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Niche Segregation in Sympatric *Lacerta agilis* and *L. vivipara*

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In some parts of the Netherlands there is much resemblance in the distribution of the lizard species Lacerta agilis and L. vivipara. In most of these places there are sympatric populations. At one such place we studied a mixed population during 7 successive years /1976-1982/. It was a heathland area in the southern part of the Netherlands, situated on inland dunes along the river Maas, called "de Hamert". In the population studied the density (expressed as number/ha) is: L. agilis 95 and L. vivipara 130. These are averages of the 7 years of study. The densities showed fluctuations in the different years of study but these fluctuations did not have mutual connections, so there are no signs of exclusion of one of the species by the other.

At the same time as the Hamert study we studied an allopatric L. vivipara population, 50 km further to the north. Also this population occurred on inland dunes along the Maas, but these dunes are situated more isolated in the river plain and they are never reached by L. agilis. Furthermore we made a study into diel time use in three big outdoor vivaria, one with only L. agilis, one with only L. vivipara and one with a mixed population.

Niche segregation in lizards is a well studied topic /Toft, 1985/, but from Europe there are only a few examples /e.g. Glandt, 1977; Korsós, 1982, 1984/. For this lecture I selected those data of our investigation, which can throw some light on the niche differences in these two species. Following Pianka /1973/I have distinguished 3 dimensions within the niche of a species, that is the spatial, temporal and trophic dimension. As in Schoener /1974/ these can be subdivided into the following six categories: macrohabitat and microhabitat, seasonal time and diel time, food type and food size. To measure niche breadth, when possible, I used the diversity index of Simpson, standardized in such a way that the values obtained varied between 0 and 1 /following Levins, 1968/. For computing niche overlap I used Pianka's index of overlap /Pianka, 1973/, so these values also range between 0 and 1.

MACROHABITAT

We only studied one macrohabitat, heathland on inland dunes, so for this I used the most recent distribution maps of the Netherlands, published in Sparreboom /1981/. Here one can see a good segregation. Out of the 141 squares of 5x5 km, in which these Lacerta's are found, only 19 have both species. L. agilis is only present in dry, sandy areas, whereas L. vivipara is also present in moister areas and on other substrates.

MICROHABITAT

Tab. 1 shows the results of a study in 1978, in which precise microhabitat notations were made of every sighting or capture of a lizard. L. vivipara is mainly found in the more dense grassy parts. L. agilis also in the more open heather parts. Computing the niche breadth of L. vivipara in the allopatric population, where it lives in a similar macrohabitat, gives a value of 0.441. From this one can suppose an influence of L. agilis on L. vivipara on the Hamert site. The presence of L. agilis appears to reduce the niche breadth of L. vivipara there.

Table 1. Microhabitat use, expressed as percentages of presence /Hamert-study, 1978/.

Microhabitats:	L. agilis	L. vivipara
patches of almost bare sand	22	1
young Calluna	6	7
old Calluna	30	3
Deschampsia flexuosa	24	36
Molinea caerulea	6	41
isolated Betula	10	4
Rubus spec.	1	5
other	1	3
niche breadth: L. agilis = 0.525 L. vivipara = 0.318	niche overlap: 0.508	

SEASONAL TIME

Data about the annual cycle of activities of the mixed population under study are given in van Nuland & Strijbosch /1981/. Looking at figure 3 of that paper it is clear that L. vivipara emerges somewhat earlier in the season and that also the beginning of the different activities /except oviposition!/ is earlier in this species. But what is also clear is that both lizards are simultaneously present in the largest part of the year.

DIEL TIME

For comparing the day-activities I used two different data sets. In the first place we searched the field consistently and systematically once every hour from 6.00 h in the morning till 21.00 h in the evening. Every visible specimen of both species was counted. Beside that we carried out a study into diel time use in the outdoor vivaria to check the field data. Tab. 2 gives the results of both studies. There is clearly much overlap in the use of the resource "time". Furthermore it looks as if the activity period of L. vivipara is somewhat shortened by the presence of L. agilis. The niche breadth of L. vivipara in the allopatric field condition is clearly more than that in the sympatric population. This is confirmed by the check investigation in the vivaria, where the allopatric L. vivipara has the same niche breadth as under allopatric field conditions. The niche breadth of L. agilis remains practically constant, in the field as well as in the vivaria and allopatric as well as sympatric.

