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I. INTRODUCTION

A number of phenological studies have been carried out on spiders of the genus *Pardosa* (Wiebes, 1960; Vlijm & Kessler-Geschiere, 1967). These wolf spiders (F. Lycosidae) are terrestrial carnivores which do not build webs to catch their prey and which are active during the day on the ground surface and vegetation. Much ecological data for the group have been collected by hand sampling or pitfall trapping. As younger instars are less readily caught in pitfall traps than the sexually mature spiders, the ecology of the latter individuals is better known. Soon after courtship and mating the females produce a cocoon (egg sac) which they carry attached to their spinnerets until the spiderlings emerge. Vlijm & Richter (1966) demonstrated that adult males of *Pardosa lugubris* exhibit increased locomotory activity during the time that the females are carrying cocoons. Vlijm & Kessler-Geschiere (1967) suggested that the increased locomotory activity during this period may increase the chances of virgin females being fertilized. These virgin females, after the main period of reproduction, would be found in sub-optimal areas where the spider density is low, and a migration of males into these habitats may result in a predominance of females in the preferred habitats, as was found by Heydemann (1960 a,b) for several spider species.

The increase of the male locomotory behaviour may be inherent to the age of the males. It seems also possible, however, that its occurrence is related to the cocoon carrying phase of the females life, *i.e.*, males...
may respond differently to females with an egg sac than they do to unfertilized females.

In an attempt to discriminate between these possibilities and, albeit in an indirect way, to elucidate the increased locomotory activity, a study was made on the behaviour of males of *P. amentata* at different stages of their adult life towards fertilized and unfertilized females.

### II. MATERIALS AND METHODS

On 26 April 1966, just before the final moult occurred, specimens of *Pardosa amentata* were collected by hand, from beside a ditch, in the neighbourhood of Amsterdam. Of these spiders (167 subadult males and 157 subadult females) about 60% had already moulted to adult by 28 April. These animals were divided into three groups (A, B and C) each consisting of 25 males and 25 females. Each group was kept in a glass container (60 x 30 x 30 cm) on a layer of moist sand. The air temperature during the day was 24°-26° C. Light was given daily from 7.30 hr until 17.30 hr.

Group A was used as the experimental group. Any dead or mutilated spider of this group was replaced by a healthy one from group B. Spiders removed from group B were replaced from group C. Most of the females constructed a cocoon on the 8th or 9th day after moulting, and the spiderlings emerged 26-28 days after moulting. Females which were retarded in their development or which had lost their cocoons prematurely, were also replaced from group B and C.

The experiments were started within one day after the final moult and, with one exception, were finished 30 days afterwards, when the number of non-mutilated males in group A had dropped below 25. During the experiments the spiders of group A were divided into 25 pairs; no special care was given to the choice of the pairs. Each pair was put into a glass box (16 x 8 x 6 cm), the bottom of which was covered with moist sand. These boxes were changed daily. They were placed under a heating lamp which produced a surface temperature of 28°-30° C. As the preferred temperature of adults of *P. amentata* is about 30° C ([Vlijm, Kessler & Richter, 1963]) courtship starts readily under these conditions.

At 9.00 hr the pairs of spiders were acclimatized for one hour to the experimental conditions. The experimental period, starting at 10.00 hr, lasted four to six hours per day. During the first 20 minutes of each hour (the observation period) the behaviour of each of the males was recorded every 30 secs, the observation time being 1 sec. per animal. Thus 1000 observations were made every hour, each of which was
expressed as a symbol reflecting the behaviour of a male at the time of observation.

The behaviour of the males was classified in the following categories (the symbols referring to each category, as used in the illustrations, are indicated in parenthesis):

A. Behaviour directed towards females:
   1. courtship and searching behaviour ($c$, Fig. 1A): this behaviour of *P. amentata* has been described in detail by Schmidt (1957), by Vlijm, Kessler & Richter (1963), by Vlijm & Dijkstra (1966) and by Dijkstra (1970);
   2. mating ($m$);
   3. approach without display ($a$): males approach females in a rather "stealthy" way, without courtship display. The abdomen, contrary to approach with display, is held near the ground (Fig. 1B). This leads to a situation where the male is touching the female with his front legs (see also Dijkstra, 1970).

B. Undirected behaviour (behaviour not directed towards females):
   1. sitting ($s$);
   2. walking: undirected locomotory activity ($w$).

Fig. 1. The position of the body of males of *Pardosa amentata* during "courtship" (A) and "approach without display" (B).

The number of times each symbol was noted per 1000 observations was counted, and the ratios obtained in this way were expressed as percentages. These percentages are taken as measures of the time spent on the different types of behaviour during the observation period.

Preliminary experiments revealed that the behavioural characteristics are unchanged during the day, at least from 10.00–16.00 hr, under the experimental conditions.

