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On the phenology of peat bog spiders

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Abstract
Phenology of common ground-living spiders on peat bogs along a transect from Bavarian mountains (Germany) through Southern Lithuania and Southern Finland up to Finnish Lapland was compared. No general pattern in changes of phenology common to all species, or most of them, could be found. However, most species had some differences in their activity patterns in different regions, indicating adaptation to the local climate. Two main patterns of phenology were found: 1) fixed time of the maximal activity (conservative pattern), e.g. *Agyneta cauta*, *Pirata uliginosus*, *Antistea elegans* and *Pardosa hyperborea*, and; 2) flexible time of maximal activity (adaptive pattern), e.g. *Centromerus arcanus*, *Oryphantes angulatus* and *Pirata piraticus*. Generally, the activity pattern of males was more stable and predictable between the regions than that of females.

Key words: Araneae, activity pattern, epigeic, peatland

INTRODUCTION

The phenology of spiders has been studied intensely in various habitats in Europe (e.g. Tretzel 1954; Merrett 1967, 1968, 1969; Schaefer 1976). Broen & Moritz (1963) deal exclusively with the phenology of peat bog spiders in Germany. Freudenthaler (1989) also provided data on phenology of peat bog species from Austria. Despite the large number of studies on life history and activity patterns of spiders, only a few papers consider the differences between these processes in relation to the habitat type, latitude or altitude (e.g. Puntscher 1980; Albert 1982; Sømme 1989).

In the present article we analyse the annual activity patterns of some spider species occurring in the same type of habitat (peat bog) along a north-south transect in Europe. The aim of this study is to compare the activity patterns of each of the species in different geographical regions varying in duration of snow free period and day length.

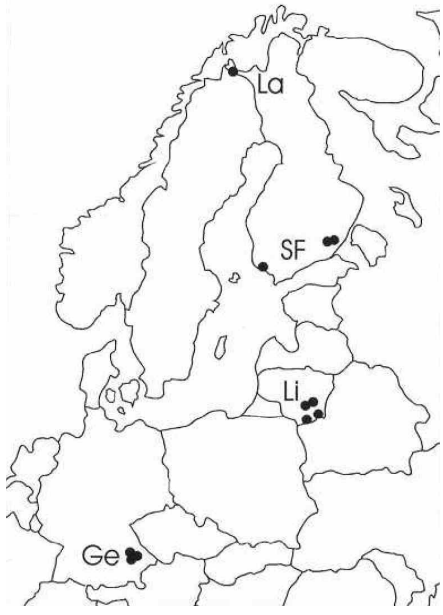
STUDY AREAS AND METHODS

Spiders were collected in peat bogs situated in Finnish Lapland (c. 69°N), Southern Finland (61°N), Lithuania (55°N) and Southern Germany (49°N) by means of pitfall traps (Fig. 1). The latitudinal transect between the most northern and southern investigated localities was about 2000 km. The animals from Lapland, Southern Finland and Lithuania were collected in lowland peat bogs, but the material in Germany was collected in mountain habitats of the National Park " Bayerischer Wald" at altitudes of 750-1185 m. Only investigations throughout the whole growing season were taken for analysis. One peat bog was studied in Lapland, three in S. Finland, four in Lithuania and four in Germany. The site in Lapland is a palsa mire, others are typical peat bogs. The climatic data for each investigated region are provided in Table 1.

As trapping periods, years, as well as number and type of traps varied between the

regions, the comparisons are based on percentages of the cumulative material collected in one region. A total of 10135 specimens were included in the analysis. The phenology diagrams were compiled separately for both sexes of a species in each region. The data from all localities of one region were summarised, and the cases with less than 10 specimens/sex/region were omitted (cf. also Appendix). The diagrams show percentages of both sexes of a species during a (usually two weeks) period from the cumulative material found in a given region. Due to slight differences in the collecting periods in some sites, the diagrams show only general patterns in activity of each species (and sex) in the studied regions.

Fig. 1. The location of studied peat bogs in Germany (Ge), Lithuania (Li), Southern Finland (SF) and Finnish Lapland (La).



