Leg Wave Behaviour of Wolf Spiders of the Genus *Pardosa* (Lycosidae, Araneae)

M. J. Koomans, S. W. F. van der Ploeg and H. Dijkstra
Free University, AMSTERDAM, The Netherlands
Dept. of Ecology, De Boelelaan 1087

Introduction

During research on reproductive behaviour of lycosid spiders a conspicuous leg movement was occasionally observed, which was characterized as "leg waving". In this movement the front leg was successively drawn back and flexed, raised, stretched forward and lowered.

Similar movements have been described as components of male courtship behaviour in *Trochosa* species (Locket, 1923, and Engelhardt, 1964), in *Pardosa* species (Kaston, 1936, Nappi, 1965, Rovner, 1968, and Vlijm & Borsje, 1969), and as a female response to male courtship in *Pardosa* species (Nappi, 1965, and Rovner, 1968).

Other observations (Dijkstra, 1968) had indicated that this type of leg movement is also performed by juvenile wolf spiders, and is not restricted to courtship situations. As a consequence, "leg waving" could have both a general and a courtship function.

In order to assess the various qualities of leg waving, an analysis of this behaviour was made in both sexes in various developmental stages of some *Pardosa* species, in different situations. This analysis can be divided into three parts:

a. ***Pattern analysis***
b. ***Comparative ontogenetic analysis:*** frequency analysis in different developmental stages.
c. ***Causal analysis:*** correlations with other behaviour and stimuli analysis.

The results of the analysis are discussed with regard to a possible function of leg wave behaviour.

Methods

a. *Subjects.* Subadult spiders of the species *Pardosa amentata* (Cl.), *Pardosa lugubris* (Walck.), *Pardosa nigriceps* (Thor.) and *Pardosa pullata* (Cl.), and 5th instar specimens of *P. lugubris* were collected in the field. During the experiment on comparative ontogeny the spiders moulted to adult and their offspring were used in the 2nd instar experiments.

The animals were housed and tested in a climate room at 20°C and 70% rel. humidity. They were kept solitarily or in groups (unisexual or mixed), according to experimental requirements.

The subjects used in the stimuli experiments were kept solitarily and were selected for leg wave readiness by touching one of the front legs of an immobile animal with a clean nylon thread (diam. 0.015 mm). This was repeated 5 times, with intervals of at least 30 sec. Spiders responding with at least two leg waves were selected as suitable test objects.

b. *Apparatus and treatments.* For the frquency and stimuli analysis a plastic testbox (18 x 12 cm, height 13 cm) was used, which contained a moistened sand-layer (1 cm) and a trapezoid-shaped stone (upper surface 8.5 x 5.5 cm, h. 4 cm). For the 2nd and 5th instar observations a smaller box (12 x 9 cm) and stone (5 x 3 x 3.5 cm), respectively, were used.

Usually, cleaned stones were used. However, in some stimuli experiments the stone was exposed to a group of 3 male and 3 female conspecifics (incentives) for at least 36 hours.

Direct light was provided only on the upper stone surface (light intensity 11,000 lx, surface air temperature 28°C).

In some stimuli experiments the spinnerets of the animals were sealed (by the method of Richter and Van der Kraan, 1970), in order to keep the stone clean from products of the silk glands. Some test animals were blinded with a paste of soot and shellac. During treatment these spiders were all anaesthetized with CO_2.

c. *Recordings.* Leg wave movements were recorded on film (32 fps) and on videotape (25 fps). The pattern was reconstructed by means of a step-by-step analysis of the frames.

The behaviour frequencies were recorded on a 20-channel Esterline-Angus recorder wired to two key-boards.

In the ontogenetic analysis, groups of 4 male and 4 female conspecifics (or groups of 8 2nd or 5th instars because these could not be sexed) were observed in the testboxes during 2 x 15 minutes per day. The results were reduced to the frequencies of behavioural elements per individual per 15 min.

In the stimuli analysis the animals were observed during periods of 30 minutes. The individual scores

