Aitchison, C. W. 1984. The phenology of winter-active spiders. J. Arachnol., 12:249-271.

THE PHENOLOGY OF WINTER-ACTIVE SPIDERS

C. W. Aitchison

Department of Entomology, University of Manitoba, Winnipeg,
Manitoba R3T-2N2, Canada

ABSTRACT

At least 54 species of spiders are winter-active in central, southern Canada, displaying phenologies which seem to be 42.6% stenochronous, 38.9% eurychronous and 14.8% winter-mature, with juveniles and adult stages overwintering. The cool climate of Manitoba appears to have prolonged the duration of the life cycles of some spiders. The family composition during the winter months is 34.6% erigonines (mostly represented by *Ceraticelus laetus* and *Sisicus* sp.), 13.8% clubionids (*Agroeca ornata*), 13.5% lycosids, 11.1% linyphiines (*Centromerus sylvaticus*), 8.8% thomisids (juveniles of *Xysticus*), 6.1% theridiids (*Robertus arcticus*), and 12.0% other families.

INTRODUCTION

Studies of spider phenology throughout the year have been done in Scandinavia, Germany, Yugoslavia and England by means of pitfall traps (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Merrett 1967 to 1969, Hauge 1976, Schaefer 1976, Toft 1976, Flatz 1979, Puntscher 1979), sieving of litter (Palmgren 1939 and 1976, Huhta 1965, Schaefer 1976, Toft 1976), beating of bushes (Palmgren 1939 and 1976, Hauge 1976, Toft 1976) and/or sweeping of undergrowth (Toft 1976). Edgar (1972) and Workman (1978) presented detailed life histories of *Pardosa lugubris* (Walck.) and *Trochosa terricola* Thorell respectively throughout the year. Within North America some research into the phenology of spider guilds from individual habitats has been completed (Muma and Muma 1949, Dondale 1961 and 1977, Schmoller 1970, Cutler *et al.* 1975, Peck and Whitcomb 1978), although field investigations by researchers are limited generally to snow-free areas or seasons.

To present a comprehensive picture of the life history of a species in its natural habitat, its activity should be monitored throughout the year. Some researchers, mostly from Europe, have continued sampling despite snow cover and have presented more comprehensive data (Polenec 1962, Huhta 1965, Büche 1966, Thaler and Steiner 1975, Toft 1976, Granström 1977, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Sutherland pers. comm.). Their findings demonstrated that certain families predominated during the winter at temperatures just below the 0°C range (Aitchison 1978), namely Linyphiinae, Erigoninae, Tetragnathidae, Lycosidae, Thomisidae and Clubionidae (Polenec 1962, Büche 1966, Kronestedt 1968, Thaler and Steiner 1975, Aitchison 1978, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980, Sutherland pers. comm.).

Several workers suggested that spiders active during the winter months often have definite types of life cycles and certain overwintering stages (Merrett 1969, Schaefer 1976, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980). To verify this in part, this

study attempts to determine 1) the types of phenologies occurring in winter-active spiders under natural conditions and their overwintering stages, 2) the duration of specific life cycles, and 3) the family composition and species abundances of different habitats over time.

The results of this study are dependent upon the definitions of the categories used, which are given here. AUTUMN is southern central Canada refers to September and October; WINTER refers to the period of snow-cover, i.e., from November until mid-April; and SPRING means mid-April and May; SUMMER is the period from June to August; WINTER-ACTIVE refers to any horizontal locomotory activity by a species during winter months; and SUBNIVEAN means under snow.

In the phenology of spiders the three standard patterns are as follows: 1) EURYCHRONOUS, having adults present all seasons, so that reproductive periods(s) may or may not be fixed time(s) of the year; 2) STENOCHRONOUS, with adults present at a certain time of the year (spring, summer, autumn); 3) WINTER-MATURE (Tretzel's [1954] "winter-reif"), with reproduction occurring at low temperatures. In all three patterns both juveniles and adults may overwinter, dependent upon the reproductive period and whether or not the species is annual or biennial. The maximum number of active males of a given species taken in pit-fall traps is regarded as indicative of the time of reproduction (Tretzel 1954).

SITE AND METHODS

The study area is located in the enlosed grounds of Canada Cement Lafarge Company, Fort Whyte, Manitoba, Canada (49° 49′N 97° 13′30″W) in an area consisting of a mixture of extensive aspen-bur oak groves *(Polpulus tremuloides–Quercus macrocarpa)* and a small meadow of long grass prairie (3500 m^2).

One transect of eight pitfall traps was placed in one of these groves and another in the small damp meadow. A third transect of four traps was placed in an ecotone area between the wood and a marshy area. The trap consisted of an inner plastic cup (diameter 7 cm, height 8 cm) containing a mixture of ethylene glycol and water, within an outer cup (diameter 8 cm, height 12.5 cm) having its upper lip level with the soil surface. During winter this was covered by a ring and a lid to exclude snow (Aitchison 1978). Traps were placed 10 m apart in the wood and meadow, and 5 m apart in the ecotone area.

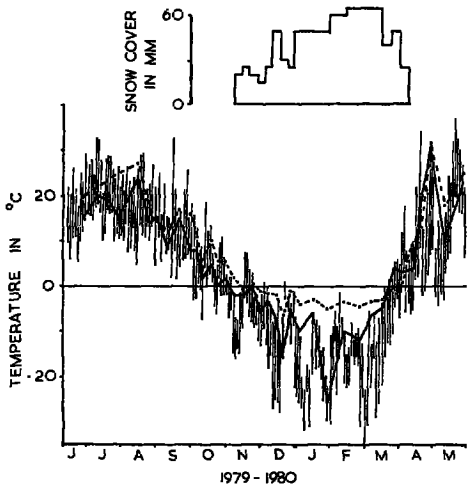

Fig. 1.–Meteorological data for June 1979 to May 1980, giving the minimum-maximum air temperatures (vertical lines) for every other day, the air temperature at the time of collection (solid line) and the mean soil surface or subnivean temperature (dashed line); in addition the duration and snow cover thickness are shown.

Sampling of the pitfall traps was completed every two weeks from April 1979 until the end of October 1981 (the snow-free period and the coldest part of the winter); and it was done weekly from late autumn until December, and from March until just after snow melt. Data from samples taken at the same sites between October 1973 and August 1975 were also incorporated into the study. The thickness of the snow cover, mean subnivean or soil surface temperatures and ambient air temperatures were noted at the times of collection (Fig. 1), with details of measurements described elsewhere (Aitchison 1978). Specimens were placed in vials of ethylene glycol by means of a brush or forceps.

In addition, 25 cm x 25 cm quadrat samples of litter were collected monthly from October 1980 until October 1981 and placed in modified MacFadyen funnels (MacFadyen 1961) for extraction to determine those species which were abundant during winter, and their densities on the soil surface. During snow-free months, spiders inhabiting the vegetative layers were sampled by sweeping in the meadow and by beating bushes in the wood.

The laboratory preparation of samples included passing them through a coarse filter, washing them with distilled water, and storing in 70% ethanol following identification to species if possible. C. D. Dondale, J. Redner and R. Carter verified some of the identifications. The carapace width of each individual was measured in mm, with species and sex noted in mature specimens. The presence of size of eggs were determined in females by dissection.

Extraction of litter samples, done in MacFadyen modified funnels (MacFadyen 1961), from the wood were done only in the non-vegetative period due to the abundance of poison ivy, *Rhus radicans*. Family composition and species abundance were determined from counts of all trapped specimens of winter-active species taken over the one year period from April 1979 until April 1980, as well as from the extracted spiders.

RESULTS

Systematic analysis of winter-active species.–A summary of the life histories of the winter-active species is found is Table 1. A total of 54 species are winter-active, as well as juveniles of *Tibellus* spp. and *Clubiona* spp., which are represented in the study area by two and three species, respectively. Of these species twenty-one are or seem to be eurychronous, with juveniles and adults overwintering; the representative families include many Erigoninae, Clubionidae, Mimetidae and Hahniidae. Twenty-three species appear to be stenochronous, with predominantly juveniles and a few females overwintering and mostly represented by the cursorial families. Eight species appear to be winter-mature, mainly linyphiines and with overwintering juveniles and winter-active adults (Fig. 2).

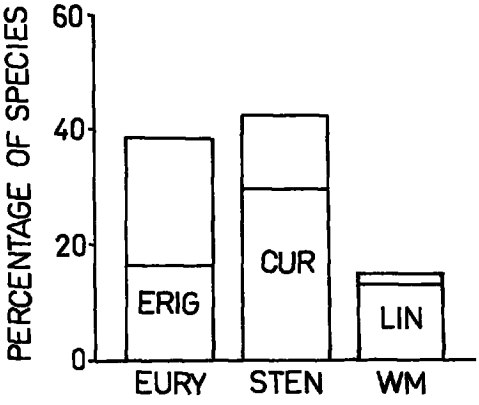

Fig. 2.–Bar graphs showing each life history pattern and the percentage of the species involved out of the total number of winter-active species. EURY means eurychronous, STEN stenochronous, WM wintermature, ERIG erigonines, CUR cursorial families and LIN linyphiines.

