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LIFE HISTORY OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE)

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ABSTRACT

In the laboratory, *P. johnsoni* oviposit successive batches of eggs with a trend toward a decrease in both number of eggs and proportion of eggs that hatch in later batches. Approximately one month elapses between copulation and the first oviposition, and another month elapses between each successive oviposition. Eggs hatch three weeks after oviposition, and spiderlings disperse from the maternal nest after another three weeks. Males mature earlier, pass through fewer molts, reach smaller adult size and have lesser adult longevity than females. There is considerable intrasexual variability in adult size, maturation time, and number of instars before reaching maturity. Males mature in 5 to 7 molts; females, 6 to 8. Instar duration and variability in instar duration is greater in later than in earlier instars. Morphometric data from the laboratory were employed for estimating the number of molts that spiders undergo in the Coastal Range of California. Spiders in nature matured later in the year and probably passed through more molts before reaching maturity (6 to 8 for males; 7 to 9 for females) than was the case for laboratory-reared spiders. Phenology and density were investigated in six populations: two from the Coastal Range of California, two from Beach habitats (sea level, next to the ocean) in California, and two from Alpine habitats (Sierra Nevada, California; Rocky Mountains, Wyoming). Densities were comparable in all populations except for one Beach population in which spiders tended to occur in patches with density 5 to 10 times greater than in other populations. The mating season in the Coastal Range tends to be two months in duration, and adult females do not survive the summer. In Beach habitats the mating season tends to be eight months in duration, and adult females are present throughout the year. Phenology with more pronounced seasonal trends in the Coastal Range is correlated with greater seasonal fluctuations in climate. Beach habitats have relatively constant, mild climate. In Alpine habitats the mating season is restricted to summer months, when snow does not cover the ground. In the Rocky Mountains, summer rain is frequent; and the mating season extends through the entire summer (approximately 3 months). In the Sierra Nevada, summer rain is rare; and the mating season is restricted to early summer (approximately 1 month). Evidence from the field indicates that males do not survive the winter in Alpine habitats; and in laboratory experiments, adult males were inferior to adult females and immatures in their ability to survive simulated winter conditions. Possible causes of interpopulational differences in phenology are discussed; and hypotheses are discussed concerning the adaptive significance of iteroparity, oviposition of infertile eggs, inter- and intrasexual size variation, intersexual variation in longevity, and other life history characteristics.

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INTRODUCTION

In the family Salticidae there are more than 4000 described species (Prószyński 1971), but published life histories of only a few of these are available (Bailey 1968, Bonnet 1933, Crane 1948, 1950, Dondale 1961, Edwards 1975, Gardner 1965, 1967, Horner and Starks 1972, Miyashita 1969, Taylor and Peck 1974). This study concerns the life history of *Phidippus johnsoni* Peckham and Peckham, an abundant, euryecious salticid with a wide geographical range in western North America, studied in the laboratory and the field. Previous studies have dealt with varied aspects of the biology of this species (Dewey 1965, Enders 1975, Hill 1975, Jackson 1976, 1977a, b, 1978a, b, c), but not its life history. The evolution of life history tactics has become an important topic in biology (see Stearns 1976); and as a major group of predatory arthropods, spiders can be expected to provide valuable subjects for studies in this area.

Recently there has been increasing interest in the phenology (seasonal changes in population composition) of spiders (*e.g.* see Edgar 1972, Merrett 1969, Robinson *et al.* 1974, Vlijm and Kessler-Geschiere 1967). The phenology of *P. johnsoni* is of particular interest because in this species phenology varies from population to population. To a lesser extent, density is also subject to interpopulational variation. These trends will be discussed in relation to climatic and other habitat differences.

The distribution of *P. johnsoni* is bounded by the Great Plains, the Pacific Ocean, northern Mexico, and southern Canada. This species occurs from sea level to timberline, occupying relatively xeric habitats such as coastal dunes and oak woodlands. However, I am not aware of populations from desert habitats, and although *P. johnsoni* has been found in areas of fairly dense vegetation, I am unaware of populations from areas with extensive closed forest canopy. Spiders from six populations were involved in this study (Fig. 1).

The salticids are diurnal vagabond predators that stalk their prey with the aid of their highly developed visual system (Land 1972). Accurately determining the total number of individuals of a vagabond species in a given area, while the spiders are wandering about, is problematic. However, *P. johnsoni* constructs conspicuous silken nests (retreats) under rocks and wood on the ground and in other similar locations (Jackson 1978c). They remain inside these at night and during inclement weather. Molting, oviposition, and sometimes courtship and mating occur inside nests. *P. johnsoni* is relatively easily located in the field when occupying nests, and this was an important factor in making this study feasible.

Oviposition, postembryonic development, and other aspects of life history were investigated in the laboratory; and these data were used in conjunction with data from the field for a more intensive study of life history of spiders from Coastal Range habitats.

STUDY SITES

Phenology and density were studied in six populations (Fig. 1), and the spiders used in laboratory studies also originated from these populations: two from the Coastal Range of California, two from the Beach habitats (sea level, next to the ocean) in California, and two from Alpine habitats. Brief descriptions of habitats will be provided here (for more detail, see Jackson 1976). Munz's (1959) classification of California plant communities was used.

Tilden Regional Park – Coastal Range. Contra Costa County, California. Rocky, grass covered slopes. Elevation: 400-600 m. Plant community: Coastal Prairie. Primary nest sites: rocks.

Mount Diablo State Park – Coastal Range. Contra Costa County, California. Rocky, grass covered slopes. Elevation: 800-900 m. Plant community: Foothill Woodland. Primary nest sites: rocks.

Point Reyes National Seashore – Beach. Marin County, California. Sand dunes, *ca.* 100 m from the ocean. Elevation: sea level. Plant community: Coastal Strand. Primary nest sites: wood on the ground.

Inglenook Fen – Beach. Mendocino County, California. MacKerricher State Park, vicinity of Inglenook Fen (Baker 1972). Sand dunes and a bluff, *ca.* 100 m from ocean. Elevation: sea level. Plant community: Coastal Prairie and Coastal Strand. Primary nest sites: Wood on ground, fence posts, dead trees.

Pothole Dome – Alpine. Mariposa County, California. Sierra Nevada, Yosemite National Park. Open, rocky area on granite dome. Elevation: 2600-2700 m. Plant community: Lodgepole Forest. Primary nest sites: rocks.

Whiskey Mountain – Alpine. Fremont County, Wyoming. Wind River Range, Rocky Mountains. Extremely rocky slopes. Elevation: 3000-3400 m. Plant community: timberline, scattered Engelmann Spruce (*Picea engelmannii*). Primary nest sites: rocks.

Climate – Habitats differ in their temperature and precipitation patterns (see Elford 1970, Lowers 1960). California has a Mediterranean climate, with relatively hot, dry summers and wet, cold winters. However, the Beach habitats have more constant and mild climate than the Coastal Range. Temperature varies little during the year; and although rainfall is much less frequent during the summer, it occasionally occurs. Another important influence is coastal fog, which ameliorates the effects of reduced summer precipitation in Beach habitats. The Coastal Range is subject to greater fluctuations in rainfall and temperature. Winter temperatures are colder and summers are hotter. Rainfall virtually never occurs during the summer, and herbaceous vegetation typically turns brown. Summers would seem less severe in Beach habitats, where the herbaceous vegetation remains green all summer.

Snow is rare in the Coastal Range habitats, and it is virtually non-existent in the Beach habitats, but in the Alpine habitats it covers the ground during the majority of the year. Although active *P. johnsoni* have been found in all months of the year in the Beach and Coastal Range populations, they are presumably inactive for much of the year in Alpine populations. Compared to Pothole Dome, Whiskey Mountain has milder summers. Rainfall is common and the herbaceous vegetation is generally green all summer. Pothole Dome receives much less summer rain. As the summer progresses and moisture from melting snow decreases, the herbaceous vegetation turns brown.

METHODS

General – Unless otherwise noted, all selections of spiders and assignments to groups for experiments in the laboratory were carried out randomly (random numbers table: Rohlf and Sokal 1969). For all statistical tests, see Sokal and Rohlf (1969). Unless otherwise noted, data given in parenthesis in the text are means ± S.D. Whenever it was necessary to touch spiders, eggs, or exuvia, a camel's hair brush was used.

Cages and Maintenance – Spiders in the laboratory were kept in cages constructed from 11 X 8 X 6 cm clear plastic boxes (Jackson 1974). Each included a ventilation hole covered by a metal screen, three cork holes, and a cotton roll partially external to the cage. The cotton was kept wet in order to provide moisture in the interior of the cage. The spiders readily constructed nests in the corner of their cages. First through fourth instars were fed vestigial winged *Drosophila melanogaster.* Later instars were fed house flies (*Musca domestica*). *Drosophila* cultures were reared in glass shell vials that were partially inserted into the cages. Using this procedure, adult *Drosophila* were continuously emerging into the spiders' cages. When house flies were used, they were introduced through the cork holes as needed in order to maintain 3 to 8 flies in the cages at all times. For house flies, the shell vial connected to the cage contained sugar cubes on which the flies fed. Temperature was maintained at 23-25°C. In the study of postembryonic development, the light regime was 11L:13D. Otherwise it was 12L:12D.

Terminology – Following the terminology of Whitcomb (1978), the stage beginning with the rupture of the chorion and ending with the first true molt will be called the postembryo. The stage that follows the first molt is the first instar, and so forth. The postembryos are relatively inactive, lack functional chelicerae, and remain inside the nest. I will restrict the term "subadult" to the instar immediately preceding the final molt. Subadult females can be identified by the outline of the epigynum, which is visible beneath the cuticle of the ventral abdomen; and subadult males are identified by their enlarged palps. After hatching the immature spider undergoes a series of molts until it is mature, after which no more molting occurs.

Postembryonic Development – An inseminated female was collected from Mt. Diablo. She oviposited in the laboratory, and when the first instar spiderlings dispersed from the maternal nest, 39 were chosen for rearing. Each was placed in an individual cage, and more or less daily records were kept. Since these individuals were not separated until they had reached the first instar, they did not provide data concerning the duration of postembryos and first instars. Therefore, complementary observations were carried out on another two sets of spiderlings. These originated from females collected at Mt. Diablo as subadults and mated in the laboratory when they matured. Thirty eggs were chosen for observations on postembryos, and 30 postembryos from another female were selected for observations on first instars. For observations on postembryos, the nest

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was opened ten days after oviposition. Thirty eggs were placed individually in a 25mm diameter plastic dish. Once hatching occurred, the relatively immobile postembryos remained in the dish, and they were monitored each day until they molted or died. The dishes were kept inside a large plastic box, provisioned with moisture by four wet cotton rolls partially interior to the cage. For observations on first instars, a nest was opened three days after hatching occurred. The postembryos were placed in a 85 mm diameter plastic petri dish, inside a large plastic box provided with moisture. Monitoring the postembryos each day, whenever one molted, the first instar spiderling was placed in an individual cage and provided with *Drosophila.* The first instar spiderlings were monitored daily until molting or death occurred.

