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CORRELATIONS BETWEEN DISTRIBUTIONS OF HUNTING SPIDERS (LYCOSIDAE, CTENIDAE) AND ENVIRONMENTAL CHARACTERISTICS IN A DUNE AREA

by

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SUMMARY

1. This study forms part of an extensive ecological programme caried out by staff members and students of the Department of Animal Ecology of the University of Leiden in the dune area "Meijendel", exploited as catchment area of the Dune Waterworks of The Hague.
2. This research is a follow-up of a previous study (VAN DER AART, 1973) on distribution analysis of hunting spiders by means of principal component analysis.
3. The aim of this study was to trace down the main environmental factor responsible for the distributions of the species studied.
4. The main environmental factor governing the distributions of the species in this study matched with the one found in the previous study based on material collected 10 years ago.
5. The "density of activity" curves for the different species in this study were the same as those found from the catches of these species made 10 years ago in a much wider area and with a slightly different sampling technique.
6. The numbers of the species of hunting spiders caught show a very strict, well-defined and reproducible relationship (Fig. 5) to a basic factor (principal component). This factor is called main environmental factor.
7. In order to get grip on the nature of the main environmental factor governing the distributions, twenty-six environmental characteristics were measured on twenty-eight sampling sites.
8. The environmental characteristics measured appeared to cluster in groups of mutually highly correlated environmental characteristics (Table VII).
9. No strict linear relation between the main environmental factor (principal component) and any environmental characteristic measured was found. The amount of light penetrating all vegetation layers approximates this ideal linear relation best.
10. The technique of principal component analysis was adapted to ecological distribution analysis in two respects: 1. The supposed additive effect of underlying factors was transformed into a more realistic proportionate effect. 2. The supposed linear relationship between an environmental factor and its effect on a biological phenomenon was substituted by an optimum curve.

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11. Canonical correlation analysis did show a very high correlation between the factor governing the distributions of the species and the factor underlying the environmental characteristics measured. Hence, both sets of variables may be thought to be dependent on one and the same basic factor.
12. The relation found between the distributions of the spiders studied and the environmental characteristics measured will be put to the test in a new independent experiment.

1. INTRODUCTION

In the dune area "Meijendel", situated between The Hague and Wassenaar in The Netherlands, at least sixteen species of hunting spiders (Lycosidae, Pisauridae, Ctenidae) occur. This dune area can be considered as a mosaic of rather different biotopes, ranging from open sandy places to sheltered poplar and birch woods in the old inner-dune valleys.

At superficial examination, at least some of the hunting spider species show differences in distribution within the study area. On the other hand it is clear that distributions must overlap considerably because up to three to seven species can be found together in any given biotope. Hunting spiders are non-specialized predators of arthropods. In this respect they resemble the Formicidae and Soricidae which are studied in the same dune area (DE BRUYN *et al.* 1972; DE BRUYN & MABELIS, 1972; DE BRUYN & KRUK-DE BRUIN, 1972; and CROIN MICHIELSEN, 1966).

In spring, the situation for predators of arthropods in general is obviously awkward, in particular for the hunting spiders. They have to consume large amounts of food for the maturation of their eggs (KESSLER, 1971), whereas at this time of the year the amount of potential prey is undoubtedly still low. Hence, at least in spring a competitive situation between hunting spider species seems rather plausible.

The coexistence of hunting spider species, which are very similar in their food requirements, life cycle and other ecological characteristics, is probably realized by differences in their niches (VAN DOBBEN, 1974; GAUSE, 1934; HARDIN, 1960; HUTCHINSON, 1957; MACARTHUR, 1967). Niche should be understood here in the sense originally given by GRINNEL (1917), *i.e.* occurrence in space and time (microhabitat), as well as in the sense of ELTON (1927), *i.e.* the relations with all the other organisms of the biotic community (function in the community). To start the analysis of the differences in niche of the hunting spider species, their distribution in space as well as their occurrence in time was studied. However, functional differences still have to be unravelled.

In a previous paper (VAN DER AART, 1973) the differences between

the hunting spider species with regard to their distributions in the field were analysed. This paper analyses the distributions in space 10 years later on sampling sites different from those used in the previous study and with a modified sampling technique. Hence, in this study the constancy of the distributions of the species were put to the test as compared with the distributions found in the earlier study (1953–1960). At present attempts are made in this paper to characterize the distribution of each species by stating the optimum value and the ecological amplitude for the main environmental gradient that is held responsible for the distribution. The optimum defines a, perhaps not realized, optimum habitat type for each species. The variance can be interpreted as a measure for the ecological amplitude of the species. In contrast to the current approach, the environmental gradient was not selected by the investigator independent of the hunting spiders but gathered from the hunting spider catches by principal component analysis. The main aim of this study is to elucidate the nature of this apparent gradient by establishing obvious relations between this gradient and environmental characteristics, which the investigator may distinguish and measure. These relations between the distributions of hunting spider species and environmental characteristics will constitute the basis for a predictive model concerning the distributions of hunting spiders in the dune area under study. How far such a model can be used for predictive purposes in areas not sampled for hunting spiders before will be put to the test in the near future.

The reason that we used multivariate analysis for this distribution analysis is based on three considerations. Firstly, one cannot be sure beforehand that only one main environmental factor affects the distributions of the species to be studied. Hence, in advance one has to reckon with a multivariate-determined phenomenon. For these phenomena multivariate methods are appropriate. Secondly, up to seven hunting spider species can be found together at any spot in our study area. Consequently the distributions do overlap a great deal and the spatial separation of the species is less clear as might be guessed from statements in literature about typical biotopes, or from firstglance inspections. Therefore a more precise quantifying description of the distributions is desirable. Thirdly, principal component analysis (PCA) and canonical correlation analysis (CCA) are appropriate tools for describing relations between variables or sets of variables, which description forms a substantial part of this distribution study.

2. MATERIAL, METHODS AND DEFINITIONS

To sample the spiders pitfall trapping with preservation fluid (formalin

4%) was practised. One hundred pitfalls of white plastic were placed in 4 square, regular grids of 25 pitfalls each, in a physiognomically inhomogeneous dune valley called "Bierlap". The distance between adjacent pitfalls was 10 m. From 15 July 1969 till 4 September 1970 the accumulated catch of each of these 100 pitfalls was collected at intervals of approximately one week.

TABLE I

Hunting spiders and their total numbers caught in 100 pitfall traps over a period of 60 weeks.

	total number
Lycosidae	
Alopecosa accentuata (Latreille)	595
Alopecosa cuneata (Clerck)	823
Alopecosa fabrilis (Clerck)	322
Arctosa lutetiana (Simon)	79
Arctosa perita (Latreille)	104
Aulonia albimana (Walckenaer)	459
Pardosa lugubris (Walckenaer)	543
Pardosa monticola (Clerck)	2,082
Pardosa nigriceps (Thorell)	1,277
Pardosa pullata (Clerck)	1,943
Trochosa terricola Thorell	3,370
Ctenidae	
Zora spinimana (Sund.)	559

A survey of the hunting spider species caught is given in Table I. The numbers of animals caught per pitfall trap are listed in Table II. Around 28 of these pitfalls (1 m radius) the vegetation and the soil were characterized by measuring a number of characteristics. The 28 sites were selected in such a way that as many biotope types as possible were represented. The number of 28 was imposed by purely practical reasons. The environmental characteristics measured are enumerated in Table III; their values at the selected sampling sites are given in Table IV.

Water and humus content were estimated gravimetrically. Lime content was determined by titration with EDTA (ethylenediaminetetraacetic acid). The insolation and reflection were measured with an AEG Lux-meter. The degree of cover by the vegetation was expressed in a decimal scale (10 classes) according to Doing Kraft (1954).

While the lycosid sampling program covered slightly more than one year, the characterization of the selected sampling sites was made only once, at the end of August 1970. Consequently the characteristics to

be measured had to be confined to those which were thought to be stable in time or, when variable, were thought to vary in a congruent way at the different sampling sites. To indicate relationships, coefficients of correlation were used. As a consequence not the absolute values of the variables are important for the analysis but only the form of the variation.

In a certain phase of our research on hunting spiders we tried the methods of capture-recapture and of sampling complete units of habitats in order to gain absolute population measurements. Both methods proved to be very time-consumming and to provide only scanty and statistically insufficient data. Moreover these methods disturb and upset the sampling area seriously. These were the main reasons for choosing a relative method of population measurement, *e.g.* pitfall trapping. Pitfall catches are influenced by: (1) the population density of the species, (2) the locomotory activity of the animals, (3) the efficiency of the trap. The efficiency of the traps used depends among others on such factors as: the size of the traps and the responsiveness of the species to the trap stimulus. For each species the efficiency of the trap is assumed to be constant. If this is true the variation in pitfall catches for each species can be regarded as a mathematical function of density and locomotory activity in the field. Both parameters are important for the chances of encounter between members of the same species as well as the chance of encounters between predators and prey or parasites and hosts. For instance, when a species occurs in two habitat types differing in structure (*e.g.* bare sand and high grass), the distance covered in the horizontal plane (locomotory activity) might be quite different. Given the same absolute density in these two habitats, the chance of an encounter of an individual with any object or condition in the field might be quite different also. Generally spoken, a pitfall catch indicates the chance of encounter of a species with any object in the field. As said before, pitfall catches do not measure the density of a species, but nevertheless represent a biological meaningful property. This biologically important statistic may be called "density of activity". "Aktivitätsdichte" (Balogh, 1958), "aktiviteitsdichtheid" (den Boer, 1958).

In the practice of this study the catches will be almost proportional to density as the species are more or less restricted to certain habitat types. Moreover, some preliminary experiments with *Trochosa terricola* in which pitfall catches were compared with absolute population measurements did not indicate differences in locomotory activity in the various habitat types, as pitfall catches and densities were obviously linearly related within the habitat types studied. Hence, in our case the catches will be likely to reflect mainly densities rather than

TABLE II

The number of individuals for each species caught in 100 pitfall traps over a period of 60 weeks.

		Species												
Pitfall no.	Angle in degrees*	*Al. accentuata*	*Al. cuneata*	*Al. fabrilis*	*Ar. lutetiana*	*Ar. perita*	*Au. albimana*	*Pa. lugubris*	*Pa. monticola*	*Pa. nigriceps*	*Pa. pullata*	*Tr. terricola*	*Zo. spinimana*	Selected sampling site no.**
1	183	2	18	0	1	0	15	0	13	67	133	72	10	
2	118	25	10	0	0	0	4	0	60	12	45	57	4	1
3	153	7	47	0	0	0	21	0	26	29	52	82	3	
4	176	2	63	0	0	0	10	0	19	44	48	99	6	
5	124	8	14	2	2	0	5	0	71	8	45	58	1	
6	103	13	3	0	0	0	3	0	71	5	26	24	5	
7	151	8	41	0	0	0	18	0	36	21	51	83	4	
8	209	0	2	0	0	0	30	1	1	15	37	65	9	2
9	125	15	20	2	2	0	9	1	29	18	45	66	1	3
10	173	4	14	0	3	0	19	1	15	29	89	52	6	
11	195	2	6	0	1	0	24	1	7	29	94	86	25	4
12	108	17	17	0	1	0	5	0	90	11	18	30	3	
13	141	10	14	0	4	0	19	0	51	5	28	62	3	
14	181	3	11	0	5	0	13	0	30	14	52	85	9	
15	195	2	17	0	8	0	11	0	8	41	107	127	22	
16	200	1	20	0	2	0	9	1	2	135	76	91	17	5
17	157	7	42	0	0	0	12	0	29	35	34	64	8	
18	196	1	19	0	5	0	11	0	10	38	69	110	11	
19	219	0	6	0	6	0	6	0	11	27	24	63	34	6
20	135	24	8	0	14	0	5	0	23	27	35	79	4	
21	174	6	10	0	0	0	7	1	24	43	86	79	16	
22	186	2	35	0	0	0	10	0	16	99	129	117	27	
23	216	0	0	0	0	0	6	0	0	62	50	121	25	
24	195	2	7	0	12	0	16	1	30	89	105	118	16	7
25	194	3	7	0	6	0	11	1	17	38	96	137	19	
26	11	3	6	0	0	3	0	0	11	3	0	5	1	
27	211	1	30	0	1	0	12	10	11	15	7	57	6	
28	265	0	7	0	0	0	1	57	0	4	3	34	9	
29	260	0	11	0	0	0	7	55	2	2	1	30	3	8
30	268	0	2	0	0	0	1	56	0	2	2	38	7	
31	68	5	16	3	0	0	3	0	41	6	5	10	1	
32	54	11	5	0	0	0	0	0	69	1	0	5	0	
33	59	4	7	1	0	0	1	1	48	2	4	13	1	
34	70	8	10	0	0	0	0	0	58	0	1	14	0	
35	202	1	24	0	0	0	22	11	58	28	17	61	16	
36	112	8	21	0	0	0	5	1	158	6	12	32	1	
37	11	1	1	0	0	0	0	0	26	1	1	2	0	9
38	21	3	0	1	0	0	0	0	22	0	0	1	0	10
39	48	15	1	2	0	0	1	0	95	0	1	4	0	11
40	205	0	25	0	3	1	22	3	35	13	46	55	15	
41	74	16	13	0	0	0	0	0	96	1	8	13	0	12
42	50	12	1	0	0	0	0	0	36	0	2	7	0	
43	46	16	2	0	0	1	0	0	71	0	2	3	0	
44	116	12	28	1	0	0	9	0	189	7	21	28	10	
45	197	1	12	0	0	0	23	1	6	110	56	55	22	
46	234	0	4	0	0	0	4	2	4	3	8	25	14	
47	104	11	16	0	0	0	6	0	170	2	17	31	0	
48	***	1	15	0	0	0	0	1	19	1	7	6	0	
49	182	3	43	1	2	0	18	1	24	53	72	97	22	13
50	221	0	2	0	1	0	4	3	14	15	72	94	32	14
51	241	0	7	0	0	0	8	17	0	13	2	31	16	
52	251	0	7	0	0	0	0	7	1	9	0	33	7	
53	276	0	1	0	0	0	0	12	0	5	0	19	2	
54	269	0	0	0	0	0	0	6	0	0	0	25	3	15
55	301	1	0	0	0	0	0	3	0	0	0	13	1	
56	246	0	11	0	0	0	8	27	0	15	0	41	11	
57	261	0	3	0	0	0	0	6	0	2	0	28	4	16
58	278	0	0	0	0	0	0	4	0	0	0	13	5	
59	267	0	0	0	0	0	0	2	0	0	0	23	2	17
60	273	0	1	0	0	0	0	5	0	0	0	25	0	18

