population and community levels. John Gilbert (Dartmouth College, Hanover, USA) found both genetic variance and environmental (inducible) effects for the length of posterior spines used for predator defense in *Brachionus quadridentatus*, the 11th rotifer species found with predator-induced spine development. His results illustrate how selection works to fine-tune phenotypic plasticity in rotifers; this was also shown by the effects on offspring fitness of differential allocation of resources to eggs (Nadia Santo *et al.*, Milan University). Control of rotifer population density by predators was addressed by Norbert Walz *et al.* (Freshwater Ecology and Inland Fisheries, Berlin, Germany), who reported an unexpected impact of freshwater mussel predation. Another contribution demonstrated density-dependent effects and regulation in natural rotifer populations using time-series analysis and complex phenomenological models (Terry Snell *et al.*, Georgia Institute of Technology, Atlanta, USA). The impact of size-dependent predation by copepods and aquatic insects on rotifer populations and assemblages was analysed in several contributions (e.g. Stephanie Hampton, Dartmouth College). This work can help us to understand the maintenance of ecological diversity at low taxonomic levels (e.g. Rainer Deneke, Brandeburg Technical University, Bad Saarov, Germany). With similar focus, Jorge Ciros *et al.* (Valencia University) analysed competitive dynamics between sympatric sibling species. Using Tilman's experimental design[1], seldom applied to animals, they showed that coexistence is possible based on differential use of algae prey.

Two reviews helped revise the interpretation of ecological interactions at community and ecosystem levels. Peter Starkweather (Nevada University, Las Vegas, USA) stressed the dual role of rotifers as predators and prey, and showed, in agreement with other participants (e.g. Ian Duggan, Waikato University, Hamilton, New Zealand), that rotifers are prominent components of aquatic food webs, in contrast with the prevailing crustacean-biased view. The second review by Ramakrishna Rao (Delhi University, India) compared the impact of predation and competition on tropical and temperate rotifer communities, concluding that top-down control is relatively more important in the tropics, with high predation pressure selecting for smaller body size. The concomitant disadvantage of small body size in competition is not so important because of the relative abundance of food in tropical aquatic ecosystems.

Prospects

Knowledge of the biology of the rotifers is approaching a mature stage. As the biology of this group becomes better understood, the role of rotifers as a key group influencing the dynamics of aquatic ecosystems becomes better appreciated. Dormancy, parthenogenesis and short life cycles give rotifers a central role in aquatic ecosystems. Their utility as experimental models for testing contemporary ecological and evolutionary theory is documented by the recent literature, and by this, and previous, symposia.

Acknowledgements

This meeting was organized by La_orsi Sanoamuang, Khon Kaen University, Thailand.

Claudia Ricci

Dipartimento di Biologia, Università di Milano, via Celoria 26, 20133 Milano, Italy (claudia.ricci@unimi.it)

Manuel Serra

Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, Apartado Oficial 2085, 46071 València, Spain (manuel.serra@uv.es)

Terry W. Snell

School of Biology, Georgia Institute of Technology, Atlanta, GA 30332-0230, USA (ts41@prism.gatech.edu)

References

1 Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press

Snakes: a new 'model organism' in ecological research?

