

The Northernmost Population of *Podarcis muralis* (Lacertilia, Lacertidae)

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Abstract. In a one year study we collected ecological data of the northernmost population of *P. muralis* in Maastricht (50° 51' N. Lat. in the Netherlands). This population consisted of about 100 adult lizards. It was probably definitely divided in two subpopulations situated close to each other which were subdivided into 5 and 2 colonies respectively, between which there was no or hardly any exchange. Sex ratio did not significantly differ from 1.0. Compared with the wall lizards of more southern populations they were found to be rather small and to grow more slowly. The age structure of the population was out of balance on account of the small numbers of some younger year classes. Only good, i. e. warmer years are likely to enable a reasonable reproduction success. The total period of activity does not differ from that in more southern regions but the reproduction period is clearly retarded and the incubation period of eggs is distinctly longer. The frequent partial reproduction failure is probably compensated by a rather high longevity, which, however, renders the population very sensitive to each factor that increases mortality. The animals have home ranges of 15–25 m² (no significant differences between sexes) and they have a considerable home range overlap. These home range sizes do not differ from those in more southern regions but the overlaps are much more frequent and therefore it can be concluded that there is a strong concentration on ecologically suitable and spatially very restricted spots. From a list of prey species based on faeces analysis *P. muralis* appears to be a non-selective feeder. On two adult specimens we found the acarine ectoparasite *Ophionyssus lacertinus*.

Introduction

The distribution of *Podarcis muralis* (LAURENTI) is mainly restricted to Central and Southern Europe. In the greater part of this area the subspecies *P. muralis muralis* occurs. The distribution of this subspecies includes France, the Channel Isles, Belgium, the Netherlands, the Rhine area in Germany, Switzerland, Czechoslovakia, Austria and the northern Balkan (MERTENS and WERMUTH 1960, STREET 1979). The northern limit of the area is roughly only just a little south of the 18° C isotherm of July. The spots of occurrence in the Benelux and W. Germany are all situated in the valleys of the Maas, the Moselle and the Rhine and their tributary valleys (MERTENS 1947, MOLLE 1953, MÜLLER 1968, 1971, 1976, PARENT 1974, 1978). The most recent distribution maps of this area (for W. Germany see MÜLLER 1976, for the Benelux see PARENT 1978)

show as the northernmost spots of occurrence the city of Maastricht in the Netherlands ($50^{\circ}51'$ N. Lat.) and somewhere near Bonn in the Rhine-valley in W. Germany ($50^{\circ}44'$ N. Lat.). Like the other spots along the northern limit of the distribution area, the city of Maastricht is a strongly isolated dot on the map. The nearest population is the one in Visé in Belgium (at a distance of about 15 kms). There used to be more places of occurrence in the southern parts of the Netherlands (VAN KAMPEN & HEIMANS 1927), but VAN BREE (1958) and also VAN DE BUND (1964) only mention Maastricht. MARQUET (1964) gave a possible occurrence on the St. Pietersberg near Maastricht but that was only based on supposition. Older literature (e. g. CREMERS 1929 and even VAN BREE 1958 and TER HORST 1960) gives more places of occurrence within the city of Maastricht, but more recent literature (VAN DE BUND 1964, TER HORST 1975) clearly gives only one place, i. e. the "Bossche Fronten".

In 1978 we studied this population of *P. muralis* and also visited all possible other places of occurrence in Maastricht and its vicinity. This study was occasioned by the fact that this last place of occurrence in the Netherlands, also being the northernmost place of the distribution area of the species, was seriously threatened by intended restorative activities on the old ramparts on which the species occurs there. In order to be able to give scientifically founded advice for the steps to be taken for the conservation of this population, taking such an extreme place on the map, we collected as many different data as possible.

Study Area

Besides occasional visits to places which seemed to be suitable within Maastricht and its vicinity and to the bordering northern parts of Belgium this study was completely carried out on the lizard population of the "Hoge Fronten" and the "Lage Fronten" in Maastricht, together forming the "Bossche Fronten". During its complete history the city of Maastricht has been a fortress. As early as in the Roman times there were fortifications with ramparts, but the oldest remains above ground-level are ruins of medieval fortifications. Most remains, however, among which also the Hoge Fronten and the Lage Fronten, are of a more recent date. They are the remains of fortifications, made by the end of the 18th century (Hoge Fronten) and in the early 19th century (Lage Fronten). The Hoge Fronten consist of a system of wide earth ridges fortified with thick stone walls, between which there are dry moats. The Lage Fronten, in the past immediately adjacent to the Hoge Fronten, forming a unity with them, are situated at a lower level and here the moats between the walls do contain water. At this moment the Hoge Fronten and Lage Fronten are nearly in the centre of Maastricht. They are now divided by a wide and busy road with houses on either side. The city of Maastricht, situated in the Maas valley on almost the most southern site of the Netherlands, has a climate which differs in many respects from that in the rest of the Netherlands (MÖRZER BRUYNS and WESTHOFF 1951). Summers are relatively warm and winters are relatively moderate there, e. g. the average of the day-time maximum temperatures of July is 23.0°C in Maastricht and 16.5°C in the rest of the Netherlands; for January these values are 5.0°C and 1.0°C respectively.

