LIFE HISTORY OF *PARDOSA MOESTA* AND *PARDOSA MACKENZIANA* (ARANEAE, LYCOSIDAE) IN CENTRAL ALBERTA, CANADA

Christopher M. Buddle: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada

ABSTRACT.   The density, fecundity, and life-cycle of *Pardosa moesta* Banks 1892 and *Pardosa mackenziana* (Keyserling 1877) were studied in a deciduous forest in central Alberta, Canada. Density estimates were lower than reported for other *Pardosa* species; they ranged from 0.46 per m^2 for male *P. mackenziana* to 2.99 per m^2 for immature *P. mackenziana*. Adult female densities were below 1 per m^2 for both species. Clutch sizes were highly variable and averaged ($\pm$ SE) 33.06 $\pm$ 1.29 for *P. moesta* and 48.37 $\pm$ 1.67 for *P. mackenziana*. Although clutch size was positively related to female size, little of the variation was adequately explained by female size alone. Several lines of evidence suggest that *P. moesta* and *P. mackenziana* require two years to mature in central Alberta, with a peak reproductive period in May and June. Females carry egg sacs into the summer months and immature spiders overwinter following the first growing season when they are still less than 5 mg in weight. After a second summer of growth, subadults overwinter and maturation occurs early in the spring.

Keywords: Lycosidae, density, fecundity, phenology, life-cycle

Wolf spiders in the genus *Pardosa* C.L. Koch 1847 are among the most conspicuous and abundant of the ground-dwelling spiders. However, little is known about the life history of many northern species of this genus in North America, even though 46 species are found in Canada, at least eight of which are distributed widely across the country (Dondale & Redner 1990). Two of these species, *Pardosa moesta* Banks 1892 and *Pardosa mackenziana* (Keyserling 1877), have been noted as being among the most abundant wolf spiders collected in deciduous forests of north-central Alberta (Buddle et al. 2000).

Significant progress has been made in understanding the ecology and biology of many *Pardosa* species in Europe, Japan, and southern latitudes in North America (e.g., Hallander 1967; Vlijm & Kessler-Geschiere 1967; Miyashita 1968, 1969; Edgar 1971a, b, 1972; Dondale 1977; Greenstone 1980; Oraze et al. 1989; Samu et al. 1998). It is commonly thought that most spiders living in temperate zones have annual life-cycles (Gertsch 1979), and this is true for many *Pardosa* from various regions including Europe, southern Canada, and the United States (Vlijm & Kessler-Geschiere 1967; Schmoller 1970; Dondale 1977; Oraze et al. 1989). However, several

Pardosa species studied from high altitudes, northern latitudes, and under cooler conditions require more than one year to complete their development (Leech 1966; Schmoller 1970; Edgar 1971b).

Other characteristics such as natural densities of *Pardosa* species and estimates of clutch size are known for many species in the United States and some regions in Canada (e.g., Eason 1969; Schmoller 1970; Dondale 1977; Lowrie & Dondale 1981), and various species from Europe (e.g., Edgar 1971b; Kessler 1971). For example, Dondale (1977) reported densities of *P. saxatilis* (Hentz 1844) between 0.8–4.4 per m^2 in southern Ontario; and as part of a detailed study of *P. lugubris* (Walckenaer 1802) in Scotland, Edgar (1971b) reported densities of various life stages between 1.7–6.2 per m^2. There is also a variety of published records on the average clutch size for many *Pardosa* species, and these range from as low as 25.5 eggs/female for the small species *P. saxatilis* to a high of 82.0 eggs/female for the larger *P. amentata* (Clerck 1757) (Marshall & Gittleman 1994).

During 1998 and 1999 I studied life history characteristics of *P. moesta* and *P. mackenziana*. The objectives were to determine the natural densities of these species, establish

their clutch sizes and assess whether the number of offspring is determined by female size, and to ascertain the life cycles of *P. moesta* and *P. mackenziana* in deciduous forests of central Alberta, Canada.

METHODS

Study site and species descriptions.—This work was done at the George Lake Field Site located 75 km northwest of Edmonton, Alberta (ca. 53°57′N, 114°06′W). There are approximately 180 ha of continuous hardwood forest at the field site, which is surrounded by agricultural land to the south and west, a lake to the east, and more than 500 ha of continuous deciduous forest to the north. Dominant tree species include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), birches (*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)), and patches of white and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill.) BSP). The study area for this research was a 2.2 ha area of upland aspen forest (Niemelä et al. 1992).

