DIVERSITY AND ECOLOGICAL ANALOGUES AMONG DESERT REPTILES

JOHN CLOUDSLEY-THOMPSON 10 Battishill Street, Islington, London N1 1TE

INTRODUCTION

Diversity is often regarded as a measure of the richness of species in a faunal region or biome. This concept provides a more useful measurement of the characteristics of a community when it is combined with an assessment of the relative abundance of the various species present. It does not, however, take into account the variety of morphological forms in the area – cursorial, fossorial, aquatic, arboreal and so on. Moreover related groups or taxa of smaller animals may not only be represented by more species than there are in taxa of larger animals in the same habitat, but they also contain more individuals of each species. There are naturally many more micro-environments in the same region than there are major habitats and, consequently, both more species and more individuals in them. Furthermore, it is a matter of opinion whether diversity should be reckoned in terms of the numbers of species present, or in the genetic variability within each of these species. More homogeneous environments must, obviously, contain fewer species than do less homogeneous environments, while the most numerous species occupy extensive habitats such as wide expanses of grassland or, in the desert biome, a sea of sand dunes rather than, say, a single tuft of perennial grass.

The diversity of reptiles lies not so much in their diversity of form as in the number of times that a particular shape or physiological adaptation has been evolved independently in different taxonomic groups. These often respond to environmental factors in remarkably similar ways. When quite unrelated species come to look alike as a result of parallel evolution in different geographical regions, they may be known as 'ecological equivalents' or, more precisely, as 'ecological analogues'. Some of the best known mammalian examples are the Fennec Fox of the Sahara, which has a number of adaptive characters that parallel those of Nearctic Kit Foxes, and the Kangaroo Rats of the North American deserts which closely resemble the Jerboas of the Palaearctic realm. Reptilian examples include the Australian Thorny Devil Moloch horridus (Agamidae) and its approximate analogue Phrynosoma platyrhinos (Iguanidae), the Horned Lizard of the North American deserts, both of which exploit a diet of ants. Analysis demonstrates that these two species are morphologically closer to one another than is either to any other species of its own lizard taxon. No lizard of any other desert region of the world has adopted a similar life style (Pianka, 1985, 1986).

Another well-known reptilian example of ecological analogues is provided by the North American Sidewinder (*Crotalus cerastes*) (Crotalinae) and its Palaearctic counterpart, the Saharan Sand Viper (*Cerastes cerastes*) (Viperinae). Both these snakes move by throwing lateral loops forward, and hide themselves by flattening their bodies and shovelling sand over their backs. They are so much alike in general appearance that, were it not for the rattle of *Crotalus cerastes* and the pits between its eyes and nostrils, the two might easily be confused (Cloudsley-Thompson, 1991).

In his analysis of the ecological niche and community structure of the lizard faunas of the North American Kalahari and Australian deserts, Pianka (1985, 1986) pointed out that both North America and Australia have long-legged species that frequent the open spaces between plants – the iguanid *Calisaurus draconoides* and *Amphibolurus* (= *Ctenophorus*) spp. (Agamidae) respectively – while each region has a medium-sized lizard-eating species (*Crotaphytus wislizeni* (Iguanidae) in North America, and *Varanus eremius* (Varanidae) in Australia. A few Kalahari – Australia species pairs are also roughly equivalent e.g. the subterranean skinks *Typhlosaurus* and *Lerista* spp. (Scincidae) and the semi-arboreal *Agama hispida* and *Amphibolurus* (= *Pogona*) *minor* (Agamidae).

In addition to the examples already mentioned, other members of the Agamidae frequently occupy similar or analagous ecological niches to those of Iguanidae. Examples include Uromastix spp. (Agamidae) of the Great Palaeractic desert and North American Sauromalus and Cachryx spp. (Iguanidae). The south-east Asian agamids Leiolepis spp. resemble North American iguanids such as Dipsosaurus dorsalis and the Australian Amphibolurus pictus (Agamidae) while the Iranian agamid Phrynocephalus mystaceus and the African gecko Geckonia chazaliae may also have many characters in common. Despite this, Pianka (1985, 1986) concluded that the differences between the ecologies of most lizard species in the three continental deserts that he studied, are much more striking than are the similarities. 'It is easy to make too much out of convergence, and one must always be wary of imposing it upon the system under consideration'.

Neverthless, recognition of convergence is an important factor in the understanding of natural selection. (Another example of convergence upon which I do not intend to elaborate here, is provided by the adaptive coloration of desert animals, including reptiles, which almost always match the sandy hues of their environment, or else are black (Cloudsley-Thompson, 1979). It is almost a tautology to state that a particular biome, such as the desert, should engender comparable adaptations in its fauna in different zoogeographical realms of the world. Pianka (1986) provides an excellent example based on scorpion predation. While scorpions are solitary prey items, they are extremely large and nutritious, thereby presumably facilitating the evolution of dietary specialization. In the Kalahari they are preyed on by *Nucras tessellata* (Lacertidae) and in Australia by *Pygopus nigriceps* (Pygopodidae). The diurnal *N. tessellata* forages widely to capture these animals in their daytime retreats, whereas the nocturnal *P. nigriceps* sits and waits for scorpions moving at night, above ground, during their normal period of activity. No North American desert lizard specializes on a diet of scorpions, but the small snake *Chionactis occipitalis* (Colubridae) appears to have usurped this ecological role.

Whereas some lizards have evolved as dietary specialists, rather more are generalists. Moloch horridus and Phrynosoma spp. eat essentially nothing but ants. The Kalahari lizards Mesalina lugubris (Lacertidae) and Typhlosaurus spp. (Scincidae) feed entirely on termites as do the Australian nocturnal geckos Diplodactylus conspicilatus and Rhynchoedura spp. as well as some day-active Ctenotus spp. (Scincidae) (Pianka, 1986). Dietary diversity occurs in many species of lizards which eat almost everything they can catch and overcome. Variations in diet also occur within the same species, both from time to time and from place to place, as opportunities present themselves and the abundance of particular prey species fluctuates.

The existence of ecological analogues and convergence among reptiles is more evident in a comparatively homogeneous biome, such as desert, than it is in more complex environments. Nevertheless it often becomes apparent in specialized ecological niches everywhere.

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