Methods

Lizards were caught with a light noose on the end of a slender twig. Sex, snout-vent length (SV-length), tail length (TL-length), weight and precise location were recorded for all lizards caught. All individuals were marked by means of toe-clipping and furthermore by applying dots of coloured nailpolish on their backs. The latter method enabled us to make observations through field glasses about behaviour and spatial occupation of individual lizards without having to disturb them.

Results

In Maastricht and its vicinity wall lizards were only found on the Hoge Fronten and the Lage Fronten. All ♂♂ caught by us (except one) as well as a number of the ♀♀ had bellies of a dark colouration. All the year through this colouration was dark red with a large number of big black patches.

In total we made 351 observations (captures, recaptures and resightings) of 65 different, marked individuals. Furthermore we made 188 sightings of unmarked individuals. The population in Maastricht turned out to consist of two subpopulations, presently more or less divided from each other, one in the Hoge Fronten and one in the Lage Fronten. In the subpopulation of the Hoge Fronten there were five colonies more or less divided in space, between which there was no or hardly any exchange of individuals during the year of study. On the Lage Fronten there were two colonies divided in space.

In order to make an estimation of the number of individuals in the group of unmarked animals we used the frequency of observing the marked individuals. This frequency turned out to depend on the activity of the animals and the surveyability of the habitat. Therefore it was separately calculated for the ♂♂ and the ♀♀ and separately for the animals of the Hoge Fronten and of the Lage Fronten. The marked ♂♂ of the Hoge Fronten proved to be sighted 8.3 times on the average, the ♀♀ 5.3 times. For the Lage Fronten these frequencies were much lower, viz. 2.1 times for the ♂♂ and 1.8 times for the ♀♀. Of nearly all sightings of unmarked animals we did record sex and location so that we can make a reasonable estimation of the number of individuals in this group of observations. So doing we come to an estimation of a total of 56 adult specimens on the Hoge Fronten and a total of 41 adult specimens on the Lage Fronten, so the whole Maastricht population should have 97 adult lizards. The sex ratio found (♂♂/♀♀) is 1.37 (for the Hoge Fronten 1.44 and for the Lage Fronten 1.22). These values do not significantly differ from equality (X^2 -test, $P > .10$).

The age structure of the population is given in Table 1. The figures in it are based on real counting for juveniles and subadults and on estimations as explained above for adults. Although the numbers of the adults are based on estimation, the difference in number between young adults and full-grown adults, however, is certainly reliable. The animals, born in 1976 (young adults), can clearly be distinguished from the group of older adults because of their smaller sizes, especially in the first half of the season. The greater numbers for animals in the higher year-classes immediately strike the eye. ROLLINAT (1934) states that juveniles lead a more secretive life but in spite of a possible

Table 1. Age structure of the Maastricht *Podarcis muralis* population in 1978

year of birth	in the text referred to as	number
1978	juveniles	8
1977	subadults	12
1976	young adults	25
≤ 1975	full-grown adults	72

underestimation of their numbers on account of this Table 1 does show that the population increase of 1978 was very slight. Judging from the numbers of subadults and young adults the increase of 1977 must also have been slight but high in 1976. Possibly the temperature and the length of the season in the year of birth plays a role in this. According to the weather data from the Royal Dutch Meteorological Institute (ANON. 1972–1978) of the last seven years 1973 and 1976 were both extremely warm, sunny and dry, whereas the years 1972, 1974, 1975, 1977 and 1978 were all rather sombre and cold in general (these data were compared with the average data of the years 1931–1960). The sunny and warm weather of 1976 is very probably the cause of the relatively large representation of that year-class. BANK et al. (1977), who studied the Maastricht lizard population in 1977, then found relatively many subadults, i. e. animals born in the preceding year. In analogy to this also the year-class born in 1973 (6th calendar year animals) within the group of the full-grown adults must be considerable. In this respect the following might be remarked. For two ♂ adults we tried to determine the exact age by analysing growth rings in haematoxiline-stained cross sections of phalanges (for method see HEMELAAR & VAN GELDER 1980). For this purpose we selected a ♂ of average size (SV-length 60 mms) and a rather big ♂ (SV-length 66 mms). In the cross sections of both specimens 5 growth rings could be seen, indicating that they were 6th calendar year animals and therefore must be born in 1973. Also this suggests an inconsistent age structure for the population.

