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# THE DISTRIBUTION OF SPIDERS AND HARVESTMEN (CHELICERATA) IN THE DUTCH NATIONAL PARK "DE HOGE VELUWE"

by

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ABSTRACT

A preliminary study is made of the distribution of Araneida and Opilionida (Chelicerata) in a National Park in The Netherlands. Special attention is paid to the influence of vegetation structure on the distribution of the spiders.

In the late summer of 1944 and the autumn of 1946 a study was made of the distribution of spiders and harvestmen in the Dutch National Park "De Hoge Veluwe". The theme of this study was suggested to me by Dr. A. D. Voûte, at that time director of the Biological Laboratory, Hoenderloo. Some years before, Quispel (1941) had investigated the distribution of Ants in the same area. Westhoff & Westhoff-De Joncheere (1942; cf. also Westhoff, 1960), who continued Quispel's work with a study of distribution and nest-ecology of the ants in Dutch woods, characterized it as the first quantitative faunistic-sociological study in The Netherlands.

Synecology was flourishing in The Netherlands at that time. Meltzer & Westhoff (1942) published an introduction to plant sociology, Westhoff, Dijk & Passchier (1942) a survey of the Dutch plant associations. Mörzer Bruyns (1947) published a theoretical introduction to biocenology, together with a biocenological study of terrestrial Mollusca. Van der Drift (1950) analysed the animal community in a beach forest floor in the National Park "De Hoge Veluwe" (before that time, Noordam & Van der Vaart-De Vlieger, 1943, had already studied the fauna of oak litter in that area). The late Lucas Tinbergen studied the rôle of song birds in the natural control of insects in pine woods (cf. Tinbergen, 1955, 1960), an investigation that was not completed. In that

period I identified the Spiders and Harvestmen collected by Van der Drift (material from "De Hoge Veluwe") and Tinbergen (material from Hulshorst, at a distance of some 30 km North of "De Hoge Veluwe"). The results of these identifications supplemented the results obtained during my own field studies, and are partly included in the present paper. In the development of my study, I owe much to the discussions I had, at that time, both with the late Lucas Tinbergen and with Joseph van der Drift.

A report of my investigations was completed at the end of 1947. Although it presented interesting aspects (the introduction of vegetation structure into the study of animal distribution was rather new), it was never published. In the course of 1948 I started my studies in the field of acarology. Even though I was regularly reminded of my earlier work, particularly when visiting the National Park, a serious idea of publication did not arise until I had returned to arachnology in connection with my comparative study of Chelicerata[1]. In comparison with mites (particularly Actinotrichida), many other groups of Chelicerata (mostly inhabitants of the soil) present little morphological diversity. Important exceptions are constituted by harvestmen and, particularly, spiders; in the last-mentioned group, the evolution of web construction enabled the colonization of completely new niches. My early study of the distribution of spiders and harvestmen, and the various methods of sampling, excellently illustrated this great diversity in evolution. In studying the distribution of ants, Quispel (1941) could confine himself to the application of a single standard method. In my study of spiders and harvestmen, several different sampling methods appeared to be necessary.

My study was little more than a first orientation. Many aspects of the problem (quantitative aspects, seasonal aspects, horizontal and vertical migration, day and night activity, etc.) could not be included in my program. The investigation, as it was finished, yet kept a particular personal value, and this personal aspect has probably also contributed to the ultimate publication[2].

The National Park "De Hoge Veluwe" is situated between Otterlo, Hoenderloo and Schaarsbergen, and extends over some 21 square miles. The soil is sandy, and in the greater part of the park the upper layer is composed of young drift-sands (partly constituting inland dunes); locally, cover sands and

[1]Mention must, however, be made here of the revisions of the Dutch harvestmen and wolf spiders that Spoek (1963) and Wiebes (1959) prepared under my guidance, and in which my material is included. Several of their ecological conclusions (particularly those published by Spoek) are also based on data collected by me at that time.

[2]The present paper is no more than a summary of the original report on my researches. All field analyses and tables are omitted. It is published in this shape in order to stimulate new investigations of the relation between vegetation structure and the distribution of Arachnids.

late-glacial drift-sand ridges occur. About half of the area consists of heathlands, grasslands and the typical pioneer vegetations of young drift-sands (Spergulo-Corynephoretum, associations of lichens); at the time of my investigations there were still many unstable inland dunes with little or no vegetation. The other half of the area is partly afforested with coniferous trees and deciduous trees (oaks, beeches, etc.), partly covered with a spontaneous vegetation of Scotch pine. The organization of the arachnid fauna of the area varies from relatively simple communities (as in the case of the inland dunes) to the very complex communities of woods (where the occurrence of spiders and harvestmen extends from the soil to the top of the trees).

