

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.

#### References

1. Robson, S.L., and Wood, B. (2008). Hominin life history: reconstruction and evolution. *J. Anat.* 212, 394–425.
2. Pontzer, H., Raichlen, D.A., Shumaker, R.W., Ocozbek, C., and Wich, S.A. (2010). Metabolic adaptation for low energythroughput in orangutans. *Proc. Natl. Acad. Sci. USA* 107, 14048–14052.
3. Wich, S.A., de Vries, H., Ancrenaz, M., Perkins, L., Shumaker, R.W., Suzuki, A., and van Schaik, C.P. (2009). Orangutan life history variation. In *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*, S.A. Wich, S.S. Utami Atmoko, T. Mitra Setia, and C.P. van Schaik, eds. (New York: Oxford University Press), pp. 65–75.
4. Charnov, E.L., and Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evol. Anthropol.* 1, 191–194.
5. Knott, C.D. (1998). Changes in orangutan diet, caloric intake and ketones in response to fluctuating fruit availability. *Int. J. Primatol.* 19, 1061–1079.
6. Smith, B.H., and Tompkins, R.L. (1995). Toward a life history of the Hominoidea. *Annu. Rev. Anthropol.* 24, 257–279.
7. Ross, C. (2004). Life histories and the evolution of large brain size in great apes. In *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence*, A.E. Russon and D.R. Begun, eds. (Cambridge, UK: Cambridge University Press), pp. 122–139.
8. Aiello, L.C., and Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36, 199–221.
9. Sibly, R.M., and Brown, J.H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *Proc. Natl. Acad. Sci. USA* 104, 17707–17712.
10. McNab, B.K. (1986). The influence of food habits on the energetics of eutherian mammals. *Ecol. Monogr.* 56, 1–19.
11. Nagy, K.A., Girard, I.A., and Brown, T.K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* 19, 247–277.
12. Pontzer, H., and Kamilar, J.M. (2009). Great ranging associated with greater reproductive investment in mammals. *Proc. Natl. Acad. Sci. USA* 106, 192–196.
13. Brown, J.H., and Sibly, R.M. (2006). Life-history evolution under a production constraint. *Proc. Natl. Acad. Sci. USA* 103, 17595–17599.
14. Morrough-Bernard, H.C., Husson, S.J., Knott, C.D., Wich, S.A., van Schaik, C.P., van Noordwijk, M.A., Lackman-Ancrenaz, I., Marshall, A.J., Kanamori, T., Kuze, N., *et al.* (2009). Orangutan activity budgets and diet: a comparison between species, populations and habitats. In *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*, S.A. Wich, S.S. Utami Atmoko, T. Mitra Setia, and C.P. van Schaik, eds. (New York: Oxford University Press), pp. 119–133.
15. Hawkes, K., O'Connell, J.F., Jones, N.G., Alvarez, H., and Charnov, E.L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. USA* 95, 1336–1339.
16. Leonard, W.R., and Robertson, M.L. (1997). Comparative primate energetics and hominoid evolution. *Am. J. Phys. Anthropol.* 102, 265–281.
17. Hofreiter, M., Kreuz, E., Eriksson, J., Schubert, G., and Hohmann, G. (2010). Vertebrate DNA in fecal samples from bonobos and gorillas: evidence for meat consumption or artifact? *PLoS ONE* 5, e9419.
18. Hernandez-Aguilar, R.A., Moore, J., and Pickering, T.R. (2007). Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proc. Natl. Acad. Sci. USA* 104, 19210–19213.
19. Tulp, N. (1641). *Observationum Medicarum Libri Tres*. (Amsterdam: Lodewijk Elzevir).

Psychology Department, Glendon College of York University, 2275 Bayview Avenue, Toronto MSN 3M6, ON, Canada.  
E-mail: [arusson@gl.yorku.ca](mailto:arusson@gl.yorku.ca)

DOI: 10.1016/j.cub.2010.10.003

## 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



Figure 1. A Kem Kem dinosaur.

The large meat-eating theropod dinosaur *Spinosaurus* is well-known, largely on the basis of its teeth and a few vertebrae, from the Kem Kem of Morocco. The curved, unserrated teeth of *Spinosaurus* are very often found for sale in local markets and fossil shops. In this artistic rendering the dinosaur is shown fishing. Artwork by Todd Marshall.

extremely unusual ancient ecosystem: one top-heavy with dinosaur predators.

