7.

Investigations on the Feeding Habits of Linyphia.

(Aran.)

By

Edwin Nørgaard, Løgstør.

The purpose of the investigations described in the present paper was to obtain some insight into the feeding habits of *Linyphia*. Notably its behaviour when it captures its prey was observed and studied experimentally in order to determine the stimuli which cause the different reactions of this behaviour.

The investigations were made partly at Løgstør, and partly at the Ecological Field Laboratory at Strandkjær (Molslaboratoriet), recently established by the Natural History Museum of Aarhus, to the director of which, Dr. H. M. Thamdrup, I tender my best thanks. I also wish to thank my friend, Mr. Johs. Petersen, teacher at the Municipal School, Løgstør, for his valuable linguistic help.

1. Methods and Material.

Most of the observations as well as the experiments were made in the natural habitat of *Linyphia* in woods and plantations, where it places its snare among twigs. Some of the experiments were carried out indoors on spiders kept in observation boxes.

To investigate the significance of vibrations in the web, a vibrator constructed like an electric buzzer (Peters 1931) was used. This vibrator is shown in fig. 1; *w* is a fine wire that vibrates in time to the armature of the buzzer. The point of this wire is placed on the web at the spot where a vibration centre is required. *sl* is an adjustable brass slide that regulates the vibrations of the wire, which passes through a hole in the short leg of the angular slide.

The spider's response to chemical stimuli was investigated by means of small pith-balls, which were placed upon the web instead of prey. These balls were used

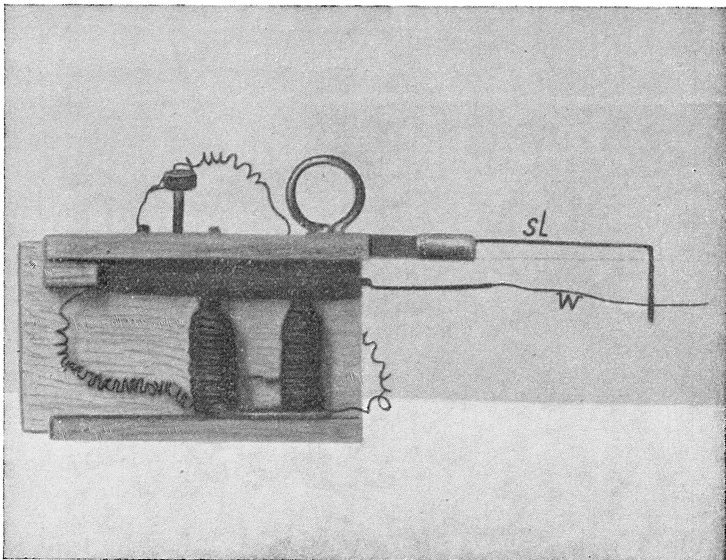

Fig. 1. The vibrator.
sl = adjustable slide.
w = vibrating wire.

either dry or moistened with a fluid containing the substances the influence of which upon the behaviour of the spider was to be tested.

The investigations were made in 1939 and the following years on the common spiders *Linyphia triangularis* Cl. and *Linyphia montana* Cl.

2. The Snare.

The snare of *Linyphia* is very characteristic and has been described by many arachnologists. So I shall give merely a brief description of it, and concerning its construction I may especially refer to Hopffmann (1936). The main parts of the *Linyphia* snare are (fig. 2):

1. The sheet, which consists of densely spun threads forming very fine, irregular meshes. The upper surface

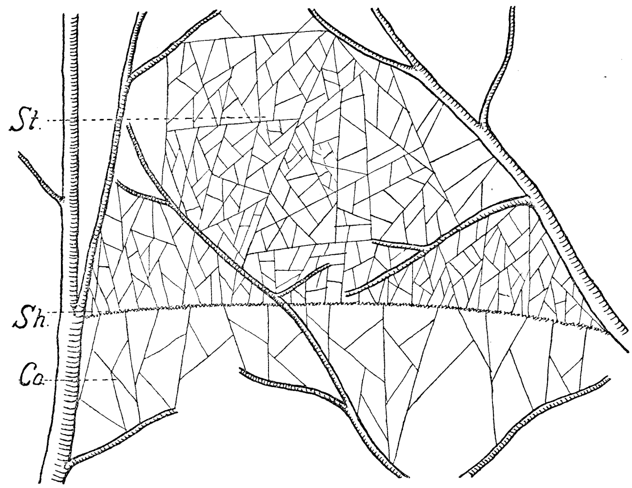

Fig. 2. The snare.
st. = the stopping web.
sh. = the sheet.
co. = the counterbalance threads.

