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IMPORTANCE OF RIVERS IN SHAPING ORIGINAL EURO-MEDITERRANEAN LIZARD HABITATS

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In pristine conditions, Mediterranean Europe was covered by dense forests during all Pleistocene and in more recent warm periods. Combined with its rather northern position this means that at that time, apart from in coastal environments, lizard habitats would have been present only where open places were formed by the action of storms, natural fires and the erosive forces of rivers. The latter will have been the most reliable and also the most important force, especially combined with the influence of large grazing and browsing animals. Variations in habitat quality in the resulting open spaces are determined by longitudinal gradients in temperature, humidity, steepness and trophic conditions. Present day ecological differentiation and some special characteristics of the lizards will be discussed in the light of these hypotheses.

Keywords: lacertids, pristine habitats, rivers, erosion

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U izvornim uvjetima sredozemna Europa je bila pokrivena gustim šumama tijekom cijelog pleistocena i u novijim toplim periodima. U kombinaciji s njenim više sjevernim položajem to znači da je u to doba, osim u obalnim područjima, staništa guštera moglo biti samo tamo gdje su postojali otvoreni prostori nastali djelovanjem oluja, prirodnih požara i erozivnih djelovanja rijeka. Djelovanje rijeka bilo je najprisutnija i najvažnija sila, posebno u kombinaciji s utjecajem velikih životinja, koje su brstile i pasle. U nastalim otvorenim prostorima varijacije u kvaliteti staništa bile su određene longitudinalnim gradijentima u temperaturi, vlazi, strmini i trofičkim uvjetima. Raspravlja se o sadašnjim ekološkim diferencijacijama i nekim posebnim značajkama guštera u svjetlu iznesenih hipoteza.

Keywords: lacertidi, izvorna staništa, rijeke, erozija

INTRODUCTION

Modern European biogeographers conclude that distribution patterns of reptiles can be explained more easily using direct environmental parameters rather than

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historical processes (e.g. VARGAS & REAL, 1997, for Iberian reptiles). Yet PORTER (1972) stated that most geographic distributions of reptiles seen today can be attributed to Pleistocene and more recent climatic changes. In these geological periods Europe had roughly two alternating combinations of environmental conditions, viz. cold climates with open landscape types and warmer climates with densely forested landscapes.

As all European lacertids are clearly diurnal and heliothermic (ARNOLD, 1987), which means they depend on a combination of warm temperatures and more or less open terrain, it is not entirely clear where these animals could have been found originally. In the warmer periods, densely closed forests still not affected by man covered nearly all of Europe. In the colder periods, i.e. during the various Ice Ages, the greater part of Europe was too cold for lizards. Then the animals survived in refuges in the southernmost regions along the Mediterranean. In the warmer interglacial periods they repopulated Europe, but then also the vegetation closed in again. This means that there seems to have been no place for lizards in the warmer periods either, dependent as they are on direct insolation.

Direct insolation only can be attained in more or less open places, where the vegetation climax, in Europe high and closed forest, is put back for some reason to earlier, more open succession stages. This means that European lizards are intrinsically bound to early or intermediate succession stages of the potentially natural vegetation.

So in the warmer periods there always has been a need for forces, spread over time and space, which put back the natural succession.

FORCES PREVENTING VEGETATION CLIMAX

In pristine conditions four different forces can be distinguished, viz.:

1) **wind**: storms can create smaller or bigger open spots in forests by blowing down old trees. Without other influences such open places are of rather short duration and are also unpredictable in time as well as in space.

2) **fire**: also the rare occurrence of natural fires can have led to open landscapes locally. For these too the temporal, as well as the spatial, predictability is very low.

3) **water**: the erosive force of water in streams and rivers and the regular inundations of low-lying delta regions have a very strong influence on local vegetation development. Given rather fixed geomorphological situations these influences are in general long lasting and also their spatial distribution shows far fewer fluctuations than wind and fire effects. This means that the water cycle provides rather reliable lizard habitats, i.e. durable, more or less open, sunny spots. This effect of rivers still can be observed, even in recent times, by looking at the northernmost distribution points of species like *Podarcis muralis* and *Lacerta bilineata*, which are both strictly river-bound in north-western Europe (STRIJBOSCH *et al*., 1980; NETTMANN & RYKENA, 1985; GRUSCHWITZ & BÖHME, 1986).

4) **grazing, browsing and rooting animals**: this force should not be neglected. Most of the animals meant here also derive benefit from the more or less durable presence of rather early stages of vegetation succession, in which the spatial distri-

bution of nutritious biomass is often considerably more profitable for them than in high, closed forests. By their actions, open spots are more or less kept open.

Probably these two latter forces, rivers and large herbivores, have been the most important creating and maintaining forces of lizard habitats in pristine European conditions. Later, man came on the scene, far outweighing the influence of rivers and the original wild animals by deforestation (farmland cultivation) and cattle breeding.