TABLE II (continued)

Pitfall no.	Angle in degrees*	*Al. accentuata*	*Al. cuneata*	*Al. fabrilis*	*Ar. lutetiana*	*Ar. perita*	*Au. albimana*	*Pa. lugubris*	*Pa. monticola*	*Pa. nigriceps*	*Pa. pullata*	*Tr. terricola*	*Zo. spinimana*	Selected sampling site no.**
		Species												
61	273	0	1	0	0	0	0	12	0	1	0	22	3	19
62	274	0	2	0	0	0	0	13	0	0	0	22	2	20
63	286	0	0	0	0	0	0	46	0	0	0	17	2	
64	270	0	1	0	0	0	0	16	0	0	0	32	2	
65	271	0	0	0	0	0	0	8	0	0	0	23	4	
66	273	0	0	0	0	0	0	17	0	0	0	25	5	
67	271	0	1	0	0	0	0	11	0	0	0	20	7	
68	278	0	0	0	0	0	0	23	0	0	0	21	4	
69	301	0	1	0	0	0	0	0	0	0	0	9	0	
70	289	0	0	0	0	0	0	4	0	0	0	10	2	
71	274	0	3	0	0	0	0	28	1	0	0	30	1	
72	277	0	0	0	0	0	1	14	0	0	0	16	4	
73	296	0	0	0	0	0	0	7	0	0	0	11	0	
74	282	0	1	0	0	0	0	16	1	0	1	18	2	21
75	273	0	1	0	0	0	0	22	0	0	0	25	5	
76	11	7	0	16	0	4	0	0	2	0	0	1	0	22
77	21	17	0	16	0	3	0	0	5	0	0	0	0	
78	16	17	0	15	0	7	0	2	6	0	0	1	0	23
79	15	11	0	20	0	5	0	0	3	0	0	0	0	24
80	21	9	1	9	0	0	2	1	11	6	0	16	6	25
81	***	6	6	3	0	5	0	2	4	6	0	37	11	
82	0	3	0	6	0	18	0	0	0	0	0	1	0	26
83	24	29	0	11	0	4	0	0	1	0	0	0	0	27
84	19	14	0	12	0	2	0	1	4	0	0	1	0	
85	25	14	1	14	0	1	0	0	9	4	0	3	0	
86	14	7	1	12	0	4	1	0	0	0	0	0	0	
87	0	3	0	9	0	8	0	1	1	0	0	1	0	
88	8	3	0	8	0	2	0	0	5	0	0	0	0	
89	23	15	0	14	0	1	0	0	6	0	0	2	0	28
90	18	9	0	12	0	2	0	0	7	0	0	0	0	
91	8	6	0	9	0	6	0	0	0	0	0	2	0	
92	11	6	1	11	0	5	0	0	2	0	1	1	0	
93	8	5	1	15	0	7	0	0	3	0	0	1	0	
94	26	9	3	6	0	2	1	0	17	0	0	1	0	
95	35	14	4	6	0	0	0	0	11	0	0	2	0	
96	27	25	1	13	0	1	0	0	1	0	0	0	0	
97	13	8	0	13	0	4	0	0	0	0	0	0	0	
98	17	14	0	25	0	4	0	0	3	0	0	0	0	
99	18	12	0	17	0	3	0	0	7	0	0	1	0	
100	36	35	10	17	0	1	0	0	29	0	0	0	0	
Mean		5.95	8.23	3.22	0.79	1.04	4.59	5.43	20.82	12.77	19.43	33.70	5.59	
Std. dev.		7.31	11.98	5.81	2.28	2.49	7.02	11.64	35.25	24.53	32.41	35.39	7.31	

* The pitfalls are ordinated by the method described in section 4.2 (Fig. 4). The ordination of the pitfalls is expressed in angle degrees with respect to pitfall no. 82.

** In the surroundings of 28 pitfalls (see section 2), 27 environmental characteristics were measured (Table IV).

*** Pitfall omitted from further analysis as the degree of correlation with the main environmental factor is very low (Fig. 4).

TABLE III

Environmental characteristics measured around 28 selected pitfall traps.

Soil	— Water content*
	— Humus content*
	— Acidity (pH-KCl)
	— Lime content**
Vegetation	— Percentage bare sand*
	— Cover on the ground by leaves and twigs*
	— Cover by mosses and lichens
	— Cover by the herb and grass layer*
	Maximum height*
	Minimum height
	Cover by *Calamagrostis epigejos**
	Cover by *Carex arenaria*
	Cover by *Festuca ovina*
	Cover by *Corynephorus canescens**
	Cover by *Urtica dioica*
	Cover by *Moehringia trinervia*
	— Cover by the shrub layer
	Maximum height
	Minimum height
	Cover by *Ligustrum vulgare*
	— Cover by the tree layer*
	Maximum height*
	Cover by *Populus tremula**
	Cover by *Crataegus monogyna**
Light	— Lux at equal grey sky*
	— Lux at cloudless sky*
	— Lux by reflection of the soil surface*

* Used in canonical correlation analysis (4.3).
** Skipped from further analysis (4.3).

activities in the various habitat types. It is obvious that an important assumption in this study is that the size of the pitfall catches reflects the degree of suitability of the habitats. For this assumption to be plausible, among others the dispersal powers of the species studied have to be so great that all the sites under study were inhabited by all those species for which these places were suitable. For the group of spiders we are dealing with here, this assumption seems to be not too unrealistic as the adults possess a high locomotory ability (VLIJM, 1966), whilst the juveniles show the phenomenon of "balooning" (RICHTER, 1970). So it may be assumed that the numbers present, and hence the numbers caught, always reflect the degree of suitability of the site.

Definitions

In the fields of ecology and mathematics the same terms are in use for different concepts and ideas. To avoid misinterpretation, terms used in this paper that may arouse confusion are defined as follows:

1. (environmental) component; an environmental variable which may or may not be relevant for the distribution of the species under study
2. (environmental) characteristic; an environmental component which can be measured by the investigator
3. (environmental) factor; an environmental component which is relevant for the distribution of the species under study
4. principal component; the mathematical description of an environmental factor or a composition of environmental factors. Let a set of n points (or vectors) be given in a p-dimensional space. Then the (first) principal component is that direction in which the dispersion (variance) of the points is maximum. The second principal component is that direction, perpendicular to the first principal component, in which the remaining variance is as great as possible. Analogously, the third principal component forms right angles to the first and second component and points in the direction of maximum remaining variance. And so on.
5. (environmental) gradient; the ecological interpretation of a principal component. That not all n points in the p-dimensional space do coincide is thought to be caused by a number of factors. Thus the interpretation is that for the first principal component the environmental factor causing the greatest mutual differences (dispersion of the points) is responsible. For the second principal component a factor of somewhat less importance is held responsible. And so on.

3. AMENDMENT OF THE PRINCIPAL COMPONENT MODEL

As the distributions of species are likely to be determined by quite a number of different factors, multivariate methods suggest themselves for analysing those distributions. Multivariate methods like principal component analysis and the related factor analysis are now widely used. However, the unfamiliarity of biologists with multivariate analysis seems to hamper their full employment and therefore obviously delays the development of special adaptations of the available techniques to the peculiarities in the field of distribution ecology.

We started from the idea, according to the definition, that the distribution of a species depends on a number of factors or a number

TABLE IV

The values of 26 environmental characteristics measured at 28 sampling :ites (Table II). All characteristics were measured at the end of August 1970. Lime content omitted. All soil samples were taken on the same day.

		Soil			*Vegetation*									
sampling site no.	pitfall no.	water content (percentage dry weight)	humus content (percentage dry weight)	acidity (pH-KCl)	percentage bare sand	cover by fallen leaves and twigs (percentage)	cover by moss layer (percentage)	cover by herb layer (percentage)	maximum height herb layer (centimetres)	minimum height herb layer (centimetres)	cover by *Calamagrostis epigejos* (percentage)	cover by *Carex arenaria* (percentage)	cover by *Festuca ovina* (percentage)
1	2	10.3	5.3	3.70	0	0	20	85	5	1	50	3	40
2	8	21.1	9.7	3.68	0	5	2	95	50	1	80	2	0
3	9	12.9	6.5	3.60	0	0	10	99	20	1	30	2	60
4	11	14.5	4.8	3.36	0	0	10	100	50	1	100	0	2
5	16	20.4	6.0	3.46	0	0	0	100	30	2	90	2	4
6	19	29.4	12.3	3.65	10	30	10	30	40	1	10	0	0
7	24	24.0	8.3	3.64	0	0	1	100	30	20	90	0	0
8	29	13.8	5.4	3.70	0	70	2	30	30	2	10	0	0
9	37	12.0	5.1	3.38	0	0	75	25	2	1	0	3	0
10	38	9.0	4.4	3.60	50	0	30	20	3	1	0	3	1
11	39	9.2	4.5	3.60	0	0	60	40	10	0	0	4	0
12	41	9.9	4.4	3.41	0	0	45	55	3	1	2	3	0
13	49	33.7	13.2	3.87	5	5	1	90	30	2	80	10	20
14	50	21.9	7.8	3.58	0	0	5	95	20	1	20	4	20
15	54	26.3	5.7	3.58	0	80	1	20	30	1	0	0	0
16	57	20.7	6.8	3.56	0	99	1	1	30	1	0	0	0
17	59	28.0	9.4	3.45	0	85	1	20	40	2	0	0	0
18	60	22.7	9.5	3.43	0	80	0	20	30	2	0	0	0
19	61	18.6	6.9	3.62	0	90	4	4	20	1	0	0	2
20	62	22.4	8.1	3.59	0	98	1	1	25	1	0	0	0
21	74	19.6	5.8	4.27	0	95	1	5	35	1	0	0	0
22	76	3.5	1.6	7.37	25	0	75	1	20	1	2	2	0
23	78	3.3	1.4	7.37	20	0	55	25	20	1	2	3	0
24	79	5.2	2.1	6.73	25	0	55	20	10	0	2	2	0
25	80	6.2	2.1	6.41	35	0	2	60	45	2	1	0	0
26	82	2.7	1.1	7.84	90	0	5	5	3	0	0	0	0
27	83	2.6	1.6	6.58	10	0	45	30	4	3	0	2	0
28	89	2.6	2.2	7.23	30	0	40	30	2	0	0	2	0

		Vegetation											*Light*		
sampling site no.	pitfall no.	cover by *Corynephorus canescens* (percentage)	cover by *Urtica dioica* (percentage)	cover by *Moehringia trinervia* (percentage)	cover by shrub layer (percentage)	maximum height shrub layer (decimetres)	minimum height shrub layer (decimetres)	cover by *Ligustrum vulgare* (percentage)	cover by tree layer (percentage)	maximum height tree layer (metres)	cover by *Populus tremula* (five-classes scale)	cover by *Crataegus monogyna* (five-classes scale)	lux at equal grey sky (× 1000)	lux at cloudless sky (× 1000)	reflection of soil surface at cloudless sky (× 100)
1	2	0	0	0	0	0	0	0	0	0	0	0	18	68	50
2	8	0	2	20	0	5	3	0	25	4	0	1	7	6	5
3	9	0	0	0	0	0	0	0	0	0	0	0	15	43	40
4	11	0	0	0	0	0	0	0	0	0	0	0	12	16	20
5	16	0	0	0	0	0	0	0	0	0	0	0	3	16	10
6	19	0	1	20	20	15	6	20	70	0	0	0	4	3	2
7	24	0	2	0	0	0	0	1	0	0	0	0	21	21	10
8	29	0	0	0	1	15	10	0	75	5	4	2	3	3	2
9	37	20	0	0	0	0	0	0	0	0	0	0	25	56	30
10	38	20	0	0	0	0	0	0	0	0	0	0	26	60	40
11	39	30	0	0	0	0	0	0	0	0	0	0	19	50	40
12	41	50	0	0	0	0	0	0	0	0	0	0	19	60	40
13	49	0	2	2	0	0	0	0	0	0	0	0	12	33	30
14	50	0	2	3	0	0	0	2	12	0	0	1	10	10	3
15	54	0	2	4	0	0	0	0	45	6	2	2	2	3	2
16	57	0	0	0	0	0	0	0	85	5	2	0	1	2	1
17	59	0	0	10	0	0	0	0	40	0	3	0	3	5	3
18	60	0	2	3	1	9	6	2	80	5	1	2	2	5	3
19	61	0	0	2	0	0	0	1	50	4	2	1	1	4	1
20	62	0	0	0	0	0	0	0	75	6	2	1	1	3	1
21	74	0	3	2	0	30	20	2	50	6	2	1	2	3	1
22	76	2	0	0	0	0	0	0	0	0	0	0	19	67	50
23	78	20	0	0	0	0	0	0	0	0	0	0	17	57	60
24	79	20	0	0	0	0	0	0	0	0	0	0	18	55	55
25	80	0	1	2	1	15	8	0	50	0	0	0	2	5	10
26	82	10	0	0	0	0	0	0	0	0	0	0	19	37	80
27	83	20	0	0	0	0	0	0	0	0	0	0	19	56	40
28	89	30	0	0	0	0	0	0	0	0	0	0	19	54	40

of complexes of correlated factors. We assume that these factors are for the moment of unknown nature.