This novel ecosystem was found in a Moroccan sequence of rocks, in the Saharan southeast of the country. These fossil deposits, called the 'Kem Kem', have been known to palaeontologists for almost a century [4]. The Kem Kem is early Late Cretaceous in age (Cenomanian: around 95 mya), comprises both continental and deltaic rocks, and has so far yielded more than 80 named taxa of fossil vertebrates [5]. What is particularly unusual about the fossils from the Kem Kem is that the vast majority collected are the remains of large predatory dinosaurs, some the size of *Tyrannosaurus rex*. In fact, more than 70 percent of described fossils from the

Kem Kem sequence are the bones and teeth of predators — almost the exact reverse of what one would expect in a modern ecosystem. On the African savannah, for instance, predators make up a much smaller component of the overall biomass: only up to around 30 percent in exceptional cases.

Even more unusual about the fossil fauna of the Moroccan Kem Kem is that prey species, especially plant-eating dinosaurs like huge four-legged sauropods and the bipedal duck-billed ornithomimids, seem to be almost completely absent. Just very rare bones of one or two species of sauropod have been described, and only the footprints of duck-billed dinosaurs have ever been reported. Where were all the prey animals to

sustain the large number of giant predatory dinosaurs? This unusual pattern has led some to believe the Kem Kem fauna to be unlike anything seen today: an example of a predator-dominated ecosystem [2,3]. However, more likely, time-averaging has had a part to play [1].

As ever in palaeontology, just because a fossil has not been found in a particular rock sequence does not mean it was not there. Although picked over for decades, and with increasing regularity in recent years, most fossils from the Kem Kem are fragmentary and not collected from their original positions in the rocks. The bulk of the fossils that come from this region are found on the surface by prospecting palaeontologists or mined and collected by local villagers who know they have a market value. A recent study of fossils from this region of Morocco [6] has suggested that because local villagers and fossil collectors know that theropod dinosaur teeth, especially those of the large predatory dinosaurs *Cacharodontosaurus* and *Spinosaurus* (Figure 1), can command a higher price they are more often available for sale in local fossil shops. This bias has filtered down into museum collections: Moroccan samples are also dominated by the remains of predatory dinosaurs, while the more boring, less saleable bones that could be attributed to plant-eating ornithomimids are rarely encountered [6]. In the Sahara, where harsh weather conditions make short work of softer bones, the hard enamel of more resistant dinosaur teeth, shed regularly through life, are much more often collected by eager palaeontologists, but the sites have rarely been surveyed carefully by professional palaeontologists.

Do the dinosaurs of the Kem Kem tell us about a system that was really ecologically unique? Sporadic fossil collecting from rocks more than 150 metres thick and continuous in the Sahara over hundreds of kilometres creates a problem of time-averaging. Added to this is the fact that most of the taxa described from this part of Morocco were bought and then only later given to museum collections, rather than being properly collected with location data in the field. All this adds up to a very tricky situation for building hypotheses about palaeoecology. Perhaps after all, the 'present is the key to the past'; better

to assume that the ecology of the Kem Kem was more similar to a modern ecosystem (we just have not found enough prey species yet for the large dinosaurs, whose numbers we might be overestimating anyway) than try to re-write the ecological rule book based on really quite inadequate fossil evidence.

#### References

1. Tomašových, A., and Kidwell, S.M. (2010). The effects of temporal resolution on species

- turnover and on testing metacommunity models. *Am. Nat.* 175, 587–606.
2. Russell, D.A. (1996). Isolated dinosaur bones from the Middle Cretaceous of the Tafilat, Morocco. *Bull. Mus. Nat. d'Hist. Nat., Paris*, 4e Série, Sec. C, 18, 349–402.
3. Russell, D.A., and Paesler, M.A. (2003). Environments of Mid-Cretaceous Saharan dinosaurs. *Cret. Res.* 24, 569–588.
4. Lavocat, R. (1948). Découverte de Crétacé à vertébrés dans le soubassement de l'Hammada du Guir (Sud marocain). *C.R. Acad. Sci.* 226, 1291–1292.
5. Cavin, L., Tong, H., Boudad, L., Meister, C., Piuze, A., Tabouelle, J., Aarab, M., Amiot, R., Buffetaut, E., Dyke, G., *et al.* (2010). Vertebrate assemblages from the early Late Cretaceous

- of southeastern Morocco: An overview. *J. Afr. Earth Sci.* 57, 391–412.
6. McGowan, A.J., and Dyke, G.J. (2009). A surfeit of theropods in the Moroccan Late Cretaceous? Comparing diversity estimates from field data and fossil shops. *Geology* 37, 843–846.