EURO-MEDITERRANEAN LIZARD HABITATS

Mediterranean Europe originally was also densely forested, a situation lasting more or less until the 14th or 15th century (DELANO-SMITH, 1979). Locally, some deforestation had occurred already before that time, but the degeneration into the barren landscape dominating most parts now is surely of a later date (KING *et al.*, 1997). Thus little is left of the original forests, because, as GRENON & BATISSE (1989) have stated: »Of all the forest systems of the world, those around the Mediterranean ... have been most degraded by human action«. Because of this it is now rather difficult to indicate pristine lizard habitats there. For the greater part, nearly all of these animals now occur in man-made and man-sustained open landscape types. However, geologically speaking this situation has existeed for only a very short time. In the long periods before, forces other than man must have provided open, sunny places. As stated before, in the author's opinion these are the rivers and the bigger herbivores.

Given the geophysical situation, a lot of Euro-Mediterranean rivers flow more or less from north to south, i.e. from relatively cold to relatively warm. This longitudinal temperature shift is strengthened by the fact that all rivers flow from high to low altitudes.

Fig. 1 shows a hypothetical river, from its origin in the mountains to its delta along the sea shore. Initially the water runs through a steep, cool or cold, but more

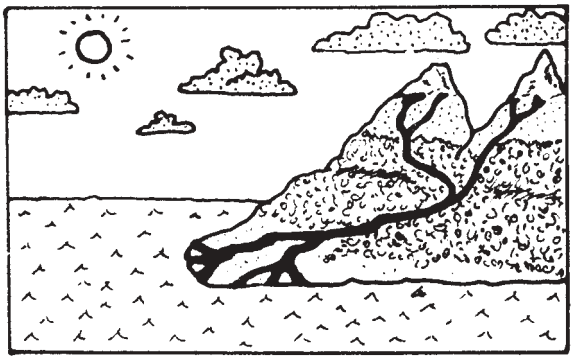

Fig. 1. Hypothetical river system from source to delta.

or less open mountain landscape. After this the mid-stream parts follow, initially with still fast running water through steep, narrow, V-shaped valleys in dense forests, but further on they may locally have formed broader, U-shaped valleys, in which meandering can already occur. At the end comes the flat delta, where the speed of the water is mostly very low and where the landscape shaping influence of the water is present more in sedimentation and inundation effects, than in erosion effects.

This also causes a second longitudinal gradient, viz. of relatively oligotrophic conditions in the upstream parts to relatively eutrophic conditions in the downstream parts, for in the erosive upper course material is removed continuously, while there is a certain accumulation in the lower course. This trophic gradient must also have been evident in the influence of big herbivores, because really big grazers with a high biomass must have shown a preference for the deltas and the broader, U-shaped valleys. Only in these parts, with enough warmth, eutrophy and stability (i.e. predictablity), enough nutrition could be produced. Relatively eutrophic conditions often mean a quick succession to climax vegetations, but in the more or less flat parts this succession is likely to be counteracted by the increased presence and actions of the big herbivores.

As a conclusion, the following qualities could be attributed to the potential lizard habitats in the various parts of a river (Tab. 1):

– in the upper course and the steep, V-shaped valleys strongly erosive forces regularly form relatively small, often isolated, open sites with a high inclination, on which great changes occur in direct insolation and also in temperature and humidity. These sites are heterogeneous in nature, and, because their relatively little surface area, show a great edge effect and accordingly are mostly present only temporarily. Their substrates are mostly hard and rocky, without substantial soil formation and therefore often of a relatively oligotrophic nature. So the main characteristics here are: small, steep, oligotrophic, unstable.

Tab 1. Qualities of lizard habitats along Euro-Mediterranean rivers in pristine conditions.

HABITAT CHARACTERISTICS	UPPER COURSE PARTS (V-shaped valleys included)	LOWER COURSE PARTS (U-shaped valleys and delta)
area	relatively small	relatively large
surface	hard	soft
inclination	steep	flat
trophic condition	relatively oligotrophic	relatively eutrophic
temperature: level / course	strongly changing / not stable	relatively high / relatively stable
humidity: level / course	strongly changing / not stable	relatively low / relatively stable
presence	for relatively short periods	for longer periods
influence of larger herbivores	small	great
situation	often isolated	mostly continuous
edge effects	great	small

– in the downstream parts (U-shaped valleys and delta) the combined effects of inundating water, sedimentation and the presence of big herbivores cause the presence of relatively large, more or less continuous and also more or less flat, open terrain. In these areas it is mostly relatively warm and dry, there is a lot to eat and the substrates are often sandy and soft. So here the main characteristics are: large, flat, eutrophic, more or less stable (at least predictable).