RESULTS

Spring and summer activity

Only two species, *Pardosa sphagnicola* (Dahl, 1908) (Fig. 2) and *Centromerus arcanus* (O.P.-Cambridge, 1873) (Fig. 6), were found in high numbers in all investigated areas. Nine species were missing in one or two of the investigated areas or were not trapped in sufficiently high numbers there to be included (Appendix). Due to low numbers, the data on females of some species were also omitted from the diagrams (Figs. 2-7).

The general patterns in the phenology of the species did not vary markedly between the regions. However, many species showed some plasticity in adapting their activity patterns to the climatic conditions of the different geographical regions.

The two following main trends in activity patterns can be distinguished:

(1) Fixed time of the maximal activity (conservative pattern)

Some species showed a short activity period at the same time of year without marked differences at different latitudes or altitudes, e. g. *Agyneta cauta* (O.P.-Cambridge, 1902), *Pirata uliginosus* (Thorell, 1856), *Antistea elegans* (Blackwall, 1841) and *Pardosa hyperborea* (Thorell, 1852). These species reach maximal abundance at the same time in all localities investigated (Figs. 3-4).

(2) Flexible time of maximal activity (adaptive pattern)

Another group of species follows an activity pattern adjusting the time of maximal activity to particular environmental conditions. The period of the highest activity is usually later in northern areas than in southern regions. These differences in time of maximal

Table 1. Climatic data from the regions investigated.

	Lapland	S. Finland	Lithuania	Germany
Yearly mean temperature (°C)	- 4.0	+ 4.2	+ 6.0	+ 5.9
Precipitation (mm)	450	550	620	1300
Snow cover (cm)	90	40	15	70
Snow free period (months)	4.5	8	9	7

activity were noticed for the species active in spring and autumn, e.g. *Centromerus arcanus*, *Oryphantes angulatus* (O.P.-Cambridge, 1881), *Walckenaeria nudipalpis* (Westring, 1851) and *Pirata piraticus* (Clerck, 1757) (cf. Figs. 5-6).

Winter activity

The winter activity of spiders on, or in, the *Sphagnum* layer was not studied. Adults of *Trochosa spinipalpis* (F.O.P.-Cambridge, 1895) were recorded in marked numbers in all localities (except Lapland) after snow melt (Fig. 7). High activity was found also for *Oryphantes angulatus* immediately after snow melt, and for *Walckenaeria nudipalpis* before first snow (Fig. 6). Both linyphiids have been found commonly on the snow cover in Northern Finland (Huhta & Viramo 1979). Many species with great activity shortly after snow melt (Appendix) were registered in Lapland. These species are supposed to be already active under the snow cover shortly before snow begins thawing. In southern regions many species usually show a short period of low activity after snow melt followed by a sudden increase of activity (e.g. *Pardosa hyperborea*; Fig. 3).

North-south comparisons

Some patterns can be noticed along the south-north transect. In the case of *Pardosa sphagnicola* prolonged maximal activity periods were registered in southern regions (Fig. 2). Prolonged periods of high activity were observed in the mountains of S. Germany for *Antistea elegans* and *Pirata hygrophilus* Thorell, 1872. Some species active in spring or early summer may have a period of low activity before reaching their maximal activity in southern regions (*Pardosa sphagnicola, Pardosa hyperborea, Pirata hygrophilus*).

Sexes

The most predictable patterns of activity were registered in males. The activity of the females usually lasted longer than that of the males. The most complicated and unpredictable situation was registered in *Pirata piraticus* (Fig. 5). The activity periods of males and females of this species seem to be almost separated in Lapland. For some reason females were not actively moving during early summer (mating period); the late summer activity period is typical to all lycosid females carrying egg cocoons or spiderlings.

