that simpler psychological rules of thumb (perhaps having to do with, for instance, the nature of relevant stimuli, and with conditional learning) are the ones produced by natural selection. From birth, parents and the newborn negotiate honestly and dishonestly with one another, providing plenty of time for the infant to learn relatively complex rules of social exchange long before the evolutionary psychologists get at it to test its reasoning capabilities.

Humans clearly differ from animals, if only quantitatively. One of evolutionary anthropology's aims is to distinguish humans from other animals, and explain the distinction. And one of the more interesting new distinctions is empathy, especially for anyone interested in altruism or cooperation. Cheney and Seyfarth here present very convincing evidence that monkeys do not act as if aware of others' mental states. Hence they cannot empathize. We humans can. Is that why we are such good observational learners and teachers – with all the consequences for cultural evolution that Boyd and Richerson address here – and why only humans might be capable of true altruism?

Anyone arguing for a distinctive human ability needs to tell us when it arose. Mellars's chapter might epitomize modern evolutionary anthropology and the book. He argues that we can detect a major increase in the sophistication of our tools, our art, and our social complexity at about 50 000 years ago. Here's the Naissance that preceded the Renaissance, and it correlated with a sudden great increase in human population density and geographic dispersal, and hence presumably changes in the intensity and nature of competition. If we could fully explain the causal route among all these events, the task of evolutionary anthropology would be well advanced. The chapters in this book give a very complete coverage of how we might continue the search.

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What are species?

Species: The Units of Biodiversity

edited by M.F. Claridge, H.A. Dawah and M.R. Wilson

Chapman & Hall, 1997.
£49.00 hbk (xvi + 439 pages)
ISBN 0 412 63120 2

This book addresses the recent furore about species concepts. The debate is a rare and fascinating case where a philosophical logjam actually affects the growth of scientific knowledge. Ernst Mayr catalysed the recent arguments about species by proposing what he felt was *the* solution, the 'biological species concept' (BSC). Mayr recommended that the idea of species as reproductively isolated 'evolutionary units' be divorced from the everyday business of classifying individuals into particular species. He overtly provided a set of ideals about how the status of species was maintained, rather than a useful definition of that status.

Mayr's heritage is a huge muddle. By postulating an ideal species – one that has reproductive isolation – rather than a practical approach to sorting actual taxa, Mayr opened a Pandora's box of alternative concepts. Evolutionists' ideas of underlying biological reality differ widely. Today we have competing species concepts based on ecological niches, mate recognition, cohesion, and various kinds of phylogenetic ideals. Philosophers have added many pages of learned discussions, but they haven't helped much either. This book is a revolutionary attempt by Claridge and the other editors to survey practical species definitions in all organisms, from viruses to mammals. For this reason alone, it deserves a place on the shelves of anyone interested in the species debate.

What concepts do the authors select? Claridge himself would have been happier if the BSC had been universally adopted, but it received only eight votes (I have allowed some authors to vote for more than one concept). A concept I liked, in which multiple morphological and/or genetic characters are used to define the gaps between species has a slight edge (nine votes), especially among prokaryologists, while Cracraft's so-called phylogenetic species concept (PSC) is neck-and-neck with the BSC, with eight votes. Finally, three authors (Goodfellow, Embley, Minelli) point out that some sort of cut-off genetic distance could be used as a rule of thumb to define species. This may seem odd, but distance-based species definitions are becoming disappointingly respectable as we obtain molecular genealogies of allopatric groups as diverse as tuataras, canids and the great apes. The bonobo, for example, is dubiously regarded as a separate species from the chimpanzee because it differs more than seems normal within species in morphology, genetics and behaviour.

Although this book is about practical applications, the musings of philosophers are represented by Hull, who is notable here because he recants his well-known 1968 diatribe against operationalism in definitions. As we might expect from a philosopher, Hull concludes that 'no one concept is clearly superior to all the others'. The most excruciating chapter is by Mayden, who constructs a hierarchical classification of 25 species concepts, and 'finds' Simpson's evolutionary concept (ESC) to be fundamental to the rest. He does not realize that the ESC will only be fundamental if you hold its ideals to be so *a priori*. Twelve of 18 authors emphasize Mayr's philosophical distinction between criteria and concepts of species, but I am hopeful about the future because three of these authors specifically reject the idea that practical species should be defined with respect to an underlying biological ideal. Arguably, Cracraft is also a philosopher, since, as systematist on a group where few new taxa exist (birds), he mainly occupies himself by redefining the levels of already well-known taxa, most recently in the birds of paradise. The weakness of the PSC is that tiny monophyletic populations and even individuals might be defined as separate species by virtue of possession of at least one diagnostic character (Knowlton, Corbet). Cracraft replies: (1) 'the application of the concept of monophyly is superfluous and unnecessary'. Cracraft's 'phylogenetic' species can then presumably be paraphyletic, polyphyletic, or phenetic. (2) His critics 'forget that species concepts are populational concepts that are used to delimit basal taxa', and that 'the PSC is not about the diagnosibility of individuals but of populations'. But Cracraft still doesn't face the problem that he might distinguish many small locally divergent populations as separate species (Knowlton).

