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Life History: The Energy-Efficient Orangutan

A study of orangutans' daily energy expenditure confirmed exceptionally slow metabolism. It suggests they evolved a lifestyle designed to minimize energy use. If so, shifting to a higher energy-use strategy may help explain how humans evolved.

Anne E. Russon

The pattern Aesop mused upon in the 5th century BCE, that animals can differ in their pace of life — tortoises being slow, hares being fast — has become one of the most important topics in modern evolutionary biology. In biology, the pace of a species' life cycle from conception to death is called its 'life history'. It is defined by the timing of events in an individual's life that are critical to survival and reproduction, e.g., longevity, age at first reproduction, gestation length, the interval between births and age at weaning [1]. Life histories reflect packages of linked traits that vary the overall pace of life from slow to fast: slow livers tend to be large, long lived, and produce few offspring, whereas fast livers tend to be small, die young, and reproduce more. The big evolutionary question is: why are there different life histories?

A new study by Pontzer and colleagues [2] brings orangutans to front stage in the study of life history evolution. Orangutans are well known for slow pace of life (Figure 1) — the

slowest of all the great apes. But because of that, they were the neglected apes of the 20th century, dismissed as sluggish, slothful and uninteresting. They have the latest age of first reproduction (over 15 years), longest intervals between births (7–9 years) and latest age at weaning (6–10 years) [3]. They also travel little, and do so slowly; they socialize little and rest a lot. Pontzer's work [2] now offers new evidence about the basis for their exceptionally slow life histories.

Generally, it appears that species' life histories have evolved to balance diverse selection pressures. For this reason, they are often called 'strategies'. For instance, they reflect the effects of major environmental challenges on mortality during adulthood (the reproductive period); species with lower adult mortality rates tend to have slower life histories [4]. Orangutan slowness is consistent with the poor and fickle food supply of Southeast Asian forests: during the worst food lows, they may survive on bark and their own fat stores for months on end [5]. Other traits are also

tied to a species' life history: notably, large body size and large brain size correlate with slow life history. A common view is that these links are due to tradeoffs in allocating energy to survival as opposed to reproduction [6]. In great apes, for instance, growth and juvenile development may be delayed or in humans gut size may be reduced, to pay the costs of growing or operating these species' large brains [7,8].

Pontzer's group [2] explored newer views that different life history strategies reflect different management of total energy use — intake and expenditure, or throughput, not just different energy allocation. Focusing on energy use emphasizes the interactions within the set of interrelated ecological, behavioral and physiological traits that characterize the species, that is, the species' 'lifestyle' [9]. Strategies for energy use seem to vary from high to low, depending on food availability and mortality threats [9–12]: abundant and reliable food supplies favor high energy-use strategies, while unpredictable food supplies or high predation risks while foraging favor low energy-use strategies. Importantly, species with access to abundant, reliable food resources may be able to reproduce more than those whose food resources are low in abundance, unreliable, or dangerous to obtain [12]. If physiology is a key factor in energy use, then metabolism must play an important role [13].



Figure 1. The slow orangutan.

Tulp's famous ape [19] shows the lassitude and morose, melancholic attitude that are among the signs that it is an orangutan (not a chimpanzee, as many have thought).

Pontzer *et al.*'s study [2] tested whether energy use is a factor in orangutan life history by measuring their metabolic rate. Many efforts have been made to assess wild orangutans' energy use, but measures are necessarily indirect, e.g., activity budgets (time spent on feeding vs. other activities), presence of ketones in urine (products of metabolizing bodily fat stores, i.e., negative energy balance), and caloric intake (nutritional content of foods eaten) [5,14]. Pontzer and colleagues [2] assessed orangutan energy use directly by measuring daily energy expenditure in active captive

orangutans, the average amount of energy an individual expends in a typical day. They chose daily energy expenditure because evidence from other species suggests it measures species' energy-use strategies: low daily energy expenditure tends to occur where food supplies are unpredictable and foraging is risky. Orangutans showed an extremely low daily energy expenditure, lower than that of human couch potatoes. In fact, among mammals, only sloths have a lower daily energy expenditure than these orangutans. This low daily energy expenditure of orangutans is

consistent with the view that lifestyle reflects food availability: orangutans' slow life history is linked to poor, unreliable food sources, low reproduction rates, and low energy use. They are consummate energy minimizers.