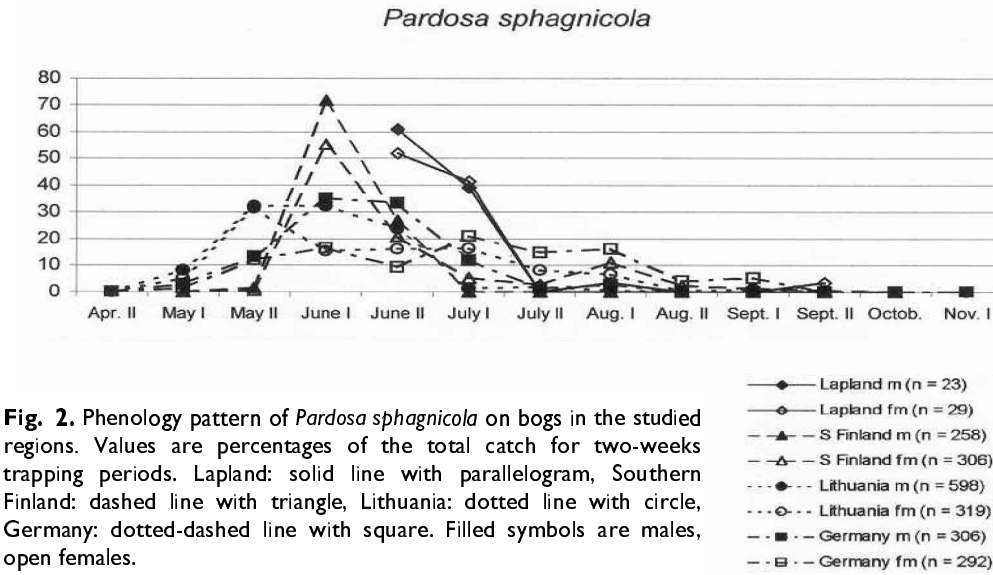


Fig. 2. Phenology pattern of *Pardosa sphagnicola* on bogs in the studied regions. Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females.

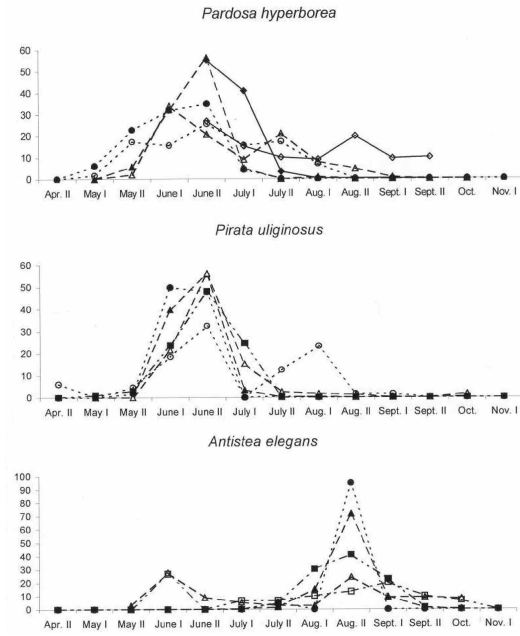
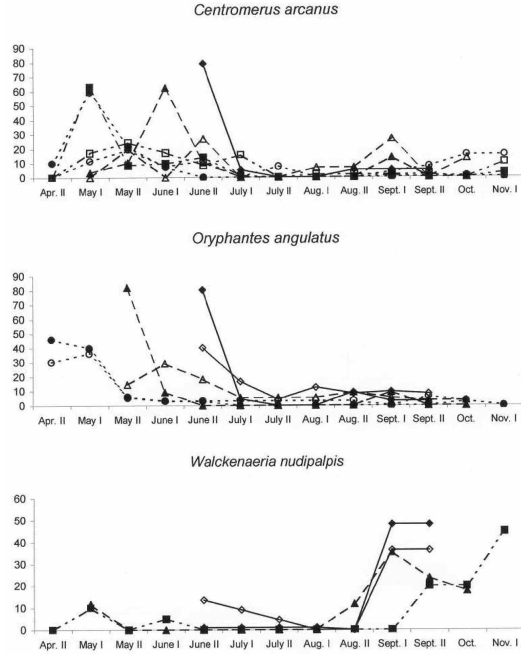


Fig. 3. Phenology of three species with "fixed time of maximal activity". Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females (cf. Fig. 2).