Oviposition and Hatching – Data concerning the number of egg batches oviposited came from 71 females collected in the field (Mt. Diablo, 14; Tilden, 57) as immatures, mated in the laboratory, and maintained until they died. Data concerning the number of eggs per batch came from 30 of these (Mt. Diablo, 14; Tilden, 16). Each female mated a single time. These spiders were maintained until death or until they ceased to oviposit. After oviposition, the female's eggs could be seen through the silk of her nest, although a bright light was sometimes necessary. Two to seven days after oviposition, the females were forced out of their nests and transferred to clean cages. The nests containing eggs were placed inside 25 X 79 mm shell vials plugged with cotton, after cutting away much of the silk. The great majority of the eggs in a given batch hatched on the same day, and this day was recorded as the date of hatching. Since the postembryos could be seen either through the door of the nest or through the silk with the aid of a bright light, it was not necessary to open the nest in order to observe hatching. The day on which a mass exodus of spiderlings occurred was recorded as the day of nest departure in this study. This day could be recorded unequivocably, since the majority of the spiderlings inside a given batch departed on the same day.

Measurements – Body length was measured to the nearest 1 mm from the antero-medial eyes to the posterior end of the abdomen, excluding the spinnerets, using a ruler. Measurements on the carapaces were made to the nearest 0.01 mm under a microscope with an ocular micrometer. Terminology for carapace features is explained in Fig. 2. When the spider molted, its carapace was shed as a single plate. Carapace measurements were made on spiders as well as their exuvia, and there were no consistent differences when the two were compared. Carapace length was measured on exuvia only, since the posterior end of the plate was obscured by the abdomen on intact spiders. Since the locations of eyes were obscure on postembryos, only length and one width (W-PLE) were measured. For W-PLE the widest location on the carapace of the postembryo was used.

Survival Under Reduced Temperature Without Food – A set of spiders from Whiskey Mountain (Alpine) were placed inside an environmental chamber in the fall and removed between 4 and 5 months later. In the late spring, the experiment was repeated with a set from Tilden, Inglenook, and some other California habitats (Non-Alpine). Each spider was inside an individual cage, in which it constructed a nest. Beginning at 23°C, temperature was lowered 5°C each day until reaching 3°C. Temperature was kept at 2-4°C, and open pans of water maintained humidity inside the dark environmental chamber.

Censuses – Phenology data were gathered by monthly censuses at Tilden, Mt. Diablo, Inglenook, and Pt. Reyes, carried out over two successive years. Pothole Dome was censused each month during the season when there was no snow cover (June through October), for two successive years. For each population, a single location was chosen as a monthly census area according to the following criteria: (1) The area gave an impression of having a population density close to the maximum for the habitat. (2) There were conspicuous objects at the borders and especially the corners of the area, such as trees, fence posts, or boulders. (3) The area could be completely searched in approximately 2 to 3 hours.

Every month, each potential nest site was searched systematically. Since *P. johnsoni* were not found under rocks and pieces of wood less than 5 cm in length, these were checked only sporadically; all larger than this were checked each time. When a *P. johnsoni* was discovered, it was taken temporarily into a glass vial, plugged with cotton. After recording the spider's body length and life stage (adult female, adult male, immature), it was released. Measurements were made with a ruler held against the glass vial, the spider could be prevented from moving, when necessary, by adjusting the cotton plug so as to press the spider gently against the bottom of the vial.

Generally, successive censuses of a given population were made three to four weeks apart. Occasionally this was not possible, but the shortest interval was ten days. A fire destroyed the Pt. Reyes census area, before the last three censuses had been made. For this reason, Population Density Census Area No. 2, which had comparable density and area, was substituted for the final censuses at Pt. Reyes. More information concerning censusing methods is provided elsewhere (Jackson 1976).

At Tilden, Mt. Diablo, Inglenook, Pt. Reyes, and Whiskey Mountain, two population density censuses were made for each population. Except for Inglenook, which will be discussed later, Population Density Census Area No. 1 was the same area as the monthly census area. Area No. 2 was another similar area. Density censuses were carried out at a time close to the peak of the mating season for each population. The methods were the same as for the monthly censuses, except that the density censuses were carried out at sunrise, usually on rainy and relatively cold days. Under these conditions, it was reasonably certain that all spiders were in their nests. All wood in the census areas was broken open with a hatchet. For evaluation of density, all living individuals were counted except for masses of postembryos and first instar spiderlings inside nests.

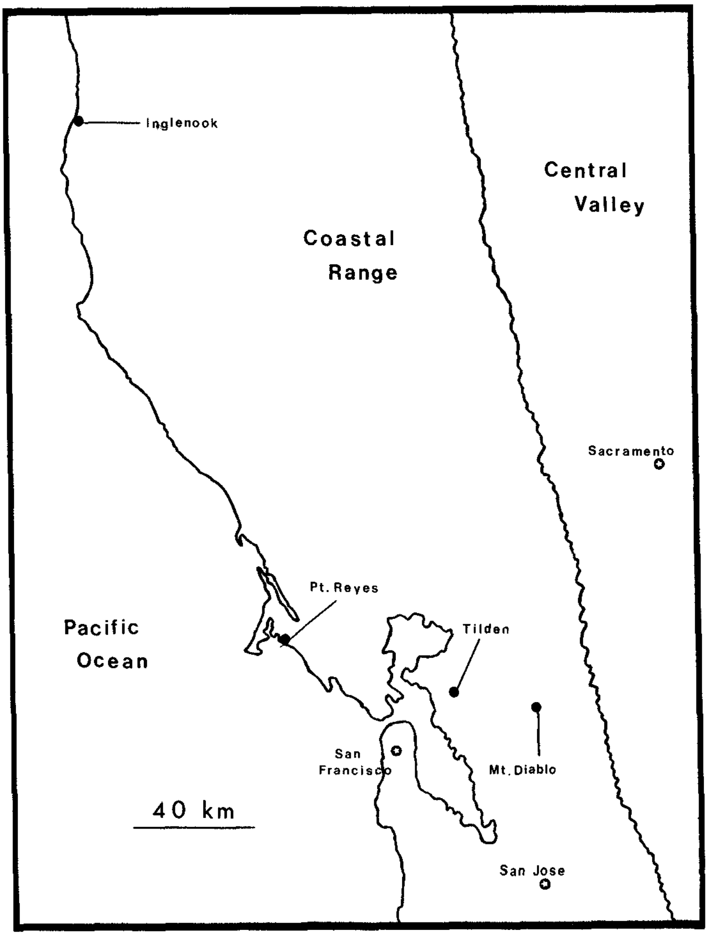

Fig. 1.–Map of northern California showing location of census areas. See Table 1.

OVIPOSITION AND HATCHING

Number of Batches – Fertile eggs are defined as ones that hatch, and a fertile female is one that oviposits any fertile eggs after copulation. A fertile batch is one containing any fertile eggs. Usually fertile batches contained some infertile eggs. Fertile females may oviposit infertile batches, which are ones that contain no fertile eggs. After copulation, infertile females either do not oviposit or they oviposit infertile eggs only.

Fertile females oviposited a series of one to five fertile batches (Table 1), sometimes followed by infertile batches; but infertile batches were never followed by more fertile batches. Some females oviposited only one fertile batch before beginning to oviposit infertile ones. Also, some females died before ovipositing any fertile batches. However, since disregarding these (Table 1, compare rows 3 and 4) does not appreciably elevate the mean number of fertile batches, death before completion of a full series of oviposition is apparently not the entire explanation for variability in the number of batches per female.

Oviposition by Infertile Females – Seventeen of 20 virgin females failed to oviposit. Two oviposited one infertile batch each, and one oviposited two infertile batches. A comparison of adult longevity of those virgins that failed to oviposit with the time between the final molt and the first oviposition of virgins that oviposited (Fig. 3) suggests

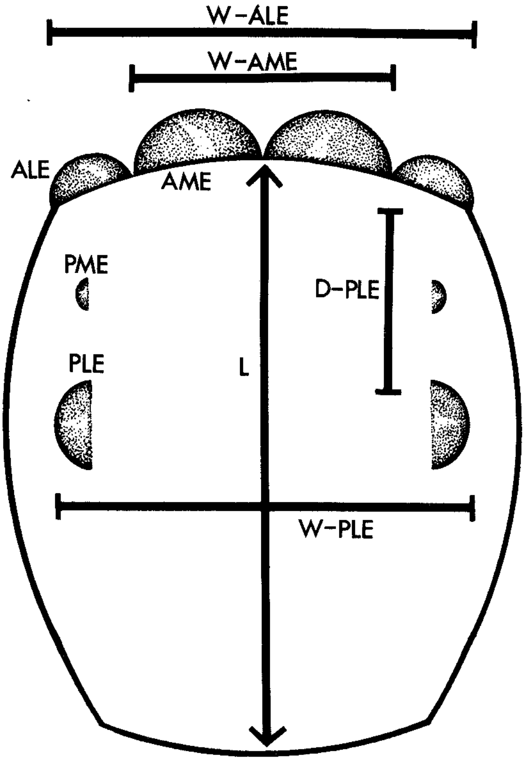

Fig. 2.–Carapace of *Phidippus johnsoni.* Eyes: anteromedial (AME), anterolateral (ALE), posteromedial (PME), posterolateral (PLE). Carapace features: distance from anterior edge of carapace, between the two AME, to posterior end of carapace (L); distance from lateral edge of one PLE to lateral edge of other (W-PLE); distances between lateral edges of the two ALE (W-ALE) and the two AME (W-AME); distance measured from the posterior edge of AME to anterior edge of PLE (D-PLE). See text for additional details.

that oviposition by virgins occurs at a time substantially after maturity, and that those virgins that failed to oviposit were generally ones that died before reaching this advanced age. Since a Mann Whitney U-test indicated that significance was approached but not reached (0.10>P>0.05), further data related to this question would be of interest.

Disregarding those females that died less than 40 days after copulation, 14 mated females failed to oviposit after mating, and 15 oviposited infertile batches only. The number of batches oviposited by infertile mated females (Table 1, compare rows 1 and 2) was fewer than the number oviposited by fertile mated females (t = 4.356, P<0.001). Copulation seems to influence oviposition somehow, and it would be of interest to compare the mechanisms involved with those known for insects (Engelmann 1970, Leopold 1976). It is not known whether mated infertile females were inseminated. However, they did not behave the same as virgin females when the date of the first oviposition is considered (Fig. 3). More time elapsed between maturity and the first oviposition for virgin females than for mated infertile females (Mann Whitney, P<0.01), suggesting that copulation influenced oviposition somehow even when mating did not produce fertile eggs. Oviposition by infertile females, including virgins, infertile batches from fertile females, and infertile eggs in fertile batches have been reported for other salticids (Edwards 1975, Horner and Starks 1972). Fertile females oviposit approximately 42 infertile eggs each (Table 1, rows 5 and 6), some of which tend to be in infertile batches and even more of which tend to be in fertile batches (Table 1, rows 7 and 8).