Pardosa moesta and *P. mackenziana* are among the most abundant wolf spiders found on the forest floor at George Lake; other *Pardosa* species encountered less frequently include *P. xerampelina* (Keyserling 1877), *P. fuscula* (Thorell 1875), *P. distincta* (Blackwall 1846) and *P. ontariensis* Gertsch 1933. *Pardosa moesta* has general habitat affinities including meadows, hayfields, marshes, bogs, lawns, gravel pits, clear-cuts, rocky shores, and deciduous forests (Wolff 1981; Dondale & Redner 1990; Buddle et al. 2000). Lowrie (1973) has suggested that western populations of *P. moesta* occur more often in wet habitats from various elevations. *Pardosa mackenziana* is usually associated with coniferous forests although known to inhabit salt marshes, bogs, beaches, and deciduous forests (Lowrie 1973; Dondale & Redner 1990; Buddle et al. 2000).

In a study of spider assemblages in north-central Alberta, Buddle et al. (2000) found that *P. moesta* and *P. mackenziana* co-occur in a variety of different age-classes of deciduous forest stands. The proportions of the two species, however, differed depending on whether the forest stand had a closed canopy. In open stands, 67.3% of the total catch of the two species was *P. moesta*. In closed canopy stands the situation was reversed as 67.8% of the total catch of the two species was *P. mackenziana*.

Pardosa moesta and *P. mackenziana* are easily distinguished in the field based on their size and coloration. *Pardosa moesta* is the smaller of the two species, with an average length of 4.95 mm for males and 5.64 mm for females, whereas the average length for *P. mackenziana* is 5.91 mm for males and 6.85 mm for females (Dondale & Redner 1990). Adult and sub-adult male *P. moesta* have a dark, shiny carapace in contrast to the lighter brown carapace with its lighter median band on male and female *P. mackenziana*. Female *P. moesta* have a dark carapace with faint median and submarginal bands. It is also possible to distinguish immature stages of the two species based on subtle difference in the coloration and patterns on the carapace; immature *P. mackenziana* have distinct white setae that outline a V-pattern on the median region of the carapace. The white setae on the carapace of immature *P. moesta* are arranged in a more scattered pattern on the carapace. Additionally, the carapace of immature *P. mackenziana* is a deeper brown color than the carapace of immature *P. moesta*. Voucher specimens of both species are deposited in the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada.

Density estimates.—Densities of *Pardosa* were estimated by haphazardly placing on the forest floor an upright bucket (28 cm diameter, 23 cm height) with its bottom removed. After the bucket was firmly placed on the forest floor the enclosed leaf-litter was searched for wolf spiders (similar to quadrat sampling used by Edgar (1971a, b)). Individual *Pardosa* were identified, counted and brought to the laboratory. This procedure was repeated 241 separate times between 23 April–15 June 1999. Three different life-stages were classified for both species: immatures, sub-adults, males and females. Results from the bucket estimates were extrapolated to the number of *Pardosa* of different life stages per m^2 of forest floor, separated into three sampling periods of approximately equal lengths (23 April–10 May, 11–27 May and 28 May–15 June).

Fecundity.—Female *P. moesta* and *P. mackenziana* carrying egg sacs, or those appearing to be gravid (i.e., found with swollen abdomens), were collected on an opportunistic

basis during the spring of 1998 and 1999 in order to assess fecundity and relationships between female size and clutch size. Many *Pardosa* species are known to produce more than one egg sac in a given season (Miyashita 1969; Edgar 1971b; Wolff 1981). However, all collections were made early in the season, ensuring that catches did not contain females with second egg sacs, which are known to contain fewer eggs (Miyashita 1969; Edgar 1971a). Data about size and fecundity were collected for a total of 66 *P. moesta* and 73 *P. mackenziana*. Live females were gently held between a piece of soft foam and a clear plastic petri dish and their carapace width (CW) was measured to the nearest 0.01 mm using an ocular micrometer. CW is easily measured and thought to be a good indicator of overall spider size, as has been shown for both web-building and hunting spiders (Hagstrum 1971; Spiller & Schoener 1990; Wise & Wagner 1992; Zimmermann & Spence 1992). Spiders were held at 25 °C under long-day photoperiod (16 h light: 8 h dark) in clear film canisters with moistened plaster-of-Paris on the bottom to maintain humidity (similar to the procedure outlined by Wise & Wagner (1992)). Many females produced egg sacs in captivity, and for most female spiders, spiderlings were allowed to hatch to determine clutch size. Due to time constraints, however, some of the specimens were placed immediately in 70% ethanol, and egg sacs were later dissected for measures of clutch size. Linear regression was used to assess the relationships between female size and number of offspring produced for each species.

