

LIFE HISTORIES AND DISTRIBUTION PATTERNS OF HUNTING SPIDERS (ARANEIDA) IN AN ONTARIO MEADOW

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ABSTRACT

Life histories and distribution patterns were reconstructed from random vacuum samples of coexistent populations of nine species of hunting spiders in an Ontario meadow. The populations of *Pardosa saxatilis* (Hentz), *Pirata minutus* Emerton, *Schizocosa avida* (Walckenaer), *S. heasmani* Dondale, and *S. crassipalpis* (Emerton) had annual life histories, and matured, mated, and oviposited in the spring or early summer. *Xysticus peltax* (O. Pickard-Cambridge) and *X. gulosus* Keyserling were also annual, but matured and mated in late summer or early autumn, and oviposited the following spring. *X. discursans* Keyserling was biennial, and matured and reproduced in the spring. *Lycosa frondicola* Emerton was also biennial, but matured in late summer and reproduced the following spring. Most of the nine species were more densely represented in the lower, moister part of the meadow, whereas *S. heasmani*, individuals of which are very similar in anatomy to those of *S. avida*, was more densely represented on the higher, dryer part, and the adults of *L. frondicola* kept largely to the edge of the meadow nearest the forest.

INTRODUCTION

Ideally, the life history of an animal species is a summary of vital events from birth to death in the average generation. Ball (1920) describes the adaptations to environment exhibited by life histories as "deep-seated and fixed modifications brought about through reaction to seasons unnumbered. . .". Wilbur, Tinkle, and Collins (1974) refer evocatively to these adaptations to environment as "selective compromises." The study of life histories leads not only to an intimate view of life within the population but also to new data useful in taxonomy and in population dynamics, particularly when coexisting populations are sampled together by a single method.

This paper examines the life histories and distribution patterns of coexistent populations representing nine species of hunting spiders in a meadow habitat. The species were selected from a large spider fauna (Dondale, 1971) on the basis of abundance and/or biomass. The combined populations of these species accounted for 56 percent of total estimated spider biomass in the meadow.

METHODS

The study site was a small, sloping, 0.8 hectare meadow near Belleville, Ontario (Turnbull, 1966; Dondale, 1971). Two 2,000 m² plots were staked out in 1966, Plot 1 on the higher, sandier part of the meadow and Plot 2 on the lower, clay-type part. Annually from 1966 to 1970 the surface litter and its spider inhabitants were sampled at 180 randomly-chosen spots, each spot being one-half m² in area (Turnbull and Nicholls,

1966). The samples were taken in nine series during the year, each series consisting of 20 samples on four consecutive days of fine weather. The earliest series of the year was taken as soon as snow left the meadow, i.e., approximately mid-April, and the latest one at the time of the first severe frosts, i.e., late October. The spiders were extracted from the litter samples by a method already described (Dondale, Nicholls, Redner, Semple, and Turnbull, 1971). Biomass measurements were obtained from specimens dried at 100°C for 24 hr.

Life histories were reconstructed partly from mean numbers and biomasses in the successive samplings, and partly from mean size of individuals as estimated from measurements of carapace width. Distribution patterns were inferred from plottings of the accumulated collection spots. Times of maturity were determined partly from pitfall captures or insectary cultures, as well as from vacuum samples.

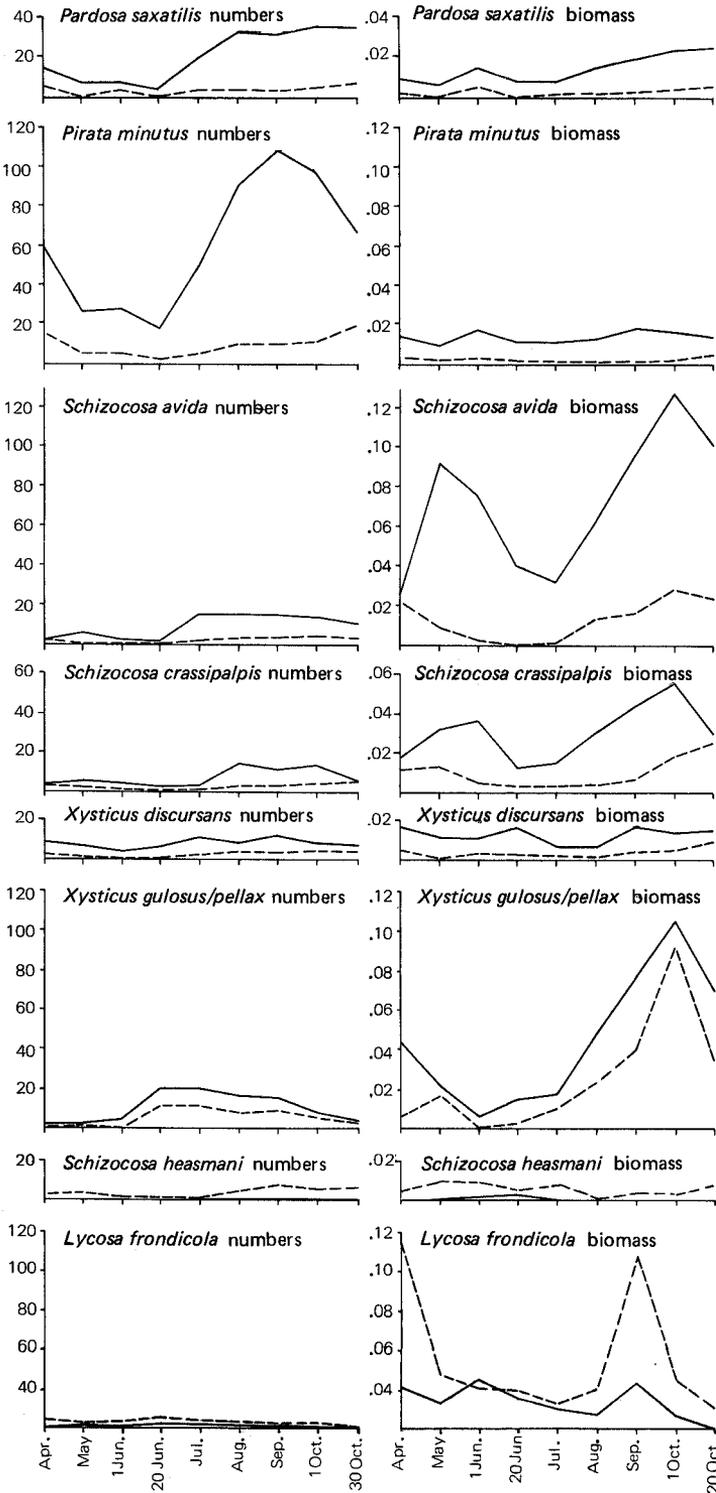
RESULTS

The number of vacuum samples on each five m² co-ordinate ranged from 2 to 21, with a mean of 11. This intense sampling over a relatively long period of time permitted reconstruction of life histories with reasonable confidence. For the annual species, four complete generations, and for the biennials, three (and parts of others) were traced. All nine species, with the partial exception of *Lycosa frondicola*, appeared to be true meadow inhabitants inasmuch as individuals could be found in all seasons in predictable numbers. They also fed and reproduced in the meadow.