Number of Eggs and Hatch Proportion – Fewer eggs are oviposited in each successive batch of eggs (Fig. 4), as is frequently the case in spiders (Bristowe 1958). Also, the proportion of the eggs that hatch (hatch proportion) decreases with each successive batch as has been reported in other salticids (Edwards 1975, Gardner 1965, Horner and Starks 1972). The trend toward fewer eggs and smaller hatch proportions is indicated by linear regression (Fig. 4) and by performing a series of paired comparisons (t-tests). In the latter, each fertile batch of a given female was compared with her previous batch, and tests for each set of batches were significant (P<0.01).

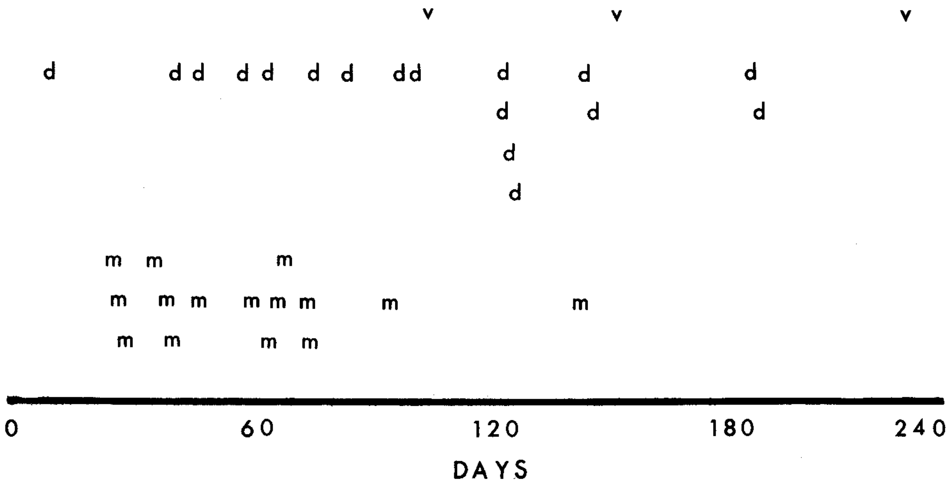

Fig. 3.–Oviposition by infertile females. Each point represents a different individual spider. *Days*: number of days elapsed since reaching maturity. *v*: First oviposition by virgin female. *d*: Death of virgin female that failed to oviposit. *m*: First oviposition by infertile, mated female.

Table 1.–Data related to oviposition. See text for definitions of "Fertile Batch" and "Fertile Female." Note: Means ± S. D. identical for digits expressed in rows 3 and 4.

	Mean ± S.D.	Max.	Min.	n
1. Total number of batches oviposited by fertile females.	3.1 ± 1.32	7	1	71
2. Number of batches oviposited by infertile mated females.	1.5 ± 0.83	4	1	15
3. Number of fertile batches oviposited by fertile females.	2.6 ± 1.14	5	1	71
4. Number of fertile batches oviposited by fertile females that oviposited at least one infertile batch.	2.6 ± 1.14	5	1	29
5. Total number of eggs oviposited by fertile females.	207.9 ± 81.84	355	68	30
6. Number of fertile eggs oviposited by fertile females.	165.5 ± 63.40	309	64	30
7. Number of infertile eggs within fertile batches. (Females that oviposited at least one infertile batch.)	69.6 ± 53.39	147	3	8
8. Total number of eggs within infertile batches. (Fertile females that oviposited at least one infertile batch.)	28.4 ± 13.68	54	12	8

Timing of Oviposition – Approximately one month (24.8 ± 5.36 days) generally elapsed between copulation and the first oviposition by fertile females. The timing was more variable for infertile mated females (43.0 ± 25.85 days). Subsequent fertile oviposition followed at approximately one month intervals (30.0 ± 13.73 days), with infertile batches being oviposited after more variable periods (39.1 ± 27.52 days). In *Metaphidippus galathea* (Walckenaer), the interovipositional interval is 14.6 days (Horner and Starks 1972).

Hatching and Dispersal – Eggs hatch three weeks after oviposition (21.7 ± 1.56 days), and the first instar spiderlings disperse from the maternal nest after another three weeks (20.3 ± 1.52 days). In *Plexippus sitipes* Karsh (Miyashita 1969), the time between oviposition and hatching is similar (27 days), and the time between hatching and dispersal is very similar in *Phidippus coccineus* Peckham and Peckham (21 days, 7 females) (Gardner 1965). In *Phidippus regius* C. L. Koch (Edwards 1975) *P. coccineus* (Gardner 1965), and *Phidippus audax* (Bailey 1968), the time between mating and the first oviposition is very similar to that for *P. johnsoni*.

POSTEMBRYOLOGICAL DEVELOPMENT

Maturation Time – In the araneid spider *Araneus diadematus* Clerck, spiderlings within single batches fall into two groups, slow and fast developers (Ramousse 1973, Reed and Witt 1972), which require greatly differing time periods in order to obtain maturity in the laboratory under identical conditions. In the laboratory, some *P. johnsoni* reached maturity after a substantially shorter time than was the case for all other individuals (Fig. 5), suggesting that slow and fast developers occur in the Salticidae also, a group not closely related to the Araneidae.

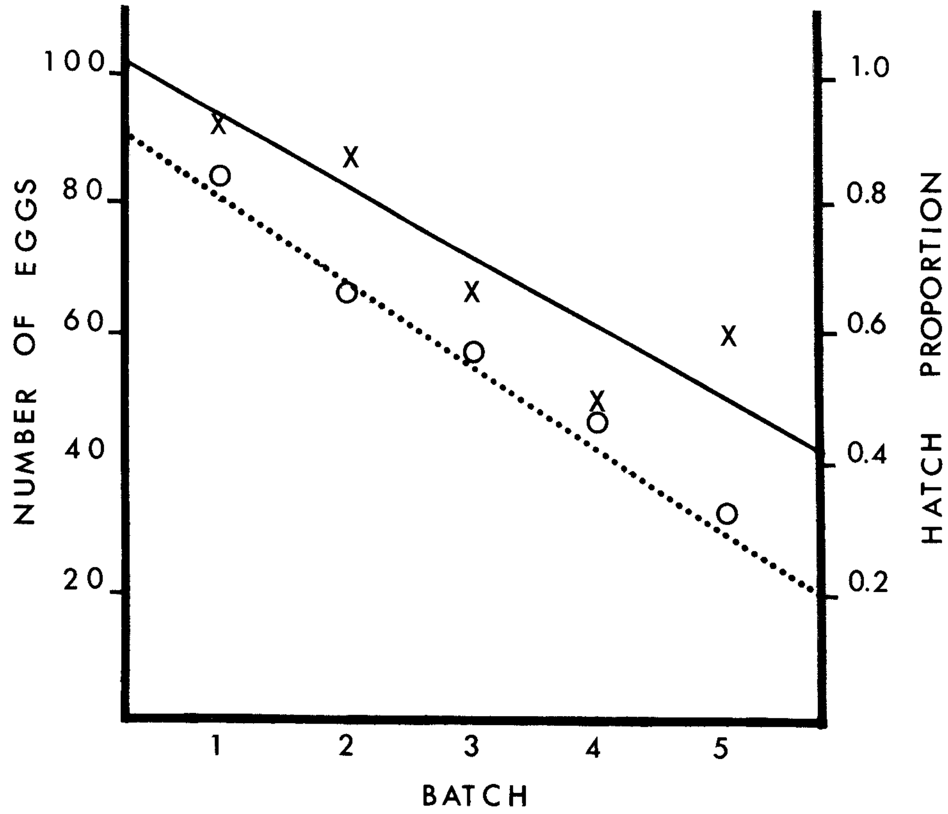

Fig. 4.—Decreasing size and hatch proportion (defined in text) of successive batches. Only fertile batches included. Both regression coefficients less than zero ($P<0.001$). Linear regression equations: Batch size (dotted line), $Y = 92.87-12.07X$; hatch proportion (solid line), $Y = 1.07-0.12X$. Sample sizes: first batch, 30; second, 26; third, 20, fourth, 12; fifth, 4.

In the laboratory, maturation time was shorter for males than for females (Fig. 5) (Mann Whitney, $P<0.001$). Earlier maturity of males was the pattern in phenology censuses also. Also when spiders were collected as subadults at Tilden and Mt. Diablo and taken to the laboratory, the males matured earlier than the females (Fig. 6) (Mann Whitney, $P<0.001$). Horner and Starks (1972) reported shorter time between hatching and maturity for 18 male *Metaphidippus galathea* (180.5 ± 21.92 days) compared to 12 females (193.2 ± 25.00 days). The standard deviations were calculated from the 95% confidence limits for the means that they provided. However, assuming that their data were normally distributed, a t-test did not indicate that their means were significantly different.

Levy (1970) proposed that spiders fall into two groups with respect to life cycles. One group consists of species for which the males and females mature after a period of time and a number of molts such that spiders originating from the same egg batch overlap in time when mature. The other group consists of ones for which males have sufficiently fewer molts than females such that they do not overlap and siblings from the same batch cannot mate with each other. *P. johnsoni*, like the majority of spiders that have been

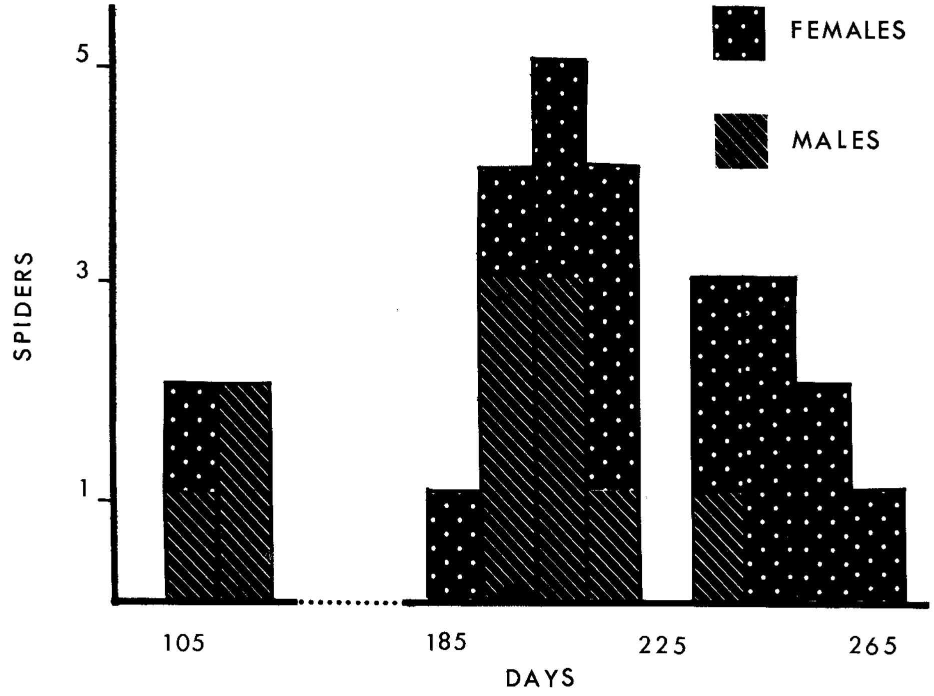

Fig. 5.–Comparison of female and male maturation time in the laboratory. Maturation time: number of days elapsed between hatching and maturity. Recorded in graph for 10-day intervals (105 represents 101-110 days, etc.).