Secondly, since it is in practice impossible to analyse in the field the influence of all factors one by one, we decided to estimate the influence of the separate factors on the distribution of the species from the combined effect of all factors. This influence was in this case measured as pitfall catches.

A third assumption was that at least a number of these factors or complexes of factors, relevant for the distributions, was the same for a number of species (they will be called common factors).

Finally we assumed that the size of the catches reflected the degree of suitability of the site. These four considerations pave the way for the use of multivariate methods, in this case principal component analysis.

The basic reasoning in principal component analysis runs as follows. A stochastic vector X (p dimensions) is characterized by a (p-dimensional) multivariate probability-density function. A number of n independent samples will give us the following data: $X_1, .., X_n$. Now the main aim of using principal component analysis is to see how far the black box which generates the vectors $X_1, .., X_n$ can be opened in order to trace down some of the probability relationships involved.

However, application of principal component analysis in distribution ecology meets two major objections (VAN DER AART & DE BRUYN, 1972). The basic model of this analysis states that the population size N of a species i on a certain site s is a linear combination of a number (r) of environmental factors.

$$N_{is} = \sum_{k=1}^{r} a_{ik} \cdot x_{ks} \qquad (1)$$

Where x_{ks} is the realized value of the k-th factor on site s and a_{ik} is a coefficient of proportion.

Thus it is essentially an additive model. However, in the situation we are dealing with (the distribution of hunting spiders), the favourable and unfavourable effects of environmental factors are as far as we can imagine combined in a multiplicative way. A factor removes a certain fraction—or if one likes a certain percentage—of the population and not a certain number. For this reason a multiplicative model seems more appropriate. In other words it is thought reasonable to assume that the relative change in population size is approximately linear to the change in the environmental factor.

For the k-th environmental factor we may write $\frac{\Delta N}{N} \approx a_k \cdot \Delta x_k$ (2)

Where

ΔN is the difference in population size between site s and the one slightly different, $s + \Delta s$

and

Δx_k is the change of the environmental factor k from s to $s + \Delta s$

Let Δs tend to zero then we obtain the following differential equation

$$\frac{1}{N} \cdot \frac{dN}{ds} = a_k \cdot \frac{dx_k}{ds} \qquad (3)$$

the solution of which is given by

$$\log N = a_k \cdot x_k + c_k \qquad (4)$$

where c_k is a constant

When a number of environmental factors is involved than it is reasonable to presume that in first instance approximately holds

$$\log N = \sum_k (a_k \cdot x_k + c_k) = c + \sum_k a_k \cdot x_k \qquad (5)$$

where $c = \sum_k c_k$

For that reason we have transformed the original data to logarithms. To avoid difficulties with zero values we have added one to the original data before transformation to logarithms.

The foregoing holds when the environmental factor operates over a limited range. As this is evidently not the case here, we have to accept that a_k is not a constant but also a function of the environmental factor itself. That is, a_k in formula 2 has to be replaced by $b_k \approx -2c'_k x_k$.

In general the curve depicting the relation between the number of individuals of a species and some environmental factor will be of the optimum type, provided that the sampling is done over a sufficiently wide range of values of the environmental factor. When, for instance, a certain species survives best at a certain level of humidity, both higher and lower humidity levels will cause a decline in the population. Wellknown are also bell-shaped or non-peaked "preference" curves for temperature, size of prey in case of predators, salt tolerance in case of water organisms, and so on. Therefore the functions relating factors to densities are clearly not so simple that they can be expressed in terms of coefficients of linear regression (formula 4).

NOY-MEIR & AUSTIN (1970), DE BRUYN (1971) and VAN DER AART (1973), by handling principal component analysis in practice in cases of evident non-linearity between variables and factors, found that more than one principal component was needed for the representation of just one factor. VAN DER AART (1973, Fig. 10A), gives an example of an imaginary factor and a number of normally distributed dummy variates on that factor.

From this artificial system of which all relations were known, samples were taken and analysed as if they were black box data obtained from the field. As a result three principal components could be extracted with Eigenvalues greater than one. However only one single factor was involved. In all those cases dealing with optimum curves the factor is brought about as a horse-shoe-like curve in the hyperplane formed by the first two principal components (Fig. 2; VAN DER AART, 1973, Fig. 10B). There is a typical and very regular twisting in the third dimension as can be seen in Fig. 1. Some theoretical aspects of these phenomena were touched on by VAN DER AART & DE BRUYN (1972). It is not yet fully clear how far the use of correlation coefficients is responsable for these findings. Mr. G. J. DE BRUYN is working on this subject at our department.

The crucial point with non-linear relationships is that the proposition of each principal component being related to just one common

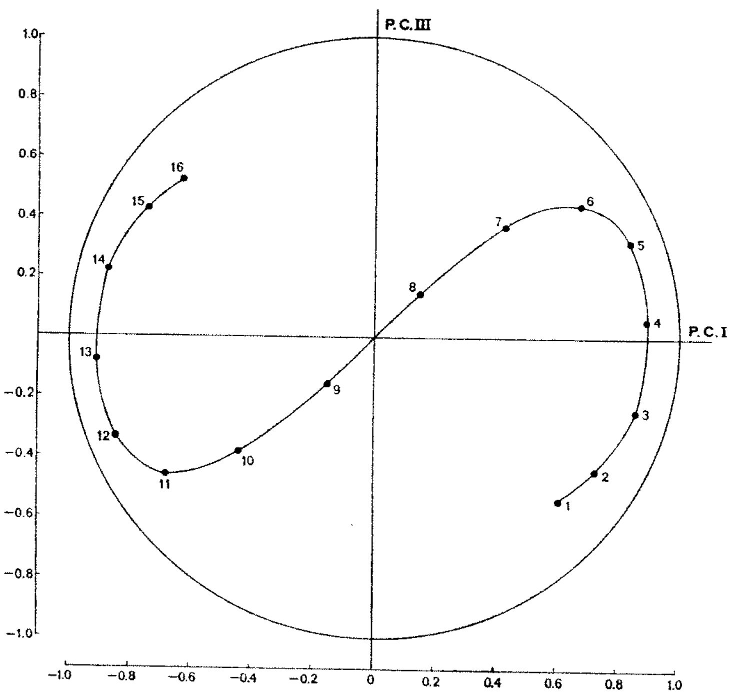


Fig. 1. Characteristic arrangement of 16 dummy variates in the hyperplane formed by the principal components I and III. The variates are normally distributed with regard to an imaginary environmental factor (data in VAN DER AART, 1973, Fig. 10, Table XI).

TABLE V

Lower half of the square, symmetrical matrix of product-moment correlations based on the log-transformed data of Table II.

1. *Al. accentuata*	1.00											
2. *Al. cuneata*	+.11	1.00										
3. *Al. fabrilis*	+.59	−.43	1.00									
4. *Ar. lutetiana*	+.02	+.39	−.23	1.00								
5. *Ar. perita*	+.40	−.43	+.80	−.21	1.00							
6. *Au. albimana*	−.03	+.76	−.41	+.55	−.40	1.00						
7. *Pa. lugubris*	−.72	−.15	−.41	−.19	−.33	−.13	1.00					
8. *Pa. monticola*	+.61	+.63	−.07	+.28	−.19	+.44	−.57	1.00				
9. *Pa. nigriceps*	−.07	+.75	−.43	+.56	−.41	+.88	−.14	+.37	1.00			
10. *Pa. pullata*	+.06	+.75	−.44	+.62	−.42	+.89	−.29	+.54	+.88	1.00		
11. *Tr. terricola*	−.44	+.64	−.80	+.48	−.72	+.72	+.28	+.17	+.77	+.73	1.00	
12. *Zo. spinimana*	−.47	+.48	−.58	+.44	−.50	+.70	+.27	−.00	+.78	+.66	+.83	1.00
Species no.	1	2	3	4	5	6	7	8	9	10	11	12

factor in the field, no longer holds. Another, yet unsolved, problem is that when there are several common environmental factors, each giving rise to an optimum curve, we are still unable to select pairs of principal components representing the relevant factors in the field.

4. RESULTS

4.1. THE DISTRIBUTIONS OF THE HUNTING SPIDER SPECIES IN THE AREA STUDIED

From the catches of the various species obtained from 100 pitfalls in a sampling period of approximately one year, the degree of similarity between distributions was estimated by calculating product-moment correlations. These were based on the log-transformed data of Table II (see Table V). From this Table V the principal components were obtained, which describe the main environmental factors in a numerical form (Table VI). These principal components and their relations to the distributions of the spider species are visualized in Fig. 2. Here a typical horse-shoe-like figure presents itself. This figure suggests—as has been explained in §3—that only one environmental factor is acting and that a non-linear relation exists between the densities of species and this single environmental factor.

TABLE VI

Matrix describing the position of 12 vectors (spider species) in the principal component space, according to the distribution relations of the spider species. Sequence of species as in Fig. 2. 100 samples (pitfall catches).

	Principal components							
	I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*
Ar. perita	−.66	+.38	+.51	+.20	+.10	−.26	+.18	−.06
Al. fabrilis	−.70	+.51	+.36	+.15	+.12	+.20	−.12	+.04
Al. accentuata	−.23	+.90	−.14	.00	+.10	+.23	+.08	+.06
Pa. monticola	+.40	+.74	−.45	−.05	+.09	.00	+.17	−.12
Al. cuneata	+.80	+.31	−.23	+.23	+.27	−.20	−.09	+.17
Ar. lutetiana	+.60	+.24	+.40	−.62	+.20	−.03	−.02	+.03
Pa. pullata	+.89	+.33	+.10	+.01	−.13	−.01	−.00	−.12
Au. albimana	+.89	+.23	+.17	+.18	+.04	+.03	−.16	−.24
Pa. nigriceps	+.90	+.19	+.23	+.18	−.07	+.04	−.03	+.13
Tr. terricola	+.92	−.28	−.03	−.02	−.01	+.01	+.08	+.05
Zo. spinimana	+.82	−.30	+.32	+.15	−.07	+.16	+.20	+.06
Pa. lugubris	+.04	−.88	−.04	+.10	+.42	+.12	+.05	−.09
Eigenvalues	6.09	3.05	1.01	0.60	0.36	0.25	0.17	0.16
Cumulative perc. of Eigenvalues	50.8	76.2	84.6	89.6	92.6	94.7	96.1	97.4

This ordination of the species is in agreement with the one found during the sampling programme of 1953 till 1960 (VAN DER AART, 1973, Fig. 11). In this earlier sampling programme a much larger area was sampled, ranging from the old inner-dune valley studied in this paper to the bare and more accidented dunes near the sea. In the two studies the arrangement of species is much the same. On the one extreme in the bare sandy biotopes, species like *Arctosa perita* and *Alopecosa fabrilis* are found. *Alopecosa accentuata* and *Pardosa monticola* occur mainly in open vegetations dominated by low herbs and grasses. A group of species with clearly distinct life habits, namely *Alopecosa cuneata*, *Arctosa lutetiana*, *Pardosa pullata*, *Aulonia albimana* and *Pardosa nigriceps*, can be found in well-developed grass and herb layers. Ac-

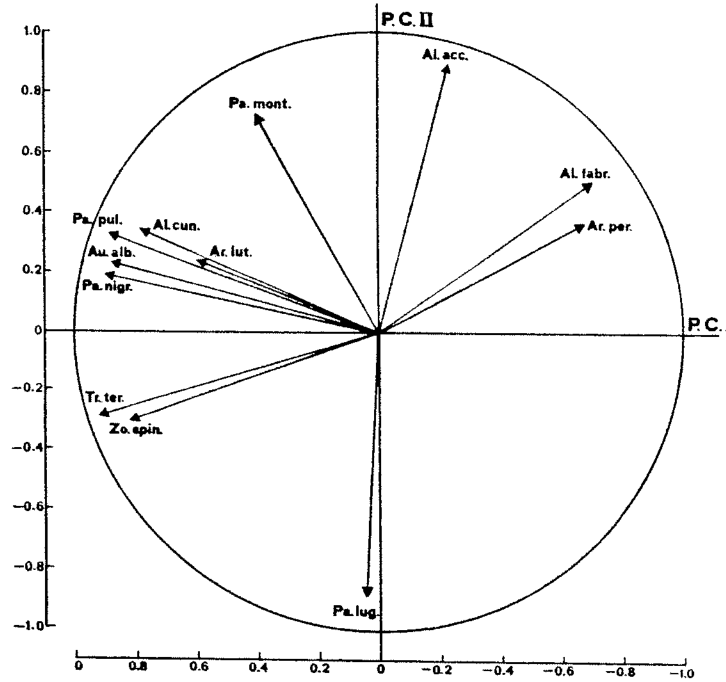


Fig. 2. Relations between the distributions of 12 hunting spider species with regard to the principal components I and II (figures in Table VI). 12 variables (hunting spider species), 100 observations (pitfall catches, data in Table II). The solution is based on log-transformed data.

cording to ENGELHARDT (1964), *Trochosa terricola* is confined to the transition zones of woods and clearings. In our study area *Trochosa terricola* is found in a comparable biotope type consisting of a well-developed grass layer with loosely dispersed shrubs. Little is known about the distribution of *Zora spinimana*. It may, however, be postulated, that the distribution of *Zora spinimana* closely resembles that of *Trochosa terricola* on account of their positions in Fig. 2 and their degree of correlation (r = + 0.83, Table V). *Pardosa lugubris* constitutes the other extreme of the gradient. It is a species frequently encountered in woods where it is often seen sunning or running over fallen leaves.

