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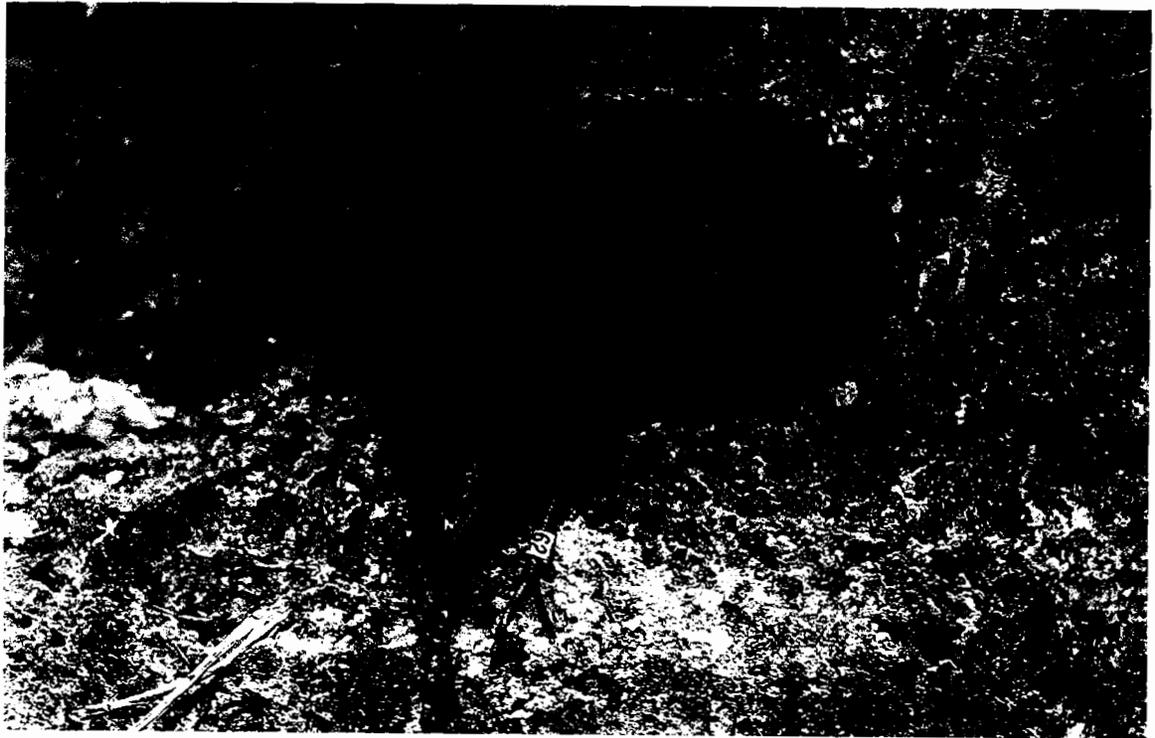
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CAN THE ALDABRA WHITE-THROATED RAIL  
*DRYOLIMNAS CUVIERI ALDABRANUS* FLY?

BY

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# CAN THE ALDABRA WHITE-THROATED RAIL *DRYOLIMNAS CUVIERI ALDABRANUS* FLY?

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## ABSTRACT

The Aldabra White-Throated Rail *Dryolimnas cuvieri aldabranus*, endemic to Aldabra Atoll (Seychelles), has long been considered the last flightless bird of the western Indian Ocean islands. However, this study represents the first quantitative approach to determine the rail's capacity for sustained, level flight. Morphological, physiological and behavioral aspects are considered in determining its actual and theoretical capacity for flight. Wing loading calculations suggest that it can fly. All other evidence, most importantly the greatly reduced breast musculature, indicate flightlessness. The Aldabra Rail originated from Madagascar, where the nominate form is volant, but only weakly. The Aldabra Rail evolved as a ground forager in the absence of any adult predation, i.e. without any apparent need to fly. This, combined with energetic advantages to becoming flightless, has led to the Aldabra Rail losing its capacity for flight.

## INTRODUCTION

Aldabra Atoll (9° 24' S, 46° 20' E) is home to the last flightless bird of the western Indian Ocean islands (Hambler et al., 1993): the Aldabra White-throated Rail (hereafter Aldabra Rail) *Dryolimnas cuvieri aldabranus*. It is currently classified a subspecies of the nominate form on Madagascar (Benson, 1967). A major difference between the two taxa is that the form on Madagascar can fly, whereas *aldabranus* is thought to be flightless (Taylor and van Perlo, 1998).