Table 1.—List of winter-active spiders at Fort Whyte, Manitoba, Canada, their patterns of life histories and the length in years and seasonal activity (largely condensed into a 12-month period from 4½ years of data, with the exceptions of one year of data for *A. aculeata* and *P. moesta*), and the total number of trapped males (M), females (F), and juveniles (J) as determined by pitfall traps: △ = 1-2 males; ● > 2 males; ☆ = male maximum; ◆ = 1-2 females; ○ > 2 females; # = female maximum. The abbreviations of life history patterns are as in the Appendix.

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
ERIGONINAE:																	
1. *Ceraticelus fissiceps*	EURY	?				△	●☆	△	△	△	△				16	1	0
												◆					
2. *Ceraticelus laetabilis*	EURY	?	△	△	●		●	△				△	●	●☆	26	11	0
			◆		◆	◆		◆	◆			◆	◆				
3. *Ceraticelus laetus*	EURY	?	●	△	●	●	●	●	●☆	△	●	△	●	●	125	78	16
			○	○	○	○	○	○	○#	◆	○	○	○	○			
4. *Ceraticelus minutus*	EURY	?	△			△	△	△	●☆			△			12	17	0
			○	◆		◆	◆	◆	○#					◆			
5. *Ceraticelus simillis*	EURY?	?				△		△	●☆		△				6	12	0
						◆	◆	◆	○#					◆			
6. *Collinsia plumosa*	SUMSTEN?	?					●☆								4	5	2
					◆				◆			◆	◆				
7. *Diplocephalus cuneatus*	SUMSTEN?	?						△							1	2	11
									◆			◆					
8. *Islandiana princeps*	EURY?	?							△			△			2	1	0
														◆			
9. *Lophomma* sp.	WM?	?													0	1	0
													◆				
10. *Pelecopsis mengei*	EURY?	?					△		△					△	3	4	0
						◆		◆	◆	◆							
11. *Pocadicnemis americana*	SUMSTEN	?						●	●☆	●					6	11	1
								◆	○	○#	○						
12. *Scotinotylus* sp.	?	?													0	1	0
				◆													
13. *Sisicus* sp.	EURY?WM	?	△	△		△	△					△		●☆	17	5	19
														○			
14. *Tapinocyba* sp. A	EURY	?				△	●	●	●☆				△		19	1	0
														◆			

Table 1 (cont.).

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
LINYPHIINAE:																	
15. *Allomengea pinnata*	WM	?											●☆		14	5	0
													○#	◆			
16. *Bathyphantes brevis*	WM?	?											△		1	0	0
17. *Centromerus sylvaticus*	WM	?						△			△	●☆	●	●	44	28	0
												○	○#	◆			
18. *Macrargus multesimus*	WM	?											△		1	3	0
												◆	◆	◆			
19. *Meioneta fabra*	SUMSTEN?	?					△	△							2	12	1
	EURY?		◆					◆	○#	◆	○		◆				
20. *Neriene clathrata*	WM?	?											△		1	4	10
21. *Porrhomma terrestris*	WM?	?													0	1	0
														◆			
22. *Oreonetides* sp.	WM?	?			△										1	0	0
THERIDIIDAE:																	
23. *Robertus arcticus*	EURY	?					△					△	△		5	3	0
						◆	◆						◆				
ARANEIDAE:																	
24. *Araniella displicata*	SUMSTEN?	1?													0	0	13
TETRAGNATHIDAE:																	
25. *Pachygnatha tristriata*	AUTSTEN?	?										●☆			3	1	18
						◆	◆										
26. *Tetragnatha laboriosa*	SUMSTEN?	1?						△							2	1	22
											◆						
MIMETIDAE:																	
27. *Ero canionis*	EURY?	?	△								△		△		3	1	0
								◆									
28. *Ero furcata*	EURY?	?												△	1	0	0
AGELENIDAE:																	
29. *Cicurina robusta*	EURY	?			△						△	●☆	●	△	16	2	0
							◆							◆			

Table 1 (cont.).—List of winter-active spiders at Fort Whyte, Manitoba, Canada, their patterns of life histories and the length in years and seasonal activity (largely condensed into a 12-month period from 4½ years of data, with the exceptions of one year of data for *A. aculeata* and *P. moesta*), and the total number of trapped males (M), females (F), and juveniles (J) as determined by pitfall traps: △ = 1-2 males; ● > 2 males; ☆ = male maximum; ◆ = 1-2 females; ○ > 2 females; # = female maximum. The abbreviations of life history patterns are as in the Appendix.

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
HAHNIIDAE:																	
30. *Hahnia cinerea*	EURY	1?	△			△	●☆	●		△		△			22	2	6
							◆		◆								
31. *Neoantistea agilis*	EURY	1?							△	●	●☆	●		△	36	38	2
						◆	○	○#	○	○	◆	○		◆			
32. *Neoantistea magna*	EURY	1?					△	●	●	△	●	●☆	●		37	9	1
							◆	○	○				◆	○			
LYCOSIDAE:																	
33. *Alopecosa aculeata*	SUMSTEN	2				●	●	●☆	●	△	△				621	136	713
						○	○	○#	○	○	○	○					
34. *Pardosa distincta*	SUMSTEN	1-2						●	●☆	△	△				100	110	267
							◆	○	○#	○	○	○					
35. *Pardosa moesta*	SUMSTEN	1-2					●	●	●☆	●					277	80	155
								○	○	○#	○	○					
36. *Pirata insularis*	SUMSTEN?	1-2						△	△						2	6	16
							◆	◆	○		◆						
37. *Trochosa terricola*	EURY	2				●☆	●	●		△	△	△			42	64	118
						○	○#	○	○	○	◆	◆					
GNAPHOSIDAE:																	
38. *Drassodes neglectus*	SUMSTEN	1?					●	●☆	●						11	2	4
										◆		◆					
39. *Drassylus niger*	SUMSTEN?	1-2						△	●☆						6	4	13
							◆	◆	◆	◆							
40. *Gnaphosa muscorum*	SUMSTEN	2?					△	●☆	●						22	7	5
								◆	○#	◆							
41. *Haplodrassus hiemalis*	SUMSTEN?	2?					△	☆△							4	2	2
							◆	◆									
42. *Zelotes subterraneus*	SUMSTEN?	2?					●	●☆	●	●	△				35	12	39
						◆	◆	○	○	◆	○						

Table 1 (cont.).

Family and Species	Life history	Length	Seasonal Activity J	F	M	A	M	J	J	A	S	O	N	D	Total trapped M	F	J
CLUBIONIDAE:																	
43. *Agroeca ornata*	EURY	1-2					△	△				●☆	●	△	85	5	15
			◆			◆								◆			
44. *Agroeca pratensis*	EURY	1-2				△	△		△		△	●☆	●	△	36	11	12
						◆						◆	○#				
45. *Castianeira longipalps*	AUTSTEN?	2?							●	△	●☆				9	7	3
							◆	◆			◆	○#					
46. *Phrurotimpus borealis*	EURY	2?					△	●☆					△		8	9	9
			◆	◆				◆	◆		◆	◆	◆	◆			
47. *Scotinella pugnata*	SPSTEN?	1?				△	●☆								6	9	1
			◆	◆				◆	◆	◆		◆		◆			
THOMISIDAE:																	
48. *Oxyptila conspurcata*	SUMSTEN/ EURY	2?						●☆	△						8	10	8
						◆	◆	◆	◆		○	◆	◆	◆			
49. *O. sincera canadensis*	SUMSTEN/ EURY	2						●☆	●						61	36	33
							◆	○#	◆	○	○	○	◆				
50. *Xysticus emertoni*	SUMSTEN	2					●☆	●	△						45	2	30
							◆			◆							
51. *Xysticus ferox*	SUMSTEN	2					●	●☆	●						63	12	79
							◆	○	○#	◆							
PHILODROMIDAE:																	
52. *Thanatus formicinus*	SUMSTEN	2				●	●☆	●	●						51	11	63
							○#	◆	◆	◆	○						
SALTICIDAE:																	
53. *Neon nelli*	EURY?	1?						△					△		2	0	1
DICTYNIDAE:																	
54. *Argenna obesa*	EURY	2?		△				●	●☆	△				●	19	25	39
			◆			◆	◆		○		◆	◆	○	○			

Appendix 1 contains general data of winter-active species of spiders, presented by family, providing other information on that species or genus, when females have eggs, the overwintering stages, life history patterns and habitat information.

Duration of life cycles.—Of those twenty-seven species for which there are sufficient data to determine the duration of life cycles, there seem to be eight species which are annual (29.6%), six annual-biennial (22.2%) and thirteen biennial (48.1%). The families Lycosidae, Gnaphosidae, Clubionidae and Thomisidae provided the strongest evidence of life cycle duration (see Table 1).

Seasonal family composition, species abundance and densities.—Consider only those species which are winter-active, family compositions and species abundances were determined for the wood and meadow from pitfall trap catches and litter extractions, and for the ecotone from the pitfall catch only. The number of individuals representing each species is sometimes inexact because it is often not possible to place juveniles in a species.