of the sheet is covered with viscid silk (E. Nielsen 1932), the stickiness of which is very effective, as the following observation will show:

I. *L. triangularis.* 22. 6. 42.
A pith-ball is dropped on to the snare. By means of a tweezer I try to pick up the ball again. It adheres to the sheet, which is raised together with the ball to the cover of the observation box, where it adheres so firmly that it cannot be removed again.

The under side of the sheet is not sticky and serves the spider as a place of residence.

2. The stopping-web, which stops the insects and makes them fall down on to the sheet.

3. The counterbalance threads, which are spun beneath the sheet to counterbalance the upward pull of the stopping-web.

L. triangularis is always found hanging with the dorsal side downwards under the sheet. Its claws pull down the sheet in small cones, and the securing thread is stretched from the spinnerets to the sheet. Violent disturbances of the snare makes the spider release its hold. It then falls down, but, suspended by the securing thread, stops a short distance above the ground.

L. montana as a rule sits outside the snare only with its front legs upon the edge of the sheet, through which it receives the vibrations caused by the entangled insects.

3. Description of the Capturing Behaviour.

Some records from my journal will give an idea of the typical course of the capture:

II. *L. triangularis.* 8. 10. 39.
A fly is dropped on to the sheet. The spider turns to the place of impact. The fly lies quiet at first. When it begins moving, the spider runs to it and bites it. The bite is succeeded by sucking.

III. *L. montana.* 16. 10. 39.
A small fly is dropped on to the snare. The spider rushes to it at once, pulls it through the sheet, bites it, and carries it by the chelicerae to the place outside the web, where it was sitting before the capture.

IV. *L. triangularis.* 31. 5. 40.
A bug *(Lygus pratensis)* is dropped on to the snare. The bug is entangled in the stopping web. The spider runs to the place beneath the bug. It shakes the web by means of its forelegs, until the struggling bug falls down on to the sheet. The spider touches the bug with its forelegs and then leaves it.

It appears from these records that the spider's behaviour when the prey is captured consists in various reactions. The first phase of the behaviour is the "turning to the prey"-reaction, in which the spider turns round and rushes towards the place where the prey hit the web. As a rule the spider does not reach this spot at once, for after hitting the sheet, the prey usually lies motionless for a short time, and the spider does not move either.

This pause is broken the moment the insect moves again, when the spider at once rushes towards it. This second phase of its behaviour will be called the "rushing to the prey"-reaction.

When the spider reaches its prey, it puts its forelegs through the sheet in front of the insect, which is thus stopped and captured by the legs of the spider, for which reason I call this phase the "stopping of the prey"-reaction. Sometimes the insect is entangled in the stopping-web, and in such cases the spider pulls the sheet by means of its forelegs, until the prey falls down. I regard this pulling of the sheet as a variation of the "stopping of the prey"-reaction, since it is carried out at the same point of the capture and in the same way: The legs of the spider are in both cases placed round the vibration centre, pulling at the web, and trying to get hold of the entangled insect. If the latter is already lying on the sheet, the pulling movements of the forelegs are few, but if it is hanging in the stopping-web, the spider carries out many vigorous pulling movements.

Having touched the prey with its forelegs, the spider sometimes leaves it again; but in most cases the spider now strikes the claws of its chelicerae into the captured insect and keeps them in this position for some time.

When the movements of the prey have ceased, a brown fluid is ejected on it, which action is followed some seconds later by sucking, during which the abdomen of the spider seesaws up and down in a peculiar way. Sometimes the spider masticates the prey between the ejection of the digestive fluid and the sucking. Thus we find the same method of sucking the prey in *Linyphia* as Bartels (1930) observed in *Tegenaria* and Braun (1931) in *Argyroneta*.