The Aldabra Rail's ability to fly has been questioned since it was first studied. Abbott (in Ridgway, 1895) describes them "flying at each other like game cocks". Frith (1977) more accurately describes this fighting behavior, making it clear that they leap at each other using their wings to assist them but certainly not flying. Abbott also states "that they are not absolutely flightless, but use their wings to assist them in leaping..." (Ridgway, 1895). Benson (1967) considered the wings so short as to render them "virtually flightless". Penny and Diamond (1971) report flying abilities similar to that of the domestic chicken, qualified by describing flapping as used to assist in jumping, which presumably means they did not believe it capable of powered flight. While such observations are commonplace

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on Aldabra, there are no records of Aldabra Rails actually flying — defined here as sustained, level flight.

The Aldabra Rail's inability to fly has thus far been inferred from behavioral observations only (principally a lack of observations of birds flying), and there has been no quantitative approach to actually determine their capacity for flight. I here describe investigations made into their actual and theoretical capacity for flight using morphological, physiological and behavioral data.

## METHODS

Wing-loading is the ratio between total wing area and body weight. Wing area was measured for 12 individuals by tracing the outline of the right wing in a notebook, superimposing this on grid paper and counting the number of squares more than half-covered by the wing. The resultant area was doubled for total wing area. Birds were weighed at capture using a 200 g Salter spring balance.

Two rails, trapped as part of a separate study, died in captivity. Their breast muscles (pectoralis and supracoracoideus) were completely excised when freshly dead. The tissue was weighed using a 50 g Pesola spring balance and compared against their body weight at capture.

The length of each primary feather was measured on both wings of four Aldabra Rails. This was done by inserting a ruler between the feathers until it was pressed gently against the skin of the wing, where the feather being measured exited the skin. The feather was then flattened against the ruler and measured. The lengths of all primaries on each wing were then summed and the percentage difference between summed values for right and left wings calculated.

Observations of Aldabra Rails were made in situations where flight would have been advantageous. These include catching birds by hand and, on one occasion, gently launching a bird about three meters up into the air. I carefully watched its behavior in the air and on landing.

## RESULTS

Results of wing-loading calculations for Aldabra Rails (Table 1) are all well within theoretical limits for volant birds, with a mean of  $0.62 \text{ g/cm}^2$  ( $\pm 0.08$ ,  $n=12$ ).

Aldabra Rails in the hand have noticeably small breast muscles. Dissection of two dead specimens corroborated this impression, showing very small breast muscles relative to total body weight. Aldabra Rails handled throughout the year (both newly caught and retrapped individuals) show no perceptible change in breast musculature, thus a larger sample size of breast weights (necessarily destructive) is unlikely to produce substantially different results.

Table 1. Wing area, total mass at capture and wing loading of adult Aldabra Rails.

Total wing area (cm <sup>2</sup> )	Mass (g)	Wing loading (g/cm <sup>2</sup> )
354	230	0.65
294	180	0.61
230	185	0.80
272	185	0.68
322	215	0.67
258	161	0.62
340	205	0.60
246	152	0.62
350	182	0.52
242	157	0.65
276	144	0.52
306	165	0.53

The fluctuating asymmetry in left and right primary feather lengths showed a consistent, unexpected bias towards longer primaries on the right wing. Further, the difference increased as primary length increased.

Table 2. Weight of breast muscle, total mass at capture and percentage of total body weight that breast muscle constitutes for two Aldabra Rails.

Breast muscle (g)	Mass (g)	%
7.15	164	4.4
5.85	201	2.9

Table 3. Fluctuating asymmetry in cumulative right- and left-wing primary feather lengths of four Aldabra Rails.

Right Wing	Left Wing	% difference
735	716	2.7
728	716	1.7
791	757	4.5
761	734	3.7

Anecdotal evidence of Aldabra Rails being unable to fly is unequivocal. In the first incident, an Aldabra Rail was cornered on a rocky ledge overhanging open water. As it leaped, fluttering, past me, I lunged for it. I failed to catch it and instead accidentally knocked it off its path while it was in mid air. Despite its flapping, it did not gain any lift or appreciable forward movement. It could not correct its course and fell quite rapidly into the water below. It swam easily to the shore and clambered out. It was seen foraging nearby within two minutes.

A second incident occurred after I had succeeded in cornering an adult bird that never attempted to fly when I captured it by hand. After briefly examining it, I took it outside and released it by gently tossing it up and away (no more than three meters vertical or horizontal). It flapped vigorously, but appeared uncoordinated in the air. I do not believe its flapping contributed any lift at all. It sawed, rolled and pitched before landing quite heavily and awkwardly. It then ran off without any obvious difficulty and was seen several times in the same vicinity over the next two days.