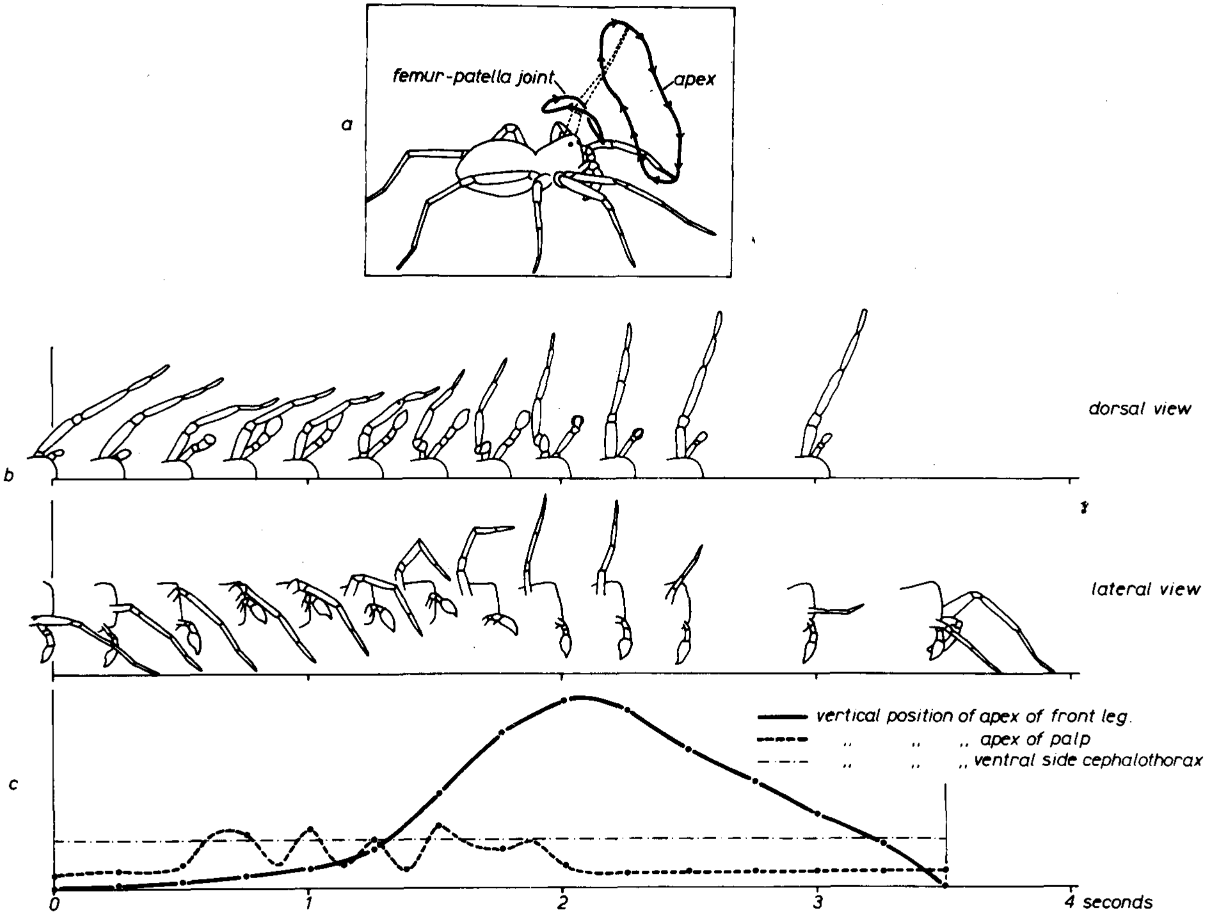

Fig. 1 – Leg wave behaviour of *P. lugubris*, subadult male.
a – Pathways of apex and femur-patella joint during the leg wave.
b – Positions of the leg during the leg wave.
c – Heights of leg and palp apex relative to cephalothorax height.

were summed.

Results and Conclusions

Pattern analysis

a. *Leg movements.* The common leg wave pattern is presented in Fig. 1. Fig. 1a shows that the apex of the front leg describes an elliptical course. The step-by-step analysis of Fig. 1b shows that the movement consists of both vertical and lateral components; the duration is 3-5 sec. The graph of Fig. 1c is derived from 1b, and shows the vertical pathways of leg and palp apex relative to cephalothorax height, plotted against time.

Usually, the body position remains unchanged during the leg wave.

Some variations in the pattern of leg waves are shown in Fig. 2a ("jerky" leg wave, mostly observed in *P. pullata* females) and Fig. 2c (*P. lugubris* adult males). Sometimes leg waves are not finished, or start from another leg position. Leg waves may be repeated 2-5 times ("series of leg waves"), either with the same leg, or alternately with both front legs.

b. *Associated palp movements.* Often leg waves are accompanied by more or less specific palp movements. These movements are mainly induced by

