

localized ectopic expression of a Hox gene, *Hox-4.6*, in the limb bud of the developing chick results in a homeotic transformation of one digit into another⁷. These results are the first direct demonstration that Hox genes actually control the patterning of the vertebrate limb.

How widespread is the homeobox? A screen for homeobox sequences, employing the polymerase chain reaction, reveals that Hox genes are present in the principal animal phyla and points to their being universal in animal metazoans. Moreover it seems that the different classes of homeodomain protein were established early during evolution, around the time of the rapid metazoan radiation some 600 million years ago (C. Kappen and F. Ruddle, Yale University). All these results suggest that the homeobox was a central player in the evolution of organismal form. Certainly

they are providing hints as to the answer to a long-standing puzzle for students of the vertebrate head — did the head arise by modification of ancestral segments in a headless ancestor, or was it made from scratch? The expression patterns of four homeodomain proteins in the mid- and forebrain of mice (A. Simone, CNR, Milan), the *Drosophila* homologues of which are required for development of the fly head, lend support to the first explanation. □

Guy Riddihough is an assistant editor of Nature.

1. Schier, A. F. & Gehring, W. J. *Nature* **356**, 804–807 (1992).
2. Kissinger, C. R. *et al. Cell* **63**, 579–590 (1990).
3. Hanes, S. D. & Brent, R. *Science* **251**, 426–430 (1991).
4. Rould, M. A., Perona, J. J. & Steitz, T. A. *Nature* **352**, 213–218 (1991).
5. Smith, D. & Johnston, A. D. *Cell* **68**, 133–142 (1992).
6. Le Mouelluc, H. *et al. Cell* **69**, 251–264 (1992).
7. Morgan, B. A. *et al. Nature* (in the press).

ECOLOGY

Pastoral plumbing

Peter D. Moore

SPATIAL and temporal heterogeneity in an ecosystem promotes the development of biological diversity and is therefore often sought after by those concerned with management for conservation purposes. In grasslands, for example, large grazing animals contribute to microhabitat diversification not only as a result of their trampling and biting of herbage, but also by defaecating and urinating in patches.

V. J. Jaramillo and J. K. Detling^{1,2} have examined the effects of patch urination on grasslands, both in terms of its effect on nutrient uptake and growth of grasses and also its subsequent influence on the grazing behaviour of herbivores. They find that the grasses tested were stimulated by treatment with artificial urine and that subsequent grazing by cattle was intensified within the patches. Evidently this will favour the development of structural heterogeneity in grassland, but its ultimate influence on species diversity is more difficult to predict.

Excretion by grazing animals is known to affect the internal nutrient cycling pattern of a range of different ecosystems, both terrestrial and aquatic, and nutrient redistribution and local concentration produced in this way can modify the growth and productivity of primary producers. Fish schools grazing in sea grass during the day and roosting amongst corals, for example, increase the local ammonium ion concentrations by over four times and this can stimulate coral growth because of the provision of

extra nutrients to the photosynthetic symbionts of the corals³. On an even smaller scale, copepod excretion has been shown by radioactive-labelling studies to create a spatial heterogeneity of phosphorus concentration that can result in patches of enriched growth amongst phytoplankton⁴. Similarly, on land, invertebrate grazers such as snails in the Negev desert consume endolithic lichens from rocks during the cool of the night, then deposit much of the nitrogen in the shade of those rocks during the day, creating pockets of eutrophicated soil⁵.

Jaramillo and Detling¹ looked at the development of patchy environments in grassland near Cheyenne, Wyoming, by applying treatments of two litres of simulated urine to selected plots while retaining untreated matched plots as controls. They then concentrated their attentions on two grass species, *Agropyron smithii*, a rhizomatous C3 photosynthesizer, and *Bouteloua gracilis*, a tussocky C4 species. Both species increased their tiller density as a result of treatment, *Bouteloua* in the first year and *Agropyron* in the second. The temporal difference in response could be related to the greater efficiency of nitrogen use in the C4 species; less nitrogen is needed for photosynthetic enzyme production, so more can be devoted to vegetative growth. The influence of the local fertilization by urine was felt outside the immediate ring of application — in the case of the rhizomatous species, this is likely to be a consequence of transport along the rhizomes, but movement in the

clump-forming species is more difficult to explain. Perhaps nitrogen transfer occurred by mycorrhizal links between individual plants of the same (or even different) species.

In a second experiment², Jaramillo and Detling observed the behaviour of cattle when presented with grassland in which simulated patch urination had taken place. Selective grazing occurred, in which the fertilized plots were favoured, and this corresponded with elevated foliar nitrogen concentration of the grass. This response by the grazing animals supports the ideas of Bazely, Ewins and McCleery⁶, which stem from their observations of the behaviour of barnacle geese (*Branta leucopsis*) on salt marshes in the Netherlands. The geese concentrated their grazing in areas that had been used for colonial breeding by herring gulls (*Larus argentatus*) and in which the foliar nitrogen content of the red fescue grass (*Festuca rubra*) was increased. A cycle of urination, fertilization, growth stimulation and increased grazing appeal seems now to be well established by these various studies.

The question of species diversity is more difficult, however. If we accept the Grime model of moderate stress leading to enriched diversity⁷, then local fertilization is more likely to stimulate the growth of 'competitor' plants and suppress those less robust in stature and aggressive in growth. But if those same patches are then subjected to increased grazing, the effect could be reversed, with fast-growing species being selectively removed by the herbivores. In practice, the establishment of species-rich grassland, according to the work of Gibson and Brown⁸, demands more than a quick fix by a selected grazing regime. They claim that centuries of very heavy grazing is the only sure way of establishing the species-rich, 'ancient' grasslands which are so highly prized by conservationists in temperate regions. There is no magic short-cut. Within our life spans we may have to make do with the patchy environment created by a leaky cow. □

Peter D. Moore is in the Division of Biosphere Sciences, King's College London, Campden Hill Road, London W8 7AH, UK.

1. Jaramillo, V. J. & Detling, J. K. *J. appl. Ecol.* **29**, 1–8 (1992).
2. Jaramillo, V. J. & Detling, J. K. *J. appl. Ecol.* **29**, 9–13 (1992).
3. Meyer, J. L., Schultz, E. T. & Helfman, G. E. *Science* **220**, 1047–1049 (1983).
4. Lehman, J. T. & Scavia, D. *Science* **216**, 729–730 (1982).
5. Jones, C. G. & Shachak, M. *Nature* **346**, 839–841 (1990).
6. Bazely, D. R., Ewins, P. J. & McCleery, R. H. *Ibis* **133**, 111–114 (1991).
7. Grime, J. P. *Plant Strategies and Vegetation Processes* (Wiley, Chichester, 1979).
8. Gibson, C. W. D. & Brown, V. K. *J. appl. Ecol.* **29**, 120–131 (1992).