Life cycle.—*Adult population dynamics:* The activity of adult wolf spiders can be assessed by using a sampling technique such as pitfall trapping. Pitfall trap catches depend on spider activity so absolute density estimates, for example, are not possible with such data. However, pitfall trap data can be used to infer the peak reproductive period for spiders as during this time male and female spider activity increases. In the present study, data generated from live-trapping and mark recapture using pitfall traps are used only to assess the activity of adult *Pardosa*, the peak reproductive period and the duration of female survival. This work was completed from May to August 1998 using enclosures previously used for experiments with ground beetles (see Nie-

melä et al. (1997)). Enclosures were located 50–60 m from the area where density estimates were obtained. Three sets of enclosures measuring 4 × 24 m in length (subdivided into six compartments per enclosure, each measuring 4 × 4 m) were made in 1989 by sinking ¾ inch (*ca.* 2.0 cm) plywood 30 cm into the ground, leaving 40–45 cm above ground. All seams were sealed with caulking and a strip of aluminium flashing 10 cm wide was screwed or nailed to the top part of the walls. Experiments were designed based on the assumption that *Pardosa* species would be unable to move between compartments. However, both *P. moesta* and *P. mackenziana* were observed climbing between compartments; nevertheless, it was still possible to monitor the population dynamics of adult wolf spiders within the enclosures and to assess the length of female survival.

Eight pitfall traps without preservative were placed in each of the 18 compartments. Traps were 1 liter plastic containers sunk into the ground so that the trap lip was flush with the substrate. Funnels were placed in the traps to prevent spiders from escaping. Traps were opened and monitored three to four times per week from early May until mid-July and about once per week until the end of August. I recorded the sex of captured *P. moesta* and *P. mackenziana*, and recorded whether females carried egg sacs.

Sixty *P. moesta* and 48 *P. mackenziana* females carrying egg sacs were marked and released on 16 June into the aforementioned compartments. Spiders were marked with a small dot of enamel paint on the carapace. A small hole was drilled into a petri dish that was placed over the spider being gently held on a piece of foam; females were maneuvered on the foam pad so their carapace was directly below the hole and a toothpick dipped in paint was inserted through the hole to place paint on the carapace. Marked females were monitored along with other live trap catches in the compartments in order to estimate how long individual *P. moesta* and *P. mackenziana* females survive in the field.

Juvenile growth and development: Understanding population dynamics of adult spiders is insufficient for an adequate understanding of life-cycles; additionally, it is essential to determine the growth of juvenile spiders through the course of the summer and to es-

Table 1.—Density (number per m²) of immature (IM), sub-adult (SA), male, and female *Pardosa moesta* and *P. mackenziana* obtained from 241 samples (14.94 m² total sampling area) between 23 April–15 June 1999.

Sample period	Area (m²)	*Pardosa moesta*				*Pardosa mackenziana*			
		IM	SA	♂	♀	IM	SA	♂	♀
23 April–10 May	4.4	2.73	0.68	0	0.23	2.04	1.13	0	0
11 May–27 May	6.2	1.29	1.77	0.48	0.81	2.42	0.48	0	0.65
28 May–15 June	4.3	1.61	0	0.92	1.61	2.99	0	0.46	1.15
Average		1.87	0.81	0.47	0.88	2.48	0.54	0.15	0.60

tablish the overwintering stage. As part of an experiment investigating the competitive interactions between *P. moesta* and *P. mackenziana*, a number of newly dispersed spiderlings were released into small arenas. The arenas were white buckets, with the bottoms removed, measuring 28 cm in diameter and 23 cm in height. The buckets were sunk 5–7 cm into the ground on 8 July 1998 and covered with fine mesh to prevent immigration and emigration. Newly dispersed spiderlings were obtained from female *P. moesta* and *P. mackenziana* used for fecundity estimates. Spiderlings from more than 10 females of each species were bulk weighed in groups of ten. A total of 237 *P. moesta* and 234 *P. mackenziana* was placed in 12 arenas between 13 July–21 July 1998. In September 1998, the leaf litter from within the arenas was sifted and searched for *Pardosa* specimens. These were weighed and then immediately returned to the arenas. As soon as the snow melted in the spring of 1999, the litter within the arenas was searched a final time and *Pardosa* were counted and weighed.