Paradosa saxatilis (Hentz).—Eggs of this small lycosid began hatching in late June or early July and continued to hatch until August. The juveniles grew until early October when they had attained approximately one-half their mean total growth (Fig. 2). Growth resumed the following May, and the first adult males appeared toward the end of that month. The latter were observed in numbers until approximately the third week of June, thereafter dwindling until the last was sighted about mid-July. The first females appeared a few days after the first males, and the first mating pairs were seen in the field at that time. Females with egg sacs were seen early in June, and by early July most of them were carrying sacs or were carrying their young massed on their backs. The young were carried thus for periods up to one week. Many of the females then constructed a second sac. The last females of the season were seen in early September, at which time the population consisted entirely of half-grown to subadult individuals. The data give a clear picture of an annual life history, with maturity and reproduction in springtime.

P. saxatilis ranged in numbers from 0.8 to 4.4 individuals annually per m², but showed a progressive decline from 4.4 to 1.6, 2.0, 1.6, and 0.8 during the successive five years of the study. Distribution on the meadow was not random but biased toward the relatively moist Plot 2 (Fig. 4). A spider of eastern Canada and the eastern United States, *P. saxatilis* inhabits marshes, bogs, roadside embankments, lawns, and hayfields as well as meadows. The species is apparently at or near the northern limit of its range at Belleville, and this may account for an apparent mean decline in numbers amounting to approximately one-half the autumn population during the winter (Fig. 1). *P. saxatilis* contributed little to total spider biomass owing to the small mean size of individuals at maturity (Fig. 2).

Fig. 1.—Mean annual population densities (number per 10 m²) and biomasses (mg per 10 m²) for populations of nine species of hunting spiders in Ontario, 1966-70. Broken line: Plot 1; solid line: Plot 2.



Laboratory matings were observed on 18 occasions, but egg production, for unknown reasons, was poor. Field-caught females with egg sacs had 27 to 32 (mean 30) eggs in the first sac and 16 to 29 (mean 21) eggs in the second. Overwintered juvenile males molted two or three times (usually two) before attaining maturity, females one to three times (usually three).

Pirata minutus Emerton.—Hatching of the eggs of this small lycosid usually began in late June, at which time females were found with young massed on their backs. Occasional females with sacs were, however, seen until October. The young grew until September or October, at which time they had attained approximately 70 percent of their mean total growth (Fig. 2). Most individuals of both sexes at this time lacked only one molt to maturity. They resumed growth the following April or early May, and the first males

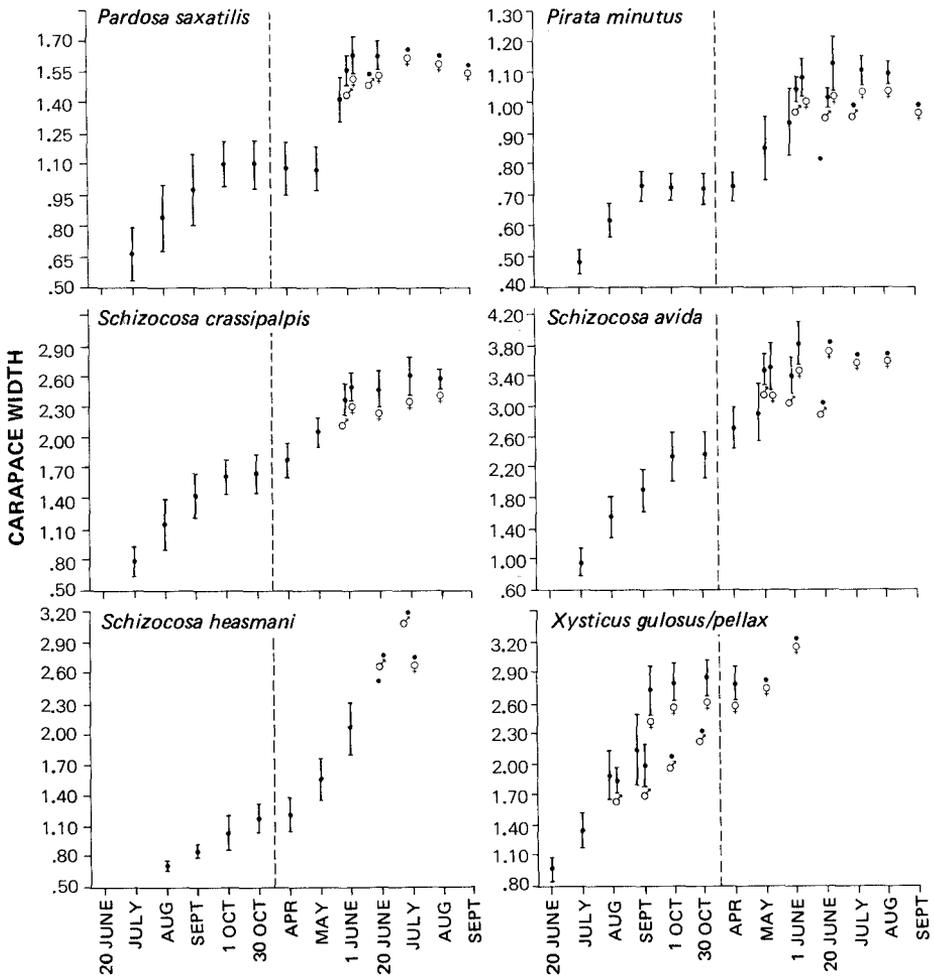


Fig. 2.—Seasonal growth in populations of seven species of annual hunting spiders in Ontario, 1966-70. Y-axis scaled in mm of carapace width; broken vertical line indicates winter; solid vertical line indicates 1 standard deviation about the mean. Number of individuals measured varied from 13 to 107 for any date.

appeared as early as 19 May. The peak of male activity occurred at the end of May or the beginning of June; the last male was seen on 19 August. Females appeared a few days after the first males, and were soon seen mating. Females with egg sacs appeared as early as the second week of June. Most females seen during late June were carrying sacs. The total number of sacs made by a female was not determined owing to the growing scarcity of females in the field and the lack of success with insectary cultures. The available data indicate an annual life history for *P. minutus* in Ontario, with maturity and reproduction in springtime.

The population of *P. minutus* ranged in annual abundance from 3.2 to 11.5 individuals per m². In spite of this density, the population contributed very little biomass (Fig. 1) owing to small mean size of the individuals at maturity (Fig. 2). Both numbers and biomass peaked in September, then declined (Fig. 1).

The population was more heavily represented on the relatively moist Plot 2 (Fig. 5), and in general the individuals kept close to the ground. Found on sphagnum bogs and similarly cool, moist habitats, this spider ranges over eastern Canada and New England. The overwintering population appeared to suffer no appreciable loss, though approximately two-thirds of the wintered population was lost before the commencement of egg hatch. Some 19 laboratory matings were observed, 11 of which terminated by the death

