1967

An investigation of the ecology of the wolf spider Pardosa groenlandica th. (Araneae Lycosidae)

David Raynor Ricards
The University of Montana

Recommended Citation

Ricards, David Raynor, "An investigation of the ecology of the wolf spider Pardosa groenlandica th. (Araneae Lycosidae)" (1967). *Graduate Student Theses, Dissertations, & Professional Papers*. 6730.
https://scholarworks.umt.edu/etd/6730

AN INVESTIGATION OF THE ECOLOGY OF THE WOLF SPIDER *PARDOSA GROENLANDICA* TH. (ARANEAE, LYCOSIDAE)

By

David R. Ricards

B.A. University of California at Los Angeles, 1947

Presented in partial fulfillment of the requirements for the degree of

Master of Arts

UNIVERSITY OF MONTANTA

1967

Approved by:

Royal Bruce Brunson
Chairman, Board of Examiners

Fred S Honkala
Dean, Graduate School

MAR 11 1968
Date

ACKNOWLEDGEMENTS

This study could never have been satisfactorily completed without the valuable assistance of several persons.

I am especially grateful to Dr. Royal Bruce Brunson of the Department of Zoology, University of Montana, who has served as my thesis director. He has been exceptionally generous of his time and assistance and his encouragement and understanding have been most appreciated.

I should like to thank Drs. Robert S. Hoffmann and George Singer, also of the Department of Zoology, University of Montana, who have provided much valuable advice and counsel during the course of my investigation.

I am especially obliged to Dr. Herbert W. Levi, Curator of Arachnids at the Museum of Comparative Zoology, Harvard University, for his generous assistance in the identification of my spider specimens and for his encouragement of my initial curiosity about wolf spider biology. His sustained interest in my efforts have contributed substantially to their fulfillment.

Dr. Howard Evans, also at the Museum of Comparative Zoology, Harvard University, has helped with the wasp identification for my study and advised me about their life history, for which I am very grateful.

In addition, special thanks are extended to Mr. and Mrs. Lloyd Tilton for their cooperation during the course of this investigation along the lakeshore of their property.

This study was supported in part by a Summer Fellowship for Secondary School Teachers of Science and Mathematics granted by the National Science Foundation.

TABLE OF CONTENTS

CHAPTER PAGE

CHAPTER PAGE

PAGE

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

INTRODUCTION

One of the more conspicuous animals among the rocks and gravel of lakefronts and river banks of the Nearctic region is Pardosa groenlandica (Thorell, 1872). This representative of the wolf spiders (Araneae, Lycosidae) may commonly be seen in these locations, immobile on an exposed rock surface in the early morning or late afternoon sunlight. The males attract attention during the remainder of the day by their active movements among the rocks in their courtship wanderings in spring and early summer. Their abundance along the shore of Flathead Lake, Montana, suggests that they are the dominant invertebrate carnivore in many riparian locations, yet they have been neglected in ecological studies.

Nørgaard (1951) has reported on the distribution in a Danish Sphagnum bog of two species of wolf spider, Lycosa pullata and Pirata piraticus. Their respective temperature and humidity tolerances restricted L. pullata to the microclimate at the surface and P. piraticus to that just beneath the surface in the stalk layer of the bog. Barnes and Barnes (1954) reported the species composition of spiders associated with the maritime sand-beach and broomsedge drift lines of North Carolina. They showed that the xeric conditions of the sand-beach drift support a less dense and totally different spider population from the mesic environment of the broomsedge drift. However, wolf spiders comprised the largest part of both populations; Lycosa modesta for the mesic and Arctosa littoralis for the xeric habitat.

Kuenzler (1958) described the niche relations of three wolf spiders in ten areas selected to represent various stages of secondary plant succession in fields of the Southeastern coastal plain. Two of these species (*Lycosa carolinensis* and *Lycosa timuqua*) prepare burrows in the soil as retreats and predominate in the more xeric, open habitats in the first to fifth year stages of succession. *Lycosa rabida*, the third species, becomes predominant in habitats at the broomsedge stage of succession beginning about the fifth year and persists in successive stages to the dry wood habitat with adequate brush understory. This corresponds with the behavior of this species as an active climber in forbes, grasses, and lower trunks or branches of trees.

Kuenzler also utilized a mark-and-recapture technique to investigate spatial relations of the three species. The distribution of the spiders within any one uniform habitat was shown usually to be random. Movements were analyzed as an estimate of home range with the result that *L. rabida* was shown to wander more extensively than the two burrowing species which appeared to remain at a particular distance from their burrows; less than nine feet for *L. timuqua* and about two and a half feet for *L. carolinensis.*

Hackman (1957) reported an investigation of two different populations of the wolf spider *Trochosa ruricola* (Deg.) in southwestern Finland. He calculated the size of the adult population along the island lakeshore which he studied, as about 1000 (10 spiders per meter of shoreline) and the total production of eggs as about 20,000 (or 200 per meter of shoreline). Calculated mortality rates were reported but admitted to be unrealistic.

In addition, the mark-and-recapture technique that Hackman employed permitted him to determine that individual females in exceptional instances are capable of having two broods (June and August) in one summer and that some females survive as adults for two summers, although the males disappeared entirely before the last molting of the new generation in August. Hackman also reported observations of prey, enemies, and movements.

Studies of spider populations, which typically include wolf spiders, have been reported for a variety of habitats and over a wide geographical distribution in the last decade. Heydemann (1960) reported on the pattern of spider succession in the newly formed land of the North Sea coast. Wiebes (1960) investigated 14 species of Lycosidae and Pisauridae occurring in the dune area of Meijendel near The Hague, Netherlands. Duffey (1962) and Cherret (1964) studied the British spider fauna inhabiting grasslands and high moorlands respectively. Neither observed Pardosa species although species of Lycosidae were collected; Pirata piraticus in sufficient numbers to permit Cherret to report population estimates for this species in his 800 square foot study grid. This was, however, an incidental aspect of his study. Cannon (1965) reported an investigation of the spider fauna of three different forest communities and an old field community in Ohio. The comparison was made only qualitatively. Peck (1966) investigated the spider population on a two-acre plot in west central Missouri comprising representative herbaceous, shrub, and composite communities. The quantitative composition of the population was restricted to the fauna above ground level which was sampled with sweep nets. The Lycosidae were represented in negligible numbers.

Turnbull (1966) studied the spider population in connection with his investigation of the predator-prey relationships among the arthropod population of a short-grass community in eastern Ontario, Canada. He utilized a forced air suction sampler which he considered 100%

efficient in collecting the spiders in the 0.25 square meter area sampled at a time. From 162 samples taken during the summer of 1962, the Lycosidae were the most commonly represented spider family and comprised 789 (44%) of the 1791 total spiders collected. Of the 42 species collected *Pardosa saxatilis* and *P. milvina* were responsible for almost 80% of the calculated biomass of the spider population. Turnbull substantiated that the numbers of spiders of different species varied from week to week although the overall population remained stable. He did not attempt to estimate the population density.

Vlijm and Kessler-Geschiere (1966) have published what to my knowledge is the most recent ecological study of spiders related to my own. They investigated the coexistence of three species of *Pardosa* in the dunes of an island along the coast of The Netherlands to identify their respective ecological requirements. Based principally on a regimen of sampling with pit-traps they demonstrated a greater abundance of *P. pullata* in the dampest locations, *P. monticola* in the arid and barren areas, and *P. nigriceps* in the willow growth above the ground layer. An apparent variation in preference of vegetation cover to open ground was noted by male and female *P. Pullata* and *P. nicriceps* related to the stage of the life cycle; the ratio being greatest immediately following the final molt and decreasing during the copulation period. A proportionate increase in the ratio of females to males was substantiated within the optimal portions of their typical environments which appeared most distinct immediately after the period of copulation. No estimate of absolute numbers in the population was attempted.

Several investigations of aspects of the life history and behavior of vaious *Pardosa* species are related to my study. Considerably the greatest part of this literature reports on the sexual biology of various species of spiders which demonstrate courtship displays as a part of their reproduction. Reports by Gerhardt (1924), Bristowe and Locket (1926), Bristowe (1929), and Kaston (1936) identify the major problems involved and their significance. More recent reports are those by Schmidt (1957) investigating factors prompting mating in *P. amentata* and by Vlijm, Kessler, and Richter (1963) relating principally to reproductive behavior -- courtship, mating, egg-sac preparation and transport, and emergence of the spiderlings. Vlijm and Dijkstra (1966 c) elaborate aspects of the reproductive behavior in relation to the systematics of four sympatric *Pardosa* species. The most recent report relative to wolf spiders and *Pardosa* in particular to my knowledge is by Hallander (1967) who describes features of the courtship display of *P. chelata* (Muller) and hypothesizes a relationship to the dry leaf litter characteristic of the species' habitat.

A major aspect of my study has been to investigate quantitatively the cursorial behavior of *P. groenlandica* in terms of the amount and orientation of movement as related to sex and age differences. An investigation of these problems has been recently reported by Vlijm and Richter (1966 b). Their study was conducted in an entirely different fashion and for a different species, *P. lugubris* (Walckenaer), but provides an interesting comparison to my own observations and conclusion which I will discuss, as in the case of all the aforementioned studies, in more detail in the pertinent sections to follow.

My study of *Pardosa groenlandica* compares most closely to that of Hackman (1957) on *Trochosa ruricola* and permits a comparison of the population characteristics of these two different species occupying similar habitats. This study seeks to extend the exact description of the cursorial activities that particularly distinquish wolf spiders by analyzing the amount and pattern of movement, daily, seasonally, and at different stages of the life cycle.

CHAPTER 1

METHODS

This report incorporates observations of the biology of Pardosa groenlandica made over a period of four summers beginning in 1961 at the Rocky Mountain Biological Laboratory, Gothic, Colorado, and continued in the summers of 1964 to 1966 at the Biological Station of the University of Montana at Yellow Bay, Flathead Lake, Montana. The principal part of the field work for this investigation was done from 21 June to 18 August, 1966, along a 100 foot lakeshore frontage (Fig. 1) on the property of Mr. Lloyd Tilton on the east shore of Flathead Lake at a location two miles north of the Biological Station at Yellow Bay. In addition the adjoining beachfronts to the north and south to a distance of 200 feet in each direction were regularly surveyed.

Flathead Lake is a natural body of water principally collected from the Swan and Flathead rivers draining more than a 250 mile length of the western slope of the Rocky Mountains including part of Glacier and Waterton National Parks. The lake level is regulated by the operation of Kerr dam and maintained between 2883 and 2893 feet elevation above sea level. The lakeshore at the location of the study area is composed of bare rocks scoured clean by their continued abrasion in response to the wave action that constantly alters the shoreline. The average volume of a random sample of 20 rocks selected in contact with the one-foot-long arms of a stick cross placed at midbeach was measured by water displacement as 108 ml. The largest rock in the sample was 507 ml; the smallest 13 ml. Sand and soil underlying the rocks reaches the surface only at about the highwater line beyond midbeach.

The study site is bounded to the west by the water of Flathead

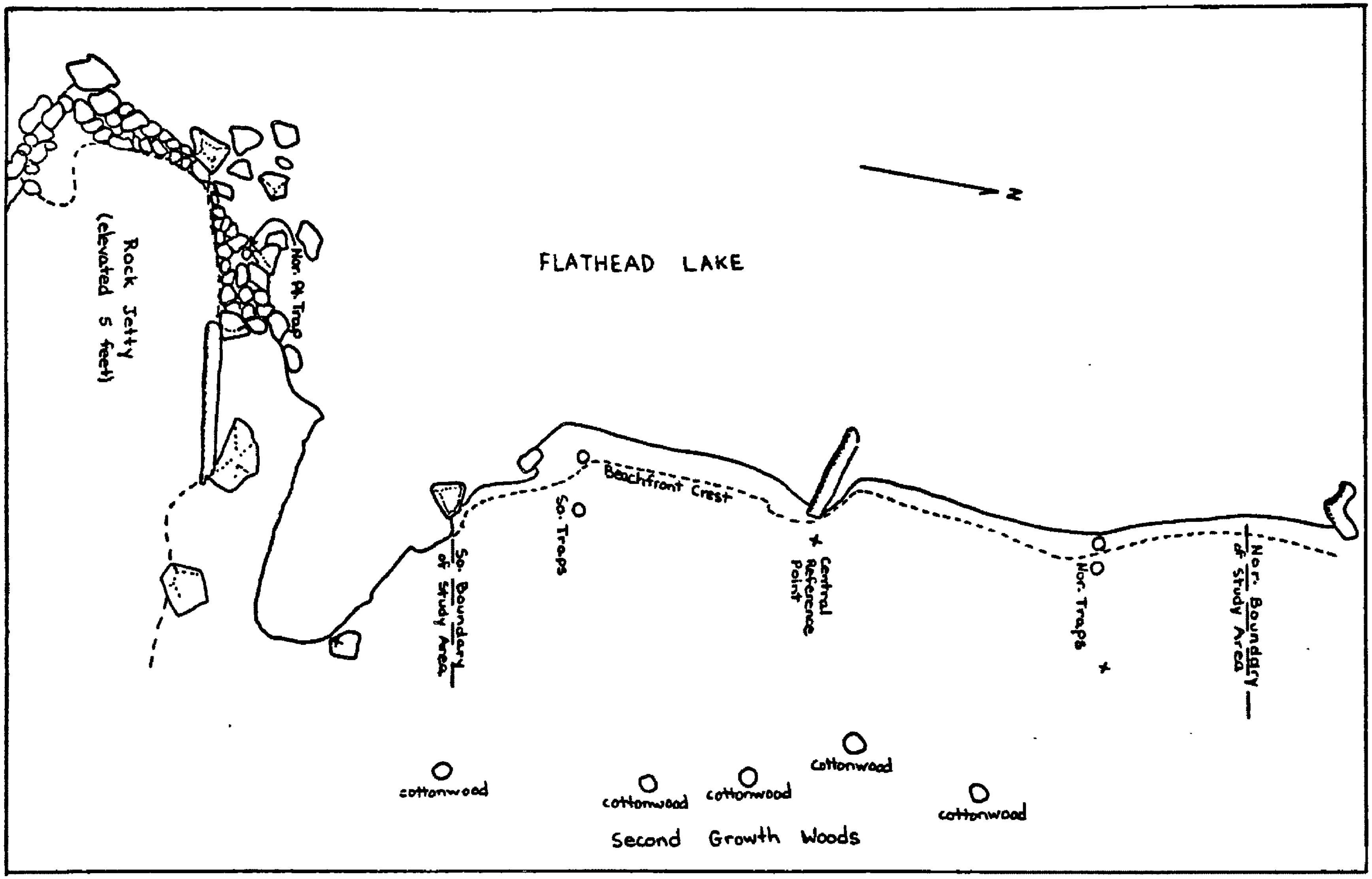


Fig. 1. Flathead Lake Beachfront of L. Tilton Property. 28 June, 1966. Scale: $\frac{1}{4}$ in. = 5 ft.

Lake and to the east by second growth wood-lots including Douglas fir (Pseudotsuga menziesii), larch (Larix occidentalis), ponderosa pine (Pinus ponderosa), and birch (Betula papyrifera). Cottonwoods and alders characteristically border the woods at the edge of the lakeshore.

Proceeding from the water's edge the first permanent vegetation is scattered wild rose (Rosa woodsii). These grow as scattered individual plants from above the high water line to the bases of the cottonwood trees at the edge of the wood-lot to the east. The width of the lakeshore, measured at the central referance point from the water's edge to the nearest cottonwood tree, was 25 feet.

The north and south limits were arbitrarily fixed but were set to encompass a representative natural portion of the lakeshore. Just beyond the southern limit a boat launching channel approximately 15 feet wide had been scraped with a bulldozer. Adjoining the channel, rocks and boulders had been hauled from the orchards on the nearby properties and had been dumped to form a jetty extending out about 50 feet from the edge of the woods and to a height of 8 to 10 feet above the lake level. The study site proper, however, was undisturbed except that the adjoining jetty appeared to have acted so as to alter the wave action enough to result in the deposition of displaced rocks on both sides of the jetty. Consequently the width of the lakeshore in the study area was greater than at any other location regularly surveyed to the north or south during this investigation. Furthermore, the lakeshore was kept free of any large pieces of driftwood.

General observations determined that the greatest concentration of P. groenlandica occurred within the area from the water's edge to midbeach. Consequently the most intensive effort was centered on this area measuring 15 by 100 feet.

The investigation of the spider population of the study site relied upon a mark-and-recapture routine. Spiders were captured in one of two ways: either, 1) grasping individuals by their legs with a pair of forceps as they exposed themselves from underneath the rocks; or, 2) by trapping them in pitfalls made from plastic dishpans. The first method was time-consuming as it required patiently awaiting the reappearance of a spider from under the rock which was sought as refuge upon the approach of the investigator. Next the forceps had to be slowly brought to a position where their open points would lie one on each side of an extended leg. At the moment judged most propitious a quick squeeze of the forceps would be made to effect the capture by pinching the leg. The method entailed considerable luck as well as patience as I would estimate that only one out of four attempts proved successful because some spiders would not permit a close enough approach with the forceps, others would avoid the grasp of the forceps by an even quicker leg movement, and still others by autotomizing the pinched member and falling free. However, this proved to be the most satisfactory method of capturing females transporting egg-sacs because they were seldom trapped in the pitfalls. Further, there was a curious advantage in that frequently a spider would extend a leg forward to touch the tips of the forceps or even to pounce at the tips of the forceps in an apparent effort to seize them. The animal's capture, however, necessitated closing the forceps at just the right moment as the spider would not prolong its grasp of the forcep points and having once contacted them appeared to avoid their renewed approach. This behavior suggested "baiting" the forceps to better attract intended captives. This proved successful by using live mayflies (Beatus sp.) and houseflies (Musca sp.) as lures. These were grasped with the forceps by their wings and presented to the spider. The struggles of the insect when presented at a distance of 5 to 6 inches would generally attract a spider to approach and seize the lure to which it would cling while being transferred to a capture jar. However, except for the few days when the mayfly hatch was especially abundant the effort of locating a suitable lure became itself excessively time consuming and the expedience of the forceps themselves as a lure was relied upon.

The second method of capture using pitfall traps proved successful and made possible the capture of large numbers of spiders. The traps were prepared using round plastic dishpans 13 inches in diameter and 4 inches deep with straight, smooth sides to which the spiders were unable to cling to climb out. These were placed in holes excavated along the lakeshore to a depth such that the brim of the pan was just slightly lower than the surrounding surface level. The rocks were replaced around the outside of the pans with 5 or 6 flat rocks selected to form an overhang projecting over the brim. These rocks were supported by 5 or 6 small sticks laid around the circumference of the pans and resting at each end on the brim of the pan. The arrangement operated as a pitfall to trap spiders as they blundered on the edge of the overhang. Enough small rocks were placed in the pitfall to provide refuge for the captives from one another and protection from the direct rays of the sun. The captives could be removed by grasping their legs with a forceps or by catching them in a small bottle into which they could be prompted by gentle prodding with a small stick or the fingers of the free hand.

Four pitfall traps were prepared and maintained in the study area proper. These were located: one at the water's edge, one at midbeach 15 feet from the south boundary, and two in the same arrangement at the same distance from the north study site boundary. (See Fig. 1). Three other traps were prepared outside the study site limits; one, 130 feet to the north at the water's edge and the other two on the north and south sides of the jetty. These locations were selected to test the amount of spider movement around the point of land and along the lakeshore.

The traps were examined each evening and the spiders were removed. These were taken to the laboratory where the numbers of marked and unmarked males, females, juveniles, gravid females, females with egg-sacs, and females with spiderlings was recorded. Because of the numbers of spiders which were trapped in the pitfalls, efforts to mark them in an individually distinctive pattern were not attempted. Instead the dorsal surface of the abdomen was painted with an identifying color spot to indicate the pitfall location where the animal was first captured. Subsequent observations were utilized principally for estimating population numbers and general movements.

The traps were operated and maintained according to the following schedule. The first trapping was done beginning 18 July, 1966, and continued for 11 days until 30 July, 1966. Trapping was then discontinued for five days by filling each trap full of rocks. This was followed by two trapping periods: 1) three days from 4 August to 7 August; and, 2) six days from 11 August to 17 August. As mentioned, the trapping data were intended primarily for analysis of population dynamics and to identify the amount of movement into and out of the study site proper. The trapping intervals were consequently intended to sample any changes occurring during the period of this study.

The individually captured spiders were kept separately in plastic containers and brought indoors to be marked for release. At the time of capture the location on the lakeshore was marked with a stick wedged upright between the rocks and a label recording the date and specimen accession number was attached.

Marking was accomplished by first immobilizing the specimen by chilling for a minute or two in the deep freeze compartment of a kitchen refrigerator. The resulting lethargy of the animal made it possible to use a small camel hair artist's brush to pinion it against the bottom of the container by pressure on the cephalothorax. When thus positioned a second artist's brush was used to paint a spot of quick-drying yellow or white enamel on certain patellae of the specimen's legs in a distinctive combination to permit future identification.

Although it was observed on occasion that when the enamel hardened, a specimen might have a leg joint immobilized, this did not appear to prove a serious handicap. Indeed the loss of an entire leg commonly occurs by natural causes. In several instances I observed individuals along the lakeshore that retained only two legs on each side.

The dorsal surface of the abdoman could also be successfully painted without ill effect. However, if the enamel was thinned with an excess of paint thinner so as to spread on contact over the animal's body and reach body openings such as the anus, spiracles, and spinnerets the result was lethal.

After marking, specimens would be kept long enough to be certain of no noticeable ill effect, commonly a couple of hours, and then released at the location of capture. This location was recorded in an individual record maintained for each specimen by determining the compass bearing and distance from a fixed, central reference point to a stick wedged upright at the location of capture.

A total of 191 different spiders, 148 females and 43 males, were in this manner identified between 21 June and 6 August, 1966, and individual records maintained for each.

During the nineteen days that the pitfalls (13" diam.) were operated a total of 962 spiders were captured for marking. Of these, 503 were trapped in the study site proper. In this collection 260 were males and 243 females.

After releasing marked specimens were "recaptured" by daily searching along the lakeshore and recording the observed location for each of the marked specimens sighted. Once a week the study site was searched at hourly intervals from 07:00 until sunset. It was observed that the spiders were most conspicuous from 09:30 to noon and from 18:00 to sunset. Consequently, most searching effort was concentrated daily during these periods. The actual procedure was to remain motionless at one location and to observe all the spiders in view a few feet in front and on each side of me to a distance of three or four feet. At this distance the painted pattern on their legs could be clearly observed and recorded. A twig could be inserted through a slip of paper with the sex, date, time and any additional remarks considered pertinant and the twig wedged upright between the rocks at the spider's observed location. The location of an unmarked spider was not recorded but it was counted in a tally which was kept of all spiders that were observed during the search period. This tally recorded the numbers of males, females, sizes (adult, immature, juveniles, and spiderlings), gravid females, and females with egg-sacs or with spiderlings clinging to them. This procedure was repeated for all spiders observed with each advance throughout the study area. Each search was concentrated to record counts and "recaptures" in two regions: 1) from the water's edge to the crest of the beachfront; and, 2) from the beachfront crest to midbeach. I would advance from south to north making a search in one region and return in an opposite direction in the other region to complete the search.

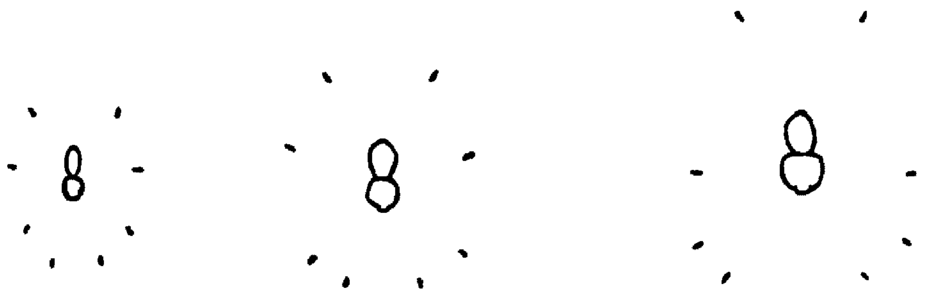
At the completion of each morning's search the position of each spider "recapture" could be determined by two measurements: 1) the distance -- to a half foot accuracy -- from the central reference point to each stick measured with a 100 foot tape measure; and, 2) the compass bearing in line with the stick from the central reference point, made using a Leitz Co. surveyor's staff compass. These measurements were noted on the paper slip marking the location of each specimen and the slips were then collected to transcribe the accompanying data to the permanent record notebook. Commonly, the evening's search continued so late as to prevent completion of these measurements at that time, in which event the sticks could be left in position and the measurements could be completed the follwing morning before the spiders became most active.

Although this procedure required more effort than one utilizing a system of prelocated quadrats, it permitted the recording of actual observed distances and avoided the limitation of an artificially imposed quadrat interval in the analysis of movement.

Juveniles were arbitrarily categorized by estimating their size in comparison to an established standard (Fig. 2). Gravid females were judged on the basis of the appearance of their swollen abdomen. In each case these categories were not always infallibly distinct -- particularly in judging juveniles -- and this was further aggravated on the occasion of an individual spider positioning itself under a protecting rock margin and remaining partly hidden. However, with patience I could approach different individuals to a distance of less than a foot. When a particular individual would duck out of sight by my too hurried movement, they would commonly reappear within a couple of minutes if I would remain immobile. Efforts to uncover them by removing the rocks under which they were hiding usually resulted only in their moving to a greater depth and staying out of sight.

I have sought to develop suitable culture techniques to maintain captive specimens for laboratory observations. During the summer of 1961 thirty-three specimens were maintained for varying periods of up to six weeks in various culture arrangements devised from eight ounce baby food jars. None of these arrangements proved very satisfactory in maintaining a suitable environment for the spiders which appeared to have a very limited humidity tolerance.

During the summer of 1964 two gallon aquaria were utilized as culture containers. The bottom of each aquarium was filled with water approximately a half inch deep with small rocks added in sufficient amount to cover the bottom to a depth of between one to two inches. This arrangement permitted the spiders a degree of freedom of movement to seek the most tolerable conditions for themselves. Six spiders were satisfactorily maintained in this arrangement for as long as six weeks.



juvenile immature adult female

Fig. 2. Size Standards Utilized for Estimation of Population Categories.

In an effort to culture greater numbers of specimens in less space, one-and-a-half quart round, plastic containers with friction lids were used during the summer of 1965. Rocks and water were included to cover the bottom in a similar manner as with the aquaria. Twenty-nine different specimens were collected and observed that summer utilizing this arrangement.

None of these arrangements were maintained for longer than six to eight weeks during the summer and consequently I have not been able to observe a complete life cycle for Pardosa groenlandica. However, I have noted a number of features about their life cycle which in my search of the literature have never been reported previously for this species. The majority of these observations pertain to the early development of the spiderlings while confined within the egg-sac. Four distinct stages of development occur which Savory (1964) reports are customarily described as embryo, pre-larva (not always present for different species), larva, and nymph. Each stage is identifiable by a characteristic ecdysis. However, he takes exception to the usage of larva in this terminology as this stage in spiders is not comparable to that in insects. In insects the larva is a free-living form capable of moving independently and feeding itself. Spiders, on the other hand, have a blind-ending alimentary canal (metabolozing the residual yolk mass from the ovum) and no functioning sense organs and truly, therefore, represent a prolongation of the embryonic state in which the organ systems are undergoing completion.

Instead of larva, Gertsch (1949) has applied the term, deutovum, utilized for an analogous stage in the development of mites.