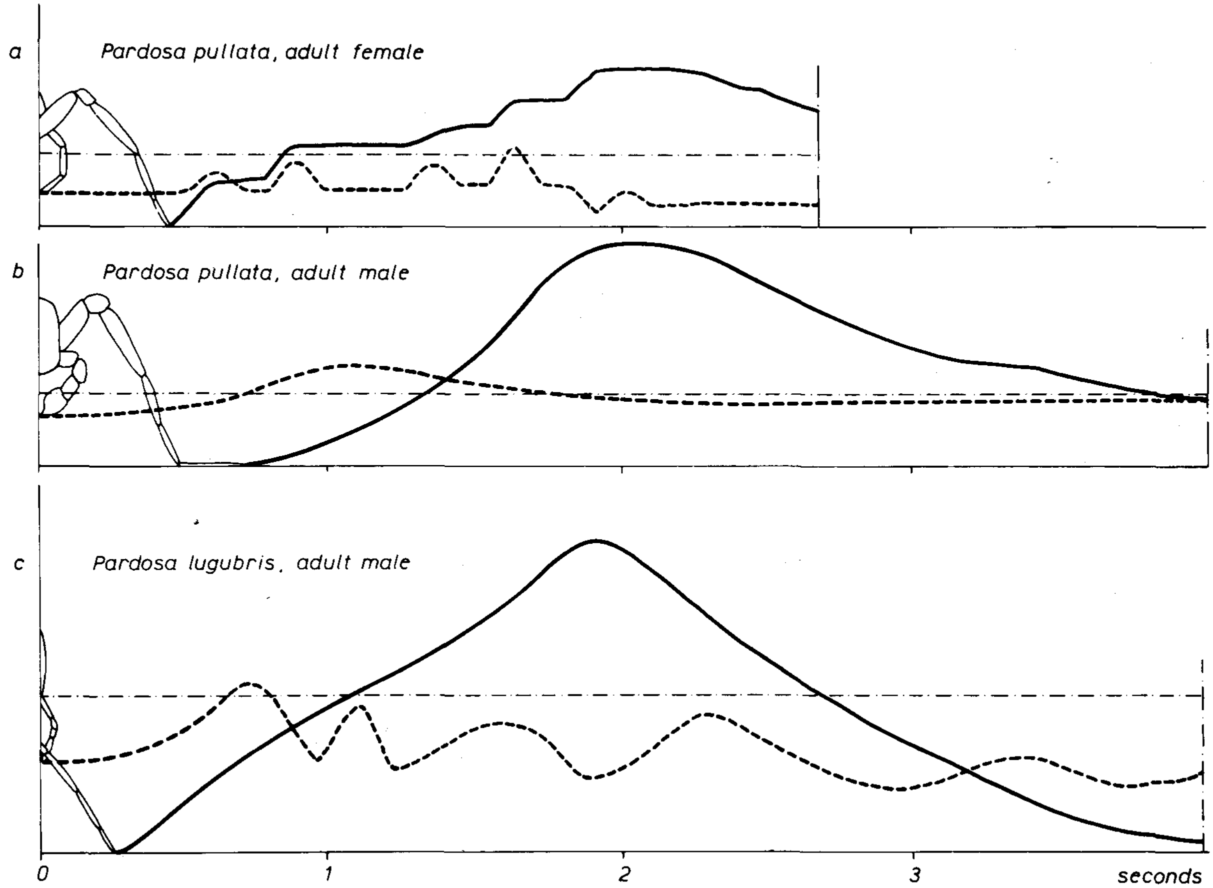

Fig. 2 —Three types of leg wave behaviour (Legend: see Fig. 1c).
a – Jerky leg wave of *P. pullata* adult female.
b – Leg wave with palp wave of *P. pullata* adult male.
c – Leg wave of *P. lugubris* adult male.

the proximal palp segments; the distal parts remain mutually fixed. There are two distinct categories:

1. Oscillatory movements. (Fig. 1b, c). These are usually restricted to the initial (upward-backward) phase of the leg wave. This category is the most common one. When the leg wave is jerky, the palp movement may be jerky also (Fig. 2a).
2. Palp wave (Fig. 2b). This movement is comparable with the leg wave movement. It starts just before the leg wave and ends at 3/4 of the leg wave. Palp waves (with or without leg waves) are only observed in adult males of *P. pullata* and in *Pardosa femoralis* Simon.

A different movement pattern was found in *P. lugubris* adult males (Fig. 2c). The leg wave itself is slightly jerky; the palp movements are oscillatory, but they last for the whole leg wave, and they are obligatory. Although this behaviour has some resemblance to the courtship behaviour of *P. lugubris,* it is markedly different in respect of both leg and palp movements. Hallander (1967) referred to a comparable behaviour as "single-display".