On an annual basis, the family composition of winter-active spiders in the wood was predominantly lycosids (represented by *A. aculeata, P. moesta* and *T. terricola*), with erigonines (*D. cuneatus* and *C. laetus*), other families, thomisids (*O. sincera canadensis*) and linyphiines next in abundance (Fig. 3a). Out of a total of 1207 specimens and over 38 species, the most abundant species are *Alopecosa aculeata* (406 of the total number of spiders) and *Pardosa moesta* (153), the moderately abundant species *T. terricola* (80), *O. sincera canadensis* (67) and *D. cuneatus* (65), and the less abundant species *C. laetus* (54).

In the meadow, the annual family composition was mainly represented by lycosids (*A. aculeata, P. distincta* and *P. moesta*), and erigonines (*D. cuneatus* and *C. laetus*) (Fig. 3b). From a total of 1217 individuals and 38 species, the most abundant species are represented by *A. aculeata* (278 specimens), *P. distincta* (167), followed by *D. cuneatus* (123), *C. laetus* (68), *P. moesta* (45) and *X. ferox* (38).

The ecotone contained the fewest species (about 17) and 333 specimens over the year, but this was partly due to only four instead of eight pitfall traps. The catch was predominately *A. aculeata* (60 specimens) and *T. terricola* (33), with *O. sincera canadensis* (17) and other less numerous families (Fig. 3c).

Overall the lycosids were most abundant on a yearly basis, dominated in all habitats by *A. aculeata,* and by *P. moesta* in the wood and by *P. distincta* in the meadow. *T. terricola* and the thomisid *O. sincera canadensis* were representative species from wooded areas,

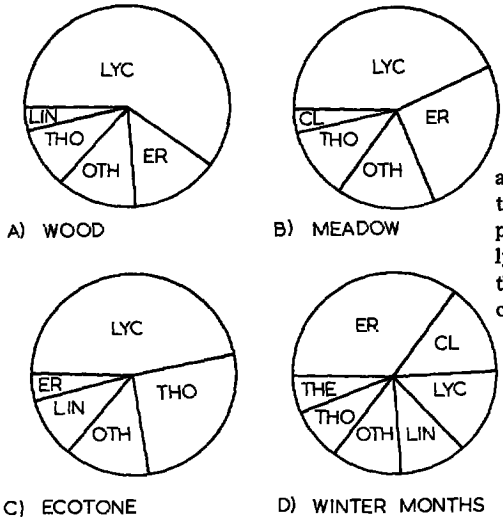

Fig. 3.—The family composition of winter-active spiders from a one year period (A to C) from three different habitats, and from all habitats pooled during winter months (D). LYC means lycosids, ER erigonines, LIN linyphiines, THO thomisids, CL clubionids, THE theridiids and OTH other families.

Table 2.–Mean seasonal densities in the numbers of individuals/m² of winter-active spiders extracted from litter. No sampling was done in the wood during spring or summer. Probably all densities are underestimated due to the small number of samples collected and escapes during collection and extraction. A is autumn, W winter and S spring and summer.

Species	Season	Meadow	Wood
Diplocephalus cuneatus	A	48.0	69.3
	W	70.7	14.7
	S	18.0	
Ceraticelus laetus	W	17.3	10.7
	S	4.0	
C. similis	A	3.2	
	W	6.7	2.7
C. minutus	A	2.7	
	W	1.3	6.7
C. fissiceps	A	1.6	
Oxyptila conspurcata	A		2.6
	S	2.0	
O. sincera canadensis	A		2.6
Xysticus ferox	A	1.6	
	W	1.3	
	S	2.0	
X. emertoni	W	1.3	
Neoantistea magna	A	2.7	
Pardosa distincta	W	1.3	
Castianeira cingulata	W		1.3
Phrurotimpus borealis	W	1.3	
Argenna obesa	W		1.3
Robertus arcticus	W		1.3

whereas the erigonines *D. cuneatus* and *C. laetus* occurred in both habitats. The numbers of the latter two species and of other small and web-building species are undoubtedly underestimated. Those species collected by sweeping and beating generally were not winter-active and therefore were not considered.

During both winters, 342 specimens of spiders, representing the majority of winter-active species, were collected from all habitats. Compared to the annual lists, a change of family composition and species dominance occurred, consisting of mainly erigonines (44 specimens of *C. laetus* and 32 *Sisicus* sp.), lycosids (20 *P. distincta* and 11 other juveniles), linyphiines (30 *C. sylvaticus*) and thomisids (25 juveniles of *Xysticus* spp.) (Fig. 3d). The erigonines are eurychronous, *C. sylvaticus* winter-mature, and both *Agroeca* spp. eurychronous with an early October male maximum.

From the litter extractions, the densities of only 15 species were determined seasonally (Table 2). Note that the densities of the larger cursorial spiders are probably underestimated, especially in the warmer months, since these animals easily fled when samples were scraped up and placed into plastic bags.

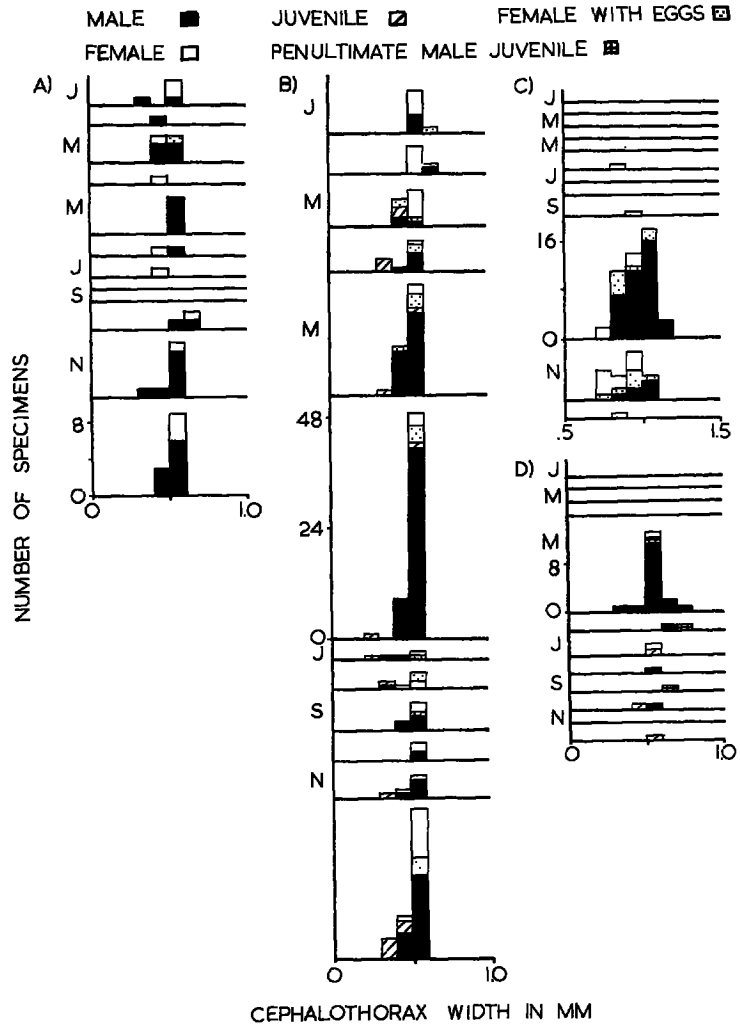

Fig. 4.–Cumulative numbers of spiders taken each month of the year, with J being January, M March, M May, J July, S September and N November (ordinate), and their varying cephalothoracic widths in mm (abscissa), for A) *C. laetabilis*, B) *C. laetus*, C) *C. sylvaticus* and D) *H. cinerea*.

DISCUSSION

Types of phenology.–Many problems arise when comparing the stated types of phenology on any one species of spider reported by one researcher with that of another. Varying methods of collection, the number of assembled specimens and definitions of seasons and of life cycle patterns complicate the issue further. In cases where few individuals of a species are collected, classification is rather tenuous and may change when more material is available, e.g., *T. pallens* from two different habitats (Hauge 1976, 1977) and *T. terricola* (Aitchison 1980 and the present work). A description of species, sex, time and place of collection seems must judicious (Merrett 1967 to 1969). The eurychronism

of Granström (1977) is possibly not valid at other latitudes, since it is defined at being an activity period of more than three months. The present definition of eurychronism may contain a wide spectrum of life cycles, accommodating the previous definition of diplochronism, i.e., those species with two reproductive periods per year. For instance, *T. terricola* is considered eurychronous and not diplochronous, and clubionids with adults present much of the year become eurychronous. In addition, the two activity periods of autumn-breeding, long-lived females, quiescent during winter and laying eggs in spring, give the impression of diplochronism (Merrett 1967), and two activity peaks of males fit that definition. The classification of life histories is especially dependent upon the collection methods used; one cannot rely solely upon data taken in sweep nets or beatings but must include sieving, pitfall traps or quadrat samples (Palmgren 1939 and 1976, Huhta 1965, Toft 1976).