The present paper is composed of two chapters. In chapter I the arachnid communities in various types of environment are analysed. In chapter II factors determining the arachnid distribution pattern are discussed. The nomenclature used here for the plant associations is that given by Westhoff & Den Held (1969); in the case of heathlands, however, I followed the nomenclature recently introduced by De Smidt (1981). The botanical nomenclature is that of Heukels & Van Ooststroom (1968) for most of the higher plants, that of Landwehr (1976) for the grasses, and that of Landwehr (1966) for the mosses.

## I. The arachnid communities of "De Hoge Veluwe"

In this chapter the arachnid communities of three types of environment will be analysed: (1) inland dunes and drift-sands vegetations; (2) heathlands; and (3) woods.

### 1. Inland dunes and drift-sand vegetations

A provisional study of the arachnid fauna of inland dunes and drift-sand vegetations was made in the period 9–11 August 1944 in two drift-sand areas in the North of the National Park, viz., the "Otterlosche Zand" and "Siberië. The inland dunes were, at that time, partly without any vegetation, partly with a vegetation of mainly *Ammophila arenaria* (L.) Link. Important parts of the drift-sand area presented a vegetation belonging to the Spergulo-Corynephoretum (with a subassociation characterized by *Agrostis canina* L. subspec. *montana* (Hartm.) Hartm. and *Festuca ovina* L.); this association can be very rich in lichens (a pervasion of lichen associations, particularly the Cladonietum destrictae). Arachnid sampling was qualitative as well as quantitative; in the last-mentioned case, spiders were collected in enclosed transects of 10 × 0.5 $m^2$. In the inland dunes, the density of the arachnid population in the

transects varied from 1 specimen (in the case of a coverage of 0%) to 8 specimens (in the case of a coverage of 35%). In the Spergulo-Corynephoretum, the density of the arachnid population in the transects varied from 12 specimens (in the case of a coverage of 50%) to 13 specimens (in the case of a coverage of 90%). Characteristic species of the inland dunes are *Philodromus fallax* Sundevall, *Arctosa perita* (Latreille) and *Euophrys petrensis* C. L. Koch; the harvestman *Phalangium opilio* Linnaeus was also collected in the inland dunes. The arachnid fauna is richer in species in the Spergulo-Corynephoretum. Besides the harvestman *Phalangium opilio* Linnaeus (also found in the top of solitary pines in this area), the following species of spiders were found in this vegetation type: *Arctosa perita* (Latreille) (less numerous than in the inland dunes, and only in the case of scanty coverage), *Steatoda albomaculata* (De Geer) (the species makes its web close to the ground, in holes among lichens, for instance), *Agelena labyrinthica* (Clerk), *Cheiracanthium* cf. *virescens* (Sundevall)[1] (the silk cells in which they harbour themselves during the day are generally found in tussocks of *Corynephorus canescens* (L.) P.B.), a *Xerolycosa* species (very young specimens were found among the moss *Polytrichum piliferum* Hedw.), *Zelotes petrensis* (C. L. Koch) (under lichens), *Aelurillus v-insignitus* (Clerk), *Hyposinga albovittata* (Westring) (web in the herb-layer), *Alopecosa fabrilis* (Clerk), *Tibellus* cf. *oblongus* (Walckenaer)[1] (in the subassociation with *Agrostis canina* subspec. *montana*). Mention must be made here also of the capture, in the inland dunes, of a single lost adult male of *Araneus diadematus* Clerck.

## 2. Heathlands

The investigation of the arachnid fauna of heathlands was carried out in two periods. In 1944 an important part of the National Park was closed to the public, and I confined myself to a small, dry heath enclosed by woods, situated on a late-glacial drift-sand ridge (investigated on 11–12 August 1944). In 1946, in the period 20 September – 2 October, dry as well as humid heathlands in various parts of the National Park (and in the adjacent estate "Planken Wambuis") were investigated; I included in my research the fine Ericetum tetralicis (properly speaking no heathland, but a moor) near the "IJzeren Man". Apart from the Ericetum tetralicis, the heathlands of the National Park belong to various subassociations of the Genisto anglicae-Callunetum (all with a humid variant characterized by the occurrence of *Erica tetralix* L. and *Molinia caerulea*) (L.) Moench. The investigation was partly qualitative, part-

[1]The immature specimens could not be identified with certainty.