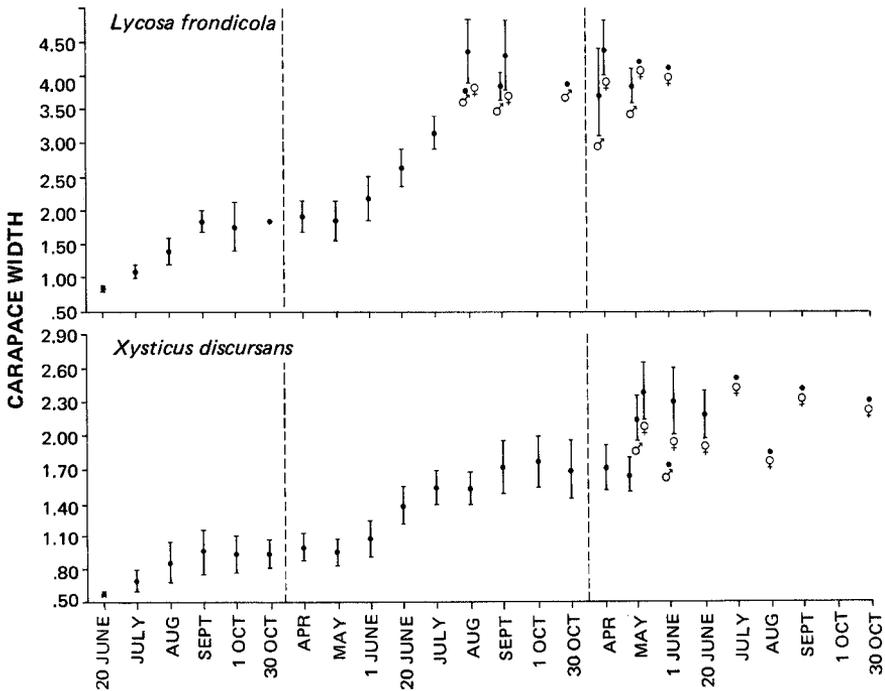


Fig. 3.—Seasonal growth in populations of two species of biennial hunting spiders in Ontario, 1966-70. Y-axis scaled in mm of carapace width; broken vertical line indicates winter; solid vertical line indicates 1 standard deviation about the mean. Number of individuals measured varied from 14 to 57 for any date.

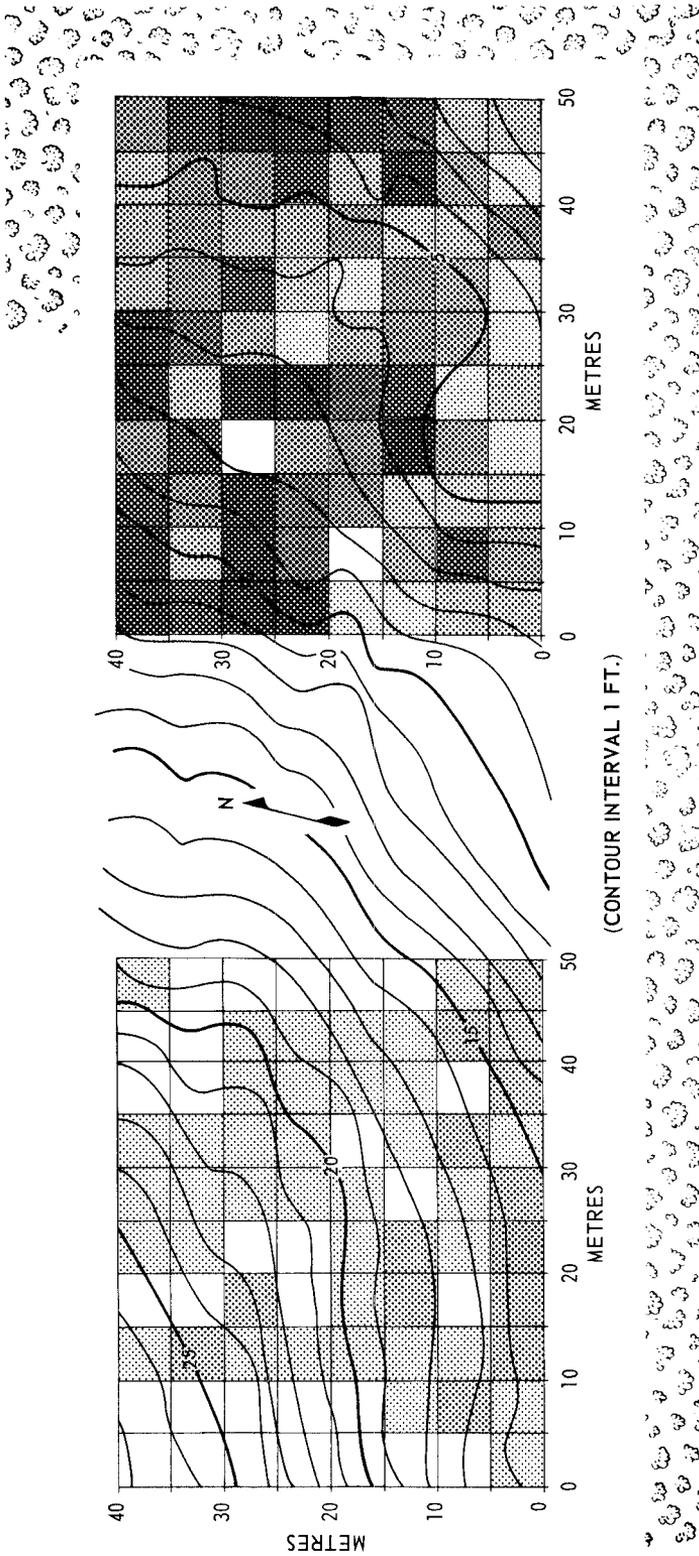


Fig. 4.—Frequency of collections of individuals of *Pardosa saxatilis* (Hentz), 1966-70. Frequency ranged from 0 (no stippling) to 33 (densest stippling) for any 5-m² quadrat.