Tretzel (1954) suggested that winter-active spiders had certain types of life cycles, but Puntscher (1979) was unable to verify this. Schaefer (1976) demonstrated that five standard types of phenology could have overwintering eggs, juveniles and/or adults; only those annual species with overwintering eggs could not possibly have winter-active representatives. The present study supports the work of both Flatz (1979) and Puntscher (1979), that winter-active species can occur in all the classes of phenology except the strictly annual, autumn-stenochronous species with overwintering eggs. Admittedly the length and type of life cycle determine the overwintering stages; the stenochronous species with annual-biennial and biennial life cycles and various-sized overwintering juveniles are the most abundant winter-active group in Canada. Despite the fact that some representatives of a winter-active species may spend winter in hibernaculae, the other active individuals of that species result in its being considered as winter-active.

Individual species of winter-active spiders collected in Manitoba frequently may only be compared to different species within the same genus; unfortunately there is a paucity of information on life cycle classification in North America and generally on that of winter-active species globally. However, there are often some similarities of phenology within a genus, which lends support to conclusions about a particular species of that genus. Genera of winter-active species, e.g., *Scotinoylus*, *Pardosa* and *Xysticus*, often have the same life history patterns in both the Palaeartic and Nearctic regions, (Thaler and Steiner 1975, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980).

The eurychronous species comprise a broad range of families, all of which have adults present throughout the year. Also included under this phenological pattern are all species previously called diplochronous. Many erigonines (Muma and Muma 1949, Tretzel 1954, Broen and Moritz 1963, Palmgren 1975 and 1976, Toft 1976, Puntscher 1979, Aitchison 1980), a few linyphiines (Broen and Moritz 1963, Palmgren 1975, Braun 1976, Granström 1977, Puntscher 1979) and mimetids (Schaefer 1971, Palmgren 1972) are eurychronous, as some species of these families are in Manitoba. The eurychronism of hahniids *Neoantistea* spp. and *H. cinerea* in Manitoba is corroborated by that of European species (Schaefer 1971, Flatz 1979), as is that of the lycosid *T. terricola* (Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1968, Hauge 1976, Schaefer 1976, Granström 1977, Workman 1978). The diplochronism of some European clubionid species, including *Agroeca* spp. (Tretzel 1954, Broen and Moritz 1963, Merrett 1967, Braun 1976, Flatz 1979), which is now defined as eurychronism, is also seen in Canada. The overwintering stages in this phenological pattern include adults and juveniles of varying size classes.

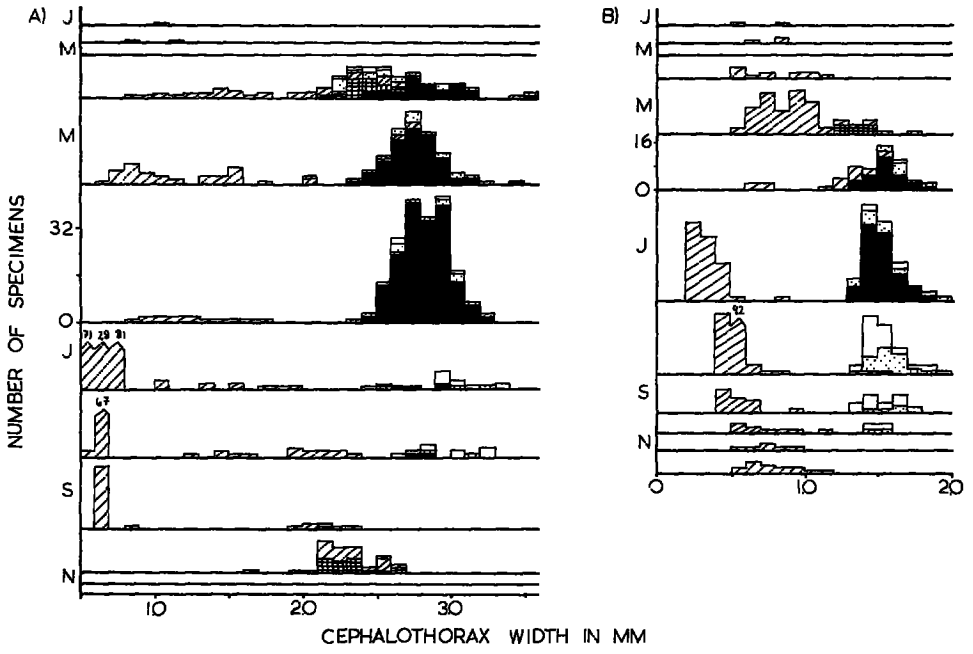

Fig. 5.–Cumulative numbers of lycosids taken each month of the year: A) *A. aculeata* and B) *P. distincta*. J represents January, M March, M May, J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

Stenochronism is demonstrated by a variety of families, some of which are typically with this life history pattern. Some erigonines and linyphiines (Muma and Muma 1949, Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1969, Schaefer 1971 and 1976, Palmgren 1975 and 1976, Toft 1976, Granström 1977, Hauge 1977, Puntscher 1979) are stenochronous, as are *D. cuneatus* and *M. fabra* of Manitoba. Some apparently typical stenochronous families include the tetragnathids (Thaler and Steiner 1975, Flatz 1979, Flatz and Thaler 1980), the lycosids (Edgar 1972, Toft 1976, Flatz 1979, Aitchison 1980), the gnaphosids (Hauge 1976, Flatz 1979, Puntscher 1979) and the thomisids and philodromids (Palmgren 1950, Broen and Moritz 1963, Merrett 1967, Schmoller 1970, Schaefer 1971 and 1976, Cutler *et al.* 1975, Toft 1976, Dondale 1977, Aitchison 1980), as corroborated by this study with the exceptions of eurychronous *T. terricola* and *Z. subterraneus*. Again various-sized juveniles and a few females overwinter.

Of the winter-mature species, the linyphiines *C. sylvaticus* and *Macrargus* spp. in Canada (Aitchison 1978, 1980) and the same species and other European genera (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Kronestedt 1968, Merrett 1969, Schaefer 1976, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980) are winter-active. The European agelenid *C. cicurea* is also winter-mature (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Flatz 1979, Flatz and Thaler 1980). Winter-active adults and juveniles overwinter.

For the majority of species in this study, agreement has been found with the current literature regarding phenological patterns and overwintering stages, as well as confirmation of other winter-active species (Huhta 1965, Büche 1966, Kronestedt 1968, Thaler and Steiner 1975, Schaefer 1976, Toft 1976, Granström 1977, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Flatz and Toft 1980, Sutherland pers. comm.). The percentages of different phenological patterns agree well with previous work (Aitchison 1980),

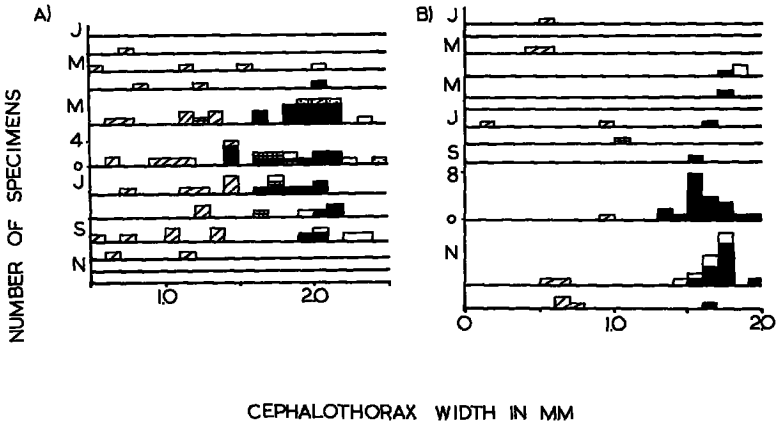

Fig. 6.–Cumulative numbers of spiders taken each month of the year: gnaphosid A) *Z. subterraneus* and clubionid B) *A. pratensis*. J represents January, M March, M May J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

with the highest percentage being of summer stenochronous species with overwintering juveniles (Schaefer 1976, Puntscher 1979, Aitchison 1980).

Duration of life cycles.–The life cycles of spiders from mid- and northern Europe are annual, annual-biennial or biennial, with the duration dependent upon environmental conditions, especially upon temperature (Huhta 1965, Almquist 1969, Edgar 1972, Schaefer 1976, Dondale 1977). For example, *P. lugubris* is annual-biennial with a biomodal distribution of female weights during the summer in Holland, but it is biennial in Scotland and Denmark (Edgar 1972, Toft 1976). Likewise *P. moesta* in Ontario is annual (Dondale 1961) and in Manitoba annual-biennial (Aitchison 1980). Furthermore, altitude can change an annual species into a biennial one (Schmoller 1970). Within *Pardosa* spp. copulation may occur in the same temperature range at two different latitudes or may be dependent upon photoperiod (Schaefer 1976, Granström 1977), introducing two more parameters affecting the length of the life cycle. Even within species of lycosids in Manitoba, the time of the male maximum varied by two weeks during two consecutive summers, dependent upon the climatic conditions at that time. As a consequence, the phenology of a species may be annual at lower latitudes (altitudes) and biennial in higher latitudes or in regions with cooler climates, such as Manitoba.