Spring cohorts: To better understand what life-stages of *P. moesta* and *P. mackenziana* overwinter in central Alberta, the specimens retained from the density estimates were weighed to the nearest mg. Some additional specimens were collected on an opportunistic basis through until 30 June 1999 to increase the sample size for these estimates. It was assumed that if these species are annual, only one weight class of individuals would be present following the overwintering period. Species requiring two years to complete development should show two size classes of individuals at the time of spring emergence, and three size classes of individuals during the reproductive period (Dondale 1961; Edgar 1972).

RESULTS

Density estimates.—A total of 117 *P. moesta* and *P. mackenziana* was counted during the 241 density estimate samplings. Immature *Pardosa* represented the most frequently encountered spiders and had the highest density estimates during most sampling periods (Table 1). Densities of sub-adults were highest between 23 April–27 May and decreased in the final sampling period; adults increased in density in the last two sampling periods (Table 1). Males of both species were encountered infrequently during the survey and thus their density estimates were low in comparison to other life stages (Table 1). Female densities averaged 0.88 per m² for *P. moesta* and 0.60 per m² for *P. mackenziana*.

Fecundity.—*Pardosa moesta* was the smaller of the two species with a mean (± SE) CW of 2.07 ± 0.02 mm, and its average clutch size was 33.06 ± 1.29 eggs or spiderlings per egg sac. *Pardosa mackenziana* had an average CW of 2.73 ± 0.02 mm and a mean clutch size of 48.37 ± 1.67. Both species showed a significantly positive relationship between female size and clutch size using linear regression (Fig. 1A, B). However, very little of the variation in clutch size was explained by female size as indicated by the low R^2 values (especially for *P. mackenziana* (Fig. 1B)).

Life cycle.—*Adult population dynamics:* Live-trapping data show that male and female *P. moesta* were most active in mid-May and early June (Fig. 2A). Peak activity of *P. mackenziana* males and females was slightly later; they were most frequently caught between late May and mid-June (Fig. 2B). Spider activity is known to vary with temperature (Dondale & Binns 1977). The high variation in live catches of adult *Pardosa* in May and June was
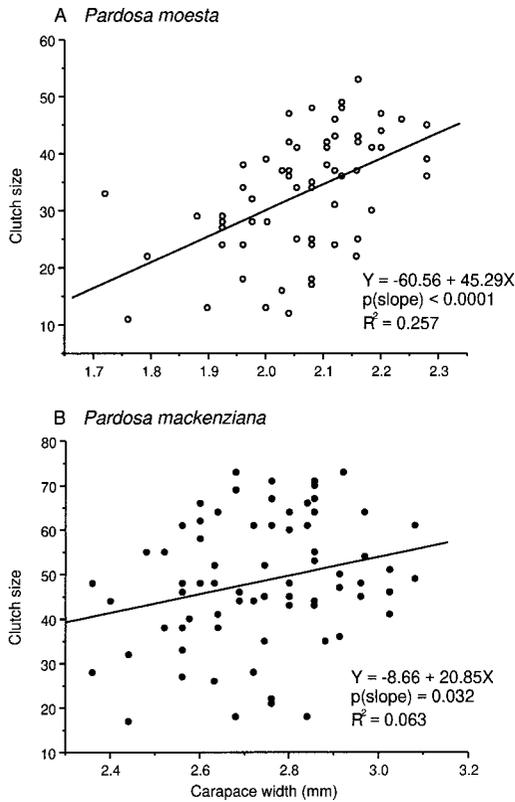
Figure 1.—Linear regression of clutch size (number of spiderlings or eggs per egg sac) against carapace width (mm) for *Pardosa moesta*, n = 66 (A) and *P. mackenziana*, n = 73 (B).
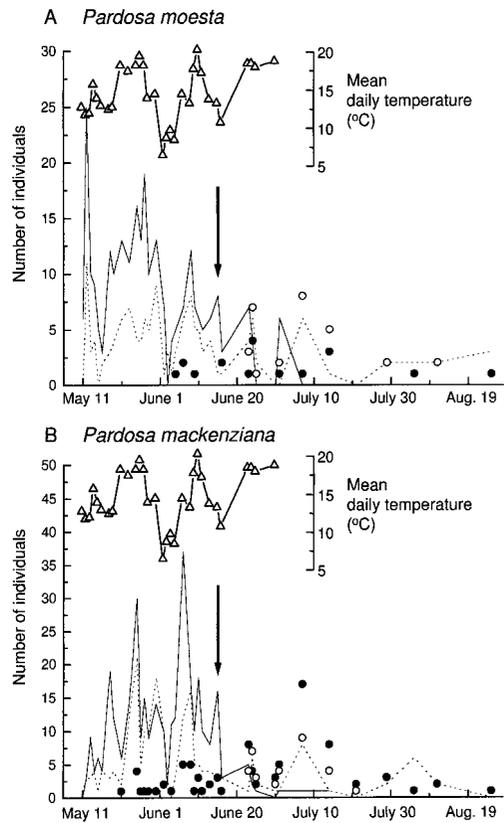