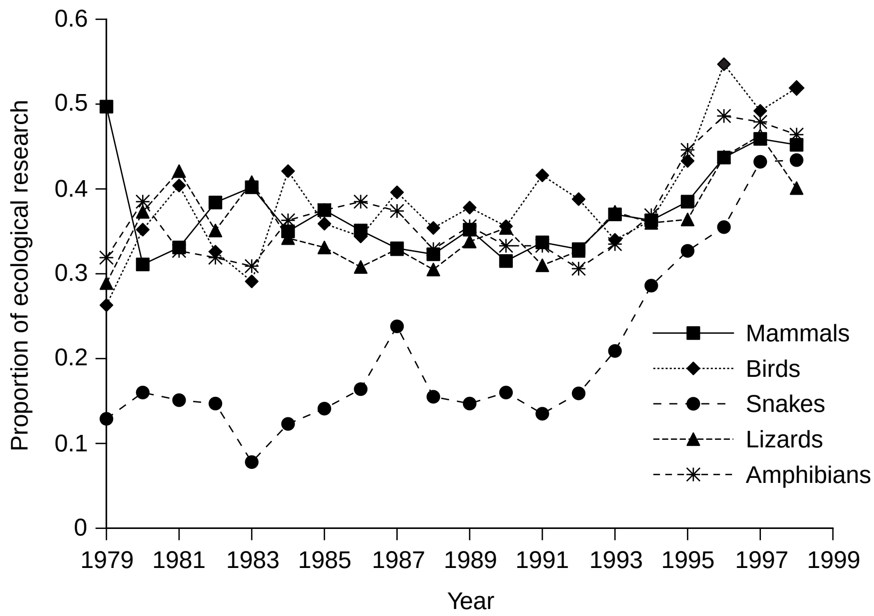
In most fields within biology, a small number of taxa receive disproportionate scientific attention. This phenomenon is evident at all phylogenetic levels (e.g. 'model species' within genera and 'model genera' within families, etc.) and operates differently within different fields of study. Particular taxa can serve as 'model organisms' for some types of question, whereas other parts of their biology attract little attention. Why does this pattern exist and what factors sometimes cause it to change? Here, we examine the growing popularity of a previously neglected lineage – the snakes – as study organisms for ecological research.

With a few notable exceptions (especially the Hymenoptera), most of the popular model organisms in behavioural ecology are vertebrates – particularly endothermic vertebrates (birds and mammals). This research emphasis is massively disproportionate to species richness, even if we restrict comparisons to within the terrestrial vertebrates. For example, there are more species of amphibians than mammals[1], but almost ten times as many papers on behaviour and ecology of mammals than of amphibians (over the period 1979 to 1998, *Zoological Records* had >32 000 entries for behaviour and ecology of mammals, and about 4000 for amphibians).

There are both costs and benefits of concentrating a high proportion of research upon a small number of taxa. The scientific benefits are perhaps most obvious. Some sorts of animal have features that expedite particular types of research (e.g. birds are generally much easier to observe than mammals). Other benefits of such taxonomic concentration of research include historical factors: there are more giants upon whose shoulders one can stand. More cynically, there might be other logistical advantages also. Those same giants (or their academic offspring) might well review your papers and be inclined to look upon them more favourably. Nonetheless, there is also a cost in generality. We cannot hope to understand the diversity of organismal tactics unless we study a diversity of organisms.

The system is not static, because the relative intensity of effort devoted to particular types of research within particular taxa varies substantially through time. Analysis of *Zoological Records* entries reveals some interesting patterns in this respect. We counted the number of entries for each major group in specific fields (Fig. 1). The relative numbers of publications per group remained fairly constant through time, with an increasing

  PII: S0169-5347(00)01853-X



Trends in Ecology & Evolution

Fig. 1. Changes in research focus over a 20-year period (1979–1998), as shown by the number of publications on ecological topics using major groups of terrestrial vertebrates. The number of ecological publications is shown as a proportion of all publications on ecology and behaviour for the group concerned. These numbers were obtained from searches in the *Zoological Records* database, using the taxonomic group name (e.g. avian or bird) and either 'ecology' or 'behav*'. For most terrrestrial vertebrates, ecological publications comprise about 30 to 40% of the total numbers of ecological and/or behavioural papers. However, in snakes ecological research was rare (usually < 20% of such publications) until the early 1990s, but has increased rapidly since that time. The increase in proportional emphasis on ecological research for snakes is statistically significant over this time period (Spearman's rank: $r_s = 0.77$, $n = 20$, $P = 0.0006$).