Low temperatures depress growth during the winter (Edgar 1972, Workman 1978) and consequently prolong the length of life of spiders in these climates. Thus it can be expected that a higher proportion of species (about 50% of the total number of species) will have longer life cycles, as shown in Denmark (Toft 1976) and in Manitoba (Aitchison 1980 and the present work). In biennial *T. terricola* as many as three sizes of juveniles overwinter, while most biennial species only had two size classes overwintering. There is overlap in the size of overwintering juveniles of lycosids especially and of clubionids to some extent, probably the result of a prolonged reproductive period in those families.

Typically the erigonines and linyphiines have biennial life cycles in Denmark (Toft 1976), although this is not true in southern Germany with five species of annual erigonines (Schaefer 1976). The absence of identifiable juveniles from these families makes it difficult to determine the duration of their life cycles.

The low mean annual temperature of Winnipeg, Manitoba (+2.2°C) and the low temperature of the litter appear to have prolonged the life cycles of some species to annual-biennial and biennial.

Family composition, species abundance and densities.—There are seasonal changes in family composition and differences in the proportions of collected families which may be associated with different trapping techniques (Puntscher 1979). The former phenomenon is clearly demonstrated when comparing the annual family composition with that of the winter (Fig. 3); annually the lycosids dominate in all habitats whereas the erigonines, thomisids and linyphiines are moderately abundant. During the winter, however, the erigonines outnumber the less abundant clubionids and lycosids.

Most winter-active spider species are in the Erigoninae and Linyphiinae, with some species overwintering as juveniles (Kronestedt 1968, Merrett 1969, Schaefer 1976), and others copulating in November and laying eggs in spring (Toft 1976). In Austria winter-active families were represented by 55.9% erigonines, 34.5% linyphiines, 8.7% tetragnathids, with lycosids and thomisids comprising most of the remainder (Thaler and Steiner 1975, Puntscher 1979). Palmgren (1965) collected linyphiines, including *M. multesimus*,

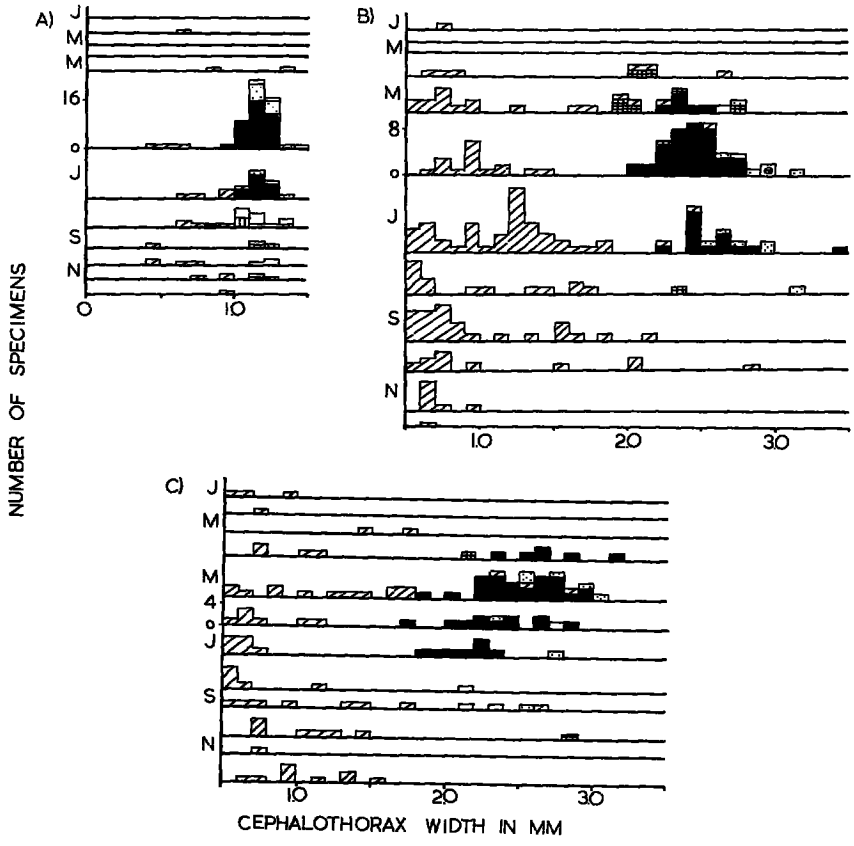

Fig. 7.—Cumulative numbers of spiders taken each month of the year: thomisids A) *O. sincera canadensis* and B) *X. ferox;* and philodromid C) *Th. formicinus.* J represent January, M March, M May, J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

erigonines and the hahniid *Hahnia mengei* Kulczynski under 60 to 80 cm of snow cover, at temperature around 0°C in Finland. When considering all winter-active stages, Polenec (1962) trapped 93.5% linyphiines in an oak wood, and 74.1% linyphiines, 5.7% each of lycosids and clubionids and 3.8% thomisids in a Yugoslavian pine wood. In Austria, Flatz (1979) encountered 47% linyphiines, 23% erigonines, 15% lycosids, 11% tetragnathids and 3% theridiids; whereas in Canada Sutherland (pers. comm.) collected 50% erigonines and 35% linyphiines. All of these families maintained winter activity in Canada, with erigonines most abundant and followed by the clubionids and linyphiines with a late October male maximum (the latter represented mostly by *C. sylvaticus*). The presence of winter-active juveniles of the genera *Pardosa* and *Xysticus* corroborates the finds of other workers (Thaler and Steiner 1975, Granström 1977, Aitchison 1978, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980).

The species abundance, considered on an annual basis, varies from that of the winter. The lycosids, in particular *A. aculeata*, were most abundant in all habitats over the year with the erigonines, *C. laetus*, moderately abundant (Fig. 3a-c). However during winter the roles change, with *C. laetus* becoming the most abundant species and the lycosid *P. distincta* a less abundant species. Other winter-active species come from the families Clubionidae, Linyphiinae, and Theridiidae, as well as the thomisid juveniles of the genus *Xysticus*.

Migration from various vegetative layers to the litter in autumn by spiders was clearly shown by the high densities of erigonines, compared to a low density in litter during the summer. Possibly relatively high densities of the thomisids do not appear in the litter until early winter, since their autumn densities are lower. Similarly, the lycosid density must have been underestimated in all seasons, because of their mobility. The high densities of *D. cuneatus* indicate that this species does not have a high activity level, compared to those of the lycosids and the thomisids (Table 2).

ACKNOWLEDGMENTS

I wish to thank Canada Cement Lafarge Company for the use of its limited access grounds; L. B. Smith for his supervision and also for critical reading of the manuscript; M. Schaefer, S. Toft, R. Carter and P. W. Aitchison for constructive comments on the manuscript; F. Kozin for translation of Slovenian; C. D. Dondale, J. Redner and R. Carter for determinations; the Canada Agricultural Research Station in Winnipeg, Manitoba, for use of laboratory space; and A. Shukla for typing. Funding was partially provided by a University of Manitoba Research Grant (no. 431-1119-60).

LITERATURE CITED

Aitchison, C. W. 1978. Spiders active under snow in southern Canada. Symp. Zool. Soc. London, 42:139-148.

Aitchison, C. W. 1980. A preliminary study of the phenology of winter-active spiders. Proc. 8th Internat. Congr. Arachnol. 1980, Vienna; pp. 61-66.

Almquist, S. 1969. Seasonal growth of some dune-living spiders. Oikos, 20:392-408.

Braun, R. 1976. Zur Autökologie und Phänologie einier für das Rhein-Main-Gebiet und die Rheinpfalz neuer Spinnenarten. Jb. nass. Ver. Naturk., 103:24-68.

Broen, B. von and M. Moritz. 1963. Beiträge zur Kenntnis der Spinnenfauna Norddeutschlands. I. Über Reife- und Fortpflanzungszeit der Spinnen (Araneae) und Weberknechte (Opiliones) eines Moorgebietes bei Greifswald. Deut. Entomol. Z., 10:379-413.

Broen, B. von and M. Moritz. 1965. Spinnen (Araneae) und Weberknechte (Opiliones) aus Barberfallen von einer tertiären Rodbodenkippe im Braunkohlenrevier Böhlen. Abh. Berichte Naturk. Görlitz, 40:1-15.

Büche, W. 1966. Beiträge zur Ökologie und Biologie winterreifer Kleinspinnen mit besonderer Berücksichtigung der Linyphiiden *Macrargus rufus rufus* (Wider), *Macrargus rufus carpenteri* (Cambridge), und *Centromerus sylvaticus* (Blackwall). Z. Morph. Ökol. Tiere, 57:329-448.

Cutler, B., L. H. Grim and H. M. Kulman. 1975. A study in the summer phenology of dionychious spiders from northern Minnesota forests. Great Lakes Entomol., 8:99-104.

Dondale, C. D. 1961. Life histories of some common spiders from trees and shrubs in Nova Scotia. Canadian J. Zool., 39:777-787.

Dondale, C. D. 1977. Life histories and distribution patterns of hunting spiders (Araneida) in an Ontario meadow. J. Arachnol., 4:73-93.

Edgar, W. D. 1972. The life-cycle of the wolf spider *Pardosa lugubris* in Holland. J. Zool., London, 168:1-7.

Flatz, S. 1979. Winteraktivität epigäischer Arthropoden (ibs. Aranei, Carabidae) im Bereich der Landesanstalt für Pflanzenzucht und Samen-prüfung Rinn (Nordtirol, 900 mNN). Unpubl. Mag. thesis, Universität Innsbruck, Austria. 75 pp.