Figure 2.—Number of *Pardosa moesta* (A), and *Pardosa mackenziana* (B) collected by live trapping in enclosures between 11 May–29 August 1998. Solid lines represent catches of males, dashed lines are females. Solid circles (●) are females carrying egg sacs, open circles (○) are re-captures for marked females (released 16 June, solid arrow). Open triangles (△) are mean daily temperatures (°C) for May and June.

partially explained by variation in the mean daily temperatures during the spring (temperatures were obtained from a weather station at Sion, Alberta, 14 km south-west of the George Lake Field Site); warm days often corresponded to peaks in adult *Pardosa* activity (Fig. 2).

Females carrying egg sacs were caught from 3 June–25 August for *P. moesta* and from 21 May–25 August for *P. mackenziana* (Fig. 2). Therefore, spiderlings could be active from late spring and into the autumn months for both species. The late season catches of females carrying egg sacs likely corresponded to the production of a second egg sac.

Marked females were released on 16 June, and individuals of both species were re-captured at various times throughout the summer (Fig. 2). Two marked *P. moesta* were re-captured on 11 August, showing that females live at least 56 days in the field after being collected, marked and returned to the enclosures

on 16 June. Female *P. mackenziana* were not found in the enclosures as long as *P. moesta*; the latest re-capture for *P. mackenziana* was 21 July, 35 days after release.

Juvenile growth and development: Spiderlings released into arenas at the beginning of this experiment (13 July–21 July) had an average weight of 0.45 ± 0.03 mg for *P. moesta* and 0.58 ± 0.04 mg for *P. mackenziana*. Weights in September were 1.30 ± 0.25 mg for *P. moesta* (n = 29), and 1.28 ± 0.12 mg for *P. mackenziana* (n = 34). Thus, *Pardosa moesta* spiderlings gained on average 2.8 times their weight, and *P. mackenziana* 2.2 times their weight between mid-July and September 1998. Leaf-litter from the arenas was
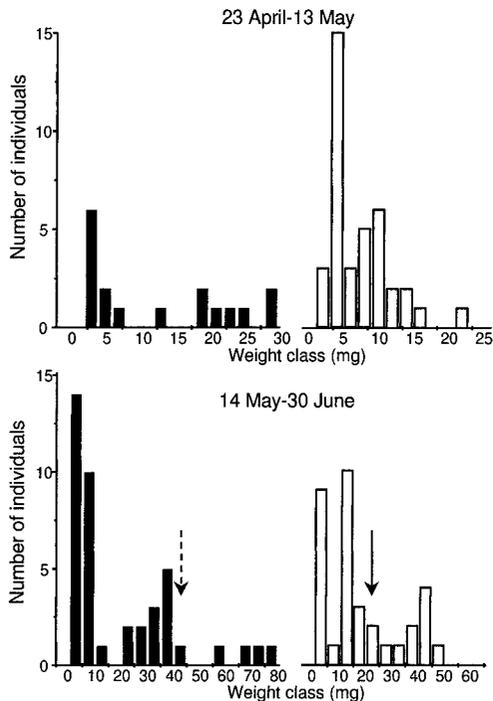
23 April-13 May