EURO-MEDITERRANEAN LACERTIDS

About the potential inhabitants, the Euro-Mediterranean lacertid lizard fauna is composed of only a few genera, of which *Lacerta* (including *Archaeolacerta* and *Timon*), *Podarcis* and *Algyroides* are the most important ones. Besides these only *Acanthodactylus* (1 species), *Psammodromus* (2 species) and *Ophisops* (1 species) occur, all of which reached Europe from Africa and Asia rather recently and already adapted to open, xeric environments (ARNOLD, 1989; 1990; BÖHME & CORTI, 1993). Within the five old-European (sub)genera two have rather big representatives (*Lacerta* and *Timon*) and three have rather small representatives (*Podarcis*, *Archaeolacerta* and *Algyroides*). In ectotherm animals the fact of being big or small also includes a number of differences in ecological needs. Big animals with their generally relatively high body weight cannot live easily on steep slopes, and cannot retreat into narrow rock crevices. Due to their relatively small skin area they evaporate relatively little (making them less water dependent) and for the (often rapid) build-up of their greater biomass they need a rather eutrophic environment with preferably a predictable, relatively high temperature. Due to their relatively greater skin area smaller animals have higher cutaneous water loss, but this is balanced by their considerably faster warming up capacity; yet this makes them more water dependent than their bigger relatives. As a result of their lower weight and measurements they can easily live on steep slopes with only rock crevices as hiding-places, while these body qualities also reduce their energy needs (i.e. the trophic condition of the environment needed).

In conclusion one can roughly state, that bigger animals are better equipped for a life in stable, dry, warm, flat, eutrophic habitats, and smaller ones in more humid habitats, which do not necesssarily have to be stable, eutrophic, flat and continuously warm.

DISCUSSION

A comparison of the qualities of the various parts of rivers and the wide ecological differentiation among lizards shows strong conformities in the pairs »lower course parts/bigger animals« and »upper course parts/smaller animals«. This means that the lower course parts offer ideal habitats to the bigger lizards, while the smaller ones can also thrive in the upper course parts.

Based on the present-day niches of the various species (e.g. ARNOLD, 1987), one can defend the hypothesis that free running rivers and their deltas, together with the actions of big herbivores, were the main providers of good lizard habitats until

early historical times. All representatives of *Lacerta* and *Timon* are typical ground dwellers, hiding in holes in the ground or in the vegetation. The biggest representatives in Europe (*Lacerta lepida* in the west and *L. trilineata* in the east) are the most thermophilic, and only occur at lower altitudes. The somewhat smaller representatives (e.g. *L. viridis* and the even smaller, but not Mediterranean *L. agilis*) not only occur further north, but can also thrive at higher altitudes and in steeper, more densely vegetated and moister environments. The genus *Podarcis* is represented by a great number of species in Europe, most of which are excellent climbers, very well adapted to living on steep, rocky substrates (ARNOLD, 1987; 1990). In those regions, in which they coexist with the more or less equally-sized *Archaeolacerta* and *Algyroides* species, due to their great abundance they might have expelled these animals to higher situated mountainous parts and the narrower, more humid clefts respectively. This possible event could also explain the heavily fragmented distribution pattern of *Archaeolacerta* and *Algyroides* in Europe. On the higher situated parts long winter periods prevent the total closing of forests, by which a more or less permanently open landscape is present there. Most *Archaeolacerta* species live in this kind of habitat. In general, the *Algyroides* species live in more shaded spots at lower altitudes (ARNOLD, 1987), in a Europe without human influence, the steeper, deeper river clefts. In particular, the habitats of *A. marchi* and *A. moreoticus* form examples of such an environment.

Podarcis itself also has relatively big and relatively small representatives, sometimes even sympatrically, e.g. *P. sicula* and *P. tiliguerta* on Corsica and Sardinia. And also then it is the case that the bigger representative lives in more open, lower-altitude sites than the smaller representative. In this way *P. sicula* could be seen as an originally more delta-bound species, *P. tiliguerta* as a riverine species. A possible indication in this direction can be seen in their strongly different escape behaviour (own observations). To escape a big potential predator like man, *P. sicula* on Corsica and Sardinia runs away only some meters, until just out of reach. Here the animal follows a wait-and-see policy, running away somewhat further when being approached again. This rather bold behaviour strongly contrasts with that of *P. tiliguerta*, which flees immediately and without stopping to safe cover, climbing behaviour often occurring during the flight. Could this difference be a remnant of a former occurrence in two different habitat types, viz. a flat, hot, open space full of big herbivores for *P. sicula* and smaller, steep, open spots for *P. tiliguerta*? Then *P. sicula* only runs away because of the risk of being trampled on by an essentially innocent herbivore, while *P. tiliguerta* knows only unpredictable and therefore more dangerous potential predators.

Due to constraints of space it is impossible to go further into the subject. Yet the author would like to stress once again that the visual aspects supporting the hypothesis posed here about the importance of rivers in forming and maintaining lizard habitats are taken away nearly completely in present-day Europe by the human impact on the landscape, especially on that of the Mediterranean region. Therefore lizards now occur in all sorts of places, where they certainly did not occur originally, or, which happens increasingly in more recent times, they have disappeared from places where they did occur originally.

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