show that 99% of the variation in their basal rates of metabolism can be accounted for by interspecific variation in body mass, food habits and altitudinal distribution. These findings, which are derived from 31% of the species and 53% of the genera in this family, give the most complete picture of the standard energetics of any diverse family of birds.

Basal rate, regarded as the standard rate of metabolism in endotherms, conforms to a power function that increases with body mass and varies with food habits, climate, body composition, a continental or island distribution, and possibly other factors. Individual and population growth rates, reproductive rates and energy expenditure in the field, at least in mammals, correlate with variation in basal rate.

Among passerine birds, one of the most distinctive families is the Paradisaeidae, which is found principally in New Guinea. This family is noted for the elaborate plumage of most males, widespread use of lek polygyny, extended longevity, low reproductive rates and diverse food habits, which vary from strict frugivory to extensive insectivory.

In an analysis of covariance, the log_{10} basal rates of 13 species of Paradisaeidae, measured in rainforest habitat at the T ec with the low-altitude frugivores. Fruit-eating species that live at altitudes greater than 1,000 m have basal rates that are 90.6% of those that live at higher altitudes. Other combinations of body mass, food habits and altitude account for the observed basal rates of the remaining species. Body mass alone accounts for 91.7% of the variation in basal rate; 97.5% of this variation is accounted for by the combination of body mass and food habits.

A low basal metabolic rate in frugivorous birds is also seen in manakins (Pipridae)9, pigeons (Columbidae)10, toucans (Ramphastidae)11, and a hornbill (Bucerotidae)12, although frugivorous passerines have higher basal rates than frugivorous non-passerines, contrary to the view that there is no difference in the basal rates of non-passerines and passerines1. An examination of the evolutionary relationships within the Paradisaeidae indicates that frugivory13 and low basal rate are plesiomorphic conditions in this family. The evolution of high basal rates in the studied species occurred at least three times in relation to movement into higher altitudes, and twice in relation to the adoption of an omnivorous or insectivorous diet. The use of phylogeny as the cause for the evolution of character states12,13 is therefore doubtful.

The remarkable plumage of males in dimorphic species of this family seem to entail very high costs during synthesis: rates of metabolism increase by at least 53% during moult in male king birds of paradise (Cicinnurus regius). However, brightly coloured males in species with sexually dimorphic plumage do not have higher basal rates than dull-coloured females of the same species (F_{2.4} = 0.46, P = 0.66), and sexually dimorphic species do not have higher basal rates than sexually monomorphic species (F_{1.8} = 0.87, P = 0.37). Furthermore, species that use lek displays do not have higher basal rates (F_{1.35} = 4.45, P = 0.079) than those that use solitary displays.

The behaviour and ecology of the Paradisaeidae has been extensively studied, but the energetics of these species have not been evaluated until now. The analysis of covariance that I used for this task is superior to the conventional phylogenetic-contrasts approach.

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brief communications

Dating of the Herto hominin fossils

The age of Pleistocene Homo sapiens fossils and archaeological material from the Bouri Formation in the Middle Awash region of Ethiopia, discovered in 1997 by White and colleagues10, has been constrained to between 160 ± 2 and 154 ± 7 kyr on the basis of isotopic dating and stratigraphic and geochemical evidence. However, our analysis of their stratigraphic and geochronological data indicate that, although the estimated maximum age (160 ± 2 kyr) is valid, the minimum age (154 ± 7 kyr) is doubtful. These important discoveries may therefore be distinctly younger than reported.

The fossils and archaeological remains occur in volcaniclastic sandstones and gravel deposits of the older part of the Upper Herto Member of the Bouri Formation. The lower boundary of this member is formed by a wide erosional surface. Immediately below this surface is a bentonite tuff (MA 97-1, 2) which has been isotopically dated to 260 ± 16 kyr. Two pumices and two obsidian clasts from the fissiliferous deposits above the erosional surface provide a relatively narrow age range close to 160 kyr, which indicates a maximum age for the deposit, but it cannot necessarily be inferred that it is “close to the actual time of deposition of this fissiliferous unit”.

