On the Biology of Eresus niger Pet. (Aran.).

By
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1. Introduction.

The present paper contains the results of investigations which I entered upon in 1930, after having read about *Eresus niger* in Emil Nielsen: De danske Edderkoppers Biologi. Some of my observations I already published in 1936; but since then I have succeeded in finding *E. niger* several times, and my knowledge of the life habits of this spider has so increased that I think I am able to give a rather complete description of its biology now.

Previous investigations on the biology of this spider have been few on account of its rareness; but on the other hand it must be said that the few biological observations on *Eresus* recorded in the arachnological literature are very interesting and highly urged me to continue my efforts to get an insight in the life history of this spider.

The material for my observations I have found in North-Jutland, partly at Legind Bjerge on the island of Mors, and partly at several places in Himmerland. Besides investigating the spider in the field on many excursions I have observed it in my private laboratory at Løgstør, where I have kept the animal in glass-boxes under natural conditions; here the experiments that will be mentioned in the following, have been made too.

During my work several persons have helped me in a valuable way, and I want to render my best thanks to them all, and especially to the following gentlemen:

Mr. V. Halse, Nykøbing Mors, who kindly guided me in the Legind Bjerge.

Mr. Johs. Petersen, Løgstør, who has accompanied me on many excursions in Himmerland, and who has given me a valuable linguistic help when I was preparing this paper.

Mr. S. L. Tuxen, M. Sc., København, who allowed me to investigate the spider collection of Zoologisk Museum, København.

Mr. Aa. Vittrup, Løgstør, who has lent me a camera and in many other ways helped me by the photographic work.

2. The Habitat.

Eresus niger has its northern limit of distribution in Denmark, and in this country it has only been found in Jutland. The localities are always vast heathery tracts, of which especially the south-facing slopes of the hills are preferred (fig. 1); but also on the plains the webs of *Eresus* can be found if only the vegetation suits the spider.

The webs are built, where the heather does not make an unbroken layer, but is standing in tufts, among which there are open patches with a low vegetation consisting of mosses and lichens and some other plants, f. inst. *Nardus strictus, Genista anglica, Vaccinium vitis-idaea,* and *Hieracium pilosella.* A view of the habitat is given in fig. 2, where the characteristic difference between

Fig. 1. Brusaa. Heathery hills. Locality for *Eresus.*

the dark, high vegetation of the heather and the light, low vegetation of the patches can easily be seen.

In addition to this description of the vegetation I

Fig. 2. Urhøje. Tufts of heather, and patches with lower vegetation. Habitat for *Eresus*.

can give a few facts about the micro-climatic conditions of the habitat. They are illustrated in tab. I, the records

Table I.

Climatic conditions in the habitat of *Eresus*, recorded at Legind Bjerge on 11. 5. 40 at 15^{30}.

	2 m above ground	in the vegetation	in different webs
temperature	10^0 C.	18^0 C.	24^0—31^0 C.
wind	stiff breeze	almost quiet	perfectly quiet

of which have been made at Legind on the 11. 5. 40. A rather cold north-west wind was blowing; but the sun was shining from a cloudless sky, and the fact that the mature males were running about by the dozen in search of the webs of the females, showed that weather conditions on that particular day were near optimum for the mating period of *Eresus*.

Sometimes only a single web is found in one patch; but in most localities more webs are found near each other forming a little group or colony in the same open

Table II.

Survey of the investigated localities.

Locality	The way of placing the webs	Number of excursions
Legind	colony	5
Vindblæs	singly	6
Aarupgaard	colony	10
Oudrup	singly	2
Urhøje	colony	4
Brusaa	colony	11

patch. A survey of the localities I have investigated is seen in tab. II. From this it will be learnt that I have been able to find colonies at most of them, so I consider

this method of placing the webs to be the most natural, and when only a single web is found, I think it must have been built by a spider emigrated from a colony in the neighbourhood.

The situation of the webs in proportion to the vegetation is shown in fig. 3. It will be seen that the webs are placed at the northern edge of the patch, a feature

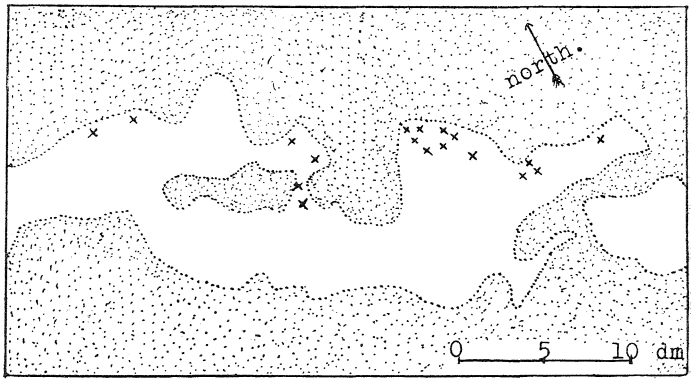

Fig. 3. Map of *Eresus*-colony at Brusaa.

which I have observed in all the colonies I have investigated. The significance of this situation of the webs is that they will be sun-lit during the greater part of the day, thus getting a temperature that is some degrees above the mean temperature of the locality (tab. I). Further it must be considered that the webs when placed close upon the surrounding vegetation are not particularly exposed to the wind, a fact which seems to be very important for this spider; for *Eresus* is very sensi-

tive to air-currents, which will appear from the following experiment:

By means of a little balloon provided with a pointed glass-pipe an air-current was directed towards the spider experimented on. The spider reacted at once, trying to escape the air-current. If it was unable to escape it lay down with its legs bent to its body, only leaving this shock-attitude when the air-current had ceased.