ly quantitative. In the last-mentioned case two different types of transects were used: transects of 10 × 0.5 $m^2$ for the total arachnid fauna, transects of 10 × 1.75 $m^2$ for the larger web spiders. In the last-mentioned case, those large web spiders were captured which occurred in a transect of which the breadth corresponded with the distance from the tip of the left to the tip of the right middle finger, with outstretched arms (1.75 m); the length of the transect (10 m) was measured with a rope (fastened to my belt) which was drawn in a chosen direction. The transect of 10 × 0.5 $m^2$ was too large for very small spiders (these could be collected in a plot of 1 $m^2$). In a transect of 10 × 1.75 $m^2$ the number of larger web spiders varied from 5 to 31. In one case the total number of spiders and harvestmen (with exception of the very small spiders) in a transect of 10 × 0.5 $m^2$ appeared to be 7. The following two spiders belong to the characteristic fauna of heathlands: *Thanatus formicinus* (Clerk) and *Philodromus histrio* (Latreille)[1]; the last-mentioned species was found also in the Ericetum tetralicis. The harvestmen *Phalangium opilio* Linnaeus and *Leiobunum blackwalli* Meade were both found in the heath; the first-mentioned species occurs also in the inland dunes and in the Spergulo-Corynephoretum, the last-mentioned species is found, elsewhere in The Netherlands, also in coastal dunes, grasslands and woods. The following species of Spiders were also found by me in the heath: *Theridion simile* C. L. Koch (elsewhere also on bushes and low plants), *Dictyna arundinacea* (Linnaeus) (web in the head of various plants and also on small shrubs), *Cheiracanthium erraticum* (Walchenaer) (also in grasslands), *Evarcha falcata* (Clerck) (also on low Scotch pines), *Pisaura mirabilis* (Clerck) (also in long grass and open woods). Characteristic differences between dry and humid variants of the Genisto anglicae-Callunetum were not yet found.

The following (larger) web spiders were found in the heath: *Uloborus walckenaerius* Latreille, *Araneus quadratus* Clerck, *Araneus redii* (Scopoli), *Araneus adiantus* (Walckenaer), *Cercidia prominens* (Westring) and *Mangora acalypha* (Walckenaer). The first-mentioned species is found in The Netherlands exclusively in the heath; the other species have a certain preference for heathlands. The small web spider *Microlinyphia pusilla* (Sundevall), mentioned in literature for low vegetations, is a common species of the heath. Heathlands close to the fringe of a wood are colonized in late summer by several web spiders from the wood (*Araneus diadematus* Clerck, *Neriene clathrata* (Sundevall), *Linyphia triangularis* (Clerck), *Meta segmentata* (Clerck), *Araneus cucurbitinus* Clerck). No significant differences were found between the

[1]In the National Park *Eresus niger* (Petagna), although very rare, is also found in heathlands. The species is not included in the present section because it was not found in my transects and plots. Until now, only a few stray males have been captured in this area.

web spider fauna of the dry and the humid variants of the Genisto anglicae-Callunetum. The structure of the heath, on the contrary, appeared to be an important factor in the distribution of the larger web spiders. The fauna of heathlands with uniform growth (sociability 5) appeared to be distinctly different from the fauna of bushy heathlands (sociability 3), i.e. heathlands with differences in the height of the heather and an alternation of dense bushes and open spaces. In bushy heathlands, up to 13 specimens of *Araneus quadratus* Clerck were found in transects of 10 × 1.75 $m^2$; in heathlands with uniform structure up to 1 specimen of this species. *Araneus adiantus* (Walckenaer), on the contrary, was slightly more numerous in rather high heather with uniform growth (up to 3 specimens in a transect); in bushy heathlands up to 1 specimen of this species was found.

The influence of vegetation structure on the fauna of the heath was also investigated by comparison with a different vegetation of similar structure, viz., a grassland (*Agrostis canina* L.) with seedlings (height about 1 m) of mainly oak and Scotch pine. *Araneus redii* (Scopoli) appeared to be very numerous in a transect with many young pines (it made a web on the pines; 23 specimens were found in a transect with 20 young pines and 3 young oaks, 6 specimens in a transect with 13 young oaks and 3 young pines). *Araneus quadratus* Clerck, which makes a web between the seedlings, was nearly equally numerous in both transects (7, respectively 9 specimens).