Pontzer and colleagues [2] suggest their findings on orangutan metabolism may shed light on human life history evolution, in line with a longstanding suggestion that critical changes in hominin evolution may owe to changing patterns of energy use [4,15,16]. They argue that if humans and orangutans differ substantially in daily energy expenditure — as their results show — there may be considerable evolutionary plasticity in metabolic physiology. Plasticity of this sort could help solve a current puzzle about human life history when compared to that of other great apes. On the one hand, human life history increases the duration of several traits in great ape life histories; for instance, longevity and gestation are prolonged, age at first reproduction delayed. On the other hand, it decreases the duration for two other traits: weaning occurs earlier, intervals between births are shorter [2]. These decreases may be due to a shift to more nutritious and more reliable food sources (e.g., meats, roots, and tubers) linked with ancestral humans' shift to savanna habitats. A strategy of higher energy use combined with greater help in parenting (perhaps by grandmothers) could increase reproductive success. Altering metabolic physiology could contribute to these changes. As a postscript, recent evidence suggests that the seeds of this shift may be evident in chimpanzees and bonobos: both can use savanna habitats, consume meats, roots and tubers, and are highly energetic in their behavior [17,18].

Daily energy expenditure is a promising addition to the kit of tools for assessing energy use. An important next step is exploring whether it can be used with wild orangutans. Activity levels in the captive orangutans tested appear similar to those of wild orangutans, based on activity budgets and travel distance, but neither of these measures assesses energy intake or expenditure accurately. These captive orangutans' daily energy expenditure increased in colder weather, probably to fuel thermoregulation, so that of wild

orangutans almost certainly differs and needs to be tested directly. Daily energy expenditure was assessed in captives from the disappearance of a dose of doubly labeled water in which the hydrogen and oxygen were replaced with a traceable stable isotope. Testing required orangutans to drink a dose of doubly labeled water and provide urine samples, daily, for two weeks. Whether this is feasible in the wild is questionable. On another tack, the seasonal differences in daily energy expenditure that Pontzer *et al.* [2] found may have important implications for wild orangutan daily energy expenditure. Bornean orangutans survive during prolonged food lows by metabolizing their own body fat and resting a lot, so their energy use should be at its lowest at this time. Who knows, during these periods, they might surpass the sloth in slowness.

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Palaeoecology: Different Dinosaur Ecologies in Deep Time?

Do dinosaurs from the Moroccan Kem Kem formation provide evidence for an ecosystem dramatically different from anything seen today? More likely the common palaeontological problem of time-averaging has had a part to play.

Gareth J. Dyke

The geological principle of uniformitarianism posits that 'the present is the key to the past'. But how similar really were ancient ecosystems, as recorded in the fossil record, to the ones we see today? Most palaeontologists would argue that there are unlikely to have been assemblages of animals and plants in the past that we cannot understand with reference to modern-day ecosystems. Perhaps, however, as palaeoecologists we have no chance: if a fossil assemblage reflects an ecological situation completely alien

to the modern world, then how would we hope to recognise it?

Just picking up fossils off the ground and counting them cannot give us a clear answer about an ancient ecosystem because of the effects of 'time-averaging'. This critical palaeontological concept addresses the mixing of fossils of different ages together into single rock layers. In other words, the organisms whose remains are found together did not necessarily live together. In a recent paper, Tomašových and Kidwell [1] demonstrate that time-averaging effects can dramatically alter

interpretations of ancient ecosystems based just on fossil collections.

Assume, for example, that based on counts of fossil species at a given site the appearance and disappearance of species seems slow or gradual and different to a modern ecosystem in a similar environment. Yet, the huge timescales involved — centennial, millennial or longer — may have created an illusion of stasis. Tomašových and Kidwell's simulations [1] show that time-averaging tends to decrease the numbers of species collected by palaeontologists that were actually dominant in an ecosystem while increasing the count of rarer ones. This finding has direct implications, particularly for vertebrate palaeontology; it has, for instance, become fashionable to speculate about the shape of dinosaur-dominated ecosystems. Several reports [2,3], based on 95 million-year-old (mya) fossils from a famous series of sites in Morocco, claim evidence for an