Flatz, S. and K. Thaler. 1980. Winteraktivität epigäischer Aranei und Carabides des Innsbruck Mittelgebirges (900 mNN, Tirol, Österreich). Anz. Schädlingskde., Pflanzenschutz, Umweltschutz, 53:40-45.

Granström, U. 1977. Ecological Studies on Spiders (Araneida) in grasslands in nothern Sweden. (in Swedish). Unpubl. doctoral thesis, Universiteit Umeå, Sweden.

Hauge, E. 1976. Spiders (Araneae) of a west Norwegian *Calluna* heath. Report no. 20, Lindås Prosjektet, Universitetet Bergen. 98 pp.

Hauge, E. 1977. The spider fauna of two forest habitats in northern Norway. Astarte, 10:93-101.

Huhta, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. Ann. Zool. Fennici, 2:260-308.

Kronestedt, T. 1968. Notes on the Swedish species of the genus *Centromerus* F. Dahl (Araneae, Linyphiidae). A faunistic report with ecological remarks. Entomol. Ts. Årg., 89:111-127.

MacFadyen, A. 1961. Improved funnel-like extractors for soil arthropods. J. Anim. Ecol., 30:171-184.

Merrett, P. 1967. The phenology of spiders on heathland in Dorset. I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. J. Anim. Ecol., 36:363-74.

Merrett, P. 1968. The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. J. Zool., London, 156:239-256.

Merrett, P. 1969. The phenology of linyphiid spiders on heathland in Dorset. J. Zool., London, 157:289-307.

Muma, M. H. and K. E. Muma. 1949. Studies on a population of prairie spiders. Ecology, 30:485-503.

Palmgren, P. 1939. Die Spinnenfauna Finnlands. I. Lycosidae. Acta Zool. Fennica, 25:1-86.

Palmgren, P. 1943. Die Spinnenfauna Finnlands. II. Pisauridae, Oxyopidae, Salticidae, Clubionidae, Anyphaenidae, Sparassidae, Ctenidae, Drassidae. Acta Zool. Fennica, 36:1-112.

Palmgren, P. 1950. Die Spinnenfauna Finnlands und Ostfennoskandiens. III. Xysticidae und Philodromidae. Acta Zool. Fennica, 62:1-43.

Palmgren, P. 1965. Die Spinnenfauna der Gegend von Kilpisjärvi in Lappland. Acta Zool. Fennica, 110:1-70.

Palmgren, P. 1972. Studies on the spider populations of the surroundings of the Tvärminne Zoological Station, Finland. Comment. Biol. (Helsinki), 52:1-133.

Palmgren, P. 1974. Die Spinnenfauna finnlands und ostfennoskandiens. IV. Argiopidae, Tetragnathidae und Mimetidae. Fauna Fennica, 24:1-70.

Palmgren, P. 1975. Die Spinnenfauna finnlands und ostfennoskandiens. VI. Linyphiidae 1. Fauna Fennica, 28:1-102.

Palmgren, P. 1976. Die Spinnenfauna finnlands und ostfennoskandiens. VII. Linyphiidae 2. Fauna Fennica, 29:1-126.

Peck, W. B. and W. H. Whitcomb. 1978. The phenology and populations of ground surface, cursorial spiders in a forest and a pasture in the south central United States. Symp. Zool. Soc. London, 42:131-138.

Polenec, A. 1962. Arahnidska Fauna in asociacije pozimi. Biol. Vestnik (Ljubljana), 10:71-83.

Puntscher, S. 1979. Verteilung und Jahresrhythmik von Spinnen im Zentralalpinen Hochgebirge. Unpubl. doctoral thesis, Universität Innsbruck, Austria. 117 pp.

Schaefer, M. 1971. Zur Jahresperiodizität der Spinnenfauna einer Ostseeküstenlandschaft. Biol.Zbl., 90:579-609.

Schaefer, M. 1976. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). Zool. Jb. Syst., 103:127-289.

Schmoller, R. 1970. Life histories of alpine tundra Arachnida in Colorado. Amer. Midl. Nat., 83:119-133.

Thaler, K. and H. M. Steiner. 1975. Winteraktive Spinnen auf einem Acker bei Grossenzersdorf (Niederösterreich). Anz. Schädlingskde., Pflanzenschutz, Unweltschutz, 48:184-187.

Toft, S. 1976. Life histories of spiders in a Danish beech wood. Natura Jutl., 19:5-40.

Tretzel, E. 1954. Reife- und Fortpflanzungszeit bei Spinnen. Z. Morph. Ökol. Tiere, 42:634-691.

Workman, C. 1978. Life cycle and population dynamics of *Trochosa terricola* Thorell (Araneae: Lycosidae) in an Norfolk grass heath. Ecol. Entomol., 3:329-340.

Manuscript received June 1983, revised November 1983.

APPENDIX

Information on the winter-active species of spiders and other species in the same genus regarding when females contain eggs, the overwintering stages, life history patterns and habitat information. The abbreviations used are as follows: eury - eurychronous; spsten - spring stenochronous; sumsten - summer stenochronous; autsten - autumn stenochronous; dipl - diplochronous; WM - winter-mature; OW - overwinter(ing); M - male; F - female; J - juvenile; pen - penultimate; and WA - winter-active.

ERIGONINAE:

Ceraticelus fissiceps (O. P.-Cambridge): Adults OW. Possibly Eury. Mostly from the wood.

Ceraticelus laetabilis (O. P.-Cambridge): F with eggs in March. Adults OW. Eury (Fig. 4a). From mixed habitats.

Ceraticelus laetus (O. P.-Cambridge): Fs have eggs in Jan, March, April and May (highest proportion). Adults and Js OW. Eury (Fig. 4b). From mixed habitats. A moderately abundant species in the meadow and less abundant in the wood.
LIT: *C. laticeps* (Em.) eury (Muma and Muma 1949).

Ceraticelus minutus (Emerton): Fs with eggs in July. Adults OW. Eury. From the wood.

Ceraticelus similis (Banks): Fs with eggs in July. Adults OW. Eury. In open areas.

Collinsia plumosa (Emerton): Pen Ms and Ms OW. Possibly sumsten M, eury F. Mostly from the wood.
LIT: *C. holmgreni* (Th.) also mature in snow-free period (Palmgren 1976).

Diplocephalus cuneatus Emerton: Js and pen Ms OW. Possibly sumsten M, eury F. From mixed habitats. A moderately abundant species in the meadow and in the wood.
LIT: *D. latifrons* (Cbr.) eury with spring reprod (Broen and Moritz 1963) and biennial with Js and WA Fs OW (Broen and Moritz 1963, Toft 1976, Flatz 1979, Flatz and Thaler 1980). *D. permixtus* (Cbr.) adults in autumn and winter, although Ms seen in March, Aug and Oct; Fs in March, May and Oct. Dipl (Braun 1976). *D. picinus* (Blw.) sumsten (Broen and Moritz 1963, Merrett 1969) or eury with spring reprod and biennial with OW Js (Toft 1976).

Islandiana princeps Braendegaard: OW adults. Eury? From mixed habitats.
LIT: *I. flaveola* (Banks) probably eury (Muma and Muma 1949).

Lophomma sp.: Only one F in Nov from meadow. WM?
LIT: *L. punctatum* (Blw.) adults OW, called dipl, eury and possibly WM, with an apparent autumn activity period and M max in March; biennial (Braun 1976); eury with winter reprod and adults OW (Broen and Moritz 1963); in northern Sweden spsten (Granström 1977). Seems to have two maturity periods (Palmgren 1976).

Pelecopsis mengei Simon: Adults OW? Eury. In ecotone area.
LIT: *P. elongata* (Wider) with WA adults (Polenec 1962, Flatz 1979). *P. paralleli* (Wider) collected in winter, adults in Aug and Sept; eury (Puntscher 1979). *P. radicicola* (L. Koch) sten Ms, eury Fs (Broen and Moritz 1963).

Pocadicnemis americana Millidge: Fs with eggs in July and Aug. Js OW. Sumsten. From the wood.
LIT: *P. pumila* (Blw.) sp- or sumsten (Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1969, Schaefer 1971, Palmgren 1976, Hauge 1977); with M max in June and Fs April to Dec and Js OW (Palmgren 1976.)

Scotinotylus sp.: One F taken Feb from the wood. WA Fs. Unknown phenology.
LIT: *S. alpigenus* (L. Koch) adults collected in summer (Palmgren 1976); many Ms and a few Fs WA under snow (Flatz and Thaler 1980).

Sisicus poss. n. sp.: Js, pen Ms and Ms OW. Eury-WM. Mostly from the meadow.
LIT: *S. apertus* (Holm) Fs taken May, July, Oct and Dec (Palmgren 1975); both sexes taken in pitfall traps in the Austrian Alps in Nov, Feb and March (Thaler pers. comm.). *S. longitarsi* Chamberlain and Ivie WA Js and adults under snow of Manitoba taiga (Sutherland pers. comm.).