I shall follow Gertsch's example and use the terms deutovum (instead of pre-larva) for the stage following the rupture of the chorion and pre-nymph (instead of larva) for the stage following the second molt but before the first free-living nymphal stage. These can be readily distinguished because the exoskeleton of the pre-nymph is not yet bristled and the appendages are much shorter than for the nymph.

CHAPTER II

FEEDING

Results

Pardosa groenlandica in common with other wolf spiders does not snare its prey but pounces on it. This is accomplished primarily as a result of the chance approach of a victim to a distance close enough to be pinioned by the extended forelegs and grasped in the chelicerae as the spider suddenly darts or jumps forward a distance of three to four inches. Frequently spiders will stalk their prey -- moving cautiously forward to come within suitable range for the final capture -- but only if the intended victim is on a closely adjacent rock.

Frequently the intended victim avoids the pouncing spider which must then wait another chance encounter. P. groenlandica, however, are capable of surviving long periods of fasting. I have observed two captive females to succomb after a minimum of 57 days without eating and three others after 53, 41, and 37 days.

I have noted 30 instances of natural prey capture and feeding behavior during observations of the study area for the summers of 1965 and 1966. I have recorded nine instances of cannibalism, eight of dipteran, and seven of mayfly (Beatus sp.) capture or attempted capture. In addition one instance each of beatle (Carabid sp.), moth, ant pupa, mosquito, butterfly, and dragonfly feeding attempts. In addition I observed the feeding behavior of 20 captive specimens maintained in containers for laboratory observation. These have been fed most successfully various dipterans. All specimens offered live dipterans have consumed them. A total of 29 feedings for 20 different specimens have thus been accomplished. In addition one specimen was observed to capture and consume a mosquito and two each to eat a mayfly.

Pardosa groenlandica appear commonly to reject ants and sow bugs (*Armadillium* sp.) as potential prey. This conclusion is based on four different observations of spider responses to ants in the study area and two observations of captive specimens. One encounter observed on 1 July, 1966, was by an adult male *P. groenlandica* that pounced at an ant which it appeared to contact with its chelicerae but did not grasp. A similar incident was observed on 3 July, 1965. On 6 July, 1965, a *P. groenlandica* was observed to move to avoid an ant approaching its location on a rock. No effort whatsoever was made by the spider to grasp the ant. On 7 August, 1965, two different spiders were seen to approach a large winged black carpenter ant crawling over the rocks but both retreated when within about one to two inches without any actual contact having been made.

One of the captive specimens (a female, number 1965.22) was observed to respond to a small black ant on 27 July, 1965, the sixth day of her captivity. The ant had found its way into the spider's container. At 10:15 the spider was observed to pounce at it but then reject the ant and make no further attempt to seize it. This specimen 21 days later ate a small dipteran which it was offered.

This reaction was also observed for specimen number 1965.1, also a female, which on 11 July, 1965, the tenth day of confinement, was offered a live black ant collected in the study area. The spider approached the ant at its first movement, but without actual contact occurring the spider subsequently appeared to avoid the ant. Three hours later the spider promptly ate a dipteran when it was offered.

The spider's response to sow bugs was tested by presenting a sow bug to a spider (number 1965.2) which was captured with an egg-sac on 25 June, 1965. At the time of capture a live sow bug was placed in the spider's container. Three days later there was no apparent change in the spider but the sow bug was undisturbed. The sow bug was not removed but a live housefly was introduced at about 10:15 the following day. When the container was re-examined at 19:30, the dismembered remains of the housefly were observed at the bottom of the container. Four days later on 4 July, 1965, the sow bug was observed intact, dead at the container with no evidence of the specimen having been eaten. This was nine days after the sow bug had first been introduced.

Thirty per cent of the natural feeding behavior observed involved cannibalism. Only one of these instances involved a female cannibalizing a recognizable male. Seven involved adult females preying on smaller spiders. One on 1 August, 1965, involved a spiderling cannibalizing another spiderling, one on 27 June, 1966, involved an adult male cannibalizing a juvenile. I would note here that in no cases of observed copulations of male and female was the male subsequently grasped and consumed.

I have noted a difference in the response of males and females to mayflies that have been used as lures (see Methods). Not infrequently the males will only tap the mayfly with their forelegs while females will unhesitatingly pounce at the lure. Indeed females will frequently pounce at any object moving within reach. Commonly when collecting spiders using forceps to grasp them by the leg the females will rush forward a distance of an inch or two to contact the forceps when they are slowly moved along the rock surface. Males on occasion do so also but only the females will re-approach the forceps two or three times if the first effort to capture is unsuccessful. After once contacting and apparently testing the forcep points, males will avoid the forceps on succeeding trials and continued effort to capture them in this manner is usually unsuccessful. On 30 July, 1965, I was using a small twig in an effort to capture a female *P. groenlandica* by chasing it into a cardboard milk carton and noted the spider to twice pounce at the end of the stick as I moved it slowly across the surface of the rock toward her.

Discussion

I believe these observations indicate that prey recognition by *Pardosa groenlandica* is primarily visual and principally in response to movement rather than to form. Though normally rejecting ants as victims, spiders will commonly respond to their movement by approaching closer. The movement of the stick and forceps in the examples related, I believe to initiate the attack response. In addition I have observed different spiders to pounce at drops of water falling nearby from a wave splashing against the beachfront rocks. When stalking spiders I have tested their possible response to sounds by whistling as loudly as possible at a distance of two or three feet -- but with no observable result. They respond immediately to any sudden movement even at distances of six to eight feet -- indicating a considerable visual acuity.

Tactile reliance is also likely in certain cases. As evidence that prey recognition is a complex behavior involving a number of diverse stimuli other than movement, I have observed a captive specimen (number 1965.20) consume a dead dipteran. This occurred on 25 July, 1965, the third day after capture of the female with her attached egg-sac. The dead fly was placed on the rock immediately in front of the spider and was ignored at the time. Some moments later the spider was observed to have grasped the dead fly with her chelicerae and to have carried it to another part of the container. I feel this incident demonstrates that movement alone is not the only effective stimulus to the feeding response.

It would appear on the basis of the observed encounters between spiders and ants that prey recognition in this instance is a learned behavior. I base this conclusion of the observed instances of spiders approaching to pounce at an ant and apparently only as a consequence of actual contact to then reject the intended victim, in contrast to other observations of spiders completely ignoring or even avoiding ants. I believe the different responses can be explained on the basis of experience as a consequence of which certain spiders avoid or ignore ants as a potential victim.

I would call attention in this regard that this avoidance apparently does not include ant pupae, at least on the basis of the single observed instance on 15 July, 1966, of a gravid female P. groenlandica grasping an ant pupa and carrying it along the beachfront. Perhaps the protective mechanism (formic acid discharge?) functions only in the adults.

The indifference of P. groenlandica to sow bugs is interesting because sow bugs occur abundantly in the same habitat.

CHAPTER III

REPRODUCTIVE BEHAVIOR

I. COURTSHIP

Results

The males' courtship behavior is noticeable by their agitated movement as they scurry over and among the rocks seeking a receptive mate. This is observed from June through the middle of August but appears to be most common during the first half of July.

Courtship starts shortly after 09:00 in the south end of the study area. As the sun's rays light the lakeshore the spiders can be observed to emerge from under the rocks to expose themselves to the sun's rays. The females will commonly thus occupy themselves for about the next three hours until the increasing temperature and intensity of the sun's light drives them to seek shelter under a protective rock. Males are more active, and after a brief initial sunning and grooming of their extremities begin searching over and among the rocks. They mostly concentrate in the beachfront and along the beachfront crest paralleling the water's edge, but also wander into the midbeach portion.

Male movement involves frantic dashes among the rocks with momentary pauses on their upper surface during which they will commonly rub together legs I and II on one side and then the other. The rubbing consists of about four or five brushes at a time and sometimes occurs simultaneously on both sides.

The course of the dashes among the rocks appears erratc and unoriented. By chance alone apparently, other spiders are sighted. When this occurs the male will face the second spider and commence waving his pedipalpi, alternately moving his pedipalpi very rapidly up and down and at intervals alternately raising one and then the other overhead. After a few moments of this the male will suddenly dash at the other spider. Most commonly the females thus approached will retreat, abandoning her site and moving to seek refuge under a rock. The male pursues, but then suddenly pauses to wave with his pedipalpi and sometimes rapidly vibrates his abdomen in a vertical plane while flexing his legs to elevate his body on the tips of the tarsi. This will be followed by another sudden dash in further pursuit.

This routine will occasionally be varied, most commonly by females with egg-sacs. Instead of abandoning her refuge, she repulses the approach of the male by extending and elevating her first two pairs of forelegs and raising her body at an angle to the substrate thus exposing her chelicerae more effectively. The approaching male then checks his advance and assumes a similar defensive attitude. Frequent contact by the forelegs of each pair will actually occur which usually results in the advancing spider springing away. Unless the female abandons her refuge and dashes off, the male will, after a few moments, retreat to continue his ranging over the rocks. If the female dashes off the male will invariably follow in close pursuit.

This same sequence appears to occur on the occasion of an encounter between two males, except that if the approached male resists the advance by assuming a defensive posture with forelegs extended and elevated there is no subsequent chase when the two later depart.

On no occasion have I observed a female press an encounter. On the contrary, they appear to ignore a male unless one dashes at them. If the female remains immobile the male will continue to display with movements of his pedipalpi and shaking his abdomen at the same time when he is within reach extending his forelegs to reach over the female's head to tap her with his tarsi on her back. If the female persists in her rejection with her forelegs and cephalothorax elevated the male will eventually abandon his effort. If, however, the female in response to the male's touch lowers her forelegs and body, the male will move astride her back to initiate the mating.

Discussion

Courtship routines by wolf spiders were first reported by Clerck (1757). Gerhardt (1924), Bristowe and Locket (1926), and Bristowe (1929) proposed the specific courtship movements to function as a means of recognition between males and females of the same species the significance of which was that such a behavior served as a species isolating mechanism. Engelhardt (1964), however, has denied this to be effective in the case of the four Trochosa species he studied in Central Europe. Studies relating to the Pardosa genus have been reported by Montgomery (1903) and Kaston (1936) who described variations in courtship behavior of various species and by Schmidt (1957) who investigated the factors releasing mating in P. amantata (Cl.) and by Vlijm and Dijkstra (1966c) who compared the courtship behavior in the P. amantata group. Most recently, Hallander (1967) has reported the details of the courtship behavior of Pardosa chelata which he studied in southern Sweden.

The male Pardosa groenlandica is typically the active partner as in the previously reported species. The male searches to locate a receptive mate and initiates the courtship display. Engelhardt (1964) hypothesizes that the males of the four Trochosa species of Central

Europe locate their partners by responding to certain scent substances specific for each species that adhere to the silk of the female draglines. My observations of the erratic, random routes of *P. groenlandica* males cause me to believe they encounter their mates purely by chance, with recognition principally dependent upon detection of movement substantiated by tactile stimuli.

Pardosa groenlandica males do not drum on the ground with their forelegs as Kaston (1936) reports for *P. modica* and Hallander (1967) for *P. chelata*. Nor do they rotate the pedipalpi during their display in the manner of *P. chelata*. *P. groenlandica* males will rub the first and second forelegs together on one side and then the other, but I have observed this commonly with isolated captive specimens and do not consider it particularly related to the courtship display. The most characteristic movements of the *P. groenlandica* display are the rapid up and down waving of both pedipalpi interrupted momentarily by one pedipalpi at a time being raised overhead and the violent vibration of the abdomen. This action is generally terminated with a sudden dash forward toward the intended partner.

The raised stance on the tips of the tarsi and the forward reach of the forelegs which Hallander (1967) reports for *P. chelata* are also typical of the courtship behavior of *P. groenlandica* males.

II. MATING

Results

I have seen mating spiders on seven occasions. The first instance was on 24 July, 1965. The male was astride the female, facing her posterior with his legs between hers and flexed under her cephalothorax.

The female remained immobile as the male contracted his abdomen rhythmically. After a few minutes the female with the male still astride moved beneath a rock and disappeared from sight.

On 26 July, 1965, I observed a male approach and mount a female. The male approached quivering his abdomen a few times while about six inches distant and then without further preliminaries he ran onto the rock where the female remained immobile and clambered onto her back from one side, turning to face her posterior. His pedipalpi were inserted into the female's epigynum alternately on the left and the right side as the male reached around first on one side with both pedipalpi and then the other. The male alternated pedipalpi, using his left while reaching around the female's right side and vice versa, for at least six times in a period of about two minutes while the female remained motionless. Then the female began to move forward carrying the male still astride her a distance of about six inches. When she turned around the male dismounted, clambering off the rear of her abdomen, the two then moving in different directions to seek concealment under adjoining rocks.

Occasionally more elaborate preliminaries occur. An example was observed on 20 July, 1966, when the male was observed to repeatedly approach the female waving his pedipalpi and extending his forelegs, which the female resisted by raising her first pair of forelegs in a defensive attitude. The male eventually succeeded in placing his forelegs over the back of the female's cephalothorax from the front and approached close enough apparently to make contact with his pedipalpi and those of the female. However, the female kept her forelegs extended to prevent the male from mounting farther. The male thereupon retreated, and then advanced in the same fashion three more times, quivering his abdomen and elevating himself on the tarsi of his legs before each advance. After about five minutes the male succeeded in mounting the female and the copulation proceeded in a manner similar to that described for the other instances.

Additional matings observed on 17 August, 1965, and on four different dates from 15 July to 16 August, 1966, are mostly similar. On 15 July the same female (number 1966.51) was observed mating on three different occasions at 10:48, 11:58, and 12:43. This same female was observed copulating again on 16 July at 11:26.

On two occasions (4 August, 1966, and 20 July, 1966) I noted two males in nuptial embrace.

Discussion

These observations demonstrate a similar mating routine. After the male gives a preliminary display by movements of his pedipalpi, forelegs, and body, if the female demonstrates her receptivity by remaining immobile. If unreceptive she may either retreat, with the male invariably following in pursuit, or assume an attitude of rejection by elevating her forelegs and the forepart of her body. In this event, the male continues to display with movements of his pedipalpi and shaking his abdomen at the same time approaching closer and by extending his forelegs to reach over the female's head to establish tactile contact on her back. If the female persists in her rejection the male will eventually abandon his effort and leave to seek another more receptive mate. If,however, the female lowers her forelegs and body, the male will move astride her back. This is commonly accomplished by the male mounting the female over her head although not invariably. The male, however, invariably faces the rear of the female which position appears necessary for the insertion of his pedipalpi into her epigynum. The actual insertion is by one pedipalp at a time as the male reaches around one side of the female and then the other. The male clasps the female with his legs inserted between hers and flexed under her cephalothorax. In this manner the male is capable of retaining his position even if the female begins to move around. Ordinarily, however, she whill remain motionless at least at first. When the male dismounts he runs forward over the rear of the female's abdomen. The copulation can last for over fifteen minutes and the female can mate frequently, at intervals of about an hour. On no occasion was the female observed to attack the male after the copulation.

This routine is generally similar to that which Hallander (1967) reports for *Pardosa chelata*. A conspicuous difference is in the behavior of the male when dismounting. Unlike *P. chelata* males which Hallander (1967) reports jump off backwards when copulation is terminated, the *P. groenlandica* males run forward over the rear of the female's abdomen. This may be a significant factor in the usual fate for the males of the two species. Hallander (1967) reports that it seems common for the female *P. chelata* to eat the male after mating. In the seven matings between *P. groenlandica* that I observed the female never attacked the male.

The akinesia of the female *Trochosa* initiated by the copulation that Engelhardt (1964) mentions is not apparent among *P. groenlandica*. Indeed I have observed females transporting males still astride their backs.

Kaston (1936) reports the length of copulation for the six *Pardosa* species he describes to vary from two minutes to about 3½ hours. Engelhardt (1964) reports the length of copulation for the Trochosa species he studied to vary from four minutes to six hours 48 minutes. Vlijm and Richter (1966 b) report the exact time of 16 observed copulations of Pardosa lugubris (Walkenaer) to vary from 90 to 300 minutes with a median of 188½ minutes. Hallander (1967) reports the length of copulation for P. chelata as normally ninety minutes. My only observation of an undisturbed mating lasted about ten minutes.

III. EGG-SAC PREPARATION

Results

The preparation of the egg-sac has been described by other investigators (Vlijm, 1962) for Pardosa amentata Cl. I have observed this on two occasions by P. groenlandica. The first was on 1 July, 1961, by specimen number 1961.10 captured three days previously under a stone on a gravel bed of the East River at the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado. This specimen was confined in an eight ounce baby food jar with a dampened wad of toweling. The specimen when examined about 20:00 that evening was observed to be in the process of preparing its egg-sac and was continuously observed during the entire process for the next hour and five minutes.

At the time my observations began the spider had prepared a silk disk approximately one centimeter in diameter in the center of the supporting strands of a horizontal web attached to the sides of the container and the crumpled folds of paper wadding. The spider was noted to continuously feel the margins of this disk with her pedipalpi while applying additional silk from her spinnerets. This activity stopped shortly and at about 20:10 the spider, while supporting herself on the strands of the web, began to deposit a viscid drop from her epigynum in the center of the disk. The droplet resembled honey in its color and viscosity. It was transparent with no evidence of individual eggs. In about ten minutes it had reached a size at least five millimeters in diameter.

When the spider stopped exuding the germinal fluid she began to cover the entire surface of the droplet with silk strands, zig-zagging from the disk at the base of the droplet to the top center but never from one side entirely across to the other. All the while only the pedipalpi and spinnerets were in actual contact with the droplet and its supporting disk. The spider stood with her tarsi on the supporting strands. Layer after layer of silk was added for the next twenty minutes after which she began to pull at the edge of the disk with her chelicerae and pedipalpi.

In a couple of minutes she had freed the edge of the disk and while supporting it on edge with her legs and pedipalpi began to rotate the sac while laying criss-cross strands of silk across the seam. Next she began to lay more covering over the egg-sac by moving it in all directions and reversing top for bottom.

The first evidence of egg-sac coloration was noticed at 20:50, as a darkening becoming a greenish-blue color around the margin of the seam. From this location the area of coloration diffused over the surface of the sac in irregular streaks and blotches. Within ten minutes the color had extended in streaks to the center of the sac's surface. All the while the spider was supporting the sac under and against her cephalothorax and bending her abdomen to bring her spinnerets in contact with the egg-sac but I can't be certain whether this was to apply additional covering or to test the surface in some fashion.

At 21:07 my handling of the jar appeared to disturb the spider which in response moved off the supporting web with the sac dragging behind by a strand from her spinnerets. The sac by now was almost entirely a dark bluish-green, mottled by only a few remaining white areas.

By the next morning the egg-sac was uniformly a dark blue-green color but noticeably darker on the underside than the top. By 4 July, 1961 the upper surface showed considerable grey portions. Two days later it appeared that the spider had turned over the egg-sac since the underside now appeared lighter than the upper side. Also at this time small brown spots were noticeable. Five days later I noted the upper surface to be lighter than the underside and concluded that the spider had again turned over the sac.

By 15 July, two weeks after the spider first prepared the egg-sac, it no longer showed any blue-green coloring. The underside was nearly all white and the dorsal side was white with irregular dark gray spots. This coloring became predominantly gray by evening.

This color change occurred in the period of a day or two and I suspect that it could be the result of the spider chewing at the surface of the egg-sac.

On 16 July, 1961, 15 days after its preparation, the egg-sac was observed unattended at the bottom of the container and was removed for preservation. The sac at the time appeared quite hard and dessicated with a wrinkled surface not noted previously. This might have been the result of the spider sucking out the contents of the sac, although the specimen had been successfully fed four times in the previous eight days, the last time being the day before the egg-sac was abandoned.

The second instance of egg-sac preparation was observed on 5 July, 1961, and was also of a confined specimen (number 1961.16) that had been captured with a very distended abdomen five days previously at the same location as specimen 1961.10. The spider's routine on this occasion was similar to the previous description except that the specimen after depositing her droplet of germinal fluid was unable to satisfactorily cover it with silk to complete her egg-sac. For at least 20 minutes she moved her spinnerets back and forth while straddling the droplet, but without depositing any silk. All the while she was pulling with her chelicerae at the margin of the disk in an effort to pull the basal disk free from the supporting webbing. The result was that the disk became folded in half and some of the droplet was squeezed out the opposite side. After this the spider appeared to abandon her efforts to finish the egg-sac and remained motionless grasping the margin of the folded disk with her chelicerae and pedipalpi for at least an hour. During this time the droplet began to dry out. Three and a half hours after the spider was observed to deposit her germinal droplet she was observed to release the remnant of the egg mass and abandon it on the floor of the container. Nothing further occurred.

The next morning the spider was examined and noted to have a slightly distended abdomen as though all the germinal fluid had not been exuded. Her abdomen was noted as noticeably distended the following day and still so three days after that (10 July, 1961) although the spider had not apparently eaten during that time. She apparently did eat a dipteran left in her container on 11 July, 1961, but there was no noticeable difference nor other special activity until her death on 15 July, 1961.

The arithmetic average of the sizes of 35 different egg-sacs I measured in my study was 6.6 mm in diameter by 3.3 mm in maximum thickness for twelve newly prepared sacs, increasing to 6.9 mm in diameter by 4.3 mm in maximum thickness for 23 older sacs. The age of the sac was determined by the stage of development of its contents; whether ova, for a new sac, or deutova or pre-nymphal stages for an older sac. The color changes occurring at different ages of the sac were also noted. In general, newly prepared egg-sacs were characteristically dark colored with noticeably blue or green tinges. The older egg-sacs were lighter and gray. Also a reliable age criterion is the condition of the seam joining the two halves of the sac around its margin. This is always expanded and shows as a white band from one to two millimeters wide in older egg-sacs beginning at about the deutoval stage when the chorionic cuticle splits.

Discussion

In comparing the two instances of egg-sac preparation, it would appear that the unsuccessful effort was the result of the spider's failing to properly enshroud the germinal droplet. I am unable to explain the cause of the spider's inability to exude the necessary silk to complete her egg-sac. It appeared by the movement of her spinnerets that she was making the effort to do so but for some reason was unable. Also, I noted that two days after her failure to complete her egg-sac she had added more strands to the webbing between the folds of paper so that any possible defect of her spinnerets could have been only temporary.

The spider's response to the abnormality is noteworthy by her persistence to free her egg-sac even though it had not been completed. But although seemingly so determined to grasp the egg-sac she ignored a substitute egg-sac from another specimen that was presented to her. This was done by using forceps to place the substitute directly in front of her. The only response was for the spider to momentarily contact the sac with her pedipalpi and the tarsi of her forelegs. No effort to grasp the sac occurred. The substitute sac was then placed on the remnant of the supporting webbing. The next morning the spider was observed straddling the substitute egg-sac and touching the surface with one leg and her left pedipalp but not actually grasping it. This was the extent of the attention the spider was seen to have given the substitute, although it was left in her container until the following morning. At no time was the spider observed to attempt to actually transport the substitute.

In contrast, Savory (1929) reports a similar instance when a captive wolf spider (his investigations were made of Lycosa amentata, L. lugubris, and L. pullata in Malvern, England), that was observed to be preparing her egg-sac, readily attached a wad of blotting-paper to her spinnerets when he offered it as a substitute for the nearly completed genuine sac.

The opposite results in these two cases, though each occurred as only single instances and with different species of wolf spiders, I believe serve to emphasize the importance of the final spinning activity in addition to the mere activity of egg-laying in eliciting the sac attachment and transport behavior.

The spiders in both cases successfully laid their eggs but only one subsequently finished her egg-sac and only this one demonstrated any attachement and transport behavior.

Based on these observations I believe that the response to transport the egg-sac is the culmination of a series of specific stimuli and corresponding responses which properly occur in an essential sequence. Each sequential step in this series of responses is dependent upon the former so that any step that is imperfectly executed disrupts and frustrates the remainder of the sequence. The emission of the germinal fluid coming earlier in this sequence than the spinning activity to enshroud the droplet would appear to be of less importance as a stimulus to egg-sac attachment.

Furthermore visual and chemo-tactile stimuli would appear to be of a very low order of importance in eliciting the egg-sac attachment and transport behavior because on 14 and 15 August, 1966, a small female was observed in the study area with a chip of bark attached by her spinnerets. Similar instances have been reported for other species of wolf spiders and other objects, such as snail shells (O'Conner, 1896). Certainly such objects could not have the identical chemo-tactile and visual stimuli of a genuine egg-sac and their attachement and transport by these females I would infer to be in response to the sequence of activities involved in egg-laying and sac completion.

CHAPTER IV

NATALITY

I. SPIDERLING EMERGENCE AND TRANSPORT

Results

I have made observations of 19 individually identifiable spiders that were observed with newly prepared egg-sacs which could be recognized by their characteristic dark blue-green color that were subsequently noted transporting spiderlings clinging to their abdomens. The interval of time ranges from nine to 22 days with a median of 17 days and a mean of 16.5 days. (See Fig. 3). Except for having been painted in an identifiable manner these spiders were unmolested in their natural habitat.

Curiosity to note if the eggs would develop without attention by the female prompted me to remove two egg-sacs from captured spiders and observe their contents at regular intervals. The egg-sacs were placed in separate stoppered vials on a shelf directly over the electric hot water heater which was the only available method of providing a reasonably constant temperature of about 25° C. One egg-sac was collected on 2 August, 1966, and observed for 16 days. When collected it measured 6 mm in diameter by 3.5 mm in maximum thickness. It was roughly disk-shaped with the upper and under surfaces gray-green in color and about one-third of the margin white, apparently the result of the expansion of the seam joining the top and bottom halves together. The following day I separated a part of this seam to examine the sac's contents which I determined to be deutova; the first stage after the rupture of the chorion. The cephalothorax and the form of the appendages

Fig. 3. Record of observations of all (70) individually identifiable female P. groenlandica resighted a total of at least five times over a period of a week from 21 June to 18 August, 1966. Date first observed and marked indicated as M. Subsequent observations indicated as x. S indicates female observed carrying spiderlings. Solid line (——) indicates the interval the egg-sac was observed to be transported. Broken line (- - - -?) indicates the probable period of egg-sac transport inferred from actual observations and the 17 day average for egg-sac transport.