All four species observed show a rather uniform pattern of leg wave, plus, facultatively, the oscillatory palp movement. The same pattern was observed in specimens of *Pardosa prativaga* (Koch), *Pardosa sphagnicola* (Dahl) and *P. femoralis.* Thus it can be concluded that leg wave behaviour is rather common

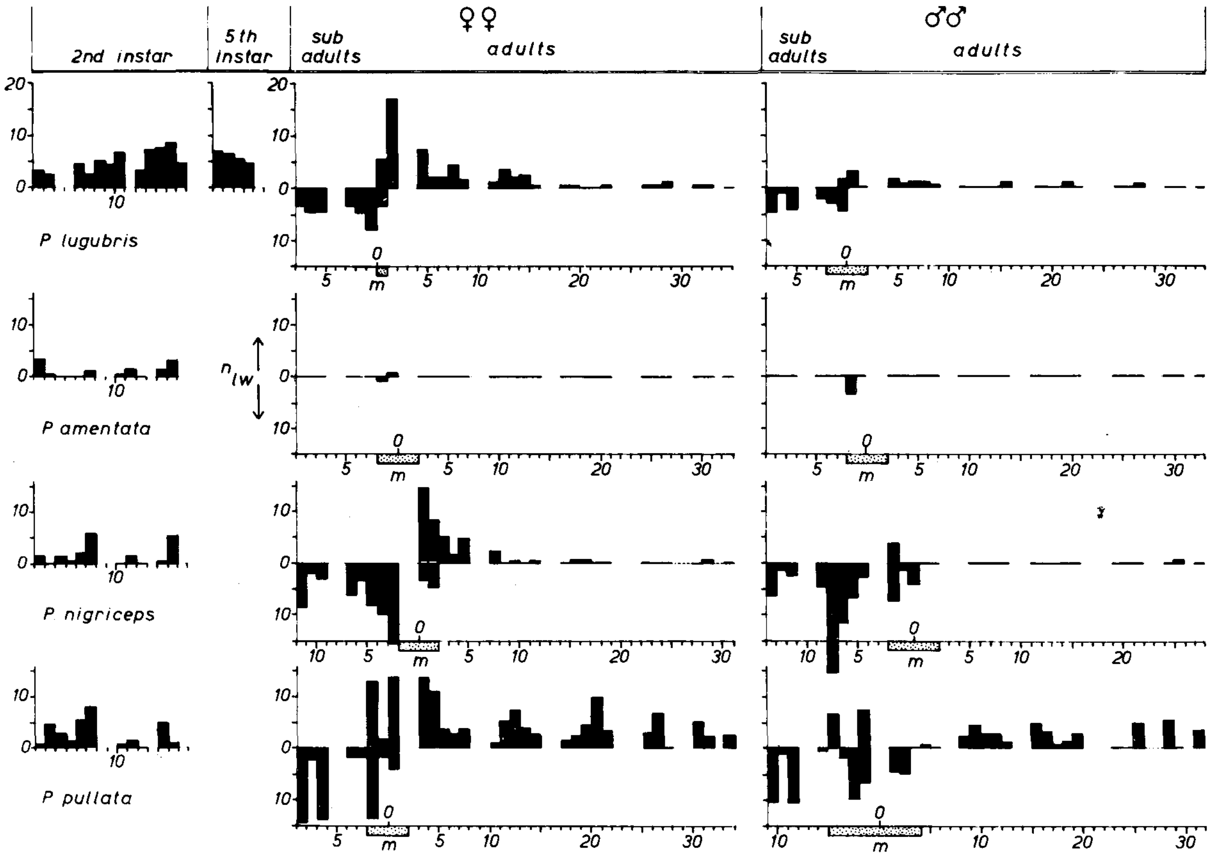

Fig. 3 – Ontogeny of leg wave behaviour in 4 species of *Pardosa*.
n_{lw} = number of leg waves per individual in 15 minutes.
m = maturation moult period.
Time indication: 2nd instar: days after hatching
5th instar: no time indication
subadults: days before maturation moult
adults: days after maturation moult

in the genus *Pardosa*.

Notwithstanding the slight variations in the pattern, the leg movements are clearly distinct from other movements, such as leg beating, leg raising or walking, especially as regards the speed of the movement.

Comparative ontogenetic analysis

Fig. 3 shows the frequencies of leg waving in the four *Pardosa*-species during the 2nd instar, the 5th instar, the subadult and the adult stage (both sexes). From these data the following conclusions are drawn:

1. Leg waving occurs in all four species studied. However, in *P. amentata* leg waving is almost absent under the chosen test conditions.
2. Leg waving occurs in all observed developmental stages. After a period of relatively high frequencies around the maturation moult, there is a rapid decline in the frequency of leg waving, except in *P. pullata*.
3. In the adult stage leg waving occurs in both sexes (*P. amentata* not taken into account). Females show more leg waving than males, except in *P. pullata*.