L. triangularis sucks its prey at the place of capture or close to it, the prey being sometimes transported a short distance to be fastened to the sheet, where this has not been destroyed during the capture.

L. montana generally sucks the prey at its resting place at the edge of the web, as will appear from the following record:

V. *L. montana*. 21. 6. 42.
A fly is dropped on to the web. The spider rushes to it, catches hold of it with its forelegs, and bites it. When the movements of the prey have ceased, the spider pulls it through the sheet and transports it to the resting place. There it is fastened to the edge of the sheet by some threads laid out by the spider, which moves its abdomen from side to side, its spinnerets alternately touching the web on either side of the prey. Then the prey is sucked.

Conclusion: The capturing behaviour consists in five phases: 1. The "turning to the prey"-reaction. 2. The "rushing to the prey"-reaction. 3. The "stopping of the prey"-reaction. 4. The bite. 5. The sucking. These five phases will be further analysed in the following chapter.

4. Experiments on the Capturing Behaviour.

a. The "turning to the prey"-reaction.

As appears from my observations, the spider at once turns to its prey when it hits the web, and my first experiments aimed at finding out to which stimuli the spider reacts in this way. Unfortunately I have not been able to cover the eyes of the spiders experimented on, so that I cannot tell exactly, how important the eyesight is for the feeding behaviour of *Linyphia;* but my experiments clearly show that quite different senses play the greatest rôle. And in addition it has been proved by Homann (1928) and Bartels (1929) that webspinning spiders are not able to perceive figures and perhaps not even movements by means of their eyesight.

The experiments on the "turning"-reaction were made in the following way: Instead of insects small objects (spruce needles, leaf-stalks, pith-balls) were dropped on to the sheet of the *Linyphia*-snare, and the spider's response was observed.

Result: When objects of suitable weight (see later on) were used, the spider turned to the place of impact in most cases; and as the spider could not possibly see the objects, we may conclude that the "turning"-reaction is released by the vibrations of the sheet. These vibrations are caused by the impact of the object and are transmitted to the spider's legs through the elastic sheet.

The results of the experiments in which I dropped different objects on to the sheet might be divided into two groups:

1. If the objects were relatively light, nearly all the experiments gave a positive result, i. e. the spider turned to the place of impact.

2. If the objects were rather heavy, the spider ran away to the edge of the sheet.

This must mean that there exists a certain weight limit at which the "turning"-reaction is replaced by an "escape"-reaction, and some experiments were made to find this limit.

Experiment: I made some balls of elder pith and other material. They were of about the same shape and size, but of different weight. These balls were dropped on to the sheet from a height of 10 cm, and the spider's response was observed.

Table 1. The spider's response to prey of different weight.

	20 mg	30 mg	45 mg	80 mg
"turning"-reaction	9	5	0	0
no reaction...................	1	1	0	0
"escape"-reaction	2	10	15	10
total	12	16	15	10
"turning"-reaction in %	75 %	31 %	0 %	0 %

Result: In Table 1 I have recorded the spider's response. From this table it appears that the weight limit in question must be between 30 mg and 45 mg.

The experiments were carried out on *L. triangularis* in the penultimate stage; perhaps the weight limit is somewhat higher for adult spiders.

b. The "rushing to the prey"-reaction.

In most cases the spider had to run some distance before reaching the prey, and an orientating stimulus must then be necessary. My observations showed that the prey must move if the spider were to find it. Accordingly it seemed most probable that the spider was guided by the vibrations of the sheet, and the experiments confirmed this supposition.

Two records from my journal will show the method used:

VI. *L. triangularis.* 15. 10. 39.
With the vibrator I touch a piece of moss lying on the sheet. At once the spider rushes to it; but having touched the moss with its front legs, it leaves it again.

VII. *L. triangularis.* 15. 10. 39. (Fig. 3).
The sheet is touched with the vibrator (*a*). The spider rushes to the spot. The vibrator is now moved and touches another spot of the sheet (*b*); the spider follows. Once more the vibrator is displaced, and the spider again changes direction. This time it comes near the remains of a fly, which had been captured and sucked some hours earlier. The spider now rushes upon this little lump, but soon leaves it again.