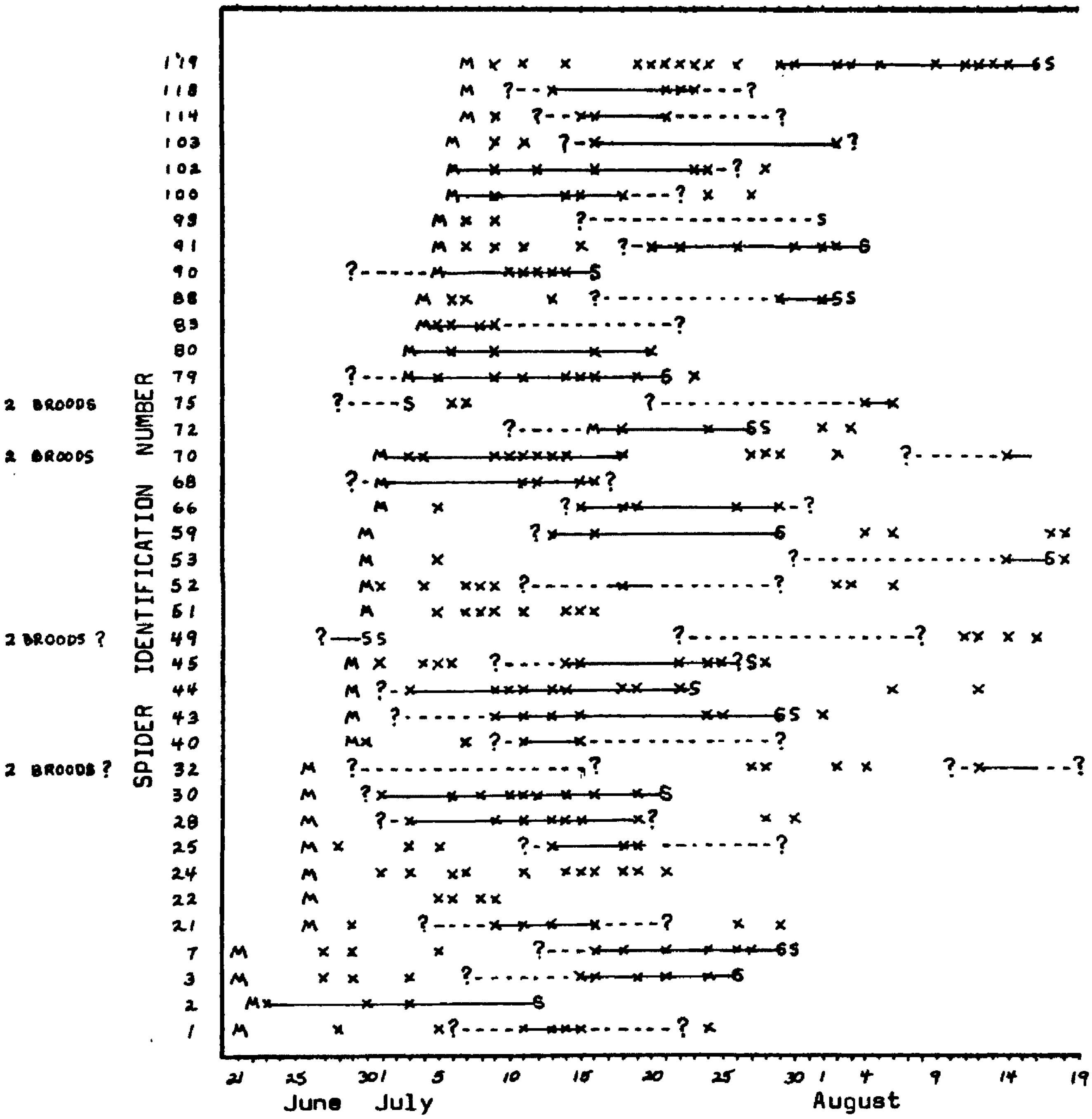
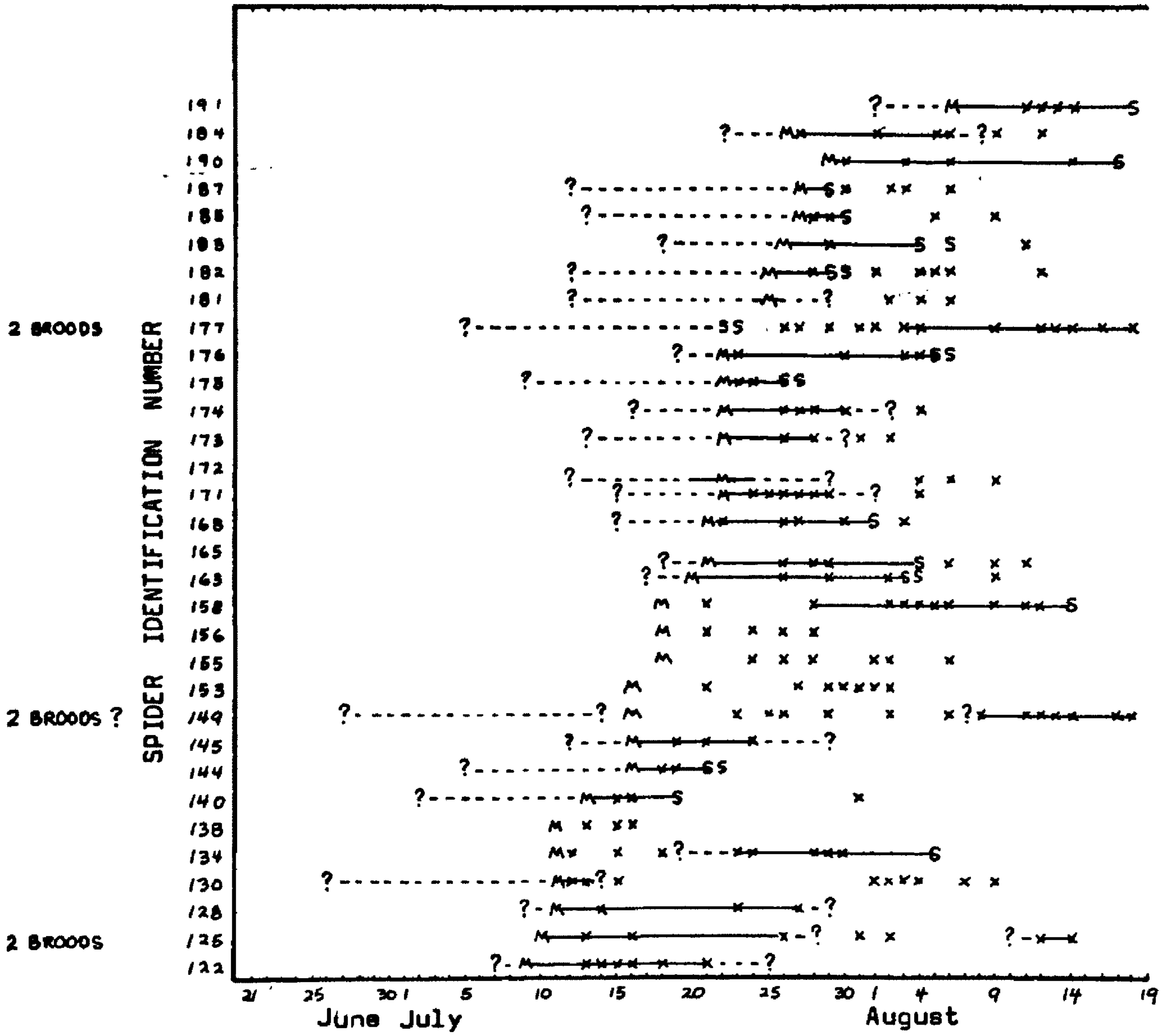


Fig. 3 (cont.) Record of observations of all (70) individually identifiable female P. groenlandica resighted a total of at least five times over a period of a week from 21 June to 18 August, 1966. Date first observed and marked indicated as M. Subsequent observations indicated as x. S indicates female observed carrying spiderlings. Solid line (——) indicates the interval the egg-sac was observed to be transported. Broken line (- - - ?) indicates the probable period of egg-sac transport inferred from actual observations and the 17 day average for egg-sac transport.



were distinct but immovable and colorless. The abdomen was yellow. The sac and its contents were molested no further and replaced in the vial with a green leaf to supply moisture on the shelf. Condensation collecting on the interior of the vial provided an indicator of the relative humidity as in excess of 95%.

The next day, 4 August, 1966, when the sac was examined an estimated 30 pre-nymphal spiderlings were noted outside the sac lying on the bottom and clinging to the sides of the vial. Apparently these had made their way out the opening made when the sac's seam was partially separated. The abdomens of the pre-nymphal spiderlings were a noticeably mottled gray and yellow color with the cephalothorax having a light gray margin around a middorsal clear yellow streak. The appendages were translucent with a gray coloring developing in the interjoint segments. Over the next several days this body coloring became conspicuously grayer as the mottled gray pattern expanded and darkened on the dorsal surface of the abdomen and margin of the cephalothorax. The appendages were readily moved but were typically extended stiffly out from the cephalothorax and not suitably positioned to support the body in locomotion. The appendages were promptly moved when touched with the point of a teasing needle.

Six days later, 10 August, 1966, the pre-nymphs had begun to molt again and their shed cuticles were laying at the bottom of the vial. As nymphal forms their appendages were longer and bristled and utilized to support the spiderlings in movement from place to place. The forelegs were measured to be about two millimeters long and equal to the total body length. The abdomen was a mottled gray and yellow color. The cephalothorax was gray around the margins with a middorsal clear yellow wedge beginning at the location of the posterior eyes and narrowing to a point at the middle of the abdomen. The appendages were colorless.

Over the next several days this coloring was noticed to darken with the middorsal wedge becoming more tan colored. On 12 August, 47 nymphs were counted, 35 of which were moving actively. Fifteen pre-nymphs which had not yet molted were also noted. Four days later (16 August), 21 active and fifteen inactive and presumed dead nymphs were counted. The observations were discontinued the following day with no additional changes apparent except that one nymph was observed grasping another and apparently eating it.

A similar developmental sequence was observed for the spiderlings of the second egg-sac which was maintained for observation except that this egg-sac was removed from the female at an earlier stage of development. This second egg-sac was collected on 3 August, 1966, and measured 6.5 mm in diameter by 4 mm in maximum thickness. It was blue-gray in color and the seam joining the top and bottom halves was not expanded. By separating the seam for about a quarter of the circumference, I was able to determine the contents of the sac to be eggs. These were clear yellow in color with no indication of any embryonic development. The sac and its contents were placed in a stoppered vial with a green leaf included for moisture as with the first egg-sac and put with it on the shelf over the hot water heater. Three days later a whitish area was noted to have developed at one end of the eggs. Two days after this (8 August, 1966) the cuticle covering this blastodermic region was shed revealing the immobile outline of the cephalothorax and appendages of the developing deutova. These had the appearance as noted for the first egg-sac. Two days later these spiderlings were actively flexing their appendages and similar in appearance to the pre-nymphs described for the first sac. These were examined daily and their development proceeded in a similar fashion to that noted for the contents of the first sac. The sac contained at least 50 active pre-nymphs on 12 August, 1966.

Between the hours of 09:20 on 15 August, 1966, and 07:30 the following morning, all but one of these pre-nymphs had molted to emerge as bristled nymphs. Forty-two individuals were counted but perhaps an equal number were clustered together on the sides of the vial about three-fourths of the distance to the top. By the following day, 17 August, 1966, the nymphs had dispersed throughout the vial. Observations were discontinued on that date.

Following their second molt the spiderlings as nymphs are fully capable of active locomotion and perhaps it is in response to their scrambling that the female begins to chew at the seam of the egg-sac, although Engelhardt (1964) is of the opinion that the female is responding to an endogenous neurosecretorily regulated course, correlated with oviposition and influenced by external temperature and is independent of any stimulus proceeding from the egg-sac or the spiderlings in it. The female's chewing at the seam allows the two halves of the sac to separate somewhat and provide more room for the activities of the confined spiderlings. The seam is noticeable at this stage as a white band approximately one millimeter wide around the circumference of the egg-sac. Eventually the female chews a hole in the seam through which the spiderlings begin to emerge. Vlijm (1963) has described this process.

I observed this of one of the females collected to examine the contents of her attached egg-sac. In the laboratory she frequently was seen to grasp her sac and chew at its margin. Upon close inspection small openings were noted at two or three locations in the seam. Through one of these perforations a nymph was seen to emerge.

To count the contents of the sac I removed it from the female and separated its two halves by tearing the sac further apart at the seam. The sac had previously been placed in a cup so that the liberated nymphs would be prevented from escaping. These began moving actively about at the bottom of the cup when the egg-sac was opened. When their number had been determined the now empty egg-sac was offered the female. She accepted it promptly, grasping it with her chelicerae, and recommenced chewing at its margin. Later she reattached it to her spinnerets from which location I assume the spiderlings would normally energe.

The spiderlings were also dropped back into the container with their mother. She reacted to the movement of one of these by extending a foreleg to touch it but otherwise she made no noticeable response. The nymph for its part began to clamber up the female's foreleg which she shook once or twice to shake it off. However, for the most part she simply remained motionless, making no effort to resist the nymphs, many of which shortly were clambering up her other legs and even her chelicerae. The nymphs ceased their activity, however, when they had located themselves on the back of her abdomen where they positioned themselves facing forward on the female and taking positions beginning from the front of the abdomen rearward. They appeared to hold their position with the tarsal claws of one foreleg or the other (not both) and by gripping the setae of the female's back between their chelicerae. They are thus capable of clinging not only to the back of the abdomen but also to its sides and underneath. They do not ride on the mother's cephalothorax.

I have records of eleven different females observed on consecutive days carrying spiderlings at the lakeshore. All but one of these was noted transporting her brood for two days. The single exception was for three days. After this period of time the females characteristically begin to move considerable distances. I surmise that in the course of these movements the young are dislodged. In observing captive females which were transporting spiderlings I have never noted any evidences of ecdysis preceeding the displacement of the nymphs. I suspect that they are unseated purely by the agitation of the female's movements and that her apparent increased wanderlust serves as an effective mechanism of dispersing the young.

Discussion

Vlijm, *et.* *al.*, (1963) reports that *Pardosa* *amentata* carries the egg-sac for about three to four weeks depending upon the temperature. Vlijm and Richter (1966 b) observed that *Pardosa* *lugubris* females tended their egg-sac for approximately three to five weeks. The 17 day median interval I observed for *Pardosa* *groenlandica* would appear to be distinctly shorter than for either of the congeneric species previously reported, although temperature is an uncontrolled variable in this comparison.

The 17 day median length of egg-sac transport observed for spiders in their natural habitat is conspicuously shorter than for five specimens kept in captivity in unnatural conditions. The latter were all carrying egg-sacs at the time of their capture from which spiderlings subsequently emerged. The interval of time ranges from 16 to 36 days with a median of a fraction more than 25 days and a mean of 26 days.

I believe the difference to be evidence of the beneficial care which the female normally provides by seeking the best exposure to the sun's light for her egg-sac. Nørgaard (1953) reports that female

Pardosa pullata Cl. when carrying egg-sacs, prefer higher temperatures in comparison with females without egg-sacs. Vlijm, et al. (1963), although unable to corroborate Nørgaard's finding in preliminary laboratory experiments with Pardosa amentata noted that females in the field would expose their egg-sacs to the midafternoon sun while remaining themselves in the shadow of the soil crevices except when a high cirrus cloud on passing before the sun just perceptibly reduced the light intensity and temperature. Within seconds Vlijm reports the females would emerge from the sheltering crevices to more fully expose themselves and their egg-sacs.

I have noted a similar behavior by female P. groenlandica which as the sun's light first falls on the lakeshore rocks will position themselves and their egg-sacs to the full force of the sun's rays but as the sun rises higher and the temperature increases will withdraw to the shade cast by the margin of a rock but commonly turning so as to have the tip of the abdomen and the attached egg-sac projecting into the sun's light. Such behavior was impossible for the five confined females and I feel this to be at least partly responsible for the greater length of time noted for the emergence of the spiderlings.

The development of the progeny in the two unattended sacs compares reasonably to that of the Trochosa species for Central Europe reported by Engelhardt (1964). When maintained under comparable conditions of about 25° C and 95% relative humidity the duration of the deutoval (described by Engelhardt as prelarva) stage is about a day. The duration of the pre-nymphal stage I observed for Pardosa groenlandica, however, was only about half of that Engelhardt (1964) reports for the four Trochosa species.

Based on the evidence of the development of the progeny in the unattended egg-sacs it would appear that so long as conditions of adequate humidity and moderate temperatures are maintained the eggs can develop to an active independent stage without special care by the female. I would infer that the principal function of the female in the transport of the eggs is to insure that the optimal humidity and temperature conditions are maintained. The specific combination of stimuli and responses by which this is accomplished merits investigation but is beyond the scope of this study.

Apparently any response to the mother by the nymphs emerging from the egg-sac is solely as a result of physical contact. At least I saw no evidence that the spiderlings would orient their movements toward the female. But if by their erratic movements they contacted some appendage of hers they would clamber up it. They would not, however, climb up the bristles of a water color brush when contacted nor its handle nor a teasing needle, although they were capable of climbing the sides of the cup enclosing them.

In this process I feel that it is entirely likely that some spiderlings never are able to attach themselves to their mother. I don't believe this to be necessarily fatal to the spiderling, though. The mother gives absolutely no care to the young she is transporting except possibly indirectly as she adjusts her position during the day to the changing light of the sun and the temperature and humidity of the air. The spiderlings for their part are entirely capable of fending for themselves, since their previous molt just before emerging from the egg-sac, but in the process of clinging to their mother for the extra two or three days they become more effectively dispersed along the lakeshore and in less immediate competition for survival. This is an advantage apparently significant enough to have become established by evolutionary processes as a characteristic of the entire family of wolf spiders.

Engelhardt (1964) reports that *Trochosa* spiderlings in Central Europe stay on their mother for about eight days. Vlijm and Richter (1966 b) observed that *P. lugubris* females transported their spiderlings from three to eight days. The two to three day interval *P. groenlandica* females transport their spiderlings is distinctly shorter.

Engelhardt (1964) surmises that the spiderlings drop off the female as they get hungry. I am of the opinion that the *P. groenlandica* spiderlings are dislodged as a result of the mother's sixfold increase in movement which occurs on the average two to three days after the emergence of the brood. Vlijm and Richter (1966 b) report a similar marked increase of activity by female *P. lugubris* at this period which they also assume to be important in helping the species to disperse.

After their dislodgement from the female the remainder of the development of these spiderlings probably resembles that for *Pardosa amentata* Cl. Vlijm, *et al.* (1963) here reported a description of the life history of this species which is very common along the banks of streams and rather humid open habitats in the Netherlands. This habitat would seem to compare closely to the preferences of *P. groenlandica* which in addition to the congeneric status of the two species suggests them to have a closely similar life history (cf. Wiebes 1960; Vlijm, *et al.* 1963; Vlijm and Kessler-Geschiere 1966).

Vlijm, *et al.* (1963) reports *P. amentata* as mostly overwintering as sub-adults in the penultimate instar. Probably ten to thirteen nymphal instars occur. The exact number has not been reported for *P. groenlandica* but 10 to 13 has been shown to be customary for spiders its size (Bonnet, 1930). They mature early in the spring from mid-March to mid-April depending upon the temperature and the courtship and reproductive activities begin within a few days.

Considerable overlap occurs in this, however, because spiders at all stages of development are numerous all during July and August.

I have noted four instances of different females preparing two egg-sacs in one summer. All were first identified during the first half of August, 1966. Certainly the spiderlings emerging from these egg-sacs will not be as far developed as their predecessors that season. How many of these survive the winter is uncertain, but a few surely must.

Hackman (1957) reports that in exceptional cases female Trochosa ruricola, wolf spiders also inhabiting a water front habitat, will survive two winters as adults. He noted six such females in his study in Finland.

I have not been able to determine if P. groenlandica are equally capable of over-wintering as adults from one summer to the next. I did test for this possibility by trapping on 8 - 9 July, 1967, in the study area to attempt to recapture some of the 1153 spiders marked the previous summer. A total of 111 spiders were captured in the four pitfalls operated at the midbeach and beachfront locations at the south and north ends of the study area but none were identifiable from the previous summer.

II. BREEDING PERIOD AND NUMBER OF BROODS

Results

Females transporting egg-sacs can be seen throughout the summer. Table 1 indicates the relative numbers of females seen with egg-sacs at intervals during the summer. These are actual counts of different females

TABLE 1

RECORD OF THE VARIATION IN THE PROPORTION OF *PARDOSA GROENLANDICA* FEMALES WITH EGG-SACS DURING THE SUMMER

1966		w/sacs	Total females	% w/sacs
6/21	Midbeach. 12:45-13:50. 27°C @ 12:45. Cirrostratus 10/10 overcast. Wind: Beaufort 3.	16	46	35
7/5	Midbeach. 11:15-12:44. 30°C @ 12:45. Clear. Calm.	12	48	25
7/13	Midbeach. 09:45-11:25 24°C @ 10:45. Scattered cumulus 3/10 overcast. Calm.	43	59	73
7/22	Midbeach. 10:00-11:10 29°C @ 11:20. Clear. Wind: Beaufort 4.	25	33	76
8/3	Midbeach. 10:10-11:10 32°C @ 11:10. Cirrostratus 4/10 overcast. Wind: Beaufort 4.	21	32	65

TABLE 2

RECORD OF THE DATES OF SUBSEQUENT EGG-SAC PREPARATION FOR A GROUP OF 28 FEMALE *P. GROENLANDICA* FIRST OBSERVED WITHOUT EGG-SACS BETWEEN 21 JUNE AND 7 JULY

	Observed		Inferred	
Never Prepared Egg-Sacs	3	(11%)	0	
Sacs Prepared by 14 July	12	(43%)	19	(68%)
Sacs Prepared by 21 July	7	(25%)	5	(18%)
Sacs Prepared by 28 July	0		3	(10.5%)
Sacs Prepared by 4 August	4	(14%)	1	(3.5%)
Sacs Prepared after 4 August	2	(7%)	0	
Total	28		28	

with egg-sacs as they were observed during census surveys through the study area. The surveys have been selected for as comparable conditions as possible considering: location; time of day; weather; and time taken for the survey. These observations indicate a threefold increase in the percentage of females with egg-sacs beginning at approximately the middle of July and continuing at least through the first week of August.

Individually marked female spiders also show an increase in mid-July of the numbers transporting egg-sacs. Table 2 summarizes the observations of these females which were seen five or more times over a period of at least a week. Twenty-eight of these when collected and marked between 21 June and 7 July had no egg-sacs but then were re-sighted with sacs which they had prepared subsequently. Twelve (43%) of these females were observed with their new egg-sacs by the middle of July.

Discussion

The numbers of females with egg-sacs prepared by the middle of July increase to 19 (68%) if the probable first date the egg-sac was prepared is inferred from the record of actual observations by using the 17 day average length of egg-sac transport.

For example, specimen number 1966.1 was seen with an egg-sac on only four occasions from July 11 to July 15. Certainly she carried her egg-sac for a longer length of time than this. The record indicates that she must have prepared her sac between 5 July, when she was seen without one, and 11 July, when she was first seen with her sac. Furthermore, it must have been transported until sometime after 15 July, but abandoned before 24 July, when she was again re-sighted without a sac. Because the average length of time females carried their egg-sacs was 17 days (determined from the record of 19 spiders observed with newly prepared egg-sacs and later with newly emerged spiderlings), I infer that specimen 1966.1 probably prepared her sac about 6 July and abandoned it about 22 July.

The records determined in a similar manner for all 28 females are summarized in Fig. 3. The results of this analysis agree with those from the census surveys that the preponderance of egg-sacs are formed by the middle of July.

After 7 July only seven females without egg-sacs at the time of capture were marked and released for observation. Three of these subsequently prepared egg-sacs, one each by 21 July, 28 July, and after 4 August. The four remaining (37%) were never observed with egg-sacs although they were observed at regular intervals all during the latter half of July. However, the similarity of their record to those four specimens numbers 70, 75, 125, and 177, all of which were observed to prepare two egg-sacs before and after an approximately two week mid-July interval, causes me to suspect that they very well may have also. This has been reported as a not uncommon occurrence in various species of wolf spiders (Vlijm, _et al_. 1963 and Vlijm and Richter, 1966).

The very late egg-sac for specimen number 1966.32 I believe to be likely a second sac prepared this summer. Its date of preparation between 4 and 12 August agrees with the observed dates for the confirmed second sacs for specimens number 70, 75, 125, and 177. Also, its small size and shriveled appearance seem characteristic of the late summer sacs (Vlijm, 1963). The sac was collected and its size measured as 4.5 by 2 mm. It contained only 17 eggs. This compares closely to the conspicuously abnormal appearance of the second egg-sac that was collected for specimen 1966.70. This was nearly rectangular (5 x 4 x 3 mm) and shriveled looking, with 23 eggs. Lastly, I have no observation record for 30 days from 26 June to 27 July for specimen number 1966.32, ample time for an egg-sac to have been prepared and the brood to have emerged before the preparation of the sac noted on 12 August.

Similar considerations lead me to suspect two possible broods for specimen number 1966.49.

Seven females are suspected or known certainly to have prepared two egg-sacs; 10% of the 70 individually identified females in my study. Four (5.7% of the 70 total females) are definitely known to have prepared a second egg-sac. By comparison Engelhardt (1964) reports 55% of the four Trochosa species of Central Europe to prepare a second egg-sac in mid-summer and Vlijm and Richter (1966 b) observed that in most cases P. lugubris females prepared a second egg-sac within a week after the emergence of their first brood.

III. PROGENY COUNTS

Results

I collected 37 egg-sacs for examination between 13 July and 17 August, 1966, outside the study area from the portion of the lakeshore immediately south of the rock jetty. They were collected in approximately equal number for the first half of July (10), the last half of July (15), and the first half of August (12). See Table 3. With the exception of June, I believe the collections are suitably distributed in time to adequately sample any variations in natality rates during the summer.

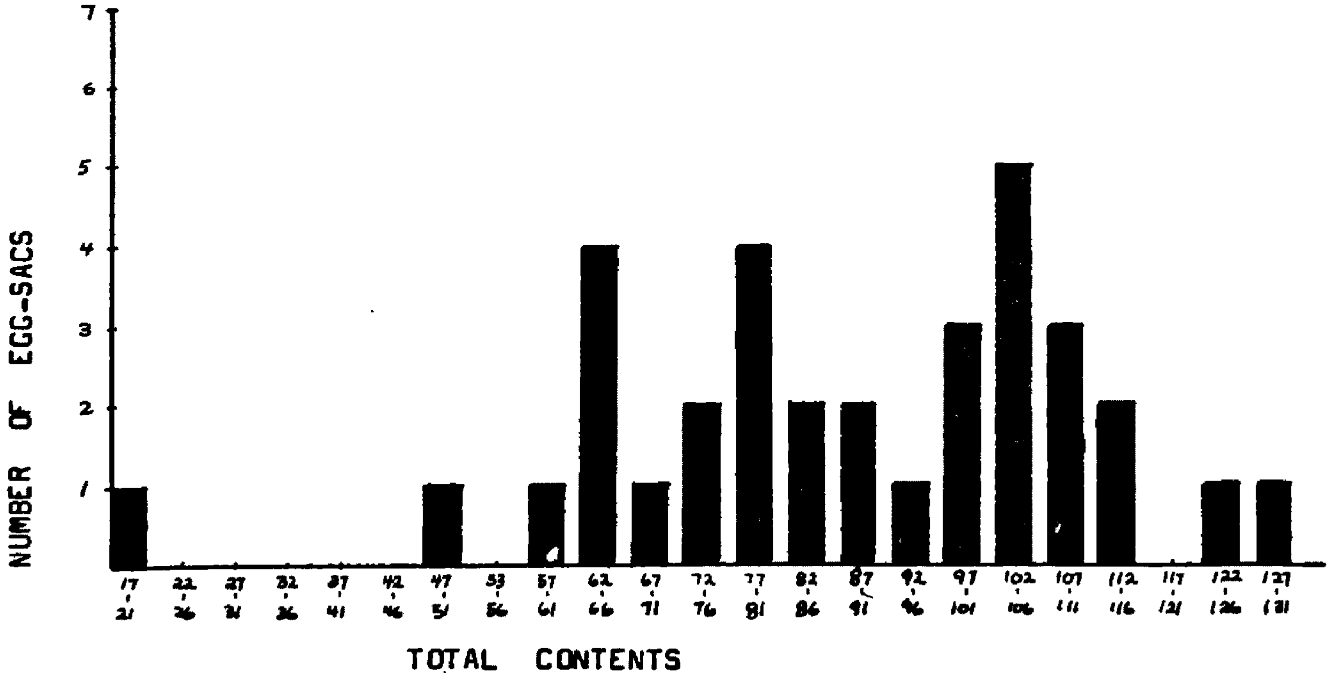
Thirty-four of these sacs were examined to note the number and stage of development of the spiderlings contained within. These were categorized as ova, deutova, pre-nymphs, and nymphs.. The arithmetic

TABLE 3

RECORD OF PARDOSA GROENLANDICA EGG-SACS COLLECTED

	Date (1966)	Number	Totals
First Half of July	7/13	10	10
Last Half of July	7/19	5	
	7/22	3	
	7/23	3	
	7/26	2	
	7/27	1	
	7/30	1	15
First Half of August	8/1	4	
	8/2	1	
	8/3	1	
	8/4	1	
	8/5	2	
	8/14	2	
	8/17	1	12

Fig. 4. Distribution of the numbers of progeny of 34 P. groenlandica egg-sacs collected between 13 July and 17 August, 1966. Median = 89; Mean = 90.



average of the contents of all 34 sacs was 90 spiderlings; the median, 91; range 17 to 127 (Fig. 4).