14 May-30 June

Figure 3.—Frequency of *Pardosa moesta* (open bars) and *Pardosa mackenziana* (solid bars) by weight class (mg) collected from 23 April–30 June 1999. Period of spring emergence given as 23 April–13 May, period of reproduction given as 14 May–30 June. Solid arrow indicates average weight for adult *Pardosa moesta*, dashed arrow indicates average weight for adult *Pardosa mackenziana*.
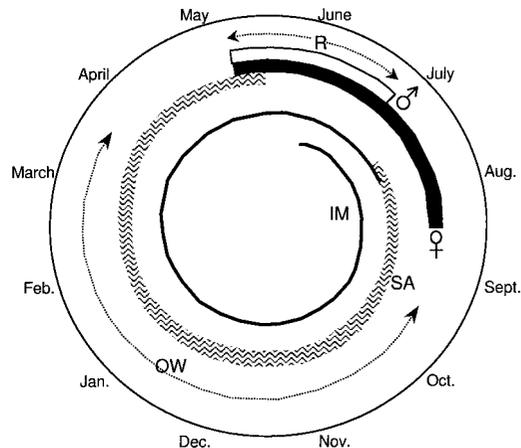

Figure 4.—Generalized life cycle of *Pardosa moesta* and *Pardosa mackenziana* in deciduous forests of central Alberta, Canada showing immatures (IM), sub-adults (SA), males, females, reproductive period (R), and overwintering period (OW).

sifted and searched again on 23 April 1999; four *P. moesta* with an average weight of 1.25 ± 0.25 mg and five *P. mackenziana* with an average weight of 1.40 ± 0.25 mg overwintered in the arenas. Although the arenas only approximated natural conditions, some spiders survived the winter and did not gain weight between September 1998 and April 1999.

Spring cohorts: Spider weights from individuals retained from the density estimates indicate that two life stages, and a few larger individuals, were present immediately following winter (23 April–13 May) (Fig. 3). During the peak reproductive period (13 May–30 June), three life stages were present for both species (Fig. 3). The majority of specimens collected fell below the average weight of adult specimens (Fig. 3). Although adult *P. moesta* and *P. mackenziana* showed a peak in activity from mid-May until late June, which would correspond to the reproductive period

(Fig. 2.), many smaller instars (i.e., < 5 mg in size) of both species were also present on the forest floor during this time (Fig. 3).

Taken together, results from the population dynamics of adults, juvenile growth and development, and from the weight classes of spring cohorts suggest *P. moesta* and *P. mackenziana* take two years to complete development in central Alberta. Both species have the same generalized life-cycle (Fig. 4); the only notable difference in life-cycles between the two species is that *P. moesta* has an earlier reproductive period than *P. mackenziana* (Fig. 2). Both species appear to have at least two overwintering periods: one as immatures and one as sub-adults (Fig. 4).

DISCUSSION

Density.—Densities of sub-adult and adult *P. moesta* and *P. mackenziana* were below 2.0 per m^2 during all sampling periods and immature densities were all below 3.0 per m^2; these estimates were lower than has been reported for other species of *Pardosa*. In Scotland, for example, Edgar (1971b) reported immature *P. lugubris* densities as high as 6.2 per m^2 for shaded areas in the spring. However, immature *P. lugubris* were also found to have low densities in clearings (Edgar 1971b); different life-stages of *Pardosa* may utilize different habitats and their densities would thus vary depending on habitat type. Immature *P.*

lugubris move from clearings to overwinter-ing areas in the autumn, and female *P. lugub-ris* carrying egg sacs may search for open ar-eas in which to sun their egg sacs and deposit their young (Edgar 1971a, b). Adult *P. moesta* are known to attain high populations in open, grassy regions (e.g., Dondale & Redner 1990; Buddle et al. 2000), which are common in the agricultural landscape within 100–200 m of the George Lake study area. Although *P. moesta* can certainly maintain populations in a closed canopy deciduous forest, densities of this species may be higher in more open hab-itats. Similarly, *P. mackenziana* may have higher densities in coniferous forests where this species is reported to be most commonly collected (Dondale & Render 1990).