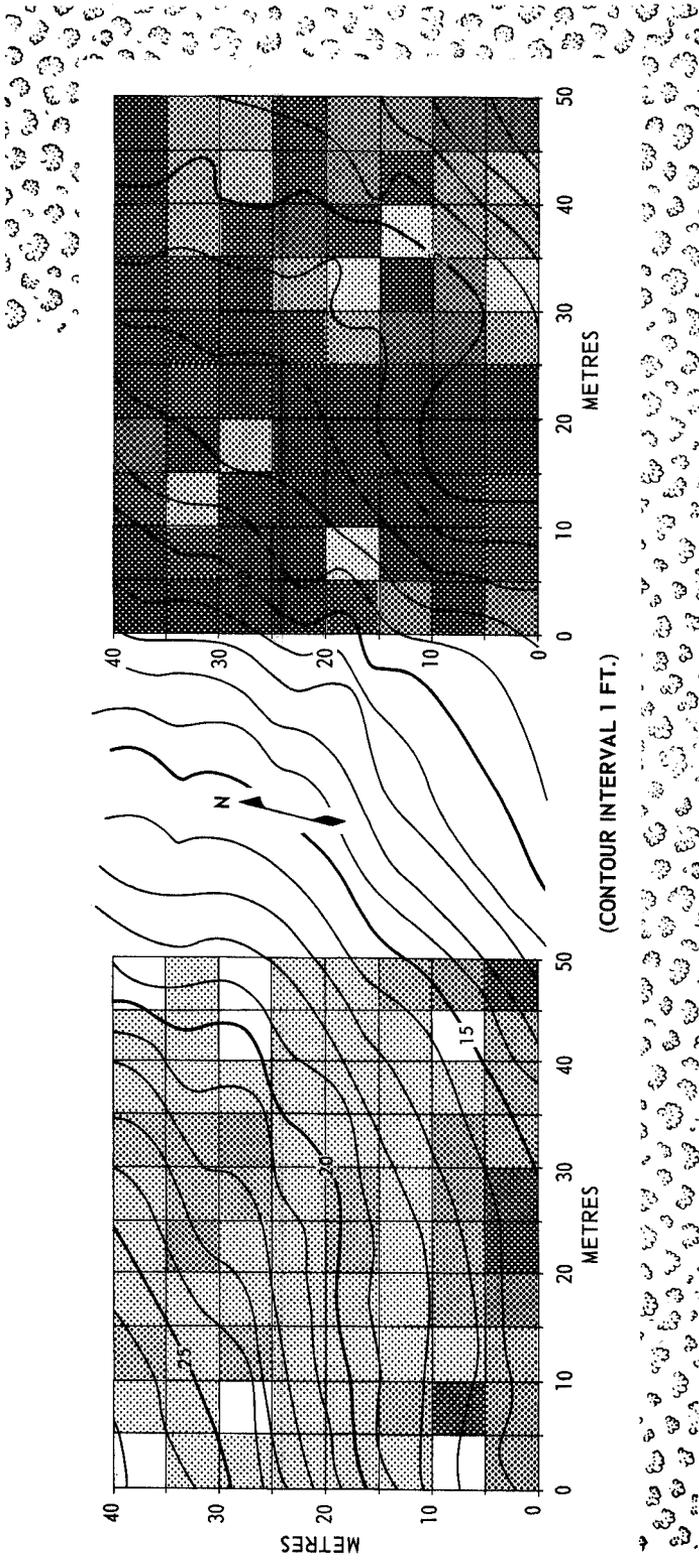


Fig. 5.—Frequency of collection of individuals of *Pirata minutus* Emerton, 1966-70. Frequency ranged from 0 (no stippling) to 130 (densest stippling) for any 5-m² quadrat.

and ingestion of the male by the female. None of these mated females laid eggs. Nineteen field-caught females had egg sacs containing 10 to 40 (mean 24) eggs.

Schizocosa avida (Walckenaer).—Egg hatch in this medium-sized lycosid commenced about 20 June and continued till late August, though most occurred during July. The young spiderlings grew until late September, at which time they had attained somewhat more than one-half of their mean total growth (Fig. 2). Activity and growth resumed the following April. Juvenile males brought indoors at this time molted only once to maturity. The first males were seen in the field about mid-May, and the last about 29 June, with a peak of activity in late May and early June. Females first appeared a few days after the first males; mating ensued, and females continued to be sighted until nearly mid-June when none appeared for an interval of 10 days. They were then seen again, carrying egg sacs or young until about mid-July, when sightings ceased for a second 10 day interval. After this, females were seen sporadically until the third week of August.

The two intervals of quiescence in mature females were studied in insectary cultures. Both coincided with times of low activity during which the females were ovipositing and incubating their eggs in shallow (approximately 2 cm deep) nestholes in the ground. On sunny days they were frequently seen holding the sac at the mouth of the hole with the chelicerae or, less frequently, standing over the hole with the sac attached to the spinnerets. At the end of the quiescent period the egg sac, now empty, was often left at the bottom of the hole.

The data indicate an annual life history for *S. avida*, with maturity and mating in the spring.

The population was at low density and appeared to be in decline. Mean annual levels of 1.5, 1.3, 1.0, 0.7, and 0.5 individuals per m² were recorded, respectively, for the five years of the study. Distribution was biased toward the moist Plot 2 (Fig. 6). The species ranges widely across southern Canada and the United States, its main habitat being open grassland. The population, in spite of low density, accounted for a large amount of biomass (Fig. 1).

Laboratory matings and ovipositions were observed in 24 instances. The females made either one or two egg sacs, the first containing 69 to 191 (mean 113) eggs, the second 49 to 59 (mean 54). In addition, seven gravid females were dissected and found to contain 90 to 298 (mean 205) oöcytes in various stages of development.

The annual curve of biomass (Fig. 1) showed two peaks, a steep one in May when the spiders were growing rapidly in the penultimate instar, and a second one, less steep but higher, at the beginning of October when growth came to a halt before hibernation. The sharp decline that followed the spring peak was tentatively attributed to attrition of the population through predation; the autumn decline is unexplained.

Schizocosa heasmani Dondale.—Eggs of this medium-sized lycosid began to hatch in late July. The spiderlings attained about 40 percent of their total growth by October. Growth resumed the following May, and subadults of both sexes were seen as late as 12 June. The first adult males were observed at mid-June; of 30 males caught in pitfall traps in 1967, most appeared between 18 June and 14 July, the final one being taken that year on 19 July. Females appeared a few days after the first males, and mating commenced at once. Females were present until nearly mid-August. A few individuals were reared in the laboratory: first instars from the field or from laboratory hatchings in September molted once monthly from September to December, and a final time before maturity in January or later. The photoperiod used in these cultures was 16 hr of light and eight hr of dark. Only males survived to maturity. Five laboratory matings were observed. The females

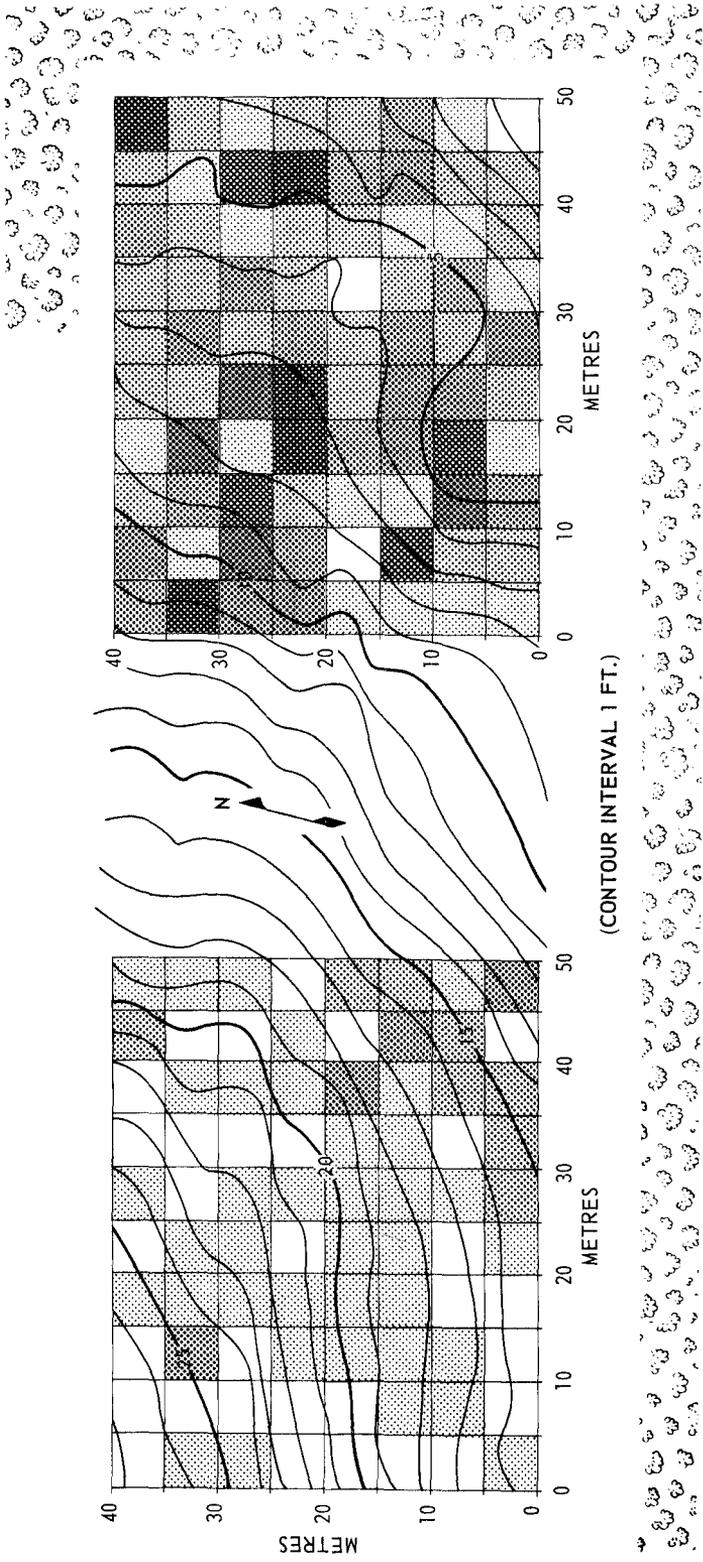


Fig. 6.—Frequency of collection of individuals of *Schizocosma avida* (Walckenaer), 1966-70. Frequency ranged from 0 (no stippling) to 17 (densest stippling) for any 5-m² quadrat.

made one or two egg sacs containing 110 to 176 eggs in the first and about 85 eggs in the second.