Discussion

The average content of 90 spiderlings is considerably fewer than the numbers of eggs Hackman (1957) reports for Trochosa ruricola. He examined a random sample of 29 egg-sacs and noted a range between 83 and 256 with a mean of 176.

Petersen (1950) has shown that there is a positive correlation between the number of eggs and the length of the cephalothorax of the female in various species of wolf spiders. This is not adequate to explain the difference between P. groenlandica and T. ruricola, however, because they compare too closely in size.

IV. SEASONAL VARIATION

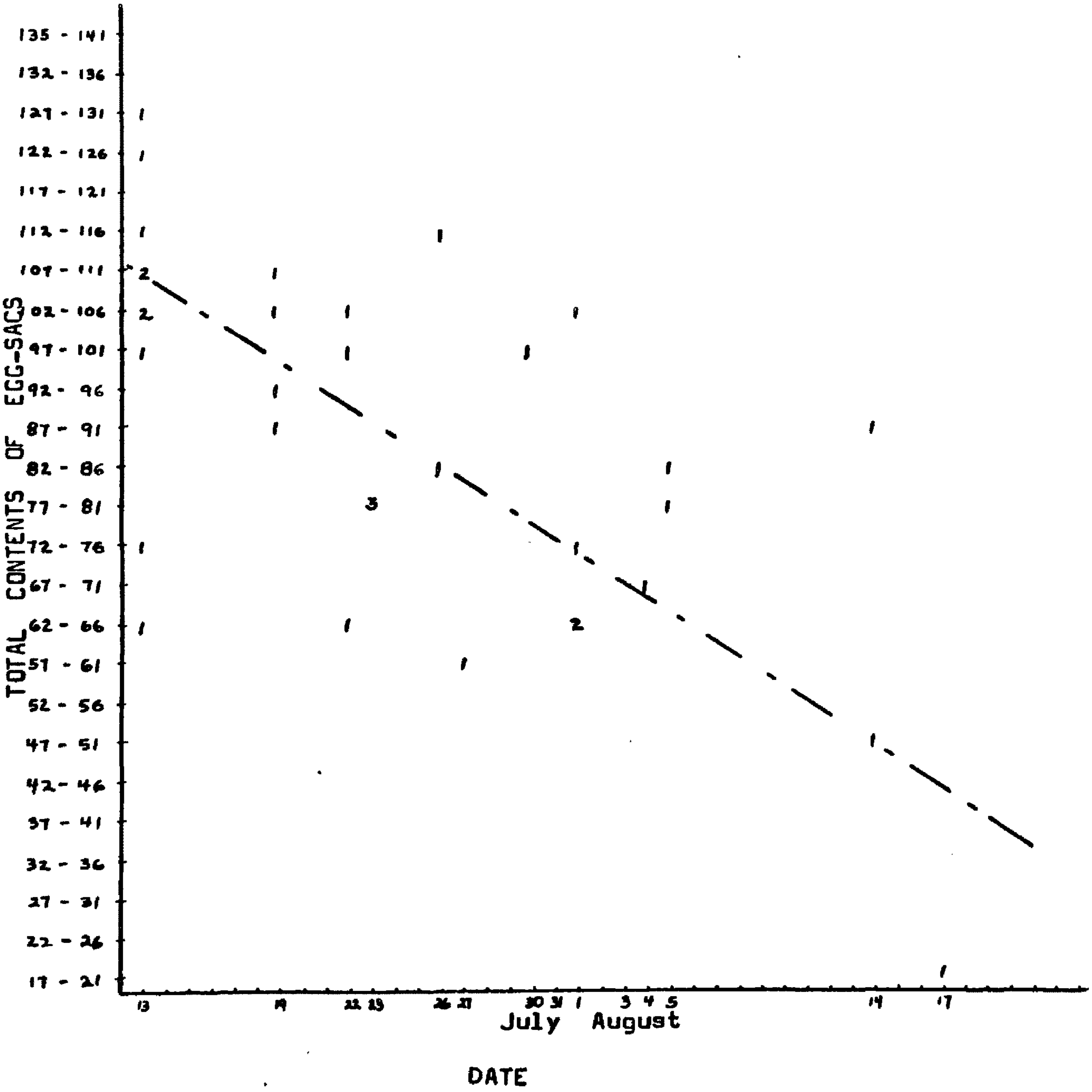
Results

The number of spiderlings in the sample of 34 sacs noticeably declines from mid-July to mid-August (Fig. 5). Ten sacs collected on 13 July had a mean of 102, a median of 105, and a range from 63 to 127. The last ten sacs collected (between 1 - 17 August) had a mean of 69, a median of 73, and a range from 17 to 103.

Discussion

It is interesting to note that a few sacs of small content occurred consistently during the sampling period. One would expect a greater number of smaller sacs with less content later in the summer because of the greater proportion of females preparing sacs for a second brood which

Fig. 5. Comparison of the total egg-sac contents to the date collected for a random sample of 34 *P. groenlandica* egg-sacs. The diagonal represents the approximate median with as many cases above as below the line.



are characteristically smaller (Vlijm, *et al.* 1963). It is less obvious why smaller sacs would occur regularly throughout the summer. In some cases they probably result as a consequence of the female's undernourishment. Bristowe (1939) has shown experimentally that the amount of nourishment can influence the fecundity of *Segestria* and *Drassodes* spiders and I think it not unreasonable to make the same inference for *P. groenlandica*. In addition, spiders are known to suffer infestations of endoparasitic namatods and this could be a factor contributing to the regular occurrence of small egg-sacs, although I made no examination for infested spiders in this population. Certainly, a genetic variability between individual spiders must be a contributing factor. I never noticed in any of the egg-sacs that I examined any evidence of parasite larvae that could have been responsible for the fewer contents.

V. REALIZED REPRODUCTION

Results

The mean number of progeny per egg-sac observed in this study was 90 spiderlings.

For the period of maximum population, roughly 7 - 16 July, 29% of the observed adult female population (274 out of 935 females) were noted with attached egg-sacs.

Discussion

Assuming that all adult females in the population in the course of the summer will prepare an egg-sac, then the average number of eggs per sac would represent a realized reproductive potential 45 times (90 ÷ 2) the previous adult population.

The actual numbers of progeny for the summer can be estimated as the product of the numbers of females with egg-sacs and the average sac content. The portion of the total population transporting egg-sacs can be calculated as the product of the percentage with egg-sacs (29%) and the average total population of female spiders (1192) during the period of maximum population taken from the data in Fig. 10. This calculation gives an approximate number of females transporting egg-sacs in the study area as 346.

The corresponding estimate for the production of progeny would be 31,140 (346 x 90 avg. spiderlings per egg sac). This would represent a crude birth rate during this period 15 times greater than the total adult population. Assuming that all adult females in the course of the summer will prepare an egg-sac, the annual production of eggs would be approximately 100,000 for the population in the study area. Taking the maximum population for the area as approximately 2,000 spiders, 100,000 eggs represents a realized reproductive potential 50 times the previous adult population.

CHAPTER V

MORTALITY AND/OR DISAPPEARANCE RATE

I. AS SPIDERLINGS

Results

Not all the contents of each sac in the sample of 34 examined showed an equal degree of development. Seven sacs contained eggs which were noticeably dry and hard or could be considered nonviable because they showed no change while the remaining contents had developed to either pre-nymphs or nymphs---two or three stages more developed. However, in three of these sacs, only a single nonviable egg was noted. One of the remaining sacs had three nonviable eggs; one, five; one, ten; and one, thirteen. Only the latter two sacs represented any considerable proportion of undeveloped eggs; 21% and 16%, respectively. In neither of these, nor any of the remaining egg-sacs examined, did I notice any evidence of internal sac parasites.

I have observed or suspected three females to have consumed portions of the contents of their egg-sacs. One specimen, number 1965.8, was collected on 1 July, 1965. Twenty-three days later during the afternoon she laid her eggs and prepared an egg-sac. This was noted to be conspicuously smaller and more flattened, only about 2 mm in greatest thickness, than a normal egg-sac. The following morning, 27 July, 1965, the spider had sucked out the contents of the egg-sac and was observed grasping its shriveled, black remnant in her chelicerae. She had been fed only once, 13 days earlier during her 27 day confinement.

This was the possible fate of the contents of the egg-sac prepared by specimen 1961.1 but if so the entire contents were not consumed. This specimen was collected on 26 June, 1961. Four days later she was noted transporting a newly prepared egg-sac. This she transported attached to her spinnerets in an apparently normal manner for the next 22 days. On the morning of 17 July, 1961, the surface of this egg-sac was first noted to be wrinkled as though the sac had begun to dry out and shrivel. I suspect now that the spider had sucked out some of its contents even though she had consumed a dipteran given her just the day before. Six days later, 23 July, 1961, the sac was noted to be considerably more wrinkled and deformed indicating a possibly second feeding on the sac's contents. She had last been fed five days previous to this and a dipteran given to her that same day was consumed by the following morning. On 31 July, 1961, she was noted to be grasping the sac between her chelicerae which continued to be her mode of transport for the next three days until on 4 August, 1961, the sac was observed unattended at the botton of the container and was removed.

The egg-sac for 1961.10 was found similarly unattended on 16 July, 1961, fifteen days after its preparation. By its shriveled appearance, not noted the previous day, I suspect it to have also been sucked-out.

I investigated the numbers of spiderlings carried by twelve different females collected between 19 July and 14 August, 1966. The median number of spiderlings was 70, the mean was 67, and the range of the sample from 17 to 115. I recorded the sizes of six of the females. All measured 1.0 or 1.1 centimeters in total length with the length of the abdomen either 0.5 or 0.6 centimeters. These six individuals of nearly equal size had an arithmetic average of 69 spiderlings with a range from 44 to 101.

Although it is not possible to determine how many spiderlings may have dropped off before the capture of the female, I did capture two females with spiderlings clinging to their backs and with their egg-sacs still attached to their spinnerets. On these occasions I know that their broods must have just started to emerge and the likelihood of their having already lost some spiderlings to be correspondingly slight. One female had 74 spiderlings and the other 54. The arithmetic average of the two broods is 64.

Discussion

The total number of nonviable eggs noted was 34 in the seven different egg-sacs. This constituted 1.1% of the 3072 total contents of all egg-sacs examined. Because I examined only two sacs in which the contents had developed to the nymphal stage, I am unable to determine the percentage of arrested development that might occur at succeeding stages. Mortality rate of the young within the egg-sac appears very low.

Vlijm, *et al.* (1963) has reported that females kept in isolation in the laboratory eventually laid unfertilized eggs and prepared an egg-sac which, however, in due time was sucked-out or abandoned. The incidences I have noted for specimens numbers 1961.1, 1961.10, and 1965.8 would appear to be in agreement with Vlijm's observation. Although I can't be certain that the spiders hadn't mated before their captivity, it seems unlikely in view of Vlijm's further report that egg-laying normally occurs very quickly after mating. It was 23 days after her capture before specimen 1965.8 laid her eggs and fours days after their capture before specimens 1961.1 and 1961.10 did. Neither does it seem likely that the eggs were destroyed due to the spider's hunger. Specimen 1961.1 had eaten just the day before the egg-sac was first noted to be a little wrinkled on 17 July, 1961. In all, she ate a total of eight times during the 24 days she carried her egg-sac. Specimen 1961.10 had been fed four times in the eight days previous to abandoning her egg-sac. The last time was the day before the egg-sac was sucked-out. Specimen 1965.8 ate only once, 12 days before she prepared her egg-sac, which she sucked out by the next day.

By comparison, specimen 1965.5 was collected transporting an egg-sac and had spiderlings successfully emerge, yet went a minimum of 22 days without eating.

There is a distinct difference between the numbers of eggs in the egg-sac and the number of spiderlings which the female transports clinging to her abdomen. A comparison of the medians, as the more conservative difference, indicates 21.3% fewer spiderlings are carried by the female than the number of eggs contained in the egg-sac.

Although these figures do not allow for the numbers of spiderlings which may have been dislodged by their mother's movements before they were collected, they compare closely to the average of the two females which I collected transporting spiderlings which had just emerged from the sac which were still attached.

It is important to also consider the size of the mother in comparison to the numbers of spiderlings transported, realizing that a larger spider could reasonably be expected to carry more spiderlings. The sample of six females measured indicated a very small variation (approximately 1 mm) in total length. The arithmetic average of the number of spiderlings transported by the sample was 70 which agrees closely to the average (67) of the total sample. I conclude therefore that the variation in size of the females in the population is insignificant as a factor determining the number of spiderlings transported.

In all these comparisons the average number of transported spiderlings is distinctly less than the number of eggs contained on the average in the egg-sac. I doubt that the decline in numbers is because of the female consuming any of her offspring, at least I didn't see the slightest such inclination on the one occasion in which I have been able to observe the female's reactions to her emerging brood. Rather I feel that it is likely that some spiderlings never are able to attach themselves to the mother. This is not necessarily fatal to the spiderlings, though, as the mother gives absolutely no care to the young she is transporting except possibly indirectly as she adjusts her position during the day to the changing light of the sun and the temperature and humidity of the air.

II. PREDATION

Results

Unexpected predators of Pardosa groenlandica were shrews. I have witnessed a shrew actually grasping a P. groenlandica in its mouth in the north point pitfall trap at 21:25 on 28 July, 1966. Although the shrew escaped when I attempted to remove it, I am certain by its appearance, size, and coloration that it was Sorex vagrans. I know these definitely occur in the study site because on the morning of 8 July, 1967, I found a dead Sorex vagrans in the south midbeach pitfall where it had been trapped the previous night. This specimen's gut was examined for evidences of P. groenlandica but nothing was noted as its stomach and the first part of its small intestine were empty. What contents remained were too disintegrated to be recognizable. In view of the known rapid metabolism of these creatures I suspect that it had consumed all spiders that had previously fallen into the pitfall then starved to death when it was unable to escape itself.

A major predator of Pardosa groenlandica is the digger wasp Anoplius ithaca, Banks (Pompilidae). This conclusion is based on repeated observations during the summers of 1964 to 1966 of these wasps grasping P. groenlandica victims to transport to their burrows along the lakeshore. I first noted this at midday on 4 August, 1964, when I chanced to notice a wasp dragging a P. groenlandica among and over the rocks. The spider appeared completely immobile and made no resistance while I watched it being transported a distance of approximately two feet. On one occasion the wasp left the spider while it flew ahead in a circular route appearing to reconnoiter so as to orient itself with its destination. The wasp then recovered the spider after appearing to make a search to locate it. The destination proved to be a burrow excavated under a flat rock beneath which the wasp disappeared with its victim. I then covered the rock with a netting, anchoring the edges with rocks, and proceeded to await the reappearance of the wasp. This occurred after an interval of between five to ten minutes but the wasp immediately disappeared again under the rock. After waiting another five minutes, I began to remove the smaller rocks from under the net in an attempt to dig out the wasp and spider. After the surrounding rocks and dirt were removed in a circle approximately eight inches in diameter and to a depth of about two inches, the wasp emerged from the dirt at the bottom of the excavation -- no distinguishable burrow entrance was apparent -- and was evntually captured in the enclosing net. From this the wasp was transferred to a collecting bottle and preserved in ethenol. It was subsequently identified by professor H. Evans, of the Museum of Comparative Zoology, Harvard University.

Further excavation of the soft, moist dirt between the rocks uncovered a total of five P. groenlandica. Although the spiders were alive only one made any active effort to escape, the others moving their legs very letharagically. Close examination revealed an oval white egg attached on the left side of the abdomen near the anterior margin of three of the spiders. Further digging uncovered the apparent remains of disintegrated spiders such as carapaces and leg segments. These and the other spiders were collected in separate bottle with a small amount of soil for further examination.

Two days later the attached egg on one of these spiders appeared withered. The spider itself was apparently normal. Three days later the egg could not be detected. There was no apparent difference in the spider and it appeared to behave normally for four more days when it was then preserved in ethanol.

The second spider when examined two days after its capture did not respond but no noticeable development of the wasp egg occurred.

The third spider when examined the second day after its capture also was alive but a white colored larva had emerged from the egg and enlarged to a size of 3 or 4 mm in length by 1 mm in diameter. It remained attached to the same location on the front left side of the spider's abdomen. Three days later (9 August, 1964) the larva had consumed the spider's abdomen and enlarged to about 10 mm in length by 4 mm in diameter. Its color was also noticeably darker. On 10 August, 1964, a second spider carcass was placed in the container but was ignored as the larva later that day was observed to have commenced spinning a cocoon in preparation to puate. This was completed by the follwing day. I kept this cocoon in its container until the next spring in hopes that the adult might emerge but apparently the pupa succumbed as no further developments occurred.

I was able to establish further details of the nature of this wasp/spider relationship on the occasion of my second observation on 31 July, 1965. On this date I noticed a digger wasp dragging a female _P. groenlandica_ along the lakeshore. This was accomplished by the wasp grasping the spider with its mandibles and dragging the spider backwards over and among the rocks. At intervals of every one or two minutes the wasp would release its prey and fly away apparently reconnoitering its route as it flew from rock to rock along the lakeshore or in a couple of five to six feet circles around its victim, each time returning to regrasp its victim and continue its journey. Also, the wasp was observed to lie on its side on the upper surface of the rocks and rub its hind legs together several times and repeatedly flick its wings in a nervous fashion.

When the march was resumed the route was continued always in a nearly straight line along the beach crest to the location of the concealed burrow. Upon arrival the wasp clambered around in a small circle before grasping the spider to pull it underground beneath the concealing rock.

For the next 20 minutes I observed the entrance continuously for the emergence of the wasp before covering the location with a mesh net as before. On returning approximately 45 minutes later the wasp was observed crawling underneath the netting and it was then successfully transferred to a collecting bottle.

The location of the burrow was fixed and that same afternoon I began the excavation of the burrow. This had been prepared in a location distant enough from the water's edge to have allowed soil to accumulate among the beachfront rocks. Included in the soil at this particular location were a number of charcoal particles from the brush burned here the previous autumn. The soil was damp but with no visible moisture. The soil was removed by brushing away the uppermost layers little by little in a six inch circle surrounding the burrow entrance. At a depth of about one-and-one-half inches a female spider was uncovered buried in moist soil beneath two rocks directly beneath the location where the wasp originally disappeared. The spider was alive and active and attempted to escape when uncovered. A white egg was noticed attached to the front left dorso-lateral margin of the abdomen.

Additional digging excavated a second spider, a juvenile, also alive but immobile except for an occasional twitching in the forelegs which with the other appendages were drawn alongside the body. It also had a egg attached in the same identical location on the abdomen. No further spiders were recovered.

The spiders recovered were place with some of the soil and charcoal particles in a small capped bottle for subsequent laboratory examination.

The next day both spiders were observed to be apparently normally active and sought to avoid the grasp of the tweezers when examined.

No observations were made for the next two days but on 3 August, 1965, both parasitized spider were dead. What appeared to be a larva was seen attached to the side of the larger spider at the location previously noted for the egg. The smaller spider showed erosion of the exoskeleton at the corresponding location but the larva itself was not observed.

Two days later the larva was still attached at the same location on the large spider's abdomen but not apparently growing. The spider itself remained intact. The small spider appeared to be decomposing, however, and as no larve was distinguishable it was preserved in ethanol.

The larger spider six days later had reached the same state and had to be discarded. This was eleven days after it first had been collected. No evidence of the wasp larva was noticeable by this time and as far as I could tell there had been no subsequent development.

The behavior of the wasp in transporting its victim was investigated further on three subsequent opportunities on 16 and 17 August, 1965. On these occasions careful measurements of the distance, direction, and time were noted for the wasp's route in transporting its victim. These are recorded in Figs. 6, 7, and 8. The straight line routes the wasps followed are noteworthy. The wasps maintained these by clambering up and down the sides of rocks in the route of march rather than seeking what would seem to be a less strenuous path among them. The wasps commonly would move backwards along its route pulling the spider, grasped by its mandibles, behind it. On two of these occasions the route proceeded for a distance of 7½ and 15 feet over water. This was accomplished by the wasp flying and dragging the spider along the surface. Flying to transport a victim was also observed for about one to two feet distance of a previous portion of the wasp's route over the rocks.

The effort exerted by the wasps in their task is impressive. The longest observed route was measured to be approximately 111 feet and this does not account for the distance traversed before the observations began nor for the vertical distance involved in clambering up and down the sides of the rocks along the route. The wasp completed its task in 9½ minutes.

Further evidence of the impressive effort exerted is in a comparison

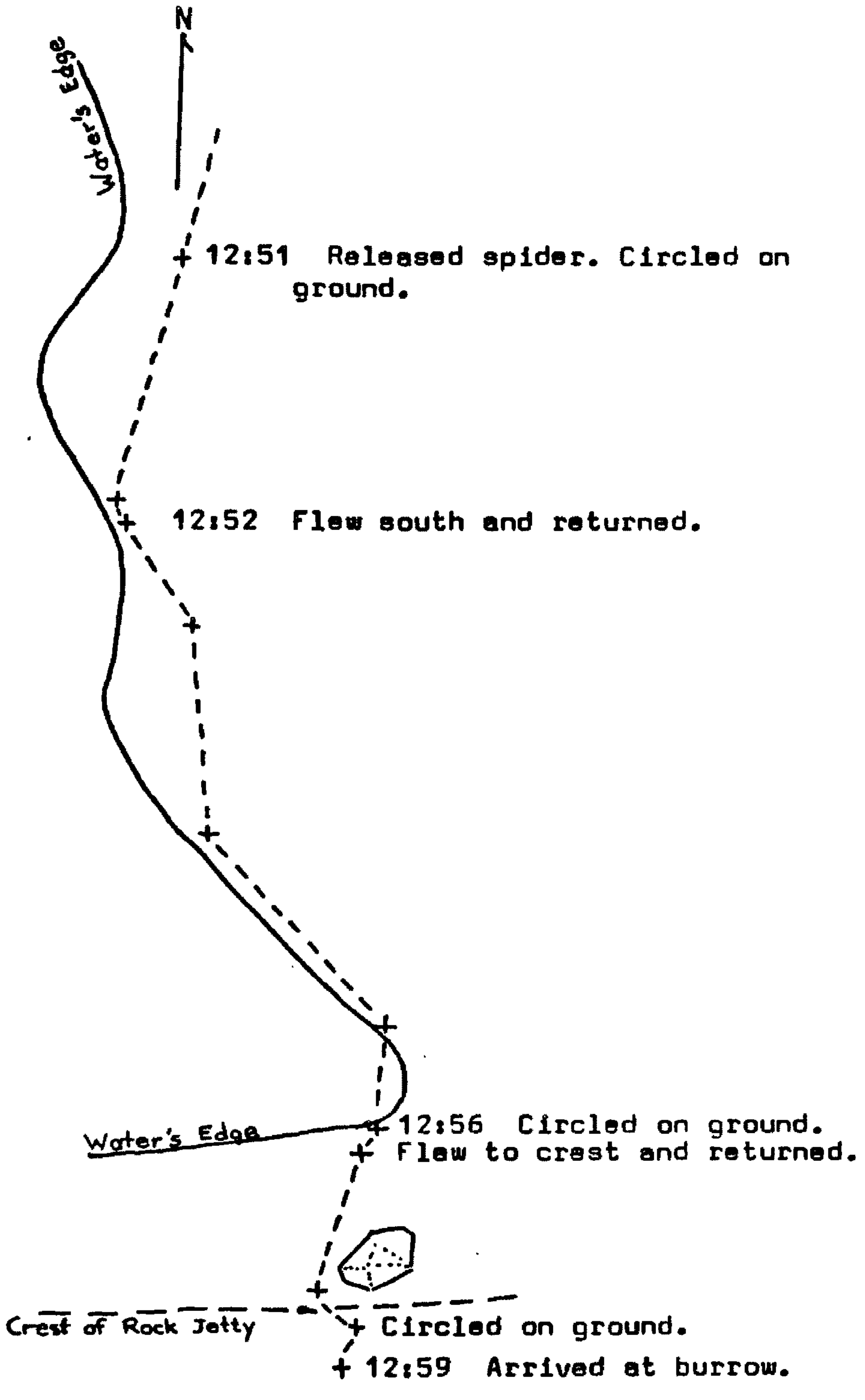


Fig. 6. Observed route of digger wasp, *Anoplius ithaca*, dragging an immature *P. groenlandica*. 16 August, 1965. Total observed distance = 111 feet. Scale: 1 inch = 16 feet.

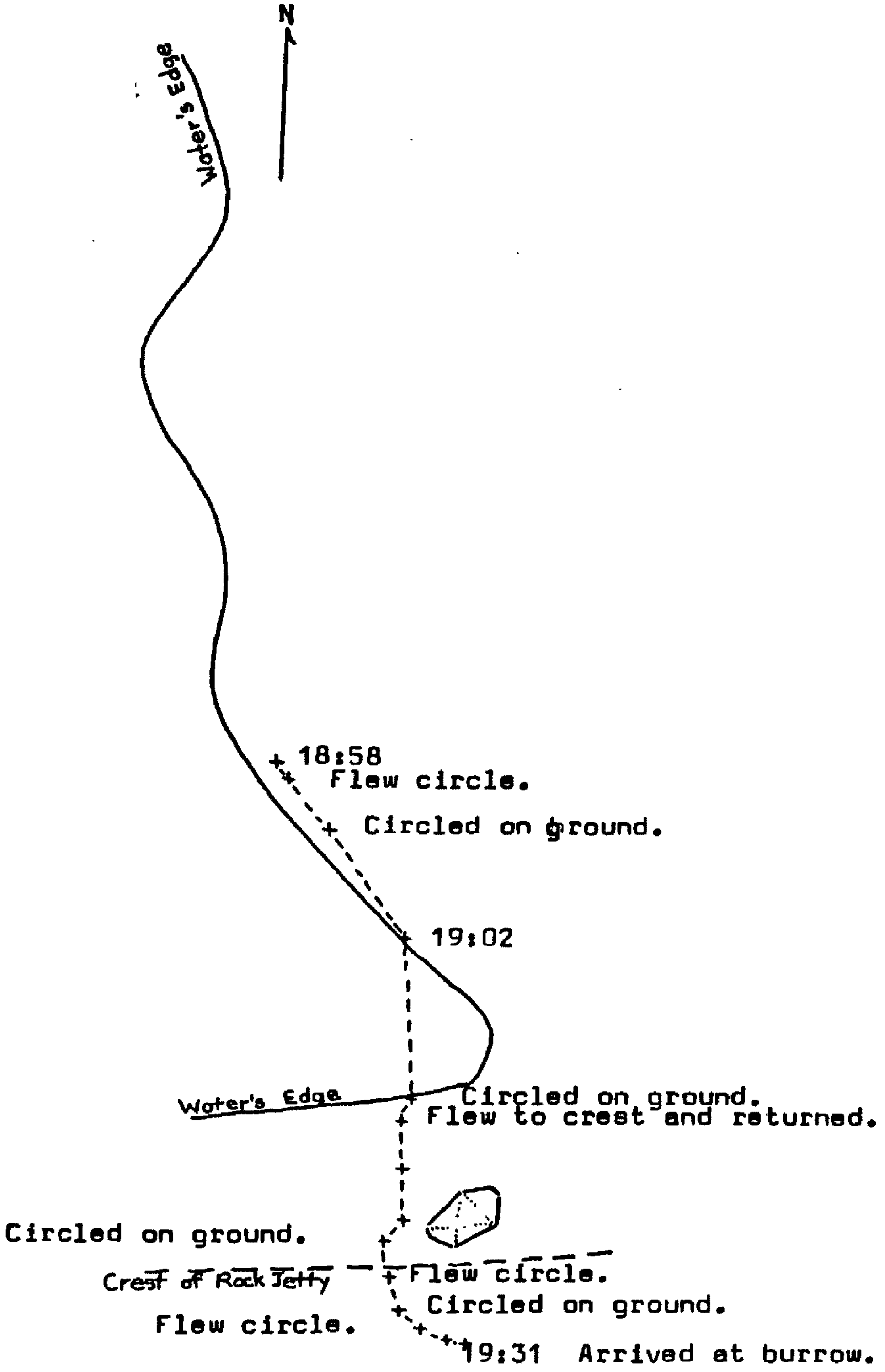


Fig. 7. Observed route of digger wasp, Anoplius ithaca, dragging gravid female P. groenlandica. 16 August, 1965. Total observed distance = 53 feet. Scale: 1 inch = 16 feet. Flight over water indicates the wasp is orienting to something besides the water's edge.

