

LIFE-CYCLES OF FOUR SPECIES OF *PARDOSA* (ARANEAE, LYCOSIDAE) FROM THE ISLAND OF NEWFOUNDLAND, CANADA

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ABSTRACT. Populations of four species of *Pardosa*, *P. fuscula*, *P. groenlandica*, *P. hyperborea* and *P. moesta*, were sampled during summer 1997 on the west coast of the Island of Newfoundland, Canada. Measurements of carapace width indicated that all four species fit a biennial life-cycle model where new individuals join the population in summer, live through the following winter, grow throughout the next year, live through the next winter, and then mature, breed and die in the year following their second winter. All species showed only one defined recruitment of new spiderlings during the sampling period, but at least two species may have extended periods of recruitment and some individuals may have an extended life-cycle.

Keywords: Lycosidae, *Pardosa*, life-cycle

At the beginning of the 20th century the conventional wisdom about araneomorph spider life-cycles was that most were annuals, either spring breeders or summer-autumn breeders (Emerton 1902). Palmgren (1939) provided one of the first exceptions when he described the two-year cycle of *Dolomedes fimbriatus* (Clerck 1757) where juveniles overwintered twice. Cloudsley-Thompson (1955) concluded that individuals of all three British species of *Amaurobius* C. L. Koch 1837 lived for about two years, overwintered twice, and spent their second winter as adults. Hackman (1957) described a similar two-year cycle for *Trochosa ruricola* (De Geer 1778). Dondale's (1961) seminal work presented quantitative data for five species of spiders in Nova Scotia, Canada: *Araniella displicata* (Hentz 1847), *Philodromus rufus* Walckenaer 1826, *P. cespitum* (Walckenaer 1802) and *Eris militaris* (Hentz 1845) were shown to be true biennials, while *Pelegrina proterva* (Walckenaer 1837) was annual. He also concluded that nine other widespread and abundant spiders were biennials. In the last decades of the 20th century a number of studies have not only clearly demonstrated annual and biennial life histories for several different species, but also reported permutations of these two basic life-cycles. That is, within these two general categories there are species that mature and breed at different times of year and species that are

intermediates between strictly annual and strictly biennial (e.g. Eason & Whitcomb 1965; Toft 1976, 1979; Dondale 1977; Stratton & Lowrie 1984).

In addition to such permutations of the annual/biennial theme, the plasticity of spider life history has been demonstrated. For example, the same species may change from annual to biennial depending on geographical location, such as *Philodromus cespitum* that was annual on the warmer Niagara Peninsula, Ontario, Canada (Putman 1967), but biennial in colder Nova Scotia, Canada (Dondale 1961). *Pardosa lugubris* (Walckenaer 1802) was annual in the Netherlands (Vlijm et al. 1963) but biennial in Scotland, and this was attributed to differences in summer temperatures (Edgar 1971a, 1972). In addition, individuals of the same population may extend their life-cycle under particular circumstances. Edgar (1972) showed that *P. lugubris* in the Netherlands varied between annual and biennial depending on environmental conditions. Workman (1978) showed that in Norfolk, U.K., *Trochosa terricola* Thorell 1856, usually biennial with the second overwintering as adults, was occasionally triennial when juveniles hatched from late or second cocoons overwintered three times before breeding in their fourth year. Leech (1966) suggested that even more extended life-cycles may occur in particularly cold conditions. He surmised that two species

from Hazen (Ellesmere Island, NWT, Canada), *Pardosa glacialis* (Thorell 1872) and *Allopecosa exasperans* (O. Pickard-Cambridge 1877), had a life-span of six or seven years, but that surmise was based on the unsupported assumption that each of the estimated six or seven instars lasted one year. These points raise a number of questions. Do spider species not yet examined have similar life histories to those already described? Do species in places not yet examined have similar life histories to those in known places? Do species at latitudes farther north than some of those previously examined show extended life histories, for example intermediate between those documented in Nova Scotia (Dondale 1961) and those hypothesised on Ellesmere Island (Leech 1966)?

The Island of Newfoundland is an appropriate location to examine these questions. The life histories of the species in this study have not been described before with the following exceptions. Ricards (1967) reported the life history of what he called *P. groenlandica* (Thorell 1872) in Montana, and Schmoller (1970) reported on what he called *P. tristis* Keyserling 1887 (identified as *P. groenlandica* by Dondale 1999) in Colorado. But as Dondale (1999) pointed out, both authors were in fact dealing with complexes of two or more species, not monospecific populations of *P. groenlandica*, so their conclusions have limited significance. Buddle (2000) reported the life-cycle of *Pardosa moesta* Banks 1892 in Alberta, and his observations are directly relevant here. Life histories of spiders on the Island of Newfoundland have essentially never been investigated. Hackman (1954) reported 220 species from the Island, but drew conclusions for only one: *Trochosa terricola* was described as biennial, although the data presented could support other interpretations.