Consequently there seems to be a fine harmony between the organism of *Eresus* and the physical factors of its habitat. Further it must be mentioned that the placing of the webs in the open patches is of great ecological value to the spider, otherwise too, as most of the insects that serve *Eresus* as a prey live in these patches and not in the high and dense vegetation of heather which surrounds them. This is particular true of the weevils and grasshoppers and bugs that feed on the plants of the low vegetation of the patches; but also many of the bigger beetles, the empty chitinous skeletons of which are found on webs of *Eresus,* are attracted by the sunny spaces of the heath.

3. **Web-Constructions.**

a. The Cribellum-thread.

The cribellum of *Eresus* is divided in two like that of *Amaurobius;* consequently the cribellum-thread of *Eresus* is also similar to that of *Amaurobius,* whose cribellum-thread is described by E. Nielsen (1932) as follows: "The capture-thread is a compound thread, composed of two straight, parallel strands and two others consisting of nothing but loops and nooses, to these four threads which originates from the spinnerets a bluish, viscid substance is attached; this is combed out of the cribellum and the single fibres are not to be distinguished in it."

The main difference between the cribellum-threads

of the two species is to be found in the number of strands, which makes four in *Amaurobius,* but six in *Eresus,* namely two straight ones and four crispy ones. Consequently the cribellum-thread of *Eresus* is very thick and strong and well adapted for the different uses that this spider makes of it, and which are to be described in the following.

b. The Silken Carpet.

The retreat is built of a thick, yellowish web which is very tough. It does not resemble the web which other spiders use when making retreats. For a long time I could not make out how it was made; but a chance observation gave the explanation.

A female *Eresus* was repairing a hole in the upper part of its retreat. Thus it was possible to make an exact investigation of its method of spinning: The spider was sitting head downwards, suspended from the web by means of the foremost three pairs of its legs. The tarsus and metatarsus of its left hind-leg were placed horizontally supported by the right hind-leg. The left hind-leg was moving fast up and down the cribellum touching the spinnerets in each movement. The thread which was combed out was pushed into a bundle on the point of the abdomen. When the bundle had reached a convenient size, *Eresus* stretched up its right hind-leg and pushed the thread to the edge of the hole which had to be repaired. Here it was smoothed a little by means of the right hind-leg, and the spider took up again the spinning position. Each new bunch of thread was connected with the preceding by a thread. During a quarter of an hour the spider combed out three bunches of cribellum-thread. Then it turned round and went up with its cephalothorax foremost and began to pull the threads and smooth them by means of its front-legs.

A microscopic investigation of the new web some

hours later showed how *Eresus* had transformed a thread designed for capturing the prey into a thick, durable carpet, which was well fit for lining the retreat-tube and making a roof over the entrance of this important part of the burrow. The crispy strands of the compound cribellum-thread were partly stretched to be straight and parallel like the two middlemost strands, and more layers of web were pasted together by the very viscous, bluish lime which the cribellum produces. A few days later the colour of the new web had grown yellow, and now it formed a compact carpet, the appearance of which did not betray that it had been made from cribellum-threads.

c. The Burrow.

It is rather difficult to form a notion of the construction of the burrow of *Eresus* when consulting literature only. Simon (1892) describes it as follows:

"Tous les autres *Eresides* sont terricoles; les femelles s'établissent, soit sous les mousses et les lichens, et creusent un trou oblique, qui peut avoir de 10 à 15 centimètres de profondeur, et le tapissent d'une toile très épaisse, jaunâtre et grossière, dont la partie supérieure est repliée et masque l'ouverture."

From this description we learn that the burrow has a subterranean part consisting of a vertical retreat-tube, which is covered by the aërial part of the burrow. This aërial part is more distinctly described by E. Nielsen (1932), who has discovered that there can be a great difference between the burrows of different individuals, and describes the two types he has found as follows:

"... one type was spread on the naked ground and consisted of a triangular, thick sheet of greyish, dense web ... Each web was fastened at one end; its shape was that of a nearly equilateral triangle and it was spread loosely over the ground; when I took hold of

the extreme end of it I could lift the whole flap so as to uncover the burrow; this was of an elongate shape, rather narrow, and situated near the spot where the web was fastened.

The other type of web was quite different from the first; it was found in the heather itself, where this was so high and dense that no sheet-web could be stretched on the ground. This type was shaped like an elongate

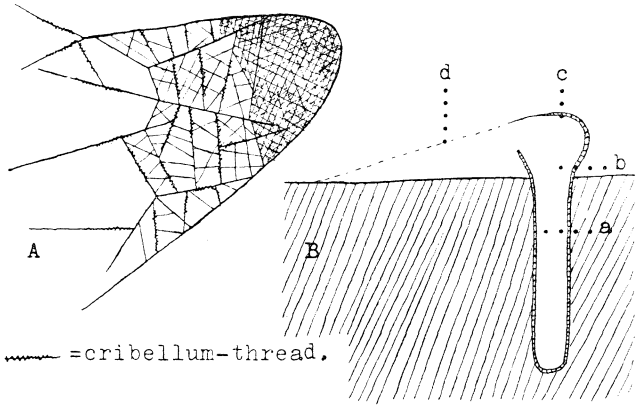

Fig. 4. A: Burrow with capture-web from above. B: Vertical section of burrow. a: The tube. b: The funnel. c: The roof. d: The capture-web.

cylinder, somewhat tapering at the ends, and with an oval opening on the upper surface and at one of the ends; at the other end the cylinder was continued in a broad sheet, the extent of which, however, was very small. At the bottom the cylinder was continuous with the lined burrow . . . ."

