

humidity and climate variations related to the North Atlantic oscillation^{11,12}, showed that none of them, taken individually, is a good explanation for the observed positive trend in cirrus occurrence and its regional distribution.

The trends in cirrus 'amount when present' over the previously defined regions of high fuel consumption are -1.9% and -4.2% for land and ocean, respectively (Table 1). The combination of a large positive trend in cirrus occurrence associated with a negative trend in the cirrus amount when present is consistent with an increasing amount of condensation-trail cirrus covering a small portion of an otherwise clear sky at the cirrus cloud level. This results in a trend in cirrus coverage (cirrus occurrence \times cirrus amount when present) of 0.0% averaged over land, rising to 2.9% over the continental regions with most air traffic. Over ocean, these values are 2.3% and 1.0% , respectively, because of the aforementioned contribution of the North Pacific Ocean to the global increase in cirrus occurrence. Both radiative transfer calculations and Earth Radiation Budget Experiment measurements of the net change in radiation associated with high, thin clouds¹³ suggest a 0.2 W m^{-2} cloud radiative forcing per 1% of condensation trail or high-level cloudiness. I therefore estimate that the trend in cirrus amount over the continental regions of high air traffic (2.9% , as discussed above) would correspond locally to an additional cloud radiative forcing of about 0.7 W m^{-2} between 1982 and 1991. A larger forcing would be expected if calculated from the beginning of commercial jet traffic until the present time. However, we cannot rule out the possibility that the observed change in cirrus amount is not due solely to aviation, or that other climate processes have not masked an even larger aviation impact on cirrus cloudiness. For instance, a previous analysis¹⁴ showed that other regions experienced large positive trends in cirrus amount between 1952 and 1981.

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High metabolic rates in running birds

The ability to increase metabolic rate during locomotion has been important in the structural evolution and evolutionary success of both birds and mammals. Greater endurance capabilities are conferred directly by greater maximal metabolic rates, which vary between species. These maximal rates are known for many mammals¹ but have not been determined for birds. We have measured oxygen consumption in a large flightless bird, the rhea, *Rhea americana*, while it was running on an inclined treadmill, and find an upper limit to aerobic metabolism that is 36 times greater than the minimum resting rate, a factorial increase exceeding that reported for nearly all mammals.

We trained two female rheas (average mass 21.8 kilograms) for two years to run on a treadmill while wearing clear plastic hoods. We then measured linear increases in rates of oxygen uptake while the birds ran up a 16° incline. The maximum rate of oxygen uptake was 2.85 millilitres per kilogram of body mass per second, reached at a running speed of 4.0 metres per second. There were no further increases in oxygen uptake when running speeds were increased to 4.7 metres per second, and plasma lactate concentrations indicated an increasing reliance on anaerobic glycolysis to provide metabolic energy at these higher speeds.

Rates of lactate accumulation (4.4 to 6.8 mM min^{-1}) and peak concentrations (24.8 mM) matched values reported for mammals running at speeds above their aerobic maximum. Remarkably, the aerobic scope

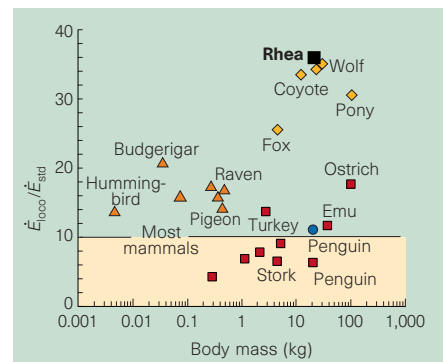


Figure 1 Factorial increases in metabolic rates above resting minimum for rheas and athletic mammals at the aerobic maximum and for other avian species at the highest rates available. Triangles, flying birds; squares, walking and running birds; circles, swimming birds; and diamonds, running mammals.

(the maximum aerobic metabolic rate divided by the minimum resting rate²) of these relatively inactive birds is more than 3.5 times those of typical mammals¹, and equals those of some of the most capable mammalian endurance runners (Fig. 1).

Although the rheas' factorial increase in anaerobic metabolism is 1.7 times greater than the highest previously reported avian values (Fig. 1), we believe that their aerobic scope is representative of birds in general. Previous avian values do not provide evidence of being upper limits; they are probably below species' maxima, but to unknown extents. Nonetheless, the minimum metabolic increase required for flight³ of 15 times the resting value exceeds the aerobic power of a typical mammal by a factor of 1.5, and most avian species can fly. Even birds with more limited endurance, such as the penguin and domestic fowl, can increase their aerobic metabolism by as much as a typical mammal^{4,5}. We suggest that, on average, the aerobic scope of birds exceeds those of mammals by a factor of two or more.