The present study sites on the Island of Newfoundland, at approximately 50°N, are farther north than previous life history work with the following exceptions. Buddle (2000) and Zimmerman & Spence (1998) reported life-cycles of lycosids and a pisaurid, respectively, from approximately 54°N in central Alberta. However, both these studies were conducted at the George Lake area dominated by hardwoods such as aspen (indicative of higher summer temperatures) in the boreal transition region, whereas the present study was con-

ducted in boreal forest dominated by fir and spruce (indicative of lower summer temperatures) (Ecological Stratification Working Group 1995). Leech (1966) reported from the Canadian arctic at approximately 82°N. Some European work has been conducted at latitudes farther north than Insular Newfoundland. For example, Toft (1976) reported from Denmark and Edgar (1971a) from Scotland, both at approximately 56°N. However, climate is not simply determined by latitude, and the generally more temperate European climate is indicated by the beech woods of the former study and the oak woods of the latter.

METHODS

Species and localities.—Four species of *Pardosa* C. L. Koch 1847 (Lycosidae) were chosen for this study: *P. fuscula* (Thorell 1875), *P. groenlandica*, *P. hyperborea* (Thorell 1872) and *P. moesta*. Full descriptions of these species can be found in Dondale & Redner (1990). They were chosen both because the taxonomy of most Canadian lycosids is well established (Dondale & Redner 1990) so conclusions could be confidently assigned to individual species and preliminary investigations in 1995 and 1996 found dense populations of these species. Such dense populations lend themselves to sampling by hand as opposed to using pitfall traps. Pitfall traps are useful measures of activity and have a long history of employment in ecological studies, but they are selective in trapping different species and different life-stages (Berghe 1992; Topping & Sunderland 1992).

The Island of Newfoundland is in the boreal shield ecozone where the climate is heavily influenced by arctic currents, many areas are exposed to particularly harsh climatic conditions and the landscape is dominated by spruce-fir forest with extensive peatlands. Within that ecozone, the populations of this study were in, or immediately adjacent to, the northern peninsula ecoregion (South 1983; Ecological Stratification Working Group 1995).

The populations chosen were all in Gros Morne National Park, Newfoundland, and were therefore largely protected from human interference. The *P. fuscula* population was on an extensive peatland immediately below and around the highest land on top of Partridgeberry Hill behind the community of Woody

Point (49°30.2'N, 57°56.9'W). The *P. groenlandica* population was at the back of a pebble-cobble beach immediately north of the mouth of Baker's Brook (49°39.5'N, 57°57.7'W). The *P. hyperborea* population was on the extensive treeless heath on the higher parts of Partridgeberry Hill behind Woody Point (49°30.0'N, 57°56.6'W). The *P. moesta* population was on the treeless coastal meadow immediately above and behind the beach at Lower Head, Shallow Bay (49°57.3'N, 57°46.2'W). Voucher specimens are deposited in the Newfoundland Museum (catalogue numbers NFM ARA-01, -02, -03 and -04).

Measurements.—Dondale (1961) concluded that carapace width (CW) was the most generally useful measurement to distinguish life history stages but the species he examined did not include lycosids. Hagstrum (1971) confirmed the essentials of that work with measurements of the lycosid *Alopecosa kochi* (Keyserling 1877). However, Toft (1976) claimed that linear measurement of tibia I gave the best discrimination between instars, but in support presented data for only one species, the linyphiid *Helophora insignis* (Blackwall 1841). His data supported the superiority of tibia I measurements for that particular species, but what is applicable to a linyphiid may not be applicable to lycosids. To resolve this question, CW and tibia I of a number of samples of the lycosids of the present study were compared.