The last incident occurred when a free-living Aldabra Rail was discovered entangled by a metal band on its right tarsus with a mat of long, human hair. How this came about is not known. The bird held its right leg in the air and did not use it at all. Two of us pursued it and caught it after about three minutes. It was able to hop, and by flapping its wings managed to move quite rapidly. On several occasions it leapt off rocks and fallen tree trunks. At no stage did it ever gain lift, nor did it attempt to fly. It appeared to be terrified and, I believe, would have flown if it could have.

## DISCUSSION

A capacity for flight is determined by three main factors: wing loading, power ( $\approx$  relative volume of flight muscles) and flapping rate (Pennycuick, 1975). Upon handling an Aldabra Rail it became apparent that calculating wing loading would be uninformative. Their wings are not substantially reduced (*contra* Benson, 1967) and they have a wing loading that lies within theoretical limits for flight (Pennycuick, 1975). They have, however, lost most of their breast musculature (this is very apparent when a bird is in the hand). Thus, they lack the power required for level flight, violating the second requirement for flight. The persistence of a large wing area, contrary to expectations of a flightless form, can be understood in the light of their nest- and chick-defense displays. In these displays wings are fanned and held vertically, which has the effect of greatly increasing the apparent size of the displaying bird (R. Wanless, unpublished data). Thus any selective pressure to evolve much smaller wings is counteracted. Asymmetry in flight organs may not compromise their efficacy in defensive displays, but would have a significant, detrimental effect in flight (Shykoff and Möller, 1999; Cadee, 2000).

The flight muscles of volant birds constitute around 15% of their body weight, with exceptions tending to be higher than this (Livezey and Humphrey, 1986; Schmidt-Nielsen, 1990). Those of the Aldabra Rail (Table 1) are considerably below the 15% average for volant birds. The bulk of flight muscles is simply too small for Aldabra Rails to engage in powered flight.

Aldabra Rails undergo an annual, simultaneous, post-breeding molt (Penny and Diamond, 1971; R. Wanless, unpublished data) and are unequivocally flightless at this time. Further, the primary and secondary feathers are generally *extremely* abraded by the onset of moult (pers. obs.); it is difficult to imagine the tattered feathers being useful in flight.

The energetic advantages of becoming flightless are well known (McNab, 1994; Feduccia, 1996). Flight muscles are amongst the most energetically demanding organs in birds (Feduccia, 1996). Reduction in the bulk of flight muscles may be adaptive (genetically based), or a result of under-development or atrophy through disuse. Whatever the cause, reduction results in a considerable energetic saving for birds that no longer need to fly. Further, powered flight *per se* demands a high metabolic rate; evolution of flightlessness allows concomitant evolution of a lowered metabolic rate, a trait common to several species of flightless rails (McNab, 1994).

White-throated Rails on Madagascar (the source population for Aldabra Rails) are, at best, marginal flyers and were probably weakly volant at the time they colonized Aldabra (Benson, 1967; Benson and Penny, 1971; Taylor and van Perlo, 1998). These birds could not have stored large amounts of fat while retaining an ability to fly due to the negative impact that this would have on wing-loading. Patrikeev (1995, in Taylor and van Perlo, 1998) describes a population of Common Coot *Fulica atra* where adults become so fat after migration that 70-80% of the population cannot fly when chased. For all landbirds on Aldabra, reproduction is closely tied to the wet NW monsoon (Benson and Penny 1971). Variable timing and amount of rainfall means that in some years rains may be late and/or far below average (Farrow, 1971; Betts, 2000). An ability to store large reserves of energy (fat) at times of abundance would be advantageous in surviving the long, dry, SE monsoon and allow birds to achieve breeding condition early in the wet season. It would further serve as an energetic insurance policy, should rains be late or fail. The original impetus for Aldabra Rails becoming flightless may well have been storing fat as an adaptation to surviving periods of scarcity.

## CONCLUSION

Aldabra Rails are ground foragers and in the absence of predation on adults, evolved on Aldabra without need to fly; even on Madagascar, where numerous predators exist, they seldom fly (Taylor and van Perlo, 1998). There are numerous and considerable energetic advantages to becoming flightless, a condition to which rallids are predisposed (Taylor and van Perlo, 1998). The complete absence of observations of the Aldabra Rail flying, especially in circumstances where flight would be highly advantageous, has led to a general belief that they are flightless. Their complete, simultaneous, post-breeding molt renders adults flightless for a time without any adverse consequences. Further, flight feathers are not maintained and become extremely abraded, rendering them highly ineffective as organs for flight. While wing loading calculations suggest the Aldabra Rail could theoretically fly, the insubstantial bulk of flight muscles and asymmetry of their wings militates against this completely. I conclude that the Aldabra Rail cannot fly.

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