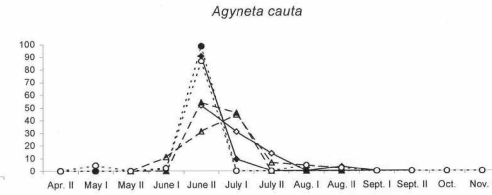


Fig. 4. Phenology of a species with "fixed time of maximal activity". Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females (cf. Fig. 2).

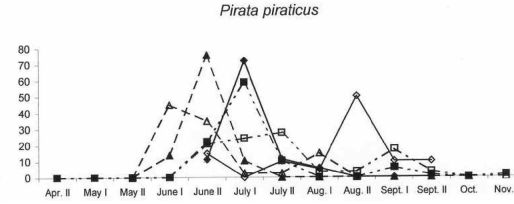


Fig. 5. Phenology of a species with "flexible time of maximal activity". Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females (cf. Fig. 2).

Fig. 6. Phenology of three species with "flexible time of maximal activity". Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females (cf. Fig. 2).

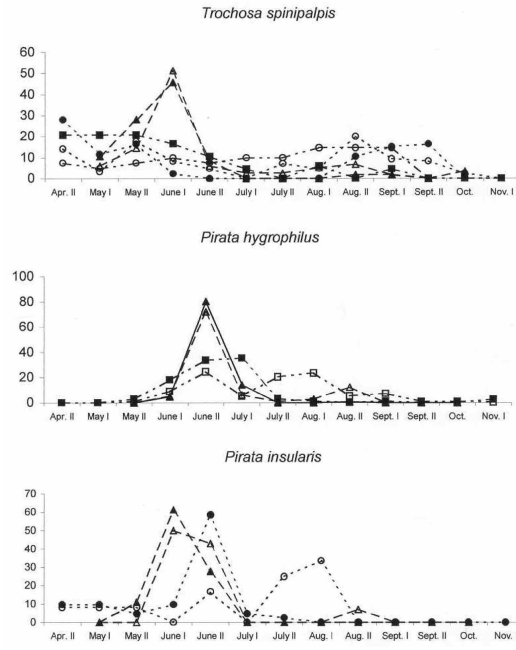


Fig 7. Phenology of three species with "untypical" activity pattern. Values are percentages of the total catch for two-weeks trapping periods. Lapland: solid line with parallelogram, Southern Finland: dashed line with triangle, Lithuania: dotted line with circle, Germany: dotted-dashed line with square. Filled symbols are males, open females (cf. Fig. 2).

Complicated cases

A few patterns remain open and difficult to explain: The maximal catch of *Agyneta cauta* in Lithuania was registered during a very short period and corresponds to that observed in Lapland, while activity periods in S. Finland and Germany are extended and correspond to each other (Fig. 4). Maximal activity of *Oryphantes angulatus* in Lithuania lasts longer than that observed in S. Finland and Lapland, where maximal abundance is immediately after snow melt and declines abruptly (Fig. 6). *Trochosa spinipalpis* is not very abundant after snow melt and shows a high increase of activity in late spring in S. Finland, while in Lithuania and Germany high numbers are registered immediately after snow melt, decreasing during spring (Fig. 7).

Mountain and lowland peat bogs

No marked differences can be distinguished between activity patterns of the same species in mountain and lowland sites. However, as regards *Pirata uliginosus* and *Agyneta cauta*, the activity in the German mountains shows similar patterns to that in S. Finland. In the case of *Centromerus arcanus, Pardosa sphagnicola* and *Trochosa spinipalpis*, activity in the German mountains is similar to that observed in Lithuania, and in the case of *Pirata piraticus* to that in Lapland. The spiders living in the German mountains have often prolonged activity periods compared to conspecifics in northern regions. It is difficult to say whether that is caused by the southern locality, altitude or other factors. In the case of *Pardosa sphagnicola* the prolonged activity period in the German mountains is observed later than that in Lithuania. This probably indicates the influence of a mountain environment.