As appears from the above quotations there seems to be different types of burrows; but a thorough analysis of all the webs, found by me during a period of 10 years, has shown that they, though different in appearance, all are constructed in the same way. They

consist of a vertical retreat-tube in the ground with a funnel-like extension at the top, which rises above the ground and is fastened to the plants. A silken carpet makes the roof that covers the entrance to the tube. In addition to the roof a capture-web is horizontally stretched among the vegetation (fig. 4 B). All the burrows consist of these main parts; but before going into details as to the construction and the use of these parts some more facts about the different types must be given. Firstly the spider has to enlarge its burrow in course of time according to the growth of its body. The last of these alterations of the burrow is most radical and is only made by the female transforming its retreat into a breeding-nest, which will be described in chapt. 6. Secondly it must be stated that the shape of the upper part of the retreat varies very much, being flat and extended in open vegetation, but lofty and arched in thick vegetation.

d. The Retreat-tube.

The retreat-tube must be supposed to be the primary part of the burrow, as the following observations will show.

In the colonies one may find all developmental stages of *Eresus*, of which the youngest individuals have only a simple short tube without a real capture-web, while the elder ones have a completely developed burrow with a large capture-web.

A second proof of the theory that the tube is the primary in the construction of the burrow I find in some experiments I have made with captured *Eresus*. Several times I have put them into glass-boxes with a layer of sand on the bottom and branches to fix the capture-web on. After some hours' stay in the box they always began digging a hole into the layer of sand.

Not until later they stretched out threads to form a sort of sheet-web from the branches to the edge of the hole.

When excavating the tube the spider uses both its palpi and chelicerae to dig out the grains of sand with. The sand is dropped close by the entrance of the tube, where it forms a little, white hill, which is easily distinguished from the surface of dark sand for the first few days. Not all the grains of sand are thrown out, which was shown by an experiment I made in the summer 1935. I removed the grains of sand and mould from one side of a tube. Then I cut it in two and placed the upper part of it with the spider in a glass-box with a layer of sand. Now I was able to observe how the spider repaired its tube and made it somewhat deeper, and it became apparent that the spider pushed the grains of sand into the silken carpet that lined the tube instead of carrying them to the surface.

The tubes of the adult females are about 10 cm. in depth and 1 cm. in diameter. By the male and the inadult female it is smaller according to their smaller bodies. As already mentioned the tube has a funnel-like extension above ground, one edge of which is lengthened and bent so as to make a roof which covers the entrance of the tube. This cover is water-proof and prevents the rain from pouring down into the tube.

e. The Capture-web.

About the capture-web of *Eresus* H. Wiehle (1931) writes:

„Von einer Betrachtung des Fanggewebes von *Eresus* möchte ich noch absehen. Ich konnte zwar in Spanien für *Eresus* feststellen, dass aus der von der Spinne als Schlupfwinkel benutzten Erdhöhle eine Art Deckennetz nach aussen und nach den nächsten Pflanzen gespannt ist, unter dem sich das Tier mit der Ventralseite nach oben lauernd aufhält; mir sind aber diese Beobachtungen

noch nicht zahlreich genug, um schon über den Netzbau der Gattungen urteilen zu können."

I am able to confirm and to some extent enlarge this description. From the edge of the roof of the retreat thick, strong silk lines are stretched to the surrounding vegetation. These lines are crossed by thinner threads in many directions, and to these threads as well as to

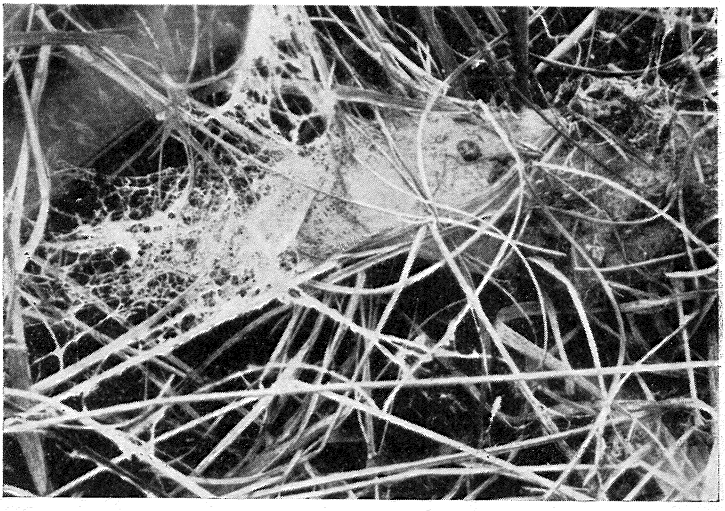

Fig. 5. Burrow of *Eresus* found in the colony at Urhøje.

the lines cribellum-threads are fixed (fig. 4 A). The web thus made is triangular in the burrows of young animals as stated by E. Nielsen (1932), but very irregular in the burrows of elder ones (fig. 5), and it also varies considerably in size.

A few times I have seen how *Eresus* fixed a cribellum-thread to a common thread. Two different ways of fixing it was observed. In both the spider began with pasting one end of the cribellum-thread to the common thread, and then it combed out a bunch of cribellum-

thread. In one case it now moved forward placing the cribellem-thread on the line to which it sticked. In the other case it stretched backwards its hind-legs placing the cribellum-thread upon the common thread in the opposite direction of which the spider was facing.