Although based on a small and rather variable population, these data indicate an annual life history for *S. heasmani*, with maturity in late spring or early summer.

Both population density and biomass were low (Fig. 1). The species is poorly known biologically owing to this fact and to the recency of its recognition as distinct from *S. avida*. Specimens of these two species are distinguishable only on subtle differences in anatomy, behavior, and ecology (Dondale, 1969). Whereas the majority of captures of *S. avida* (and of *S. crassipalpis*), for example, were made on the relatively moist Plot 2, the majority of captures of *S. heasmani* were made on the dryer Plot 1 (Fig. 7). The physiological mechanism by which this preference is effected has not been investigated.

Schizocosa crassipalpis (Emerton).—Hatching of the eggs of this medium-sized lycosid commenced between early and mid-July and continued till the end of August. The spiderlings attained approximately 50 percent of their mean total growth by the end of September, when growth ceased for the season (Fig. 2). They resumed activity and growth the following April, and large juveniles were seen as late as 11 May. There was then a period of near-zero sightings of these subadults until the appearance of the first mature males about 21 May. Males were present in numbers until mid-June, after which they disappeared rapidly, the last one being seen on 29 June. The first females appeared a few days after the first males, and mating commenced at once. Females were seen until approximately 20 June (in 1967), after which there was a 10-day lull; they then reappeared until 20 July, and a second lull occurred. The last female was sighted that year on 24 August. The periods of low adult activity were associated with oviposition, as in female *S. avida*. Several females were found in shallow nestholes during these times. Females made one or two egg sacs, the first containing 36 to 74 (mean 50) eggs, the second 17 to 43 (mean 26) eggs. *S. crassipalpis* is annual, with maturity and mating in the spring.

Mean annual density of the population of *S. crassipalpis* on the meadow varied from 0.5 to 0.9 per m² during the course of the study. In spite of this low density, biomass was relatively high (Fig. 1) owing to the moderately large average size of mature individuals of this species. Found in the Great Lakes region and northern New England, *S. crassipalpis* appears to be a true grassland spider. The meadow population showed the same distribution pattern as that of *S. avida*, but differed from the pattern for *S. heasmani* (Figs. 7, 8). The peak of male activity for *S. crassipalpis* occurred one or two weeks later than that for *S. avida*, and approximately three weeks earlier than for *S. heasmani*.

Xysticus pellax (O. Pickard-Cambridge) and *X. gulosus* Keyserling.—Egg hatch in these thomisids commenced early in June. The juveniles grew rapidly, as indicated by the curve of seasonal biomass (Fig. 1), adults appearing approximately three months later (Fig. 2). In 1967, the year in which most pitfall trapping was done, males of *X. pellax* appeared from 18 August to 26 September, and males of *X. gulosus* from 30 August to 31 October. Females were rarely trapped, those of *X. pellax* appearing from early September to mid-October, and those of *X. gulosus* from late September to late October. Mating occurred in the autumn, and only females of these species were seen the following spring. Females with egg sacs were found deep in the grass litter of the meadow in May and early June. The available data indicate an annual life history, with maturity and mating in late summer or early autumn, and with oviposition the following spring.

Individuals of these two species are extremely similar to each other, and we were able to separate only the adults. Turnbull, Dondale, and Redner (1965) reported that adults of

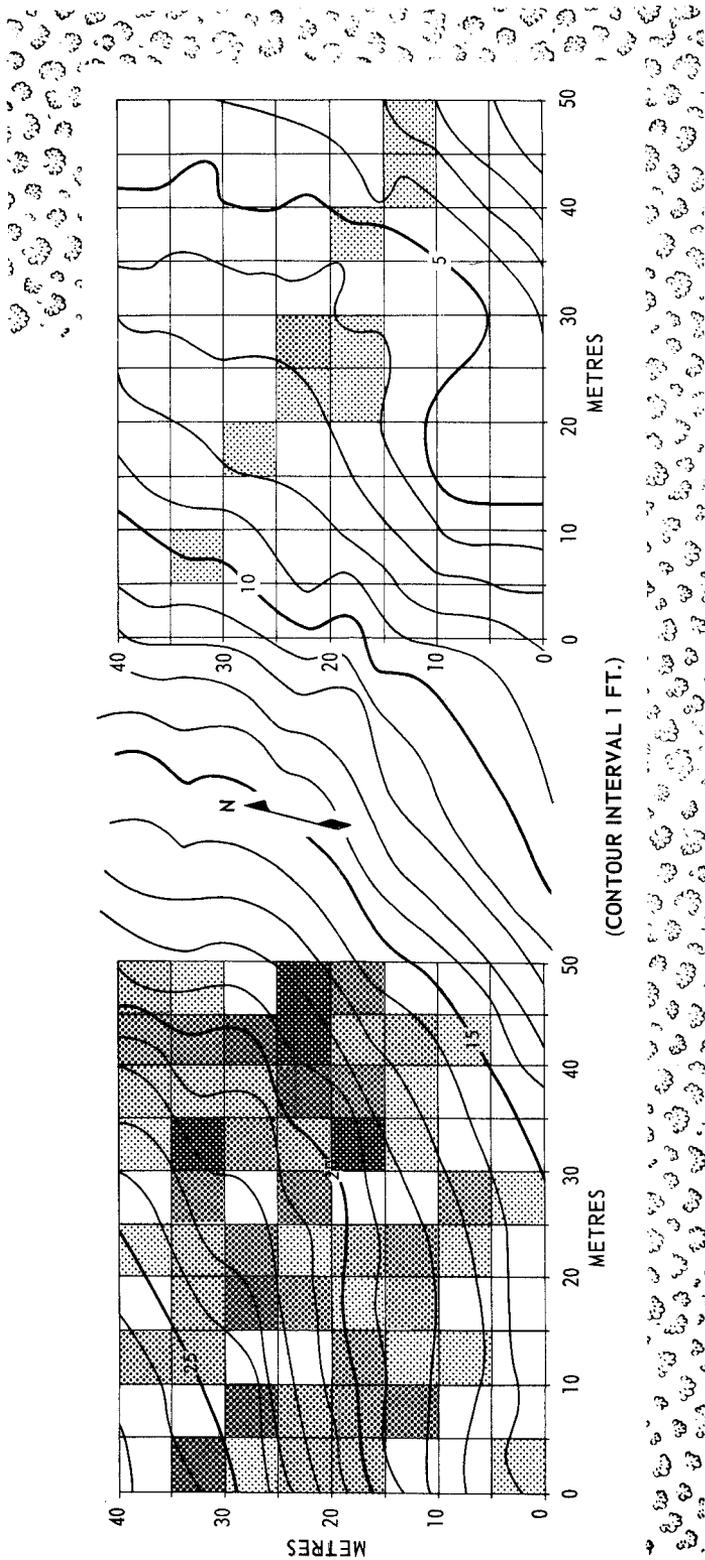


Fig. 7.—Frequency of collection of individuals of *Schizocosa heasmani* Dondale, 1966-70. Frequency ranged from 0 (no stippling) to 12 (densest stippling) for any 5-m² quadrat.

