

Putting the Species back into Community Ecology

Ecology and Natural History of Desert Lizards

by Eric R. Pianka, Princeton University Press, 1986. £56.80/\$45.00 hbk, \$19.00 pbk (x + 208 pages) ISBN 0 691 08148 4



Ecologists have no difficulty defining 'community': it is the set of all the species in an area, or possibly, some subset of these species defined taxonomically (e.g. a bird community) or trophically (e.g. a plant or herbivore community). Community ecology should be about large numbers of species – just how many species are there, how do they interact, and so on? What community ecologists study, however, are rather small numbers of species, and, apparently, ever smaller numbers as the discipline develops. In 1975, in the volume edited by Cody and Diamond¹ about 40% of 13 papers tabulated or figured 75 or more species; a further three papers considered the numbers of species directly (and other papers were largely theoretical). A decade later, in the volume edited by Diamond and Case², the comparable number was 12% of 17 papers, and two more considered the number of species directly; the majority of studies considered less than 25 species.

The reasons for this trend may include the need to understand the mechanisms of interaction between species and the difficulty of performing experiments on more than a handful of species. They might also involve the uncertainty that community ecologists are experiencing in the debate between, for instance, the Florida and California schools³, about how to analyse community patterns.

Understanding the details and mechanisms of interactions between small numbers of species is a laudable goal. But the factors influencing small numbers of trophically and taxonomically related species are

not necessarily the same factors as those that affect much larger groups. To a rough approximation, community ecology is becoming the ecology of guilds rather than communities. It is against this background that I find Pianka's new book on Australian, African and American desert lizards so interesting: it is about community ecology on a large scale.

Some areas in Western Australia support 42 different species of lizards. There are fairly typical lizards, nearly legless subterranean skinks, snake-like pygopodids, and some large predatory varanids. In the Kalahari of Namibia and Botswana, the lizard faunas are about half as rich, and sites in the USA and Mexico have only from 6 to 11 species. In each of the three areas, Pianka has assembled extensive data on habitat use, prey use, and morphology of the species. He, and Princeton University Press, are to be commended for presenting these data in full, in 30 pages of appendices. And, for those of us not knowing what the species look like, the text is illuminated with line drawings and 29 colour photographs, making this an especially attractive volume.

Why are there differences in the numbers of species? Conventional wisdom might suggest that the richest communities would occur where other potential competitors are scarce. The Australian varanids may replace the scarce predatory mammals, the pygopodids may replace certain snakes. In contrast, the numbers of insectivorous lizards positively correlate with the numbers of birds both across and within the three deserts.

Perhaps there are more species in climatically predictable areas, because in such areas species can be more ecologically specialised and more species can be fitted together. Yet, there is not a good correlation between species richness and dietary or habitat specialisation. Indeed, most of the species in all three areas show a strong preference for ants, termites and beetles. Moreover, there are more species in areas which, other things being equal, have a greater variability in rainfall. And it is rainfall that, in these arid areas, is likely to drive the abundance of food resources. So, it appears that resource unpredictability increases – rather than diminishes – species richness.

The overwhelming impression given by Pianka's studies is of the differences between the communities. The richness of the Australian communities comes by adding species with strategies well-represented

in North America (15 versus five diurnal, ground-dwelling species) as well as species adopting poorly represented strategies (10 versus one widely foraging diurnal species, and also 10 versus one nocturnal species). Certainly, there is the famous example of convergence between species which show extreme dietary specialisation on ants (*Moloch* spp. of Australia and *Phrynosoma* spp. of North America). Overall, however, it is the differences between the communities that are most striking. Interpreting the interactions between these species in terms of competition and its effects on niches may be satisfactory for small subsets of the species, but the entire communities suggest that existing theories are inadequate.

Despite all the differences, Pianka finds some abstract similarities between the three deserts. The first similarity involves the overlap in prey and microhabitat use. The raw data for these studies are the proportional uses, p_i , of the various prey or habitat categories. We can ask how much overlap is there between each species and the species nearest to it in diet (or habitat), the next nearest species, and so on. Overlap plotted against rank (nearest, next nearest, etc.) is an inevitably decreasing function. But how do these functions differ from what we might expect? Pianka produces a plausible null hypothesis by shuffling the observed p_i values for each species, among all the diet (or habitat) categories that the species exploits.

In all three areas the same patterns hold. The lizards overlap in their use of prey species more than we would expect, and in their choice of habitats less than we would expect. These communities seem to follow the rule that the species tend to feed on similar prey species but in different places.