The capture-web is so tough and viscous that it is able to keep hold of even rather strong beetles as *Cicindela campestris* and *Geotrupes stercorosus*. That these big and vigorous beetles do not manage to get off the web is also due to the method in which *Eresus* catches them, a method which will be described in the following chapter.

4. **The Feeding Habits.**

a. The Prey.

Eresus has the peculiar custom to place the rests from its meals on the outer wall of its retreat, fixing them with threads so that they cannot fall off. Of what importance this may be for the spider itself I cannot tell; but for the investigations it was very important as the burrow of *Eresus* in this way provided me with the menu of the spider. This fact has also been observed by previous investigators, and Jensen-Haarup (1904) gives the following list of insects, the emptied chitinous skeletons of which he has found on the web of *Eresus:*

„Grasshoppers: *Gomphocerus* sp. (1). Bees: (1). Ants: (1). Beetles: *Calathus cisteloides* (1); *Onthophagus* sp. (1); *Diacanthus aeneus* (many); *Barynotus obscurus* (1); *Morychus aeneus* (several); *Cneorrhinus geminatus* (many); *Cleonus glaucus* (many); *Carabus arvensis?* (1, thorax only); *Carabus catenulatus* (2); *Geotrupes typhoeus* (2).“

Apart from the last named species I have found the same insects myself on the burrows. Besides *Geotrupes stercorosus* and *G. vernalis* were found on almost all the webs. And in spring the bright coloured elytra

of *Cicindela campestris* were often seen decorating the webs.

Beetles are thus the main prey of *Eresus*, but also other insects will be caught by the spider, f. inst. grasshoppers and bugs. Bigger species of beetles are most obvious; but smaller beetles are found in so great a number that they must be the common food of the spider.

b. The Lurking Attitude.

When waiting for a prey to enter upon its web *Eresus* is sitting head upwards in the funnel-like part of the tube. Its front-legs are stretched forwards grasping the threads of the roof. The significance of this position is clear, when considering that *Eresus* like most other sedentary spiders has no great faculty of vision. Its perception of the surrounding world is mainly due to its sense of touch. In the above mentioned position the spider is able to perceive the slightest vibrations of its web by means of its front-legs, as the funnel-like part of the tube is placed in the elastic vegetation so that any movement of the capture-web will be transmitted to it.

c. The Capturing.

How *Eresus* captures its prey will be learnt from the following few records from my journal:

1. Spider 39:45. Datum: 20. 9. 39. At 17^{05} a *Geotrupes* is placed upon the web. The spider arrives at once and catches one hind-leg of the beetle from below the web. The beetle soon grows quiet, and 17^{10} the spider drags it down into the tube.

2. Spider in the colony at Legind. Datum: 11. 5. 40. At 10^{25} a *Cicindela* is placed upon the web. It struggles to get off the web; but not until two minutes later the spider leaves the tube, catches the right front-leg of the beetle by its chelicerae and pulls the prey against the capture-web, so that it soon is all entangled in the

cribellum-threads. Three minutes later the beetle is quiet, and it is dragged down into the tube.

3. Spider 40:1. Datum: 13. 5. 40. At 8^{10} a *Cicindela* is placed upon the web. The spider arrives immediately to a hole in the web and tries to catch the prey with its front-legs; but the beetle manages to get away from the hole to the opposite side of the web. The spider climbs after it, hanging under the web. Now it is able to reach the beetle, catches one hind-leg of it and pulls it against the web. Three minutes later the beetle is quiet, and it is dragged down into the tube.

These records show the method, generally used by *Eresus* when capturing its prey. According to Peters (1931) I comprise the capturing behaviour into three main points:

1. leaving the tube for the prey.
2. catching the prey.
3. transport of the prey to the tube.

The first of these points includes the reactions of the spider from the moment that it receives the first vibrations through its web until it gets to the place where the prey is. Generally the spider rushes to the prey at once, so that the first part of the capturing behaviour only lasts a few seconds; but sometimes the spider climbs cautiously to the prey, hesitating now and then, and only moving nearer when the prey is struggling to get off the web. In these cases it may last 1—2 minutes, until the spider reaches the prey. As a rule the spider climbs under the web with its ventral side upwards as already described by H. Wiehle (1931).

The second point consists of many reactions, which are performed in the course of a very short time. When the spider has reached the prey, it stretches forward its front-legs and tries to get hold of one of the legs of the prey, preferably a hind-leg. Several times I have seen a spider touch the head, the thorax, and the elytra

of a beetle, till at last it took hold of one of its legs. Then it drags the prey farther down into the viscous cribellum-threads, so that it can hardly move any longer. At the same time it bites the leg, keeping it between its chelicerae until the movements of the prey are less violent. The comparatively short, thick legs and the stout chelicerae of *Eresus* must be very useful when forcing a vigorous beetle down into the entangling capture-web.

Some three minutes after the bite the prey stops struggling, and the spider now transports it to the tube, where it will be devoured. It is impossible to see how *Eresus* treats the prey after having dragged it down into the tube; but some hours later it will be found fixed to the outer wall of the retreat. Its head has been removed, and its interior has been sucked out. "Il y a lá un exemple de digestion externe qui mériterait d'être étudié plus en détail," Berland (1932) writes. Further particulars about this interesting point cannot be given yet.