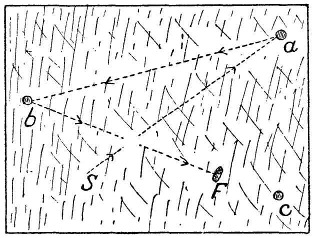

Fig. 3. Track of spider (VII).
s = the spider's starting point.
f = the dead fly.
a, b, and c = vibration centres in succession.

These experiments show that the vibrations of the sheet are the orientating stimulus that guides the spider to its prey. Notably the last-mentioned experiment shows how the spider constantly runs towards the place from which the vibrations radiate. A series of similar experiments was made in 1942, and the results are recorded in Table 2. Two important facts appear from this table:

1. Running to the vibration centre is a very constant factor of the behaviour, as 83 per cent. of 30 trials were positive. It is so constant, indeed, that we must compare it with other forms of bodily orientation to a particular type of stimulus, for instance the phototactic movements of certain moths to the light, and consequently we may speak of a positive vibrotaxis in *Linyphia*.

2. Comparing the number of positive reactions of each individual in the first, second, and third test, we see that it gradually decreases, a fact which may be due to an inhibition of the vibrotactive movement, no doubt caused by the negative result of the first (or second) "rushing to the prey"-reaction.

c. The "stopping of the prey"-reaction.

There is some difference between the individual specimens of *L. triangularis* as to which insects they

Table. 2. The influence of vibrations upon the behaviour of Linyphia.

No.	reaction to 1st impact	reaction to 2nd impact	reaction to 3rd impact	number of positive reactions
1	+	+	0	2
2	+	+	+	3
3	+	+	+	3
4	+	+	+	3
5	+	+	+	3
6	+	0	0	1
7	+	+	+	3
8	+	+	0	2
9	+	+	0	2
10	+	+	+	3
number of positive reactions	10	9	6	25
in %	100 %	90 %	60 %	83 %

eat, and which they reject. As food I have tried to use flies, mosquitos, bugs, and ants. The ants were always rejected, while flies and mosquitos were always eaten. The bugs *(Lygus pratensis)* were consumed by some individuals and rejected by others. This fact may be explained by the supposition that the aversion to bugs is an individually acquired quality, whereas the aversion to ants is a specific inborn quality.

When *Linyphia* in the "stopping"-reaction puts its forelegs through the sheet to stop the prey, it receives certain stimuli, by which eatable and uneatable prey is distinguished, as the following observation will show:

VIII. *L. triangularis.* 8. 10. 39.

A bug *(Lygus pratensis)* is dropped on to the snare. The spider runs to the struggling bug and touches it with its forelegs, but leaves it again at once and runs to the opposite edge of the sheet, where it pulls its forelegs alternately between its chelicerae. Another bug is dropped on to the snare. The spider runs to it, touches it with its forelegs, leaves it, and cleans its forelegs as before.

The stimuli received by the spider are probably of a chemical nature, because a cleaning reflex such as just described is usually released by offensive chemical stimuli. This also agrees with the results of Blumenthal (1935), who has stated that spiders are able to test the chemical qualities of the prey by means of a special sense organ, called the "tarsal organ", which is situated on the tarsus of the legs and the pedipalps.

d. The bite.

It was observed that the spider did not always bite the captured prey, but left it some minutes after the capture.

IX. *L. triangularis.* 15. 10. 39.
A fly is killed and dropped on to the sheet, and the spider is allured to it by means of the vibrator. It touches the fly with its forelegs, but does not try to bite it. A few minutes later it leaves the fly without sucking it.

X. *L. triangularis.* 24. 6. 42.
A fly is killed and dropped on to the web. The spider turns to the prey. I touch the fly with the vibrator. The spider rushes to it, and is now sitting with its legs round the prey. Once more I touch the fly with the vibrator, and now the spider strikes its chelicerae into the prey. A few minutes later the spider transports the fly to a spot not far from the place of capture and fastens it to the sheet by some threads. Then it begins sucking the prey, the seesawing movements of its abdomen being very distinct.

As shown in the above quotations, the bite does not follow automatically upon the capture of the insect; but it must be regarded as the spider's response to a vibration stimulus after the capture. For further control I have made the following experiments: A pith-ball is dropped on to the snare, and the spider is enticed to it. Again the vibrator touches the ball, and the spider then bites it. This experiment was carried out with many individuals, and in nearly all cases I succeeded in making the spider bite the pith-ball.