Life-cycles.—Critical information for all four species was whether adults survived the winter and the general nature of the population immediately after the winter. Samples were therefore taken just after snow-melt at each site (May or early June). Preliminary observations in 1995 and 1996 indicated that no adults were seen until July, except adult *P. groenlandica* which appeared in June. Therefore in 1997, sampling of *P. groenlandica* commenced in May and of the other species in June. At each sampling I tried to catch at least 50 specimens. I achieved this in all but the June samples of *P. groenlandica* and *P. fuscata*, when bad weather made these two larger and less numerous species harder to find. In one instance, *P. groenlandica* in June, it was necessary to sample the population on two consecutive days, June 1 and 2. Sampling dates and numbers caught for each species in 1997 are as follows. *P. moesta*: June 2, 98;

July 7, 99; August 14, 143; September 14, 88. *P. hyperborea*: June 5, 74; July 3, 75; August 11, 55; September 15, 66. *P. fuscata*: June 5, 48; July 9, 135; August 11, 54; September 15, 104. *P. groenlandica*: May 15, 60; June 1 and 2 combined, 37; July 4, 68; August 12, 62; September 13, 74. Spiders were caught with an aspirator and transferred to snap-cap plastic vials. Only one spider was put in each vial to avoid intraspecific aggression and cannibalism. Spiders were taken to the laboratory, placed in a deep-freeze until comatose and then placed directly into 75% ethanol for storage and later examination.

Although considered superior to pitfall traps for present purposes, hand collection nevertheless has two principal imperfections: lycosids are weather-sensitive (Vlijm & Kessler-Geschiere 1967) and may not be visible except under warm and windless conditions, and data from hand collections can be misleading because of conscious or unconscious size-selection by the collector. To offset weather problems, collections were made as far as possible on favorable days, when at least two individuals of the selected species were visible in a five-minute preliminary inspection. To offset size-selection, a conscious effort was made to catch all individuals seen of the target species irrespective of size.

Life-stages identified.—Three separate life-stages were identified: immature, subadult and mature. Mature contains a single instar and is clearly defined as adult males with fully developed functional palps and adult females with fully developed functional epigyna. The boundary between mature and subadult is clear cut. Subadults are close to becoming mature, presumably within a molt or two of maturity (although total number of molts and number of molts within the subadult stage are unknown). Secondary sexual characters are pronounced but not complete: male palpal tarsi are significantly swollen with ventral surfaces showing pronounced ogee curves; developing female epigyna have obvious lateral sclerites. Immatures are either smaller specimens showing no differences that would indicate their future sex, or larger specimens with males showing at most a slight thickening of the palpal tarsi and females showing no development of the lateral epigynal sclerites and distinguishable from potential males only by virtue of having no sign of any palpal

Table 1.—Males and females (raw data) caught in 1997. (%) = females with cocoons.

	<i>P. fuscula</i> ♂, ♀	<i>P. groenlandica</i> ♂, ♀	<i>P. hyperborea</i> ♂, ♀	<i>P. moesta</i> ♂, ♀
June	0, 0 (0%)	2, 4 (0%)	0, 0 (0%)	0, 0 (0%)
July	19, 18 (89%)	2, 2 (50%)	21, 15 (47%)	35, 26 (4%)
Aug.	1, 6 (83%)	0, 5 (20%)	0, 24 (54%)	17, 50 (92%)
Sept.	0, 3 (0%)	0, 1 (100%)	0, 30 (80%)	0, 42 (43%)

swelling. The immature life-stage contains several instars. The boundary between immature and subadult is not always clear cut, and conclusions drawn from the data must be in light of this imprecision. In addition to these three stages, very small newly or recently hatched spiderlings will be referred to occasionally. These were easily identified because in previous years females of all four species carrying spiderlings had been caught and so the size range of new spiders was well known.

RESULTS

Measurements.—One example will illustrate the relative usefulness of measurements of the two different body parts. Figure 1 compares measurements of CW and tibia I length of the July 7 *P. moesta* sample and shows that both yield essentially similar information with the two different cohorts definitively separated and both larger and smaller cohorts spread over five or six units.

Life-cycles.—Numbers of individuals with different CWs for all four species populations are displayed in Figs. 2–5. Numbers of males and females caught and the percentage of those females carrying a cocoon are shown in Table 1. All four species fit the generalized life-cycle illustrated in Fig. 6. Adults appear around the end of June and the sexes are present in approximately equal proportions in July. Males then either vanish by August or decline rapidly in numbers and have gone by September. Based on the synchrony of the sexes, the mating season is principally late June and July. Females persist to at least mid September (when sampling stopped) but do not survive the winter. The breeding season (here defined as females carrying cocoons) is July through to September. New spiders hatch in mid to late summer and join a population consisting partly of mid-size immatures (hatched the previous year) and partly of ma-

tures that have just produced the new young. The two cohorts of immature individuals present at the end of the year survive the following winter and by the next spring have grown. The cohort of smaller immatures now becomes the mid-size cohort that will grow throughout the year. The cohort of larger immatures becomes sub-adult at or before the beginning of the year and then matures, breeds to produce a cohort of new spiderlings and in turn dies before the end of the year. In each species only one recruitment of new spiderlings was seen within the sampling period and there was no direct evidence that females make more than one cocoon. Individual species are considered below.