## 3. Woods

Woods constitute very complex communities where the occurrence of spiders and harvestmen extends from the soil to the top of the trees. Few forest-dwelling animal groups present a diversity, a variety of adaptation, comparable with that of spiders. This diversity must be taken into account in an analysis of the arachnid population of a wood, and various methods are indeed required for the study of the different ecological types. In my preliminary study I distinguished five ecological groups: (a) the fauna of the trunks of trees; (b) the fauna of leafy branches of trees and shrubs; (c) the web spiders occurring between the elements of a wood; (d) the soil fauna; (e) the fauna of the herb-layer. These five groups are dealt with below in the same order.

### (a) The fauna of the trunks of trees

The fauna of trunks was studied, in the period 13–15 August 1944, in the following way. Spiders and harvestmen were captured, from the foot of the trunk up to a height of 2 m, during 15 minutes (generally, in the last 5 minutes

little or nothing was captured). Notes were made on the species of tree and on the breadth of the trunk (the average section). The most characteristic element of the fauna of the trunks is constituted by the spider *Drapetisca socialis* (Sundevall). On beeches with a section of 50 cm the number varied from 5 to 19 (average 10–11); on oaks with a section of 30 cm the number varied from 1 to 2; on spruce fir with a section of 30 cm this number was 15; and on Scotch pine with a section of 30 cm the number varied from 1 to 2. The preference for beech and spruce fir is generally attributed to the smooth surface of the bark. Two species of harvestmen were found on trunks: *Mitopus morio* (Fabricius) (on beech and spruce fir) and *Oligolophus tridens* (C. L. Koch) (on oak). Harvestmen are facultative and temporary inhabitants of the trunk; their range extends from the soil up to the top of the trees. Little attention was paid, during my research, to the species occurring in crevices of the bark, and under loose bark. Species from other parts of the wood can be found accidentally on the trunk.

### (b) The fauna of leafy branches

At the beginning of my investigation material from leafy branches was collected by beating branches during standard spaces of time (thirty or fifteen minutes). This took place in the period 13–15 August 1944, whilst additional material was collected on 5 October 1946. In 1946 I collected also entire leafy branches in bags, which were afterwards searched for Arachnids (cf. Tinbergen, 1960: 270–273). The entire arachnid material, collected according to the last-mentioned method by the late Lucas Tinbergen at Hulshorst, was also identified by me; it is included in the following discussion (it yielded, among others, valuable results with reference to vertical distribution).

The material dealt with in the present subsection pertains to Arachnids occurring on deciduous leafs and Conifer needles, to Arachnids occurring on (or beneath) the bark of branches, and to Arachnids constructing a web between the elements of leafy branches.

The following data with reference to vertical distribution are mentioned here. Adults of *Mitopus morio* (Fabricius); adults and immatures of *Philodromus aureolus* (Clerck)[1]; and immatures of *Paroligolophus agrestis* (Meade), *Oligolophus hanseni* (Kraepelin), *Xysticus audax* (Schrank), *Araneus diadematus* Clerck and *Tetragnatha obtusa* C. L. Koch were found in samples from Scotch pine taken at Hulshorst on 10 September 1946 at a height of 8–9 m.

[1]The immature specimens are all mentioned under *P. aureolus*; part of the material could belong to *P. cespitum* (Walckenaer), a closely related, but much rarer species.

Immatures of *Leiobunum rotundum* (Latreille), *Theridion* spec.[1] and *Araneus sturmi* (Hahn) were found in samples from Scotch pine taken at Hulshorst on 4 January 1947 at a height of 7–8 m. Adults of *Enoplognatha ovata* (Clerck), *Achaearanea lunata* (Clerck), *Linyphia triangularis* (Clerck) and *Tetragnatha obtusa* C. L. Koch; immatures and adults of *Xysticus lanio* C. L. Koch, *Theridion pallens* Blackwall and *Meta segmentata* (Clerck); and immatures of *Pistius truncatus* (Pallas), *Diaea dorsata* (Fabricius), *Clubiona* spec.[1] and *Anyphaena accentuata* (Walckenaer) were found in samples from oak taken at Hulshorst on 9 August 1946 at a height of 5–7 m. It may be repeated here that the harvestmen fauna of the tops of trees depends on the fauna of the soil.

According to my own samples, Arachnids are most numerous on oak, least numerous on beech; Scotch pine and spruce fir take intermediate positions between oak and beech. In the National Park, the greatest number of species was found on Conifers (solitary Scotch pines in the drift-sand area, where there is little predation by birds, are rich in species); at Hulshorst the greatest number of species was found on oak and beech.

The following species were found exclusively on Conifers: *Lathys humilis* (Blackwall), *Theridion tinctum* (Walckenaer), *Araneus sturmi* (Hahn) (Hulshorst); *Philodromus emarginatus* (Schrank), *Xysticus audax* (Schrank), *Dendryphantes rudis* (Sundevall) (Hulshorst and "De Hoge Veluwe"); *Clubiona trivialis* C. L. Koch and *Theridion pinastri* L. Koch ("De Hoge Veluwe").

