Ice-age Ecology

Frozen Fauna of the Mammoth Steppe: the Story of Blue Babe

by R. Dale Guthrie, *University of Chicago Press, 1990. £31.95/$45.95 hbk, £13.50/$19.50 pbk (xiv + 323 pages) ISBN 0 226 31122 8*

The 'mammoth steppe' was the vast expanse of grassland that existed across much of Europe, Northern Asia and North America during the ice ages, supporting an abundant and diverse mammalian community. 'Frozen fauna' refers to the carcasses of large mammals preserved within the permafrost of Alaska and North Siberia, providing a unique window onto ice-age life. And 'Blue Babe' is one such carcass: a complete adult male bison, 36000 years old, unearthed in Alaska in 1979 and tinged with blue from the mineral vivianite.

Most of the best-known frozen carcasses (especially mammoths) are from Siberia. Guthrie has read much of the Russian literature, giving an enlightening account of how the corpses were entrapped and preserved. The process of preservation is akin to mummification, the flesh becoming dried by the separation of water into surrounding ice.

The detailed postmortem carried out on Blue Babe illustrates how much information can be retrieved about the life and death of an individual animal, as well as the appearance and ecology of its kind. Coat distribution and colour, display organs, sexual dimorphism, food trapped in tooth spaces, and even wounds received in fights, combine to allow a convincing discussion of the ecology and behaviour of Pleistocene bison in comparison with their living relatives. Blue Babe himself appears to have been brought down by lions – witness claw scratches on his hind quarters and paired puncture marks on his head, each pair separated by precisely the width between the lion's canines, and a chip of lion tooth found in his hide.

The book extends much further than the phenomenon of 'frozen fauna' in general or Blue Babe in particular. It provides an in-depth study of the ice-age ecosystem. Guthrie's unique strength is that he is both ecologist and palaeontologist, combining profound understanding of both the arctic ecosystem and the Pleistocene fossil and climatic record. At times, one forgets that one is reading about an ecosystem that has been extinct for thousands of years.

Pollen studies show the mammoth steppe as a rich grassland, combining plant species characteristic today of steppe and tundra habitats (some have termed it 'steppe–tundra'). For most of the last half million years at least, it formed a huge band south of the ice sheets, and was only occasionally interrupted by brief warmer periods when woodland became established. The vegetational zones of the ice age were not simply those of today pushed southwards; true mammoth steppe no longer exists anywhere, and steppe and tundra are widely separated zones. According to Guthrie, the key to the mammoth steppe – in contrast to today's zonation of boreal forest and boggy, unproductive tundra – was aridity. The complex climatic changes of the ice ages produced lower precipitation, stronger drying winds and cloudless skies in the far north, which – with the very long daylight hours of summer – combined to increase insolation, reduce the annual period of snow cover and provide a deeper summer thaw of permafrost. The result was a high-productivity grassland, with a much greater carrying capacity and diversity of large mammals than today. Mammoth, horse and bison were the most important species; others included musk-ox, woolly rhinoceros, lion and reindeer.

Some palaeobotanists have denied the existence of a productive mammoth steppe, and Guthrie goes to considerable length to rebut their arguments, both in terms of the interpretation of pollen data and the evidence of the mammal fauna. Collections of bones from Siberian and Alaskan mines are measured in tons, and many species display extreme body size and strong sexual dimorphism – indicators of high summer productivity.

Nonetheless, on the mammoth steppe, productivity was exceptionally seasonal, severe winters keeping populations well below summer carrying capacity. Guthrie doubts that large mammals 'escaped' by very long migrations southwards. Abundant summer forage allowed prodigious growth and energy storage (especially in ruminants); in the winter they survived on fat reserves and reduced activity.

The demise of the mammoth steppe came toward the end of the last ice age, about 12000 years ago, when it was squeezed out by the encroaching zonation of tundra in the north and boreal forest in the south. The mammoth fauna was adapted to neither of these vegetational belts, and Guthrie believes that this was the reason why many large mammal species went extinct at this time. Other authors see a role for humans, which had been absent over much of the mammoth steppe for most of its history, but had begun to colonize north of 60° N after about 15000 years ago, when advances in technology enabled them to survive the cold climate and lack of trees for wood.

The 'keyhole on the past' presented by Guthrie graphically illustrates how time-shallow present ecosystems are, relative to the age of most of the species comprising them. Today's species have lived through great environmental upheavals and community rearrangements, so the study of their 'optimization' to present-day habitats can only partly explain why they are the way they are.

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Evolutionary Novelty

Evolutionary Innovations

edited by Matthew H. Nitecki, *University of Chicago Press, 1990. $51.75/£35.95 hbk, $20.75/£14.25 pbk (x + 330 pages) ISBN 0 226 58694 4*

There is hardly any topic that is of greater interest to the broad spectrum of evolutionary biologists than the subject of evolutionary innovations. The idea of an evolutionary novelty and attempts to understand the consequences of such novelties have been of interest to population biologists, geneticists, paleontologists, and developmental and evolutionary morphologists for many years. This book brings together a diversity of perspectives on evolutionary innovation and provides an extremely timely and stimulating overview of the topic.

The chapters in the book are divided into four themes: the nature of evolutionary innovations (containing one chapter by Joel Cracraft); genetics and development (three chapters); morphology and physiology (four chapters); and paleontology (three chapters). Matthew Nitecki opens this volume with an introduction in which he notes that 'innovations cannot be explained by any single cause'. Although Nitecki suggests that 'we are not able to define the concept precisely', most authors in fact do a good job of

defining what they mean by an 'evolutionary innovation'.