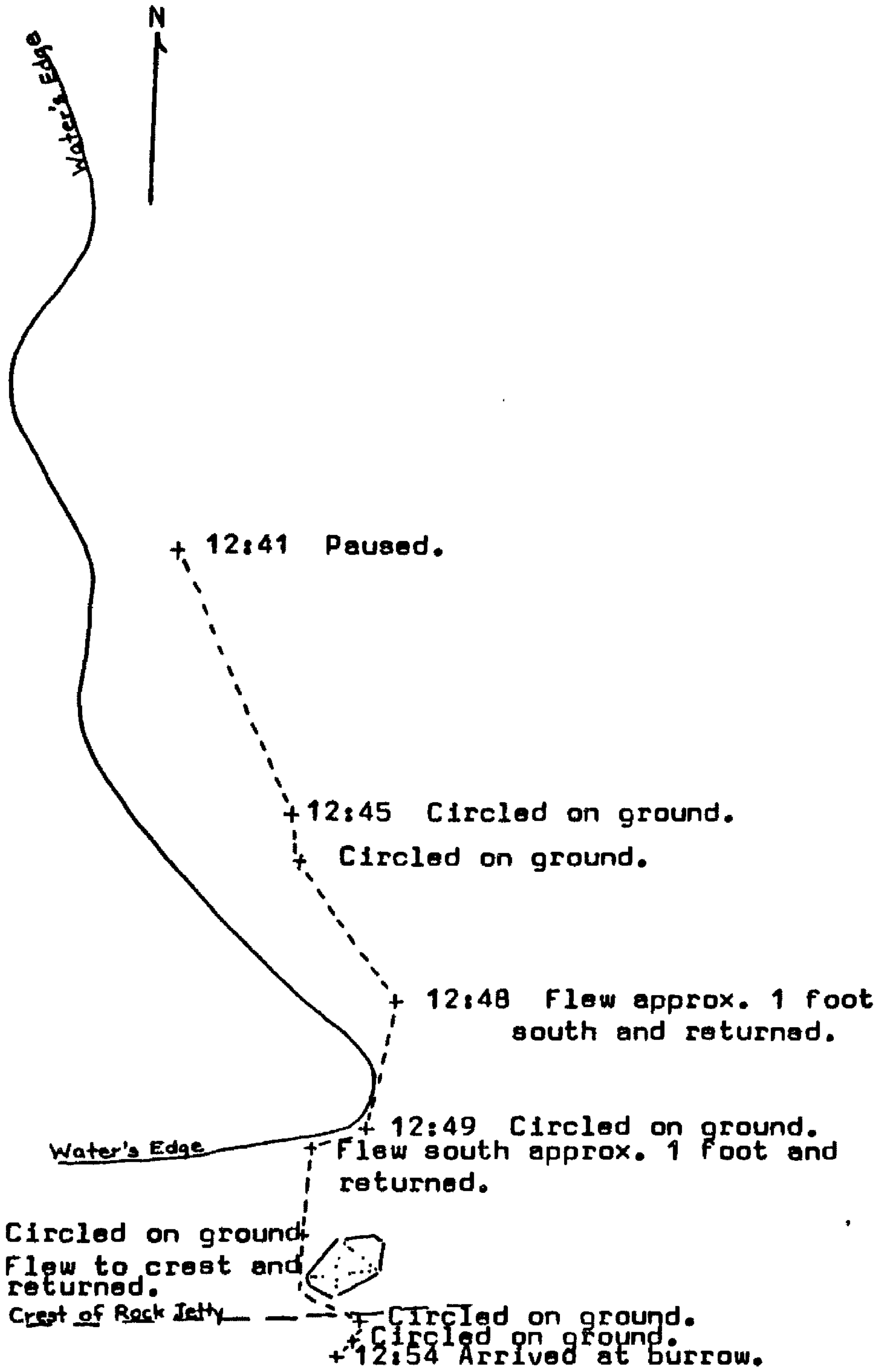


Fig. 8. Observed route of digger wasp, Anoplius ithaca, dragging an immature P. groenlandica. 17 August, 1965. Total observed distance = 76 feet. Scale: 1 inch = 16 feet.

of the weight of the spider and wasp. These weights had been determined on a previous occasion for the specimens collected 31 July, 1965, one of which was a large female spider with attached egg which had been uncovered in excavating the wasp burrow on that date. The day following the spider's capture it was weighed on a Fisher analytical balance and measured as 83.5 milligrams. The wasp that had been captured emerging from that burrow weighed 25.0 milligrams, one-third as much.

Another aspect of the wasp's behavior meriting consideration is the manner of its locating and recognizing its victims. I have noted several pertinent observations. These wasps are most commonly observed flying erratically back and forth along the lakefront crest. They frequently alight on the rocks but never stop their constant activity as they will groom themselves by stroking their antennae and rubbing their hind legs together and then scramble around the margin of the rock, flit to an adjoiing rock a couple of feet away and duck underneath, to reappear a moment later at the top of the next neighboring rock where the grooming process is repeated before the wasp takes to the air again. In this fashion an area about two feet square will be visited for perhaps a minute or two before the wasp moves further along the beach.

Such behavior gives the impression of a purely random, trial and error search. I have noted occasions when immediately following the departure of a wasp, spiders have appeared from underneath rocks in the immediate locality suggesting that the wasp if it had been relying upon some special sensory ability to detect its prey could have done so. Indeed, I have recorded observations (25 July, 1965) of wasps flying directly over exposed male spiders and even alighting on the same rock (10 August, 1965) with no apparent reaction by either.

This indifference is not restricted to male spiders as the same lack of reaction has been observed (19 August, 1965) regarding a female with attached egg-sac noted in full view at approximately two inches distance from a wasp that only a moment later was noted to fly in pursuit of a spider flushed from under a rock. This wasp was observed on this same occasion to completely ignore a juvenile spider immobile in full view on the top of a rock past which the wasp flew within about half an inch.

This is not invariably the case, however. On 19 July, 1966, I witnessed an encounter between a digger wasp and a female P. groenlandica with attached egg-sac. The female was sunning herself alongside a wood chip and had just moved about two inches to the edge of the top of the rock when a digger wasp alighted on an adjacent rock. There was no immediate reaction by either the spider or the wasp. The latter, however, by moving about on the rocks appeared to encounter seemingly by chance the location the spider had just a moment earlier occupied alongside the wood chip. At that moment the wasp appeared to become aroused and began to move about the spot in a more agitated fashion frequently testing the rock surface at that location with her antennae. In the course of these movement the wasp was observed to encounter and actually make contact with the spider which had made no effort to escape nor any other obvious reaction. In response to the actual contact, however, the spider raised her two pairs of forelegs in the customary defensive attitude. The wasp continued to advance, and, although contact was again noted, the wasp did not persist in her approach and broke off contact to fly away. The spider then resumed her resting attitude in the sun.

I witnessed another encounter on 9 August, 1966. On this occasion a struggle ensued lasting approximately three minutes and was initiated by the spider, an unmarked female, running forward to encounter the wasp which had alighted on the rock during its search along the lakeshore. The spider grasped the wasp with her chelicerae and the wasp responded by bending her abdomen forward to sting the underside of the spider when they disappeared over the edge of the rock in each other's grasp. A moment later the wasp reappeared over the edge of the rock leaving the spider immobile on the ground. The wasp proceeded to groom herself--wiping her head and antennae and lying on her side to rub her hind legs together --then after a minute proceeded to walk around the spider first in one direction then the other before grasping the spider with her mandibles and starting to drag it backwards from underneath the rock. After pulling the spider out into the open, the wasp again began grooming herself before starting to clamber south over the rocks, a distance of about a foot. Next the wasp flew back to grasp the spider to begin dragging it away.

Four minutes later as the wasp continued dragging the spider along the lakeshore her route brought her to an encounter with an adult male _P. groenlandica_, which at the approach of the wasp and her burden was observed to move to make contact with his extended forelegs. At this the wasp retreated but without any pursuit occurring. A minute later the wasp again approached the male spider and contact re-occurred. At this the spider was seen to raise his right leg-III, wherewith the wasp withdrew under an adjoining rock and the spider abandoned his position and disappeared from view among the rocks. Two minutes later the wasp was seen to emerge grasping a marked female _P. groenlandica_. The original victim which the wasp had abandoned on encountering her new prey was subsequently located and preserved in ethanol.

This new victim was then transported southward along the lakeshore to the water's edge at the location of the inlet alongside the rock jetty. Here the wasp was observed to lose her grip on the spider as she clambered along a log extending into the water; and her victim slid off the log into the water. The wasp was seen then to fly circles in an apparent search for her victim, which although floating on the surface, had in the meantime been washed among some rocks along the water's edge a couple of feet from which it fell into the water. After approximately five minutes the wasp was lost from view as she appeared to abandon her search for the spider.

One remaining incident of special note was witnessed on 15 August, 1966, when a wasp dragging an immobilized spider along the lakeshore was robbed of its prey by another spider which was seen to rush forward, grasp the wasp's victim and snatch it away beneath an adjoining rock. The wasp subsequently recovered its victim which had apparently been abandoned by the robber spider. This incident bears a close resemblance to that observed on 9 August, 1966. On both occasions wasps dragging their victims were approached by another spider which appeared to initiate the actual encounter.

Discussion

There are several noteworthy aspects to these last two mentioned incidents. On both encounters it was the spider which was observed to approach the wasp to initiate actual contact between the two. This suggests that the spider apparently approaches the wasp mistaking it for a more easily subdued prey and that the wasp's role is more to lure the spider to attack than to herself be the aggressor.

Secondly, although the same wasp was involved in the two encounters observed on 19 July, 1966, in the first encounter the wasp perservered in the conflict and in the second it withdrew. It may be significant that the first encounter was with a female P. groenlandica whereas the second was with a male. I suspect that the wasps are able to distinguish between the two sexes, because I have never identified a male victim in the eight instances for which I have records in the summers of 1965 or 1966. Moreover, in neither encounter actually observed between wasps and male spiders did the male fall victim; and on two different occasions (25 July and 10 August, 1965) I have noted male spiders in full view to be ignored by apparently searching wasps. As males typically have a proportionately very small abdomen and in all cases I have noted the parasitizing egg has been fixed at the same identical location on the abdomen, I feel there is cause to suspect a possible limiting factor restricting the wasp parasitism to females and immature spiders. This suspicion is reinforced in the incident in which the wasp withdrew from engaging with the male but was observed immediately afterwards with a second female victim.

I believe the routes observed demonstrate that the wasps were orienting themselves to their destination. I think this is most likely to be visual landmarks along the lakeshore such as the large rock which was exposed quite prominently and past which each route traveled although the position of the sun or polarized lighting of the sky as is known to function in the orientation of beach spiders (Papi, 1963) could equally be operative in this instance.

Finally there is the question of prey recognition. Wasp, while transporting their prey along the lakeshore, will regularly release them to fly unburdened ahead to orient themselves with their destination. During her reconnaissance a wasp will travel several yards away from where the spider has been left and be gone for as long as a minute or two, yet return with only momentary hesitation to recover her victim. This apparently would demonstrate that the wasp is not limited to responding purely to recognizable movement, yet I have noted several instances when spiders in full view of apparently searching wasps have been ignored. The incident in which the floating spider was washed away as a result of which the wasp was unable to relocate her prey would appear to demonstrate that the wasp places major reliance upon the immediate topography of the locality rather than the form or possible odor of her victim. Although the wasp never located her prey she did return several times to the location at which she last grasped it and if she was relying upon odor to do so it would seem she could have as equally well detected the odor of her prey floating nearby on the surface of the water.

It is difficult for me to be very conclusive in assessing the effect of the wasp predation on the P. groenlandica population. The wasps are active all summer long. The earliest I have had occasion to notice wasps searching along the lakeshore is 27 June; the latest, 16 August. I am certain that their activities commence much before this (perhaps in April) and persist until probably October. I would judge their activities to be most intense during the first half of August.

Although the wasps begin their daily activities with the first sun to light the lakeshore and continue until sunset, their greatest diurnal activity is concentrated at midday.

I have had only two occasions in which to note shrews along the lakeshore so I have no adequate means of judging how important a predator they are of the *P. groenlandica* population. However, the *P. groenlandica* population is considerable, and the capability of the shrews demonstrably adequate.

I suspect four other possible vertebrate predators although none of these actually have been observed to capture any *P. groenlandica.* The most suspect are chipping sparrows (*Spizella passerina*). I have noted these on several occasions as they hop individually or in pairs from rock to rock along the beachfront crest repeatedly darting their head at something among the rocks. I have never been able to observe what it is that they grasp but I have never been conscious of any considerable numbers of seeds lying among the rocks and the portion of the lakeshore in which the sparrows' activities are concentrated is too far from the water's edge for mayflies to be very abundant.

The three remaining suspects are garter snakes (*Thamnophis sp.*), Leopard frogs (*Rana pipiens*), and toads (*Bufo boreas*). Although I have never actually seen toads in the study area they are known to be common in such localities and could be expected to be more active at night. The garter snakes and leopard frogs are frequently seen among the rocks alongalong the water's edge and although I have never observed either to actually capture any *P. groenlandica* I feel both to be perfectly capable and they both frequent the locations where the *P. groenlandica* population is concentrated.

CHAPTER VI

POPULATION DYNAMICS

I. DENSITY

Results

The marking method I utilized in this investigation permits an estimation of the size of the Pardosa groenlandica population within the study area. The calculations necessary are fundamentally those based on the principle of the "Lincon-Peterson index" which can be expressed by the relationship $\frac{P}{M} = \frac{S}{R}$ in which P is the population size, M the number of marked specimens available for recapture, S the total number of individuals in one collecting sample, and R, the number of resighted marked specimens in the sample. The last three items are known from the record of observations maintained during the course of the investigation and consequently permit the calculation of the population size as, $P = \frac{M \cdot S}{R}$.

Figure 9 summarizes the population estimates made for the numbers of males and females separately at five intervals during the period of this investigation. The actual calculations are detailed in Appendix A.

A selective bias in the operation of the pitfalls between captures of male and female spiders is apparent. A total of 664 males were trapped compared to 396 females in the corresponding period or 67.7% more males than females. This bias is exaggerated even further by considering that by the last half of July the male population is declining to approximately half the size of the female population.

Because of such an extreme bias the trap recaptures have not been included in the calculations for the female population. Instead these

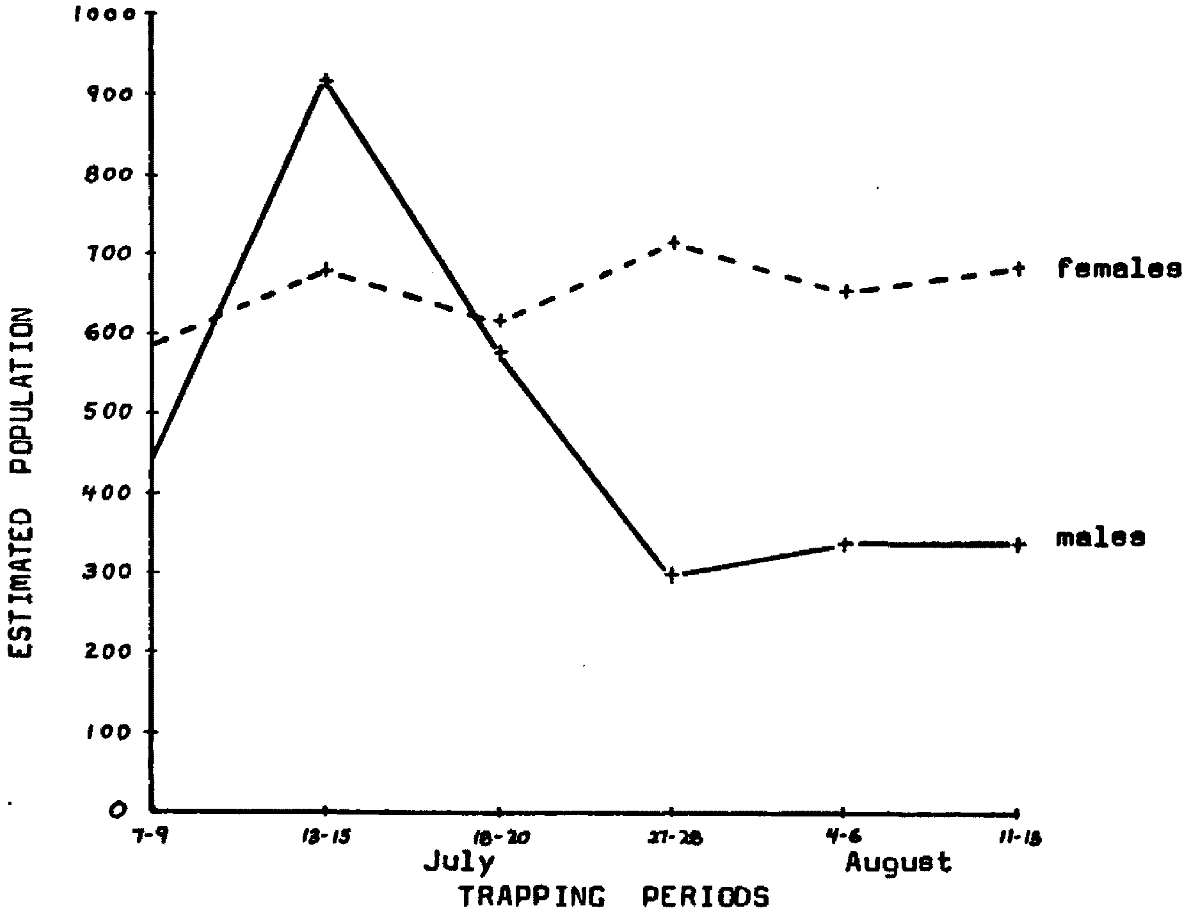


Fig. 9. Pardosa groenlandica population estimated by the Lincoln - Peterson Index analysis of all painted spiders marked in the study area and observed during census surveys at selected three day intervals. The actual calculations are detailed in Appendix A.

have utilized observations from the census surveys only in which the sample size consisted of those spiders sighted in the study area following the procedure described previously in the methods section of this account.

An essential condition to the reliability of the population estimated by a mark-and-recapture method is that there must be no significant movement of animals into or away from the trapping area. To test for this possibility additional traps were located outside the study area (see Methods). Spiders trapped in these pitfalls were marked and records kept of the numbers subsequently trapped in the study area as well as the number of spiders from the study area trapped outside it. Table 4 summarizes these counts. It is apparent that there is a slight movement of spiders into and out of the study area. The degree of emigration calculated by comparing the total number of marked spiders trapped out of the study area (27) to the total number trapped and marked within it (1060) amounts to 2.5%. This level of emigration increases to 3.2% (22 ÷ 674) if only the males are considered which is probably the more valid figure because of the apparent bias in the operation of the pitfalls previously mentioned.

Immigration likewise needs to be considered. This can be approximated by considering the numbers of spiders marked outside the study area which were recaptured within it. Considering only the numbers of males as before, 7.3% (10 of 136) of the spiders marked north of the study area were retrapped within it and 21.7% (15 of 69) of those marked to the south. This by itself would seem to indicate a net immigration of spiders into the study area. I doubt that this actually occurred very significantly.

TABLE 4

EVIDENCE OF THE DEGREE OF IMMIGRATION AND EMIGRATION OF PARDOSA GROENLANDICA DURING THE PERIODS OF TRAPPING BETWEEN 19 JULY AND 12 AUGUST, 1966

A. The number of Previously Marked Spiders Trapped at a Distance of 130 Feet North or South From the Study Area (Emigration).

Far North Trap			Far South Trap		
Males	Females		Males	Females	
12	2	(wht.)	3	0	(wht.)
3	1	(yel.)	4	2	(yel.)
15	3	Total	7	2	Total

B. The Number of Spiders Marked Outside the Study Area That Were Subsequently Recaptured Within It (Immigration). Grn. = First Marked 130 Ft. to North. Pink = First Marked 130 Ft. to South.

North Traps			South Traps		
Males	Females		Males	Females	
9	3	(grn.)	1	0	(grn.)
5	0	(pink)	10	9	(pink)
14	3	Total	11	0	Total

The influences of immigration and emigration upon the estimation of population size can be best minimized by sampling the population at closer intervals. An adequate procedure is that employed by Schnabel utilizing the summation of the total resightings (R) and products of numbers of marked animals available (M) and numbers resighted (S). The calculations for the estimate of population (P) then is performed as $P = \frac{M.S}{R}$. Figure 10 summarizes the estimated numbers of males and females so calculated based on records of the census surveys through the study area. The actual calculations are detailed in Appendices B and C.

Discussion

A major assumption implied in an indexing method to estimate population is that marked and unmarked individuals are equally susceptible to being recaptured. From my observations, the painted spiders certainly did not appear to behave any differently and I have no reason to suspect that their normal longevity was affected. It is possible that during the course of the census surveys through the study area that the painted spiders were the more conspicuous but I feel this possibility is minimized by the bareness of the lakeshore, the special care I took to be as observant of all spiders as possible, and the large size of each sample.

The adult population can be noted to be at its peak (2177 maximum on 16 July) for a period of about a week in the middle of July and then begin to decline. The average total adult population for 4, 5, and 6 August is only 65.6% of the corresponding population for 18, 19, and 20 July. Of interest is to note the disproportionate reduction in the numbers of male spiders during this population decline. For example, there is a 47% decline in the average number of males for 11, 12, and 13 August,

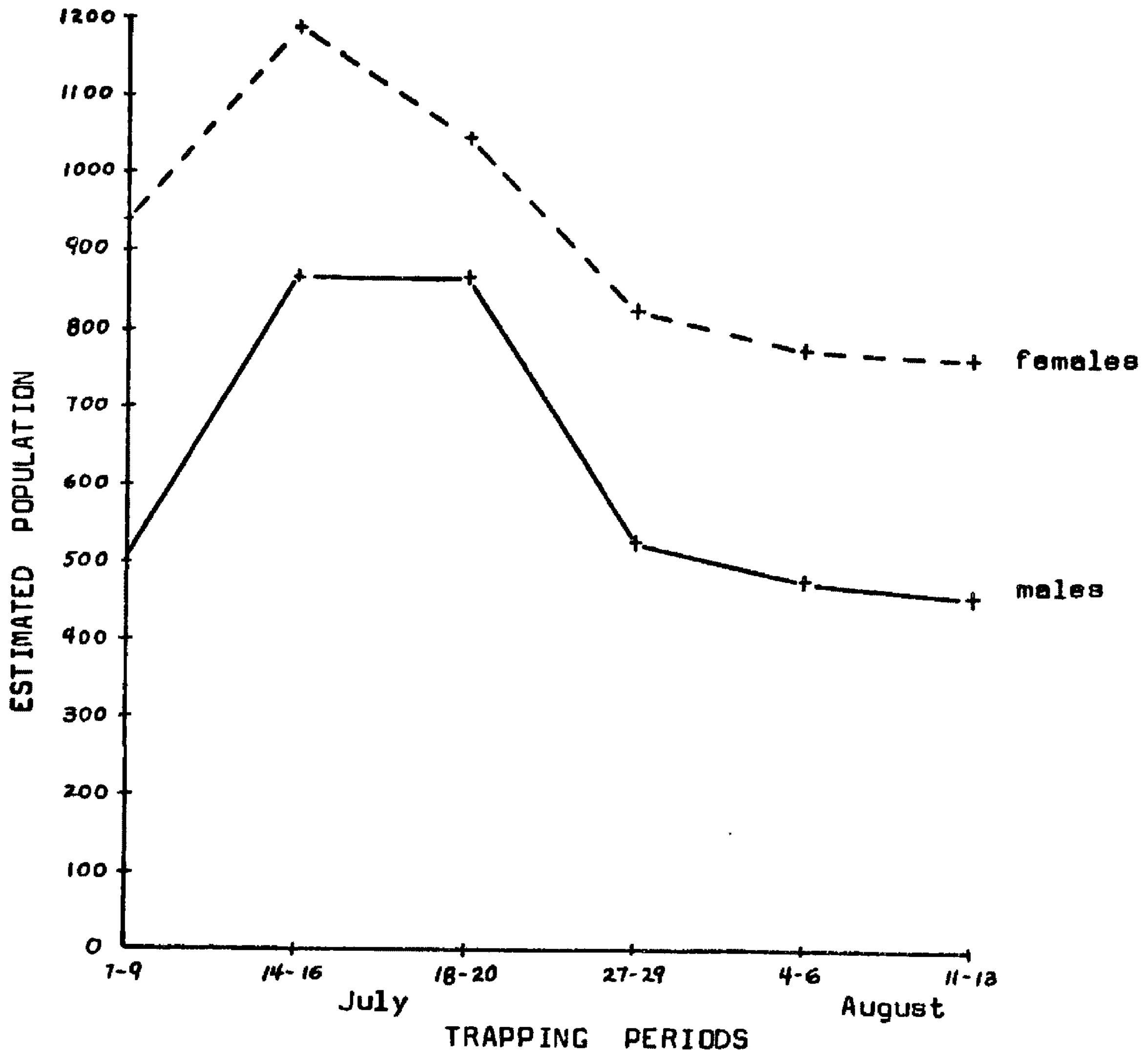


Fig. 10. Pardosa groenlandica population estimated by the Schnabel analysis of all painted spiders marked in the study area and observed during census surveys at selected three day intervals. The actual calculations are detailed in appendices B and C.

compared to the average number of males for 18, 19, and 20 July. For females there is a corresponding 27% decline. Hackman (1957), and Vlijm, *et al.* (1963), and Vlijm and Kessler-Geschiere (1966 a) report general observations of a corresponding disproportionate decline of males in the *Trochosa ruricola* and *Pardosa amentata* populations they investigated indicating the phenomenon to be a generally common occurrence among wolf spiders.