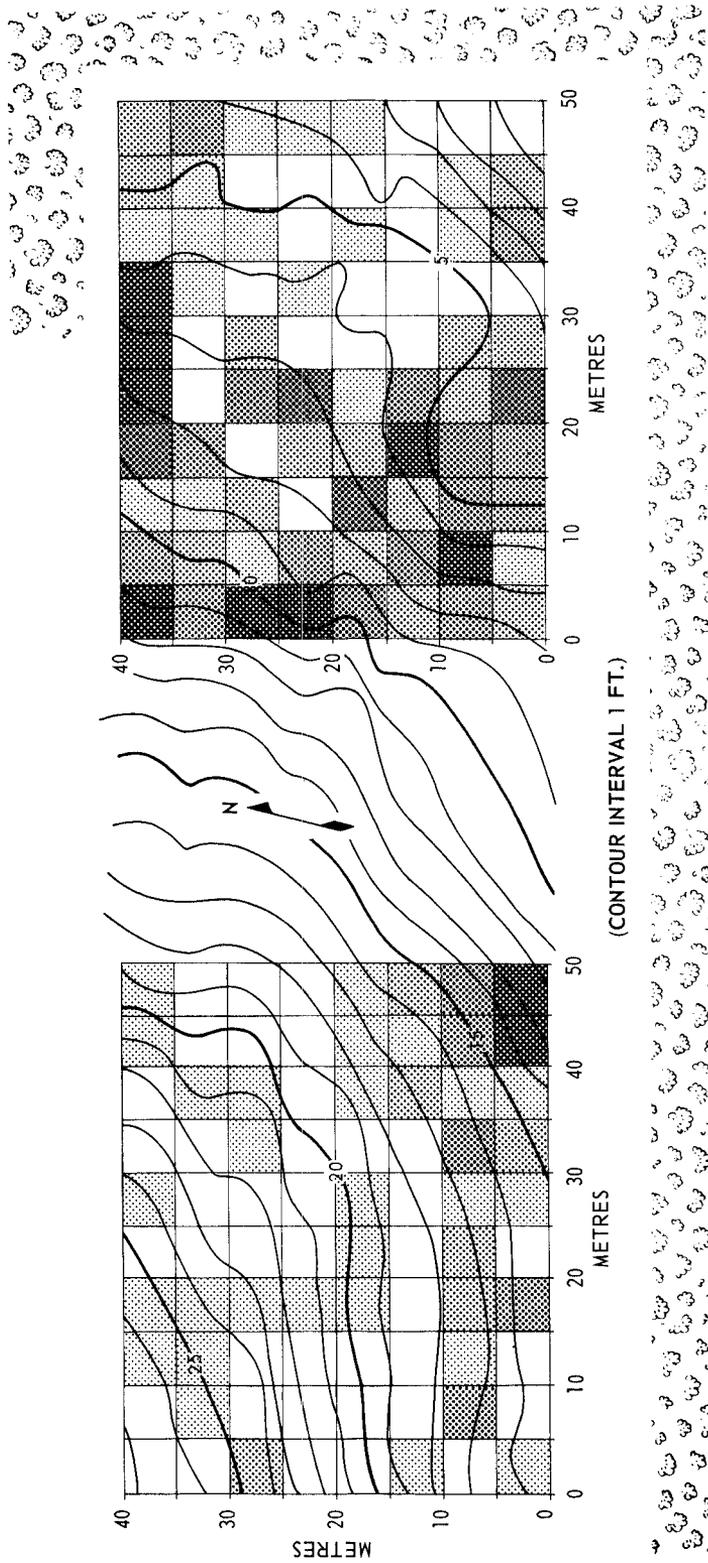


Fig. 8.—Frequency of collection of individuals of *Schizocosa crassipalpis* (Emerton), 1966-70. Frequency ranged from 0 (no stippling) to 19 (densest stippling) for any 5-m² quadrat.

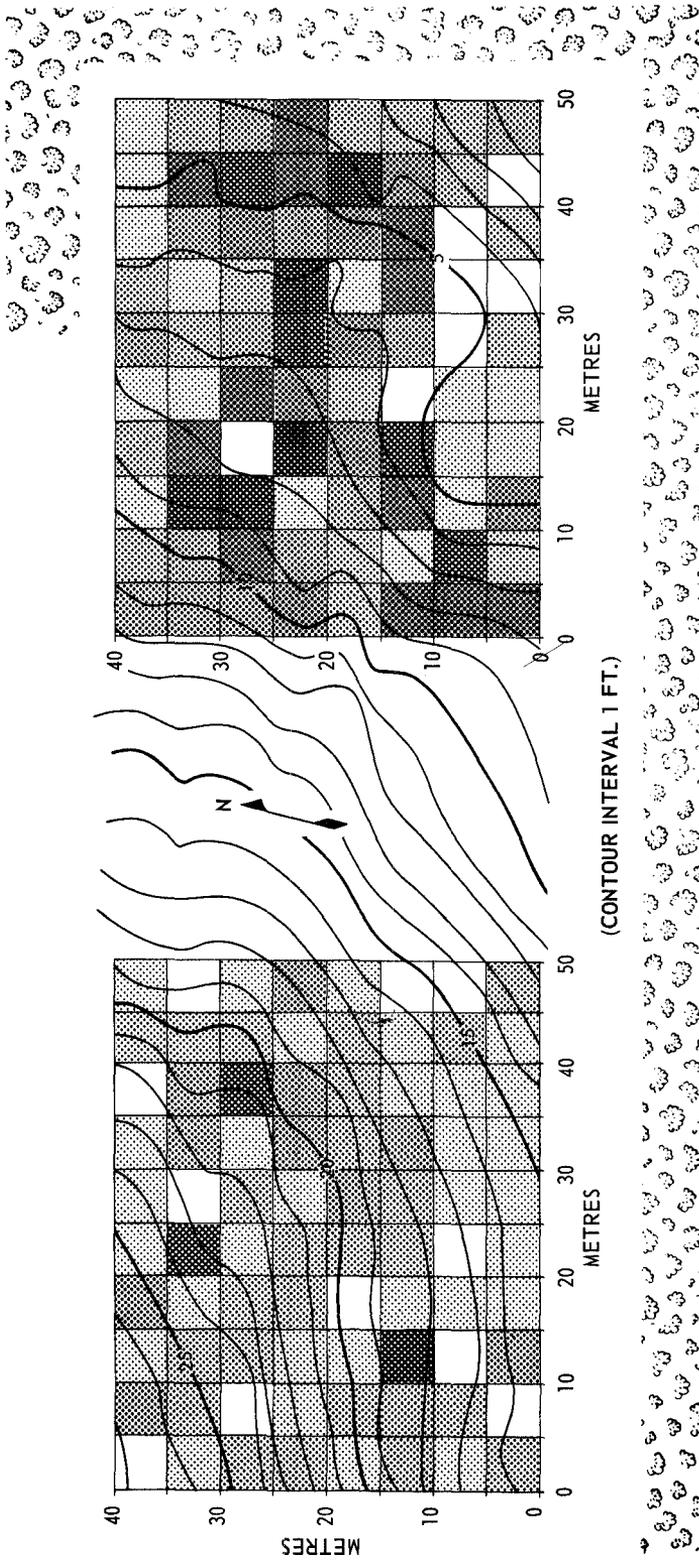


Fig. 9.—Frequency of collection of individuals of *Xysticus pellax/gulosus*, 1966-70. Frequency ranged from 0 (no stippling) to 20 (densest stippling) for any 5-m² quadrat.