Cracraft's chapter on the study of novelties at different hierarchical levels presents an excellent cautionary framework for the subsequent papers. He uses avian flight as an example of an innovation and asks how one might test for the *causal* importance of such an innovation in promoting evolutionary diversification. Cracraft is not sanguine about the utility of the concept of 'innovation' for explaining evolutionary patterns. I am more optimistic: I feel that novelties do contain causal explanatory content even though, as emphasized in the chapter by Karel Liem, many contingent ecological events may limit the resolution of our historical tests. Despite historical contingencies, certain novelties such as gene duplication (or the duplication of structural elements of organismal design) appear to have repeatable, well-defined and significant consequences for evolutionary diversification[1,2].

Most of the other chapters in this volume focus on specific facets of the notion of an evolutionary innovation, and almost all make interesting reading. Gerd Muller focuses on novelties that arise by epigenetic modifications of organs within a particular body plan while James Cheverud takes a quantitative genetic approach to measuring phenotypic correlations among characters. Karel Liem and Jeffrey Jensen extend previous discussions of key morphological innovations to emphasize the role of ecological factors and phylogenetic testing of hypothesized novelties. The role of physiological novelties is addressed by Warren Burggren and William Bemis, who clearly outline the importance of considering the function of morphological features, noting that novelties in function may be relatively uncorrelated with underlying structural features. David Jablonski and David Bottjer provide a paleontological perspective on evolutionary novelties and emphasize the important point that 'evolutionary novelties are not randomly distributed in time and space'.

The one chapter that stands out as an exceptional contribution to our understanding of innovations is that by Rudolf Raff *et al.*, on novelties during early development. This chapter is a lucid explication of the value of mechanistic studies of character origination and provides evidence that many commonly repeated aphorisms about the role of development in evolution may be far off the mark. For example, Raff *et al.* note that (1) developmental events 'which happen together or sequentially in time are not necessarily tightly coupled mechanistically'; (2) 'early development may actually be less integrated and constrained than some later stages'; (3) 'clearly homologous adult structures can be shown to arise from different embryonic regions and to express apparently different modes of development'; (4) 'regulatory mechanisms are not necessarily tightly constrained in early echinoid development'; and (5) much of the molecular variation in early development appears to have little effect on morphogenesis.

The key issue underlying the data presented in the chapter by Raff *et al.* is that a study of *mechanisms*, not mere morphological *patterns*, is a critical feature so far lacking in most studies of development and evolution. I agree, and would go further to say that evolutionary biologists (especially developmental and evolutionary morphologists) may have been badly misled by too intensive a focus on gross structural patterns[3]. The study of mechanisms, both developmental and functional, that underlie structure may reveal very different principles of organismal design and patterns of constraint (or a lack thereof) from those revealed by comparative research on structure alone.

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References

1 Lauder, G.V. (1981) *Paleobiology* 7, 430–442

2 Lauder, G.V. and Liem, K.F. (1989) in *Complex Organismal Functions: Integration and Evolution in Vertebrates* (Wake, D.B. and Roth, G., eds), pp. 63–78, John Wiley

3 Lauder, G.V. (1990) *Annu. Rev. Ecol. Syst.* 21, 317–340

Ecology Textbooks

Ecology: Individuals, Populations and Communities (2nd edn)

by Michael Begon, John L. Harper and Colin R. Townsend, *Blackwell Scientific Publications, 1990. £35.00 hbk, £17.50 pbk (xii + 945 pages) ISBN 0 86542 111 0*

Ecology (3rd edn)

by Robert E. Ricklefs, *W.H. Freeman, 1990. £21.95 hbk (xii + 896 pages) ISBN 0 7167 2077 9*

If books were species, here would be a pair to excite the interest of literary ecologists. Both aim to exploit the same resource, the pockets of undergraduate ecology students. Although they evolved allopatrically, they are sympatric in the English-speaking world. Are there significant differences in their ecological characteristics? Can we predict the outcome of their competitive encounter? Will they continue to coexist?

First impressions suggest that they may be complete competitors. They are virtually identical in physical dimensions and differ in page number by around 5%. Their spines bear the same title, although the Begon, Harper and Townsend volume (BHT) boasts a colon (appropriate enough in a text once described[1] as containing a *nouvelle cuisine*) and qualifying clause. Both are written with great clarity and vigour; BHT's parental trio has produced a virtually seamless offspring, despite the inherent risk that it might be chimaeric.

Ricklefs casts his net wide. In an opening chapter devoted mainly to an essay on the growing impact of the human race on the environment, he uses Haeckel's definition as an indication of the scope of ecology. The subsequent chapters include such matters as dominance hierarchies, reciprocal altruism and the evolution of sex ratios, together with the material that is more generally regarded as the central province of ecology. In fact, this edition of Ricklefs' book is less wide ranging than its predecessors, which ran to chapters on population genetics and the history of evolution. Nevertheless, it must still be the most comprehensive volume to bear the title *Ecology*.

The new edition also retains the emphasis on the importance of natural history, fleshed out with many delightful words and pictures. In the 11 years since the second edition appeared, Ricklefs has made substantial alterations to the content of the book and its arrangement. Nonetheless, there are several areas in which a mid-seventies ethos has remained.