Table 2 shows a survey of the sizes and weight of the Maastricht wall lizards. We have no exact measurements of juveniles and we could measure only one subadult. The SV-length of juveniles could be estimated at 25–27 mms, which corresponds well with the values given for it (ROLLINAT 1934, FRETEY 1975). The length values found for adults are in general somewhat less than those given for France (ROLLINAT 1934, ANGEL 1946, FRETEY 1975). Also VAN BREE (1958) already mentions that the wall

Table 2. Length (in mms) and weight (in grams) of *Podarcis muralis*; only measurements on individuals with complete tails are used; figures show $\bar{x} \pm$ s. d. (range)

	subadults	adult ♂♂	adult ♀♀
<i>n</i>	1	26	13
total length	112	173.8 ± 11.8 (149–188)	168.3 ± 7.4 (157–184)
snout-vent length	41	59.0 ± 4.0 (49–64)	61.4 ± 3.7 (55–66)
tail length	71	114.9 ± 8.2 (97–125)	106.9 ± 4.9 (100–118)
SV-length/TL-length	1.73	1.95 ± 0.08 (1.79–2.11)	1.75 ± 0.10 (1.54–1.88)
weight	1.6	5.04 ± 0.74 (3.7–6.3)	4.93 ± 0.61 (4.0–5.7)

lizards of Maastricht are relatively short. The differences in total length, SV-length and weight between ♂♂ and ♀♀ are not significant, but the difference in TL-length is (*t*-test, *t* = 3.19, *P* < .01) and so is the ratio SV-length/TL-length (*t*-test, *t* = 6.79, *P* < .01).

Figure 1 shows a graphic representation of the average SV-length in the successive months of the year. For this we used measurements of all individuals. From it one can deduce an average increase of SV-length by 1.7 mm/month for 3rd calendar year animals, whereas ≥ 4th calendar year animals show an average of 0.6 mm/month. This method can well be used for the 3rd year class but is less adaptable for the group of ≥ 4th calendar year animals. Therefore we also determined individual length increase in recaptured animals. The latter method gives us the following growth data: the 3rd calendar year animals have an average increase in SV-length of 1.9 mm/month (*n* = 2) and the ≥ 4th calendar year animals have 1.1 mm/month (*n* = 36). These figures indicate that young adults grow 1.5–2 mms/month (in SV-length!) and older adults about 1 mm/month. We captured too few subadults (2nd calendar year animals) to apply similar calculations. Therefore we calculated growth data for this age class from the difference in mean SV-length of juveniles at the end of the season (October) and that of 3rd calendar year animals in the early season (April). On the basis of a growth season of 6 months (April till October) the increase in SV-length is 3.6 mm/month. All growth data found by us are rather little compared with those of ROLLINAT (1934) and ANGEL (1946).

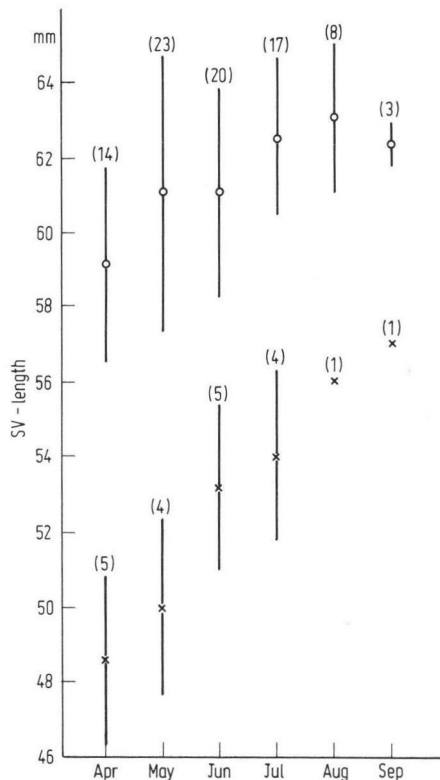


Fig. 1. SV-length (in mms) in the successive months of the year for two different age classes; shown is ± s.d. (n). × = 3rd calendar year animals; o = ≥ 4th calendar year animals

Using measurements on regularly recaptured animals we could calculate an average tail growth of 2.6 mm/month for adult animals with complete tails ($n = 15$). Animals with regenerating tails had an average of 8.7 mm/month ($n = 11$). This difference is significant (t -test, $t = 2.69$, $P < .02$).