DISCUSSION

There is a paucity of information regarding how well species activity patterns correspond with their life histories. Some studies indicate that these two processes do not always correspond to each other (Toft 1976, 1978; Dondale 1977; Albert 1982). On the other hand, it is known that the life history of a species is not always stable; for example, some species have different life histories in different habitats (Huhta 1965; Almquist 1969). The annual activity pattern is a flexible feature, and it allows the adaptation of the life history to the conditions existing in special habitats. A. Hänggi (unpublished data) found that the time of maximal activity of *Pirata piraticus* can differ markedly even in closely situated (1.5 km apart) peat bogs in Switzerland.

In the present study, despite a similar habitat structure and probably the same microclimatic conditions in the *Sphagnum* layer, spider species show variable activity patterns in peat bogs of different latitudinal and altitudinal zones. No strict general patterns in changes of phenology common to all species

(or a large species group) can be distinguished along the south-north transect. The analysed data show that for almost every species the activity patterns vary to some extent between the different geographical regions.

In a group of species, the maximal activity seems to be connected to a particular time of the year (fixed/conservative pattern). It is difficult to believe that the climatic or other environmental conditions happen to be favourable for them at that time in all regions, as there are great differences along the study transect, e.g. a two-month period without sunset in Lapland. In another group the maximal activity is clearly connected to environmental conditions of a particular locality (flexible/adaptive pattern). The most typical pattern responding to situations in different regions was found in *Pardosa sphagnicola*. This species had postponed activity in northern regions (Lapland) and prolonged activity in southern regions (Lithuania and Germany). Despite the higher altitude the activity patterns in mountain localities seem to be more influenced by their southern location than by their altitude.

In general, the present phenology patterns fit well with data from bogs in Northern Germany (Broen & Moritz 1963). Only *Walckenaeria nudipalpis* had a different pattern, with a peak in January in Northern Germany. This difference may be partly explained by different collecting periods (no winter trapping in our material). The data of *Pirata uliginosus* from Austria (Freudenthaler 1989) do not show any differences compared with the present study. The activity of *Centromerus arcanus* in Austria (Freudenthaler 1989) was similar to that observed in Southern Germany and it differed from the activity found in northern regions. This illustrates the flexible activity patterns of the species.

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Appendix. Phenology of peat bog spiders. Maximal numbers in % of the total catches in each region are given in numbers; **M, FM** = 30-50%; **m, fm** = 10-30%; m, fm = 5-10%; xx = <5%; x = singleton. M, m = male; FM, fm = female; time periods without sampling are marked in grey.

	Apr. II	May I	May II	June I	June II	July I	July II	Aug. I	Aug. II	Sept. I	Sept.II	Oct.	Nov. I	Total
Pardosa sphagnicola														
Lapland males					**61**	**M**								23
Lapland females					**52**	**FM**		xx			x			29
S. Finland males			xx	**72**	**m**									258
S. Finland females			xx	**55**	**fm**	fm	xx	**fm**	xx	xx	xx			306
Lithuania males		m	**32**	**32**	**m**	xx	xx	xx						598
Lithuania females		fm	**31**	**fm**	**fm**	**fm**	fm	fm	x	xx				319
Germany males		xx	**m**	**35**	**M**	**m**	xx	xx						306
Germany females		xx	**fm**	**fm**	fm	**21**	**fm**	**fm**	xx	fm				292
Pardosa hyperborea														
Lapland males					**55**	**M**	xx	x	x	x				720
Lapland females					**27**	**fm**	fm	fm	**fm**	fm	fm			583
S. Finland males			m	**M**	**56**	xx		x						121
S. Finland females			xx	**34**	**fm**	fm	**fm**	fm	xx	xx				280
Lithuania males		m	**m**	**M**	**35**	xx								66
Lithuania females		x	**fm**	**fm**	**26**	**fm**	**fm**	fm						58
Pirata uliginosus														
S. Finland males				**M**	**56**	xx	x	xx		x		xx		554
S. Finland females				**fm**	**56**	**fm**	xx	xx	xx			xx		237
Lithuania males			xx	**50**	**M**		xx							355
Lithuania females	m		xx	**fm**	**32**		**fm**	**fm**	x	x				65
Germany males		x	xx	**m**	**48**	**m**								102
Germany females		**fm**		**fm**	**38**			**FM**						13
Trochosa spinipalpis														
S. Finland males		**m**	**m**	**46**	m				x	x		xx		57
S. Finland females		fm	**fm**	**51**	fm	xx	xx	fm	fm	xx		xx		117
Lithuania males	**28**	**m**	**m**	xx					**m**	**m**	**m**			86
Lithuania females	**fm**	xx	**fm**	fm	xx		fm	xx	**20**	fm	fm	xx		85
Germany males	**21**	**21**	**21**	**m**	**m**	xx	m	m		xx				67
Germany females	fm	xx	fm	fm	fm	fm	fm	**15**	**15**	**15**				41