This description of the capturing method gives an idea of the reactions of the spider; but it is much more difficult to make out to which stimuli from the prey the spider reacts in the mentioned way. Only one fact about the stimuli has been experimentally stated. As it is possible to allure the spider to the capture-web by means of a vibrating pincette, an experiment I have made several times, it is evident that the stimuli that make the spider leave the tube, are vibrations in the web caused by the struggling prey.

The method of capturing just described is used nearly always; but sometimes the spider meets more unusual cases, and then it shows that it is able to meet them in a rather effective manner, which will appear from the following two records:

4. Spider 40:2. Datum: 28. 5. 40. At 13^{02} a *Geotrupes* is placed on the web. The spider arrives immediately

and catches the prey in the usual manner. At 13^{05} a *Carabus* happens to get upon the web. The spider then drops the *Geotrupes* to the ground and catches the other beetle, which is transported to the tube at 13^{09}. Two hours later (15^{10}) the spider leaves its tube, climbs to the ground and fetches the dead *Geotrupes,* which now is transported to the tube.

5. Spider in the colony at Brusaa. Datum: 25. 8. 40. At 15^{16} a grasshopper is placed on the web. The spider climbs cautiously to the struggling prey. At 15^{19} it catches one hind-leg of the grass-hopper, which at the same moment makes a violent jerk and jumps away leaving its caught hind-leg upon the spider's web. The spider then climbs to the upper side of its web and walks searching all over it. Afterwards it goes down into the tube with the leg of the grasshopper.

How are these observations to be explained? The spider in case 4 could not possibly see the beetle from its tube, and the beetle was not fixed to the spider's web in any way. I think the only explanation must be that the spider really remembered the beetle. Phenomenons in spiders' behaviour due to memory have been observed earlier by other arachnologists, f. inst. E. Meyer (1928) and M. Bartels (1929). It is necessary, however, to emphasize that the term "memory" when used in the explanation of the behaviour in animals only means that the animal carries out an action which would be due to memory if carried out by a human being; but it is not sure that the psychical functions are identical.

As to case 5 the explanation may be as follows: The spider is not satisfied to get a leg only, as "catching a leg" usually means "getting a prey", and therefore it inspects the whole web, and only when it cannot find the prey, it climbs down into the tube with the leg of the grasshopper. It is not my intention to say that the spider is able to compare the result of its catching in

this case with the results generally attained when catching a prey. I only think that "catching a leg" and "getting a prey" are two integrative parts of the very situation that is able to satisfy the state of excitation the spider has attained by the first part of the capturing behaviour. When not satisfied the spider tries to find the prey on the web, but only finds the leg, which is then accepted as a prey and carried down into the tube.

Before concluding this chapter I shall make some remarks concerning the opinion of H. Wiehle (1939), when he writes as follows: „Nach meinen Beobachtungen fand ich also bis jetz vor allem bei cribellaten Spinnen Anklänge an das Radnetz und seine Fangmethode. Ich bin weit davon entfernt, die Cribellaten mit Simon als zusammengehörige Sektion aufzufassen, ich habe ferner auch beobachtet, dass bei *Eresus* die Cribellumfäden in ganz anderer Weise zum Fang benutzt werden, mir scheint es aber dennoch von Bedeutung zu sein, dass bei den genannten Cribellaten Einzelfäden zum Signalisieren der Beute und als Fangvorrichtung eine Rolle spielen."

I think, however, that the construction of the capture-web as well as the capture habits by *Eresus,* as I have observed them and described them above are very similar to those of the *Argiopidae,* and there is no reason for excepting *Eresus* when mentioning cribellate spiders with „... Anklänge an das Radnetz und seine Fangmethode."

5. **The Males.**

a. Appearance.

Until the last moult the males possess the same velvetlike fur of black hairs as the females and do not differ from these in the shape of their bodies either. After the penultimate moult, however, the males can be distinguished from the females by the shape of their palpi, the tarsus of which being thick and spindle-

shaped in the male while slender and cylindrical in the female (fig. 7).

After the last moult the male highly differs from the mature female (fig. 6). It is much smaller than the female, and it has the brigth colours which made Warburton (1909) write that it is „perhaps the most striking member of our spider fauna, the abdomen being scarlet, with four (or sometimes six) black spots edged with white hairs. The cephalothorax is black with red on the postero-lateral borders."

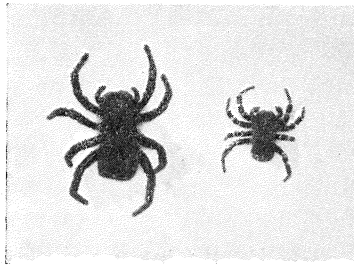

Fig. 6. Female and male. Natural size.