proportion of effort devoted to ecology (as a proportion of all research) for all major taxa. However, the proportion of these studies devoted to ecology rather than behaviour showed an interesting shift in one lineage: the snakes. The proportion of 'ecological' research within the general 'behaviour and ecology' field was surprisingly similar among groups (usually around 35%), and remained consistent through time (Fig. 1). However, in snakes ecological research was rare until the early 1990s, but since then has climbed rapidly. The proportion of research effort devoted to ecological topics in snakes now equals that in the other terrestrial vertebrates (Fig. 1). Indeed, the covers of several high-impact journals have recently featured research on snake ecology (e.g. *Journal of Animal Ecology* 63, 1994; *Nature* 379, 1996; *Proceedings of the Royal Society B* 265, 1998; *Ecology* 80, 1999), a situation not even dreamed of in earlier years. Thus, the literature on snake ecology provides an opportunity to ask why a lineage can (quite suddenly) begin to serve as a popular 'model' organism for a particular kind of research.

The increasing scientific attention paid to snake ecology reflects several factors:

- Logistics: the development of miniature radiotransmitters has made it feasible to carry out field studies on large, cryptic, secretive animals that are rarely active and (in some cases) are difficult or dangerous to handle[2,3]. Thus, ecological studies of snakes were revolutionized by this new technology.
- Competition: as behavioural ecology increased in popularity, empty scientific niches filled rapidly. Most large endothermic vertebrates were intensively studied, at least in Europe and North America. Given this level of relative saturation, researchers looking for novel ecological projects began to consider 'unpopular' organisms more seriously.
- Resources: the burgeoning environmental awareness movement also began to take a broader taxonomic perspective on what should be protected (and therefore investigated). In some cases, conservation resources flowed to nongame wildlife, encouraging ecological research on large, charismatic (but nonendothermic) predators, such as snakes.
- Social attitudes: the traditional Judeo–Christian view of serpents is exceedingly antagonistic, but environmental education has facilitated a more tolerant approach. Thus, taxpayers are (slightly) less likely to view expenditure on snake ecology as a total waste of effort.
- Fashionable concepts: snakes are terrible study organisms for some questions, but excellent for others. In particular, snakes demonstrate extraordinary plasticity in a plethora of ecological and life history traits, such as growth rates, direction and degree of sexual dimorphism, mean adult body sizes, dietary habits and reproductive biology[2,3]. Such plasticity is well suited to experimental studies. With increasing emphasis on experimental ecology, snakes have become more attractive study systems.
- Historically unique events: undoubtedly, accidents of history have also played a role. Pioneering workers, such as H.S. Fitch[4], inspired a generation of snake ecologists. There is no easy way to evaluate such impacts, but heartfelt dedications to mentors in snake ecology texts[3] suggest that such effects might have been considerable.

The validity of such speculations is difficult to evaluate and their generality is even less easily discerned. The factors that cause research on particular taxa to wax and wane through time might well differ substantially across different types of organism, and it would be interesting to have other taxonomic perspectives on this issue. Individual researchers (ourselves included) generally profess total ignorance as to why they are attracted to (and thus, have chosen to work on) a particular taxonomic group. Nonetheless, we applaud the emerging challenges to taxonomic chauvinism within ecological research, and look forward to the day when the distribution of research effort within our field more closely mirrors the phylogenetic diversity of living organisms.

Richard Shine
School of Biological Sciences A08, University of Sydney, NSW 2006, Australia (rics@bio.usyd.edu.au)

Xavier Bonnet
Conseil Général des Deux Sèvres, Centre d'Etudes Biologiques de Chizé, CNRS, 79360, Villiers en Bois, France (bonnet@cebc.cnrs.fr)

References

1 Pough, F.H. *et al.*, eds (1996) *Vertebrate Life* (4th edn), Prentice-Hall
2 Seigel, R.A *et al.*, eds (1987) *Snakes: Ecology and Evolutionary Biology*, Macmillan
3 Seigel, R.A. and Collins, J.T., eds (1993) *Snakes: Ecology and Behavior*, McGraw-Hill
4 Fitch, H.S. (1999) *A Kansas Snake Community: Composition and Changes over 50 Years*, Kreiger