Figure 2 gives a survey of the length of the active season and the dates of various phases in the reproduction cycle in 1978. This diagram was drawn up based on direct observations of animals in their natural habitat. The ♂♂ come out of hibernation very early, one month before the ♀♀. The ♂♂ therefore have an active period of about 9 months, the ♀♀ have one of about 8 months. In spite of this northern place of occurrence this period hardly deviates from that in more southern areas, e.g. ROLLINAT (1934) also gives 9 months for Central France, so does ANGEL (1946); SAINT GIRONS and DUGUY (1970) give 12 months for the ♂♂ in the lowlands of Central France (in wintermonths they regularly interrupt their hibernation) and 9 months for the ♀♀ and for a mountain population in the Pyrenees 8 months for ♂♂ and 6.5 for the ♀♀; WEBER (1957) gives 9 months for southern Switzerland and AVERY (1978) about 8.5 months for Central Italy. From this it can be deduced that the Maastricht population is active during a period just as long as in the more central parts of the distribution area of the species. The reproduction time, on the contrary, might be called at variance. In Maastricht it is roughly the period from half April till half June. ROLLINAT (1934) gives March and April for Central France and WEBER (1957) late March till early May for Southern Switzerland. We determined reproduction time on the basis of a number of, partly occurring simultaneously, components of the behaviour of the lizards. A clear couple formation was seen from half April till half June. ROLLINAT (1934) found couple formation from late March. WEBER (1957) also describes couple formation and states that this is maintained for some time also after copulation. We also saw ♂♂ and ♀♀ sticking together after the copulation period and occasionally it even occurred in summer and autumn. The phenomenon of fighting ♂♂ is given by many authors as taking place from late March (for France see ROLLINAT 1934, ANGEL 1946, FRETEY 1975; for Switzerland see WEBER 1957). In Maastricht this period was relatively late and relatively short. According to the most authors courtship behaviour immediately succeeds the period of fighting ♂♂ and also in Maastricht it was the same period. We saw copulations in May and the first half of June. The mean duration of copulation was 55 seconds (min. 15 seconds, max. 120 seconds). WEBER (1957) gives an average of 30 seconds. Also ROLLINAT (1934) mentions that the duration of copulation is very short. Also ROLLINAT (1934) mentions that the duration of copulation is very short.

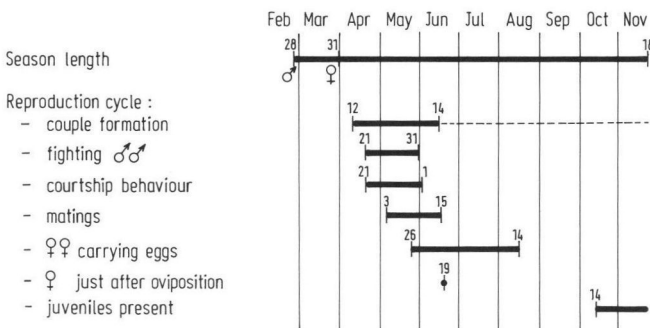


Fig. 2. Season length and time of year for various phases in the reproduction cycle

The occurrence of mating scars on the sides and bellies of ♀♀ after copulation, as described for various Lacertidae (e.g. KRAMER 1937) was found only twice by us, despite regular searches for them. This is probably due to the very short duration of copulation. We saw only three times a ♀ clearly carrying eggs (May 26, June 14 and August 14). So oviposition happens probably during a very long period in Maastricht. Most authors on *P. muralis* give as the latest date of oviposition half June. COOPER (1965) says that oviposition, rather independent of the temperature of the environment, takes place one month after fertilization. Seen in that light the late sighting of a pregnant ♀ forms a distinct indication of the retarded reproduction period in Maastricht. From the sighting on June 19 of a ♀ with distinct skin-folds on the flanks, which according to ROLLINAT (1934) indicates recent oviposition, it appears that eggs can also be deposited at an earlier date. In Maastricht the first juveniles were sighted as late as October 14. Considering literature on *P. muralis*, this is extremely late in the season (e.g. ROLLINAT 1934: July; ANGEL 1946: late July—early September). Most authors give an incubation period of 9–11 weeks and state that it highly depends on temperature (ROLLINAT 1934, ANGEL 1946). COOPER (1958) studied this dependence of temperature experimentally and arrived at incubation periods of <7 weeks (with a day and night temperature of 26.7°C) and > 5 months (with day temperatures of 18.3°C and night temperatures of 12.8°C). This clearly demonstrates the high dependence of temperature and probably explains the late occurrence of juveniles in Maastricht.