The structural basis of the rheas' aerobic power indicates that respiratory structure–function relationships, previously undetermined for birds, are quantitatively similar to those of mammals throughout most of the respiratory system, and are consistent with the concept of reasonable animal design⁶ (Table 1). Rheas, like aerobic mammals, achieve maximal high rates of oxygen uptake with existing cardiovascular and muscular structures, rather than by

Table 1 Mitochondrial volume densities and capillary densities of rhea muscles

Muscle	Bird A		Bird B	
	V_m (%)	N_c (mm^{-2})	V_m (%)	N_c (mm^{-2})
Iliotibialis lateral	10.1	803	6.5	787
Gastrocnemius	11.8	864	7.9	642
Pectoralis	4.2	411	4.2	469
Humerotriceps	4.3	619	4.9	508

Mean mitochondrial volume densities (V_m) and capillary densities (N_c) for leg muscles (iliotibialis and gastrocnemius) were 9.04% and 774 mm^{-2} , respectively; values for wing muscles (pectoralis and humerotriceps) were 4.37% and 502 mm^{-2} , respectively, for the rheas. Values for equivalent leg muscles of similarly sized mammals: for a 28-kg dog, $V_m = 9.1\%$ and $N_c = 884 \text{ mm}^{-2}$; for a 26-kg goat, $V_m = 3.4\%$ and $N_c = 719 \text{ mm}^{-2}$.

qualitative adjustment. Rhea heart mass (267 grams) conforms to that predicted for a mammal of the same body size and aerobic power. Volume densities of mitochondria in leg muscles are similar to those of mammals of the same size and aerobic capacity, whereas those in the relatively inactive flight muscles are only half as large and correspond to values reported for less aerobic mammals (Table 1).

Given that 30% of the rhea's body mass consists of leg musculature, rates of oxygen uptake by mitochondria per millilitre during locomotion at the aerobic maximum appear to fall within the range reported for mammals. Capillary densities in the rhea leg and flight muscles, like the mitochondrial volume densities, also parallel values reported for the muscles of athletic and less mobile mammals.

In contrast to the apparent conservation of structure-function relationships in most of the respiratory system, our results suggest that there are basic differences in the performance of the lungs of birds and mammals. We could not measure the lung volumes of the rheas directly, but in birds these are normally slightly more than half of those of mammals of the same mass^{7,8}. The rheas therefore achieved maximum oxygen flux rates, equal to those of the most aerobic mammals of their size, using lungs that are probably only half as large. This supports the general belief that avian lungs provide relatively more function per unit volume than mammalian lungs^{8,9}.

Although the aerobic limits of rheas and athletic mammals are similar, the metabolic power available in practice, and their functional needs, are not. Unlike dogs, horses and other athletic mammals that sustain high metabolic rates for hours during predation and migration, rheas do little or no sustained running and are poor at dissipating metabolic heat loads¹⁰. Rheas have apparently not been under strong selective pressures like those that promoted the aerobic power of extant running mammals. Large flightless birds lead fairly inactive lives, and may have lost the ability to fly primarily because of a lack of predation. Why rheas have an aerobic power that greatly exceeds their apparent functional needs remains a puzzle.

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The Thomas Jefferson paternity case

The DNA analysis of Y-chromosome haplotypes used by Foster *et al.*¹ to evaluate Thomas Jefferson's alleged paternity of Eston Hemings Jefferson, the last child of his slave Sally Hemings, is impressive. However, the authors did not consider all the data at hand in interpreting their results.

No mention was made of Thomas Jefferson's brother Randolph (1757–1815), or of his five sons^{2,3}. Sons of Sally Hemings conceived by Randolph (or by one of his sons) would produce a Y-chromosome analysis identical to that described by Foster *et al.* Further collaborative data (for example, the whereabouts of any of those who might have been involved at conception) are needed to confirm that Jefferson did indeed father his slave's last child, as claimed in the title. We know Thomas Jefferson was there, but how about Randolph Jefferson and his sons?

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If the data of Foster *et al.* are accurate, then any male ancestor in Thomas Jefferson's line, white or black, could have fathered Eston Hemings. Plantations were inbred communities, and the mixing of racial types was probably common. As slave families were passed as property to the owner's offspring along with land and other property, it is possible that Thomas Jefferson's father, grandfather or paternal uncles fathered a male slave whose line later impregnated another slave, in this case Sally Hemings. Sally herself was a light mulatto, known even at that time to be Thomas Jefferson's wife's half sister^{3,4}.

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Foster et al. reply — It is true that men of Randolph Jefferson's family could have fathered Sally Hemings' later children. Space constraints prevented us from expanding on alternative interpretations of

our DNA analysis, including the interesting one proposed by Davis. The title assigned to our study was misleading in that it represented only the simplest explanation of our molecular findings: namely, that Thomas Jefferson, rather than one of the Carr brothers, was likely to have been the father of Eston Hemings Jefferson.

It had been suggested to us earlier (by Herbert Barger, who also helped to recruit the descendants of Field Jefferson who participated in our study) that Isham Jefferson, son of Thomas Jefferson's brother Randolph, might have been the father of one or more of Sally Hemings' children. Barger's proposal was based on a statement⁵ that Isham was reared by Thomas Jefferson; he suggested that Isham could have been at Monticello or at Snowden (Snowden was across the James River from Scottsville, which is about 20 miles from Monticello) when Eston Hemings was conceived. But it is not known for certain that Isham was at Monticello at that time, whereas it is documented that Thomas Jefferson was. From the historical knowledge we have, we cannot conclude that Isham, or any other member of the Jefferson family, was as likely as Thomas Jefferson to have fathered Eston Hemings.

We know from the historical and the DNA data that Thomas Jefferson can neither be definitely excluded nor solely implicated in the paternity of illegitimate children with his slave Sally Hemings. When we embarked on this study, we knew that the results could not be conclusive, but we hoped to obtain some objective data that would tilt the weight of evidence in one direction or another. We think we have provided such data and that the modest, probabilistic interpretations we have made are tenable at present.

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