The main problem in dating the fissiliferous horizon is how to establish a younger age limit. The Upper Herto Member is capped by the stratigraphically important Waddeo Vitric Tuff (WAVT, M A 92-1). Unfortunately, this has proved difficult to date isotopically because of contamination by older feldspar
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phenocryts, so the only available constraint on the age of the deposit is the maximum age inferred from the volcanic clasts.

To establish a minimum age, the major elements and 11 trace elements (Zn, Cu, Cr, Zr, V, Sc, Nb, Ba, Sr, Nb and Y) of glass shards of the Waideto Vitric Tuff were geochemically analysed and used for correlation with previous, already dated Pliocene tuffs — Clark et al. refer to an unnamed tuff from the Konso region of southern Ethiopia, more than 500 km away. Although this tuff is geochemically comparable to the Waideto Vitric Tuff, it had not itself been dated either; however, the age of the immediately overlying Konso Silver Tuff (TS 120), 154 ± 7 kyr, was used as the younger age limit for the fossiliferous deposits of Middle Awash.

However, this “geochemical correlation”, which is methodologically not comparable to a real stratigraphic correlation, is highly speculative. Isotope investigations and rare-earth-element analysis are both needed before the correlation can be accepted with confidence. The recognized geochemical similarities do not mean that the two tuffs from Middle Awash and southern Ethiopia definitely belong to the same volcanic eruption event — they simply indicate similar petrogenic conditions and are not necessarily of the same age.

It is even difficult to find a particular eruptive centre on the basis of such limited data, because many Quaternary volcanic centres of similar silicic composition are located within the Main Ethiopian Rift between the Afar Depression and southern Ethiopia. Several volcanic deposits of roughly similar composition, but of different ages, should therefore be expected in the Pliocene succession of the whole Main Ethiopian Rift.

We contend that the narrow age range of the H. sapiens fossils and archaeological remains from the Upper Herto Member of the Middle Awash, as estimated by Clark et al., is too optimistic. A real minimum age can be established only if a volcanic horizon can be dated directly in or above the fossiliferous succession. Until then, only the maximum age of 160 kyr can reliably be used for this important anthropological material, although the fossils and archaeological remains could be considerably younger than this.

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Clark et al. reply — Faupl et al. question our confidence in the geochemical correlation that anchors the younger age constraint of 154 kyr on the Herto antiquities. According to convention, we reported the tephrochem-

Figure 1 Average results from electron-probe microanalyses of distinct glass populations from multimodal Konso-region tephra glass, compared with unimodal Konso tephra TA-55, the correlative Upper Herto Waideto Vitric Tuff (MA92-1) and older unimodal Konso tephra. Tephra are placed in relative stratigraphic context on the basis of field observations in the Konso region. Major elements are recalculated to 100% anhydrous and are plotted as percentage by weight of oxide on the x-axes. Symbols are used to show the glass populations from a given tephra layer.

Figure 1 Average results from electron-probe microanalyses of distinct glass populations from multimodal Konso-region tephra glass, compared with unimodal Konso tephra TA-55, the correlative Upper Herto Waideto Vitric Tuff (MA92-1) and older unimodal Konso tephra. Tephra are placed in relative stratigraphic context on the basis of field observations in the Konso region. Major elements are recalculated to 100% anhydrous and are plotted as percentage by weight of oxide on the x-axes. Symbols are used to show the glass populations from a given tephra layer.

The eruption that produced the WAVT, which is more than 2 m thick and is preserved in the Upper Herto Member (MA92-1) and in the Konso region (TA-55), was comparable in volume to large eruptions that produced other ash-fall deposits that have been tephrostratigraphically and tephrochonologically correlated between sites in the Middle Awash, the Turkana Basin and the Gulf of Aden. Although the identification of specific volcanic sources of these large eruptions would be desirable, it is not a prerequisite for tephrochemical correlation.

Field observations in the Konso region place the TA-55 marker horizon stratigraphically below the Konso Silver Tuff dated at 154 kyr. This, as well as the identification of this marker horizon stratigraphically above the 160-kyr fossil-bearing sands of the Upper Herto Member of the Bouri Formation, Middle Awash, Ethiopia, provides convincing evidence that the Upper Herto archaeological and palaeontological remains, including the newly identified Homo sapiens idaltu, are securely constrained to be between 160 ± 2 and 154 ± 7 kyr old, as we stated.

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