Conclusion: If the prey moves after the capture, the spider bites it, whereas a non-vibrating prey is rejected.

e. The sucking.

Just as a special stimulus was necessary to make the spider pass from the "stopping"-reaction to the bite, so also a fresh stimulus is necessary to induce it to let the sucking succeed the bite.

XI. *L. triangularis.* 22. 10. 39.
A pith-ball moistened with water is dropped on to the snare. The spider is enticed by means of the vibrator. It touches the vibrating ball with its forelegs and bites it. Half a minute later it lets the ball go and leaves the place. After that it sits still, cleaning its pedipalps, which are pulled alternately between the chelicerae.

XII. *L. triangularis.* 22. 10. 39.
A pith-ball moistened with fly soup is thrown on to the web. The spider is enticed by means of the vibrator. It catches the ball by its chelicerae, bites it, and begins sucking. It sucks the pith-ball for 8 minutes and then leaves it.

These experiments were repeated in 1942 with pith-balls moistened with water, ant soup, and fly soup, and the results are recorded in Table 3. Only one experiment was carried out on each individual, and only the cases in which the spider was lured to bite the ball

Table 3. The spider's treatment of pith-balls moistened with different fluids.

pith-ball moistened with	number of tests	number of cases in which sucking took place
water	3	0
fly soup	3	2
ant soup	3	0

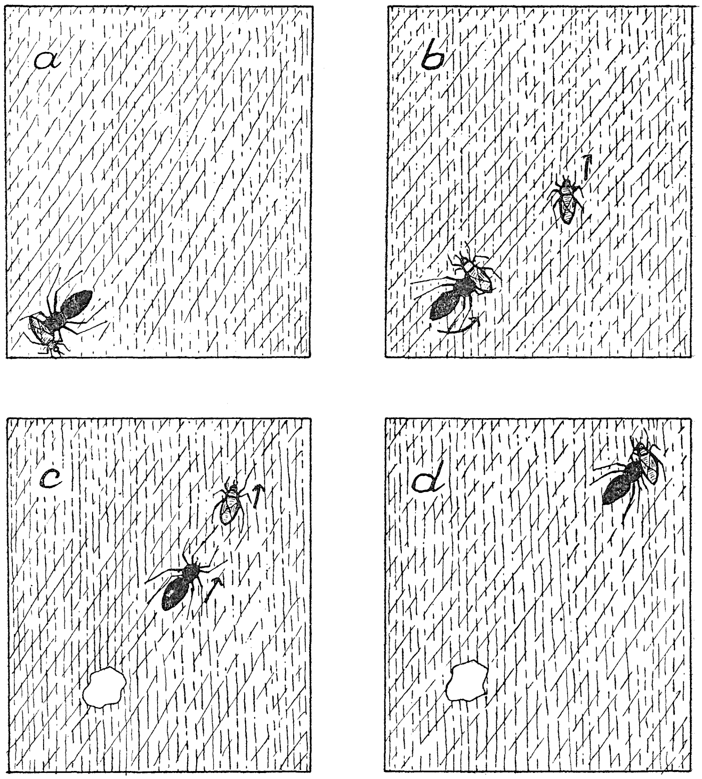

Fig. 4. Illustrating the situation in record XIII.

are included in this table. It will be seen that it was impossible to make the spider suck the balls moistened with water or ant soup, while two of three balls moistened with fly soup were sucked, one of them for 10 minutes, and the other for 6 minutes, before the spider left them.

When the balls moistened with water or ant soup were rejected after the bite, the spider cleaned its pedipalps in the way described in quotation XI.

It is worth noticing that the forelegs are cleaned when the spider has received an offensive chemical stimulus during the "stopping"-reaction, while it is the pedipalps that are cleaned after a disgusting chemical stimulus during the bite. We may then conclude that the chemical stimulus is received by the tarsal organ of the forelegs during the "stopping"-reaction, and by the tarsal organ of the pedipalps during the bite.

f. *Linyphia*'s response to a vibration stimulus from a second prey.