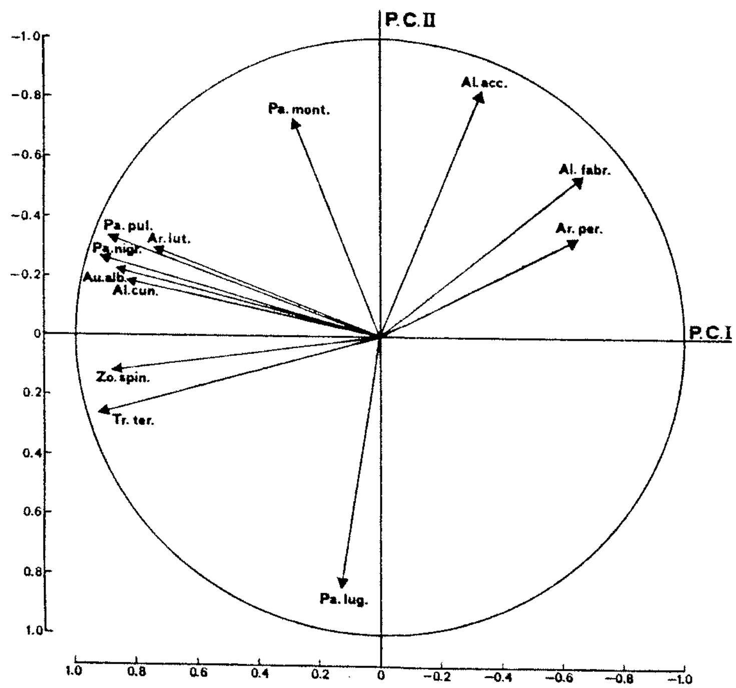


Fig. 3. Relations between the distributions of 12 hunting spider species with regard to the principal components I and II. 12 variables (hunting spider species), 28 observations (pitfall catches). Log-transformed data used.

As has been mentioned above, 28 out of the 100 sampling sites were selected to characterize the biotopes from which the animals were sampled. It is therefore interesting to know whether these selected sampling sites had been representative enough to reveal the distribution relations between the spider species as found in the complete set

of 100 samples (Fig. 2). To this aim a principal component analysis was applied to the catches of these 28 pitfalls alone. The result is given in Fig. 3. From a comparison of Fig. 3 with Fig. 2 and the underlying coefficients of correlation, it is concluded that these 28 pitfalls represent the 100 pitfalls fairly well. A few remarks about the selection of the 28 pitfalls can be found in section 4.3.

4.2. ORDINATION OF THE BIOTOPES ON ACCOUNT OF THE OCCURRENCE OF THE HUNTING SPIDER SPECIES

The species can be arranged on account of their distributions. Similarly the sampling sites can be arranged on account of their species composition. Both procedures, known as R- and Q-technique respectively, reveal the same factors relevant for the distributions. For the ordination of pitfalls by principal component analysis one starts from the transpose of Table II (thus, columns and rows interchanged). For reasons explained in a previous paper (VAN DER AART, 1973) one has to center (mean equal to zero) and standardize (standard deviation equal to one) the data per species before applying principal component analysis to the transpose of a species-in-site data matrix (Table II). The results of this analysis are given in Fig. 4 in which the pitfalls are ordinated according to the composition of the catches of the different spider species. As mentioned already in §2 the study area "Bierlap" is an inhomogeneous dune area, lowlying and mainly covered by poplar and birch woods. In this area four more or less homogeneous sites were selected, each of which has been sampled by 25 pitfalls placed in a square grid.

The first site (pitfalls 1–25) was dominated by a luxurious growth of *Calamagrostis epigejos* with some dispersed shrubs of *Crataegus monogyna*. The second site (pitfalls 26–50) had a very low vegetation of mainly mosses and lichens. At the rim a nearby wood of *Populus tremula* was invading the site with young stems and shoots accompanied by growth of *Calamagrostis*. The third site (pitfalls 51–75) consisted of a homogeneous poplar wood. The fourth site (pitfalls 76–100) may be characterized as a largely bare plain with sparse tussocks of *Corynephorus canescens*, lichens like *Cornicularia aculeata* and *Cladonia foliacea*, and sparse *Ammophila arenaria* and *Calamagrostis* sprouts. The ordination of pitfalls on account of the hunting spider catches as visualized in Fig. 4, suggests a gradient of bare sand, via low herb and grass vegetations to vegetations dominated by well-developed *Calamagrostis epigejos*. The other end of the gradient is characterized by vegetations with *Crataegus* bushes, birch trees to dense *Populus tremula* woods. Not all pitfalls fit equally well into this gradient, as is indicated by the varying distances of the dots representing the pitfalls to the centre of the figure: the more a dot is situated to the centre, the less the spider species catches in the pitfall represented by this dot are coherent with the gradients indicated.

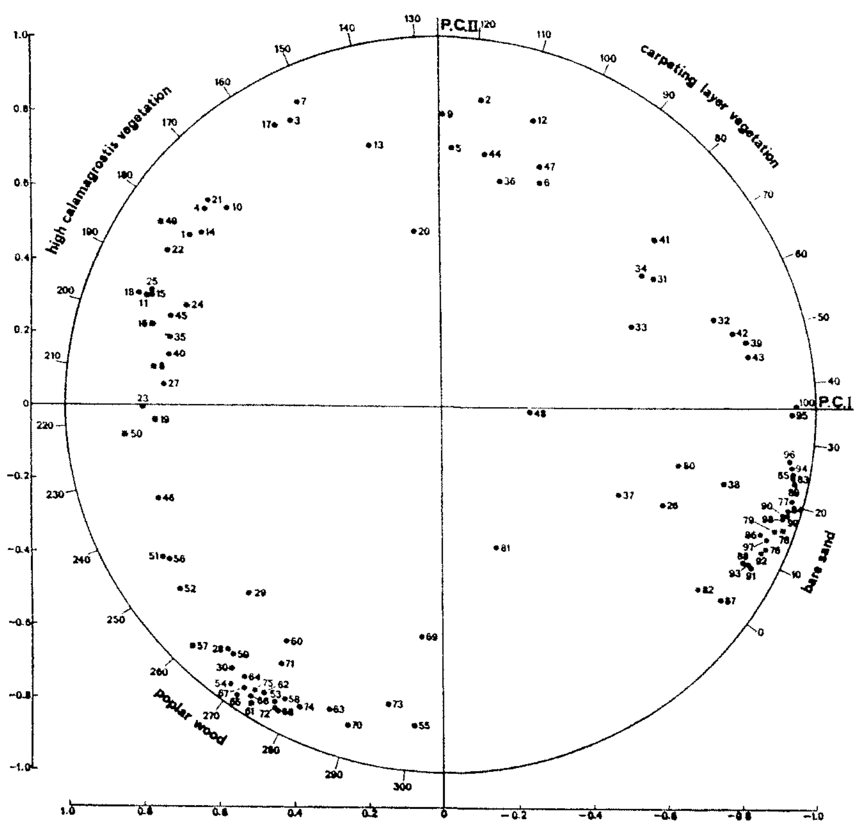


Fig. 4. Ordination of the pitfalls (biotopes) by the first two principal components based on the log-transformed normalized data of Table II. 100 variables (pitfalls), 12 observations (hunting spider species). The 28 selected sites are marked with an asterisk.

4.3. CORRELATIONS BETWEEN DISTRIBUTIONS OF SPIDER SPECIES AND ENVIRONMENTAL CHARACTERISTICS

Principal component analysis. As shown in the previous section, the pitfalls (biotopes) can be linearly ordinated on account of their catches of spider species. It is evident that in this case the gradient found is closely linked to the degree of development of the vegetation, as the

biotopes sampled are ordinated from bare sand to those situated in poplar woods. To obtain a better characterization of this gradient, the immediate surroundings of 28 out of 100 pitfalls were selected for measuring a number of environmental characteristics. The best procedure for selection undoubtedly should have been to pick out biotopes lying equidistantly along to the gradient of the ordinated pitfalls. This procedure would avoid unnecessary duplication on the one hand and exclude the risk that large parts of the gradient are accidentally not sampled on the other hand. In this way the main environmental factor would be sampled at approximately regular intervals. However, this very elegant procedure could not be applied here as the measuring of the environmental characteristics had to be done simultaneously with the pitfall sampling, whereas the ordination of the biotopes (pitfalls) could obviously only be done after the sampling was completed. Thus the selection of the environment of 28 pitfalls for characterization of the gradient of which they are a part had to be done by intuition, which after all proved to be moderately successful (see Fig. 4). These selected biotopes were characterized by measuring quite a number of environmental characteristics (Tables III and IV and §2). The main correlations within and between the groups of spider species and environmental characteristics are mentioned in Table VII. The correlation between groups is given by the mean value of the product-moment correlations between the separate variables. In Table VII the gradient runs from top to bottom, both for the spider species and for the environmental characteristics. In practice Table VII was derived from a joint principal component analysis of both species and environmental characteristics. The coefficients of correlation for the spider species in Table VII deviate slightly from those in Table V as in the latter the correlations are based on the catches in 100 pitfalls, whereas in Table VII the correlations are based on the catches in the 28 selected pitfalls only. The high correlation between acidity (pH–KCl) and bare sand is likely to be the result of an artificial situation because the fourth group of biotopes (pitfalls 76–100) was situated on a bare plain arisen by dumping of excavated sand which has a pH much higher than that of the superficial layer of undisturbed sand.

The calciumcarbonate content proved to be extremely low in all sites examined, so accurate figures could hardly be obtained. Moreover, no significant correlation of lime content with the abundance of any spider species was found, so lime content was skipped from further analysis.

It is not easy to see which vegetational characteristics are the most important ones. According to VAN HEERDT & MÖRZER BRUYNS (1960) there is a relation between the occurrence of hunting spiders and the

TABLE VII

CORRELATION SCHEME

	environmental characteristics			hunting spider species
+0.82 +0.48	pH-KCl bare sand* *Corynephorus canescens**	+0.73 ⟷	+0.77	*Arctosa perita* *Alopecosa fabrilis*
	+0.55			
	cover by moss layer			+0.56
	+0.68			
+0.65 +0.90	lux at equal grey sky* reflection of soil surface* lux at cloudless sky*	+0.73 ⟷		*Alopecosa accentuata*
	+0.59			+0.60
	Carex arenaria	+0.58 ⟷		*Pardosa monticola*
	+0.37			+0.37
+0.46 +0.58	cover by herb layer* *Festuca ovina* *Calamagrostis epigejos**	+0.56 ⟷	+0.72 +0.79 +0.89 +0.72	*Pardosa pullata* *Arctosa lutetiana* *Pardosa nigriceps* *Aulonia albimana* *Alopecosa cuneata*
	+0.29			
+0.31	min. height herb layer humus content*	+0.54 (to *Zora spinimana*, *Trochosa terricola*)		+0.71
	+0.28			
+0.51 +0.20 +0.81 +0.29 +0.53 +0.47 +0.99	water content* *Urtica dioica* cover by shrub layer *Ligustrum vulgare* max. height herb layer* *Moehringia trinervia* min. height shrub layer max. height shrub layer	+0.40 (to *Zora spinimana*, *Trochosa terricola*)	+0.83	*Zora spinimana* *Trochosa terricola* ↓
	+0.34			+0.26
+0.83 +0.87 +0.83 +0.78	*Crataegus monogyna** cover by tree layer* fallen leaves and twigs* max. height tree layer* *Populus tremula**	+0.79 ⟷		*Pardosa lugubris*
−0.32 (first to last group)				−0.32 (first to last group)

N.B. Between successive variables coefficients of correlations are given. Between two groups of variables the mean value of the coefficients of correlation concerned is stated.
* Used in canonical correlation analysis.

structure of the vegetation. Following LENSINK (1963) we did start from the idea that phytosociological taxa are not appropriate entities for the descriptions of animal habitats. Vegetational characteristics were selected such that in the first place a good description was obtained of the *structure* of the vegetation as contrasted to the *specific composition*. Therefore the cover by mosses and lichens was taken as one characteristic, as both groups grow promiscuously and define the structure and penetrability of the lowest vegetation layer. The amount of light penetrating the vegetation layers was measured by a lux meter placed either on the soil surface or respectively on top of the moss layer. Therefore, the degree of cover by the moss and lichens layer is discounted in these lux data, due to the dimensions of the lux meter. Since in sandy biotopes nearly always some *Ammophila arenaria* sprouts can be found, a closed carpet of lichens like *Cladonia* spp. and *Cornicularia* sp. and mosses like *Dicranum scoparium* is more open to entering light than biotopes classified as "bare sand".