The following species were found exclusively on deciduous trees: *Xysticus lanio* C. L. Koch, *Pistius truncatus* (Pallas), *Diaea dorsata* (Fabricius), *Enoplognatha ovata* (Clerck) (Hulshorst); *Anyphaena accentuata* (Walckenaer), *Theridion pallens* Blackwall (Hulshorst and "De Hoge Veluwe"), *Philodromus dispar* Walckenaer and *Ballus depressus* (Walckenaer) ("De Hoge Veluwe").

*Philodromus aureolus* (Clerck) appeared to be one of the most numerous inhabitants of trees; on the average one third of a sample consisted of this species. On Scotch pine the species was also found in winter.

Results obtained at Hulshorst indicate that the total number of arachnid specimens on Scotch pine decreases in the course of winter. Apart from predation and natural mortality, this decrease can also be the result of migration to more sheltered spots.

### (c) The web spiders occurring between the elements of a wood

The present subsection is devoted to the spiders (mainly the larger ones) which construct their web between the elements of a wood. I investigated transects of 10 × 1.75 $m^2$ according to the method described in section 2 of

[1]The immature specimens of these species could not be identified with certainty.

chapter I. Three types of wood are successively discussed: Scotch pine wood, Beech wood and Oak wood.

## Scotch pine wood

The web spider fauna of the Scotch pine wood changes in the course of its development from young plantation to old wood. In a transect of 10 × 1.75 $m^2$, in a field with seedlings of Scotch pine (height about 1 m) with a density of 20 specimens per transect, I found (on 18 September 1946) the following larger web spiders: 1 ♀, 1 juv. *Araneus diadematus* Clerck, 7 ♀ *Araneus quadratus* Clerck, 23 juv. *Araneus redii* (Scopoli), 1 ♀ *Meta segmentata* (Clerck), 2 juv. *Araneus cucurbitinus* Clerck and 1 juv. *Araneus* spec.[1].

In a spontaneous vegetation of Scotch pine in the drift-sand area, the web spider fauna of two solitary pine trees (with different structure) were investigated on 2 October 1946. In a pine-tree with "open" structure I found 4 ♀ *Araneus diadematus* Clerck, 3 juv. *Araneus* spec., 1 juv. *Tetragnatha* spec. In a pine-tree with "dense" structure I found 7 ad. *Araneus diadematus* Clerck, 7 juv. *Araneus displicatus* (Hentz), 3 juv. *Araneus* spec., 2 juv. *Tetragnatha* spec.[1] and 1 ad. *Linyphia triangularis* (Clerck).

The distribution of web spiders in woods of Scotch pine was subsequently investigated, in the period 2–8 October 1946, in four stages of the wood: (a) an open plantation (height of the trees about 1–2.5 m, planted at distances of 1 m); (b) a thirty-year-old pine wood (complete coverage, height of the trees about 7 m, planted at distances of about 1 m, many dead branches in the lower part of the trees); (c) an older pine wood (coverage 70–80%, height of the trees about 12 m, distances between the trunks about 3 m); (d) a hundred-year-old pine wood (distances between the trunks 6 m and more). *Araneus diadematus* Clerck was found in (a) with an average density of 4 ♀ per transect; in (b) *Araneus diadematus* Clerck was nearly completely absent; in (c) *Araneus diadematus* Clerck occurred with an density of 1–2 ♀ per transect; in (d) no *Araneus diadematus* Clerck was found. It is interesting that in another part of the last-mentioned pine wood, which had an interplantation of young spruce-firs, *Araneus diadematus* Clerck was present (webs between the young spruce firs and the trunks of the pines). Several other species of the larger web spiders are found in the pine woods of the National Park, among which *Linyphia triangularis* (Clerck), *Cyclosa conica* (Pallas) and *Zilla diodia* (Walckenaer); the last-mentioned two species are particularly numerous in dense woods with many dead branches.

[1]Several of the immature specimens could not be identified to species.

In woods of Scotch pine with an undergrowth of deciduous shrubs, the occurrence of *Araneus diadematus* Clerck depends on the structure of the undergrowth. In an undergrowth of scattered shrubs 3 ♀ *Araneus diadematus* Clerck were captured in one transect; in a dense undergrowth no *Araneus diadematus* Clerck was found (in this dense undergrowth webs of *Linyphia triangularis* (Clerck), *Meta segmentata* (Clerck) and immature *Meta* cf. *mengei* (Blackwall) were found).