Pardosa moesta males and females appeared in July (Table 1). Males peaked in July, declined in August and were gone by September. That was similar to *P. fuscula*, whereas males of the other two species had gone by August. Breeding was slightly later than in the other species because only 4% of females carried cocoons in July and it was not until August and September that a significant percentage of females had cocoons. New spiderlings (modal CW 0.6 mm) appeared in September (Fig. 2), later than in *P. hyperborea* and *P. groenlandica* but the same time as *P. fuscula*. The apparent shrinkage of immatures between June and July is an artifact of sampling.

Pardosa hyperborea males and females appeared in July (Table 1), and males were seen only in July. Significant percentages of females carried cocoons in July, August and September. New spiderlings (modal CW 0.6 mm) appeared in August (Fig. 3). No new spiderlings were caught in September despite 80% of females carrying cocoons in that month. The group of immatures in September with modal CW of 1.0 mm is seen as the new spiderlings of August grown to that size. The similar group of small immatures in August

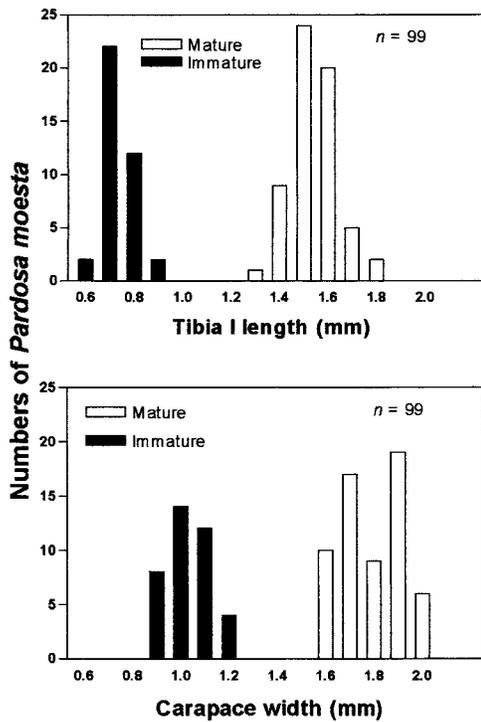


Figure 1.—Comparison of measurements of carapace width and tibia I length for the same sample of *Pardosa moesta* July 1997.

(CW 0.9–1.1 mm) is not seen as new spiders hatched the previous month (July) because neither adults nor cocoons were seen until July, and no new spiderlings were seen in that month. Therefore the two groups of immatures in August, lying between CW 0.9 and 1.6 mm, are seen as one group with a wide size range. That same group grew to occupy the range CW 1.1–1.8 mm in September. Therefore the breaks in the data at CW 1.2 mm in August and CW 1.6–1.7 mm in September are artifacts of sampling.

Pardosa fuscula males and females appeared in July (Table 1). Males had declined significantly by August and were gone by September. Breeding was in July and August with over 80% of females carrying cocoons in each of those months. New spiderlings (modal CW 0.6 mm) (Fig. 4) appeared in September.

Pardosa groenlandica males and females appeared in June (Table 1), the earliest appearance of adults in this study. Males were present in June and July but were gone by August. Females were still seen in September. Females carried cocoons in July and August,