Tapinocyba sp. A: OW Fs ? Eury. From mixed habitats.
LIT: *T. insecta* (L. Koch) sten M, eury F (Broen and Moritz 1963); *T. pallens* (Cbr.) reprod in Oct and population peak in Nov; eury? (Huhta 1965, Hauge 1976); or spring or summer reprod and dipl (Tretzel 1954, Palmgren 1975 and 1976, Hauge 1977). WA adults under snow (Flatz and Thaler 1980). *T. simplex* (Em.) WA F under taiga snow (Sutherland pers. comm.).

LINYPHIINAE:

Allomengea pinnata (Emerton): WA Fs. WM. From mixed habitats.
LIT: *A. scopigera* (Grube) autsten (Palmgren 1975) and annual (Schaefer 1976); eury with autumn max (Granström 1977).

Bathyphantes brevis (Emerton): Only one M in Nov from ecotone area. WM?
LIT: *B. gracilis* (Blw.) dipl with summer-winter copulation periods (Broen and Moritz 1963). *Bathyphantes* sp. J WA under taiga snow (Sutherland pers. comm.).

Centromerus sylvaticus Blackwall: Fs with eggs in Oct and Nov. (In the laboratory at low temperatures Fs trapped in Oct produced egg cocoons in early Nov which OW, with Js hatching in April). Adults WA. WM (Fig. 4c). From the wood.
LIT:WA and WM (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Kronestedt 1968, Merrett 1969, Schaefer 1976, Aitchison 1978 and 1980, Flatz 1979, Flatz and Thaler 1980) as well as annual (Schaefer 1976). *C. expertus* (Cbr.) called WM (Broen and Moritz 1963, Büche 1966, Schaefer 1976), while *C. prudens* (Cbr.) summer-winter dipl (Broen and Moritz 1963). *C. subalpina* Lessert active under snow at subzero temperatures (Puntscher 1979).

Macrargus multesimus (O. P.-Cambridge): Wa adults. WM. From the wood.
LIT: Ms mid-June and F June and July (Palmgren 1975), F WA under taiga snow (Sutherland under prep.). *M. rufus* (Wider) WM (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Hauge 1976, Toft 1976), and M max Feb to March with Feb max in eury Fs; annual-biennial species (Broen and Moritz 1963, Merrett 1969, Toft 1976). Adults all year except June and July (Huhta 1965); WA Fs (Flatz 1979, Flatz and Thaler 1980).

Meioneta fabra Keyserling: One F with eggs in July. Js and Fs OW. Sumsten M, eury F? From the wood.
LIT: *M. beata* (Cbr.) mature March to Oct with M max in May and June; Fs in April and May; eury (Braun 1976); WA adults (Flatz 1979). *M. gulosa* (L. Koch) eury/dipl, with Fs in winter traps until Nov; M max in July (Puntscher 1979). *M. nigriceps* (Simon) adults July to Sept; active under snow and dipl (Puntscher 1979). *M. rurestris* (L. Koch) eury with summer reprod (Broen and Moritz 1963) and WA (Flatz 1979, Puntscher 1979, Flatz and Thaler 1980). *M. saxatilis* Blw. with WA F (Polenec 1962).

Neriene clathrata Sundevall: One F with eggs in July. Js and pen Ms OW. WM (eury F)? From open areas.
LIT: Sp- or sumsten annual with OW Js (Merrett 1969, Schaefer 1971, Toft 1976).

Porrhomma terrestris (Emerton): Only one M in Dec from the wood. WM?
LIT: *P. convexum* (Westring) eury (Braun 1976) and WA adults (Flatz 1979). *P. montanum* Jackson eury with summer reprod (Broen and Moritz 1963). *P. pygmaeum* (Blw.) eury with winter max, even under snow (Palmgren 1975, Granström 1977).

Oreonetides sp.: only one M in March from the wood. WM?
LIT: *O. abnormis* (Blw.) Ms active during summer (Merrett 1969). *O. vaginatus* (Th.) Ms in June, Fs in May and Aug (Palmgren 1975), and WA with adults seen May to Oct, and dipl (Puntscher 1979). *Oreonetides* sp. nr. *flavus* Em. WA F under taiga snow (Sutherland pers. comm.).

THERIDIIDAE:

Robertus arcticus (Chamberlain and Ivie): WA adults. Eury. From the ecotone area.
LIT: *R. arundineti* (Cbr.) Ms mid-May to mid-June, and Fs April to mid-July (Broen and Moritz 1963); Ms April to Dec, Fs April to Oct (Palmgren 1974); eury (Hauge 1976). *R. lividus* Blw. with Ms Nov, Dec and Feb and F in Dec (Polenec 1962). *R. scotinus* Jackson dipl with autumn and winter max (Huhta 1965). *R. truncorum* (L. Koch) WA under snow (Puntscher 1979). *Robertus* sp. Js active under snow (Flatz 1979).

ARANEIDAE:

Araniella displicata (Hentz): Only Js taken; elsewhere Js and Fs collected on snow (probable OW stages). Sumsten or autsten? From mixed habitats.
LIT: With two generations of Js at all times of the year (Dondale 1961); Ms in July and Fs June and July (Palmgren 1974).

TETRAGNATHIDAE:

Pachygnatha tristriata C. L. Koch: Js OW and even found in webs 60 cm above snow cover on days near 0°C. Autsten? From mixed habitats.
LIT: *P. clercki* Sund. an annual sumsten (Toft 1976); eury (Tretzel 1954). *P. degeeeri* Sund. A dominant WA species (Thaler and Steiner 1975, Flatz 1979, Flatz and Thaler 1980). *P. listeri* Sund. eury with summer reprod (Broen and Moritz 1963) and with WA M (Polenec 1962).

Tetragnatha laboriosa Hentz: Js OW. Annual and sumsten? From mixed habitats.
LIT: Ms June to Sept with July max, and Fs June to Aug (Muma and Muma 1949). *T. montana* Simon and *T. striata* L. Koch both sumsten and annual (Schaefer 1976, Toft 1976).

MIMETIDAE:

Ero canionis Chamberlain and Ivie: From the wood. OW Ms. Eury?
Ero furcata Villers: one M in Dec from the wood. Eury?
LIT: Spring-autumn dipl with M max in autumn (Schaefer 1971, Palmgren 1972) or in May, and biennial with two J sizes OW (Almquist 1969). Mostly active in summer and autumn as spider feeders (Merrett 1968, Hauge 1976). Eury with summer reprod and biennial (Toft 1976). One J WA (Flatz 1979).

AGELENIDAE:

Cicurina robusta Simon: WA adults. Eury. From the wood.
LIT: *C. cicurea* (Fab.) WM (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Büche 1966) and WA adults under snow (Flatz 1979, Flatz and Thaler 1980). *C. arcuata* Keys. and *C. ludoviciana* Keys. WA (Peck and Whitcomb 1978). [One J agelenid WA under taiga snow (Sutherland pers. comm.)].

HAHNIIDAE:

Hahnia cinerea Emerton: Js and Ms OW. Eury and apparently annual (Fig. 4d). From mixed habitats.
LIT: WA F under taiga snow (Sutherland pers. comm.). *H. helveola* Simon WM (Merrett 1968); *H. nava* (Blw.) possibly dipl (Merrett 1968) or eury/ dipl with May max (Schaefer 1971), or sumsten (Tretzel 1954). *H. pusilla* L. Koch eury with summer reprod (Polenec 1962, Broen and Moritz 1963); active between Feb and July (Tretzel 1954); Ms March to June, and Fs Aug, Nov and Dec (Hauge 1976); WA Ms (Flatz 1979) and adults (Polenec 1962).

Neoantistea agilis Keyserling: Fs with eggs May to Aug. WA Fs. Eury and possibly annual. From the wood.

Neoantistea magna (Keyserling): Fs with eggs in June. WA Fs. Eury and possibly annual. From open areas.
LIT: Previously called *N. riparia* Keyserling (Aitchison 1980).

LYCOSIDAE:

Alopecosa (Tarentula) aculeata Clerck: Fs with eggs or cocoons from April to Aug (few after June). Two size classes of Js, including pen Ms, OW. Sumsten and biennial (Fig. 5a). Mostly from the wood, although an abundant species in all habitats.
LIT: Sten (Granström 1977); adults collected only in autumn and early winter (Huhta 1965); sten with July M max and Ms seen until Aug and Fs until Oct (Puntscher 1979); eury with summer reprod (Tretzel 1954). *A. accentuata* (Walck.) dipl with spring reprod and possibly biennial (Schaefer 1976). *T. barbipes* Sund. with WA adults (Polenec 1962). *A. cuneata* (Cl.) with WA adults and Js (Flatz 1979). *A. pulverulenta* (Cl.) sumsten (Broen and Moritz 1963).

Pardosa distincta Blackwall: Fs with eggs or cocoons May to Oct (July-Aug max). Between one and two size classes of Js OW. Sumsten and annual-biennial (Fig. 5b). From open areas, and an abundant species in the meadow.