Although densities of immature *P. moesta* and *P. mackenziana* remained between 1.29–2.99 per m^2 during all three sampling periods at George Lake, sub-adult and adult densities varied more dramatically by sampling period. Sub-adult densities of both species decreased as spring progressed as sub-adults molted to sexually mature adults during the peak repro-ductive period from mid-May to late June. Male densities were low for both species, which may reflect their higher mobility; males may have been better able to escape when the bucket was placed on the forest floor.

Fecundity.—Measures of both female spi-der size and fecundity varied considerably in *P. moesta* and *P. mackenziana*. Overall, how-ever, both species were substantially larger than the average for Canada. *Pardosa moesta* has previously been reported as having an av-erage CW (± 1 SD) of 1.91 ± 0.14 mm (n = 20) and the average CW for *P. mackenziana* has been reported as 2.55 ± 0.17 mm (n = 136) (Lowrie & Dondale 1981; Dondale & Redner 1990). The clutch size of 48.37 for *P. mackenziana* is close to the estimate of 50 re-ported by Lowrie & Dondale (1981) but was substantially lower than the estimate of 57.5 provided by Schmoller (1970) for alpine pop-ulations in Colorado.

In general, the average female size of a spi-der species is positively correlated with av-erage clutch size (Marshall & Gittleman 1994). Using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittle-man (1994), and unpublished data for *P. xer-ampelina*, I used linear regression to assess the strength of this relationship for *Pardosa*
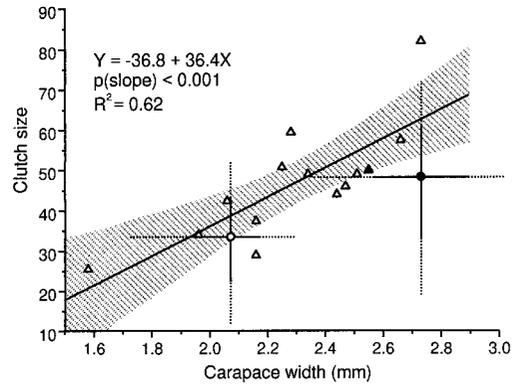

Figure 5.—Linear regression of clutch size against carapace width (mm) for 14 species of *Par-dosa* (△) using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittleman (1994) and C. Buddle (unpubl. data). Shaded area repre-sents the 95% confidence limits for the regression line. Solid triangle (▲) represents a published esti-mate for *Pardosa mackenziana* (from Lowrie & Dondale (1981)). Estimates for *Pardosa moesta* (○) and *Pardosa mackenziana* (●) from George Lake are averages with one standard deviation (solid hor-izontal and vertical lines) and range (dashed hori-zontal and vertical lines) for both carapace width and clutch size.

species. Using data for 14 species of *Pardosa*, there is a positive relationship between spe-cies size and clutch size, and close to two-thirds of the variation in clutch size is ex-plained by species size ($R^2 = 0.62$, Fig. 5). Clutch size for *P. moesta* at George Lake is close to what can be expected based on its size alone. However, the estimates for *P. macken-ziana* from George Lake fell farther below what was expected, and out of the 95% con-fidence limits for the regression line (Fig. 5). Thus, understanding variation in fecundity de-mands more than simply an understanding of size.

Within a species, however, there are strong relationships between female size and fecun-dity for both web-building and hunting spiders (e.g., Wise 1979, 1993; Enders 1976; Beck & Conner 1992; Simpson 1995). Although pos-itive relationships characterized both *P. moes-ta* and *P. mackenziana*, female size is clearly not the only determinant of fecundity. Kessler (1971) showed that food shortages can affect the number of eggs in two species of *Pardosa*. Furthermore, in a study of food limitation on the reproductive output of the pisaurid *Dolo-*

medes triton Walckenaer 1837, Spence et al. (1996) also showed that food limitation may be important in determining clutch size, but that these effects may vary with female size. Clutch size is dependent on the individual condition of the female; and this will vary depending on various factors such as environmental conditions, prey availability, and habitat type.