The largest numbers of *Arctosa perita* and *Alopecosa fabrilis* were caught on bare sand, whereas the optimum biotope for *Alopecosa accentuata* is strictly open with a more or less closed layer of mosses and lichens. A group of five species *viz.* *Pardosa pullata*, *Arctosa lutetiana*, *Pardosa nigriceps*, *Aulonia albimana* and *Alopecosa cuneata* is limited to high grass vegetations. *Pardosa monticola* is most abundant in a closed carpeting layer of short grasses. *Zora spinimana* and *Trochosa terricola* are found in habitats with a herb and grass layer which exceeds a minimum height of about 20 cm. It might be said that for the latter, a ground-dwelling species, this minimum height of vegetation ensures a humid environment, which might be the ultimate factor, as this species is shown to be susceptible to dessication (ENGELHARDT, 1964). The next set of environmental characteristics of Table VII is correlated with luxurious undergrowth of shrubs in a moderately wet environment. This type of vegetation with a well-developed damp litter and humus layer harbours a variety of species, though none of them is entirely restricted to it. *Pardosa lugubris* occurs most frequently in woods with a more or less closed surface of last year's leaves on the ground.

A more detailed insight in optimum and ecological amplitude for the separate spider species under study with regard to the main environmental factor may be obtained from Fig. 5. In this figure, 100 biotopes are ordinated according to the gradient found in Fig. 4. As a measure of distance between biotopes in Fig. 5 the numerical value corresponding to the angle in degrees measured with respect to the biotope surrounding pitfall no. 82 (zero value) was used (see Fig. 4 and Table II). On the vertical axis, the numbers of individual spiders caught (for arithmetic reasons increased by one) are given on a log-

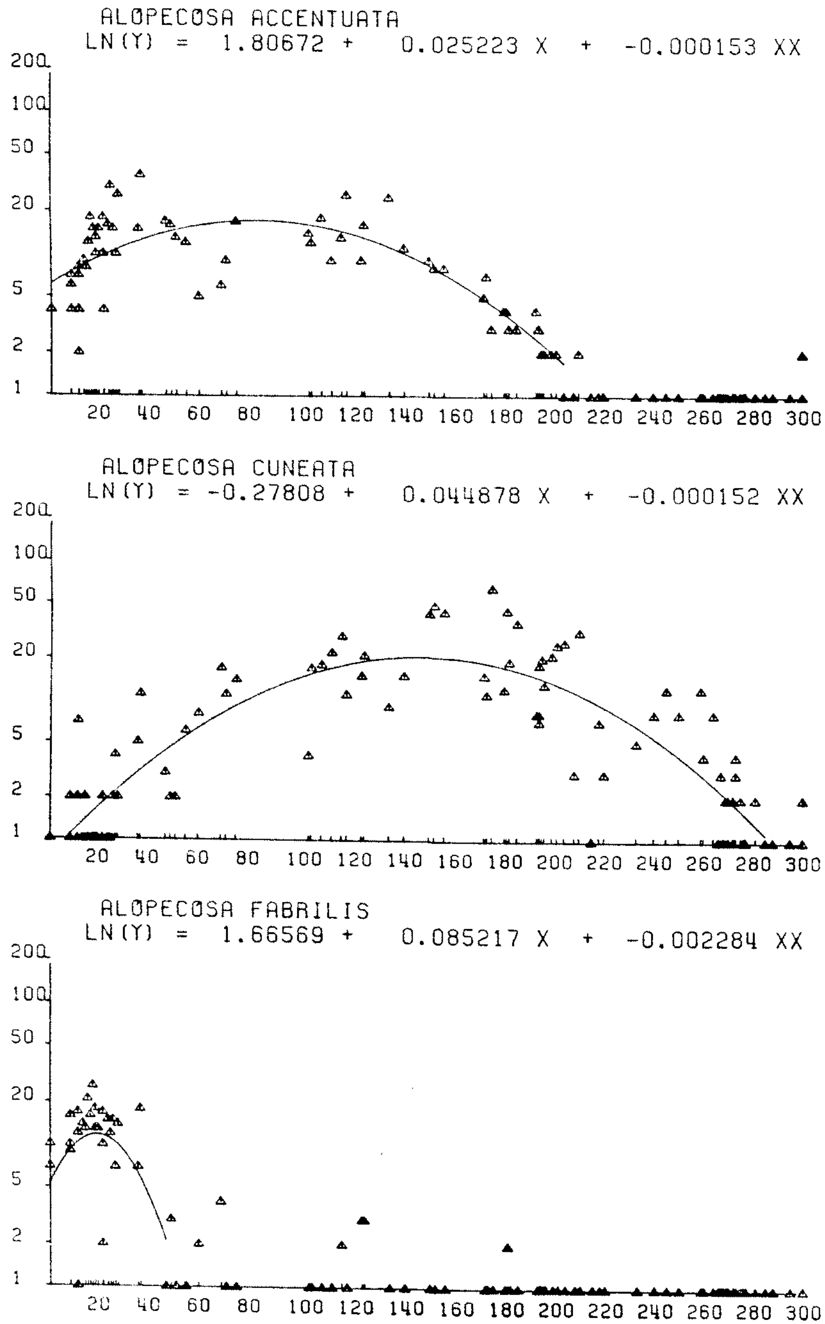


Fig. 5. The number of animals caught per pitfall trap (data in Table II). The pitfalls (biotopes) are ordinated on the basis of the main environmental factor. Second degree polynominals (regression lines) are plotted within the interval over which they were calculated.

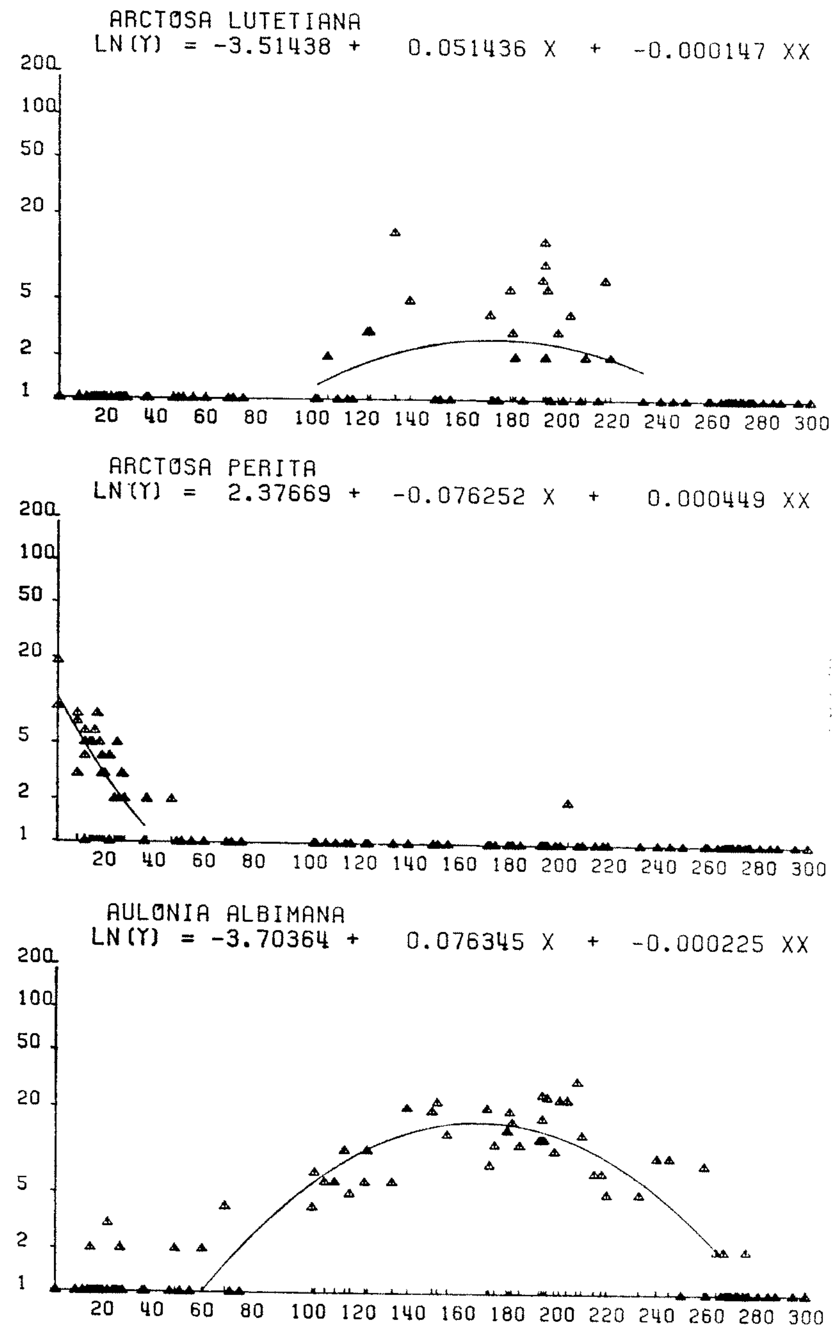
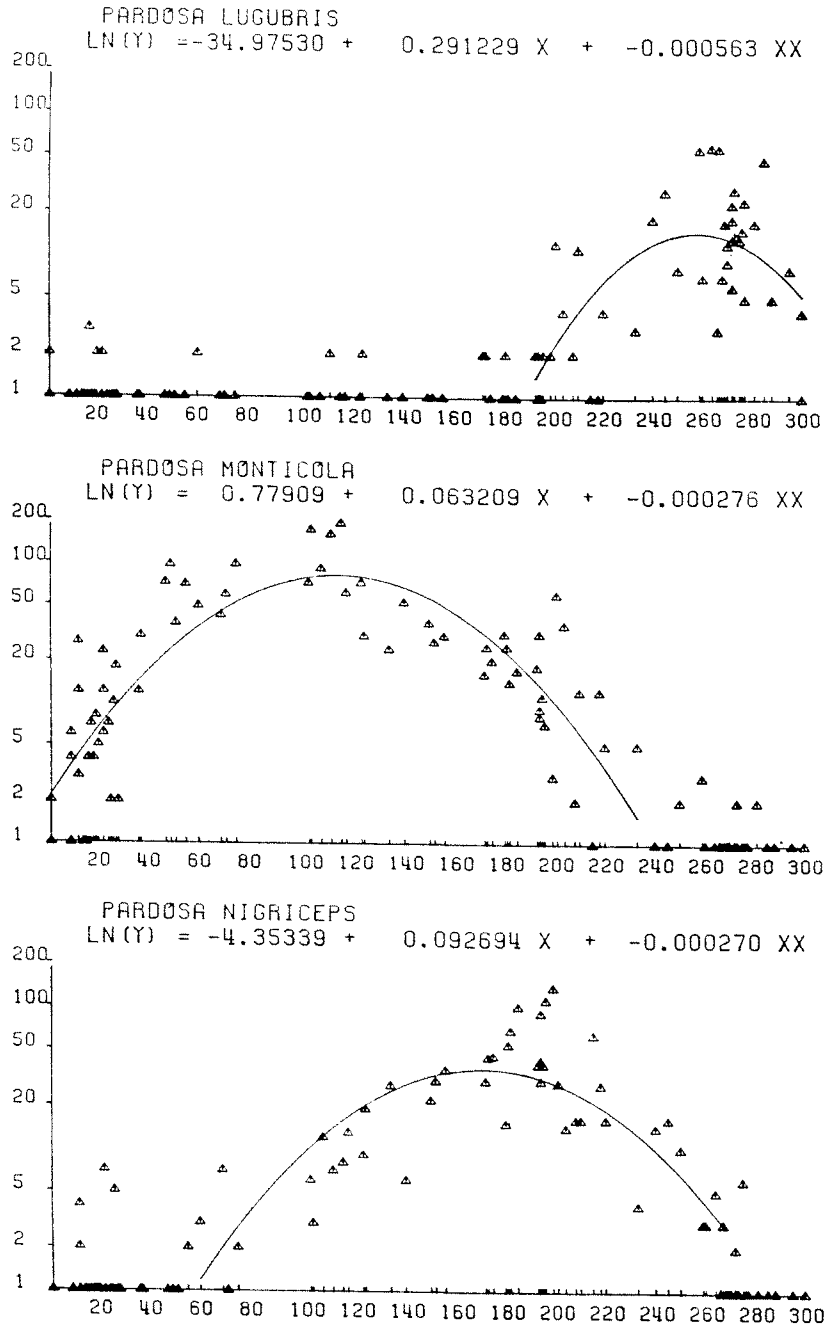


Fig. 5. continued.