The ratio of adult males to females is consistently imbalanced in the period from July to mid-August as indicated in Figure 10. It is closest to unity during the mid-July population peak but even then there is approximatley 29% more females than males and this increases to better than 60% by August. Savory, (1964 p. 59) reports that "All reliable investigations of the proportions of the sexes in the recently hatched young agree that their numbers are approximately equal...." and I would assume this to be true for *P. groenlandica*.

Heydemann (1960 a) reported a comparable increase in the proportion of females to males for *P. purbeckensis* which he related to the areas of optimal habitat. The importance of this he proposed (1960 b) to be the benefit to the species resulting from the liberation of the young in the most suitable environment. Vlijm and Kessler-Geschiere (1966 a) noted a comparable phenomenon for the three *Pardosa* species they investigated which was synchronized to follow immediately after the period of copulation. They related this to the increased daily activity of the males and consequent dispersion to suboptimal biotopes. They felt this helped insure a greater fertilization rate in those habitats where and when few females were present.

I believe another factor contributing to these disproportionate ratios between the sexes is the greater longevity of the females. Figure 11 summarized the observations I noted in my investigation and indicate the median observed age of females as twice that for the males. Vlijm and Richter (1966 b) noted that adult P. lugubris females in their investigation survived three times as long (six months : two months) as the males.

At its maximum in mid-July the population density was calculated for the beachfront as 4.08 spiders per square foot and 0.70 spiders per square foot for the midbeach portions of the study area. This represents an extremely great concentration of animals. Of course, these are the densities for the peak population which declines by approximately 35% within two weeks, but the average densities for the total adult population for the entire six week period are: for the beachfront, 3.09 spiders per square foot; and, for the midbeach, 0.51 spiders per square foot. My impression based on general field observations is that it is too great a density to represent the average actual situation although I realize that all the spiders in a given area observed cannot be expected to be in view.

A measure for comparison is provided by Hackman's report (1957) of the approximate density for a population of Trochosa ruricola. This is a wolf spider commonly found along rocky coasts in Finland and similar in its habits to P. groenlandica with the major exception that the females retire with their egg-sacs to burrows prepared under rocks in suitable locations to avoid flooding by the tides and waves. On the basis of his investigation, Hackman determined a density of approximately ten adult spiders per meter of shore track. This was calculated utilizing observations of 224 spiders marked on 24 and 25 August, 1954 (131 males and 93 females) of which 33 (21 males and 12 females) were resighted in a sample of 155 spiders sighted during a five hour search on 25 August, 1954. Allowing a survival rate of 0.96 per day, the total adult population Hackman calculated by the Lincoln formula was approximately 980. This was in approximate agreement to the population he estimated for the previous year (about 1100) calculated by the Lincoln formula utilizing the total number of individuals marked in 1953 (132) of which 25 were recaptured in a sample of 211 spiders observed during the period June to July, 1954.

A comparable calculation is possible from the date in my investigation utilizing the estimate of the maximum adult population for mid-July, 2059, divided by the length in meters of shoreline in the study area, roughly 22. This is twice the density Hackman reports for Trochosa ruricola, yet considering both determinations as admitted approximations, it would not seem too unreasonable.. Certainly the burrowing habit for T. ruricola, for which there is nothing comparable by P. groenlandica, might be expected to tend to disperse T. ruricola females because of the necessity for locating suitable burrowing sites.

II. DISPERSION

Results

The census surveys were conducted separately for the beachfront and midbeach regions. This has permitted the separate calculation of population densities for these portions of the study area. They provide additional verification that the P. groenlandica population is concentrated along the beachfront at the water's edge. See Table 5. The calculations utilized the average population of males and females separately

TABLE 5

ESTIMATED POPULATION DENSITIES OF <u>PARDOSA GROENLANDICA</u> BASED ON THE SCHNABEL ANALYSIS OF ALL PAINTED SPIDERS MARKED IN THE STUDY AREA

	Beachfront (300 Sq. Ft.)		Midbeach (1200 Sq. Ft.)	
Date	Avg. Pop.	Density/Sq. Ft.	Avg. Pop.	Density/Sq. Ft.
July				
7,8,9	males: 237	9.79	262	0.22
	females 531	1.77	405	0.34
	total: 768	2.56	667	0.56
14,15,16	males: 460	1.53	407	0.34
	females: 764	2.55	428	0.36
	total: 1224	4.08	835	0.70
18,19,20	males: 479	1.59	388	0.32
	females: 657	2.19	396	0.33
	total: 1136	3.78	784	0.65
27,28,29	males: 357	1.19	172	0.14
	females: 505	1.68	324	0.27
	total: 862	2.87	496	0.41
August				
4,5,6	males: 274	0.91	205	0.17
	females: 493	1.64	287	0.24
	total: 767	2.55	492	0.41
11,12,13	males: 321	1.07	140	0.12
	females: 499	1.66	270	0.23
	total: 820	2.73	410	0.35

at selected three day periods taken from the Schnabel analysis of daily population estimates (Fig. 10). Each average is divided by the area in square feet of the appropriate region to give a calculated estimate of the numbers of spiders per square foot. This permits a consideration of the concentration of males compared to females for both the beachfront and midbeach regions.

Discussion

It is apparent that consistently for July and the first half of August there is a distinctly greater concentration of the population in the beachfront region. The disproportion is greatest for the total population in mid-August when the density at the beachfront is 7.8 times greater than at midbeach. This would appear to be due largely to the continued decline in the number of males at midbeach from the peak at mid-July. The beachfront and midbeach densities are most nearly equal the first week of July but even then the beachfront density is 4.5 times greater than at midbeach. The average population density for the beachfront for the entire summer is 6.1 times greater than at midbeach.

There is a consistent disproportion for the population density of both males and females. The beachfront density of males is 5.9 times greater than the midbeach density of males; for females it is 6.5 times greater.

Certainly, the non-uniform distribution of population must be due to many factors. The variation to be expected in temperature and humidity between the beachfront and midbeach portions must be important (see Table VI). The difference in exposure to the sun's light probably contributes substantially. I believe a major influence also is the greater

TABLE 6

COMPARISON OF TEMPERATURES MEASURED AT MIDBEACH AND AT THE WATER'S EDGE

	Ground Level Air Temperature	Rock Surface Temperature	Subsurface Rock Temperature
Midbeach	42°C	52°C	37°C
Water's Edge	31°C	39°C	27°C

Temperatures Measured on 18 August, 1966, at 16:30 with a Mercury Laboratory Thermometer.

abundance of food along the water's edge where aquatic insects, such as mayflies, will emerge as adults.

III. MOVEMENT

A major effort of this investigation has been to analyza the movement of Pardosa groenlandica. Common reference to these spiders as "wolf spiders," which search to pounce upon their prey, identifies their cursorial ability as a major aspect of their life activities. Specific problems considered are: Over how great a distance do these spiders customarily range? Is there a significant difference in movement between males and females? Is there a significant difference in movement at different stages of the spider's life history -- such as between females with egg-sacs and those without? Are movements by these spiders recognizably oriented? and if so, to what?

I have followed the analysis of movement proposed by Brant (1962) for small rodents. His method seemed to apply best to the linear pattern of movement of these spiders along the narrow confines of the lakeshore. Brant's analysis employs the maximum straight line distance (M) in feet between the captures for each individual and the arithmetic average (av.M) for a number of animals. It also includes the average distance (av.D) between successive captures for each individual and the average time (av.T) in days, of the time between one capture and the next. In addition, I have included the average distance between one recapture and the next for each female with an egg-sac (av. D. sac) and for each female without an egg-sac (av.D.w/o sac), and the maximum distance for each female with an egg-sac (M. sac). All distances are measured in feet to a half a foot accuracy.

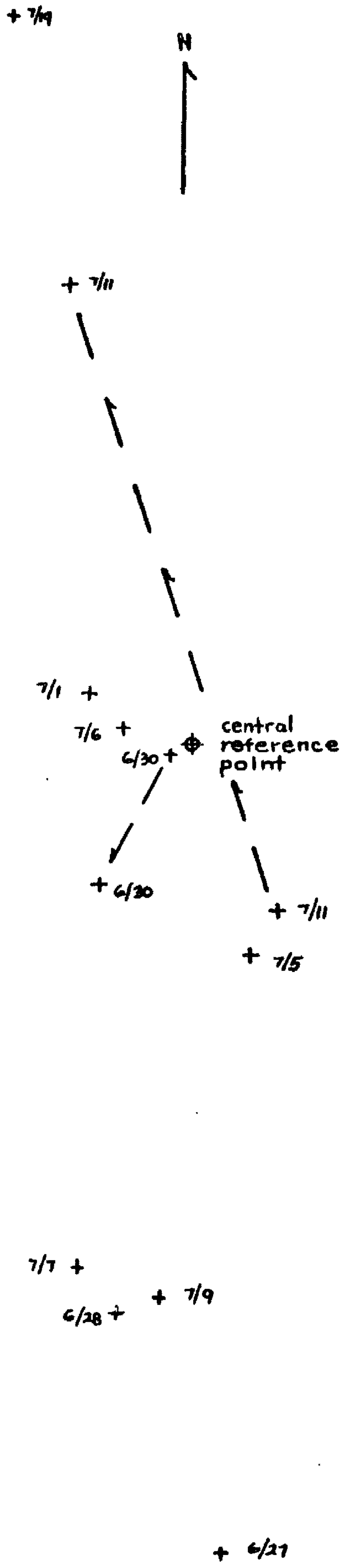


Fig. 11. Record of resightings for male Pardosa groenlandica, number 1966.17. Scale: 1 inch = 8 feet.

Distances between successive captures (D):

capture	date	days interval (t)	D in ft.	remarks
1	6/27	-	-	
2	6/28	1	13	
3	6/30	2	25½	
4	6/30	½	6½	beach-front
5	7/1	½	9	
6	7/5	4	14	
7	7/6	1	12	
8	7/7	1	25	water's edge
9	7/9	2	3½	"
10	7/11	2	18½	beach-front
11	7/11	½	30½	
12	7/19	8	14	dead. Nor. bch-front trap
	Totals:	22½	171½	

Maximum distance between captures (M), measured between captures 1 and 12 = 73½ feet.

Av.t. = 22½ ÷ 11 = 2 days.

Av.D. = 171½ ÷ 11 = 15.6 feet.

Av.M. = 73½ ÷ 2 = 36.75 feet.

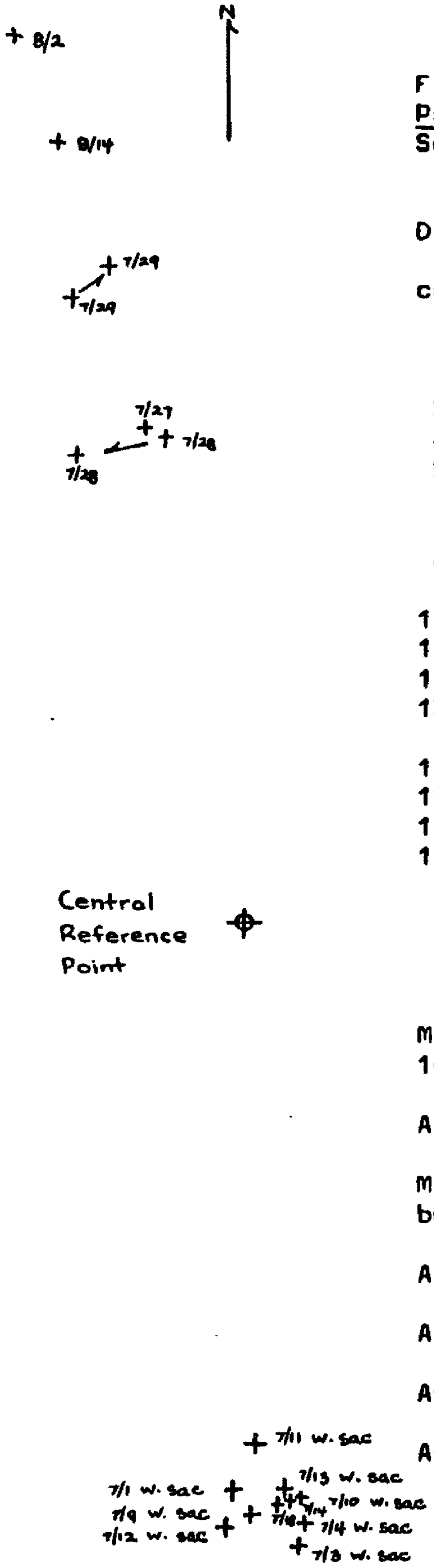


Fig. 12. Record of resightings for female <u>Pardosa groenlandica</u>, number 1966.70. Scale: 1 inch = 8 feet.

Distances between successive captures (D):

capt.	date	days interval (t)	D in ft.	remarks
1	7/1	-	-	w. egg-sac
2	7/3	2	3½	" "
3	7/4	1	1	" "
4	7/9	5	2	" "
5	7/10	1	3	" "
6	7/11	1	3	" "
7	7/12	1	3½	" "
8	7/13	1	3	" "
9	7/14	1	½	" "
10	7/18	4	½	" "
11	7/27	9	48	no egg-sac
12	7/28	1	½	11:48
13	7/28	½	3½	17:37; water's edge
14	7/29	½	7	13:24
15	7/29	½	2	16:47
16	8/2	3½	11	gravid?
17	8/14	12	5	Nor. bch.-front trap w. egg-sac
	Totals:	44	97	

Max. distance (M) between captures 2 and 16 = 68 feet.

Av.M. = 68 ÷ 2 = 34 feet.

Maximum distance with egg-sac (M.sac) between captures 2 and 6 = 4½ feet.

Av.t. = 44 ÷ 16 = 2.7 days.

Av.D. = 97 ÷ 16 = 6 feet.

Av.D. w. sac = 20 ÷ 9 = 2.2 feet.

Av.D. w/o sac = 77 ÷ 7 = 11 feet.

These parameters were determined from a map of each individual spider's movements prepared from field notes which recorded the compass bearings and distances for each location at which it had been sighted. The map was prepared to a scale of 1 inch = 8 feet and maintained for each individually marked spider. Figures 11 and 12 provide representative examples for a male and female spider with the accompanying summary.

Results

Data were thus recorded between 21 June and 13 August, 1966 for a total of 70 females and 17 males each of which had been re-sighted a minimum of five times over a period of at least a week. Data for the other 106 individually marked spiders was not used in this analysis as I felt it was not complete enough to be adequately representative.

Figure 13 shows the comparison of maximum straight line distance (M) between males and females. The respective medians with half the observed cases at a greater distance and half at a less distance are 56 feet and 59 feet. The arithmetic average (av.M) respectively are males, 48.7 feet, and females, 73.8 feet.

Figure 14 shows a comparison of the average distance between successive recaptures (av.D) for 16 male spiders and 55 females without egg-sacs. All of these are included in the collection of 70 spiders for which a minimum of five re-sightings over a period of at least a week had been made. The mean average distance between successive recaptures for the males is 14.5 feet; for the females, 30.5 feet. The respective medians are: for the males, 14 feet; for the females, 19.5 feet.

A total of 36 females were observed transporting egg-sacs that

Fig. 13. Comparison of the maximum straight line distance in feet between recaptures (M) for 71 female and 17 male *Pardosa groenlandica*. Ordinate in ten foot intervals.

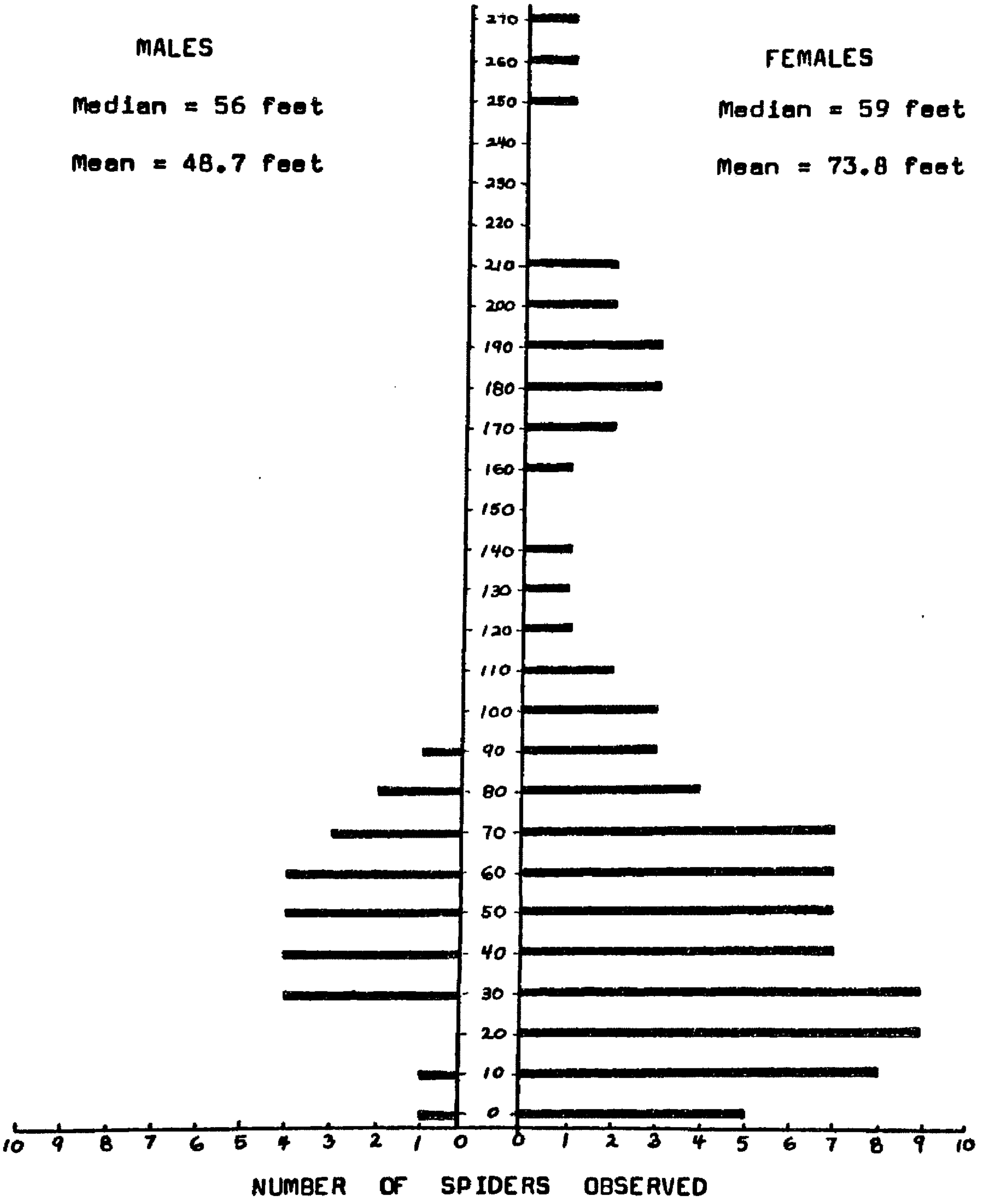
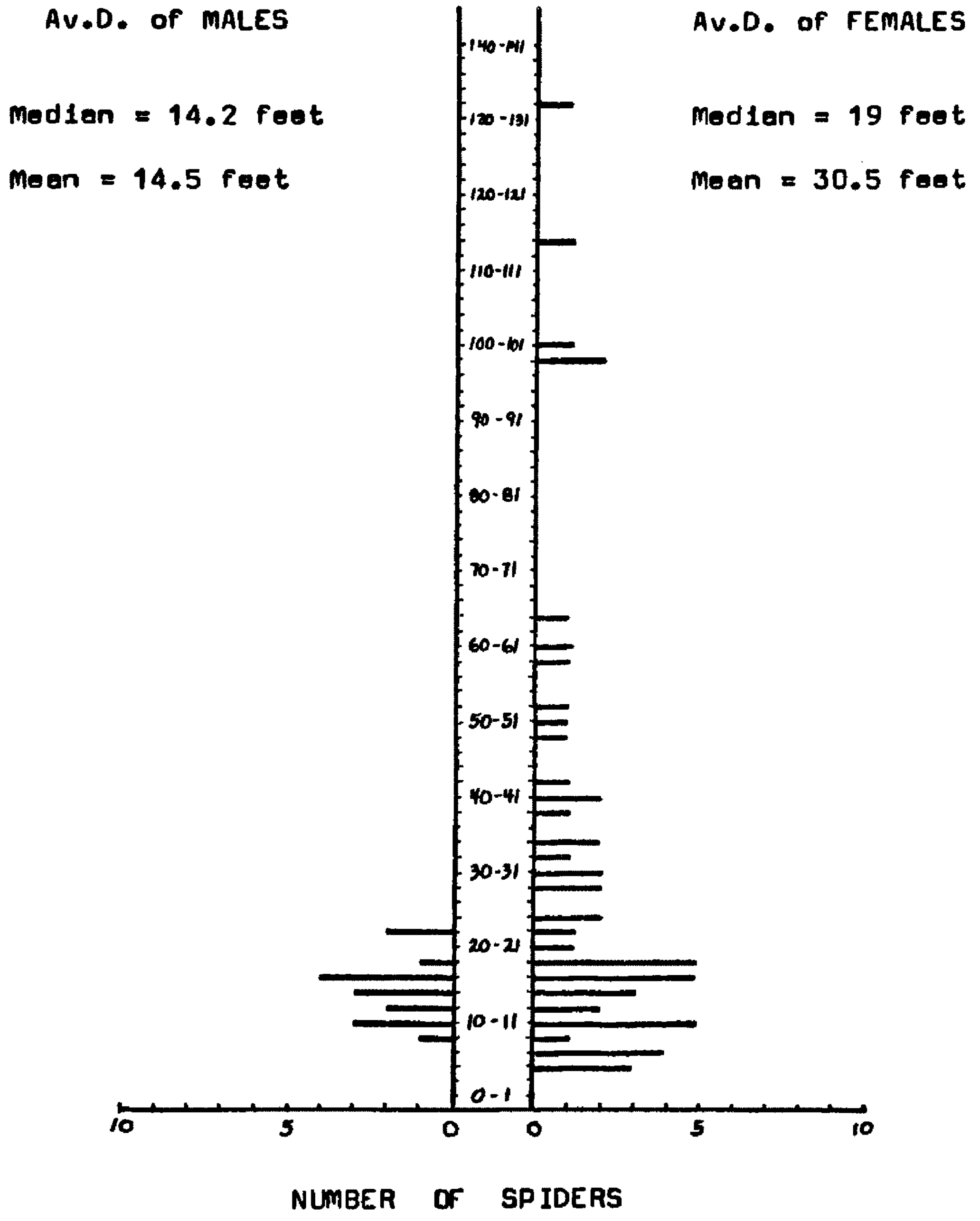


Fig. 14. Comparison of the average distance between successive resightings (Av.D.) of 16 male and 55 female *P. groenlandica* (without egg-sacs) all of which were sighted a minimum of five times over a period of at least a week. Ordinate represents distance at two foot intervals.



were seen on at least two occasions subsequent to the emergence of their brood. Figure 15 allows a comparison of the average distance between resightings while transporting the cocoon and afterwards. There is a six-fold increase in the mean distance traveled by females after emergence of the brood than while transporting the egg-sac.

Figure 16 presents records of the average time in days between successive "recaptures." The shorter interval for males is consitent with the generally more limited range of movement and greater exposure as a result of their courtship displays. Males consequently are re-sighted more frequently during their occupancy of an area.

Evidence for orientiation of movement was tested by comparison of the observed distribution of the spiders in the study site to what could be expected for a purely random distribution. The mathematical model for this random distribution can be calculated as a Poisson distribution.

The analysis required dividing the study area into suitably sized quadrats and determining the number of marked spiders observed for each. The quadrat size selected was a 2 by 2 foot square, 500 of which were required to subdivide the 20 by 100 feet size of the study area. These quadrats were drawn as a grid using the scale of one inch equals eight feet. The same scale was used to plot from the record of compass bearings and distances the location at which each marked spider had been resighted. This was done on a separate piece of waxed paper. This was then superimposed upon the grid of quadrats and allowed the numbers of spiders seen within each quadrat to be counted.

A frequency distribution of the number of quadrats with varying numbers of spiders (from 0 to 6 or more for females and from 0 to 3 or more for males) was made (Tables 7 and 8).

Fig. 15. Comparison of the average distance between successive resightings (Av.D.) of 36 female Pardosa groenlandica with egg-sacs and the same females after abandoning their egg-sacs. All were sighted a minimum of five times over a period of at least a week. The ordinate represents distance in feet with the maximum as 55 feet and over.

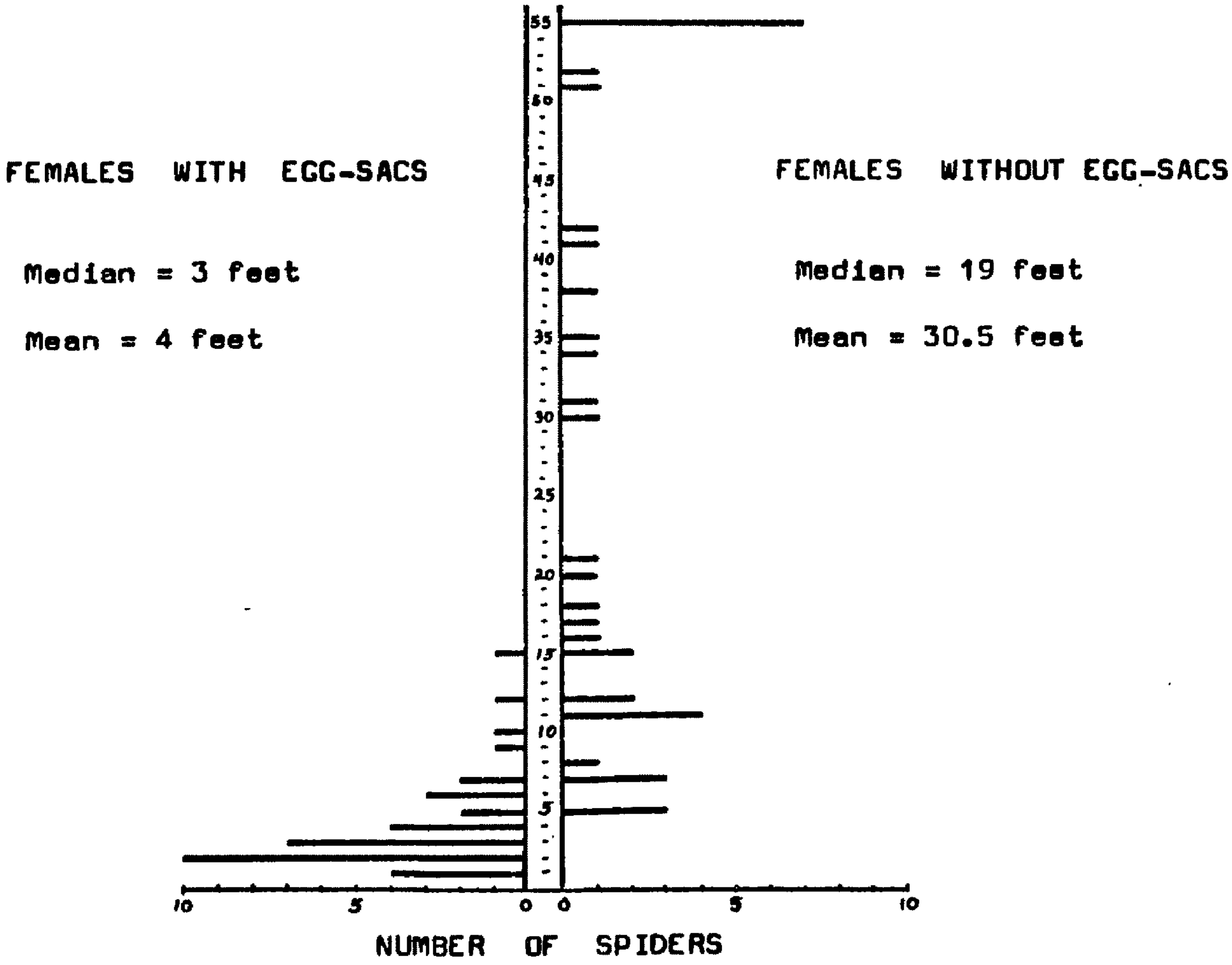


Fig. 16. Comparison of the average time in days between successive resightings (av.T.) for 69 female and 17 male *Pardosa groenlandica* observed between 21 June and 18 August, 1966. Ordinate represents days.