In the first experiment the behaviour of males towards females,
which had moulted at the same time as the males, was recorded. In this experiment the locomotory activity ("walking") of the females was also recorded, in the same way as for the males. In a further series of experiments the behaviour of males towards "standard" females was analysed. Two types of females were used as standards: females 6–9 days after moulting to adult which were not carrying cocoons, and older females which were carrying cocoons. The latter were the same animals as used in the first experiment. Females of 6–9 days old were derived from a stock of subadult females collected on 26 April and kept in the dark at 10° C, in order to postpone the final moult. When put into glass containers under the conditions described above, they moulted to adult within two days. No difference in the behaviour of these females, as a consequence of this procedure, was observed.

III. RESULTS AND CONCLUSIONS

1. Behaviour of males towards females of the same age, during the first 30 days after the final moult.

On 16 days, over a period of more than four weeks, starting on the first day after moulting, the behaviour of the animals of group A was tested. The behaviour was recorded during a period of 5 hours on each day, i.e., a total of 5000 observations per day. The percentages, reflecting the total time spent on courtship, approach without display, mating, sitting and walking by the males, are indicated in Fig. 2A,B.

Time spent on "courtship" increased during the first 9 days, was maximal one day before the females constructed their cocoons, and then decreased to a rather constant level during the period the females carried cocoons. A second increase occurred at the end of the experimental period, after the emergence of the spiderlings. From incidental observations it appeared that this period of enhanced courtship activity is continued until the females construct a second cocoon.

"Mating" was maximal one day before cocoon construction and decreased thereafter. "Approach without display" was low during the first part of the experimental period, but increased after cocoon construction. The level was fairly constant during the period in which the females carried cocoons. "Sitting" decreased gradually until just before cocoon construction, after which there was an increase, sudden at first, up until the spiderlings emerged (about 28 days after moultting). "Walking" increased rapidly in the first days to a rather constant level, showing a slight decrease around the time of cocoon formation.

It was considered that "undirected behaviour" of the males might be affected by the locomotory activity of the females. Female locomotory
Fig. 2. Time (mean percentages of 5 observation periods per day) spent by specimens of *Pardosa amentata*, during the first weeks after the final moult, on different categories of behaviour. *A*: Behaviour of males directed towards females (the line indicates the total percentage of these categories); *B*: Undirected behaviour of the males (the line indicates the total percentage of these categories); *C*: The percentage of time spent on walking by the females. The period during which the females carry their cocoons is indicated (*cocoons*). The vertical bars indicate the range of the percentages of the 5 observation periods of which the means are also indicated (dots).
activity (equivalent to "walking" in males) is indicated in Fig. 2C. It increased up to the time of cocoon construction after which a decrease occurred up until the spiderlings emerged, when a second increase occurred.

The experiment indicates that the degree of "undirected" and "directed" behaviour in males changes with time.

2. Behaviour of males towards standard females.

To test whether the changes in behaviour, as observed in the first experiment, were due to the stage in the reproductive cycle of the females or to the age of the males, males of different ages were tested against standard females.

a. On the 8th, 17th, 27th, and 34th days after the final moult the behaviour of the males of group A was tested towards females which had moulted to adult 6-9 days previously. Females of this age were preferred because in experiment 1 the highest courtship and mating rates were shown a few days before cocoon construction, which normally takes place 8-9 days after the final moult.

The results, regarding directed behaviour, are presented in Table I. Only small differences were found in "courtship" of males at 8, 17 and 27 days after the final moult. At the 34th days "courtship" was markedly reduced. This reduction may be due to senescence of the males. The rise of "sitting" is in accordance with this supposition. At this time of the experiments only 23 of the 75 males had survived. "Mating" was low except in the group of 8 days old males.

<table>
<thead>
<tr>
<th>categories</th>
<th>δ: 8 days</th>
<th>δ: 17 days</th>
<th>δ: 27 days</th>
<th>δ: 34 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>c</td>
<td>49.2</td>
<td>45.3</td>
<td>42.1</td>
<td>18.7</td>
</tr>
<tr>
<td>a</td>
<td>2.4</td>
<td>1.7</td>
<td>1.5</td>
<td>1.2</td>
</tr>
<tr>
<td>m</td>
<td>7.3</td>
<td>0.2</td>
<td>2.1</td>
<td>1.1</td>
</tr>
<tr>
<td>w</td>
<td>14.7</td>
<td>19.5</td>
<td>19.0</td>
<td>18.3</td>
</tr>
<tr>
<td>s</td>
<td>26.4</td>
<td>33.3</td>
<td>35.3</td>
<td>60.7</td>
</tr>
</tbody>
</table>

b. 24 days after moulting, the behaviour of males of group A, towards females without cocoons and females carrying cocoons, was tested. After being tested with a female of 6-9 days old for three obser-
vation periods, the males were immediately thereafter confronted with cocoon carrying females for another series of three observation periods. The results are given in Table II. “Courtship” values were high towards the unfertilized females and low towards cocoon-carrying females, whereas the reverse was true for “approach without display”. When the experiment was repeated, using the males of group B, and modified by presenting the females in the reverse order, the same conclusions could be drawn.