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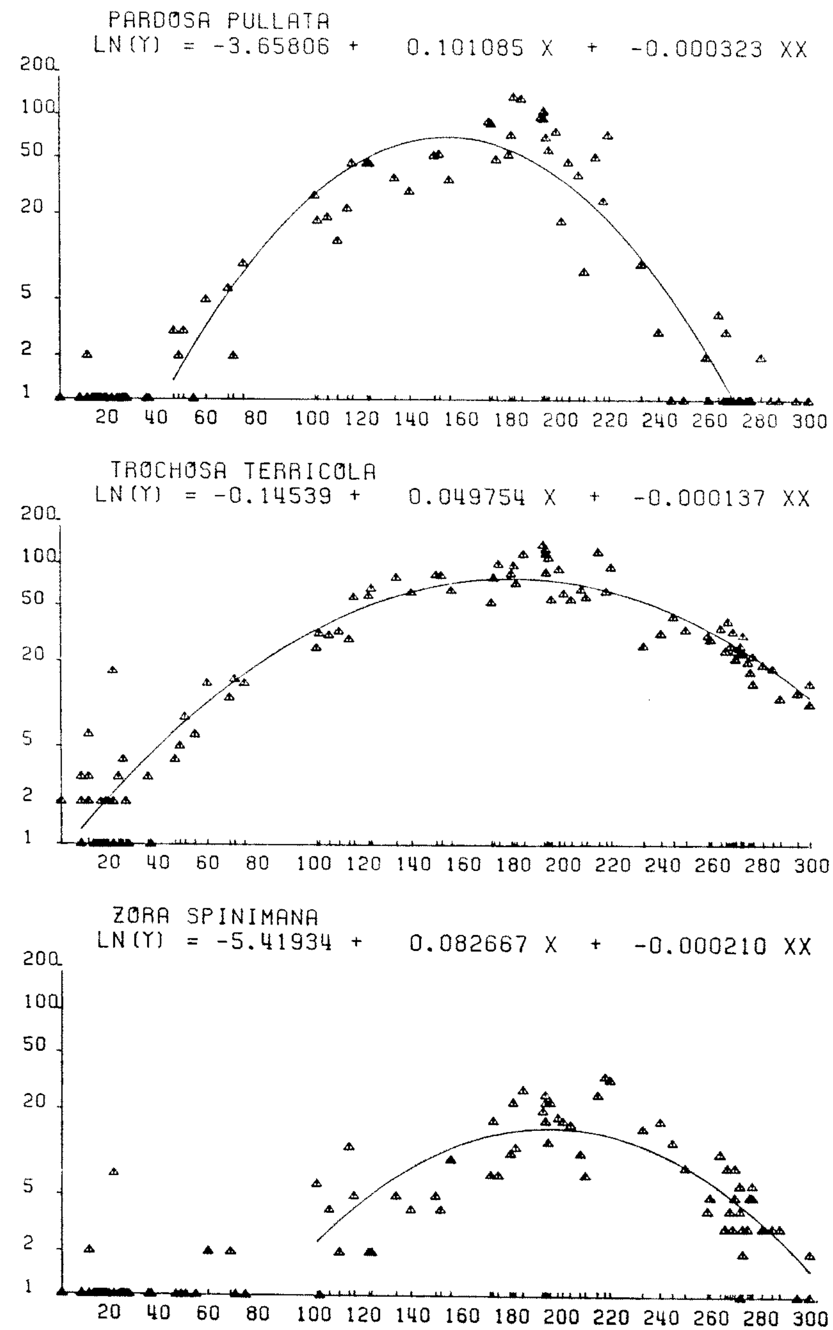


Fig. 5. continued.

arithmic scale. The "density of activity" (see §2) is plotted against the main environmental factor in Fig. 5. At first glance it is clear that these "density of activity" curves vary considerably from species to species. As a general trend it can be seen from Table II that the mean catch per pitfall shows a strong positive correlation with the standard deviation and so with the variance. This phenomenon is very often encountered in distribution ecology. Its backgrounds and implications are given a great deal of attention by A. O. BEALL (1942) and TAYLOR (1961). Thus a positive relation is to be expected in Fig. 5 between the heights of the curves and their widths (ecological amplitude). Notwithstanding this, in Fig. 5 clear differences are displayed in flatness or peakedness of the different curves, indicating various degrees of indifference or sensitivity, respectively, of each species to the main environmental distribution factor. For example the distribution of *Alopecosa fabrilis* is strongly affected by this factor, in contrast to *Alopecosa accentuata* which behaves more indifferently to it.

It is worthwhile to compare Fig. 5 of this study with Fig. 18 of the previous one (VAN DER AART, 1973). When comparing these figures one has to bear in mind that in Fig. 18 of the earlier study the numbers caught are plotted on a linear scale, whereas in Fig. 5 a logarithmic scale was used. Moreover in Fig. 18 (VAN DER AART, 1973), the main environmental factor (gradient of biotope classes) is presented in classes of 20 degree units each, whereas in Fig. 5 of this study an ordinal scale is used. It was encouraging to find that for all species the "density of activity" curves proved to be unchanged, particularly as the last study was undertaken 10 years later in a much more restricted area and with a modified sampling technique. In Fig. 5 seconddegree regression lines were fitted in that part of the gradient in which the numbers caught were not approximately zero. The positions of the optima for the species in both figures are alike, and so are the ranges of biotope classes in which the species occur. The curves for *Alopecosa accentuata* are broadly topped, with some indication of a depression in the middle; perhaps there might be two optimum biotopes, one more overgrown than the other. It was suggested by some authors (WIEBES, 1960; EDGAR, 1971; VAN DER AART, 1973) that hunting spiders during their life cycle might move from one biotope type to another. Juveniles might be found on places different from those frequented by adults. It is also known that fertilized females of some species move to more open places. The curve for *Alopecosa accentuata* is composed for all the developmental stages of this species, which might have brought about the peculiar shape. Generally, as far as lycosids are concerned, the different developmental stages (juveniles, subadults, males and females) may live in slightly different habitats.

Particularly females carying cocoons move away from the places frequanted by juveniles, subadults and males in order to stay at sites which are more exposed to the sun. The numbers caught in this study hardly permit splitting up into different developmental stages in order to analyse their separate distributions. To this subject a separate paper will be devoted in which the data of this study and our former studies will be combined.

For *Pardosa pullata* now a much better description of the distribution was obtained, as in this study an old innerdune valley was sampled in which *Pardosa pullata* is found frequently. In the first study, however, also areas more near to the sea were sampled, and although those areas proved to fit well into the gradient of biotope classes, no *Pardosa pullata* populations appeared to be established in those areas near to the sea. Therefore, in the first study only a fragmentary characterization of the distribution of this species in relation to the main environmental factor could be given.

The fact that in our dune study area *Pardosa pullata* is not present in seemingly suitable biotopes situated within 1500 m from the sea is remarkable. From the literature on the distribution of *Pardosa pullata* it is evident that the species is found in a wide range of biotope types. According to BRISTOWE (1958) it occurs on piles of pebbles on beaches as well as in the parks of London. It is the only *Pardosa* species in England, Scotland, Wales and Ireland found on mountains over 2000 feet. From the work of BREYMEYER (1969) it is known that in wet meadows in Poland *Pardosa pullata* can withstand submergence for over three months. The feature these biotopes have in common is that they are moist or at least water is within reach of the spiders. It might well be that in our rather dry dunes, the biotopes nearer to the sea are slightly more, and so just too dry compared to those at the landward side. *Zora spinimana*, a species studied by us for the first time, was caught in rather low numbers. The optimum biotope class for this species tends to be slightly more to the more wooded side of the scale as compared to *Trochosa terricola*. As for *Arctosa lutetiana* and *Aulonia albimana* it should be said that we do not know whether the low numbers of *Zora spinimana* caught are due to a low density or to a more hidden way of life (minor locomotory activity). No special linkage to lichens was found as might be guessed from the scanty observations in Britain (PARKER & COLEMAN, 1973). It is clear that it is worth trying to gain a better grip on the nature of the main environmental distribution factor. For this purpose, the 28 selected biotopes were ordinated by the same method as used in Fig. 5. In Fig. 6, those environmental characteristics which show a clear relation to the principal component (main factor) were plotted. It would have been ideal if we had hit

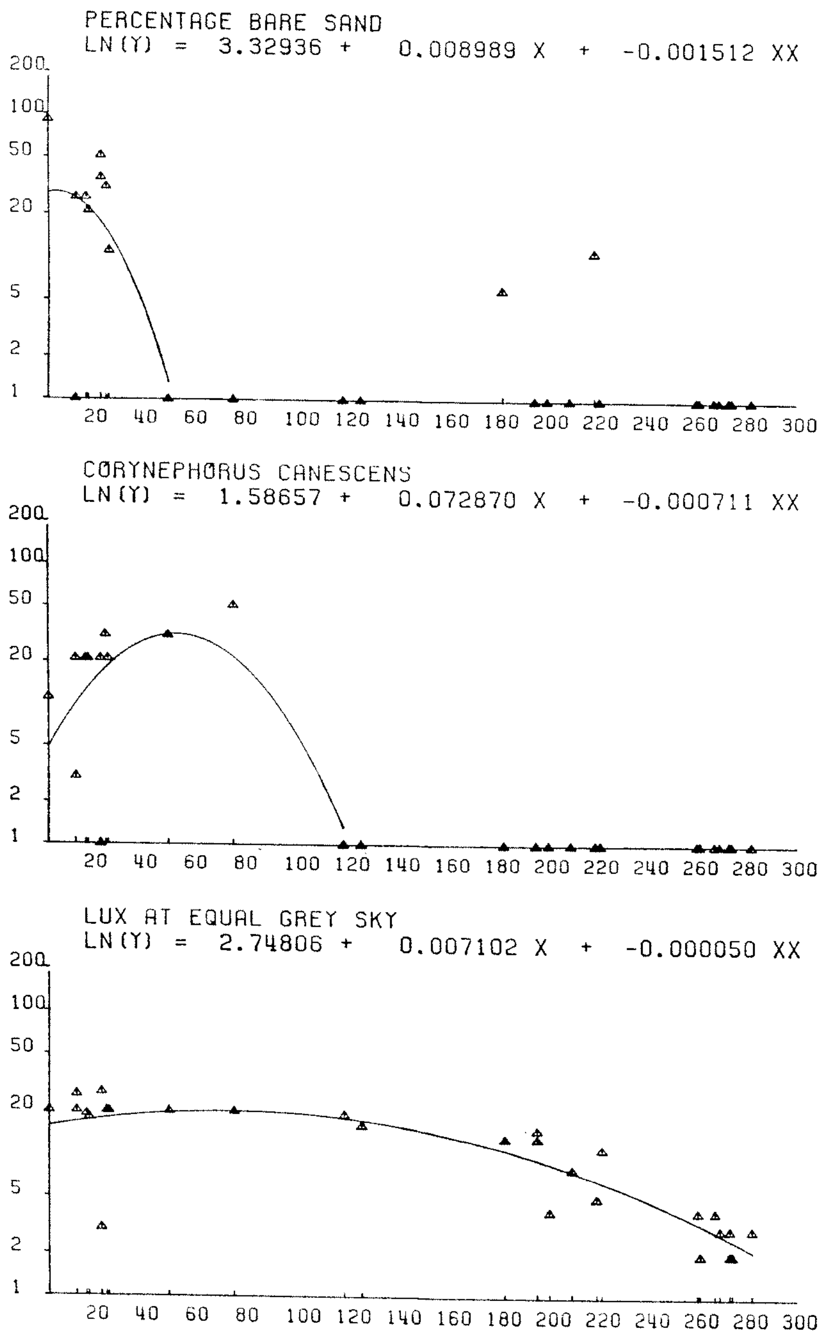
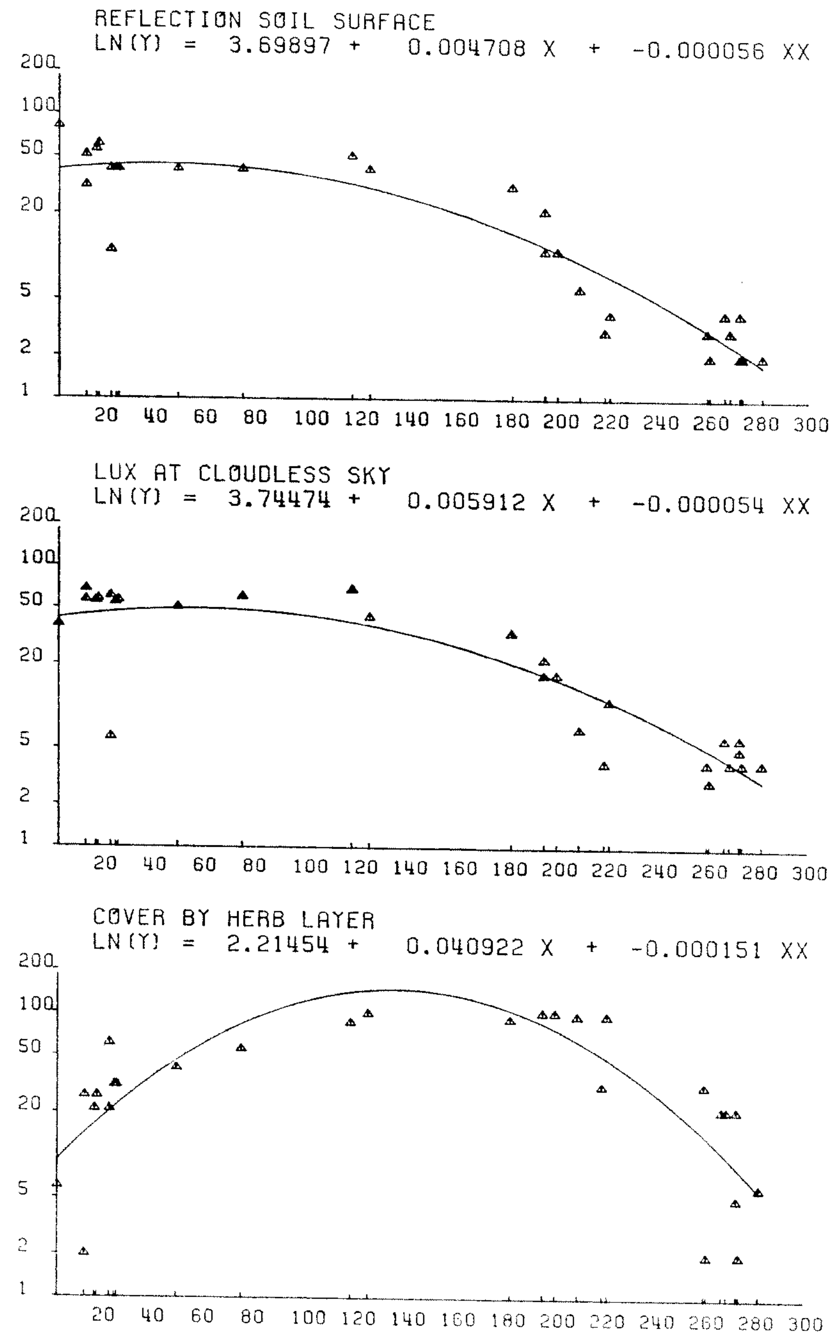


Fig. 6. The intensity of environmental factors (data in Table IV) over the range of biotopes ordinated on the basis of the main environmental factor. Second degree polynomials are plotted within the limits between which they were calculated.