Table 2. Niche breadth /A/ and niche overlap /B/ in time use /based on average percentages of visible presence per hour during 8 days of observation on sunny summer days/.

A. NICHE BREADTH:

	L. agilis		L. vivipara	
	sympatric	allopatric	sympatric	allopatric
in the field:	0.743	-	0.558	0.663
in vivarium:	0.769	0.779	0.578	0.668

B. NICHE OVERLAP:

in the field:		0.895
in vivarium:	- allopatric:	0.966
	- sympatric:	0.938

As far as one can speak of segregation, L. vivipara, as in its yearly cycle, tends to become active earlier and to stop its activities sooner. The explanation for this should partly be found in size differences between these two species and in the fact that the preferred body temperature /P.B.T./ of L. vivipara is lower /Sveegaard & Hansen, 1976, give the following P.B.T.-values for field conditions in Denmark: L. agilis 33.7°C and L. vivipara 32.3°C/. L. vivipara, being smaller, warms faster and because its P.B.T. is lower it reaches the required temperature earlier. Because of its bigger size L. agilis cools down more slowly in the afternoon which enables it to remain active longer and later.

FOOD

As all lizard species are protected by law in the Netherlands, a good thing I think, no specimens may be killed, not even for investigation purposes, and therefore it was not possible to carry out stomach analyses. So we resorted to the analysis of faecal pellets. As our results with L. vivipara /see Tab. 3/ fit in rather well with published data about this species, based on stomach analyses /Avery, 1966; Koponen & Hietakangas, 1972; Sirbu, 1977; Pilorge, 1982/, we conclude that this method is suitable. Analysing faeces one finds only fragments of the prey species, making the study of food size impossible. So we resorted to food type. Because both species feed rather opportunistically on that which is present in abundance, their niche breadth cannot be called large, and despite some distinct differences in menu the overlap is high.

As most of the segregation found is caused by spatial segregation we started to search for explanations in this field. Up to now we have followed two lines in this: the possible

Table 3. Frequencies /in %/ of food items belonging to different prey species groups in faecal pellets of Lacerta agilis /n = 177/ and L. vivipara /n = 98/.

	L. agilis	L. vivipara
Araneida	23.5	34.5
Acarina	8.9	5.0
Opilionida	5.6	5.5
Myriapoda	0.8	0.6
Odonata	0.2	-
Orthoptera	1.4	0.2
Dermaptera	0.3	0.2
Thysanoptera	0.4	2.7
Heteroptera	8.9	4.8
Homoptera	10.6	25.0
Coleoptera - adults	21.6	5.2
- larvae	1.4	0.4
Hymenoptera	6.2	2.6
Formicoidea	6.4	2.7
Diptera	2.5	9.4
Lepidoptera - adults	0.3	0.4
- larvae	0.5	0.6
insect-larvae	0.3	-
Oligochaeta	0.3	0.1
niche breadth: Lacerta agilis = 0.321 Lacerta vivipara = 0.242		
niche overlap: 0.811		

presence of interspecific chemocommunication and the analysis of certain physiological constraints in both species. In both studies we use exclusively animals out of the mixed field population. In a small scale experiment on chemocommunication, using tongue flicking frequency as a measure, we found a clear reaction in L. vivipara on the trail of L. agilis. So the smaller L. vivipara is conscious of the recent presence of L. agilis even when it cannot see its possible competitor. Further experiments are required to give more detailed information.

In the other line of experiments we measure evaporative water loss in a completely dry environment. Here we found a clear difference between the two species. In specimens with body lengths of 3 - 6 cm the mean evaporative water loss (expressed as mg water loss/g body weight/hour) is: L. agilis 9.51 ± 4.87 /n = 22/ and L. vivipara 15.69 ± 7.41 /n = 16/. This difference is significant /Student-t-test, $P < 0.01$/. So in equally sized specimens L. agilis loses water slower than L. vivipara. This finding fits in well with the segregation found in macrohabitat as well as in microhabitat. It also can give further explanation for the segregation found in time use.

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