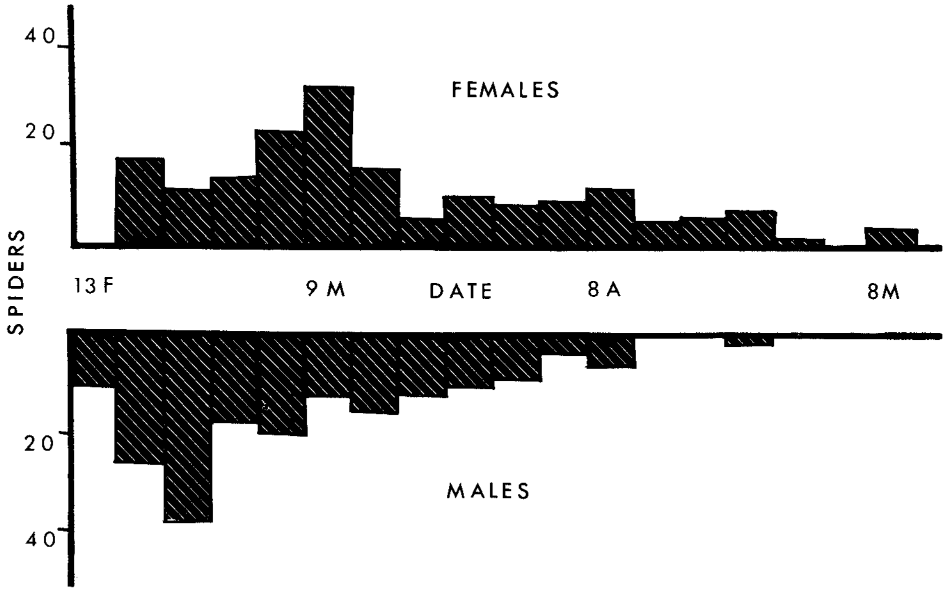

Fig. 6.–Comparison of female and male maturity date. Spiders collected as subadults at Tilden and Mt. Diablo. Matured in laboratory. Maturity date: day on which spider reached maturity. Recorded in graph for 5-day period (13 February represents 11 Feb.-15 Feb., etc.).

investigated, belongs to the first group. Robinson and Robinson (1978) have suggested that the second group is more prevalent in the tropics.

Spiders from the laboratory matured earlier than those from the field (compare Fig. 6 and 7) (Mann Whitney, P<0.001). Gardner (1967) reported earlier maturity of laboratory reared *P. coccineus* compared to ones in the field. More plentiful food, higher temperatures, different light regimes, and other factors might be involved.

Number of Molts – In the laboratory, males of *P. johnsoni* molted fewer times before reaching maturity compared to females (Table 2). The shorter maturation time of males (Fig. 5) is related to this difference. Although a Mann Whitney test on these data does not indicate a significant difference, significance was approached; and when the data from the field, involving a greater number of spiders, is considered, there is a significant difference (P<0.001) in the number of times females and males molt before reaching maturity.

There is also considerable intrasexual variation in the number of molts before maturity (Table 2). Intra- and intersexual variation in the number of molts before maturity, with males maturing in fewer molts occurs also in *Phidippus audax* (Taylor and Peck 1974), *Phidippus regius* (Edwards 1975), and *Philaeus chrysops* Poda (Bonnet 1933). The data of Bonnet, Edwards, and Taylor and Peck are summarized in Table 2, and Mann Whitney tests were carried out. The number of molts for males compared to females differs

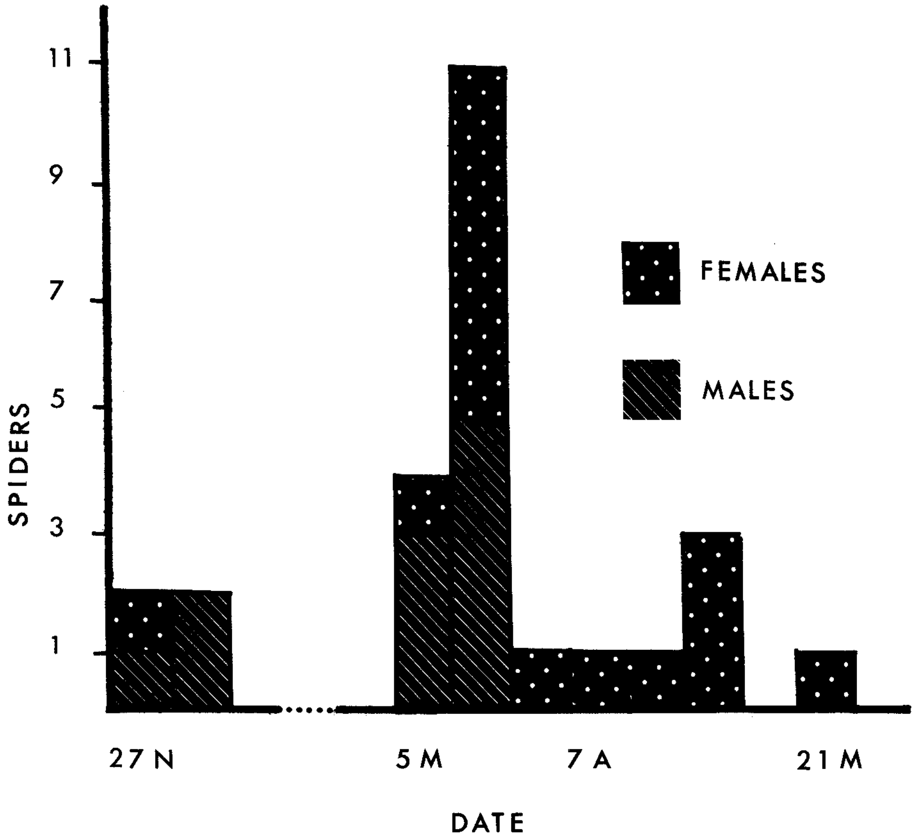

Fig. 7.–Comparison of female and male maturity date (defined in Fig. 6) of spiders reared from eggs in laboratory. Recorded in graph for 11-day periods (27 Nov. represents 22 Nov. -2 Dec., etc.).

Table 2.–Number of individuals of *Phidippus johnsoni, Phidippus audax, Phidippus regius,* and *Philaeus chrysops* that matured after different numbers of molts. Lab: spiders reared from eggs in laboratory. Field: spiders collected as large immatures at Tilden and Mt. Diablo. Data for *P. audax* from Taylor and Peck (1974); *P. chrysops,* Bonnet (1933); *P. regius,* Edwards (1975).

SPECIES	SEX	LOCATION	NUMBER OF MOLTS BEFORE MATURITY						
			5	6	7	8	9	10	11
P. johnsoni	Male	Lab	1	6	6	2	0	0	0
		Field	0	2	20	43	0	0	0
	Female	Lab	0	6	8	4	0	0	0
		Field	0	0	3	71	15	0	0
	Both	Lab	1	12	14	6	0	0	0
		Field	0	2	23	114	15	0	0
P. audax	Male	Lab	0	0	3	6	0	0	0
	Female	Lab	0	0	1	2	17	0	0
P. regius	Male	Lab	0	0	0	5	22	8	0
	Female	Lab	0	0	0	1	13	12	1
	Both	Lab	0	0	0	6	35	20	1
P. chrysops	Male	Lab	0	3	5	0	0	0	0
	Female	Lab	0	0	7	1	0	0	0
	Both	Lab	0	3	12	1	0	0	0

significantly for the laboratory data from *P. audax* ($P<0.001$) *P. regius* ($P<0.05$), but not for *P. chrysops.* It is apparently a common phenomenon in spiders for the male to mature after fewer molts than females (Bristowe 1958).

Duration of Instars – The durations of the postembryo stage and the first four instars tend to be only a few weeks (17.0 ± 2.14 days) (Table 3). Later immature instars tend to be longer (60.6 ± 38.75 days) (Mann Whitney, $P<0.05$). Later instars are also more variable, as indicated by the coefficients of variation (means 12.1 for postembryo through instar 4; 61.2 for instars 5 and 6; Mann Whitney, $P<0.05$). The subadult instar tended to be relatively long in duration. The postembryo showed especially little variation in duration, being 16 days for each spider. In *P. regius* (Edwards 1975), the postembryo was consistently 14 days in duration. Later instars were of increasing duration. Both Miyashita (1969) and Horner and Starks (1972) reported great variability in instar duration in the salticids they reared, and other investigators (Horner and Starks 1972, Taylor and Peck 1974) reported greater variation in later instars.

Bonnet (1930) pointed out a relation between adult body size of spiders and the number of preadult molts. Spiders measuring 8 to 11 mm when adults tend to molt 7 or 8 times, which is consistent with the data for *P. johnsoni* (Table 2).

Table 3.–Duration (days) of instars of immature spiders. "Subadult" defined in text. Spiders that died during the instar are excluded.

INSTAR	MEAN ± S.D.	Max.	Min.	n
Postembryo	16.0 ± 0.00	16	16	29
1st instar	19.5 ± 2.37	24	16	29
2nd instar	14.7 ± 2.46	20	12	37
3rd instar	15.7 ± 2.01	20	13	36
4th instar	19.3 ± 3.53	30	15	34
5th instar	50.8 ± 39.00	159	17	32
6th instar	79.0 ± 36.00	136	24	17
7th instar	74.3 ± 6.03	80	68	3
Subadult	83.1 ± 36.18	145	19	26

Body Size – Compared to the distensible abdomen, which changes in size with feeding within a single instar, the cephalothorax is rigid with its size remaining relatively constant during a single instar. Numerous authors (salticids: Bailey 1968, Crane 1948, Dondale 1961, Edwards 1975; see Hagstrum 1971, for references concerning other spider families) have used measurements from the carapaces of spiders as indicators of instar size. When the coefficients of variation for the five features measured on the carapaces of *P. johnsoni* are compared, there is no indication that different features are more variable than others. Also there is no indication that variability changes with instar. For each feature, overlap tends to occur in the later instars but not in the earlier ones (Table 4, Fig. 8).