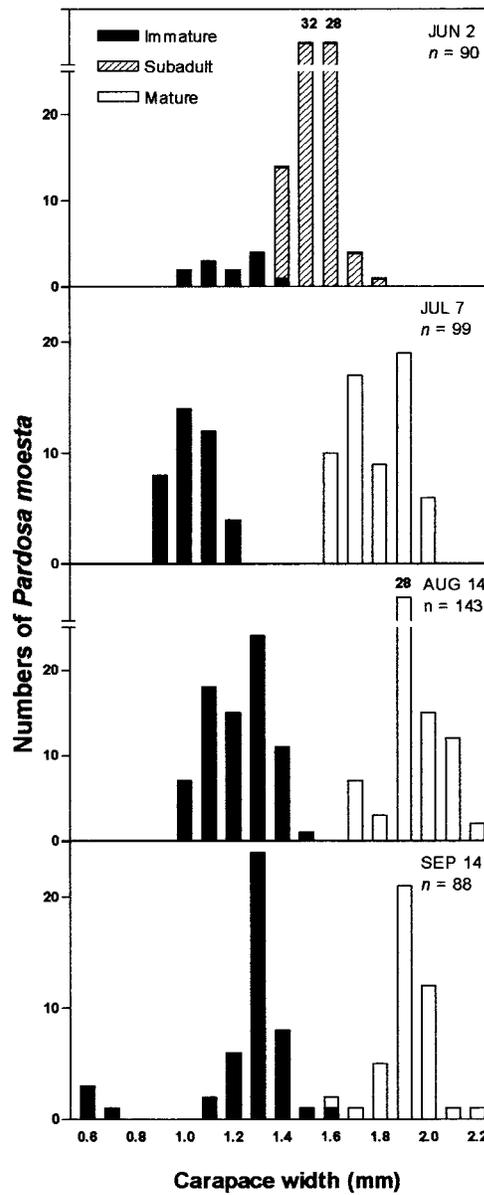


Figure 2.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa moesta*.

and a single female with a cocoon was caught in September. New spiderlings (modal CW 0.8 mm) appeared in August (Fig. 5), and had grown to modal CW 1.0 mm by September. The single subadult taken in July (CW 3.4 mm) was the latest observation of this stage for any of the four species. Small numbers of small immatures (CW 0.8 mm) were also seen

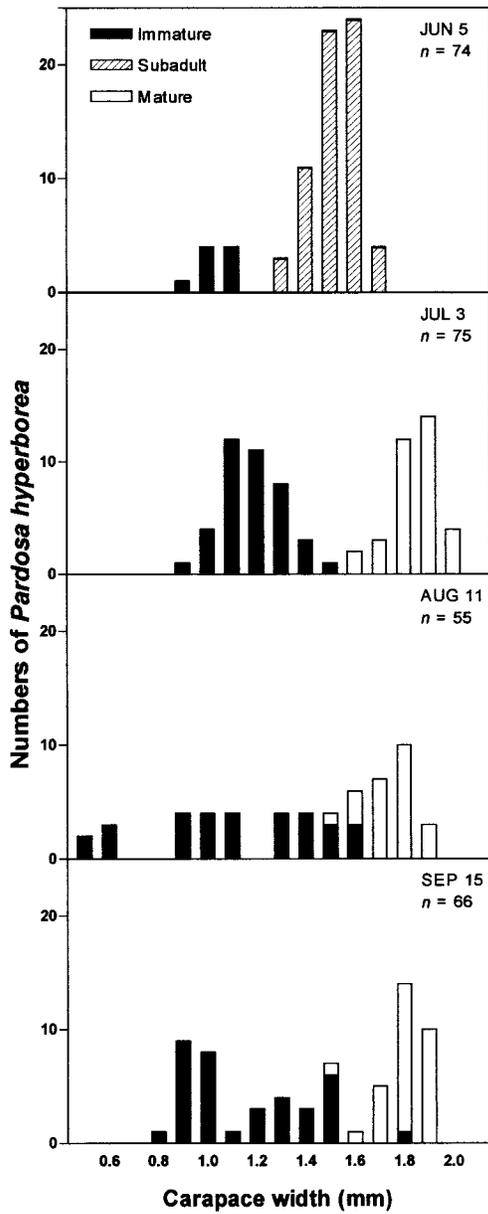


Figure 3.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa hyperborea*.

in June and July. In July these might have been a small number of early-hatching new spiderlings because both sexes had been present the previous month, but the same explanation is not applicable to June because there was no evidence of cocoon production in that month. This is the only species of this study where subadults were seen in September. The