Some experiments were carried out to investigate how *Linyphia* reacted when offered a second prey during the capture. One of the experiments will be given in detail:

XIII. *L. triangularis.* 2. 10. 39. (Fig. 4).
A bug is dropped on to the snare. The spider rushes to it, stops it, and bites it (fig. 4 a). While it is doing this, I drop another bug on to the snare. The spider is somewhat alarmed and turns round with bug No. 1 between its chelicerae (fig. 4 b). Bug No. 2 continues its flight. The spider lets go bug No. 1, which falls down through the sheet, and rushes to bug No. 2 (fig. 4 c), which is captured, bitten, and sucked (fig. 4 d).

The experiment was repeated with other individuals, and the second prey was dropped on to the sheet at different phases of the capture. A general view of the results of these experiments is given in Table 4, from

Table 4. The influence of a second impact on the behaviour of a spider during a capture.

No.	treatment of the first prey	reaction	remarks
1	bite	+	
2	sucking just commenced	(÷)	the spider somewhat alarmed
3	first prey has been sucked for 1 minute	÷	
4	do. for 4 minutes	÷	
5	do. for 10 minutes	÷	

which it appears that the spider responds to a second stimulus while it is biting prey No. 1. When the sucking has just commenced, the spider is somewhat alarmed, but it does not let prey No. 1 go. Later on during the sucking the spider does not respond to a second stimulus in any way. All the reactions of the capturing behaviour are now inhibited.

g. The relative strength of the capturing instinct.

It is important to investigate the relation of strength between various instinctive habits, and here some information will be given about the feeding habits and the sexual habits of *Linyphia*. First I shall quote the following passage from E. Nielsen (1932): "One day in July at 8,40 a. m. I observed a pair *(L. triangularis)* in copulation in a snare at the base of a pine. Several times in the course of about 3 hours pine-needles dropped into the snare or flies flew against the stopping-web. Whenever one of these things happened, the female rushed to the spot in order to bite out a needle or to hunt a fly ... Whenever the female left the male, he walked about for a long time as if searching for something".

I have made similar observations myself, and I shall quote a somewhat different situation:

XIV. *L. triangularis*. 5. 6. 40.

A pair is in copulation in a snare. An accidental disturbance of the web makes the female fall down from the sheet. The male now runs about the snare, while the female hangs suspended by her securing-thread under the web. A fly drops into the snare. The male rushes to it and catches it. I take the female and place her on the sheet, where she walks about. The male does not react in any way, but goes on sucking the prey.

These observations clearly show that the food instincts are able to repress the sexual instincts and accordingly must be stronger than these; a thing which is known from other spiders, too, as it must be the most obvious explanation of the fact that among several spiders the male suddenly from being a “sexual partner“ turns into a “prey“, which is devoured by the female.

5. Conclusion.

The capturing behaviour of *Linyphia* is a complex behaviour consisting of several reactions, which do not follow automatically upon one another, but each of them requires a special impulse in order to appear. In Table 5 I have given a schematic view of this behaviour as I must understand it from my observations and experiments.

Table 5. Survey of the feeding behaviour.

1. The spider receives a vibration stimulus
   - a. of a suitable force ↓ *turning to the prey*
   - b. too strong ↓ *escape*
2. Continued vibration stimulus ↓ *rushing to the prey*
3. The spider receives a chemical stimulus
   - a. of prey ↓ *stopping the prey*
   - b. of uneatable matter ↓ *rejecting the prey* (cleaning of forelegs)
4. The spider receives a vibration stimulus of captured prey ↓ *biting the prey*
5. The spider receives a chemical stimulus
   - a. of prey ↓ *sucking the prey*
   - b. of a strange nature ↓ *rejecting the prey* (cleaning of pedipalps)

Peters (1931) has stated that the mechanism of the capturing behaviour of *Epeira diademata* is a series of reactions, each of which is caused by an external stimulus. This agrees with the facts found concerning the capturing behaviour of *Linyphia;* but there is the great difference between the two spiders that the behaviour of *Epeira* is much more complicated and plastic than the behaviour of *Linyphia.* A further comparison between the capturing behaviour of these two spiders must, however, be put off for the present.