Because the abdomen is distensible, body length was highly variable, even for the same individual during the same instar. Abdomen sizes were defined as follows: the diameter of a slender abdomen is conspicuously less than that of the cephalothorax; and the diameter of a fat abdomen is conspicuously greater than that of the cephalothorax. Fat abdomens were especially common on gravid females. After oviposition, body length often changed dramatically. For example, a ninth instar female may be as much as 15 mm in body length when gravid, but only 11 mm after oviposition. Immatures were prone to have fat abdomens before molting and slender ones afterwards, although changes in body length were usually less dramatic than in the case of ovipositing females. Adult males never had

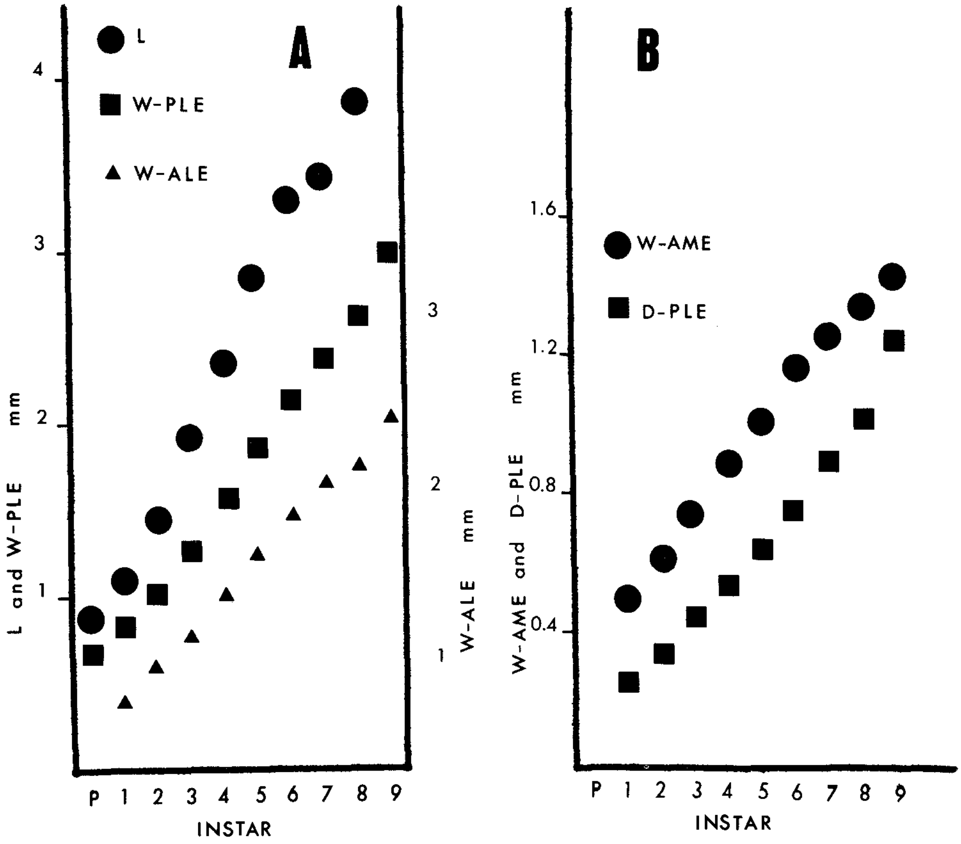

Fig. 8.–Relation between carapace features (defined in Fig. 2) and instar. Each point represents a mean. See Table 4 for sample sizes and coefficients of variation.

Table 4.–Variability and overlap of carapace features (defined in Fig. 2) of different instars (Pe: postembryo) C. V.: coefficient of variation. For a given instar, overlap occurs (indicated by +) if the mean minus one S. D. of the instar is less than the mean plus one S.D. of the previous instar. N: number of spiders measured. (*, not recorded).

Carapace Feature		Instar									
		Pe	1	2	3	4	5	6	7	8	9
L	C.V.	3.26	2.42	6.94	5.03	5.45	5.40	4.48	3.78	4.09	*
	Overlap	*	0	0	0	0	0	0	+	+	*
	N	10	18	24	26	26	28	16	52	12	*
W-PLE	C.V.	1.49	2.07	4.14	4.34	5.36	4.96	5.59	5.91	7.64	4.25
	Overlap	*	0	0	0	0	0	0	0	0	0
	N	10	33	25	27	28	31	28	16	55	12
W-ALE	C.V.	*	2.82	4.22	4.20	3.52	3.03	4.32	4.01	6.30	4.53
	Overlap	*	*	0	0	0	0	0	0	+	0
	N	*	33	25	27	28	31	28	16	55	12
W-AME	C.V.	*	2.01	3.99	4.27	3.37	2.96	3.86	4.10	5.32	2.15
	Overlap	*	*	0	0	0	0	0	+	+	+
	N	*	33	25	27	28	31	28	16	55	12
D-PLE	C.V.	*	3.90	5.14	3.18	3.24	3.90	10.43	7.95	12.72	6.49
	Overlap	*	*	0	0	0	0	0	+	+	0
	N	*	33	25	27	28	31	28	16	55	12

fat abdomens. Postembryos and first instars tended to have body lengths of approximately 2 mm; second instars, 4 mm; third, 6 mm; fourth, 7 mm; fifth, 7 to 8 mm; sixth, 8 to 12 mm; seventh, 8 to 13 mm; eighth, 10 to 14 mm; and ninth, 11 to 15 mm.

Instars of Spiders in Nature – As for the laboratory-reared spiders, adult males from the field tend to be smaller than adult females (Table 5). These spiders were collected as adults or subadults at Mt. Diablo. From the measurements made on each spider, a judgement was made for each concerning the instar to which it belonged. For spiders that were collected as subadults, the subadult exuvium was measured in addition to the spider. When all measurements were compared with the means and standard deviations for laboratory reared spiders of known instar (Fig. 8), there was one instar that each field-collected spider resembled most in size. The spider was judged to belong to this instar. No single measurement was adequate alone, as was also the case in Edgar's (1971a) study of lycosid life history. Determination of instars of spiders from the field was based on an assumption that the relation between size and instar for laboratory-reared spiders is applicable in nature. The accuracy of this assumption cannot be determined with data presently available.

Males in the field, as in the laboratory, seem to mature after fewer molts than females (Table 2) (Mann Whitney, $P<0.001$). Earlier maturity, fewer molts before maturity and smaller adult size of males compared to females is a rather general trend in spiders

Table 5.–Sexual dimorphism. Carapace features defined in Fig. 2. Measurements: mean ± S.D. (mm). All t-values, $P <0.001$. Sample sizes: females, 63; males, 41.

CARAPACE FEATURE	FEMALES	MALES	t
W-PLE	2.8 ± 0.20	2.4 ± 0.16	10.044
W-ALE	2.2 ± 0.16	2.0 ± 0.12	8.123
W-AME	1.3 ± 0.08	1.2 ± 0.07	7.511
D-PLE	1.1 ± 0.12	0.9 ± 0.10	8.169

(Bonnet 1930, 1933, Bristowe 1958, Juberthie 1954, Levy 1970, Peck and Whitcomb 1970). *P. johnsoni* from the field tend to be larger than those reared in the laboratory, possibly because they molt more times before reaching maturity.

LONGEVITY AND MORTALITY

Survival of Immatures – The proportion of laboratory-reared spiders that survived for the duration of each instar varied little, and it was relatively great for each (Table 6). Overall survivorship from hatching to maturity was relatively high in the laboratory. Nine spiderlings involved in the study of postembryonic development either escaped, were accidentally killed, or were intentionally killed and preserved as representatives of each instar. Of the 30 remaining spiderlings, only four died before they reached maturity. In contrast, Bonnet (1933), Edwards (1975), Gardner (1965), Horner and Starks (1972), and Miyashita (1969) reported relatively higher mortality among salticid immatures, as seems generally true in studies of spider postembryonic development (*e.g.* see Bonnet 1930, Deevey and Deevey 1945). There may be a number of reasons for the relatively high survivorship of *P. johnsoni* in this study. The rearing procedure, providing continual food and moisture, was different from that used in other rearing studies, suggesting that this procedure may be particularly useful, at least for some species. Another factor may be that the prey provided (Diptera) are known to be an important part of the diet of *P. johnsoni* in the field (Jackson 1978a). Although some spiders evidently require considerable variety in their diet during development (Miyashita 1968), Diptera alone are adequate for survival of *P. johnsoni* in the laboratory. Suzuki and Kiritani (1974) showed that a varied diet can affect fecundity in spiders, and this has not yet been investigated in *P. johnsoni.*

Comparison of Male and Female Adult Longevity – Adult spiders tend to survive 3 to 4 months in the laboratory, with females surviving longer (126 ± 58.3 days) than males (94 ± 47.7 days; $t=4.079$, $P<0.001$). There also is evidence from the phenology censuses that male longevity is shorter than that of females in nature. Greater longevity of females in the laboratory compared to males has been reported in *P. coccineus* (Gardner 1965), *P. audax* (Bailey 1968), and in spiders from other families (*e.g.*, see Bonnet 1930, Deevey and Deevey 1945). Assuming the data of Horner and Starks (1972) are normally distributed, the differences in longevity between females (222 ± 72.6 days, 20 females) and males (184 ± 77.4 days, 20 males) is not significantly different, although we may expect a difference if the sample size were increased.

Mortality in the Laboratory – When a dead or dying spider was seen in the laboratory, casual observations were made of the spider's behavior, location, and condition. A few spiders were accidentally or intentially killed, and one that had been collected from the field died in the laboratory as a result of parasitization by an acroserid fly. Otherwise, the cause of death in the laboratory was unknown. Among both those spiders used in observations of postembryonic development and numerous others reared from immatures collected from the field, death of immatures frequently occurred during molting. Edwards (1975) reported that most deaths he witnessed in the laboratory involved spiders that were molting, and this seems to be a particularly vulnerable time for spiders (Turnbull 1973).

The appearance of the dead spiders varied greatly. In some cases, the spider's abdomen was collapsed, and its legs were curled under its body. This was true of all spiders that

Table 6.–Survival rates of immature spiders (Pe: postembryo).

INSTAR OF IMMATURE	Pe	1	2	3	4	5	6	7
NUMBER OF SPIDERS	30	30	37	36	35	33	15	3
PERCENTAGE THAT SURVIVED TO NEXT INSTAR	97	97	100	100	97	97	93	100

died during molting, for example. Dessication would seem to be involved in these deaths, although the causes of dessication are not known. However, other dead spiders did not have collapsed abdomens, and some females had greatly distended abdomens. Dead spiders without collapsed abdomens sometimes had their legs curled under their bodies, but others had legs extended stiffly perpendicular to the body. In some cases, spiders were lethargic for a day or more before death, moving sluggishly when prodded with a brush. In other cases, spiders seemed normal as shortly as one hour before death. Two spiders were found dead with flies held in their fangs, apparently having died while feeding. The great majority of dead spiders were found outside their nests.