## Beech wood

In a beech wood without undergrowth a qualitative study of the web spiders was made on 25 September 1946. Larger web spiders were found, on the one hand, between dead branches on the ground (by which the distribution is very irregular), on the other hand between the lowest branches of the trees and the dead branches on the ground. In the dead branches on the ground I found many specimens of *Meta segmentata* (Clerck), and smaller numbers of specimens of *Araneus diadematus* Clerck, *Araneus gibbosus* (Walckenaer)[1], *Tetragnatha* spec., *Theridion* spec.[2] Between the low branches of the trees and the dead branches on the ground many webs of *Araneus diadematus* Clerck were found, and small numbers of *Meta segmentata* (Clerck), *Araneus gibbosus* (Walckenaer), *Araneus cucurbitinus* Clerck and *Cyclosa conica* (Pallas).

## Oak wood

The web spider fauna of oak woods was investigated in the period 26 September – 7 October 1946. The types of oak wood studied by me varied from dense coppice to normal mature oak wood; all belonged to the Querco roboris-Betuletum.

The web spider fauna of dense coppice resembles that of young dense pine woods: *Araneus diadematus* Clerck is absent, whilst *Zilla diodia* and *Cyclosa conica* are present. As soon as the structure of coppice or young oak wood becomes more open, by cutting, *Araneus diadematus* Clerck makes its appearance (at first in small numbers), whilst *Zilla diodia* (Walckenaer) and *Cyclosa conica* (Pallas) gradually disappear. In a mature oak wood with trees up to 18 m and a coverage of about 80%, *Araneus diadematus* Clerck can be rather numerous (I found up to 7 ♀ in a transect of 10 × 1.75 $m^2$); numerousness depends on the density of the undergrowth. *Araneus gibbosus* (Walckenaer) was regularly found. *Cyclosa conica* (Pallas) and *Zilla diodia* (Walckenaer)

[1] *Araneus angulatus* Clerck is found in the National Park on trees at the fringe of woods and along forest-roads.

[2] Several of the immature specimens could not be identified to species.

were not present in mature oak woods; *Linyphia triangularis* (Clerck) and *Meta segmentata* (Clerck), on the contrary, can be numerous (in well-developed undergrowth I found up to 12 ♀ *Meta segmentata* (Clerck), and up to 6 ♀ *Linyphia triangularis* (Clerck) in a transect).

### (d) The soil fauna

Some preliminary researches pertaining to the soil fauna of woods in the National Park were carried out by me in 1944 as well as in 1946. Besides that, numerous Arachnids collected by Van der Drift in various woods in the National Park were also identified by me; this material was only partly mentioned by Van der Drift in his analysis of the animal community in a beech forest floor (Van der Drift, 1950). The data collected in this way, have enabled me to prepare the following survey of the common Arachnids of the soil in woods in the National Park. In the present subsection, the fauna of the surface and the fauna of the deeper layers are discussed separately.

#### The fauna of the surface

The commonest harvestmen of the upper layer of the soil in deciduous woods were *Rilaena triangularis* (Herbst) (mature in spring and early summer), *Oligolophus tridens* (C. L. Koch) (mature in late summer and autumn) and *Mitopus morio* (Fabricius) (mature in summer and autumn). In woods of Scotch pine *Paroligolophus agrestis* (Meade) (mature in autumn and winter) and *Oligolophus hanseni* (Kraepelin) (mature in winter) are more common. As mentioned above, several of these harvestmen are also found on the trunk and in the top of trees. The commonest spiders of the upper layer of the soil of woods were: *Pardosa lugubris* (Walckenaer) and *Haplodrassus silvestris* (Blackwall) (deciduous woods), and *Trochosa terricola* Thorell and *Agroeca brunnea* (Blackwall) (deciduous as well as coniferous woods).

#### The fauna of the deeper layers

The harvestman *Nemastoma lugubre* (Müller) is found in the deeper layers of deciduous woods, but actively moves on the surface in the period September–December. The jumping spider *Neon reticulatus* (Blackwall), found in oak woods, probably is an inhabitants of both the upper and lower layers of the soil. As to the common spiders of the deeper layers of the soil, mention must be made of the following species: *Hahnia helveola* Simon (greatest density in the H-layer; the species was found in woods of beech, oak and Scotch

pine), *Robertus lividus* (Blackwall) (deciduous woods), and various species of the family Linyphiidae and Erigonidae (these have the greatest density in the F-layer; several species move actively on the surface during certain periods of the year). Mention must be made of the following common Linyphiidae and Erigonidae: *Macrargus rufus* (Wider) (deciduous woods, woods of Scotch pine; the species moves actively on the surface in spring), *Microneta viaria* (Blackwall) (deciduous woods; after *Hahnia helveola* Simon the commonest spider in the deeper layers of the beech wood), *Lepthyphantes flavipes* (Blackwall), *Centromerus sylvaticus* (Blackwall), *Centromerus dilutus* (O. P.-Cambridge), *Walckenaera cucullata* (C. L. Koch), *Walckenaera obtusa* Blackwall (all five species were found in deciduous woods).