Finally some imformation about the ecological value of the capturing behaviour of *Linyphia* will be given. As *Linyphia* is a sedentary spider, it does not go out in search of prey. Instead of this it waits for the prey to fall into the snare. Therefore it must be able to meet every situation that may arise when something falls into its snare, and this is indeed the case. For instance, if the prey is of a suitable weight, the capturing reactions are released; but if it is rather heavy and consequently would be dangerous to attack, an escape-reaction is released. The value of thus being able to "test the dangerousness" of the prey at a distance is obvious.

Another valuable feature of the capturing behaviour is the inhibition of all capturing reactions, which occurs the moment the spider begins sucking. In the opposite case the spider might be forced to run about the sheet endlessly capturing prey without getting any food.

The fine agreement between the habits and the senses of this spider is also worth noticing. *Linyphia* lives in a web which is a fine instrument for transmitting movements, and accordingly it is the sense of touch and orientating mechanisms depending on vibrations which are developed in this spider. The world of *Linyphia* is a world of vibrations, where touch stimuli accompanied by chemical stimuli play the greatest rôle, while the sense of sight is of slight importance.

References.

Bartels, M.: Sinnesphysiologische und psychologische Untersuchungen an der Trichterspinne *Agelena labyrinthica*. Z. vergl. Physiol. 10. 1929.

Bartels, M.: Ueber den Fressmechanismus und den chemischen Sinn einiger Netzspinnen. Rev. Suisse Zool. 37. 1930.

Blumenthal, H.: Untersuchungen über das "Tarsalorgan" der Spinnen. Z. Morph. Ökol. d. Tiere. 29. 1935.

Braun, F.: Beiträge zur Biologie und Atmungsphysiologie der *Argyroneta aquatica*. Zool. Jahrb. Abt. Syst. Ökol. 62. 1931.

Homann, H.: Beiträge zur Physiologie der Spinnenaugen I. Z. vergl. Physiol. 7. 1928.

Hopffmann, W.: Bau und Leistung des Spinnapparates einiger Netzspinnen. Jena. Z. f. Naturwiss. 70. 1936.

Nielsen, E.: The Biology of Spiders. I—II. København 1932.

Peters, H.: Die Fanghandlung der Kreuzspinne. Z. vergl. Physiol. 15. 1931.

Dansk Oversigt.

1. Formaalet med disse undersøgelser har været at faa et indblik i fanghandlingen hos *Linyphia* og eksperimentelt eftervise, hvilke sansepaavirkninger der udløser de forskellige enkeltreaktioner af denne handling.
2. Betydningen af vibrationer i nettet er undersøgt ved hjælp af en vibrator (fig. 1). Edderkoppens reaktion paa forskellige kemiske paavirkninger undersøgtes ved at anbringe hyldemarvskugler vædet med de paagældende stoffer paa nettet.
3. Nettet (fig. 2) bestaar af tæppet, spærrevævet og modtrækstraadene.
4. Fanghandlingen bestaar af følgende fem faser: 1) "dreje mod byttet"-reaktionen. 2) "løbe til byttet"-reaktionen. 3) "stoppe byttet"-reaktionen. 4) biddet. 5) udsugningen.
5. "dreje"-reaktionen udløses ved byttets anslag mod nettet. Ved løbet til byttet orienteres edderkoppen af nettets vibrationer. Under "stoppe"-reaktionen modtager edderkoppen kemiske pirringer ved hjælp af tarsalorganet, hvorved den bliver i stand til at adskille spiselige og uspiselige byttedyr. Biddet finder kun sted, hvis byttet bevæger sig, i modsat fald kasseres det. Ved biddet foregaar endnu en adskillelse af spiselige og uspiselige dyr. Indtil udsugningen paabegyndes, reagerer edderkoppen paa sædvanlig maade overfor et nyt bytte; efter ud-

sugningens paabegyndelse reagerer den overhovedet ikke paa anslag af nyt bytte. Det vises, at ernæringsinstinktet er stærkere end kønsinstinktet.

6. *Linyphia* lever i et net, der er en virkningsfuld leder af vibrationer. Det er saaledes i fuld overensstemmelse med dette forhold, at de fleste af fanghandlingens enkeltreaktioner igangsættes og orienteres af de paavirkninger, edderkoppens sanseorganer for føleindtryk modtager.