A second similarity involves the extent to which the species shift their diets from site to site. We might expect the total competition suffered by a species Q to be related to the sum of the products between overlap in diet with each of the other species A, B, C, \dots , and the corresponding density, X_A, X_B, X_C, \dots . Calculating this sum for species Q , at each site it occurs (I, II, ...) gives a measure of species Q 's performance as a 'resident' (the smaller the sum, the better the performance). We can now ask how species Q would manage at a particular site (say, site I) if it adopted the diet it chooses at the other sites at which it occurs. To obtain measures of this 'alien' performance, we calculate the summed overlap-density products for species A, B, C, \dots , at site I, using species Q 's diet first at site II, then III, and so on. If species

Q occurs at three sites, this gives us six comparisons of performance of resident versus alien diet (resident at I, versus alien at II and III, resident at II, versus alien at I and III, etc.).

In eight of nine North American, 18 of 19 Kalaharan, and 31 of 49 Australian species, the resident diets gave a better performance, on average, than the alien diets. In only one species (in North America) did the resident do worse than the aliens (all the rest were ties). Simply, every species appears to adjust its diet at each site to reduce the total competition from the other species present.

Pianka's book has some simple yet important messages. Some of what he finds conforms to existing theory of competition and niches. But particularly when we look at issues at a larger organisational scale, the differences in his communities are not

easy to explain. We are unlikely to develop ideas about the large scale features of communities in a vacuum, yet studies of large numbers of species are rare. The breadth of Pianka's study – as well as its detail – makes it a unique contribution.

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References

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Behavioural Ecology

Behavioural Ecology: Ecological Consequences of Adaptive Behaviour

edited by R.M. Sibly and R.H. Smith, Blackwell, 1985. £48 hbk, £19.50 pbk (ix + 620 pages) ISBN 0 632 01359 1

Relying on economic models inspired by principles of natural selection, behavioural ecology has enjoyed considerable success in predicting certain aspects of the behaviour of individual animals¹. Given a reasonable (though incomplete) understanding of individual behaviour, we can ask if that knowledge suggests predictions about significant attributes of single populations or communities of co-occurring species². In 1984 the British Ecological Society met to explore the implications of adaptive behaviour for the dynamics, regulation, and stability of populations. The resulting volume no doubt will advance ecologists' interest in examining behavioural strategies as mechanistic bases for population-level phenomena.

The book's 34 papers are allocated among five sections. The first, entitled 'Selective Review', lacks a common behavioural theme, although three of the seven papers consider life history theory. The second through fifth sections are more focused. The respective sections discuss foraging, spacing behaviour, breeding behaviour, and social organization as plausible foundations for predicting or interpreting population dynamics. Some of the papers report original results. Several contributors offer highly selective, but informative, reviews of their previous papers.

The book is not intended as a survey of contemporary behavioural ecology, despite the collective breadth of the five sections. The more specific aim is to expand the scope of behavioural ecology toward an effective interaction with theories of population growth and regulation. Neither the difficulty nor the potential significance of this objective should be understated. A few of the papers discuss interesting topics, but forge only weak links between behavioural and population ecology. There is little new in the general statement that behavioural variation among individuals can induce variation in survival or fecundity, which in turn influences a population's expected growth rate. However, a number of the papers achieve a successful and perceptive integration of the economics of behaviour and population dynamics. I liked Parker's contribution; using game theory, he calculates expected fitnesses for

individuals engaged in a predator-prey arms race. The game lacks an evolutionary stable solution by design. Given coupled equations for predator and prey densities, Parker demonstrates numerically that cycles in the frequencies of the behavioural strategies can drive cycles in the population sizes of both predator and prey. Perhaps a more important lesson is that quantitative hypotheses about population dynamics may be generated rigorously by allowing the parameters of growth equations to depend on a model of adaptive behaviour.

Only five papers in the book discuss interactions involving two or more species. As Schoener³ points out, one can propose possible behavioural bases for a community's properties in two different ways. Behaviour may be incorporated into population dynamics, as suggested in the volume under review. Secondly, behaviours such as dietary choice⁴ and habitat utilization⁵ of different species can be compared to an expectation under interspecific independence, or studied in an experimental manipulation of densities. In other words, a knowledge of behaviour may help us understand a lot more than demography. The book's intended focus on population dynamics probably discourages discussion of community ecology. Ecologists with an interest in behavioural mechanisms underlying natural communities should consult the symposium edited by Price⁶, as well as the volume by Sibly and Smith.