PHENOLOGY

General Comments – The data for the two years are summed at each month for each population (Fig. 9-13), since the data for each year showed virtually the same pattern. Also, these patterns are consistent with more casual observations outside the monthly census areas, both at these habitats and at other similar habitats. The "mating season" is the time period during which adult males and females are simultaneously present in the field, confirmed by observation of courting or mating pairs in the field during each of these months.

The immatures are classified into two groups: ones less than 6 mm in body length, probably first through third instars; and ones greater than 6 mm, probably belonging to the fourth and later instars. As in the laboratory, males in nature mature earlier than females, at least in the Coastal Range. In the censuses, there was a preponderance of males at the beginning of the mating season. Also, I spent many days at Mt. Diablo and Tilden previous to the mating season, collecting spiders in areas other than the census areas. Many adult males, especially ones in nests with exuvia, were found previous to finding the first newly matured females.

Comparison of Beach and Coastal Range – Beach and Coastal Range populations have distinctly different phenologies (compare Fig. 9 and 10 with Fig. 11 and 12). In the Coastal Range, there was a short mating season, a month or two in duration. In contrast, the mating season in Beach populations extended through two thirds of the year. In the Coastal Range, the subadults matured nearly synchronously in the spring. At Beach habitats, subadult males and females matured throughout the prolonged mating season. The more pronounced mating season in the Coastal Range is probably an adaptation to the more seasonal climate in the Coastal Range.

Primarily wood was searched in the Beach habitats. Except during the density censuses, the small crevices in wood were not broken open and searched for spiders. Comparing density (Table 7) with phenology census data (Fig. 11 and 12) suggests that had wood been thoroughly searched in this way each month, a greater proportion of immatures 6 mm or less in length would have been uncovered, but the other categories would have been only negligibly affected.

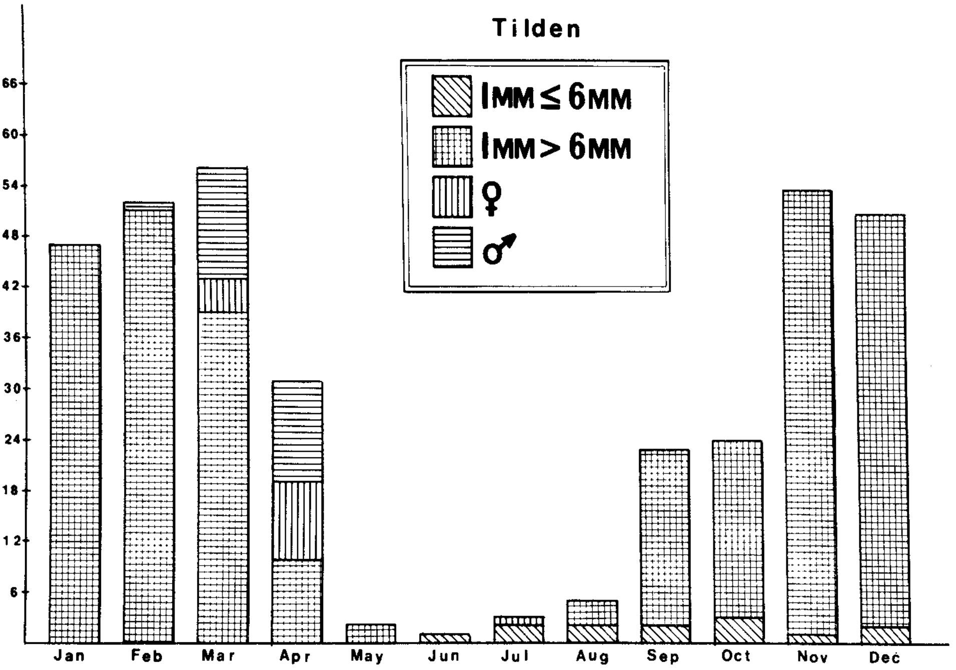

Fig. 9.–Phenology at Tilden Regional Park, Contra Costa Co., California. Number of individuals found during monthly censuses. Sum of data for two years.

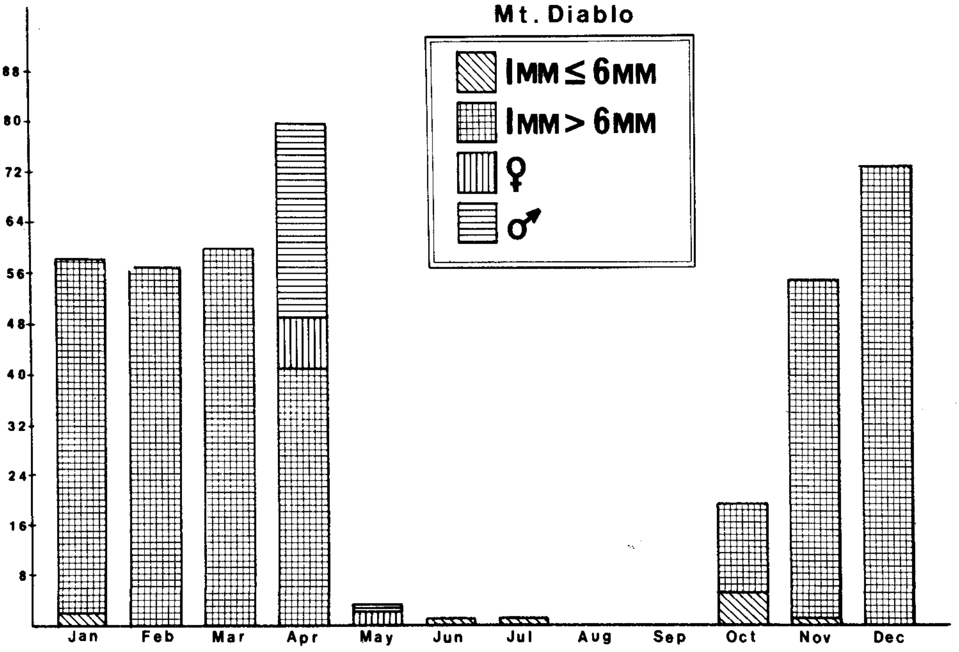

Fig. 10.–Phenology at Mt. Diablo State Park, Contra Costa Co., California. Number of individuals found during monthly censuses. Sum of data for two years.

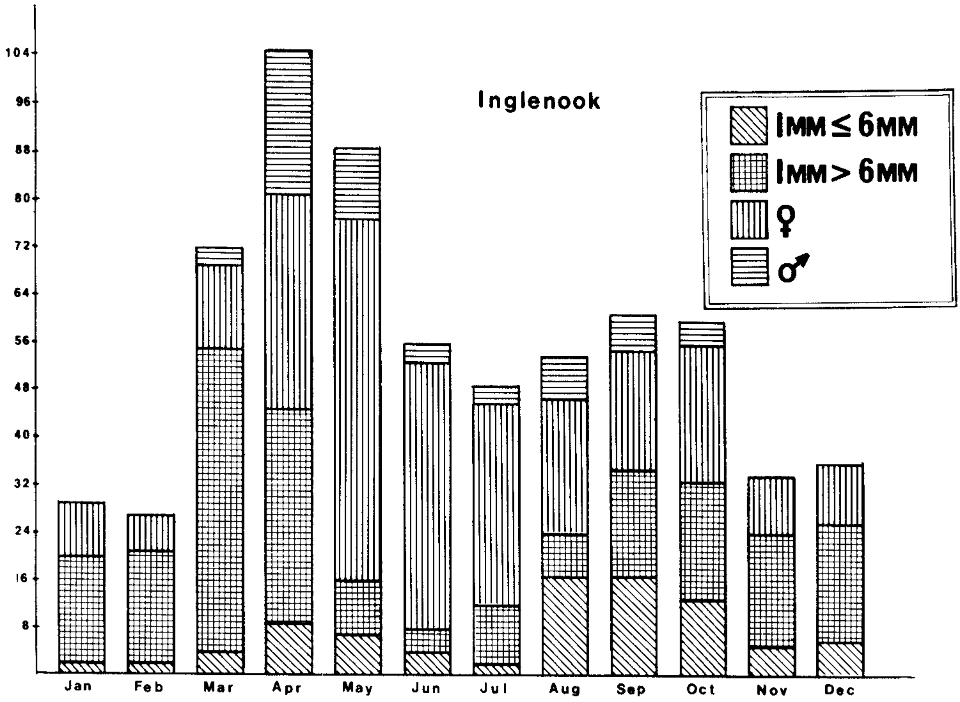

Fig. 11.–Phenology at Inglenook Fen, Mendocino Co., California. Number of individuals found during monthly censuses. Sum of data for two years.

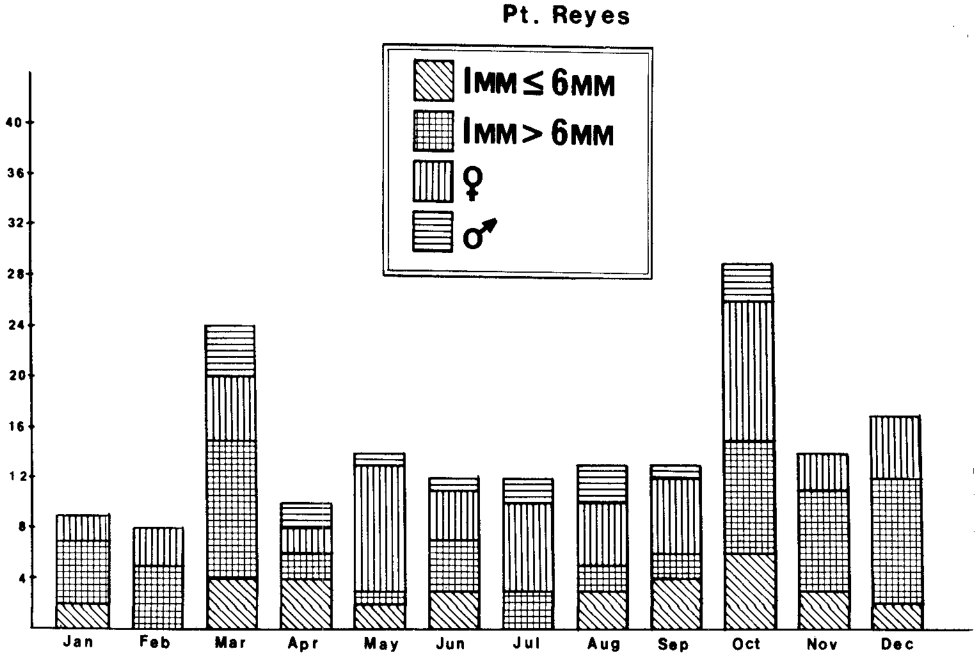

Fig. 12.–Phenology at Pt. Reyes National Seashore, Marin Co., California. Number of individuals found during monthly censuses. Sum of data for two years.