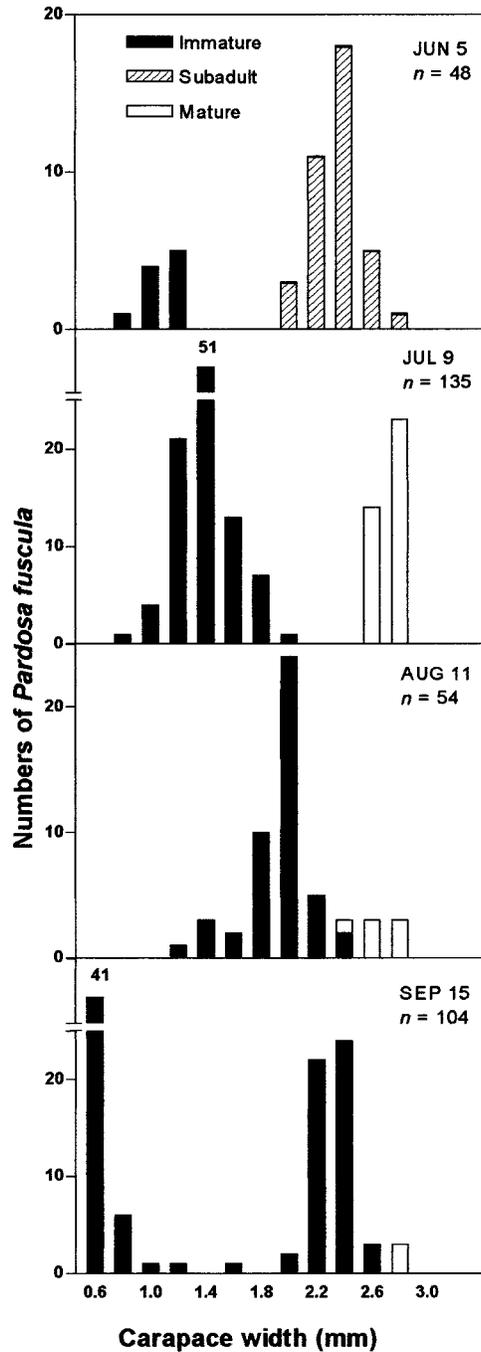


Figure 4.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa fuscula*.

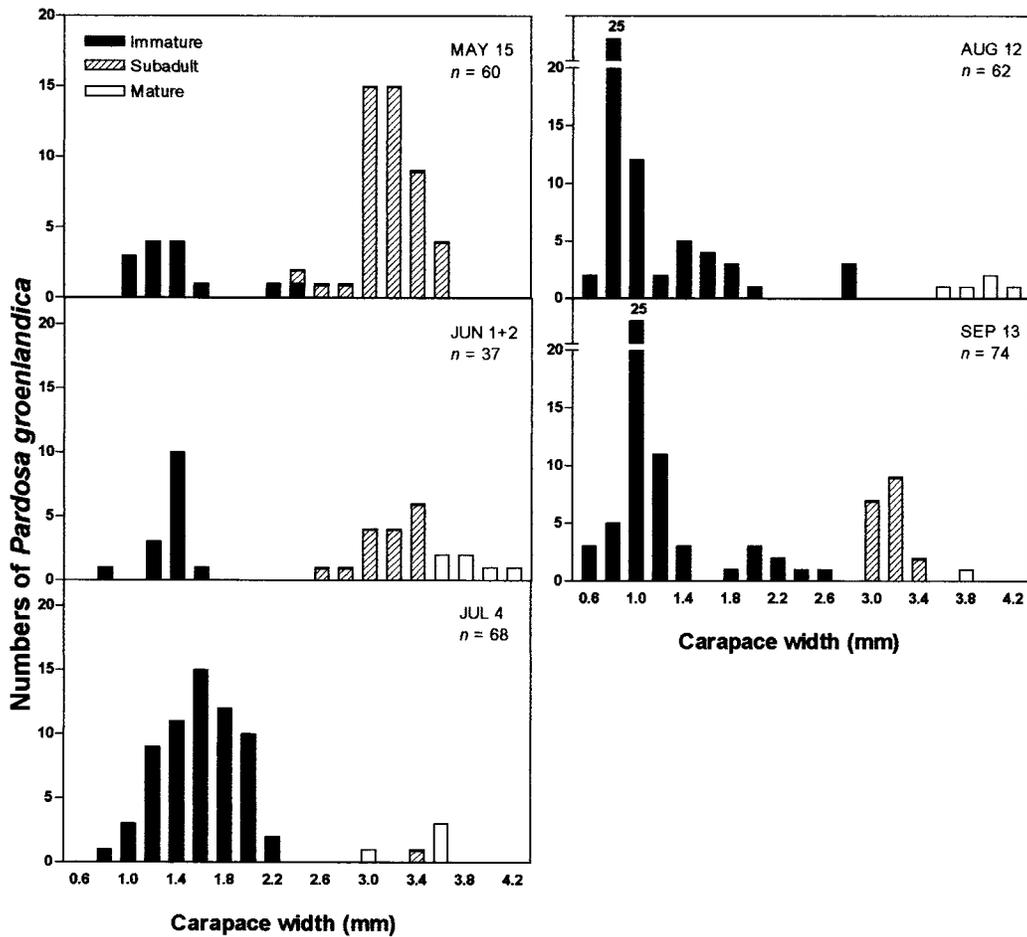


Figure 5.—Frequency distribution of carapace width measurements of the monthly 1997 samples of *Pardosa groenlandica*.

smaller immatures seen in September (modal CW 1.0 mm) were new spiders hatched the previous month (August) with one month's growth, and the smallest of this group may be a few new spiders hatched in September. The larger immatures (modal CW 1.9 mm) are seen as persistent juveniles from the previous year that were not large enough to become subadults, possibly in combination with some slightly older individuals hatched the previous month.