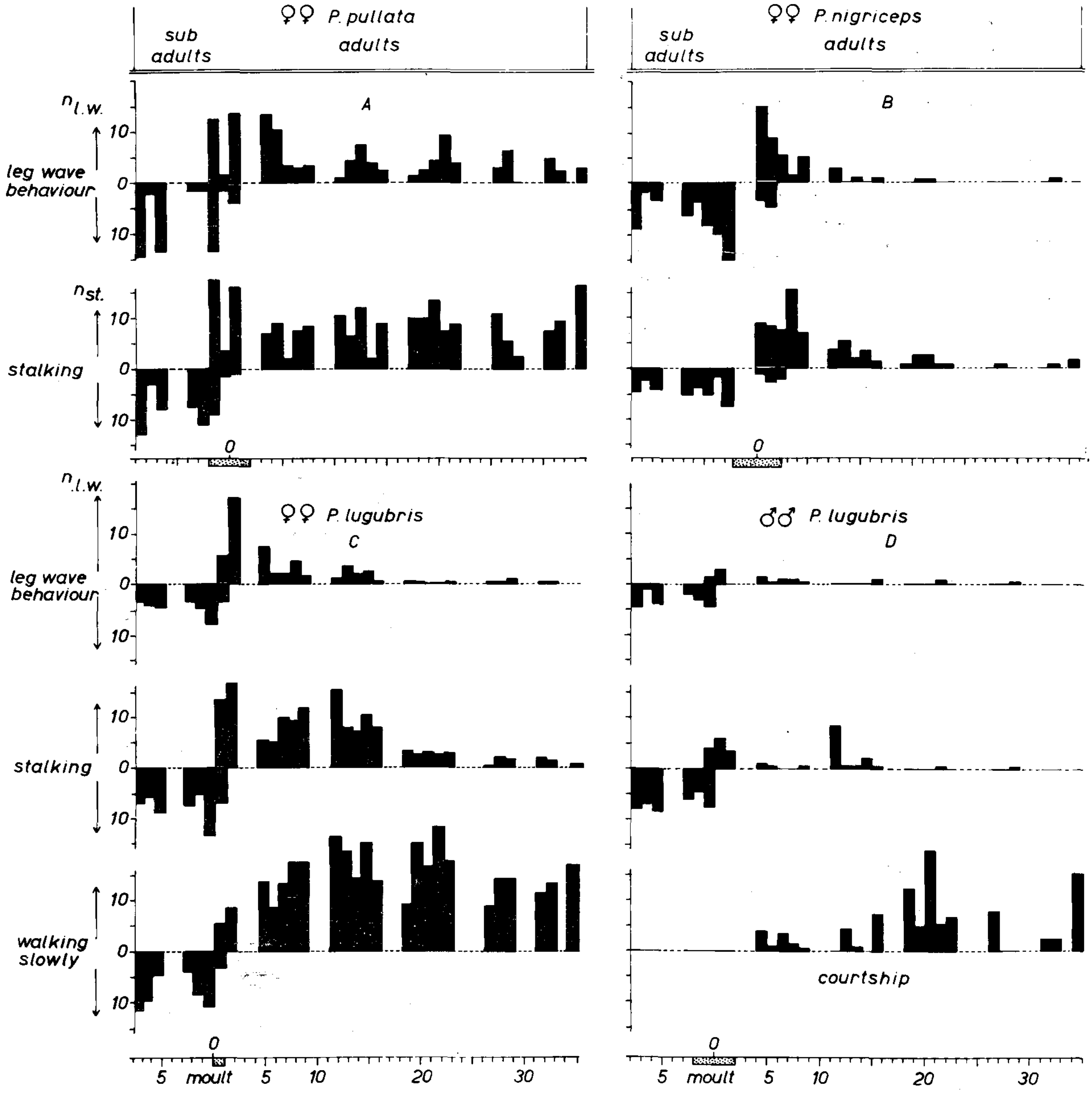

Fig. 4 —Behaviour correlated with leg waving (Legend: see Fig. 3).
a – *P. pullata* females: leg waving and stalking.
b – *P. nigriceps* females: leg waving and stalking.
c – *P. lugubris* females: leg waving, stalking and walking slowly.
d – *P. lugubris* males: leg waving, stalking and courtship display.

Causal Analysis

a. *Behaviour correlated with leg waving.* During the ontogenetic analysis other behaviour of the spiders was also recorded, in order to find possible correlations between leg waving and other elements of *Pardosa* behaviour. In Fig. 4 the frequencies of leg waving are compared with those of stalking, walking slowly and courtship display.