We determined the home range of those animals which were spotted at least 5 times (minimum polygon method, see e.g. BROOKS 1967). For the ♂♂ ($n=16$) we arrived at $25.0 \pm 18.0 \text{ m}^2$ (range 5.1–62.5 m^2) and for the ♀♀ ($n=7$) at $14.3 \pm 19.0 \text{ m}^2$ (range 2.2–54.6 m^2). The difference in home ranges of ♂♂ and ♀♀ is not significant (t -test, $t = 1.29$, $P > .10$). These home range sizes of 15–25 m^2 correspond well with the values known from more southern regions, e.g. WEBER (1957) gives about 15 m^2 for Southern Switzerland and BOAG (1973) gives an average of 23 m^2 (range 6–42 m^2) for ♀♀ and of 26 m^2 (range 10–52 m^2) for ♂♂ in Central Italy (also without significant differences between the sexes). We also calculated the range of activity as defined by WHITE (1964). Then we did find significant differences between the sexes. The ranges of activity, calculated after horizontal spreading, i.e. after the east-west and north-south dispersion of the animals given in coordinates on a map of the study area, were $10.5 \pm 6.4 \text{ m}$ for the ♂♂ and $10.6 \pm 8.5 \text{ m}$ for the ♀♀, but after vertical spreading on the walls, i.e. after the data concerning the height of the points of every sighting, they were $1.8 \pm 1.1 \text{ m}$ for the ♂♂ and $0.9 \pm 0.6 \text{ m}$ for the ♀♀. The latter difference is significant (t -test, $t = 2.22$, $P < .05$). So the ♂♂ often occur on higher places on the walls. The maximum height of occurrence on the walls had an average of $3.1 \pm 1.8 \text{ m}$ for the ♂♂ and of $1.6 \pm 1.0 \text{ m}$ for the ♀♀ which is also a significant difference ($t = 2.24$, $P < .05$). Furthermore we plotted the calculated home ranges on maps of the walls in order to examine to what extent overlapping took place. Now we used the data of all animals we spotted at least 3 times. Table 3 gives a survey of these overlaps. The most striking detail of this Table is the fact that a very large percentage of the home ranges of the ♀♀ has a total overlap with those of ♂♂ while there is hardly any total overlap for the ♀♀ mutually. Furthermore in all cases the home ranges of the ♀♀ turn out to overlap completely or partially that of a ♂, which cannot be said of the ♂♂. Only BOAG (1973) gives data on

Table 3. Frequency (in %) in which home range overlap occurs in *Podarcis muralis*

	♂♂ total overlap	partial overlap	no overlap	♀♀ total overlap	partial overlap	no overlap
♂♂ (n = 25)	28	32	40	12	56	32
♀♀ (n = 11)	82	18	—	9	45.5	45.5

home range overlap for *P. muralis*. He found a ♂ × ♂ overlap of about 8% and a ♀ × ♀ overlap of about 18%, while the ♂ × ♀ overlap was nearly 100%. Compared with our data his percentages of intrasexual home range overlap are low but the percentage of intersexual overlap is high. This latter phenomenon is undoubtedly due to the fact that in Maastricht there are home ranges of ♂♂ that lie completely isolated.

Only 3 times we saw a sudden migration of an individual over a distance of > 50 m, once in the Lage Fronten and twice in the Hoge Fronten. This concerned only ♂♂ and in one of these cases (in the Hoge Fronten) it caused exchange between two separated colonies. These migrations can occur very rapidly, e. g. one ♂ migrated 70 m in 90 minutes, another ♂ 67 m in 65 minutes.

In order to obtain an insight in the food items of the lizards we collected, in July and August, a number of faeces pellets, which are often excremented when manipulating (measuring and weighting) them just after capture. In these pellets one can often recognize remains of prey species. Table 4 shows a survey of the food items found. From this list, which only gives a rough indication, it appears that *P. muralis* is not very selective as far as food is concerned so takes what is available. The list comprises purely terrestrial animals and species that occur in wall cracks and holes as well as animals living in the vegetation. The fact that the lizards also used the nearby vegetation for foraging was established by us more than once.