DISCUSSION

Measurements.—Since measurements of CW and tibia I yielded essentially the same information either could have been used here. However, CW was adopted because it was

easier to manipulate the carapace into position for measurement. This is contrary to the opinion of Toft (1976) who argued that tibia I was easier to measure and used a linyphiid as an example. No doubt this discrepancy is due to the morphology of the taxa under consideration: what is true for lycosids may not be true for linyphiids. The use of CW to establish life-cycle stages has frequently been reported, for example by Almquist (1969), Workman (1978) and Putman (1967).

Life-cycles.—The four life-cycles demonstrated here are essentially similar to biennial species elsewhere, for example *P. lugubris* in Scotland (Edgar 1971a), *Trochosa ruricola* in Finland (Hackman 1957), *P. moesta* and *P. mackenziana* (Keyserling 1877) in Alberta

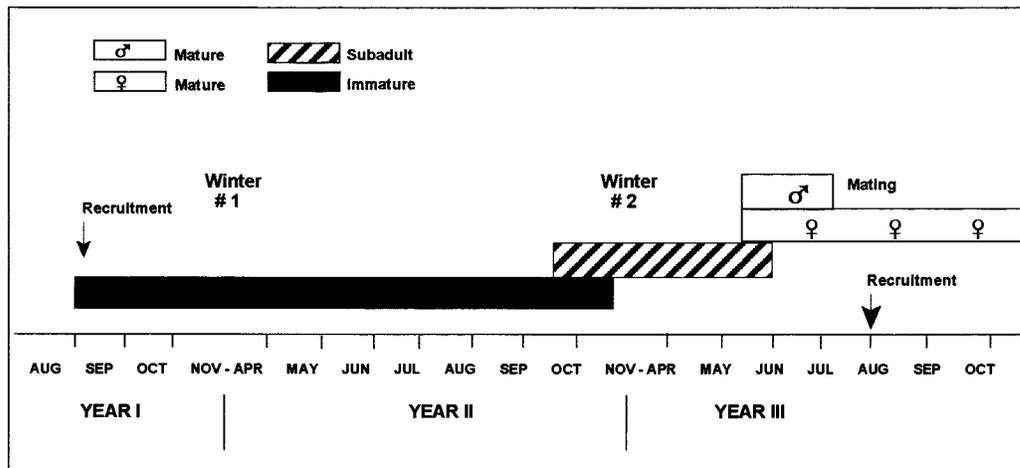


Figure 6.—Generalized life-cycle of *Pardosa moesta*, *Pardosa hyperborea*, *Pardosa fuscula* and *Pardosa groenlandica* on the Island of Newfoundland, Canada.

(Buddle 2000), *Dolomedes fimbriatus* in Finland (Palmgren 1939) and *D. triton* (Walckenaer 1837) in Alberta (Zimmermann & Spence 1998), *Philodromus rufus* and *P. cespitum* in Nova Scotia (Dondale 1961), *Araniella displicata* in Nova Scotia (Dondale 1961) and *Eris militaris* in Nova Scotia (Dondale 1961). Others, such as the three British species of *Amaurobius*, are biennials but the second overwintering is as adults not as older immatures (Cloudsley-Thompson 1955).

Pardosa moesta is the only one of the present four investigated elsewhere, and the biennial life-cycle of this species in Alberta (Buddle 2000) differs from the present work only in detail. In Alberta mating was mid-May to early June (July in Newfoundland) and cocoon-carrying early June through August (principally August and September in Newfoundland). These differences can be attributed to climate. In Alberta the population lived in the boreal transition ecoregion dominated by hardwoods with a mean annual precipitation of ca. 500 mm and the following mean temperatures: annual 1°C, summer 14°C and winter -13.5°C. The Newfoundland population lived in the northern peninsula ecoregion dominated by conifers with a mean annual precipitation of ca. 1150 mm and the following mean temperatures: annual 3°C, summer 11°C and winter -4.5°C (Ecological Stratification Working Group 1995).