Prior observations had suggested a correlation between leg waving and stalking. The latter behaviour is an extremely slow and stealthy way of locomotion, clearly different from walking. Walking slowly is intermediate between stalking and walking as regards the speed of locomotion. It has the characteristics of walking (Dijkstra, 1968) and is therefore used as a parameter for locomotory activity.

From Fig. 4 it appears that, in the course of time, leg waving and stalking are parallel in their frequencies. In *P. pullata* (Fig. 4a; males not shown but following the same trend) the frequencies remain relatively constant. In *P. nigriceps* (Fig. 4b; males not shown but following the same trend) and in *P. lugubris* (Fig. 4c, d) the frequencies of both leg waving and stalking decline shortly after the maturation moult.

Fig. 4c shows that in *P. lugubris* females the average frequency of walking slowly does not change much throughout the adult stage. The same holds for males and females of all four species (results not presented here, see Van der Ploeg, 1971). Thus there is no obvious correlation between leg waving and locomotory activity.

The results of sequence-analysis (not shown here: see Van der Ploeg, 1971) support these conclusions. Especially in *P. lugubris,* but also in *P. nigriceps* and *P. pullata* leg waving was preceded and followed by stalking more frequently than could be expected by chance. No such conclusion could be drawn with respect to sequences of leg waving and walking slowly.

In the Introduction the possible function of leg waving in courtship situations was mentioned. In Fig. 4d the frequencies of leg waving and courtship are shown for *P. lugubris* adult males. These graphs show that a decrease of leg waving is attended with an increase of courtship display. The same holds for *P. nigriceps* adult males (not shown here).

b. *Stimuli analysis.* In order to find a causal explanation of leg wave behaviour, the possible significance of some social cues as leg wave stimulating factors was investigated in *P. pullata* subadults. These animals were selected on leg wave readiness (see Methods, a.), except the animals in exp. 8 (see Table 1).

The following factors were experimentally investigated:

- the presence or absence of conspecifics (incentives);
- the presence or absence of products of silk glands;
- the role of the eyesight.

In some experiments the leg waves performed on the upper surface of the stone, or on the edge of upper and lateral surface, were separately recorded. The criterion for "edge" was simultaneous contact of the spider with both surfaces. Series were recorded in order to assess whether the significance was due to these repetitions.

The results of the stimuli experiments are shown in Table 1. The following conclusions are drawn:

1. Leg waving is stimulated by the products of silk glands of conspecifics (exp. 1-3, untreated subjects; Wilcoxon's signed value test: total n: $p = 0.001$, series: $p = 0.01$).
2. On top of "exposed" stones (see Methods, b.) more leg waving occurs than on top of "cleaned" stones (exp. 3-5; total n: $p = 0.005$, series: $p = 0.05$). There is no significant difference between the absolute leg wave frequencies on the edges of cleaned and exposed stones, respectively.
3. On the edge of both cleaned and exposed stones more leg waving/time occurs than on top (total n: $p = 0.005$, series: $p = 0.005$), when the time spent in sitting at the edge or on the top is taken into account (not shown in Table 1).
4. Sealed as well as blinded spiders show relatively little leg waving at the edge.
5. A single spider (exp. 8) on exposed stones shows most leg waving on the top; on cleaned stones it shows more leg waving at the edge.

Single spiders sitting still on cleaned stones, did so for up to 95% of the time near the edge, with the front of the body turned towards this edge. On exposed stones, most of the time while immobile was spent on the middle of the stone (data not shown here).

Experiment	Treatment		Cleaned Stone				Exposed Stone			
					% edge				% edge	
nr.	subjects[1]	incentives[2]	total n	series	total n	series	total n	series	total n	series
1	–	–	15	7	(not recorded)		33	15	(not recorded)	
2	–	sealed	8 } 64	4 } 38	(not recorded)		15 } 124	12 } 60	(not recorded)	
3	–	–	41	27	71%	70%	76	33	50%	42%
4	sealed	–	–	–	–	–	84	36	30%	33%
5	sealed	sealed	65	27	45%	44%	–	–	–	–
6	sealed + blinded	–	–	–	–	–	41	21	17%	19%
7	sealed + blinded	sealed	52	27	12%	19%	–	–	–	–
8	–	*not present*	34	20	59%	55%	170	53	6%	9%

[1] In exp. 1 & 2: the same 2 ♂♂, 2 ♀♀. In exp. 3 to 7: the same 3 ♂♂, 2 ♀♀. In exp. 8: 2 ♂♂, 2 ♀♀.