It may be remarked here that litter of solitary pines in the drift-sand area has a different fauna, characterized among others by the presence of *Centromerita bicolor* (Blackwall) and *Walckenaera monoceros* (Wider).

### (e) The fauna of the herb-layer

Several of the larger web spiders found in the herb-layer (*Meta segmentata* (Clerck), *Linyphia triangularis* (Clerck)) are dealt with in subsection (c) devoted to the web spiders occurring between the elements of a wood. The herb-layer is often very rich in spiders, particularly the smaller web spiders. In a wood of Scotch pine (height about 10 m, coverage of the trees 70%, with scattered shrubs of oak and birch, a herb layer of *Vaccinium myrtillus* L. and *Molinia caerulea* (L.) Moench, and a moss-layer of *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum scoparium* Hedw.) a plot of 1 $m^2$, in which the herb-layer mainly consisted of *Vaccinium*, was investigated on 16 August 1944. The following spiders were found on that occasion: 1 juv. *Episinus* spec., 1 ♀ *Floronia bucculenta* (Clerck), 1 ♀, 1 subad. *Linyphia triangularis* (Clerck), 8 juv. *Neriene clathrata* (Sundevall), 1 ♀ *Theridion bimaculatum* (Linnaeus), 5 juv. *Meta* spec., 1 juv. *Clubiona* spec., and 2 ♀, 1 juv. *Lepthyphantes* spec. div.[1] (a total of 22 spiders, among which 21 web spiders).

## II. On factors influencing arachnid distribution, with particular reference to vegetation structure

Spiders and harvestmen are predators (harvestmen feed also on dead bodies of small animals, and on vegetable food, such as rotten fruit) which do not depend on particular plants as source of food. Humidity and temperature are important factors in the distribution of harvestmen (cf. Martens, 1978: 39–

[1]Several of the immature specimens could not be identified to species.

41); sunlight is an important factor in the distribution of harvestmen and spiders. In chapter I of the present paper it is demonstrated that the structure of the environment is also an important factor in the distribution of spiders. Recently, Barkman (1979) published an introductory paper on the investigation of vegetation texture and structure, with particular reference to The Netherlands. Leaf size, leaf consistency, leaf orientation, life forms and growth forms are mentioned by him as structural characters of vegetation. The structure of the environment further includes: phenological characters (differences in structure connected with cyclic, e.g. seasonal, changes), structural characters of the soil (e.g. structure and thickness of litter, structure of the mineral soil), the structure of the bark of trees, and the distances between the various elements of a vegetation. In a thorough study of the rôle of structural characters in the distribution of spiders, these characters should be first analysed separately. I must confine myself here to some preliminary remarks. Growth forms of plants (e.g. bushy heather) and distances between elements (e.g. between the trunks of trees in a wood) are very important factors in the distribution of the larger web spiders[1]. Leaf size and leaf consistency could be important factors in the distribution of species living on trees and shrubs (e.g. those genera of Thomisidae of which some species are found on deciduous trees, other species on Coniferous trees; for an analysis, phenological characters could be more or less eliminated by studying also the fauna of larch, a deciduous coniferous tree). The structure of the soil could, for instance, be an important factor in the distribution of those spiders generally occurring on litter of deciduous trees (e.g. *Pardosa lugubris* (Walckenaer)), and in the distribution of species spinning a web amongst litter (*Hahnia*, Linyphiidae, Erigonidae; in the case of *Hahnia helveola* Simon, the spider is generally found in the H-layer, whilst the web is probably mainly between the elements of the F-layer[2]). In the case of the soil, the influence of structure could be (also) through microclimate. The structure of the bark of trees is apparently an important factor in the distribution of species living on the trunk. Evidently, vegetation structure is one of the most important factors influencing the distribution of spiders.