	Apr. II	May I	May II	June I	June II	July I	July II	Aug. I	Aug. II	Sept. I	Sept.II	Oct.	Nov. I	Total
Centromerus arcanus														
Lapland males					**79**	x			x	x	x			19
S. Finland males		x	**m**	**62**	**m**					**m**				29
S. Finland females			**fm**		**27**			x	fm	**27**		**fm**		15
Lithuania males	m	**59**	**m**	m					x		x	x		101
Lithuania females		**fm**	**19**	fm	**fm**		fm			x	fm	**fm**	**fm**	26
Germany males		**63**	m	m	**m**	xx				x			xx	94
Germany females		**fm**	**24**	**fm**	fm	**fm**		x	x	x	x		**fm**	58
Walck. nudipalpis														
Lapland males					x	x	x	x		**48**	**48**			100
Lapland females					**fm**	fm	xx			**36**	**36**			44
S. Finland males		**m**							**m**	**35**	**m**	**m**		17
S. Finland females			x		**fm**	x		x	x			**36**		11
Germany males		**m**		x							**m**	**m**	**45**	20
Germany females		x		x	x	**22**		**22**			x		x	9
Pirata insularis														
S. Finland males			**m**	**61**	**m**									18
S. Finland females				**50**	**FM**				x					14
Lithuania males	m	m	xx	m	**59**	xx	x							41
Lithuania females	x	x	x		**fm**		**fm**	**33**						12
Oryph. angulatus														
Lapland males					**80**	xx			m	xx	xx			66
Lapland females					**40**	**fm**	xx	**fm**	fm	fm	fm			72
S. Finland males			**82**	x						x				11
S. Finland females			**fm**	**29**	**fm**	fm	fm	fm	fm	fm	xx	xx		55
Lithuania males	**46**	**M**	m	x	x							x		35
Lithuania females	**FM**	**36**	fm	x	x	x	x	x	x		fm	x		33
Antistea elegans														
S. Finland males						x	xx	**m**	**72**	m	xx	x		198
S. Finland females			xx	**28**	xx	fm	xx	xx	**fm**	fm	fm	fm		112
Lithuania males							x		**95**					20
Lithuania females	**fm**		**fm**	x	**42**		x							12
Germany males							xx	**M**	**41**	**m**	x			66
Germany females				**27**		fm	fm	**fm**	**fm**	**fm**	**fm**	fm		30
Pirata piraticus														
Lapland males					**m**	**72**	**m**	x						18
Lapland females					**fm**		**fm**	x	**50**	**fm**	**fm**			20
S. Finland males				**m**	**76**	**m**								29
S. Finland females				**45**	**FM**	x	x	**fm**						40
Germany males					**m**	**59**	xx			m	x		x	68
Germany females					**fm**	**fm**	**28**	x	x	**fm**	x			29
Pirata hygrophilus														
S. Finland males				xx	**80**	**m**			x					126
S. Finland females				fm	**72**	fm	x	xx	**fm**					97
Germany males			xx	**m**	**M**	**35**	xx	xx	xx	xx	x	xx	xx	678
Germany females			xx	fm	**24**	fm	**fm**	**fm**	fm	fm	xx	xx	xx	449
Agyneta cauta														
Lapland males					**91**	m								32
Lapland females					**52**	**FM**	**fm**		x					29
S. Finland males					**54**	**M**								37
S. Finland females				**fm**	**FM**	**44**	fm	xx	x					45
Lithuania males				xx	**98**									127
Lithuania females		xx		x	**86**			xx	x					44
Germany males					**40**	**40**	**m**							10