At Tilden (Fig. 9) and especially at Mt. Diablo (Fig. 10) *P. johnsoni* largely disappeared from the census areas during the summer. The small immatures spend the summer in shrubs and trees in the vicinity, from which they can be readily extracted by beating the limbs over a piece of cloth or a wire screen and in which they can be found, occasionally, occupying nests. However, immatures were not found in the shrubs and trees at other times of the year. Also, adults were rarely found in shrubs and trees. Probably the longevity of adults, especially males, is short in the summer in the Coastal Range, since few were found at this time. There is no evidence that any adult females survive the long period between mating seasons in the Coastal Range. Only a few adult females survive this long in the laboratory, with continuous food and moisture and mild temperatures. On the other hand, many females in the Beach populations apparently survive the brief period between mating seasons in these habitats.

Alpine Populations – It was not possible to carry out monthly censuses at Whiskey Mt., but using other information a probable hypothesis can be proposed concerning phenology. I visited Whiskey Mt. three times, each time during a different year and month (June, July, August). In July and August, I found immatures, adult males and adult females. In June, snow still covered the ground in some places, and it had only recently melted in the areas searched. At this time adult females and immatures of all sizes were present, but no adult males were found. However, when subadult males collected at this time were taken to the laboratory, they soon matured. At approximately the same time of the year, adult males were found at Blacktail Butte, a lower elevation site (2100 m) in Grand Teton National Park, Wyoming, which is at approximately the same latitude as Whiskey Mountain. Based on these observations, it seems likely that males mature soon after the snow melts on Whiskey Mountain and that the mating season extends through the summer until the next winter's snow arrives.

The phenology at Whiskey Mountain apparently contrasts with that at Pothole Dome (Fig. 13), where there is a very short mating season only a few weeks in duration, at the

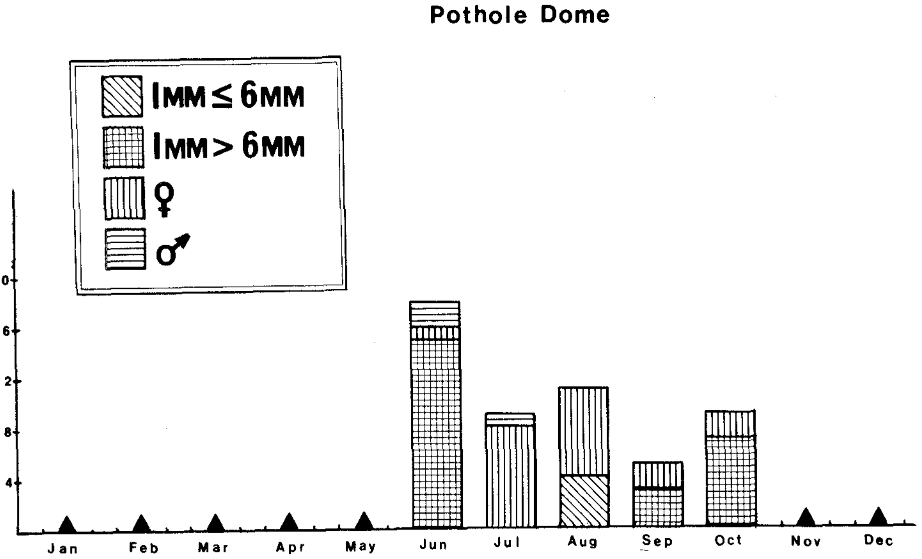

Fig. 13.–Phenology at Pothole Dome, Mariposa County, California. Number of individuals found during monthly censuses. Sum of data for two years. Ground covered by snow during months marked by triangles.

Table 7.–Population densities in different habitats. Number of nest sites (rocks and pieces of wood 5 cm or more in length) in each census area estimated by counting those in a randomly chosen sector. Inglenook Census Area No. 1 consisted of the monthly census area (A) plus an additional contiguous area (B). In Inglenook Census Area No. 2, there were only 4 pieces of wood (A: area covered by wood; B: remaining area). Number of nest sites not estimated for Whiskey Mountain Census No. 2. Only one census carried out at Pothole Dome.

CENSUS	INGLENOOK			POINT REYES	TILDEN	MT. DIABLO	WHISKEY MT.	POTHOLE DOME
	A + B	A	B					
NUMBER 1								
Area (M^2)	51,327	1974	49,353	1923	4181	5574	1431	1328
Spiders per 1,000 M^2	2.41	34.45	1.13	8.31	6.93	6.46	3.49	6.77
Spiders per 10,000 nest sites	347.33	416.66	288.95	36.23	191.79	169.01	8.40	21.64
Area of Sector (M^2)	1510			84	232	279	41	51
NUMBER 2								
Area (M^2)	455	61	394	2044	5806	3716	6967	
Spiders per 1,000 M^2	65.90	490.77	0	5.38	10.68	8.34	6.89	
Spiders per 10,000 nest sites				35.71	216.78	234.84		
Area of Sector (M^2)				93	290	186		

beginning of the summer. Again males seem to mature soon after the snow melts in the early summer. During both years an extra census was carried out at Pothole Dome very soon after the snow melted, a week or two previous to the census reported for June in Fig. 13. Although numerous adult females and immatures were found, only two adult males were present. These males had probably just molted since they were in nests with exuvia. As in the Coastal Range, males vanish later in the summer, as conditions become more xeric. Conditions do not become so xeric on Whiskey Mountain, and the contrast in phenology seems to be a reflection of this climatological difference.

Oviposition in Nature – The months during which oviposition occurs correspond approximately with the mating season (Table 8). Eggs, postembryos, and/or first instar spiderlings inside nests were found either during the phenology censuses or in neighboring areas during most of the year in the Beach habitats and throughout the summer in Alpine habitats. The egg shells found at Pothole Dome in May and at Whiskey Mountain in June were in unoccupied nests. These were perhaps remains from batches oviposited in previous summers. The relatively few eggs, postembryos, and masses of first instar spiderlings in nests in the Coastal Range were found in the early summer. A possibility that needs consideration is that ovipositing females go under very large boulders that I could not overturn by hand. Heat and desiccation would present less severe conditions in these locations. Also, they might go into holes in the ground. This was suggested by an adult female with eggs found in a hole containing a bumble bee (*Bombus*) nest (Charles Griswold, pers. comm.).

DENSITY

General Comments – Apparently few, if any, spiders were missed by the density census methods. In the case of one of the Tilden censuses, I collected each *P. johnsoni* that was found. When the area was searched again the next day, no additional *P. johnsoni* were discovered.

Table 8.–Seasonal occurrence of oviposition in different populations. Census (phenology census area; see text): counted number of nests found containing eggs, postembryos, and/or masses of first instar spiderlings. Nests containing egg shells, but no living progeny given in parentheses. Other (sites in the vicinity of the census areas): only qualitative data available. Presence: +; absence: –. Pothole Dome not visited November to April; Whiskey Mountain not visited September to May. No monthly censuses made at Whiskey Mountain. No progeny or egg shells found at Mt. Diablo, Tilden, Pt. Reyes and Inglenook in January, February, November and December.

POPULATION		MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT
Mt. Diablo	Census	0	0	0	0	0	0	0	0
	Other	–	–	+	+	–	–	–	–
Tilden	Census	0	0	2	0	1	0	0	0
	Other	–	–	+	+	–	–	–	–
Pt. Reyes	Census	0	0	1	4	1	1(1)	1(5)	1(2)
	Other	–	–	+	+	–(+)	+(+)	–	–(+)
Inglenook	Census	0	0	3	8(4)	6(44)	10(20)	0(8)	2(2)
	Other	+	+	+(+)	–	+(+)	+(+)	+	+(+)
Pothole Dome	Census			0	0(1)	0	0	0	0
	Other			–(+)	+(+)	+	+(+)	+	–
Whiskey Mountain	Other				+(+)	+(+)	+(+)		

Except for Inglenook, densities calculated with respect to area are quite similar (Table 7). However, density varies greatly with respect to number of nest sites.

Patchiness – At Inglenook the phenology census area was a 260 X 8 m rectangle along one side of a fence which enclosed cattle. The cattle were on the opposite side of the fence from the census area. All other density census areas were more nearly square in shape. In order to obtain a more nearly square area at Inglenook Census Area No. 1, the area searched was extended beyond the phenology census area to a parallel fence at the opposite side of the pasture. This was a very heterogeneous area with respect to nest sites. Wood was concentrated near the fences, especially in the vicinity of the monthly census area. Comparing density inside the phenology census area with that for the remainder of Census Area No. 1, the difference is dramatic (Table 7). Census Area No. 2 for Inglenook was an area containing four dead trees on the ground. Again, a very heterogeneous area was censused. In Table 7, the density of Area No. 2 as a whole can be compared to the density calculated for the approximately 61 m^2 liberally estimated as the area covered by the dead trees. All spiders in this census were found on the dead trees. In summary, spiders occurred at Inglenook censuses in patches in which density could be five to ten times greater than at the other census areas. Census areas at the other habitats were rather homogeneous with respect to nest sites. These trends seemed to apply not only to the census areas but generally within the habitats.

Table 9.–Survival of spiders under reduced temperature and without food. Frequencies with which males survived compared (chi square tests of independence) with those for female and immatures. (*, P <0.05; **, P <0.005).

Spiders: Population of Origin	Survived	Females	Males	Immatures
Alpine	Yes	11	0	67
	No	2*	3	46*
Non-Alpine	Yes	71	3	
	No	16**	29	

Another characteristic of Inglenook is that patches containing nest sites and spiders tended to occur as islands in the sense that distances greater than the width of the patch frequently separated it from other patches. Patches occurred at clumps of trees, along wood fences, and at other such places, separated by open sand dunes, open prairies, or other unsuitable space. This was also true of Pt. Reyes to a lesser extent. In contrast, in other habitats space containing nest sites and spiders tended to be very extensive. Unsuitable space tended to form islands or a patchwork within a connected suitable space.

WINTER SURVIVAL

Two of the conditions associated with winter were simulated in the laboratory: lack of food and cold temperature (Table 9). A more realistic simulation of winter should include gradual changes in photoperiod, for example, which would permit the spider to prepare for diapause. However, even with the relatively superficial simulation that was employed, more than half of the females and immatures survived. In contrast, few males survived, consistent with observations from nature. Evidently, adult females and immatures, but not adult males, survive the winter in Alpine habitats, since adult females and immatures, but not adult males, were found when the snow melted in early summer.

The repeat of the experiment using non-Alpine spiders (Table 9) is interesting in showing that the capacity to withstand prolonged periods under reduced temperatures and without food is not restricted to Alpine spiders. Each of 3 males, 3 females, and 21 immatures from Whiskey Mountain, maintained and fed under normal laboratory conditions during this same time period, died before the other spiders were removed from the refrigerator. Each of the spiders that survived in the laboratory experiment was provided food and water when removed from the environmental chamber. The 3 males died within one week of the end of the experiment; each female and immature lived at least three weeks before they were preserved.