[1]Chacón & Eberhard (1980) investigated factors affecting the "efficiency" of artificial spider webs. It appeared that the functioning of these "webs" is influenced, among others, by the height above the ground (more insects lower down), the inclination of the "webs" (more insects in nearly vertical "webs"), and the density of the "webs" (more and smaller insects in denser "webs"). These factors are closely connected with the possibilities of vegetation structure.

[2]Stevenson & Dindal (1982) found that spider species richness was significantly greater in curled litter than in flat litter. In the case of *Enoplognatha ovata* (Clerck), they found more spiders when special leaf types were present, whilst a significant interaction occurred between leaf type and month (the increase in body size, during development, is associated with greater need for space).

## REFERENCES

BARKMAN, J. J., 1979. The investigation of vegetation texture and structure. — In: M. J. A. WERGER (ed.), The Study of Vegetation (The Hague, Boston, London): 123–160.

CHACÓN, P. & W. G. EBERHARD, 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. — Bull. Brit. Arachnol. Soc., 5: 29–38, figs. 1–9.

DRIFT, J. VAN DER, 1950. Analysis of the animal community in a beech forest floor. — Tijdschr. Ent., 94: 1–168, front., figs. 1–15, tab. 1–25, A–C.

HEUKELS, H. & S. J. VAN OOSTSTROOM, 1968. Beknopte school- en excursieflora voor Nederland (twelfth edition): 1–425. Groningen.

LANDWEHR, J., 1966. Atlas van de Nederlandse bladmossen. — Bibl. Kon. Ned. Natuurhist. Ver., 15: 1–504, 38 figs., 394 pls.

—, 1976. Atlas van de Nederlandse grassen en een aantal adventieven en gekweekte soorten. — Bibl. Kon. Ned. Natuurhist. Ver., 20: 1–362, textfigs., 207 pls.

MARTENS, J., 1978. Spinnentiere, Arachnida. Weberknechte, Opiliones. — Tierw. Deutschl., 64: 1–464, 815 figs. Jena.

MELTZER, J. & V. WESTHOFF, 1942. Inleiding tot de plantensociologie. — Bibl. Ned. Natuurhist. Ver., 6: 1–326, 37 phot., 6 figs. 's-Graveland.

MÖRZER BRUYNS, M. F., 1947. Over levensgemeenschappen: i–x, 1–195. Deventer.

NOORDAM, D. & S. H. VAN DER VAART-DE VLIEGER, 1943. Een onderzoek naar samenstelling en betekenis van de fauna van eikenstrooisel. — Ned. Boschb. Tijdschr., 16: 470–492.

QUISPEL, A., 1941. De verspreiding van de mierenfauna in het Nationale Park De Hoge Veluwe. — Ned. Boschb. Tijdschr., 14: 183–201, 258–286, figs. 1–11.

SMIDT, J. T. DE, 1981. De Nederlandse heidevegetaties. — Wetensch. Meded. Kon. Ned. Natuurhist. Ver., 144: 1–87.

SPOEK, G. L., 1963. The Opilionida (Arachnida) of The Netherlands. — Zool. Verh. Leiden, 63: 1–70, figs. 1–13.

STEVENSON, B. G. & D. L. DINDAL, 1982. Effect of leaf shape on forest litter spiders: Community organization and microhabitat selection of immature Enoplognatha ovata (Clerck) (Theridiidae). — Journ. Arachnol., 10: 165–178, figs. 1–5, tab. 1–4.

TINBERGEN, L., 1955. Onderzoek over de dynamiek van insecten bevolkingen in Veluwse bossen. — Akademiedagen Kon. Ned. Akad. Wetensch., 8: 140–149.

—, 1960. The dynamics of insect and bird populations in pine wood. — Arch. Néerl. Zool., 13: 259–473.

WESTHOFF, V., 1960. Bosmieren en mierenbossen. — Lev. Nat., 63: 121–128.

WESTHOFF, V., J. W. DIJK & H. PASSCHIER, 1942. Overzicht der plantengemeenschappen in Nederland. — Bibl. Ned. Natuurhist. Ver., 7: 1–79. 's-Graveland.

WESTHOFF, V. & A. J. DEN HELD, 1969. Plantengemeenschappen in Nederland. — Bibl. Kon. Ned. Natuurhist. Ver., 16: 1–324, 36 figs.

WESTHOFF, V. & J. N. WESTHOFF-DE JONCHEERE, 1942. Verspreiding en nestoecologie van de mieren in de Nederlandse bosschen. — Tijdschr. Plantenziekten, 48: 138–212.

WIEBES, J. T., 1959. The Lycosidae and Pisauridae (Araneae) of The Netherlands. — Zool. Verh. Leiden, 42: 1–78, figs. 1–112.