X. pellax had only been collected in pitfall traps whereas those of *X. gulosus* were taken on substrates above the ground. This was later refuted, as adults of both species were taken together in pitfall traps (Dondale, 1971; Sauer, 1972). Individuals (both species treated as one) occurred in somewhat greater frequency on Plot 2 than on Plot 1 (Fig. 9).

Both species range from the arid plateaus of northern Mexico to southern Canada (Turnbull, Dondale, and Redner, 1965). It is possible that their life histories reflect adaptation to a brief rainy season followed by a long, dry one such as is found in the southern part of the range. Oviposition there would coincide with the onset of rain, and development of the young and mating would be completed before the dry season began. Mated females would survive the dry season, which, in more northerly latitudes, becomes the cold season.

The combined annual population density of the two species in the meadow was very low, though autumnal biomass was fairly high owing to the population's adult composition (Fig. 1). The sudden decline in biomass during October signified the disappearance of the males. There may also have been winter mortality of females.

Xysticus discursans Keyserling.—Hatching of the eggs of this thomisid commenced in June. The juveniles grew until September, at which time they had attained approximately 40 percent of their mean total growth (Fig. 3). They resumed growth the following May or early June, and had attained the subadult stage by September, when growth again ceased. These subadults became active the following May, and adults appeared during that month, i.e., some 23 months after the spiders of that generation hatched. Males were present from 3 May until 4 July. Females appeared about 12 May, when mating commenced, and were found until October, though most appeared from mid-May to approximately 20 June. Oviposition is presumed to have occurred during late spring.

The five years' collections from the population of *X. discursans* are grouped to show a single generation from hatching to death (Fig. 3), though in fact a new generation hatched, and an older one matured and mated, each spring. Hence there were two subpopulations, separable statistically from each other on mean carapace width, representing two generations in the field throughout autumn, winter, and the early spring; these were (1) the small individuals that hatched during the past year, and (2) subadults that had hatched two years earlier. In the same way, there were three subpopulations representing three generations during the summer months; these were (1) newly hatched spiderlings, (2) the half-grown juveniles that had hatched the previous year, and (3) the parents of the newly hatched. From these facts we can deduce a biennial life history for *X. discursans* in Ontario, with maturity and mating in the spring.

The population of *X. discursans* was consistently low in the meadow (Fig. 1), averaging 1.1 individuals per m² or less annually, and most captures were from Plot 2 (Fig. 10). The species ranges widely in North America, and its habitat appears to be grassland and open woodland (Turnbull, Dondale, and Redner, 1965).

Lycosa frondicola Emerton.—Hatching in this medium-sized lycosid began in June. The young spiderlings grew until early September, at which time they had attained approximately 40 percent of mean total growth (Fig. 3). They resumed activity and growth the following spring and matured in August of that year. Adult males were found from 30 July through late summer and autumn, and again the following April, May, and June, the greatest numbers appearing during the last week of April and the first week of May. Adult females appeared from early August through late summer and autumn, and again from April to early July. The mating period was not determined precisely, though it is presumed to have occurred during the period of peak male activity. One mating took

place in the laboratory in December, under a 16 hr photoperiod. Gravid females were found in shallow nestholes in the ground in early May, and females with newly-hatched young on their backs were seen during the third week of June. A single egg sac was opened on 16 June and was found to contain 97 eggs.

The meadow population of *L. frondicola* fell into two size groups, which indicated two different generations, in the field during autumn, winter, and early spring. These were (1) half-grown juveniles that had hatched the previous spring, and (2) adults that had hatched two years previous. Similarly, there were three generations during the summer. One generation matured and reproduced each year. These facts indicate a biennial life history for *L. frondicola* in Ontario, with maturity occurring in late summer and reproduction the following spring.

Mean annual population density of *L. frondicola* was low during the course of the investigation, though the adults produced strong peaks of biomass in autumn and spring, particularly on Plot 1 (Fig. 1). The decline in biomass just before winter suggests that the adults vacated the meadow for other wintering sites, returning early the following spring. It was suspected that adults were restricting their activity to the southern and eastern margins of the meadow near the forest edge whereas the young were more randomly distributed. The cumulative collections confirmed this (Figs. 11, 12). Such spatial separation between adults and young may confer a survival advantage on the population of *L. frondicola*, though this is partly speculation until more fully investigated.

L. frondicola ranges from the Rocky Mountains to eastern Canada and New England. It occupies both grassland and open woodland, and mature individuals may spend time in both kinds of habitat.

DISCUSSION

The literature dealing with the life histories of hunting spiders in temperate latitudes indicates that in many species hatching, development to maturity, and reproduction are accomplished in approximately one year. In this category belong the lycosids *Pardosa lugubris* (Walckenaer) (Edgar, 1972), *P. ramulosa* (McCook) (Yeargan, 1974), and *Pirata subpiraticus* (Boesenberg and Strand) (Hamamura, 1971), and the salticid *Metaphidippus protervus* (Walckenaer) (Dondale, 1961). It should be noted, however, that temperature regimes can influence this; in *P. lugubris*, part of the Dutch population requires two years to reach maturity rather than one (Edgar, 1972), and in Scotland, where summers are brief and cool, the population of *P. lugubris* is completely biennial (Edgar, 1971a, 1971b). Other examples of this temperature effect are found in the philodromid genus *Philodromus* (Dondale, 1961; Putman, 1967; Almquist, 1969), as well as in several other families (Almquist, 1969). *Pardosa pseudoannulata* (Boesenberg and Strand), on the other hand, is said to have two or more generations per year in Japan, and to be capable of continuous development in greenhouse cultures (Kawahara, Kiritani, and Kakiya, 1974).

It is among the species of lycosids of which the individuals grow to medium or large size that we often find an apparently consistent biennial life history. Individuals of *Tarentula kochi* Keyserling, for example, hatch in the spring, reach sixth instar by the first autumn of life, and mature the succeeding autumn, in California (Hagstrum, 1970). Essentially the same pattern occurs among species of *Trochosa* (Hackman, 1954; Engelhardt, 1964) and of *Geolycosa* (Kurata, 1939; Wallace, 1942; McCrone, 1965). McCrone (1965) points out that in some parts of Florida the population of *Geolycosa patellonigra* Wallace mates in the spring, in other parts in the autumn, and in a few others in either