There is a lot of fascinating biology and systematics in the book. Species names in bacteria must be on a single approved list, and, since 1980, new species must all be named in a single journal (Goodfellow *et al.*). How sensible; why not do the same with all organisms? Lichen species names are considered under the International Code to apply only to the the fungal partner of the

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symbiosis. Unfortunately, the algal partner is very important, and may vary within a single thallus, leading to lot of difficulty in the concept of individuals, let alone species (Purvis). Recent DNA samples of soil bacteria and other prokaryotes reveal a wealth of unknown, uncultivable types; it is quite likely that these forms outnumber eukaryotic species, as well as far outranking them in overall DNA diversity. Species definitions applying mainly to eukaryotes (like the BSC) can hardly be called general, since they can only apply to a small twig on the tree of life (Embley and Stackebrandt).

Finally, a word about the BSC: it is not well known that its practical application, known as the 'polytypic species concept', pre-dated Mayr by about 50 years and was generally accepted in bird, insect and mammal systematics until recently (the PSC and distance-based species concepts are now eroding that consensus). Corbet provides perhaps the best and most spirited recent defence of the BSC: 'A species is a set of contemporary individuals that [are capable of interbreeding to an extent that] precludes the coexistence in the same place of discrete subsets ...'. I have added square brackets to indicate that reproductive isolation could be viewed as a supporting statement about causes, rather than a required part of the definition. The species problem will, I guess, drag on until evolutionists, systematists and philosophers agree on a criterion of the *status* of species, and leave the underlying causes – 'biological reality', reproductive isolation, cohesion, phylogeny and so on – of that status open.

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Behavioural ecology at thirty-something

Behavioural Ecology: An Evolutionary Approach (4th edn)

edited by J.R. Krebs and N.B. Davies

Blackwell Science, 1997.
£26.50 pbk (viii + 456 pages)
ISBN 0 86542 731 3

Because it is a synthetic field, the precise time of the birth of behavioural ecology is hard to pin down. The subject emerged during the late 1960s and early 1970s from five schools of thought: (1) Tinbergen's four questions[1], (2) connections between ecology and behaviour, (3) economic models of behaviour, (4) evolutionarily stable strategies, and (5) kinship, social evolution and breeding systems. However, the roots of behavioural ecology were to illuminate the role played by behaviours of individuals in determining the distribution and abundance of animals, with the intention of providing answers to questions that are central to ecology. Early on, behavioural ecologists recognized the importance of reciprocity: behaviour influences population processes, and the outcomes cause selection on behaviours themselves. Thus, population processes can be fully understood only via the behaviour of individuals, and in terms of the evolutionary pressures that have forged them[2]. Detractors tend to characterize behavioural ecology as too inward-looking, focusing on 'optimality' of this or that behaviour. However, all organisms face tradeoffs and behavioural ecology is concerned with how we can analyse these tradeoffs.

The vantage from this book is that behavioural ecology is outward-looking and expansive and involves links across different levels of biological organization. For example, the first part of the book shows how behavioural ecologists have revitalized the interest in linking mechanism and function, to the point that an author writes 'Behavioural ecologists and physiologists share a mutual interest in each other's efforts...recent developments in behavioural ecology have had an impact on the way physiologists started to think in evolutionary terms ...'. More generally, the expansive approach means that behavioural ecology involves links across levels of biological organization.

I was particularly pleased to see a chapter on information use, because the entire business of life involves 'guessing what was on the other side of the hill'[3,4]. This chapter, like the book, traverses a wide range of subjects and levels – from Bayesian analysis of information to the role of the hippocampus in information processing – as the questions are analysed. This, indeed, is the future of behavioural ecology. I was also particularly pleased to see chapters on mechanism and genetics. Even a dozen years ago, many behavioural ecologists would have considered such studies 'too reductionist'. The chapter on genetics, appropriately titled the 'Social Gene', makes the case for analyzing tradeoffs faced by organisms in the context of strategic thinking, rather than the usual infrastructure of population genetics. On the other hand, the chapter on life histories was too rooted in the past, and particularly ignored state-dependent life histories[5]. There are wonderful chapters on the phylogenetic foundations of behavioural ecology and population structure that emphasize historical constraints. This is important: we must understand the role that history plays in shaping the tradeoffs that organisms face. (One of the past charges against behavioural ecology, as too adaptationist, was the claim that historical constraints were ignored.)

The forward- and outward-looking approach is followed in most chapters, where the future and new horizons are identified. These include information processing ability of animals and its implication, quantifying the fitness consequences of recognition mechanisms[6], the integration of structure and function in sperm competition, the roles of multiple signals in animal communication, the influence of social cues on mating preferences (mate-copying), and the evolution of multiple mating. These horizons will help guide the next generation of researchers as they analyse the key questions.

The maturity of behavioural ecology, as a conceptual discipline, is clear throughout the volume. For example, the pieces for a unified science of sociality consist of theories concerning ecological constraints, kin selection, social dominance and reproductive skew. Together they determine the dynamics and structure of families. This unified theory leads to a set of 15 predictions, which will guide experimental and observational work. It is now possible to conduct experiments and observations in systems that even 10 years ago seemed inconceivable and to analyse the data using computer intensive methods.

Most fittingly, the last chapter deals with individual behaviour, populations and conservation. Considering that conservation is almost always concerned with small numbers of individuals, it is amazing that conservation biologists pay such little attention to individual behaviour: there is a need for the study of individual behaviour in conservation[7]. There are a couple of important gaps – no chapters on the behavioural ecology of disease or plant behavioural ecology (plants face tradeoffs too, and plant structure can be viewed in analogy to animal behaviour).

Behavioural ecology is indeed in its prime. In the future behavioural ecologists will embrace a wide range of techniques, from gene splicing to computational descriptions of behaviour to magnetic resonance imaging, as we move towards deeper understanding of how organisms deal with the challenges put to them by the environment.

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