[2] Incentives: the same 3 ♂♂ and 3 ♀♀ in all experiments.

total n = total number of leg waves
series = number of series of leg waves
% edge = % of leg waves by an animal sitting on the edge of the stone

Table 1 – Leg wave frequencies in *P. pullata* subadults.

Discussion

Pattern and Ontogeny

The leg wave pattern is generally the same in all species studied, in all developmental stages observed, and in both sexes. Such does not hold for e.g. courtship patterns, but it does for e.g. locomotory movements.

Leg waves are often associated with the oscillatory palp movements. In the leg wave of *P. lugubris* adult males the palp movements are obligatory. Thus "leg wave behaviour" can be considered as a behaviour that consists of both leg and palp movements.

The palp moving of *P. pullata* adult males was referred to as "courting" by Vlijm and Borsje (1969), as the pattern of palp waving resembles the basic palp movement in the courtship display of *P. amentata, P. nigriceps* and *Pardosa hortensis* Thor. (see Vlijm & Dijkstra, 1966). The main difference concerns the time-scale and the rhythm of the movement.

Leg waving occurs in all developmental stages observed, especially in the pre-adult and early adult phases (except *P. pullata*). The decrease in leg waving, simultaneously with the increase in courtship frequency in *P. lugubris* and *P. nigriceps* adult males, suggests that in these species leg waving is "replaced" by courting. Analogously, leg waving in adult females could be replaced by specific *reactions* on courting.

Eliciting stimuli

The results of the experiments indicate that "exposed" stones stimulate leg waving. Tactile, tactochemical or olfactory stimuli from such substrates could possibly be perceived by sense organs which have been found on spider palps and legs (e.g. Kaston, 1936, Keller, 1961, Barth, 1967, Hegdekar and Dondale, 1969). Tactile stimuli might be sufficient (cf. the selection procedure on leg wave readiness with a nylon thread: Methods, a.).

The experiments with solitary and with blinded spiders suggest that the eyesight is important. Crossing the edge of the stone the animal passes into a different space, light and temperature condition. The perception of this change of condition might be a stimulus for leg waving.

"Exposed" substrates or the mentioned changes of condition may stimulate the "expectation" of encounters with other spiders which, particularly on clean substrates, could not easily be detected.

Even leg waving itself could be a stimulus: spiders sometimes react with leg waves to leg waving by other spiders (Rovner, 1968, Van der Ploeg, 1971).

Possible function

The results of the experiments cannot be unambiguously interpreted. Thus any indications about the function of leg waving must be speculative.

According to the situations in which leg waving occurs, the movement could have a sensory function (towards conspecifics, light, warmth; cf. the tongue of snakes). However, in the experiments insufficient evidence for this hypothesis was obtained.

The rather stereotyped (pattern, speed) movement suggests that leg waving has been ritualized to a display. Thus, being a signal, it should have a *social* function. Because leg waving is common in most species observed, it cannot be an intraspecific recognition signal (except the leg waves of *P. pullata* and *P. lugubris* adult males).

Leg waving may be considered in the context of conflict behaviour. There are at least two arguments for this hypothesis:

a. In the maturation moult period the spiders are in an internal conflict situation. In this period much leg waving occurs.
b. Situations in which other spiders can be "expected" (cf. the stimuli experiments) are conflict (approach-avoidance) situations. In such situations both leg waving and stalking frequently occur.

One of the supposed functions of courtship is the suppression of non-sexual tendencies (Platnick, 1971). Such an inhibition of agonistic responses could also be a function of leg waving. Hence leg waving could be a general agonistic display with a threat or appeasement function.

In this line of thought the occurrence of leg waving in adult males might be related to the degree of ritualization of the courtship display. In *P. pullata* the males show more leg waving in the presence of a female (Den Hollander et al., 1973). In "pre-mating" situations it sometimes consists of palp waves only. Thus *P. pullata* may have a poorly ritualized courtship display (males attempting copulation by "catching" the females), namely leg waving.

Within the so-called "*pullata*-group", the courtship of *P. sphagnicola* could be ritualized to some extent: leg waving is part of the courtship. In *P. prativaga* (*pullata*-group), and in *P. amentata, P. lugubris* and *P. nigriceps* (*amentata*-group) courtship is strictly ritualized as it contains no leg waving.

Thus both leg waving and courtship could be considered displays with an aggression-lowering function; in some species leg-waving is replaced by courtship. However, in most species leg waving occurs throughout the adult stage (although not in all individuals); presumably it retains the appeasement function, and is probably displayed by smaller animals. This might also be the explanation for the leg wave of *P. lugubris* adult males: here the leg wave is somewhat more ritualized and it could serve as an aggression-lowering display in non-courtship situations (cf. the observations of Hallander, 1967).