Apart from these generalizations, at least

two of the present four species had a longer period of recruitment than immediately apparent from the data. Within the sampling period (which ended mid September) all species showed one recruitment of new spiderlings: *P. fuscula* and *P. moesta* in September and *P. hyperborea* and *P. groenlandica* in August. However, a significant number of *P. hyperborea* and *P. moesta* in September carried cocoons that would have hatched after sampling stopped. The single *P. groenlandica* female (with a cocoon) caught in September is not an adequate basis for further discussion. Whether such an extended period was due to females carrying single cocoons over a longer period or to some females carrying more than one cocoon, whether this might be expressed bimodally, and the implications of this for both synchrony of the sexes and the size range of the life-stages will be discussed below.

Production of two or more cocoons by one female over an extended period has been reported for several lycosids. Some reports were based on the direct evidence of marking techniques (e.g. Vlijm et al. 1963 for *P. amentata* (Clerck 1757), *P. monticola* (Clerck 1757), and *P. nigriceps* (Thorell 1856) in the Netherlands). Others were based on indirect evidence such as length of the cocoon-carrying season (e.g. Eason (1969) for *P. lapidicina* Emerton 1885 in Arkansas; Vlijm & Kessler-Geschiere (1967) for *P. pullata* (Clerck 1757), *P. nigriceps* and *P. monticola* in the Nether-

lands; Edgar (1971a) for *P. lugubris* in Scotland; Tóth *et al.* (1997) for *P. agrestis* (Westring 1862) in Hungary). These species all had an early start to mating followed by a minimum four-month cocoon-carrying season, but there are suggestions of two cocoons in a shorter period. For example, both Wolff (1981) for *P. moesta* and Buddle (2000) for *P. moesta* and *P. mackenziana* surmised that a second cocoon was likely because they were carried over 3 mo. In the present study there is only the indirect evidence of duration and late start of the cocoon-carrying season to indicate how many cocoons females carried. None of the four species here had cocoons before July, whereas they were typically seen in May or at latest June in reports of two cocoons elsewhere. The cocoon-carrying periods of all four present species seem shorter than reported elsewhere, but there was an unobserved, extended cocoon-carrying season for at least two species after sampling stopped in September as discussed above. Overall, the late start and shortness of the cocoon-carrying season suggest that second cocoons were not usual. But whether from one cocoon or two, *P. moesta* and *P. hyperborea* had extended recruitment periods. These might result in bimodal recruitment and they have implications for both synchrony of the sexes and the range of sizes of life-stages.

One type of bimodality was reported by Samu *et al.* (1998) in *P. agrestis*, where a long reproductive period had synchronous peaks of males and females in May and August, each preceded by a peak of subadults, with new spiderlings present from early June to October. The present study is clearly distinguished by the shortness of the cocoon-carrying period, the late start to mating and the lack of a double peak of subadults. However, there may be an unobserved, bimodal peak in recruitment produced by late hatching cocoons as predicted by Edgar (1971b) for *P. lugubris* in Scotland.

An extended recruitment period could affect synchrony because some late-hatched spiderlings might not mature in concert with the majority of immatures that have just overwintered for the second time. Therefore some individuals could be triennial, taking an extra year to mature, as reported for *Trochosa terricola* (Workman 1978). This might explain the presence in July and early appearance in

September of subadult *P. groenlandica*, the presence of small immature *P. groenlandica* in June and July, and the large immature *P. hyperborea* embedded among the adults in September. On the other hand, Edgar (1971b) showed that late hatched spiderlings rapidly catch up in size with their counterparts from an early hatch, thereby reducing or obliterating the anticipated bimodal age distribution of these two cohorts.

The wide variation in size-range of life-stages seen in the present study has been reported for other lycosids, for example by Eason & Whitcomb (1965), Almquist (1969) and Eason (1969). An extended period of recruitment would increase the number of instars occurring together, which would increase the size-range of life-stages, particularly the immatures that contain several instars. There may also be differences between early and late-hatched spiderlings. Edgar (1971b) reported that later spiderlings tended to be heavier than earlier (but whether heavier equals a larger CW is uncertain). On the other hand, Buddle (2000) said that later spiderlings were substantially smaller than earlier. Against this must be balanced the report that later spiderlings tend to catch up with earlier ones (Edgar 1971b). Either way, size difference of new spiderlings will to an extent increase the spread of the size-range of subsequent life-stages, particularly of the immatures. Overall, such variations in size do not obscure the general conclusions of the present work, but may mask subtle attributes of the populations.

The present work has increased the knowledge of spider life-cycles in northern localities, compared these four species to other biennials, and suggested that some individuals may extend their life-cycle beyond 2 yr. The question of whether and to what extent spiders can extend their life-cycles to accommodate increasingly difficult environmental conditions awaits further studies at more northern latitudes or perhaps higher elevations.

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