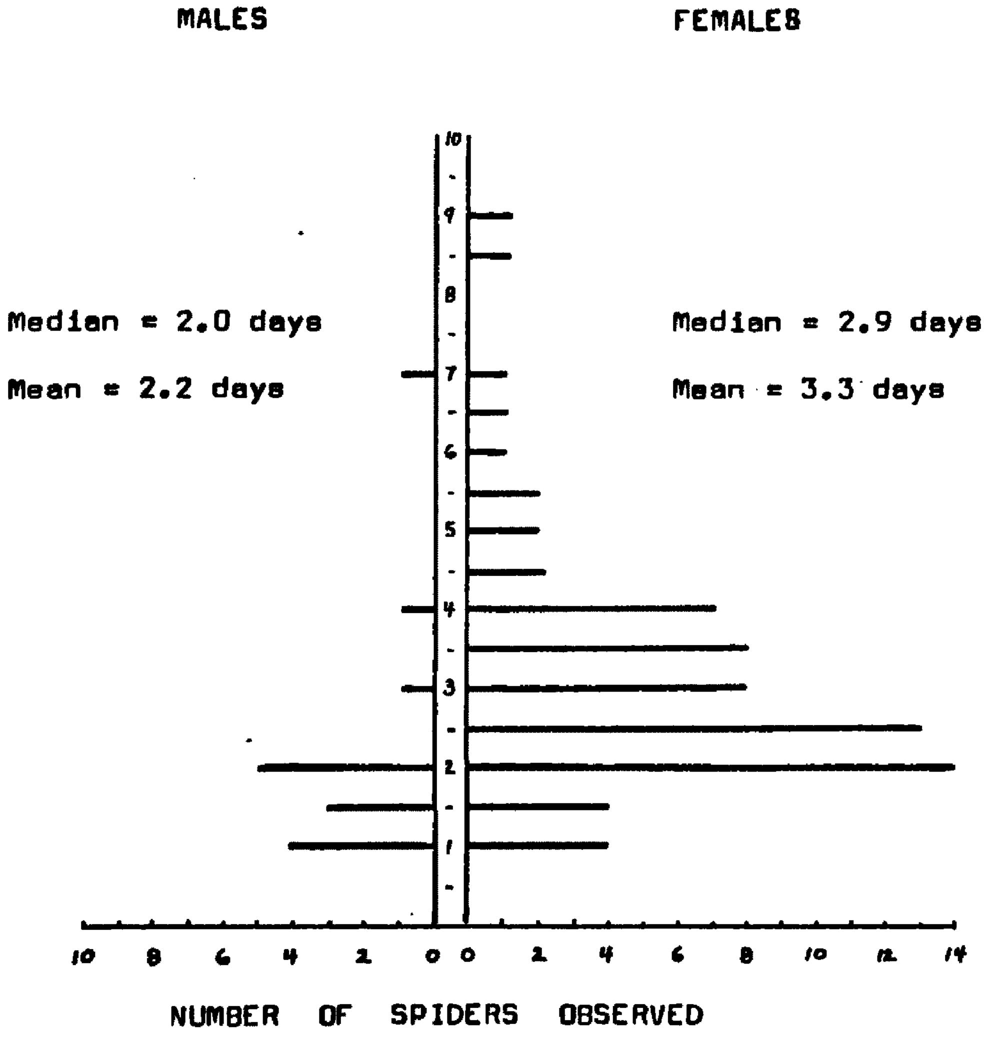


TABLE 7

FREQUENCY DISTRIBUTION OF THE NUMBER OF QUADRATS WITH FROM 0 TO 6 OR MORE FEMALE PARDOSA GROENLANDICA OBSERVED FROM 21 JUNE TO 12 AUGUST, 1966, COMPARED TO THE NUMBERS EXPECTED BY CHANCE AS CALCULATED BY A POISSON DISTRIBUTION

No. Female P. g. Per Quadrat	No. of Quadrats Observed	No. of Quadrats Expected for a Poisson Distribution
0	323	201.7
1	85	183.1
2	37	83.1
3	20	25.3
4	12	5.7
5	9	1.0
6+	14	0.2

TABLE 8

FREQUENCY DISTRIBUTION OF THE NUMBER OF QUADRATS WITH FROM 0 TO 3 OR MORE MALE PARDOSA GROENLANDICA OBSERVED FROM 21 JUNE TO 12 AUGUST, 1966, COMPARED TO THE NUMBERS EXPECTED BY CHANCE AS CALCULATED BY A POISSON DISTRIBUTION

No. Female P. g. Per Quadrat	No. of Quadrats Observed	No. of Quadrats Expected for a Poisson Distribution
0	394	368.2
1	77	112.7
2	15	17.2
3+	14	1.9

The observed distribution was then compared to the expected frequencies for a random distribution as calculated by the Poisson series:

$$P = \frac{N}{e^m} + \frac{N\ m}{e^m} + \frac{N\ m^2}{2!\ e^m} --- \frac{N\ m^n}{n!\ e^m} - 1$$

where N = the number of quadrats sampled (500) and m = the mean number of organisms per quadrats (454 ÷ 500 = 0.908). The actual calculations for this study are detailed in Appendix D for females and Appendix E for males. The results are tabulated in Table 7 and Table 8 in comparison to the observed distribution.

The differences in the observed and the calculated random distributions were tested by the chi-square method. The actual calculations are detailed in Appendix F.

By inspection of the maps prepared of each individual spider's movements, one notices that these movements were predominantly north and south, parallel to the lakeshore. The water's edge and the narrowness of the lakeshore restrict the east-west movements of the spiders in the study area. But one becomes curious whether there is a general pattern of movement in one direction or the other. I tested this possibility by inspecting the map prepared of the movements of each individual spider and locating the midpoint between the extreme locations that the spider had been sighted. The position of this midpoint was then compared to the location at which the spider was first sighted. If this midpoint was north of the location at which the spider was first sighted by a distance equal to or greater than the average distance between recaptures (av.D), I recorded this spider as having migrated northward in its movements along the beach during the course of this study. Movement south could be recorded similarly. The amount of migration was recorded in

TABLE 9

FREQUENCY DISTRIBUTION OF THE NUMBERS OF INDIVIDUALLY INDENTIFIABLE _P. GROENLANDICA_ MOVING NORTH OR SOUTH FROM THEIR FIRST LOCATION ISGHTED ONE OR MORE TIMES THEIR AVERAGE DISTANCE BETWEEN RECAPTURES (Av. D.)

		Numbers of Females	Numbers of Males
Migration Northward	4+ Av. D.	2	0
	3 Av. D.	6	2
	2 Av. D.	10	4
	1 Av. D.	13	5
No Migration		12	2
Migration Southward	1 Av. D.	10	3
	2 Av. D.	11	1
	3 Av. D.	2	0
	4+ Av. D.	4	0
	Totals=	70	17

Intrepreted as Evidence of the Dispersion of Female _P. g._ in Approximately Equal Numbers North- and Southward Along the Lakeshore.

comparison to the calculated average distance between captures (av.D). Table 9 summarizes these observations.

Discussion

Hackman (1957) studied the movements of a related wolf spider Trochosa ruricola (Deg.) along a Finnish beachfront by dividing his study area into eight sections each about ten meters long and recorded the section in which each marked specimen was released and subsequently resighted the following summer. Records were made for a total of 30 males and 65 females recaptured after overwintering in the summers of 1954 and 1955. His analysis showed that 87% of the males but only 58% of the females were recaptured in the same locality in which they were released the year before. Six per cent of the males and 15% of the females were recovered at a distance of more than 30 meters from their release point. His conclusion was that the male spiders, in spite of their hunting activity (and mating activity in May), moved very little along the shore and that the females were less stationary. He surmised by way of explanation that perhaps the search by the female for the egg-sac might be responsible for their greater amount of movement. He further commented on the abandonment by the spiders in September of the shoreline areas to move to hibernation areas at the uppermost portion of the stony shoreline or into the adjacent pine forest.

Kuenzler (1958) sought to determine the size of the home ranges for each of the three species of wolf spiders that occupied old-field habitats in Georgia. He recognized that the inadequacy of his sample (42 specimens total) limited his analysis to ".....only a very rough, probably minimum, approximation" (op.cit., p. 498). He employed two different methods. First, he measured the area enclosed within the polygon formed by connecting the outermost loci of all the recapture points for each specimen captured four or more times. Second, he followed the method proposed by Dice and Clark (1953) and measured the distance of each recapture locus from the center of activity of every spider, which was recaptured two or more times, to construct a frequency histogram of the square roots of these "activity radii". His conclusions were that all home ranges for the three species were relatively small. The major part of the burrowing spiders' activity out of the burrow is spent at a particular distance from it (usually less than 9 feet for the most active species). Lastly, the non-burrowing species wander in a more-or-less random fashion over its home range.

Vlijm and Richter (1966) investigated quantitatively aspects of the activity of Pardosa lugubris (Walckenaer) at different stages of its life cycle. Their data were obtained by observations of 20 adult males and 20 adult females of comparable ages released within the confines of a rectangular area measuring 1.80 m by 0.87 m by 0.20 m, filled with a mixture of sand and loam. Humidity, lighting, and temperatures were carefully manipulated to resemble conditions in the natural habitat of the spiders. The behavior of the confined specimens was reported to be not noticeably different in comparison to similar spiders observed in the field. The test group was observed from 15 March to 16 May, 1964. The location of all animals during this interval was marked on a plan of the container every half hour during a period of eight hours. The sixteen observed points per day per spider were utilized as a measure of "the daily activity" by determining the total length of the line formed by connecting each point in chronological order.

Their results indicated that the general level of activity of males during the observed reproductive period was greater than for females. The maximum mean weekly activity of twenty males was 1 2/3, the maximum observed for 20 females (1500: 900).

My analysis of average maximum straight line distances (av.M) and average distance between successive recaptures (av.D) do not permit direct comparison to the mean weekly activity analysis by Vlijm and Richter. However, the av.M and av.D do reflect a general level of activity and as such indicate that female P. groenlandica are more active than the males during the last half of June to mid-August. This is in general agreement to Hackman's (1957) conclusion for Trochosa ruricola (Deg.). I feel the discrepancy between these results and those reported by Vlijm and Richter may reflect an artificality imposed by their experimental scheme. For example, I have observed maximum straight line distances of 203, 209, 252, and 265 feet for female P. groenlandica. I have recorded eleven other instances of females with a maximum straight line distance between 100 and 200 feet. I feel the dimensions of the observation arena Vlijm and Richter utilized would tend to suppress a comparable degree of activity. I believe this to be borne out by the observation that during the period following the emergence of their brood the females "....became increasingly active, often preferring to move along the wall of the arena" (Vlijm and Richter, 1966: 224). Although they report that the test animals did not show any abnormal behavior in comparison to those observed in the field there is no indication that individual spiders were marked in the field and their degree of movement measured.

Further, their experimental scheme assumes a certain spatial density but there is no indication how this was tested under natural conditions.

There appears to have been no quantitative investigation of the natural population of this species.

Lastly, the study was discontinued while the increasing activity of the females was still rising. More conclusive results would require observations recorded until the activity had peaked out. The greatest maximum distances I observed were all for specimens marked and observed after the middle of July.

The pattern of activity fluctuations reported for different stages in the life cycle of female P. lugubris conform generally to those I have substantiated for P. groenlandica. The difference in activity that Vlijm and Richter (1966) report for female P. lugubris before and after the emergence of the spiderlings from the egg-sac conform generally to those I have substantiated for P. groenlandica females. They noticed about a 3 1/3 increase (1500: 450) in the mean daily activity of the female on the fourth day after the emergence of the spiderlings. By comparison, I determined a sixfold increase in the mean distance traveled by the same female after the emergence of her brood than while transporting the egg-sac.

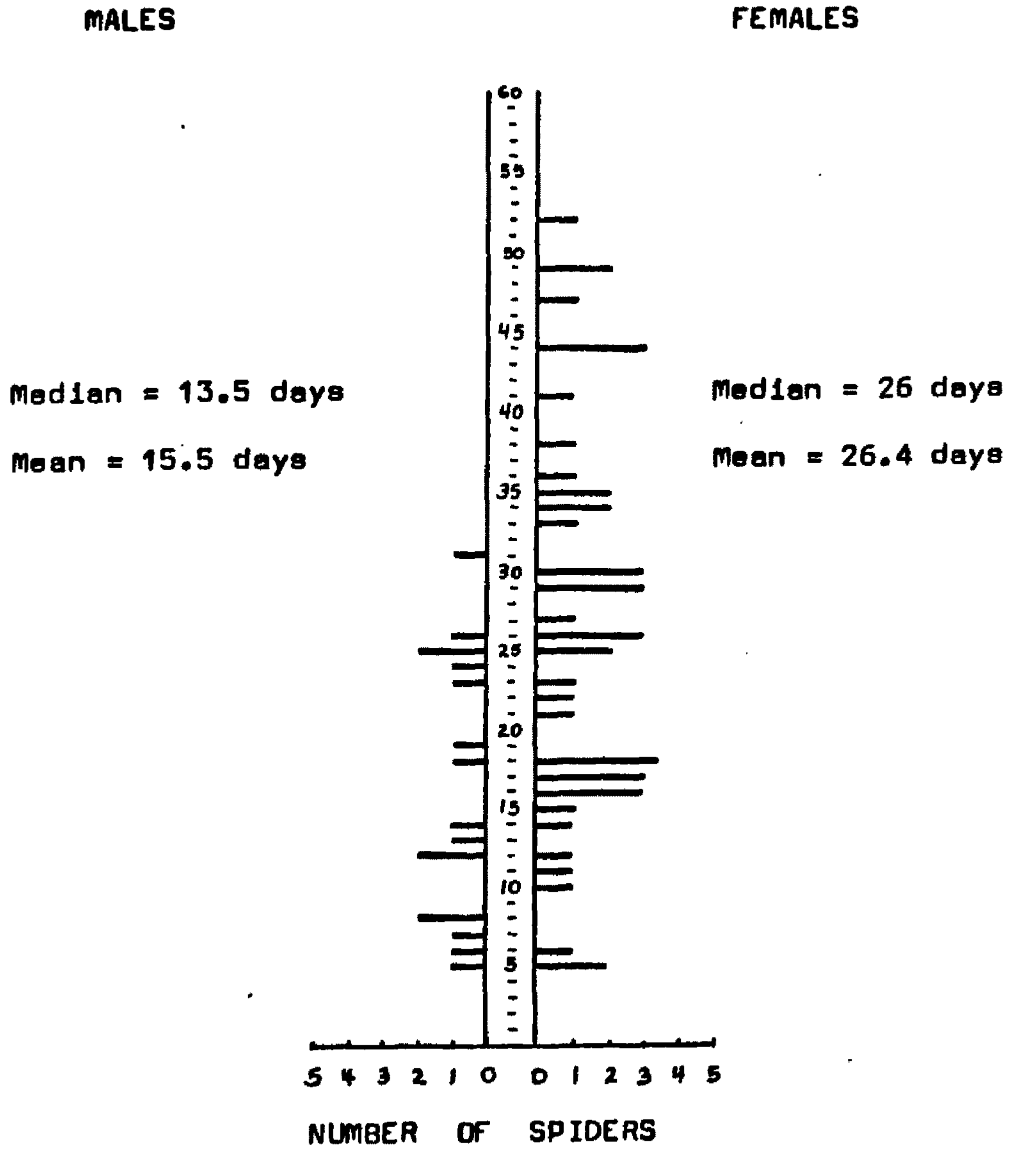
The comparison of maximum straight line distance (av.M) between males and females in this study is in general agreement with Hackman's observation that females move farther than males.

Hackman's inference that females might move more as a consequence of their searching for a suitable place for the nest burrow is not applicable to P. groenlandica which prepare no such burrow. However, field observations do indicate that there is a greater concentration of females with egg-sacs in certain locations along the lakeshore than in others. These females are seen nearly always in the region between the beachfront crest and midbeach. They are very infrequently seen in the beachfront region and on only three occasions did I see females with attached egg-sacs at the water's edge. Only one female with an egg-sac was trapped in either of the two beachfront pitfalls compared to six trapped in the midbeach pitfalls. Furthermore, the preferred locations at midbeach appear to be those lighted earliest by the morning sun. Those sections along the lakeshore that were shaded until noon by adjacent trees were largely ignored by females with egg-sacs. Consequently one might surmise an increased activity by females in moving to one of the locations of optimum exposure.

I would suggest two other possible explanations for the greater movement by females than males. The first is that females are able to range over a greater distance because they live longer. The maximum observed life span for a marked male spider was 31 days; for a female, 52 days. Figure 17 illustrates the comparison in detail. The shorter life expectancy for males is further corroborated by field observations of the numbers of spiders observed at different intervals during the summer. Thus a total of 462 sightings of male spiders was made during a regimen of hourly counts from 07:00 to 20:20 on 9 July compared to a total of only 66 for a similar regimen on 6 August. For the same dates respectively a total of 321 and 189 sightings of females were made, thus indicating a considerably greater decline in the numbers of males (86% fewer) than for females (41% fewer).

Engelhardt (1964) reports that supposing natural conditions, _Trochosa spinipalpis_, _T. robusta_, _T. ruricola_, and _T. terricola_ males can live up to 23-to-27 months, whereas the females of the spring generation can live up to 27-to-28 months, and those of the autumn generation

Fig. 17. Comparison of the observed life span in days of 17 male and 47 female *Pardosa groenlandica*. 21 June to 18 August, 1966. Ordinate in days.



Median = 13.5 days

Mean = 15.5 days

Median = 26 days

Mean = 26.4 days

up to 33-to-34 months.

Vlijm and Richter (1966 b) report that half the males in their study died within a month (end of April) and the remainder within two months (by the end of May) but almost all females lived until September and some till the end of October. This corresponded to a comparable phenomenon in the field where males were observed to decrease in numbers just after the copulation period, whereas females survive for some months.

A second explanation for greater movement by females than males is the consequence of my suspicion that females go without eating while carrying the egg-sac. This inference is based on my observations that the major food source for these spiders, other than themselves, is the insect life concentrated along the water's edge. The water's edge is where mayflies (Beatus sp.) as aquatic nymphal forms molt to emerge as adults. It is to the water's edge that adult winged insects are observed principally. Females transporting egg-sacs, however, with few exceptions were never observed along the water's edge. Their preferred locations appeared to be in the midbeach region. Furthermore, I believe that the attached egg-sac would prove a great hindrance to any successful hunting activity. Consequently, the hunger resulting from this enforced fast prompts the female (subsequent to the emergence of the brood and the abandonment of the egg-sac) to commence an active search for food. Although I realize that this hypothesis is merely conjecture on the basis of general field observations, it is in conformance with the measured movements of females which show a sixfold increase on the average in the mean distance traveled after emergence of the brood than while transporting the egg-sac. Though this increase could be prompted by a variety of causes, I feel it is not unreasonable to infer that hunger is a major one. Also, Vlijm and Richter (1966 b) report that during the three to five week period that the P. lugubris females transport their egg-sacs they consume very little food.

The chi-square results indicate that there is much less than one chance out of a hundred ($P < 0.01$) that the observed distributions of either the male or female Pardosa groenlandica would occur purely by chance. This indicates conclusively, therefore, that these animals are orienting themselves to something and responding in a selective fashion to some particular influences in their immediate environment.

I cannot establish definitely the factors to which the spiders are orienting. However, I can hypothesize certain possibilities which might be of some merit in suggesting possible future endeavors by interested investigators.

The most important factor influencing the orientation of these spiders, I feel, is the water line itself. Certainly, this requires orientation by the spiders if only as a physical barrier. However, I feel that it functions much more dynamically than this. For one, I suspect that the aquatic insects that emerge as adults along the water line provide a major food source to support the abundant spider population. Second, as spiders orient to this food source along the water line they increasingly must orient to one another. This is perhaps most apparent in courting males that appear to concentrate along the beachfront in response to the greater density of females that can be observed feeding there. Thirdly, the water line functions effectively to modify the temperature and humidity of the microenvironment. These creatures must avoid excessive temperature (Nørgaard, 1952). This is done by seeking shelter under the rocks at midday and by remaining close to the water's edge. Table 6 is illustrative in this regard in showing a comparison of temperatures at selected locations along the shoreline. The concentration of females with egg-sacs at midbeach is significant as suggesting a modification of their temperature and humidity preference at this stage of the life cycle.

It is apparent by a consideration of the results in testing for a general pattern of movement or migration along the lakeshore that nearly as many females moved south as moved north from their location where first sighted and to a comparable distance (Table 9). That is, eight females moved north three or more times their average distance between recaptures compared to six that moved south an equal amount. It is possible to conclude that there is no unidirectional movement or migration of females along the lakeshore.

I believe the sample of 17 cases is too limited to properly analyze the movement of males along the lakeshore. A more adequate sample (31 males) was obtained from the numbers of marked spiders recaptured in the pitfall traps at the two ends of the study site. These were spiders which had previously been marked and released after capture in the pitfalls at the south end of the study area and had subsequently moved northward along the lakeshore.

During this same period (19 days trapping in three intervals from 10 July to 14 August) there were 27 male and 16 female recaptures in the two south pitfalls of spiders which had moved in an opposite direction along the lakeshore. Table 10 compares these results. It is evident that about equal numbers of males are moving in either direction so that no unidirectional shift in the male population is occurring.

The data for female recaptures would appear to indicate a southward

TABLE 10

SUMMARY OF THE

NUMBERS OF TRAP RECAPTURES OF *PARDOSA GROENLANDICA* PREVIOUSLY MARKED AT THE OPPOSITE END OF THE STUDY AREA

Trapping Period	North Pitfalls (2)		South Pitfalls (2)	
(1966)	Males (yel.)	Females (yel.)	Males (yel.)	Females (yel.)
18 - 29 July (12 days)	16	2	10	11
4 - 6 August (3 days)	7	5	8	3
11 - 14 August (4 days)	8	0	9	2
Totals	31	7	27	16

Interpreted as Evidence of the Dispersion of Male *P. g.* in Approximately Equal Numbers North- and Southward Along the Lakeshore.

migration. A fraction more than twice as many females were recaptured moving south as were moving north (16 south to 7 north). However, this conflicts with evidence from the records of individual female movements which I believe to be more reliable because of the larger sampling (70 spiders compared to 23) over a longer period of time (46 days compared to 19).

My records of movements do not provide any evidence of especially defended territories by P. groenlandica. The closest approximation is during the period when the females carry their egg-sac. Then their movements are reduced and they will congregate in those midbeach localities which apparently have the most suitable exposure to the sun. However, I have not observed any individuals defending a particular locality for their exclusive occupancy. When two females with egg-sacs encounter one another they appear to accommodate to one another by simply moving apart so as to equally space themselves throughout the area. Vlijm and Richter (1966 b) report that Pardosa lugubris with attached egg-sacs also are very tolerant of one another.

Males appear entirely mobile and cannot be identified to any particular locality during the summer.

CHAPTER VII

SUMMARY

A dense population of wolf spiders, Pardosa groenlandica Th., was investigated at a location on the east shore of Flathead Lake (Lake County), Montana, in the vicinity of the Biological Station of the University of Montana at Yellow Bay. The investigation was conducted during the summers of 1954 to 1967 to study aspects of the life history and population dynamics of these spiders. In addition, observations of reproductive behavior were made in June and July, 1961, at the Rocky Mountain Biological Laboratory, Gothic, Colorado.

A mark-and-recapture method was utilized from 21 June to 18 August, 1966 to obtain data on the spiders in the 2,000 square feet study area. Some of the spiders were marked for individual identification by painting their legs or backs with quick-drying enamel paint in a distinctive pattern. A total of 148 adult female and 43 adult males were thus marked and observed. In addition, six plastic dishpans were installed along the lakeshore as pitfall traps and maintained during the summer of 1966. The spiders thus captured were marked to identify the trap location but not in an individually recognizable pattern. During the nineteen days that the pitfalls were operated a total of 962 spiders was marked. Of these, 260 males and 243 females were trapped in the study area proper. "Recaptures" consisted for the most part of re-sighting the marked spiders during the census surveys conducted at nearly daily intervals through the study area. In addition, spiders were recaptured frequently in the pitfalls.

The data thus obtained have made possible an analysis of the reproductive behavior, natality, mortality and/or disappearance rate, and population dynamics for this species which has never been reported previously.

With regard to reproductive behavior, the courtship routine of the male P. groenlandica is described. Mating behavior is described on the basis of observations of seven different instances. Egg-sac preparation is described based on two observed instances which allow a comparison of normal and abnormal behavior. A hypothesis emphasizing the importance of the spinning activity enshrouding the germinal emmision to eliciting the attachment and transport behavior by the female is proposed. The length of egg-sac transport was determined to be 17 days for the nineteen cases observed. Eggs and spiderlings were determined to continue their development without attention by the female if kept at saturated humidity and constant moderate temperature. In this species development proceeds as egg, deutova, pre-nymph, and nymph before the emergence from the egg-sac. However, development appeared to occur conspicuously faster in response to the female's sunning activities. After their emergence from the egg-sac, spiderlings were transported on the backs of the female for two days with but one exception (three days) of the total of eleven different instances observed.

Aspects of natality investigated were the breeding period and number of broods, number of progeny, seasonal variations in natality, and the realized reproduction. The preponderance of the egg-sacs was shown to be prepared by mid-July although females with egg-sacs can be observed along the lakeshore throughout the summer. Four females were identified positively to have prepared two egg-sacs during the summer. Ten additional females were suspected to have prepared two egg-sacs. The total represents 20% of all the females for which records were kept in this study. The mean contents of 38 egg-sacs examined was 90 spiderlings. The number of spiderlings noticeably declined as the summer progressed. Ten egg-sacs collected between 1 - 17 August had a mean content of 69 spiderlings. A few sacs of small content, however, consistently occurred. For the mid-July period of maximum population, 29% of the observed adult females were noted with attached egg-sacs. Assuming that all the adult females in the population in the course of the summer prepared an egg-sac, the annual production of eggs would have been approximately 100,000. This represents a realized reproductive potential 50 times the previous adult population.

The percentage of arrested development of the young within the egg-sac was observed to be only 1.1% of the total contents of all 34 egg-sacs examined. Female consumption of the contents of apparently late-season and unfertilized egg-sacs occurred occasionally. There was a distinct difference between the mean numbers of eggs in the egg-sac (90) and the number of spiderlings transported on the back of the female (67).