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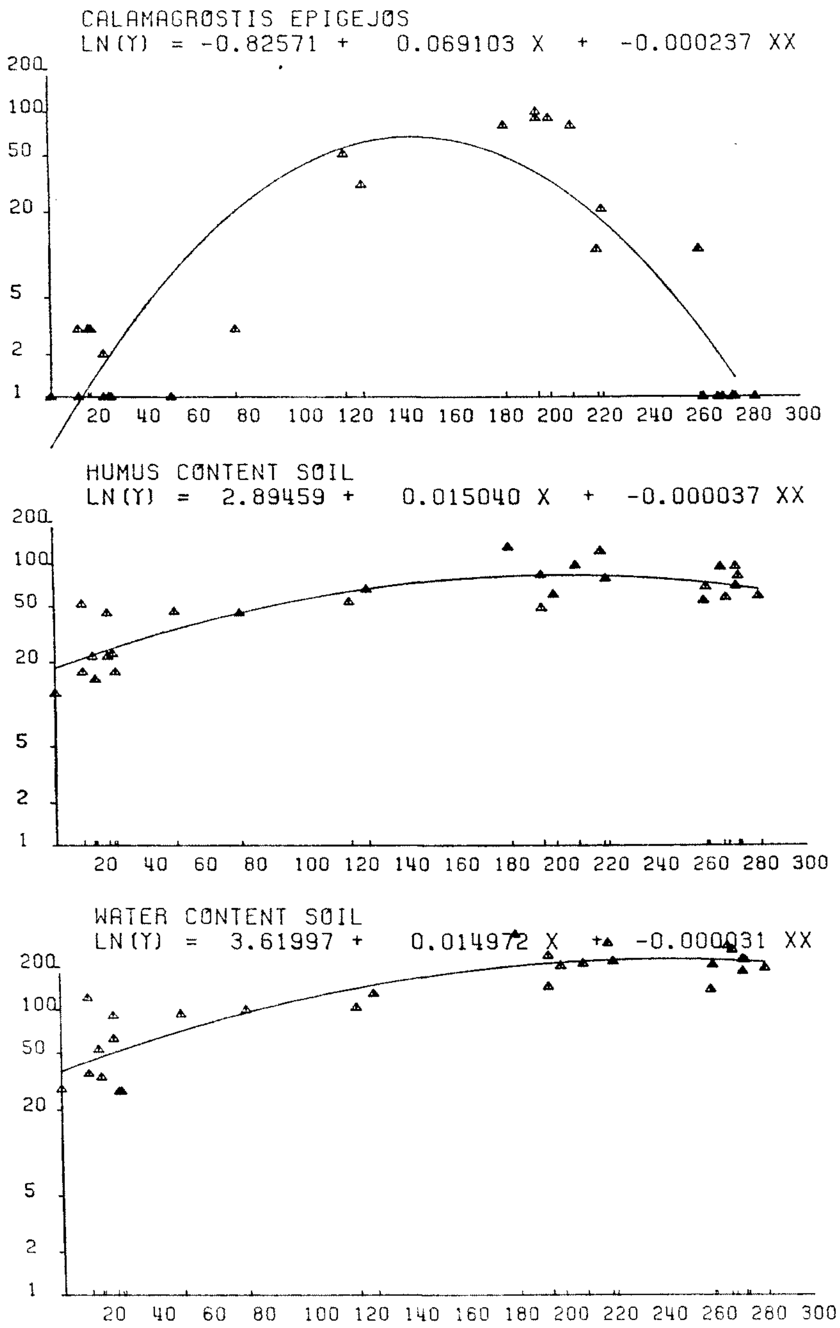

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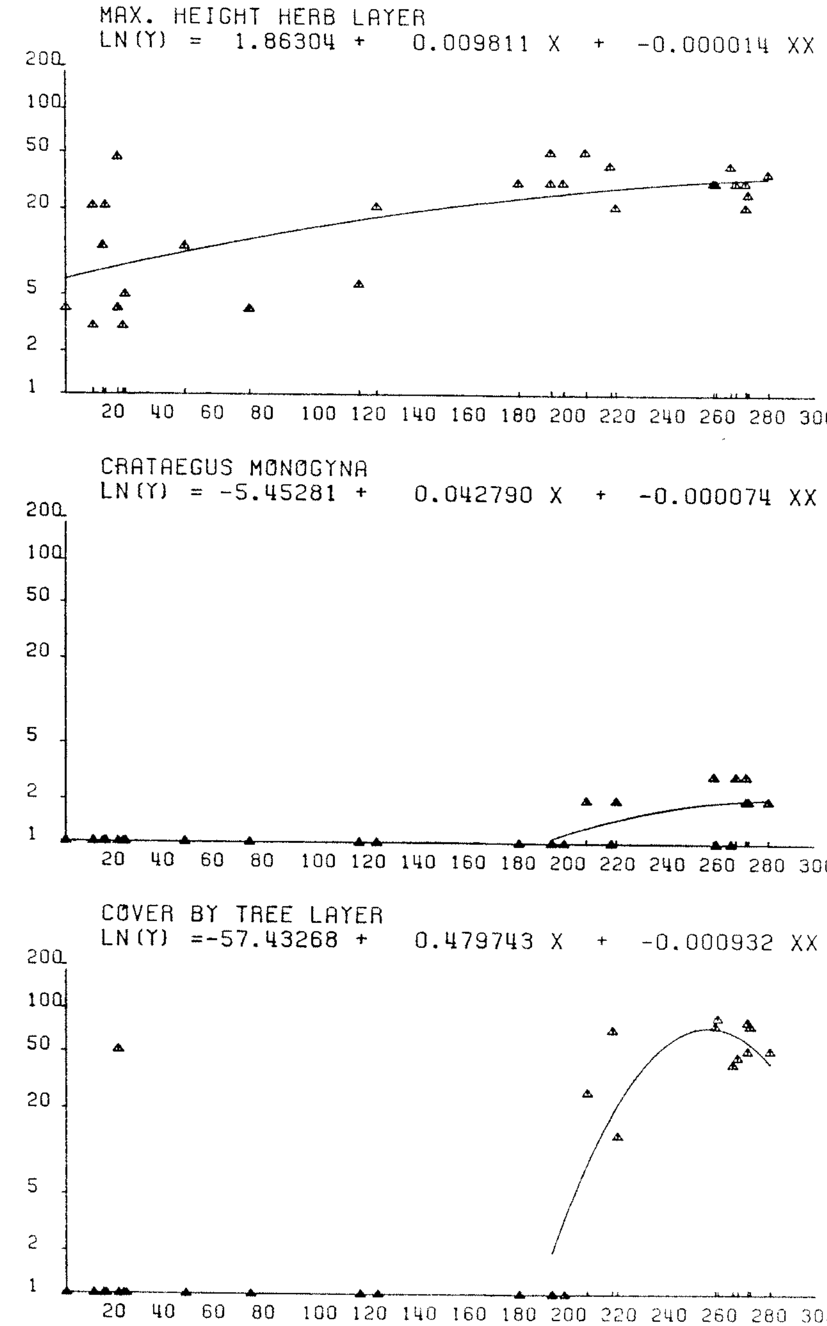

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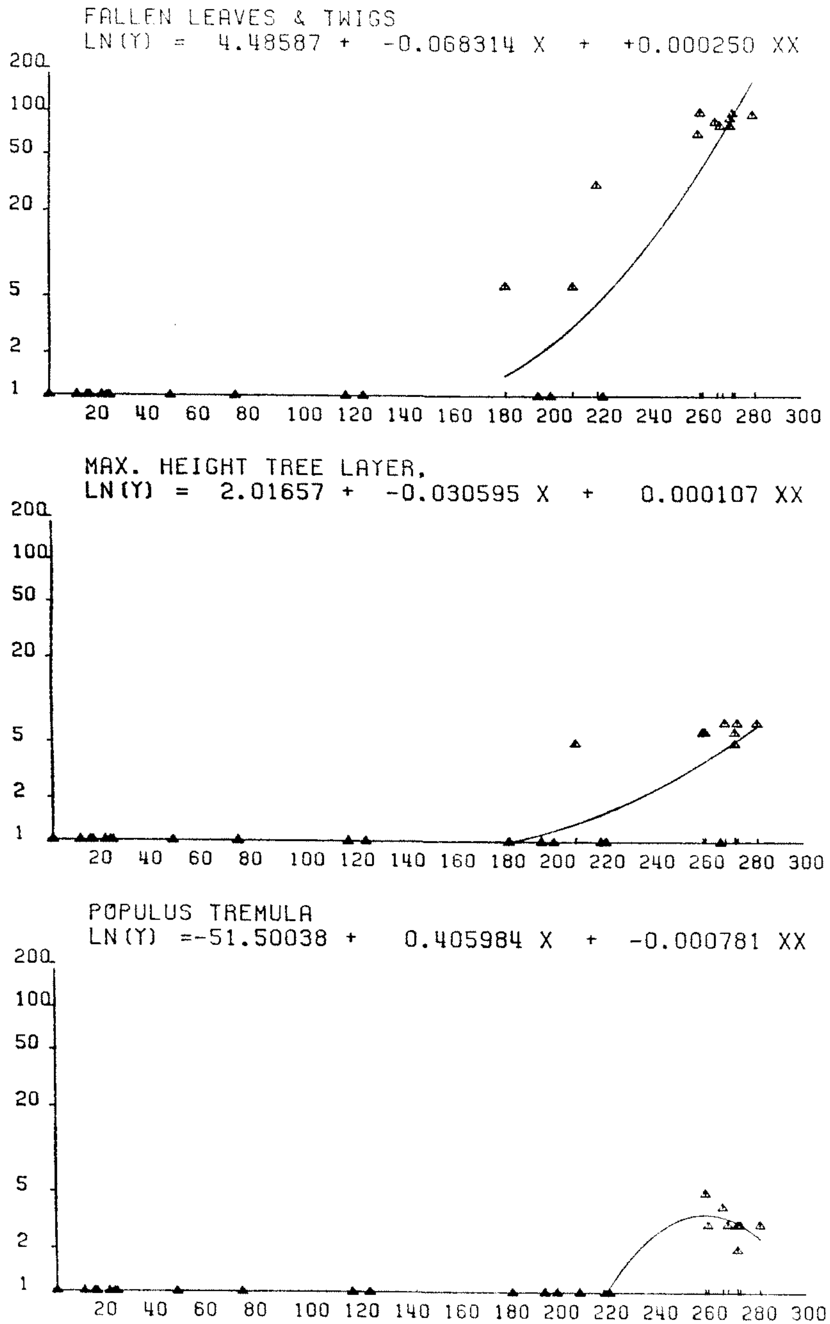

Fig. 6. continued.

upon an environmental characteristic whose intensity had proved to be linearly related to the principal component. Such an environmental characteristic would have enabled us to characterize the main factor (principal component). However, such a simple characteristic was not found. For the moment the main distribution factor can best be characterized by a number of environmental characteristics as plotted in Fig. 6.

It is obvious from this Fig. 6 that the characteristics measured are related to the principal component in a way similar to what we have seen in Fig. 5 for the spider species. Both species and environmental characteristics are based on one and the same principal component (main environmental factor) derived from Fig. 4. This result is also clear from Table VII in which both species and environmental characteristics are ordinated on the basis of their optimum values for this main factor. In fact there appear to be so many environmental factors at work and these are so closely related that it is impossible to say which one is playing the vital role in determining the distribution of a species. One should be well aware of the fact that the method used indicates the coherence between distributions of species and environmental characteristics. The causal relationships, however, still remain unknown.

Canonical correlation analysis. Canonical correlation analysis in this case aims to analyse the interrelations between two sets of variables, both measured on the same sample sites. The canonical correlation is in essence not the correlation between the variables themselves but between the canonical variates of the two sets, so between a weighted combination of the variables of either set.

A canonical correlation analysis can easily be interpreted in terms of principal components in the way of principal component analysis of two sets of variables with such a rotation that the components of the first set show a maximum correlation with the corresponding components of the second set. In the first place canonical correlation is of use for predictive purposes, in which one set of variables (environmental characteristics) act as a predictor for a second set of variables (species). Secondly canonical correlation has some advantages compared to a joint principal component analysis in the sence that only the underlying factors are compared and not also the specific variances of each of the sets. Thus the picture we get may be somewhat more clear.