About the nature of this red colour Berland (1932) writes: "chez les *Micrommata* elle est due à un pigment carotinoïde, tandis que chez les *Eresus* elle tient à des phenomènes d'interference." And about the significance of the red colour Gerhardt (1928 b) writes: "Seltsam ist, dass *Eresus*-Weibchen zwar schwächere Geschlechtsgenossinnen, nicht aber die kleinen Männchen überfallen. Es liegt nahe, hier an einen Einfluss der bunten Färbung des Männchen zu denken

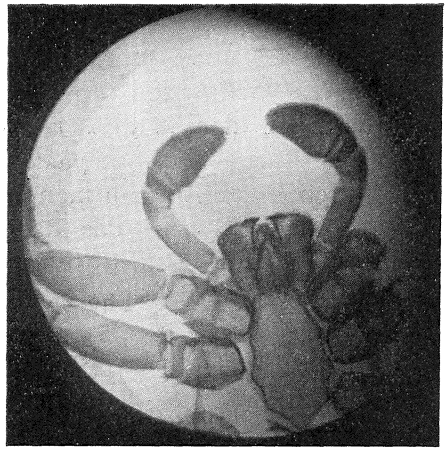

Fig. 7. The cast cuticle of male, showing the form of the palp in the penultimate stage.

und sie im Darwin'schen Sinne als "Warnfarbe" zu betrachten; doch wird man mit derartiger Annahme so lange vorsichtig sein müssen, als nicht ein giftiger oder wenigstens schlechtschmeckender Stoff nachgewiesen worden ist, der das Männchen für das Weibchen mit Wahrscheinlichkeit als ungeniessbar erscheinen lässt. Von allen südeuropäischen Spinnen mit extremem Geschlechtsdimorphismus, der die Männchen dem Weibchen gegenüber zwerghaft klein erscheinen lässt, ist *Eresus* die einzige, die ich kenne, bei der das Männchen durch das Weibchen nicht gefährdet ist."

Until sexual maturity occurs the life of the male spider is like that of the inadult female; but after the last moult its ability of spinning has diminished, as the cribellum is no longer able to produce any thread. Common threads from the spinnerets are still produced, and the male is seen to lower itself down from branches of the heather, and it has always a securing-thread stretched out wherever it walks. One single time I saw a mature male dig down into the ground; but it was the only rest of the instinct for building a retreat-tube I ever noticed. Still it must be stated that the mature male does not feed at all after the last moult.

b. Time of Sexual Maturity.

Jensen-Haarup (1904) found an adult male of *Eresus* at the web of a female in the spring of 1904. Other Danish records of adult males are also from spring-time. Therefore it was surprising to read that Berland (1932) writes, "le male d'*Eresus niger* apparait, en general, dans la seconde quinzaine de Septembre"; but far more surprised I was, when the first male *Eresus* I ever saw, moulted for the last time on 18. 8. 39. I tried to make it copulate with a mature female, but did not succeed, and the male died on 30. 8. 39. Another male died at its last moulting in the beginning of September the same

year; it had not been able to pull out its very thick palpi from the old skin.

Next time I saw mature males was on an excursion to Legind on 11. 5. 40, when more than a dozen adult males were running among the heathern shrubs of the hills. Now the question was if the mature males hibernated after their last moult, or if there were two mating periods, one in autumn and another in spring. Investigations in the autumn of 1940 have shown that the first of these alternatives seems to be the right one.

In 1940 I discovered a rather big *Eresus*-colony at Brusaa, Himmerland. In this colony I found a male in the penultimate stage on 16. 8. 40. This male reached sexual maturity by the last moult on 23. 8. 40. Two days later (25. 8. 40) I visited the colony again, and then I found the cast cuticles of males in the upper part of four burrows. I dug out one of these burrows, and the mature male was found in the tube. On 22. 9. 40 I made a new excursion to Brusaa, and then I found the cast cuticle of a male in one more burrow. I dug out this burrow, and in it the mature male was hiding. Besides this I observed that now the burrows of the females were shut for winter, the inhabitants having spun a sort of sheet-web obliquely across the entrance of the tube. It is then clear that no copulating can take place before the opening of the burrows, which is not likely to happen until next spring.

The conclusion must be that the males (as well as the females) reach sexual maturity in autumn and then hibernate in their burrows. At the beginning of May of the following year the males leave their tubes and start searching for the burrows of the females. It is most likely that this last hibernation only takes place at the northern limit of the distribution of *Eresus,* while in more southern countries this spider probably copulates in autumn immediately after the last moult.

c. Activity and Orientation.

The adult males of the sedentary spiders have to find the females in their webs or retreats. This task requires a considerably increased activity and a great ability of orientation by the male. Thorough investigations upon activity and orientation by *Eresus* do not exist as far as I know. Therefore I shall give an account of the results at which I have got as to the male spiders of *Eresus*. Of course it would be much easier to experiment with a more common species than with the few *Eresus*-specimens that could be obtained, and I hope to take up again these investigations when more material is obtainable.

A constant observation of the captured males showed that they were quiet during the greater part of the day and night, only walking about their glass-boxes, when the sun was shining into the laboratory during a few hours in the morning. To investigate if the effect of the sun-rays was due to an increased intensity of light or an increased intensity of heat, the following experiment was made:

The bottom of six flat, round glass-boxes was covered with a sheet of sooted paper. These small boxes were placed in three bigger ones, two in each. In each of these bigger boxes there was a thermometer, too. One male *Eresus* was put into each of the small boxes, and the three apparatuses were placed under varied conditions as to light and heat. The experiment lasted from 15^{24} to 15^{39}, and the results are shown in table III.

The foot-prints in the soot showed a much greater activity by the spider in direct sun-light than by those in diffuse daylight. This greater activity must be due to a greater intensity of light, as the temperatures in app. no. 1 and app. no. 3 were the same.