Table 5 gives the frequency of recently broken or regenerated tails in adult lizards. In total roughly 2 out of every 3 adults have lost their tail in their lives. The differences between ♂♂ and ♀♀ and between the animals of the Hoge Fronten and of the Lage Fronten are not significant (X^2 -tests, $P > .30$). Many authors use the frequency of broken tails as a standard of the predation pressure, e. g. BOAG (1973). Only this author mentions frequencies of broken tails for *P. muralis* (in Central Italy): ♂♂ 52.5%, ♀♀ 46.5%, total adults 50.7%. His frequencies are clearly lower than those found by us. We suppose that our higher percentages do not reflect a higher predation pressure but a mean higher age of our adults, which enhances their chance of a broken tail. In 1978 we saw only 6 specimens with a recently autotomised tail. All these recent autotomisations occurred in June and July (4 out of 6 even within one week in late June).

Only twice we saw ectoparasites on the Maastricht wall lizards. In both cases they were mites of the species *Ophionyssus lacertinus* (BERLESE). This is interesting because this mite has never been found on the other Lacertidae of the Netherlands (*Lacerta agilis* and *L. vivipara* have *Ophionyssus saurarum* (OUDEMANS)) but it does occur on Lacertidae in Southern Europe (e. g. *Lacerta viridis* and *Podarcis sicula*).

Table 4. Determinable remains of prey in faeces (of July and August) of *Podarcis muralis* (× = several bits, number of items unknown)

Prey items belonging to:	number of items found
Oligochaeta (<i>Lumbricus terrestris</i>)	2
Mollusca	1
Isopoda (<i>Oniscus asellus</i>)	1
Orthoptera – Acrididae	×
– Tettigoniidae	×
Dermaptera (<i>Forficula auricularia</i>)	3
Hemiptera – Heteroptera	3
– Homoptera – Cicadellidae	6
– Aphanidae	> 3
Lepidoptera	5
Diptera – Nematocera – Tipulidae	1
– Mycetophilidae	1
– Brachycera – Asilidae (or Rhagionidae)	1
Hymenoptera – Chalcididae	1
– Formicidae (<i>Formica</i> and <i>Lasius</i>)	7
– other Aculeata-families (a. o. <i>Halictus</i> sp.)	8
Coleoptera (a. o. Staphilinidae, Cantharidae, Lagriidae, Curculionidae, Chrysomelidae)	10
Arachnoidea – Araneidae – Salticidae (<i>Salticus</i> sp.)	1
– Linyphiidae	2
– Opiliones	1
– Acari (<i>Oribatula</i> sp.)	1
(<i>Tectocephus velatus</i>)	1

Table 5. Frequency (in %) of regenerated or recently broken tails in adult *Podarcis muralis*

	♂♂		♀♀		total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Hoge Fronten	26	61.5	18	72.2	44	65.9
Lage Fronten	11	45.5	9	66.7	20	55.0
total	37	56.8	27	70.4	64	62.0

Discussion

As during the period the wall lizards were active on the Hoge Fronten and Lage Fronten in Maastricht we also searched for them on all other places in the vicinity, mentioned in literature as possible places of occurrence, and found none, we state that the population in the Netherlands is only restricted to the animals of the Hoge Fronten and Lage Fronten. On some places we did see *Lacerta vivipara* (also on old walls, e. g. also on the Hoge Fronten!) and possible this species was wrongly taken for wall lizard in the past.

As a permanent marking system we used toe clipping. Eleven out of 65 animals captured proved to have damaged toes when caught for the first time, so for this species it is necessary to use a code in which more toes are involved. Most natural damages occurred with the long second toe of the hind legs and we never found damaged inner toes. We never saw regeneration of toes, as mentioned by ANGEL (1946).

The fact that the Maastricht wall lizards had in general a very dark belly colouration might indicate that this population has already taken a very isolated position during a long period. HERTER (1940) mentions an increase of such dark pigments in populations that are more strongly isolated and smaller.