In our case the 12 spider species as one set and a number of environmental characteristics as the second set were subjected to canonical correlation analysis. For computational reasons not all characteristics measured could be used as the number of variables (species + char-

TABLE VIII

Canonical correlation analysis on the distribution of 12 hunting spider species and 15 environmental characteristics. Based on log-transformed data (n+1). Original data in Tables II and IV. 28 common samples.

	canonical coefficients				*canonical structure*			
canonical variate no.	I	II	III	IV	I	II	III	IV
canonical correlation	0.99999	0.99891	0.9963	0.98365				
Spider species								
1. *Arctosa perita*	−0.142	−0.005	−0.207	0.232	−0.480	0.247	−0.339	0.298
2. *Alopecosa fabrilis*	−0.014	−0.029	0.051	0.076	−0.576	0.426	−0.086	0.190
3. *Alopecosa accentuata*	−0.310	0.253	0.380	−0.217	−0.433	0.800	0.079	0.200
4. *Pardosa monticola*	−0.070	0.064	−0.198	0.133	0.154	0.651	−0.053	0.216
5. *Pardosa pullata*	0.742	0.197	−0.139	−0.046	0.867	0.350	0.195	0.187
6. *Arctosa lutetiana*	0.283	−0.182	−0.154	−0.005	0.802	0.170	−0.080	−0.002
7. *Pardosa nigriceps*	−0.122	0.815	0.516	−0.672	0.873	0.312	0.265	0.027
8. *Aulonia albimana*	−0.014	−0.324	0.274	0.559	0.793	0.158	0.411	0.379
9. *Alopecosa cuneata*	−0.080	−0.173	−0.232	0.185	0.597	0.183	0.330	0.130
10. *Zora spinimana*	0.385	−0.163	−0.423	−0.049	0.907	−0.101	0.143	−0.092
11. *Trochosa terricola*	−0.269	−0.184	0.281	0.204	0.800	−0.211	0.408	−0.073
12. *Pardosa lugubris*	−0.081	−0.002	0.275	−0.179	−0.001	−0.785	0.395	−0.222
Environmental characteristics								
1. percentage bare sand	0.036	−0.038	−0.012	−0.086	−0.391	0.304	−0.382	0.190
2. cover *Corynephorus canescens*	−0.154	−0.123	−0.252	0.196	−0.581	0.454	−0.444	0.170
3. lux grey sky	0.539	−0.291	−0.366	0.340	−0.111	0.717	−0.301	0.468
4. reflection soil surface	−0.921	−0.369	0.173	1.042	−0.319	0.802	−0.163	0.420
5. lux cloudless sky	−1.026	0.912	0.287	−1.030	−0.272	0.817	−0.206	0.295
6. cover herb and grass layer	−0.073	0.221	0.308	−0.229	0.504	0.496	0.318	0.023
7. cover *Calamagrostis epigejos*	0.418	0.061	−0.131	0.189	0.778	0.330	0.355	0.303
8. humus content soil	−0.086	−0.420	0.668	0.485	0.667	−0.419	0.133	0.110
9. water content soil	0.316	0.243	−0.793	−0.372	0.673	−0.497	0.116	−0.196
10. max. height herb & grass layer	−0.164	−0.137	0.218	0.126	0.484	−0.497	0.394	−0.026
11. cover *Crataegus monogyna*	0.098	−0.296	−0.128	0.232	0.016	−0.740	0.299	−0.054
12. cover tree layer	−0.931	0.265	0.001	0.026	0.064	−0.830	0.166	−0.280
13. fallen leaves and twigs	0.343	−0.014	−0.607	0.018	0.002	−0.901	0.083	−0.230
14. max. height tree layer	−0.412	0.174	0.500	−0.140	−0.104	−0.792	0.312	−0.166
15. cover *Populus tremula*	−0.551	−0.231	0.414	0.084	−0.181	−0.852	0.207	−0.271

acteristics) has to be smaller than the number of samples (28). Hence 15 environmental characteristics were chosen for this purpose, *i.e.* those correlating best with the catches of the spider species. They are marked with an asterisk in Table III. The data obtained from this analysis are given in Table VIII. The first 4 canonical correlation coefficients proved to be very high (over .90). This means that the underlying factor(s) of both sets of variables do correlate extremely well and hence are indishinghuishable and hence may be thought to be the same.

In Table VIII under the heading of canonical structure the loadings of the variables on the canonical variates are given. The vizualisation of part of the canonical structure is given in Fig. 7. These loadings are comparable to the loadings on principal components as given in Table VI and Fig. 3. Close comparison of the canonical structure (Table VIII and Fig. 7) with the principal component structure (Fig. 3) reveals a far reaching identity between the principal components I and II and the canonical variates I and II. Since the canonical correlations are extremely high it is clear that both sets of variables,

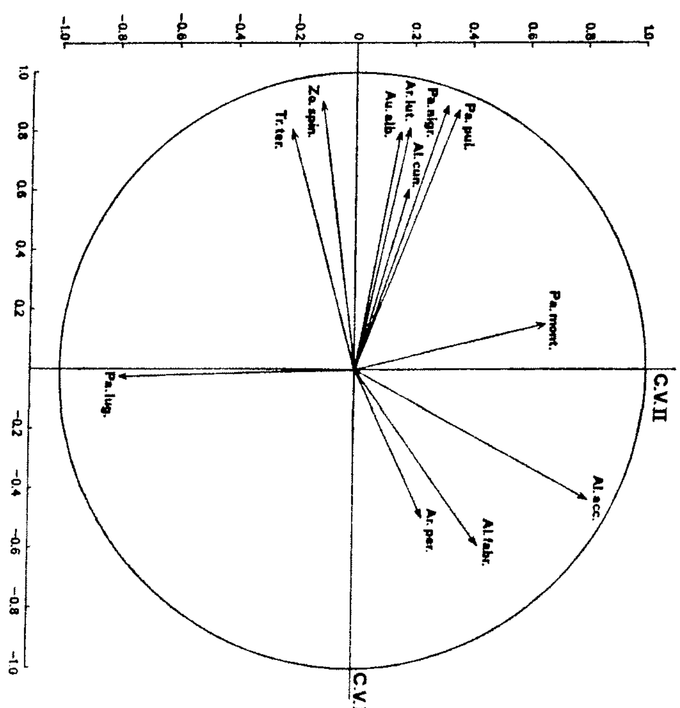

Fig. 7. Arrangement of the distributions of 12 hunting spiders in the hyperplane formed by the canonical variates I and II. Data in Table VIII.

the catches of the spiders and the values of the environmental characteristics are determined by the same factors. Moreover, these factors are not different from the ones found by principal component analysis.

As set forth in §3, non-linear relationships between variables and a basic factor give rise to a more-dimensional hyperplane of a definite shape. It may be concluded from the high canonical correlations that the hyperplanes of the two sets are of the same shape. The fact that we find more than one high canonical correlation not necessarily means that more then one basic factor is involved. We may just have to do with only one factor to which the variables are not linearly related. It may be concluded from the very regular shapes of the curves in Figs. 5 and 6 that this is the case here.

5. DISCUSSION

In the dune area under study, hunting spiders constitute a numerically important group of non-specialized predators of soft-skinned arthropods. In a previous paper their spatial distributions were studied (VAN DER AART, 1973). These distributions showed a wide overlap. However, clear differences between the distributions of species were shown to exist. The distributions proved to be linked to the structure of the vegetation or some related factor. It was the aim of this study to provide preliminary data for elucidating the nature of that factor. A more detailed and more extensive study is undertaken at the moment, in order to analyse the factors underlying the distributions of a variety of arthropod species in a more profound way. In the latter study the number of animal species sampled is larger and the area sampled is much larger. Besides, characteristics of microclimate, soil and vegetation are measured at more than a hundred sampling plots.

Since the study reported in this paper was undertaken 10 years after the previous one (VAN DER AART, 1973), it was worthwhile to check whether the spatial distributions of the species were still the same. A comparison of Fig. 2 of the present paper with Fig. 11 of the 1973 paper shows that the ordination of the species on the main environmental factor is basically the same, notwithstanding the fact that the sampling in this study was done with a modified sampling technique within a much shorter time and within a much more restricted area. This result is, however, not surprising as spider populations have proved to be fairly stable in numbers in time and to respond to changes in the vegetations fastly and precisely (VAN DER AART, 1973). Hence, the numbers caught represent very well the suitability of the biotope for each species.

Since the result of this ordination by principal component analysis

was very similar to the one of the previous study it is concluded that the main environmental factor causing this ordination is still the same. The main aim of this study was the identification of this main environmental factor (principal component). For this purpose 26 environmental characteristics were measured and plotted against the principal component in Fig. 6. Now it might be taken for granted that the chance is small that one of the 26 selected characteristics is the main environmental factor we were looking for. In fact, most of the environmental characteristics measured show optimum-curve-like responses to the principal component, indicating that these characteristics are dependent on the main factor rather than being identical with the main factor.

The only approximate linear relation to the main factor is shown by the characteristics describing the attenuation of incident light. Unfortunately, light intensity was more or less constant over a fairly wide range of the barer biotope types. This is no doubt due to the way in which light was measured. The lux meter of circular form with a diameter of 7.5 cm and 3 cm high, had necessarily to be placed on top of the moss layer and even could not be placed correctly in short grass vegetation. The measurements should have been done in the same stratum as the one in which the spiders live. As this was not the case, no distinction could be made between bare sand and areas covered by a carpeting layer of some centimeters height. However, it is clearly evident that these areas differ from the point of view of hunting spiders. Should we have been able to measure the amount of light entering on the level in which spiders live, *i.e.*, within and underneath short carpeting layers, then the differences with bare sandy areas are likely to be more pronounced.

In that case a more linear relationship between light intensity and the principal component would have been operative over nearly all biotope classes, and so a fairly ideal indicator for the principal component would have been found. It is of course by no means certain that hunting spiders mainly react to the degree of light intensity. It has up till now only been shown that the amount of incident light is correlated with the main factor. However, it is tempting to think of light as a proximate factor, since these spiders possess a well-developed visual power and are active at daytime. It is of course also possible that the spiders react to a closely linked factor like, for instance, the spectral distribution of light which is known to be different in different vegetation types.

It is evident that the main factor affecting the distribution is not related to plant species, as, for instance, *Calamagrostis epigejos* and *Festuca ovina* have the same effect on the spider species composition.

The same is true for *Populus tremula*, *Betula* sp. and *Crataegus monogyna*. The structure of the vegetation layer in which the species actually walk around seems not to be important either: moss carpets occur in dry sunny biotopes as well as in poplar woods, and both biotopes harbour different species.

Of course light is not the only characteristic showing a linear relation to the gradient "bare sand-woods". Also the humidity of the air is most likely linearly and positively correlated to this gradient. As spiders are very susceptible to dessication, such a factor might be of vital importance too. The same holds for a number of other characteristics like the decreasing fluctuations of day and night temperatures along the gradient, and other micrometeorological characteristics showing decreasing amplitudes. To which factor the spiders primarily react can only be determined in laboratory experiments. However, what we are able to do with the method exposed here is to pinpoint the intensity of the main factor (principal component) by measuring the environmental characteristics correlated with it as is done in Fig. 6. Another elegant property of the method of principal component analysis is that even when the nature of the main factor is not fully understood as in this case, the response of each species to that factor can be analysed and graphed (Fig. 5). Figs. 5 and 6 both form the essence of the present distribution analysis. The information laid down in these figures 5 and 6 and the underlying data form the basis for a distribution model for the hunting spiders studied. This set of relationships (model) will be put to the test.

In a new independent experiment in a nearby dune area never sampled before it will be tested whether the relations found are valid and strict enough to predict the hunting spider species composition and their respective numbers in certain biotopes after measuring a limited number of environmental characteristics. A preliminary test experiment of limited scope is meanwhile in progress.

Some more has to be said about the method of principal component analysis and the use of the similarity index in the relational matrix. Principal component analysis, being a fundamental technique in multivariate analysis, is now progressively used in a wide scala of sciences, *e.g.* social sciences, economics, earth sciences as well as in biology. However, the basic structure of principal component analysis is not always in agreement with the structure in nature. The basic premisses of principal component analysis not only include simplifications of the truth, but sometimes even downright misconceptions conflicting with the natural situation.

In this paper *a.o.* an attempt was made to incorporate more realistic conditions in principal component analysis. No doubt we are only at

the beginning of adapting multivariate techniques to the peculiarities of, for instance, distribution ecology. These improvements will certainly increase the value of these techniques as analytic tools in complex phenomena. An important point raised by WILLIAMSON (1972) is the choice of the similarity index. In this study as well as in the previous one (VAN DER AART, 1973) the product-moment correlation as an index of similarity was used as it is the most common version of principal component analysis. So, in fact the data were standardized as to means and variances. Of course this procedure brings about loss of information, *e.g.* the mean number of animals caught is omitted from the analysis. This is not a serious loss, since the mean number of animals caught depends among others on such complexes as the behaviour of the species towards pitfall traps. Information about differences in means would be very difficult to interpret, as nothing sensible can be said about these differences. As regards standardizing the variances it may be said that by not standardizing the variance, the ordering of species by the main environmental factor may interfere with the ordering of the species as to their variance. As pointed out by WILLIAMSON (1972) this effect can, in some circumstances, hide the resemblance of species reactions to environmental factors. Moreover, the use of simple correlations in the relational matrix expresses very clearly a wellknown and at first glance interpretable type of relation in contrast to other indices including covariances.

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