Most likely, a one year life cycle normally occurs in the field, at least in the Coastal Range and Beach habitats. However, since a relatively short portion of the year is free from snow in the Alpine habitats and since immatures can survive several months without food when exposed to cold temperatures, consideration needs to be given to the possibility that some *P. johnsoni* in Alpine habitats remain immature longer than one year. It is noteworthy that 102 spiders collected in June at Whiskey Mountain as small (body length 6 mm or less) immatures survived in the laboratory until October or longer before preserved or used in the experiment involving refrigeration, and each remained immature.

GENERAL DISCUSSION

Iteroparity – In *P. johnsoni*, as in probably the majority of spiders (Bristowe 1958), iteroparity occurs. That is, eggs are oviposited in successive batches, rather than in a single batch (semelparity). From models of Murphy (1968) and Charnov and Schaffer (1973), iteroparity would be predicted when the risks of complete failure of batches is great and when survival rates of adults are relatively high compared to immature survival rates. For *P. johnsoni*, destruction of eggs by predators, desiccation, and other factors might be a major risk. Also, future studies should look at whether the small immatures are subject to relatively high mortality due to desiccation and the shortage of suitably small prey when they emerge in the late spring and early summer. Factors such as these might place a positive selection pressure on females that spread their eggs in time among a number of batches. This characteristic could be viewed as "insurance" against environmental risks.

Emlen (1973) suggested that physical limitations might influence the number of eggs per batch in some species. Gravid females of *P. johnsoni* have greatly distended abdomens; and immediately after oviposition, their abdomens are much smaller in size. The number of eggs per batch might be increased by decreased egg size, increased abdomen distension or both. However, smaller eggs would produce smaller spiderlings at hatching, and there might be a great disadvantage for smaller spiderlings related to feeding, dessication, and growth rate (see Lawlor 1976). The advantages related to increased abdomen distension might be countered by disadvantages such as decreased agility, which might lead to increased susceptibility to predation or decreased feeding efficiency.

Decreasing Batch Size and Hatch Proportion – Another characteristic related to oviposition is the decreasing number of fertile eggs in successive batches. There are a number of factors which might favor early batches over later ones for a given female. In the Coastal Range, oviposition begins in the spring, and later batches are oviposited in the summer. Summers are hot and dry, and dessication may be a greater risk in the summer for spiderlings and eggs. Also, small insects probably become less available to the spiderlings as the dry season approaches. Female survival rates also may decrease in the summer. These factors would favor females that invest a greater proportion of their total reproductive effort in the first batch and decreasing proportions in each successive batch, resulting in decreasing number of eggs in later batches.

Absolute batch size will not be discussed here. For an interesting discussion of this subject, see Enders (1976).

Decreasing hatch proportion in successive batches might be simply the result of sperm depletion or loss of sperm or egg viability over time. Another possibility is suggested by the fact that the spiderlings of some species, including *Phidippus regius* (Edwards 1975), feed on infertile eggs before departing the egg sac (Valerio 1974). It is not known whether this occurs in *P. johnsoni.* It would be interesting to investigate the hypothesis that sterile eggs in fertile egg sacs have been selected for as "trophic eggs" (Wilson 1971). Since later batches are oviposited at a time of the year when conditions are probably less favorable for the spiderlings, possibly a greater proportion of sterile eggs are included as a result of selection favoring females that provide increased nourishment per spiderling in the later batches. Provision of sterile eggs, fed upon by the spiderlings, could be viewed as an alternative to provision of more yolk per egg.

Intersexual Size Variation – In *P. johnsoni,* males tend to be smaller than females, which is a very common occurrence in other arthropods and in animals in general Following Ghiselin's (1974) arguments, it will be proposed that the body size of male *P. johnsoni* is the result of an evolutionary compromise resulting from two types of intermale competition. Competition by "male dispersal" is analogous to a race in which the males that find and mate with the largest number of females within a certain time period are favored. Selection for early maturation by males, accomplished by molting fewer times before maturity and resulting in smaller adult body size is expected. An additional factor is that the benefit (in terms of fitness) for the male is probably greatest for males that mate with newly matured females after cohabitation (Jackson 1976) since these females are the most likely to oviposit fertile eggs and the least likely to mate with additional males. Males that mature earlier will encounter a greater number of subadult females.

Competition by "male combat" evidently occurs in *P. johnsoni* also (Jackson 1976), and this form of competition favors larger males. When two males encounter the same female, an aggressive interaction ensues and the larger male tends to drive away the smaller and mate with the female. However, selection related to male combat seems not to be sufficient in magnitude to result in males being larger than females.

Various factors probably favor larger size in females. One of these is probably the ability to store food that will be incorporated into eggs. Also there is probably selection for greater longevity related to oviposition over a prolonged period of time. This may select for larger size. For example, larger individuals may be able to store a greater quantity of fat, enabling them to more effectively endure periods of food shortage that may occur during the summer, waiting to oviposit when conditions become favorable. Also, females tend to remain inside their nests with their eggs, and there may be selection favoring endurance with relatively little food during this period. If females defend the eggs from parasites and predators during this time, this might be still another factor favoring larger size.

Intrasexual Size Variation – Great intraspecific variation in size and number of molts between hatching and maturity has been reported for spiders belonging to a wide variety of families (Levy 1970). In some cases, proximate factors such as nutrition and temperature influence the number of instars that occur (Bristowe 1958, Browning 1941, Jones 1941, Juberthie 1954, 1955). In other cases, as in *P. johnsoni*, the number of instars varies even when feeding, temperature, and other factors are held constant. Variable number of preadult instars are known to occur in various insects also (Chapman 1969). Intrasexual variation in the number of instars may be related to factors favoring intrasexual variation in maturity date and size. For females, variation in the maturity date of her offspring might be the result of selection acting on females similar to that discussed in reference to iteroparity. That is, it could be related to insurance against all progeny happening to mature at a time that is unpredictably unfavorable (see Cohen 1966). In the case of males, it was suggested earlier that opposing selection pressures favor larger and smaller adult size (also see Robinson and Robinson 1978). Perhaps natural selection favors the female that produces some optimal mix of male size classes in her progeny.

Difference in Female and Male Longevity – Shorter longevity of males compared to females seems to be a common pattern in animals. Greater susceptibility of males to predators, due to more conspicuous coloration, for example, might be a factor in the field. However, this longevity difference occurs with *P. johnsoni* in the laboratory also. In the laboratory, predation was absent; food was plentiful; and the males and females were kept under identical temperature and light regimes.

Males seem to be adapted to a lifestyle that emphasizes courtship, mating, and searching for females, in conjunction with greater vagility and earlier maturity, at the expense of maintenance functions that serve to prolong survival. Copulation is the male's only investment in the next generation. In contrast, females produce eggs stocked with yolk, oviposit successive batches over a period of several months; and remain at the maternal nest until the spiderlings hatch and disperse. These factors favoring prolonged life of females are not operative on males.

Causes of Interpopulational Variation in Phenology – Response to photoperiod and synchrony of adult mortality are possibly the two major factors responsible for phenology differences in populations of *P. johnsoni*.

During the summer in the Coastal Range (Fig. 9 and 10), adults, especially males, die; eggs hatch; and the next generation begins. In the laboratory, with continual food and constant 24°C temperature, spiders require 6 to 7 months after hatching before reaching maturity; and possibly greater time is required in the field, where temperature and feeding are not as uniform. Perhaps the immature spiders in these populations generally are not able to mature much before the spring mating season. However, the relatively synchronous maturation that occurs in the field suggests that other factors are involved as well, one of which might be photoperiod characteristics.

In the Beach habitats (Fig. 11 and 12), where adults are probably not subject to environmental conditions during the summer that are as severe as those in the Coastal Range, females tend to survive and oviposit through the summer and into the fall. Compared with the Coastal Range summer mortality of adults seems to be a lesser factor in synchronizing the life cycle. However, there is a mating season in the spring marked by a preponderance of spiders, especially males, maturing at this time; and perhaps this is related to response to photoperiod. The less distinct nature of the mating season in the Beach populations may be due to lesser influence of summer mortality in these populations and perhaps a less sharply tuned response to photoperiod.

At Whiskey Mountain the mating season probably corresponds to the period during which the ground is not covered by snow. Males do not seem to survive the winter in Alpine habitats, and subadults mature soon after the snow melts in early summer. Although the importance of photoperiod is not known, winter mortality alone must be a major factor sychronizing the maturity of males. At Pothole Dome (Fig. 13) males are abundant in early summer, but they become difficult to locate when conditions become increasingly xeric later in the summer. In this case the combination of summer and winter mortality of males would seem to be of major importance in synchronizing the early summer mating season.

Intraspecific phenology differences among populations in different habitats occur in European lycosid spiders (Bonnet 1930, Edgar 1971b). Individuals from populations in the more southern part of some species' ranges mature in a single year; but in more northern populations, most individuals require two years. In New Guinea there is intraspecific variation in the phenology of some Araneidae. More pronounced seasonal trends occur in some populations; less, in others (Robinson *et al.* 1974). Intraspecific differences in life history characteristics have been reported in birds (Baker 1938, Johnston 1954), fish (Schaffer and Elson 1975), crustaceans (Strong 1972), insects (Babcock and Vance 1929), and plants (Clausen *et al.* 1948) also; and in some cases, experimental work has shown variation to be ecotypic. An ecotype is a genetic subunit or variety within a species, adapted to local environmental conditions (Turesson 1922). Future work with *P. johnsoni* should address the question of whether populations vary ecotypically in the manner in which individuals respond to photoperiod and other environmental factors.

Comparative Studies – One of the most powerful tools for investigating evolutionary problems is the comparative method, and several observations from the literature suggest that a comparative study of spider life history strategies would be productive. For example, Gardner (1965) reported that *Phidippus clarus* Keyserling is semelparous. From the arguments presented earlier, it would be predicted that mortality represents a lesser risk for eggs and immatures in this species compared to iteroparous species such as *P. johnsoni*, *P. coccineus*, and *P. regius*. In Kaston's (1970) especially thorough study of the black widow spiders (*Latrodectus*), several intriguing differences in life history characteristics are evident when these spiders are compared to *P. johnsoni* and other spiders.

Latrodectus may begin to oviposit infertile batches followed by additional fertile batches. There is no clear trend for decreasing number of eggs per batch and hatch proportion in successive batches. The number of days between copulation and the first oviposition was highly variable. *Latrodectus* (Theridiidae) are not closely related to the salticids, and there is presently insufficient information available to warrant a discussion of the ultimate causation of these life history differences. Certainly it seems that important differences exist in the life histories of different species of spiders, and our understanding of the evolution of these differences can very likely be clarified by comparative studies.

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