To investigate if the male *Eresus* is really heliotropic (in the sense: seeking light by preference) an experi-

Table III.
Experiment on activity in male *Eresus*.

apparatus no.	light	temperature	activity
1	direct sunlight	30° C.	high
2	diffuse daylight	20° C.	slight
3	diffuse daylight	30° C.	slight

ment was made with some individuals. They were singly placed in glass-boxes. In each box there was a sun-lit part and a shady part. The spiders were watched for a quarter of an hour, and they were seen to run about the whole box, but they seemed to prefer the sun-lit part of it. Remembering that the females of *Eresus* build their retreat-tubes in the sun-lit, open patches of the heath, it will easily be understood of what ecological importance it is that the mature males are heliotropic. It prevents them from a useless running about the shady, heather-covered places, where no females are to be found.

6. **Biology of Propagation.**

a. The Copulation.

As already mentioned *Eresus* (both male and female) reaches sexual maturity in autumn, but the copulation does not take place until the following spring.

The copulation of spiders has especially been investigated by Gerhardt, who in his paper from 1928 describes the copulation of *Eresus walckenaeri,* which lives in the Mediterranean countries. My observations on *E. niger* has shown that the copulation of this species completely agrees with that of *E. walckenaeri,* which was to be expected, too, as Gerhardt (1928 a) had succeded in copulating *E. niger* ♂ with *E. walckenaeri* ♀.

The course of the copulation is described in the following record from my journal:

13. 5. 40. At 11^{23}: A male runs about on the web of a female with peculiar stiff steps and trembling abdomen. The female runs to one edge of the web pulling the threads with small, convulsive jerks. The male climbs toward the female who looks as if she would catch him by her chelicerae. It does not happen, however. Instead of this she pushes the male under her by means of her front-legs and palps. The male now applies his left palp to the epigyne of the female, and the pair takes up a position as shown in fig. 8. At 11^{45}: The copulation continued until now with small interruptions, and as far as I could see the male used his left palp all the time.

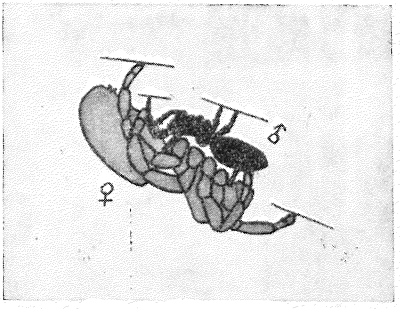

Fig. 8. Copulation.

As to the finer details of the insertion of the palp I must refer to Gerhardt (1928 a).

The male just mentioned kept on staying on or by the web of the same female, although more adult females resided in the same cage, and I observed copulation several times, even after the female had made its egg-cocoon. On 24. 5. 40 the male was found dead under the web where it had stayed.

b. The Egg-cocoon.

Simon (1892) describes the egg-cocoon of *Eresus* like this: "Le cocon n'est pas très gros, il est aplati et lenticulaire, formé d'une double enveloppe dout l'externe est épaisse, floconneuse et d'un blanc jaunâtre, tandis que l'interne, beaucoup plus serrée, est d'un blanc nacré.

Les oeufs sont petits et si fortement agglutinés qu'on ne peut les isoler sans les écrasser."

To this desription must be added that the loose outer layer of the cocoon is made of cribellum-threads, a fact which is already mentioned by Bertkau (1882), and which I am able to substantiate. I have also observed how the female during the whole period from the making of the cocoon till the hatching of the eggs covers the cocoon with new layers of cribellum-threads, whenever it is disturbed in its burrow.

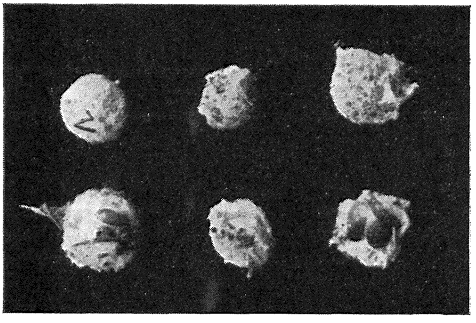

Fig. 9. A series of egg-cocoons.

Further it must be established that many foreign bodies are always spun into the loose layer of the cocoon so that it is more or less camouflaged. As a rule the camouflage consists of rests from the meals, f. inst. wings and antennae of bigger beetles and headless smaller beetles, but also vegetable substances and grains of sand are used. Fig. 9 shows a series of cocoons, from which the variation as to camouflage is very evident.

The diameter of the cocoons, which I have examined, varies from 8.5 mm. to 9.5 mm. The thickness varies considerably owing to the development of the eggs, from about 3 mm. in the newly made cocoon to more than 6 mm. just before the hatching of the eggs, the number of which being about 80.

Simon (1892) writes the following about the manner in which the *Eresidae* treats their egg-coocoons: "Les *Stegodyphus* déposent leurs cocons dans leur toile, les *Eresus* tiennent le leur entre leurs pattes, fortement appliqué sur le sternum."

It must be established, however, that *Eresus* like *Stegodyphus* generally fixes its egg-cocoon under the roof of its burrow in the morning and takes it down into the tube for the night. During the day the cocoon is then hanging in the upper part of the burrow, exposed to the sun-rays, while the female takes up its usual capture-attitude at the entrance of the tube. If the egg-cocoon is then touched, the spider at once rushes towards it, catches it by its palps and chelicerae, and carries it down into the tube.

c. The Breeding-nest.

As already mentioned the upper part of the burrow is transformed into a breeding-nest. This transformation is commenced at the time of copulation, but it is not completed until a few days before the hatching of the brood.

At first the capture-web is enlarged, and the part of it which covers the tube is thickened and made more arched. Gradually it grows yellow and gets the aspect that characterizes the "silken carpet". From the other edge of the tube another web is now stretched out, which at last in connection with the converted capture-web forms a completely closed breeding-nest (fig. 10).