The age structure of the population and also the very retarded occurrence of the juveniles indicate that this population probably has its problems with reproduction. The period of activity of the Maastricht wall lizards does not differ from that of more southern populations, it is true, but reproduction time is distinctly later and also the incubation period of the eggs is most likely to be much longer. The secretive life of the juveniles (e. g. ROLLINAT 1934, KRAMER 1938) might also in Maastricht indicate a shorter incubation period than found by us, but the occurrence of juveniles in late July or August as mentioned for France is certainly an impossibility here. Moreover the fecundity of ♀♀ is in Maastricht probably rather low. It is namely dependent on the size of the ♀♀ (e. g. ANGEL 1946) and on temperature (e. g. SAINT GIRONS & DUGUY 1970). Our lizards proved to have smaller mean sizes than those in more southern regions. Also the much slower growth of the Maastricht lizards has a similar effect. In their studies on a mountain and a lowland population of *P. muralis* in France SAINT GIRONS and DUGUY (1970) could clearly show that the lower temperatures in the mountains caused a strong fecundity decrease in the ♀♀. The upper limit in the mountains was said to be exclusively established by the impossibility to reproduce on higher places. The same should apply for the northern limit of the distribution areas of egg-laying reptiles (SAINT GIRONS and SAINT GIRONS 1956). The possible correlation between a good reproduction success in Maastricht and extremely warm years in the Netherlands also points in the direction of reproduction problems. This might only be compensated with an increase of longevity. The fact that both adults of which we established the exact age were 6th calendar year animals, despite their size differences, might indicate a rather high longevity for the Maastricht wall lizards. In this short study we could not estimate natality and mortality rates but all data we collected point out that both must be low. An increase of mortality for whatever reason (e. g. inconsiderate restoration of the old walls with consequent loss of wall cracks and of hiding places in the vegetation on and near the walls) will immediately result in a serious threat to the survival of this population.

The determinations of home ranges show that the size of home range of the Maastricht *P. muralis* is equal to that of more southern wall lizards but that the overlap is larger. This is probably an indication that the niche of this species in Maastricht is spatially more restricted. Many authors (e. g. SAINT GIRONS and SAINT GIRONS 1956, VANDEN EECKHOUT 1956, PARENT 1978) state that *P. muralis* in the northern parts of its distribution is much more restricted to warm, open and sunny rock boulders and/or walls than in more southern regions. Therefore it is possible that locally higher densities can be reached in the sequestered occurrence of small populations of *P. muralis* in the northern parts of its distribution, resulting in more home range

overlapping. We do not believe that such relatively high densities with rather vast home range overlaps cause the relatively high frequencies of broken tails found by us. ROLLINAT (1934) states that territorial and other fights among wall lizards cause loss of tails, it is true, but all recent tail losses we found took place outside the period of many fights. In a large natural population of *P. muralis* WEBER (1957) never saw tail losses as a result of mutual fighting. As stated above we suppose that our high broken tail frequencies are rather an indication of a relatively high longevity for our lizards.

The list of prey items draws a picture of a random feeder. Most of the species preyed on were abundant during the complete season and from that we conclude that food is not a restrictive factor in the northern distribution of *P. muralis*.

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References

- ANGEL, F. (1946) Faune de France 45: Reptiles et Amphibiens. Lechevalier, Paris.
- ANON. (1972–1978) Maandelijks Overzicht der Weersgesteldheid. Koninklijk Nederlands Meteorologisch Instituut. Jg. 69–75, uitgave 94 a.
- AVERY, R. A. (1978) Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from Central Italy. *J. Anim. Ecol.* **47**: 143–158.
- BANK, J., KRUIJNTJES B., PAULISSEN, P. (1977) De herpetofauna in de Hoge Fronten te Maastricht (unpublished inventarisatie-report).
- BOAG, D. A. (1973) Spatial relationships among members of a population of wall lizards. *Oecologia (Berl.)* **12**: 1–13.
- BREE, P. J. H. VAN (1958) Notes on the wall-lizard, *Lacerta muralis* (LAURENTI) 1768, in the Netherlands. *Nat. Hist. Mndblad* **47**: 8–11.
- BROOKS, G. R. (1967) Population ecology of the ground skink, *Lygosoma laterale* (Say). *Ecol. Monogr.* **37**: 71–87.
- BUND, C. F. VAN DE (1964) Vierde herpetogeografisch verslag. *Lacerta* **22**: 1–72.
- COOPER, J. S. (1958) Observations on the eggs and young of the wall lizard (*Lacerta muralis*) in captivity. *Brit. J. Herpetol.* **2**: 112–121.
- COOPER, J. S. (1965) Notes on fertilisation, the incubation period and hybridisation in *Lacerta*. *Brit. J. Herpetol.* **3**: 218–220.
- CREMERS, J. (1929) De muurhagedis, *Lacerta muralis* (Laur.), te Maastricht. *Nat. Hist. Mndblad* **18**: 68.
- FRETEY, F. (1975) Guide des reptiles et batraciens de France. Hatier, Paris.
- HEMELAAR, A. S. M., GELDER, J. J. VAN (1980) Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Neth. J. Zool.* **30**: 129–135.
- HERTER, K. (1940) Über Vorzugstemperaturen von Reptilien. *Z. vergl. Physiol.* **28**: 105–141.
- HORST, J. Th. TER (1960) De verspreiding der Amphibia en Reptilia in Zuid-Limburg. *Nat. Hist. Mndblad* **49**: 105–118.
- HORST, J. Th. TER (1975) Gaat de laatste vindplaats van de muurhagedis in Nederland verloren? *Nat. Hist. Mndblad* **64**: 36–39.
- KAMPEN, P. N. VAN, HEIMANS, J. (1927) Fauna van Nederland. III. Amphibia en Reptilia, p. 56–57. Sijthoff, Leiden.