Acknowledgements

The authors are indebted to Prof. Dr L. Vlijm and Mrs Drs A. Kessler-Geschiere for their comments on this paper, and to Mr G. W. H. van den Berg for making the drawings. H. Dijkstra acknowledges financial support from the Netherlands Organization for the advancement of pure research (Z.W.O.).

Summary

A leg wave is a movement in which the front leg of a spider is successively drawn back and flexed, raised, stretched forward and lowered. It may be accompanied by oscillatory palp movements or by a palp wave. It is different from other movements as regards the pattern and the speed.

This behaviour occurs in the juvenile and in the adult phase of several wolf spider species (genus *Pardosa*). After a peak frequency of leg waving in the maturation moult period, there is a rapid decline (except in *P. pullata*), simultaneously with an increase in courting frequency.

Leg waving is correlated with stalking, but not with locomotory activity. Leg waving is stimulated by conspecifics and their silk gland products, and by changes in space, light or temperature conditions which make the spider expect conspecifics.

Thus, rather than a movement with a sensory function, leg waving may be considered an agonistic display with an aggression-lowering function. This is also part of the courtship function complex. Hence leg waving might be replaced by courtship if the species has a strongly ritualized courtship (e.g. *P. amentata*); if not, leg waving forms part of the courtship or it functions as courtship (e.g. *P. pullata*).

References

BARTH, F. G. 1967: Ein einzelnes Spaltsinnesorgan auf dem Spinnentarsus: seine Erregung in Abhängigkeit von den Parametern des Luftschallreizes. *Z.vergl.Physiol.* **55**: 407-449.

DIJKSTRA, H. 1968: Sexueel en agonistisch gedrag bij *Pardosa amentata.* Doct. verslag, Free University, Amsterdam, and State University of Groningen. (unpublished).

ENGELHARDT, W. 1964: Die mitteleuropäischen Arten der Gattung *Trochosa* (Koch) (Araneae, Lycosidae). *Z.Morph.Ökol.Tiere* **54**: 219-393.

HALLANDER, H. 1967: Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O. F. Müller). *Oikos* **18**: 145-150.

HEGDEKAR, B. M. and DONDALE, C. D. 1969: A contact sex pheromone and some response parameters in Lycosid spiders. *Can.J.Zool.* **47**: 1-4.

HOLLANDER, J. den, DIJKSTRA, H., ALLEMAN, H. and VLIJM, L. 1973: Courtship behaviour as species barrier in the *Pardosa pullata* group (Araneae, Lycosidae). *Tijdschr.Ent.* **116**: 1-22.

KASTON, B. J. 1936: The sense involved in the courtship of some vagabond spiders. *Entomologica am.* **16**: 97-167.

KELLER, L. R. 1961: Untersuchungen über den Geruchssinn der Spinnenart *Cupiennius salei* Keyserling. *Z.vergl.Physiol.* **44**: 576-612.

LOCKET, G. H. 1923: Mating habits of Lycosidae. *Ann.Mag.nat.Hist.* **12**: 493-502.

NAPPI, A. J. 1965: Notes on the courtship and mating habits of the wolf spider *Lycosa helluo* Walck. *Am.Midl.Nat.* **74**: 368-373.

PLATNICK, N. 1971: The evolution of courtship behaviour in spiders. *Bull.Br.Arachnol.Soc.* **2**: 40-47.

PLOEG, S. W. F. van der 1971: Wuiven van enige *Pardosa*-soorten (Lycosidae). Doct. Verslag, Free University, Amsterdam (unpublished).

RICHTER, C. J. J. and KRAAN, C. van der 1970: Silk production in adult males of the wolf spider *Pardosa amentata* (Cl.) (Araneae, Lycosidae). *Neth.J.Zool.* **20**: 392-400.

ROVNER, J. S. 1968: An analysis of display in the Lycosid spider *Lycosa rabida* Walck. *Anim.Behav.* **16**: 358-369.

VLIJM, L. and BORSJE, W. J. 1969: Comparative research of the courtship behaviour in the genus *Pardosa* (Arachn., Araneae). II: Some remarks about the courtship behaviour in *Pardosa pullata* (Cl.). *Bull.Mus.natn.Hist.nat., Paris,* **41**: 112-116.

VLIJM, L. and DIJKSTRA, H. 1966: Comparative research of the courtship behaviour in the genus *Pardosa* (Arachn., Araneae). I: Some remarks about the courtship of *P. amentata, P. hortensis, P. nigriceps* and *P. lugubris. Senckenberg.biol.* **47**: 51-55.