A major predator of the P. groenlandica population was the digger wasp Anoplius ithaca Banks (Pompilidae). Eight instances are reported in detail to describe aspects of recognition and mutual responses by the wasps and spiders, manner of prey transport and orientation of the wasp to its burrow. Two hypotheses are proposed based on these observations. First, that the spider initiates the actual encounter with a wasp by pouncing at it as an intended victim. Second, that the wasp rejects adult male spiders as suitable victims.

The shrew Sorex vagrans was established for the first time as a predator of this species.

Aspects of the population dynamics investigated were density, dispersion, and movement. The adult population was noted to be at its peak (2177 maximum on 16 July, 1966) for a period of about a week at mid-July and then to begin to decline. At the end of the first week of August, the population had declined by 34.4%. A disproportionate reduction in the numbers of male spiders was noted during this period; the numbers of males declined 20% faster than for the females. It was observed in mid-August that there were 60% more females than males. This is surmised to be a consequence of a greater longevity by females.

The estimated density of the maximum adult population at mid-July was calculated for the beachfront as 4.08 spiders per square foot and for the midbeach portion as 0.70 spiders per square foot. Described in terms of the length of the water line for the study area, the density was 22 adult spiders per meter of water frontage. This is twice the density reported by the previous most comparable study.

The dispersion of both males and females was tested by comparing the observed distribution to a Poisson distribution as a mathematical model for a purely random spacing. These calculations indicated that there was much less than one chance out of a hundred ($P < 0.01$) that the observed distribution of either males or females would occur purely by chance. This seemed to be in response to the differences noted in temperature, humidity, and light exposure between the beachfront, along the water's edge, and the midbeach portions of the lakeshore. The greater abundance of food along the water's edge also was hypothesized to be a contributing factor.

The analysis of movement was conducted for a total of 70 females and 17 males that were marked in an individually recognizable manner and had been re-sighted a minimum of five times over a period of at least a week. In general, females were determined to move greater maximum distances than males (the mean for the males was approximately 48 feet compared to 73 feet for the females) and a greater average of distance between successive recaptures (the mean for the males was 14.5 feet compared to 30.5 feet for the females). The amount of movement by females was noted to vary with different stages in the life cycle, so that the median of the average distance of movement between successive recapture for females increased more than six times, from 3 to 19 feet, after they abandoned their egg-sacs. This was hypothesized to be significant for effective dispersal of the spiderlings.

Comparison of these results to similar studies previously reported is made.

BIBLIOGRAPHY

BIBLIOGRAPHY

LITERATURE CITED

Barnes, B.M. & Barnes, R.D. 1954. Ecology of spiders of the maritime drift lines. *Ecology*, 35: 25 - 35.

Bonnet, P. 1930. La mue, l'autotomie et la regeneration chez les araignees. *Bull. Soc. Hist. nat. Toulouse.* 59: 237 - 700.

Brant, D.H. 1962. Measures of the movement and population densities of small rodents. *Univ. Calif. Pub. Zool.* 62(2): 105 - 84.

Bristowe, W.S. & Locket, G.H. 1926. The courtship of British lycosid spiders and its probable significance. *Proc. Zool. Soc. Lond.* 22: 317 - 47

Bristowe, W.S. 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. *Proc. Zool. Soc. Lond.* 99: 309 - 58.

________ 1939. *The Comity of Spiders.* Vol. I. 332 pp. London, Ray Society.

________ 1941. *The Comity of Spiders.* Vol. II. 228 pp. London, Ray Society.

________ 1958. *The World of Spiders.* 304 pp. London, Collins.

Cannon, S.S. 1965. A comparison of the spider fauna of four different plant communities found in Neotome, a small valley in south central Ohio. *Ohio J. Sci.* 65(3): 97 - 110.

Cherrett, J.M. 1964. The distribution of spiders on the Moor House National Nature Reserve, Westmorland. *J. Anim. Ecol.* 33: 27 - 48.

Clerck, C. 1757. *Svenska Spindlar.* 154 pp. Stockholm.

Dice, L.R. & Clark, P.J. 1953. The statistical concept of home range as applied to the recapture radius of the deermouse (*Peromyscus*). *Contrib. Lab. Vert. Biol.* Univ. Mich. 62: 1 - 15.

Duffey, E. 1962. A population study of spiders in limestone grassland. *J. Anim. Ecol.* 31: 571 - 99.

Engelhardt, W. 1964. Die mitteleuropaischen Arten der Gattung Trochosa C. L. Koch, 1848 (Aranea, Lycosidae). *Z. Morph. Okol. Tiere* 54: 219 - 392

Evans, H. 1948. Biological notes on two species of *Anoplius* (Hymenoptera: Pompilidae). *Ent. News* 59: 180 - 4.

Evans, H. & Yoshimoto, C. 1962. The ecology and nesting behavior of the Pompilidae (Hymenoptera) of the northeastern United States. *Misc. Publ. Ent. Soc. Amer.* 3(3): 83.

Gerhardt, U. 1924. Neue Studien zur Sexualbiologie und zur Bedeutung des sexuellen Grossendimorphismus der Spinnen. *Z. Wiss. Biol.* 1: 507 - 38.

Gertsch, W.J. 1949. *American Spiders.* D. Van Nostrand, Inc. Toronto, New York, and London. 285 pp.

Hackman, W. 1957. Studies of the ecology of the wolf spider *Trochosa ruricola* Deg. *Comment. Biol. Soc. Sci. Fenn.* 16: 1 - 34.

Hallander, H. 1967. Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O.F. Muller). *Oikos* 18: 145 - 50.

Heydemann, B. 1960 a. Die biozonotische Entwicklung vom Vorland zum Koog. I. Teil. Spinnen (Araneae). *Abh. Math.-Naturw. Kl. Akad. Wiss. Lit. Mainz.* 11: 747 - 913.

new land
N sea coast
succe

________ 1960 b. Verlauf und Abhängigkeit von Spinnensukzessionen im Neuland der Nordseeküste. *Verh. dt. zool. Ges.* 24: 431 - 57.

Kaston, B.J. 1936. The senses involved in the courtship of some vagabond spiders. *Entom. Amer.* 16: 97 - 196.

________ 1948. *Spiders of Connecticut.* State Geol. Nat. Hist. Survey Bull. 70: 1 - 874.

Kuenzler, E.J. 1958. Niche relations of three species of Lycosid spiders. *Ecology* 39: 494 - 500.

Montgomery, Jr., T.H. 1903. Studies of the habits of spiders, particularly those of the mating period. *Proc. Acad. Nat. Sci.* 55: 59 - 145.

Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. *Oikos* 3: 1 - 21.

O'Conner, F.S. 1896. Spider carrying snail-shell. *Irish Nat.* 5(11): 299.

Papi, F. & Tongiorgi, P. 1963. Innate and learned components in the astronomical orientation of wolf spiders. *Ergoebnisse Biol.* 26: 259 - 280.

Peck, W.B. 1966. The population composition of a spider community in West Central Missouri. *Amer. Midland Natur.* 76(1): 150 - 7.

Petersen, B. 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. *Experientia* 6(3): 96 - 8.

Savory, T.H. 1929. On wolf-spiders' memories. *Ann. Mag. Nat. Hist.* London. 10(4): 524 - 28.

_______ 1964. *Archnida.* Academic Press. London and New York. 291 pp.

Schmidt, G. 1957. Mitteilung uber sexualbiogische Beobachtung an *Pardosa amentata* (Cl.) *Zool. Anz.* 58: 16 - 23.

Thorell, T. 1872. Om nagra Archnider fran Gronland. *Ofvers. Kongl. Vet. Akad. Forh.* 29: 147 - 66.

Turnbull, A.L. 1966. A population of spiders and their potential prey in an overgrazed pasture in eastern Ontario. *Can. J. Zool.* 44(4): 557 - 83.

Vlijm, L. 1962. Vorming van de eicocon bij de wolfspin *Pardosa amentata* (Lycoisdae). *Levende Nat.* 65(2): 25 - 8.

_______, Kessler, A. & Richter, C. 1963. The life history of *Pardosa amentata* C. (Araneae, Lycosidae). *Ent. Ber. Amst.* 23: 75 - 80.

_______, & Kessler-Geschiere, A.M. 1966 a. The phenology and hibitat of *Pardosa monticola*, *P. nigriceps*, and *P. pullata* (Araneae, Lycosidae). *J. Anim. Ecol.* 36(1): 31 - 56.

_______, & Richter, C.J.J. 1966 b. Activity fluctuations of *Pardosa lugubris* (Walckenaer), Araneae, Lycosidae, during the breeding-season. *Ent. Ber. Anst.* 26: 222 - 30.

_______, & Dijkstra, H. 1966 c. Comparative research of the courtship-behaviour in the genus *Pardosa* (Arach., Araneae). *Senck. biol.* 47(1): 51 - 55.

Wiebes, J.T. 1960. De wolfspinnen van Meyendel (Araneae, Lycosidae en Pisauridae). *Ent. Ber. Amst.* 20: 56 - 62, 69 - 74, 83 - 9.

APPENDIX

APPENDIX A.

Calculations of *P. groenlandica* population estimates by the Lincoln-Peterson index analysis of all painted spiders marked in the study area and observed during census surveys at selected three-day intervals. P = average estimated population for the three day period; M = number of spiders marked in the pre-census period; s = total number of spiders sighted during the three day census period; and R = total number of marked spiders resighted during the three-day census period.

7, 8, 9 July

Males:
M (to 7/8) = 38
S = 559
R = 48

$$P = \frac{M \cdot S}{R} = \frac{38 \times 559}{48} = \frac{21{,}242}{48} = 443$$

All Females:
M (to 7/8) = 81
S = 423
R = 58

$$P = \frac{M \cdot S}{R} = \frac{81 \times 423}{58} = \frac{34{,}263}{58} = 591$$

13, 14, 15 July

Males:
M (to 7/14) = 40
S = 323
R = 14

$$P = \frac{M \cdot S}{R} = \frac{40 \times 323}{14} = \frac{12{,}920}{14} = 923$$

All Females:
M (to 7/14) = 102
S = 422
R = 63

$$P = \frac{M \cdot S}{R} = \frac{102 \times 422}{63} = \frac{43{,}044}{63} = 683$$

18, 19, 20 July

Males:
M (to 7/19) = 67
S = 172
R = 20

$$P = \frac{M \cdot S}{R} = \frac{67 \times 172}{20} = \frac{11{,}524}{20} = 576$$

All Females:
M (to 7/19) = 122
S = 174
R = 34

$$P = \frac{M \cdot S}{R} = \frac{122 \times 174}{34} = \frac{21{,}228}{34} = 624$$

27, 28, 29 July

Males:
M (to 7/28) = 192
S = 137
R = 88

$$P = \frac{M \cdot S}{R} = \frac{192 \times 137}{88} = \frac{26{,}304}{88} = 299$$

All Females:
M (to 7/28) = 295
S = 380
R = 157

$$P = \frac{M \cdot S}{R} = \frac{295 \times 380}{157} = \frac{112{,}100}{157} = 714$$

4, 5, 6 August

Males: M (to 8/5) = 216
S = 91
R = 58

$$P = \frac{M\ S}{R} = \frac{216 \times 91}{58} = \frac{19{,}656}{58} = 339$$

All Females: M (to 8/5) = 329
S = 314
R = 156

$$P = \frac{M\ S}{R} = \frac{329 \times 314}{156} = \frac{103{,}306}{156} = 662$$

11, 12, 13 August

Males: M (to 8/12) = 242
S = 52
R = 37

$$P = \frac{M\ S}{R} = \frac{242 \times 52}{37} = \frac{12{,}584}{37} = 340$$

All Females: M (to 8/12) = 362
S = 288
R = 151

$$P = \frac{M\ S}{R} = \frac{362 \times 288}{151} = \frac{104{,}256}{151} = 690$$

APPENDIX B. Estimate of male *P. groenlandica* population by analysis after Schnabel of all spiders marked and resighted during census surveys through the study area. P = estimated population; S = total male spiders seen; M = total marked male spiders available; and, R = total number of marked male spiders resighted during census survey.

Date (1966)	S		M		R		M·S		M·S		R		$P = \frac{M\cdot S}{R}$	
June 21		29												
22	34	6	1	1	0	0	34	6	34	6	0	0	-	-
23	-	7	-	3	-	1	-	21	-	27	-	1	-	27
24							no observations							
25	12	19	3	3	0	0	36	57	70	84	0	1	-	84
26							no observations							
27	35	13	14	14	0	2	490	182	560	266	0	3	-	89
28							no observations							
29	30	18	15	15	1	0	450	270	1010	536	1	3	1010	179
30	28	21	18	18	3	3	504	378	1514	914	4	6	379	152
July 1							no observations							
2							no observations							
3	-	21	23	23	-	2	-	483	-	1397	-	8	-	175
4	-	30	26	26	-	3	-	780	-	2177	-	11	-	198
5	-	42	29	29	-	6	-	1218	-	3395	-	17	-	199
6	36	55	31	31	7	7	1116	1705	2630	5100	11	24	239	213
7	73	16	35	35	17	3	2555	560	5185	5660	28	27	185	210
8	17	19	38	38	2	3	646	722	5831	6382	30	30	194	213
9	239	195	38	38	15	8	9082	7410	14913	13792	45	38	331	363
10							no observations							

APPENDIX B. (Continued)

Date (1966)		S		M		R		M·S		M·S		R		P = $\frac{M \cdot S}{R}$	
July	11	44	19	38	38	0	0	1672	722	16585	14514	45	38	369	382
	12	-	21	40	40	-	2	-	840	-	15354	-	40	-	384
	13	29	20	40	40	2	2	1160	800	17745	16154	47	42	378	385
	14	35	30	40	40	1	2	1400	1200	19145	17354	48	44	399	394
	15	151	58	40	40	4	3	6040	2320	25185	19674	52	47	484	419
	16	28	-	40	40	1	-	1120	-	26305	-	53	47	496	-
	17							no observations							
	18	86	33	23	20	7	3	1978	660	28283	20334	60	50	471	407
	19	33	8	42	25	1	1	1386	200	29669	20534	61	51	486	403
	20	-	12	73	25	-	8	-	300	-	20834	-	59	-	353
	21	45	68	79	42	10	33	3555	2856	33224	23690	71	92	468	258
	22	-	14	101	45	-	6	-	630	-	24320	-	98	-	248
	23	206	33	111	46	75	11	22866	1518	56090	25838	146	109	384	237
	24	-	25	121	48	-	16	-	1200	-	27038	-	125	-	216
	25	-	24	124	51	-	15	-	1224	-	28262	-	140	-	202
	26	23	46	125	58	12	28	2875	2668	58965	30930	158	168	373	184
	27	14	33	125	58	6	18	1750	1914	60715	32844	164	186	370	177
	28	17	11	131	61	8	9	2227	671	62942	33515	172	195	366	172
	29	50	12	137	61	37	10	6850	732	69792	34247	209	205	334	167
	30	-	9	143	61	-	6	-	549	-	34796	-	211	-	165
	31							no observations							
Aug.	1	-	22	143	61	-	12	-	1342	-	36138	-	223	-	162
	2	30	28	143	61	16	17	4290	1708	74082	37846	225	240	329	158
	3	-	27	143	61	-	11	-	1647	-	39493	-	251	-	157
	4	19	6	143	61	10	2	2717	366	76799	39859	235	253	327	158

APPENDIX B. (Continued)

Date (1966)	S		M		R		M·S		M·S		R		$P = \frac{M \cdot S}{R}$	
Aug. 5	-	5	153	63	-	5	-	315	-	40174	-	258	-	156
6	28	33	160	68	18	23	4480	2244	81127	42418	253	281	321	151
7	no observations													
8	no observations													
9	5	9	165	68	2	5	825	612	82104	43030	255	286	322	150
10	no observations													
11	6	17	164	68	2	14	984	1156	83088	44186	257	300	323	147
12	11	12	169	73	10	6	1859	876	84947	45062	267	306	318	147
13	-	6	170	74	-	5	-	444	-	45506	-	311	-	146
14	-	10	170	74	-	8	-	740	-	46246	-	319	-	144
15	no observations													
16	-	10	173	76	-	7	-	760	-	47006	-	326	-	144
17	10	15	173	76	6	11	1730	1140	86677	48146	273	337	317	143

APPENDIX C. Estimate of female P. groenlandica population by analysis after Schnabel of all spiders marked and resighted during census surveys through the study area. P = estimated population; S = total female spiders seen; M = total marked female spiders available; and, R = total number of marked female spiders resighted during census survey.

Date (1966)	S		M		R		M·S		M·S		R		P = $\frac{M \cdot S}{R}$	
June 21														
22	44	25	3	3	1	0	132	75	132	75	1	0	132	-
23	-	17	5	5	-	1	-	85	132	160	1	1	132	160
24							no observations							
25	17	53	5	5	0	0	85	265	217	425	1	1	217	425
26							no observations							
27	58	10	15	15	2	0	870	150	1087	575	3	1	362	575
28							no observations							
29	27	14	21	21	2	1	567	294	1654	869	5	2	331	434
30	37	30	28	28	1	3	1036	840	2690	1709	6	5	448	342
July 1							no observations							
2							no observations							
3	-	47	47	47	-	8	-	2209	-	3918	6	13	-	301
4	-	40	54	54	-	6	-	2160	-	6078	6	19	-	319
5	-	48	58	58	-	8	-	2784	-	8862	6	27	-	328
6	40	48	62	62	3	6	2480	2976	5170	11838	9	33	574	356
7	52	8	76	76	9	0	3952	608	9122	12446	18	33	507	377
8	12	21	81	81	3	3	972	1701	10094	14147	21	36	481	393
9	187	142	82	82	21	22	15334	11644	25428	25791	42	58	605	444
10							no observations							
11	14	38	87	87	1	7	1218	3306	26646	29097	43	65	620	448

APPENDIX C. (Continued)

Date (1966)		S		M		R		M·S		M·S		R		P = $\frac{M \cdot S}{R}$	
July	12	-	27	98	98	-	14	-	2646	-	31743	-	79	-	402
	13	15	59	98	98	1	15	1470	5782	28116	37525	44	94	639	399
	14	22	82	102	102	2	18	2244	8364	30360	45889	46	112	660	409
	16	131	107	102	102	8	19	13362	10914	43722	56803	54	131	809	434
	16	18	-	102	102	1	-	1836	-	45558	-	55	-	828	-
	17							no observations							
	18	55	48	55	55	3	14	3025	2640	48583	59443	69	145	704	410
	19	20	36	66	56	2	13	1320	2016	49903	61459	82	158	609	389
	20	-	15	81	59	-	2	-	885	-	62344	84	160	-	390
	21	50	63	84	66	14	15	4200	4158	54103	66502	99	175	546	380
	22	-	33	97	73	-	10	-	2409	54103	68911	-	185	-	372
	23	179	48	115	83	44	11	20585	3984	74688	72895	143	196	522	372
	24	-	36	127	85	-	17	-	3060	-	75955	-	213	-	357
	25	-	39	148	90	-	13	-	3510	-	79465	-	226	-	352
	26	22	76	154	98	7	30	3388	7448	78076	86913	150	256	521	339
	27	29	84	176	101	13	32	5104	8484	83180	95397	163	288	510	331
	28	32	88	191	104	14	34	6112	9152	89292	104549	177	322	504	324
	29	69	76	200	105	29	33	13800	7980	103092	112529	206	355	500	317
	30	-	92	214	106	-	49	-	9752	-	122281	-	404	-	303
	31							no observations							
Aug.	1	-	46	214	106	-	20	-	4876	-	127157	-	424	-	300
	2	41	104	214	106	24	42	8774	11024	111866	138181	230	466	486	297
	3	-	89	214	106	-	39	-	9434	-	147615	-	505	-	292
	4	43	69	214	106	18	26	9202	7314	121068	154929	243	531	488	292
	5	-	42	222	107	-	21	-	4494	-	159423	-	552	-	289
	6	50	135	225	109	18	73	11250	14715	132318	174138	266	625	497	279

APPENDIX C. (Continued)

Date (1966)	S		M		R		M·S		M·S		R		P = $\frac{M \cdot S}{R}$	
Aug. 7							no observations							
8							no observations							
9	4	53	240	111	2	26	960	5883	133278	180021	268	651	497	277
10							no observations							
11	15	57	240	111	8	29	3600	6327	136878	186348	276	680	496	274
12	21	102	245	117	7	54	5145	11934	142023	198282	283	734	502	270
13	-	93	249	118	-	53	-	10974	-	209156	-	787	-	266
14	-	84	249	119	-	49	-	9996	-	219252	-	836	-	262
15							no observations							
16	-	68	254	125	-	34	-	8500	-	227752	-	870	-	262
17	25	78	254	125	9	36	6350	9750	148373	237502	292	906	508	262

The expression $\frac{Nm^n}{n!e^m}$ where N is the number of quadrats, m is the mean number of organisms per quadrat and e=2.718, the base for natural logarithms, permits the determination of the expected occurrences of organisms by purely random distribution of female Pardosa groenlandica in this study ~~are~~ as follows:

N = 500 and log N = 2.69897; m = 0.908 and log m = 9.95809-10; and e = 2.718 and log e = 0.43429

For 0 spiders per quadrat: $\frac{N}{e^m} = \frac{500}{2.718^{0.908}}$

$$\text{Log}\ \frac{500}{2.718^{0.908}} = 2.69897-(0.43429)(0.908)=2.69897-0.39434= 2.30463$$

$$\frac{N}{e^m} = \text{antilog}\ 2.30463 = \underline{\underline{201.7}}$$

For 1 spider per quadrat: $\frac{Nm}{e^m} = \frac{500(0.908)}{2.718^{0.908}}$

$$\text{Log}\ \frac{500(0.908)}{2.718^{0.908}} = 2.69897+(9.95809-10)-0.43429(.908)= 12.26272-10$$

$$\frac{Nm}{e^m} = \text{antilog}\ 2.26272 = \underline{\underline{183.1}}$$

For 2 spiders per quadrat: $\frac{Nm^2}{2!e^m} = \frac{500(0.908)^2}{2.1(2.718)^{0.908}}$

$$\text{Log}\ \frac{500(0.908)^2}{2(2.718)^{0.908}} = 2.69897+2(9.95809-10) - \left[0.30103+0.43429(0.908)\right]$$

$$= (22.61515-20) - 0.69537 = 21.91978-20$$

$$\frac{Nm^2}{2!e^m} = \text{antilog } 1.91978 = \underline{\underline{83.1}}$$

For 3 spiders per quadrat: $\frac{Nm^3}{3!e^m} = \frac{500(0.908)^3}{(3.2.1)(2.718)^{0.908}}$

$$\text{Log}\ \frac{500(0.908)^3}{6(2.718)^{0.908}} = 2.69897+3(9.95809-10) - \left[0.77815+0.43429(0.908)\right] = 1.40075$$

$$\frac{Nm^3}{3!e^m} = \text{antilog } 1.40075 = \underline{\underline{25.2}}$$

For 4 spiders per quadrat: $\frac{Nm^4}{4!e^m} = \frac{500(0.908)^4}{(4.3.2.1)(2.718)^{0.908}}$

$$\text{Log}\ \frac{500(0.908)^4}{24(2.718)^{0.908}} = 2.69897+4(9.95809-10) - \left[1.38021+0.43429(0.908)\right] = 0.75678$$

$$\frac{Nm^4}{4!e^m} = \text{antilog } 0.75678 = \underline{\underline{5.7}}$$

For 5 spiders per quadrat: $\frac{Nm^5}{5!e^m} = \frac{500(0.908)^5}{(5.4.3.2.1)(2.718)^{0.908}}$

$$\text{Log}\ \frac{500(0.908)^5}{120(2.718)^{0.908}} = 2.69897+5(9.95809-10) - \left[2.07918+0.43429(0.908)\right] = 0.01590$$

$$\frac{Nm^5}{5!e^m} = \text{antilog } 0.01590 = \underline{\underline{1.0}}$$

For 6 or more spiders per quadrat:

$$500 - (201.7+183.1+83.1+25.2+5.7+1.0) = 500-499.8 = \underline{\underline{0.2}}$$

APPENDIX E.

The expression $\frac{Nm^n}{n!e^m}$ where N is the number of quadrats, m is the mean number of organisms per quadrat and e=2.718, the base for natural logarithms, permits the determination of the expected occurrences of organisms by purely random spacing in a number of quadrats. The calculations for the expected random distribution of male Pardosa groenlandica in this study are as follows:

$N = 500$ and $\log N = 2.69897$; $m = 0.306$ and $\log m = 9.48572-10$; and $e = 2.718$ and $\log e = 0.43429$

For 0 spiders per quadrat: $\frac{N}{e^m} = \frac{500}{2.718^{0.306}}$

$$\text{Log } \frac{500}{2.718^{0.306}} = 2.69897-(0.43429)(0.306)=2.6989.7-0.13289= 2.56608$$

$$\frac{N}{e^m} = \text{antilog } 2.56608 = \underline{\underline{368.2}}$$

For 1 spider per quadrat: $\frac{Nm}{e^m} = \frac{500(0.306)}{2.718^{0.306}}$

$$\text{Log } \frac{500(0.306)}{2.718^{0.306}} = 2.69897+(9.48572-10)-(0.43429)(0.306)$$

$$= (12.18469-10)-0.13289 = 2.05180$$

$$\frac{Nm}{e^m} = \text{antilog } 2.05180 = \underline{\underline{112.7}}$$

For 2 spiders per quadrat: $\frac{Nm^2}{2!e^m} = \frac{500(0.306)^2}{(2.1)(2.718)^{0.306}}$

$$\text{Log } \frac{500(0.306)^2}{2(2.718)^{0.306}} = 2.69897 + 2(9.48572-10) - \left[0.30103+0.43429(.306)\right]$$

$$= (21.67041-20)-0.43392 = 21.23649-20$$

$$\frac{Nm^2}{2!e^m} = \text{antilog } 1.23649 = \underline{\underline{17.2}}$$

For 3 or more spiders per quadrat:

$$500 - \left[368.2 + 112.7 + 17.2\right] = \underline{\underline{1.9}}$$

APPENDIX F. Calculations for the Chi-Square Test to Compare the Observed and Theoretically Expected Random Distributions of Male and Female *Pardosa groenlandica*.

For Females:

No. of females per quadrat:	0	1	2	3	4	5	6+
Observed (f_o):	323.0	85.0	37.0	20.0	12.0	9.0	14.0
Expected by Poisson distribution (f_e):	201.7	183.1	83.1	25.2	5.7	1.0	0.2
$f_o - f_e$	120.3	-98.1	-46.1	-5.2	6.3	8.0	13.8
$(f_o - f_e)^2$	14,472.1	9,623.6	2,125.2	27.0	39.7	64.0	1,904.0
$\frac{(f_o - f_e)^2}{f_e}$	71.7	52.5	25.5	1.1	6.9	64.0	952.0

$X^2 = \sum\left[\frac{(f_o - f_e)^2}{f_e}\right] = 1173.7$ Degrees of freedom (df) = 5 $P < 0.01$

For Males:

No. of males per quadrat:	0	1	2	3+
Observed (f_o):	394.0	77.0	15.0	14.0
Expected by Poisson distribution (f_e):	368.2	112.7	17.2	1.9
$f_o - f_e$	25.8	-35.7	-2.2	12.1
$(f_o - f_e)^2$	665.6	127.5	4.8	146.4
$\frac{(f_o - f_e)^2}{f_e}$	1.8	11.3	0.28	77.0

$X^2 = \sum\left[\frac{(f_o - f_e)^2}{f_e}\right] = 90.4$ Degrees of freedom (df) = 3 $P < 0.01$