

accompanying paper by Wu *et al.* (Wu, Holmes, Davidson, Cohn and Kedes, *Cell*, 9, 163; 1976), who have hybridised total histone mRNA to single-stranded DNA from the histone plasmids pSp2 and pSp17.

Since the mRNAs hybridise only to the complementary coding sequences, the arrangement of coding and non-coding regions can be seen directly in the electron microscope after a novel treatment with T4 gene 32 protein which preferentially stains the single-stranded regions of the histone plasmid DNA-histone mRNA hybrids (Wu and Davidson, *Proc. natn. Acad. Sci. U.S.A.*, 72, 4506; 1976). As expected, they found three RNA:DNA hybrid regions on pSp2 and two on pSp17 accounting for the five histone genes, interspersed with spacer DNA—definitive proof that each gene is only repeated once in each repeat unit. Direct measurements allow them to independently assign most of the duplex regions to specific histone genes, constructing a map which agrees with those obtained by other methods.

Portmann, Schaffner and Birnstiel

(page 31 of this issue of *Nature*) have also directly demonstrated by electron microscopy five coding regions interspersed with spacer DNA in the *Psammechinus* repeat unit DNA cloned in phage lambda, by making use of the fact that the AT-rich DNA of the spacer regions denatures at a lower temperature than the GC-rich coding sequences forming open loops along the DNA. The GC-rich regions correspond well in size to the individual histone protein sequences.

Detailed sequencing of the repeat unit at the nucleotide level is now underway, made possible by the ability to obtain pure DNA fragments by cloning in phage or plasmids. Before too long, nucleotide sequencing may well have identified any regions of homology between the non-transcribed DNA in these and other genes, or between the histone spacer sequences themselves. Preliminary evidence (Cohn *et al.*, *Cell*, *op. cit.*), indicates that most of the histone spacer sequences are unlikely to be shared with other genes, and that there is also little homology between the individual spacer sequences. □

keeping population levels steady.

Hogarth concludes with speculation on the causes of extinction of dragons: despite persistent accounts of dragons and similar animals even in the present century, the typical mediaeval dragon was certainly extinct by the late 18th century. One contributing factor was commercial over-exploitation, primarily for pharmacological purposes. Only once was conservation legislation passed to protect dragons. This was in Rhodes, in 1345, when the king forbade any knight to attempt to slay a local dragon (although Hogarth conjectures that this edict stemmed from concern for the knights, not the dragon). If we accept the notion that dragons were extreme K-selected animals, then their rapid extinction under the diverse pressures exerted by man is not surprising (see for example, *Nature*, 257, 737–738; 1975).

Hogarth's article is undoubtedly seminal, but I find it in some respects excessively uncritical. In discussing the evolution of dragons, and other "related species such as the cockatrice and griffon". Hogarth suggests they "probably originated as a distinct group only 5,000 years ago". Quite apart from the inherent implausibility of this statement, it is well to begin by getting clear the morphological details of the animals loosely grouped together here. These can be obtained from bestiaries, or from any heraldry text. Setting aside relatively minor differences, such as whether the feet have talons or claws, or whether the head has teeth or a beak, the basic difference is that the griffon and the canonical dragon are six-limbed (four legs, two wings), whereas the wyvern and cockatrice are four-limbed (two legs, two wings).

This is an absolutely fundamental distinction. One of the most conservative features of vertebrate evolution is the tetrapod morphology: this may be seen in any museum exhibit of the

## The ecology of dragons

from Robert M. May

ALTHOUGH much studied in earlier times, dragons and their ilk have been largely neglected in the recent upsurge of interest in animal ecology and behaviour. An article by Hogarth (*Bull. Brit. ecol. Soc.*, 7[2], 2–5; 1976) seeks to remedy this neglect.

In view of the lack of contemporary observational evidence, Hogarth necessarily relies on a survey of earlier sources. Most of these are from the 17th and early 18th century, an age when scientific curiosity was flowering. Later publications are increasingly sceptical, although Hogarth notes published doubts on the existence of dragons as early as Caxton's (1481) *Mirror of the World*.

Dragons appear to have been both omnivorous and voracious. Different records testify to their diet having been highly variable in both composition and quality: one dragon ate two sheep every day, and another which was kept captive by Pope St Sylvester consumed 6,000 people daily. The population density was also highly variable (presumably in a way which correlated with the per capita food requirements): "in England, indigenous dragons were solitary and it is doubtful whether the resident population averaged more than a few dozen, although occasional migrant flocks of up to 400 were seen: in India, by contrast, the marshes and mountains were described as being 'full' of dragons". Estimates of their life table parameters are scrappy, but

there seems to be general agreement on a typical lifespan of the order of  $10^2$ – $10^4$  years.

The sexual display behaviour of dragons includes at least one remarkable and unparalleled manifestation, recorded by an 18th century author: "Dragons, being incited to lust through the Heat of the Season, did frequently, as they flew through the Air, Spermatise in the Wells and Fountains". This may be conjectured to have had adaptive value in reducing intrinsic fecundity. Such long-lived beasts would seem to have been at the extreme K-selected end of the r–K continuum, and would therefore be likely to exhibit behaviour which had the effect of

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500,000,000 years of evolution from lobe-finned fishes through amphibians and reptiles to birds and mammals. This underlying conservatism in skeletal structure, despite great variation in outward form and function, probably reflects the relative ease of modification of genes which govern timing in development, as opposed to those governing basic structure (see for example, King and Wilson, *Science*, **188**, 107–116; 1975). The wyvern and cockatrice have this basic vertebrate tetrapod morphology, but the six-limbed dragon and griffon do not. The probable ancestry of these latter two, as an entirely separate group, therefore dates back at least to the Devonian. This basic distinction applies to other now-extinct beasts: despite superficial similarities, unicorns belong with the familiar tetrapods, but the pegasus belongs with the six-limbed dragon-griffon vertebrate phylum, as do centaurs. Some angels (the humanoid-plus-wings kind) also belong in this phylum, but in view of the bewildering complications of angel morphology (once one includes cherubim, seraphim, and so on: see Davidson, *Dictionary of Angels: Including the Fallen Angels*, Free Press, 1967), this point is best not pursued.