Pardosa moesta Banks: Fs with eggs or cocoons form June to Oct (Aug max). Two size classes of Js OW. Sumsten and annual-biennial. From the wood, where an abundant species, moderately abundant in the ecotone area and present in the meadow.
LIT: In Ontario an annual species (Dondale 1961). *P. amentata* (Cl.) and *P. lugubris* sp- or sumsten (Broen and Moritz 1963, Toft 1976, Granström 1977), with WA Js (Flatz 1979). The latter species is annual-biennial in the Netherlands (Edgar 1972) and biennial with two sizes of OW Js in Scotland and Denmark (Edgar 1972, Toft 1976). *P. palustris* (L.) and *P. pullata* (Cl.) with WA Js and adults (Flatz 1979). *P. saxatilils* (Hentz) sumsten and annual (Dondale 1977).

Pirata insularis Emerton: Fs with eggs or cocoons May to July. Seems that two size classes of Js OW. Sumsten? and annual-biennial? From open damp areas.
LIT: *P. piraticus* (Cl.) sumsten and annual (Schaefer 1976) or annual-biennial (Toft 1976). Adults seen in summer with a possible June M max (Palmgren 1939, Merrett 1968). *P. minuta* Em. sumsten and annual (Dondale 1977).

Trochosa terricola Thorell: Fs with eggs or cocoons April to Sept. Three size classes of Js OW. Eury with spring reprod and biennial. Mostly from the wood, where a moderately abundant species, as in the ecotone.
LIT: Dipl with spring-summer reprod (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Huhta 1965, Merrett 1968, Hauge 1976, Granström 1977, Workman 1978); spsten and biennial (Aitchison 1980); eury with summer reprod and biennial (Toft 1976); WA adults (Polenec 1962, Flatz 1979). *T. spinipalpis* Cbr. with WA Ms and eury (Polenec 1962). *T. pratensis* (Em.) biennial (Dondale 1961).

GNAPHOSIDAE:

Drassodes neglectus (Keyserling): Two size classes of Js (and Fs?) OW. Sumsten M, eury F? and annual? From the wood.
LIT: *Drassodes* spp. probably sten with OW Js and probably biennial (Schmoller 1970).

Drassylus niger (Banks): Fs with eggs in May. Seems that two size classes of Js OW. Sumsten and annual-biennial? From mixed habitats.
LIT: M max late May-early June; Fs late May to mid-Aug (Cutler *et al.* 1975).

Gnaphosa muscorum (L. Koch): Fs with eggs June to Aug. Js OW (two size classes). Sumsten and possibly biennial. From the wood.
LIT: Sumsten (Tretzel 1954, Puntscher 1979); WA Fs (Puntscher 1979). Probably biennial, laying eggs July and Aug with OW Js (Schmoller 1970). Ms July; Fs with cocoons June and July (Palmgren 1943). *G. leporina* (L. Koch) Fs all seasons and Ms in summer (Merrett 1967); *G. parvula* Banks Ms late May June, Fs late May to mid-Sept (Cutler *et al.* 1975).

Haplodrassus hiemalis (Keyserling): Two size classes of Js OW. Sumsten and possibly biennial? From the wood.
LIT: *H. dalmatensis* (L. Koch) sumsten with adults May to Sept (Braun 1976). *H. signifier* (L. Koch) Ms May and June (Tretzel 1954, Broen and Moritz 1965, Merrett 1967, Hauge 1976) and WA Fs and Js (Hauge 1976, Flatz 1979). *H. sorenseni* (Strand) sumsten (Broen and Moritz 1963).

Zelotes subterraneus L. Koch: Fs with eggs May and June. Two sizes of Js and Fs OW. Sumsten? and biennial? (Fig. 6a). Mostly from the wood.
LIT: Eury with summer reprod (Tretzel 1954, Broen and Moritz 1963); Ms all summer (Palmgren 1943) except mid-July and with Aug M max; Fs May to Oct, Js May to late Sept (Cutler *et al.* 1975); dipl spring-autumn (Muma and Muma 1949). *Z. latreilleii* (Simon) probably dipl, with adults April, May, Aug and Sept (Tretzel 1954, Hauge 1976); Ms March to Sept with May max and Fs April to Nov (Merrett 1968). *Z. serotinus* L. Koch with summer reprod and biennial, with two size classes of OW Js (Almquist 1969). *Z. pretrensis* (L. Koch) with WA M (Flatz 1979).

CLUBIONIDAE:

Agroeca ornata Banks: Fs Jan, April and Dec, all with eggs. Js and adults OW. Eury and annual-biennial. Mostly from open areas.
LIT: Dipl with an 18-month life cycle (Aitchison 1980); Ms late May (max), June, mid-Aug to Oct; Fs and Js May to Oct (Cutler *et al.* 1975).

Agroeca pratensis Emerton: Phenology like that of *A. ornata* (Fig. 6b).
LIT: *A. brunnea* (Blw.) dipl with spring reprod (Polenec 1962, Broen and Moritz 1963) and WA M (Flatz 1979) and adults (Polenec 1962). *A. proxima* (Cbr.) with an 18-month life cycle and OW eggs producing adults by Aug (Almquist 1969); dipl and annual-biennial with Fs present all year except in July (Merrett 1967); sten M, eury F (Tretzel 1954, Broen and Moritz 1963). *A. striata* (Kulczynski) probably sumsten with OW Fs (Braun 1976).

Castianeira longipalps (Hentz): Fs with eggs in Oct. Pen Js OW. Autsten with OW eggs? and biennial? From mixed habitats.

Clubiona spp: *C. johnsoni* Gertsch, *C. abboti* L. Koch and *C. kastoni* Gertsch all present in the study area, having WA Js in mixed habitats.
LIT: *C. compta* L. Koch with WA Js and F (Flatz 1979).

Phrurotimpus borealis Emerton: Fs with eggs in Jan and summer months. Js and Fs OW. Eury with spring reprod and probably biennial. From the wood.
LIT: Adults seen May to July (Peck and Whitcomb 1978).

Scotinella (Phrurolithus) pugnata (Emerton): WA Fs. Spsten M and eury F; annual? from the wood.
LIT: *Phrurolithus festivus* (L. Koch) Ms May to July with June max and Fs May to Sept; sten M and eury F (Tretzel 1954).

THOMISIDAE:

Oxyptila conspurcata Thorell: Fs with eggs from April to July. Js and Fs OW. Sumsten M, eury F and probably biennial. From mixed habitats.

Oxyptila sincera canadensis Dondale and Redner: Fs with eggs June to Sept and in Nov. Js and Fs. OW. Sumsten M, eury F biennial (Fig. 7a). Mostly from the wood where moderately abundant, and less abundant in the ecotone.
LIT: *O. atomaria* (Panzer) with WA Ms (Flatz 1979) and dipl (Polenec 1962); and *O. brevipes* Hahn with WA Fs (Polenec 1962). *O. bryante* Gertsch with seemingly sumsten Ms, and Fs seen throughout warm months (Cutler *et al.* 1975). *O. trux* (Blw.) dipl with spring-summer reprod (Broen and Moritz 1963); Ms with a short early summer activity period (Merrett 1967); Ms April to Oct with a June max, Fs May to Oct (Palmgren 1950).

Xysticus emertoni Keyserling: Fs with eggs May and Aug. Js and pen Js OW. Sumsten and biennial. From mixed habitats.

Xysticus ferox (Hentz): Fs with eggs May and June. Apparently two size classes of Js OW. Sumsten and biennial (Fig. 7b). From mixed habitats, and a less abundant species in the meadow.
LIT: *X. cristatus* (Cl.) spsten (Schaefer 1971) and biennial (Toft 1976); Ms with prolonged spring-summer activity and Fs April to Oct (Merrett 1967); WA F (Flatz 1979). *X. erraticus* Blw. and *X. pini* Hahn with WA Fs, and the latter sten (Polenec 1962). *X. gulosus* Keys. and *X. pellax* (Cbr.) autsten and annual (Dondale 1977). *X. luctuosus* (Blw.) sumsten (Broen and Moritz 1963); *X. punctatus* Keys. with two generations of Js at all times of the year, i.e. biennial (Dondale 1961); *Xysticus* spp. generally sumsten (Cutler *et al.* 1975) and with WA Js (Flatz 1979).

PHILODROMIDAE:

Thanatus formicinus Clerck: Fs with eggs from May to July and in Sept. Two size classes of Js OW. Sumsten M, eury F and biennial (Fig. 7c). Mostly from open areas.
LIT: Ms May and June (max), Fs May to Aug with OW Js (Palmgren 1950). *Th. rubicellus* Mello-Leitão June to Oct with June-July reprod (Schmoller 1970). *Th. striatus* L. Koch sten (Palmgren 1950); adults May to July (Merrett 1967); and spsten and annual (Schaefer 1976).

Tibellus spp.: Both *T. oblongus* (Walckenaer) and *T. maritimus* (Menge) present in the study area. WA Js from open areas.
LIT: Js of *T. oblongus* taken throughout the year (Almquist 1969).

SALTICIDAE:

Neon nelli (Peckham and Peckham): Js OW. Eury? and annual? From the wood.

DICTYNIDAE:

Argenna obesa Emerton: Fs with eggs April, May and July. Js and adults OW. Eury with summer reprod? and biennial?
LIT: *A. subnigra* (Cbr.) Ms May to mid-July (Broen and Moritz 1965).