- KRAMER, G. (1937) Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen. *Z. Morphol. Ökol. Tiere* **32**: 752–783.
- KRAMER, G. (1938) Angaben zur Fortpflanzung und Entwicklung von Mauer-Eidechsen. *Senckenbergiana* **20**: 66–80.
- MARQUET, P. L. (1964) Enkele gegevens over de amphibien en reptielen van het Land van Caestert. *Publ. Wetensch. Belg.-Nederl. Commissie Besch. Sint-Pietersberg*, nr. **8**: 59–60.
- MERTENS, R. (1947) Die Lurche und Kriechtiere des Rhein-Main-Gebietes. Kramer, Frankfurt.
- MERTENS, R., WERMUTH, H. (1960) Die Amphibien und Reptilien Europas. Kramer, Frankfurt.
- MOLLE, F. (1953) Herpetologische Beobachtungen in der Südeifel. *Aquar. Terr. Z.* **6**: 294–296.
- MÖRZER BRUYNIS, M. F., WESTHOFF, V. (1951) The Netherlands as an environment for insect life. IXth Intern. Congress of Entomol., Amsterdam (67 pp.).
- MÜLLER, P. (1968) Zur Verbreitung der Mauereidechse, *Lacerta muralis* (LAURENTI 1768) im Saarland. *Faunist.-Florist. Notizen aus dem Saarland* **1**: 5–6.
- MÜLLER, P. (1971) Biogeographische Probleme des Saar-Mosel-Raumes dargestellt am Hammelsberg bei Perl. *Faunist.-Florist. Notizen aus dem Saarland* **4**: 1–14.
- MÜLLER, P. (1976) Arealveränderungen von Amphibien und Reptilien in der Bundesrepublik Deutschland. *Schriftenreihe für Vegetationskunde* **10**: 269–293.
- PARENT, G. H. (1974) Mise au point sur l'herpétofaune de la Belgique, du Grand-Duché de Luxembourg et des territoires adjacents. *Bull. Soc. Natural. Luxemb.* **79**: 79–131.
- PARENT, G. H. (1978) Contribution à la connaissance du peuplement herpétologique de la Belgique. Le caractère relictuel d'âge Atlantique de l'aire du lézard des murailles, *Lacerta muralis muralis* (LAURENTI) au Benelux. *Nat. Belg.* **59**: 209–222.
- ROLLINAT, R. (1934) La vie des reptiles de la France centrale. Delagrave, Paris.
- SAINT GIRONS, H., DUGUY, R. (1970) Le cycle sexuel de *Lacerta muralis* L. en plaine et en montagne. *Bull. Mus. Hist. nat. Paris* **42**: 609–625.
- SAINT GIRONS, H., SAINT GIRONS, M. C. (1956) Cycle d'activité et thermorégulation chez les reptiles (lézards et serpents). *Vie et Milieu* **7**: 133–226.
- STREET, D. (1979) The reptiles of Northern and Central Europe. Batsford, London.
- VANDEN ECKHOUT, J. P. (1956) Les reptiles de Belgique. *Serpents-Lézards. Nat. Belg.* **37**: 41–50.
- WEBER, H. (1957) Vergleichende Untersuchung des Verhaltens von Smaragdeidechsen (*Lacerta viridis*), Mauereidechsen (*L. muralis*) und Perleidechsen (*L. lepida*). *Z. Tierpsychol.* **14**: 448–472.
- WHITE, J. E. (1964) An index of the range of activity. *Amer. Midl. Naturalist* **72**: 369–373.

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