In brief, wyvern and cockatrice can be envisaged as radiations from the basic vertebrate theme. But dragons, griffons, centaurs and angels belong to an entirely different lineage, the evolutionary history of which is shrouded in mystery.

The loose association of these two fundamentally different groups provides a striking example of the pre-Darwinian tendency to regard each species as a separate act of creation, rather than to trace logical phylogenetic relationships.

On the other hand, grouping together dragons, wyverns and the like is understandable in the light of the similarities of their ecology, behaviour and superficial appearance. They provide a dramatic example of evolutionary convergence, in the face of phylogenetic differences at least 400,000,000 years old. Such convergence implies some very tight evolutionary constraint somewhere in the "dragon" niche, a constraint hardly hinted at in Hogarth's account of their highly generalist diet and behaviour. This constraint may lie in the tendency exhibited by most dragons of record to be obsessive custodians of hordes of gold.

I conclude with the time-worn call for further research, modified by the highly contemporary remark that (if the above speculation is correct) such research may yield the literally golden fruits that grant-giving agencies increasingly desire. □

## Primate behaviour and ecology

The Sixth Congress of the International Primatological Society was held at Cambridge on August 23–27, 1976. Aspects of the conference dealing with behaviour and ecology are discussed below.

from F. P. G. Aldrich-Blake and Miranda Robertson

THE theoretical thrust of much primate work in the late sixties and early seventies was loosely socio-ecological; features of social organisation such as group size and composition were related to broad ecological categories of habitat such as 'forest' or 'savanna'. While this approach sought an evolutionary explanation of primate societies, it was insufficiently precise both in its treatment of causal mechanisms of social change and in its measurement of critical ecological variables. Recent work has placed a greater emphasis on the adaptive strategies of individuals in their dealings with society and the environment.

Notable in this respect was a paper by R. M. Seyfarth, D. L. Cheney and R. A. Hinde (University of Cambridge), which sought to provide a conceptual framework within which to interpret inter-individual behaviour. Primate societies, they pointed out, can be analysed at three different levels: interactions between individuals; the long-term relations to which interactions give rise; and the structure resulting from those relationships. While patterns of interaction between individuals are often apparently complex, they may be governed by relatively simple principles. For example, networks of social grooming among adult females of four species of primate had many features in common, despite being drawn from groups of differing size and degree of genetic relatedness. Computer simulation showed that these features could be accounted for by a preference for females of high rank as grooming partners and competition for access to these preferred females. Interactions between individuals have long-term effects on their relationships: grooming partners are more likely to form coalitions during aggressive encounters than are pairs that have had fewer friendly interactions in the past. Thus the optimum individual strategy should be to maximise the benefit derived from others by maximising the time spent interacting with animals of high rank. A similar theoretical approach can be used to explain many other aspects of social behaviour; the different behaviour of immature males and females, for instance, can be related to

strategies for maximising their fitness as adults.

In contrast, sessions on ecology produced few conceptual syntheses, despite a striking increase in the quality and quantity of research in this field. Detailed accounts of primate communities in Asia, Africa and the Americas were presented, the most notable being that of T. T. Struhsaker (New York Zoological Society) and his associates in the Kibale Forest, Uganda. In all areas, leaf eaters attained higher biomasses than fruit eaters, and these higher than insectivores, but otherwise few general principles emerged. Indeed discussion revealed dissent on aims and methods, let alone conclusions.

We still do not know what factors limit the population of any primate. Availability of food is clearly a plausible candidate; K. Milton's (New York) studies of the howler monkeys of Barro Colorado Island and their habitat suggest that fruit and young leaves of suitable quality may be in short supply at some seasons. Food intake may be limited as much by the need to avoid toxins as to obtain nutrients. Milton showed that many potential foods were rich in phenolic compounds, and J. S. Gartlan and D. B. McKey (University of Wisconsin) likewise demonstrated the presence of toxins in most plant products in the Douala-Edea forest of Cameroon. On the other hand T. Iwamoto (Miyazaki University), in bioenergetic studies of Japanese monkeys in evergreen forest and gelada baboons in Ethiopian montane grassland, obtained figures suggesting that primates used only a tiny proportion of the potential food available. T. H. Clutton-Brock (University of Sussex), and other participants in the concluding discussion, considered that problems of measuring food availability were so intractable, at least in tropical forest, that any attempts were doomed to failure.

S. A. Altmann (University of Chicago) suggested that attention should be focused on species living in relatively simple habitats, and presented a mathematical model of optimal diet, to be tested on savanna baboons in Kenya. For foraging strategies to be adaptive, he pointed out, animals must eat enough of the various foods available to stay above the minimum for every nutrient and below the maximum for every toxin, at the least possible cost. While the model related these factors with elegance and simplicity, many participants thought it likely to founder on the practical problems of measuring cost, including as it does such diverse elements as energy expenditure, time, and risk of predation. Clearly we must wait some years yet before the value of this and competing approaches becomes clear.