ECOGRAPHY 19: 305–312 Copenhagen 1996

Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain

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Romero J and Real R 1996 Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain Ecography 19 305–312

We have analysed the relations between the distribution areas of *Bufo bufo* and *Bufo calamita* in the south of the Iberian Peninsula In order to characterise the localities where the species were found we used 24 environmental variables and we tested their influence on the distribution of both species by nonparametric methods By means of logistic regression we calculated the odds of finding one or other species in a locality The environmental parameters that increase the probability of presence of each species and of both species together are related with the climatic stability and with the climatic subregions *Bufo bufo* is more likely to be found in areas where the climate is more predictable probably because in these areas it may exert its competitive superiority over *B calamita* In zones with very low climatic stability *B calamita* is more likely to be found than *B bufo* probably because *B bufo* lacks the ability to adapt to unpredictable conditions In areas with intermediate climatic predictability *B bufo* is present, but it would be prevented from removing *B calamita* and so the odds of finding each species are equilibrated In these areas there would be a balance between the superior competitiveness of *B bufo* and the higher adaptability of *B calamita* With the same logistic equation we characterise the typical habitats of each species and also the environments shared by both species

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The localities where a determinate species has been recorded are usually represented by its distribution area However, the area occupied by a species is not as homogeneous and static as the simple representation of points in the two dimensions of a distribution map might suggest According to the geographical scale or degree of resolution adopted, there are zones where the species is absent inside the distribution area and also fluctuations in the density of the species (Margalef 1974 p 240, Antúnez and Mendoza 1992) Thus, the distribution of the species is more or less heterogeneous, presenting a mosaic structure that is generally caused by the alternation of patches of different environmental characteristics (Rotenberry and Wiens 1980, Wiens 1985) However, it is not easy to approach the internal complexity of the distribution area unless a small area is studied (see, for example, Rotenberry and Wiens 1980)

The common toad *Bufo bufo* L and the natterjack toad *Bufo calamita* Laurenti are both widely distributed in the Iberian Peninsula Notwithstanding several authors have reported local scale differences in their distribution in the south of the Iberian Peninsula and have pointed out microenvironmental differences in the places where one or the other species is present (Beebee 1983, Antúnez et al 1988) However, macroenvironmental factors may also play an important role in the local distribution of *Bufo bufo* and *B calamita*

Accepted 2 February 1996

ISSN 0906-7590

All these characteristics of *B calamita* can allow it to adapt to zones with irregular precipitation and temperatures, which are therefore unpredictable, in contrast to what occurs to *B bufo*, which tends towards stable and predictable climate Pluviometric irregularity is not an inconvenience for *B bufo* only when the pluviometric regimen is high, and so the presence of water pools for reproduction is guaranteed

Competence and predation

A possible cause of the low abundance of *B calamita* in the mediterranean subhumid subregion could be competition with *B bufo* in the woodland areas in the different stages of larvae and adult

Heusser (1972) and Andren and Nilson (1985a, b) pointed out competition between *B bufo* and *B calamita* in larvae, subadult and adult stages Beebee (1977 1979) and Beebee et al (1990) affirm that *B bufo* removes *B calamita* from certain pools, frequently after structural changes on the habitat occur According to Beebee (1977), widespread encroachment by tall vegetation in heathland areas previously inhabited by *B calamita* have created shade, which may have enabled the common toad to enter as a successful competitor Moreover, Beebee (1979) supports that the encroachment of *B bufo* into habitats previously occupied mainly by *B calamita* is an important mechanism underlying natterjack declines in Britain According to Heusser (1972) and Beebee and Beebee (1977) *B bufo* tadpoles exert inhibitory effects on the growth of younger *B calamita* larvae, although the effects of growth inhibitors in nature is yet to be shown Thus, *B bufo* may also exert its superiority during larval development, since both species coincide in their breeding season in the study area (Barbadillo 1987, Gracia 1988, Diesener and Reichholf 1992), leaving *B calamita* with advantages only in more ephemeral breeding sites (Banks and Beebee 1987), which are not frequent in the mediterranean subhumid region

Predation might also play a role in zones with odds much more favourable to *B bufo* than to *B calamita* Beebee (1983) has pointed out this observing that the tadpoles of *B bufo* predate the tadpoles of *B calamita*, and Banks and Beebee (1987) have also shown that *B bufo* tadpoles may predate *B calamita* embryos

The areas shared by both species

The existence of wide zones where the odds of finding both species are similar can be due to the temporary ponds where *B bufo* advantage is minor According to Toft (1985) the majority of anuran species worldwide may occur syntopically in ephemeral ponds In such ponds very little food partitioning has been found (Heyer 1973, 1974), but tadpoles are specialised in their ability to feed in different positions in the water column Other habitat partitioning may be the time period in which they occur in the ponds as larvae, but this does not happen in our study area, because both species coincide in their breeding season (Barbadillo 1987, Gracia 1988, Diesener and Reichholf 1992) However, in areas with both predictable precipitation and temporary ponds, there might be a balance between the competitive superiority of *B bufo* and the higher adaptability of *B calamita* to the drying up of the ponds, thus enabling the coexistence of both species with similar odds

Notwithstanding, the interpretation of the results should not lead to the conclusion that areas with the odds in favour of one or the other species are ecological optima for that species We cannot affirm, for instance, that *B bufo* adapts better to one or other zone of the study area but we can affirm that some zones have climatic and environmental conditions that make it more favourable for *B bufo* than for *B calamita*

Conclusions

The logistic regression indicates that the factors that allow us to forecast the presence of *B calamita* instead of *B bufo* does not depend on the temperature mean values but on intraannual instability of temperatures and interannual instability of precipitation The adaptations that *B calamita* presents allow it to live in places where the climatic unpredictability is high *Bufo calamita* is able to increase the speed of metamorphosis, so that if a pool is drying, because the rainfall has been lower or the temperatures have been higher, then the period of metamorphosis is shorter

In the subhumid mediterranean subregion and the high mountain subregion the climatic stability allows *B bufo* to exert its competitive superiority over *B calamita*, and thus the odds are in favour of *B bufo*

The same logistic function explains the zones where the odds of finding both species are similar These zones are characterised by intermediate climatic stability Here there is a certain balance between the superior competitiveness of *B bufo* and the higher adaptability of *B calamita*, which is not removed from the zone since the relative climatic instability does not allow the total hegemony of *B bufo*

Acknowledgements – We are grateful to A Antunez, for comments on earlier versions of the manuscript

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