Life cycle.—The population dynamics of adult *P. moesta* and *P. mackenziana* were inferred from live pitfall trapping, a technique that depends on the activity of individual spiders. Focussing on these data, it appears that *P. moesta* and *P. mackenziana* follow a pattern typical for life histories of *Pardosa* in temperate zones: sub-adults must overwinter since mating occurs early in the spring, males die shortly after the reproductive period, and females carry egg sacs into the summer months (Turnbull 1966; Edgar 1971a). There were only two notable differences in adult activity between the two species: female *P. moesta* may live longer than *P. mackenziana*, and the reproductive period for *P. moesta* is slightly earlier than for *P. mackenziana*, a finding also noted by Wolff (1981).

By itself, the phenological data for adult populations could be interpreted to mean that both species have annual life-cycles. However, data about juvenile growth and development and weight classes of spring cohorts establish that more than one year is required for these species to mature. The numerous small (i.e., < 5 mg) individuals of *P. moesta* and *P. mackenziana* found in the early spring would require at least one more year to complete their development. Also, *P. moesta* and *P. mackenziana* spiderlings held in outdoor arenas did not reach the sub-adult stage in their first growing season and would require an additional overwintering period to complete their development.

During the period of spring emergence, weights of immature *Pardosa* specimens did not fall into a single weight class but were spread over several weight classes (Fig. 3). This may reflect the different cohorts produced from early (i.e., mid-May until June) compared to mid-season (i.e., late June until July) egg sacs from the previous summer. Spiderlings dispersing from mid-season egg sacs would not have the same potential for growth and development before the onset of cooler conditions compared to spiderlings dispersing from early season egg sacs. This suggests that overwintering for immature *P. moesta* and *P. mackenziana* may be facultative rather than obligatory; immature spiderlings may overwinter at different stages in their development. However, the reproductive period for both species is early in the spring, suggesting that the second overwintering stage primarily consists of sub-adults.

To ensure synchrony of the mating period, spiderlings from mid-season egg sacs would have to gain proportionally more size during their second summer compared to those from early season egg sacs. *Pardosa* may accomplish this by altering the number of instars to reach maturity, as instar number is flexible in many spider species (e.g., Miyashita 1968; Edgar 1972; Toft 1976; Zimmermann & Spence 1998). Edgar (1971a) also showed that although the second egg sacs of *P. lugubris* had fewer eggs, the eggs themselves were heavier, possibly in preparation for cooler winter conditions.

A small number of female *P. moesta* and *P. mackenziana* carry egg sacs much later in the season than the majority of the populations (i.e., late August, Fig. 2). Since spiderlings emerging from these egg sacs would be substantially smaller than those emerging earlier in the season, it is possible that spiderlings from late season egg sacs may slow down their development and stretch their life cycle over two additional growing seasons. By implementing a three year life cycle, synchrony of mating would be ensured. However, because only a small proportion of female *P. moesta* and *P. mackenziana* carry egg sacs in late August, it is unlikely that many individuals in the central Alberta populations of these species would exhibit three year life-cycles. Most egg sacs are carried in early or mid-season, suggesting the majority of individuals of *P. moesta* and *P. mackenziana* have biennial life cycles.

A two year life cycle for *P. moesta* and *P. mackenziana* is similar to that found for *P. lugubris* in central Scotland (Edgar 1971b), and for several species living at high altitudes (Schmoller 1970). Further south it is probable that *P. moesta* and *P. mackenziana* have annual life cycles. Schmoller (1970), for example, suggested that in high altitude regions of Colorado, *P. mackenziana* exhibits annual life

cycles. *Pardosa lugubris* has an annual life-cycle on the European mainland (Vlijm et al. 1963), and a biennial life-cycle in central Scotland (Edgar 1971b). The difference in life-cycle is attributed to cooler conditions in Scotland. However, Edgar (1972) also showed that the life cycle of *P. lugubris* in the Netherlands may vary from annual to biennial depending on environmental conditions and the timing of spiderling dispersal. A mixed annual-biennial life cycle has also been suggested for *P. tesquorum* (Odenwall 1901) in central Saskatchewan (D.J. Buckle unpubl. data). Another variation in *Pardosa* life-cycles has been shown for *P. agrestis* (Westring 1861) in central Europe. Here, Samu et al. (1998) report a bimodal life-history pattern, with reproductive periods in May and August. Undoubtedly, *Pardosa* life-cycles are remarkably flexible, and this may aid in explaining their dominance in many terrestrial ecosystems.

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