Scarcely one week after the hatching of the brood the female begins to fill the interior of the breeding-nest with cribellum-threads. She is combing out threads from the cribellum almost continually during 2—3 days. Her abdomen is diminishing. The spinning-movements are growing more slow, the number of movements a minute sinking from 140 to 50. At last the female is

found dead in the breeding-nest, which is now quite filled with cribellum-threads, among which the spiderlings are creeping.

Tab. IV shows the different dates for the making of the breeding-nest and for the development of the brood

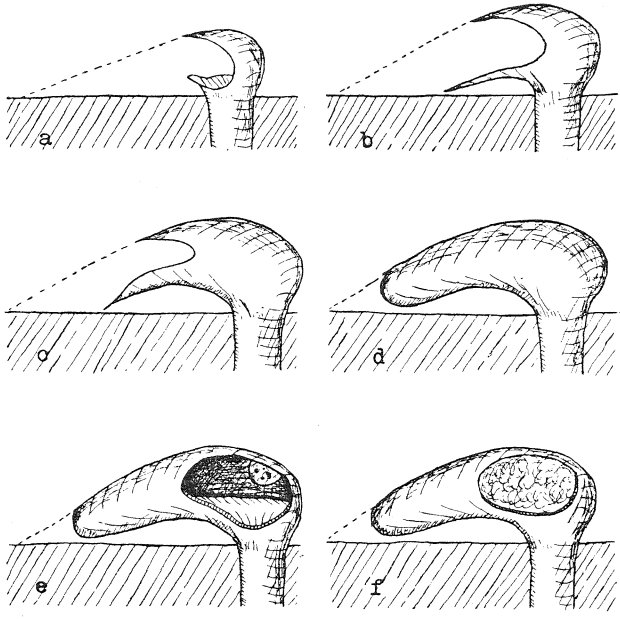

Fig. 10. a—d: Developmental stages of the breeding-nest. e: Breeding-nest opened to show the placing of the egg-cocoon. f: Breeding-nest filled with cribellum-threads.

by 3 females observed in captivity. In addition to these I have found more than 10 breeding-nests in the field, and they were all filled with cribellum-threads, in which the dead and shrunk female was lying. As to the use of the cribellum-threads nothing positive can be said.

As late as 13. 10. 40 at Brusaa and 15. 10. 40 at Vindblæs I found breeding-nests, in which the spiderlings were still living. They had separated the tube into small

Table IV.
Survey of the breeding-period of *Eresus niger*.

spider no.	breeding-nest commenced	egg-cocoon made	breeding-nest finished	young ones emerged	spinning of cribellum-threads commenced	female died
39. 38.	?	?	2. 7. 39	6. 7. 39	11. 7. 39	13. 7. 39
40. 2.	15. 5. 40	18. 5. 40	16. 6. 40	18. 6. 40	25. 6. 40	27. 6. 40
40. 19.	?	?	26. 6. 40	28. 6. 40	3. 7. 40	6. 7. 40

chambers by means of horizontally and vertically placed sheet-webs, so that only one or a few individuals lived in the same chamber. Probably they hibernate in this way and do not leave the breeding-nest until the following spring.

d. Life Cycle.

As I never succeeded in wintering *Eresus,* I cannot exactly tell how long this spider lives; but by comparing some material collected at Legind on 30. 6. 39 some idea of the age of the spider may be given. In tab. V there is a survey of the individuals found on this day. I have arranged them in four groups. Group 1

Table V.
Survey of *Eresus*-individuals found at Legind on 30. 6. 39.

Group no.	description	length of body	propagation and death
1	mature individuals	13—14 mm.	1939
2	individuals that reached sexual maturity in the autumn of 1939	8.6—11 mm.	1940
3	small individuals	5—7.4 mm.	1941?
4	eggs and brood	....	1942?

(females only) had egg-cocoons or brood. Group 2 reached sexual maturity in the autumn 1939 and would consequently have propagated in the spring 1940. As to the groups 3 and 4 the dates of propagation are more problematic; but they are stated as the earliest date at which propagation might take place. From this it appears that a mature *Eresus* at least attains an age of three years.

7. Summary.

1. The habitat is dry heath with a sparse vegetation of heather.
2. The burrows are placed in patches with low vegetation and often form small colonies. Thus the spider benefits from the favourable micro-climatic conditions of the patches.
3. The burrow is built of a carpet made of cribellum-threads. It consists of a vertical retreat-tube and a horizontal capture-web.
4. *Eresus* feed on beetles mainly, the capture-threads being so strong and viscous that even big beetles stick to them.
5. The capture-habits of *Eresus* are to some extent similar to those of an orbweaver. It was shown, too, how *Eresus* is able to vary its habits.
6. The males as well as the females reach sexual maturity in autumn, then hibernate in the closed retreat-tubes, and copulate in the following spring.
7. The activity of the males is highly stimulated by the sun-rays. The copulation is like that of *Eresus walckenaeri*.
8. The egg-cocoons are camouflaged by foreign bodies spun into the outer layer of cribellum-threads. It is fixed to the roof of the burrow like that of *Stegodyphus*.
9. The upper part of the retreat is transformed into a breeding-nest, which after the hatching of the brood is filled with cribellum-threads, the use of which has not yet been discovered. The young ones hibernate in the tube of the breeding-nest.
10. The age of mature *Eresus* must be estimated at 3 years at least.

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