School of Geography, Archaeology and Palaeoecology, Queen's University, Belfast, Elmwood Avenue, Belfast, BT7 1NN, UK.  
E-mail: [garethdyke@gmail.com](mailto:garethdyke@gmail.com)

DOI: 10.1016/j.cub.2010.10.001

## Social Evolution: War of the Worms

The discovery of a non-reproductive soldier caste in a clonally reproducing trematode greatly extends the taxonomic distribution of eusociality and reaffirms the importance of relatedness in the evolution of reproductive altruism.

Philip Newey and Laurent Keller

There is great variability in degrees of sociality within the animal kingdom. The most elaborate forms are found in species such as ants and termites, where division of labour is associated with a caste system in which queens monopolize reproduction and workers do all the other colony tasks, such as brood care and foraging. In recent years, the presence of specialized reproductive and non-reproductive castes has been uncovered in several other arthropods, including gall-forming aphids [1], thrips [2] and snapping shrimps [3]. A new study [4] now greatly extends the taxonomic range of these eusocial systems by describing the occurrence of specialised reproductive and soldier morphs in the parasitic trematodes or fluke worms.

Trematodes have a complicated lifecycle involving several distinct stages and several hosts (Figure 1). *Himasthla* sp. B infects the California horn snail, *Cerithidea californica*, as its second intermediate. Once in the host, the parasite exhibits repeated clonal reproduction of rediae, which then produce more of themselves or give rise to dispersive offspring (cercariae). All these individuals are clones of the diploid larvae that infected the host. While studying trematodes in marine snails, Hechinger *et al.* [4] observed that rediae occurred in two distinct morphological forms (Figure 2). The

larger, or primary, morph is that of the reproductive rediae already described in the literature. The other, secondary, morph is much smaller and more mobile, with relatively larger mouthparts. Importantly, the two morphs differ greatly in their reproductive abilities. While 96% of the

reproductive rediae contain embryos and/or dispersive cercariae, none of the smaller morphs show any sign of reproduction. Moreover, detailed censuses showed that the smaller morph is unable to undergo a transition to the much larger reproductive morph, thus indicating that it is fully sterile.

There are also important behavioural differences between the two forms. The larger, primary morphs are almost all located in the visceral mass of the host, mainly in the region of the gonads. The smaller form is distributed more widely throughout the host, but primarily within the mantle, which is the

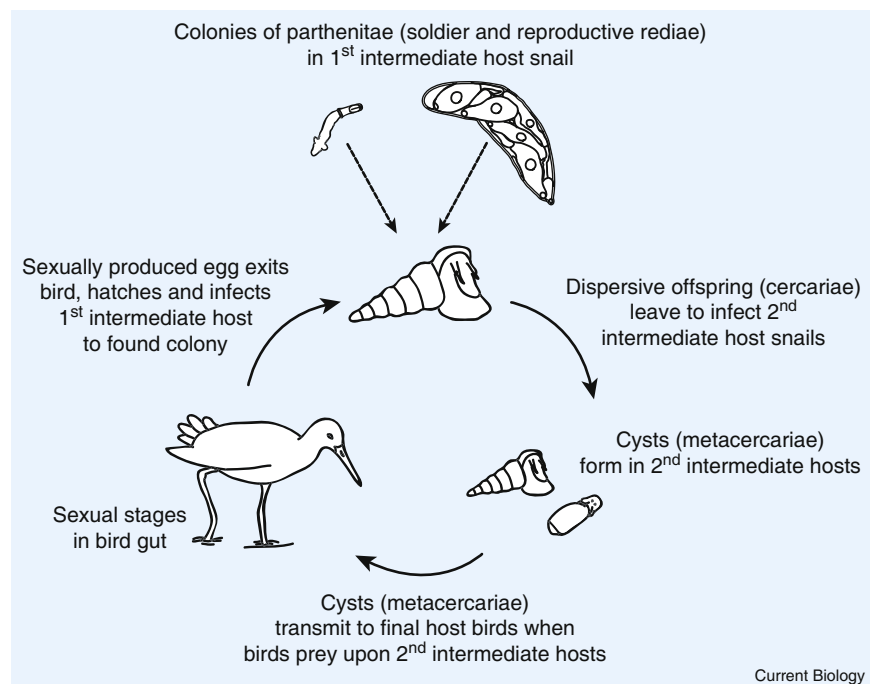


Figure 1. The complex life cycle of the trematode *Himasthla* sp. B.

As illustrated, the life cycle of the trematode *Himasthla* sp. B involves several sequential forms and three hosts. (Courtesy of Ryan Hechinger; reproduced with permission from [4].)