**Table II**

The levels of “courtship” (c), “approach without display” (a), “mating” (m), “sitting” (s), and “walking” (w) of males of *Pardosa amentata*, 24 days after the final moult, towards females without cocoons (♂ × ♀ – c) and towards females carrying cocoons (♂ × ♀ + c). The data represent the mean percentages obtained in 3 observation periods for each pair.

<table>
<thead>
<tr>
<th>categories</th>
<th>♂ × ♀ – c</th>
<th>♂ × ♀ + c</th>
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<tr>
<td>c</td>
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<tr>
<td>a</td>
<td>4.0</td>
<td>11.9</td>
</tr>
<tr>
<td>m</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>w</td>
<td>18.7</td>
<td>20.3</td>
</tr>
<tr>
<td>s</td>
<td>39.6</td>
<td>44.9</td>
</tr>
</tbody>
</table>

The results presented in sections a and b strongly suggest that the behaviour of males towards females, at least during the first four weeks of the adult stage, largely depends on the stage of the reproductive cycle of the females.

c. It is possible that the greater locomotory activity of the males in the field at the time when most females are fertilized and are carrying cocoons may be due to the fact that males exhibit during this period less directed activity towards females. To study the validity of this hypothesis, the behaviour of the males of group A was tested, at days 11, 18 and 22, towards both types of standard females presented simultaneously. The directed behaviour of the males was recorded in a slightly modified way: it was noted whether “courtship”, “mating” or “approach without display” was directed towards the female without cocoon or to the cocoon carrying female. The percentages of directed behaviour (the mean of five observation periods for each day) are presented in Fig. 3. The results indicate that there was no difference in the total time spent by males on directed behaviour towards females with or without cocoons. However, as in the previous experiments, most of the behaviour directed towards females without cocoons was “courtship” and towards cocoon carrying females “approach without display”.
Fig. 3. Time spent by males of Pardosa amentata at 3 different days on “courtship” + “mating” \((c + m)\), “approach without display” \((a)\) and total time spent on directed behaviour \((a + c + m)\) towards females with and without cocoons, presented at the same time. The data are the mean percentages of 5 observations per day. Hatched bars: behaviour directed towards the females without cocoons; open bars: behaviour directed towards females with cocoons.

IV. DISCUSSION

In the Introduction it was suggested that the increased locomotory activity exhibited by males of several Pardosa species after the main period of copulation, observed in the laboratory (Vlijm & Richter, 1966) and in the field (Vlijm & Kessler-Geschiere, 1967), might be due to different reactions of the males towards fertilized and unfertilized females. From the experiments presented in this paper it appears that males do indeed behave differently to females depending on the phase in the reproductive cycle of the latter. Males showed more “courtship” towards and mated more frequently with females without a cocoon, whereas they spent more time on “approach without display” towards females carrying a cocoon. However, from the last experiment it appears that males do not show a preference for unfertilized females when confronted with the two types simultaneously. The males spent
the same time on each type. Therefore, the increased locomotory activity observed in the field is probably not related to the behavioural differences observed.

The level of undirected behaviour (i.e., "walking" and "sitting") in males during the first four weeks after moult was rather constant. The absence of increased locomotory activity in the presence of females with cocoons is probably a consequence of the experimental set-up. The test boxes were relatively small (16 × 8 cm). In this situation the male can only walk a short distance before meeting a female. In the field, as well as in the large experimental box used by Vlijm & Richter (1966), the situation is clearly very different in this respect. Therefore, in our experiments "undirected behaviour" may tend to be under-represented.

In the experiments described it is likely that optical stimuli were most important with regard to the behaviour of the male. Under natural conditions other stimuli may be of relatively greater importance. Undirected locomotory activity in the field presumably ends whenever (1) a female is seen or (2) some other stimulus is received from a female. Females with cocoons exhibit less locomotory activity than females without cocoons. Spiders respond more to motile objects than to static ones (Dzimirsky, 1959). Hence, males receive less optical stimuli from females with egg sacs. Females of P. amentata do not produce silk threads when they carry a cocoon (Richter, 1970), while females without cocoons produce a special type of silk (Richter & Stolting, in preparation), which serves as a stimulus for males. Similar observations were reported by Engelhardt (1964) in Trochosa species. Thus, females carrying cocoons will also provide less chemical stimuli than females without cocoons. There is therefore considerable evidence that the increased locomotory activity in Pardosa males, after the main period of copulation, is correlated with the fact that most females in this period, in the optimal habitats, present very few stimuli for the males. Therefore, during this period, the chances of the unfertilized females to meet males will be increased.

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