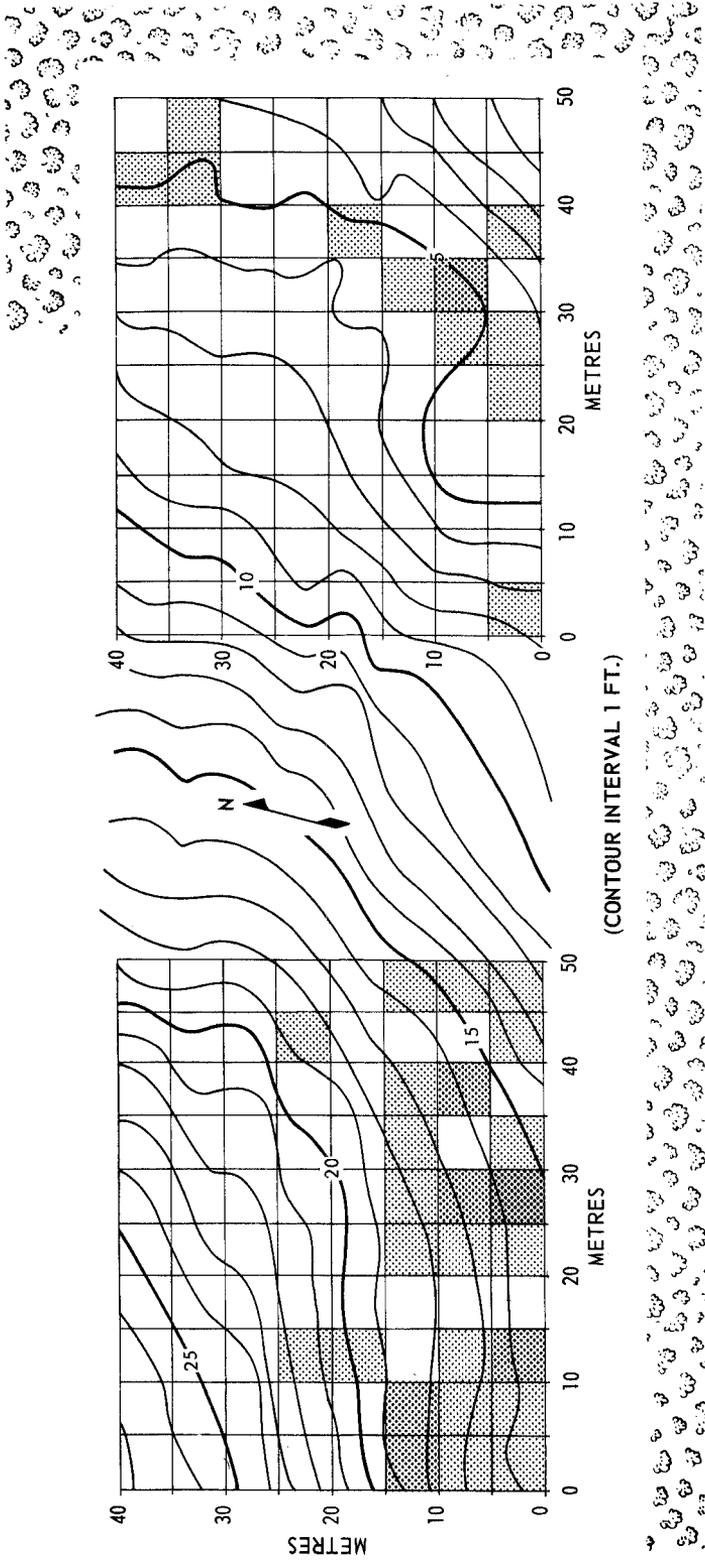


Fig. 11.—Frequency of collection of adults of *Lycosa frondicola* Emerton, 1966-70. Frequency ranged from 0 (no stippling) to 5 (densest stippling) for any 5-m² quadrat.

time of year, according to individual. McCrone was unable to separate the seasonal forms on any anatomical characters. Eason and Whitcomb's (1965) claim that *Lycosa rabida* Walckenaer and *L. punctulata* Hentz are annuals needs supportive field data.

The Ontario populations studied by us are either annual (*Pardosa saxatilis*, *Pirata minutus*, *Schizocosa avida*, *S. heasmani*, *S. crassipalpis*, *Xysticus pallax*, *X. gulosus*) or biennial (*X. discursans*, *Lycosa frondicola*). In most of them, maturation, mating, and oviposition occur in spring, though *X. pallax* and *X. gulosus* mature and mate in late summer or autumn and oviposit the following spring, and *L. frondicola* matures in late summer and mates (probably) and oviposits the following spring. It appears, then, that hunting spiders are generally either annual or biennial according to species, with some modification by temperature, and that within both categories there may be spring or autumn maturity. In autumn maturing species, either annual or biennial, mating may occur in autumn or spring, but oviposition is always delayed until spring.

The seasonal separation of maturity times permits greater species diversity in a given habitat, as interaction between coexisting populations would decrease survival. Differences in diel activity periodicities among populations, and among the stages of a single population, can further reduce the possibility of destructive interactions (Dondale, Redner, and Semple, 1972). The separation of peak mating times by a few weeks in *X. pallax* and *X. gulosus* and in the three species of *Schizocosa* coexisting in the meadow suggest that survival is promoted when interaction is minimized, particularly at mating time.

Species diversity may also be promoted by the occupation of different microhabitats by different populations within a single habitat. Kuenzler (1958) suggested that *Lycosa rabida* is separated from the sympatric *L. timuqua* Wallace and *L. carolinensis* Walckenaer by the acrobatic shrub foraging of *L. rabida* and the small home ranges of *L. timuqua* and *L. carolinensis*, both of the latter being burrowers. Vlijm and Kessler-Geschiere (1967) studied the spatial factors that separate three coexisting populations of *Pardosa*: *P. pullata* (Clerck) was most abundantly represented on damp, vegetated ground, *P. nigriceps* (Thorell) was dominant in the plant layer, and *P. monticola* (Clerck) was virtually restricted to dry, bare ground. Richter, Hollander, and Vlijm (1971), working with populations of *P. pullata* and *P. prativaga* (L. Koch), individuals of which are extremely similar and which are even believed to interbreed to some extent in nature, found that the populations tended to restrict their activities respectively to open grassland and to "transition areas." There were additional differences in courtship, rate of development, longevity, and in the ability to disperse on wind currents. Hallander (1970) similarly found that individuals of *P. pullata* showed affinity for short grass, sphagnum, or open marshes where the relative humidity was 90 to 100 percent and temperatures fairly cool, whereas individuals of the sympatric *P. lugubris* preferred leaf litter where the relative humidity was 60 to 90 percent and temperatures warmer. Duffey (1962) reported a partial difference in the vertical strata occupied by individuals of *P. pullata* and *P. nigriceps*, the former close to the ground and the latter several centimetres above ground level. Edgar (1971b) described a series of spatial (and temporal) adaptations among the stages of *P. lugubris* whereby movement between the woodland perimeter and adjacent grassy clearings apparently reduced the possibility of cannibalism.

Vogel (1972a) described a series of "habitat mosaics" in the mountains of Colorado in which populations of seven species of *Pardosa*, each representing a different species group, develop and move about, showing for the most part slight preferences for different levels of moisture or altitude, or of time of adult appearance. She also studied three other

species of *Pardosa*, populations of which coexist in dry, grassy hillsides. These were more puzzling, however, and no separating factors were identified; moreover, the three were members of a single species group. In a second study, Vogel (1972b) found that the amount of cover afforded by grass or fallen leaves apparently determined which of two species of *Pardosa* was the more abundantly represented in a particular area. Rich plant cover was associated with the presence of individuals of *P. falcifera* F. Pickard-Cambridge, poor cover with those of *P. sternalis* (Thorell), and intermediate cover with individuals of both species in varying proportions.

The spatially separating factors that we have deduced for various hunting spiders in the present study are of the same kinds as those just reviewed. The species pair *Schizocosa avida* and *S. heasmani* affords the best example: the majority of individuals of *S. avida* were caught on Plot 2, where the soil was moist and the plant cover relatively thick and diverse, whereas the majority of individuals of *S. heasmani* were caught on Plot 1, where the soil was sandy and dry, and the plant cover sparser and more simple. The preference of adults of *Lycosa frondicola* for the edge of the meadow close to the forest, in contrast with the juveniles, which were taken more randomly on the meadow, is equally interesting and invites further investigation.

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