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THE EFFECT OF SOME ABIOTIC FACTORS ON THE DISTRIBUTION AND SELECTION OF HABITAT BY THE CARABID BEETLES IN THE CENTRAL SIERRA MORENA MOUNTAINS (SW Córdoba, Spain)

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COLEOPTERA
CARABIDAE
ECOLOGIE
DISTRIBUTION
ANALYSE CANONIQUE

RÉSUMÉ — Le rôle des facteurs abiotiques dans la sélection de l'habitat par les Coléoptères Carabiques est étudié. La zone étudiée est située au NW de la province de Cordoue (Espagne). Afin de caractériser l'aire nous l'avons replacée dans son cadre géologique, édaphique et climatique. Les techniques de récolte et les méthodes de préparation sont celles habituellement utilisées en entomologie. Une analyse de corrélation canonique des espèces présentes dans l'aire et des variables édaphiques du milieu a été réalisée. Les résultats montrent que certaines espèces sont conditionnées par divers paramètres abiotiques : température, humidité et texture du sol. D'autres facteurs (taux de matière organique et taux d'argile) ont une influence sur la distribution totale des espèces. Enfin, la caractérisation des biotopes par l'ensemble de leurs paramètres physico-chimiques met en évidence leur colonisation par des groupes d'espèces à des taux différents de probabilité.

COLEOPTERA
CARABIDAE
ECOLOGY
DISTRIBUTION
CANONICAL CORRELATION

ABSTRACT — The effect of certain environmental abiotic factors on the selection of habitat by the Carabid beetles is studied. The area in which the study was carried out is located in the northwest of Cordoba, Spain. The edaphic and microclimatic features of 75 sampling stations were studied in order to characterize the area. Collection and preparation techniques were those currently used in Entomology. The results show that the presence of certain species in the area is correlated to some abiotic parameters such as temperature, humidity and soil texture whereas other factors like organic matter content and clay percentage affect the overall distribution of the species. Thus, the joint effect of the physical-chemical parameters has a determining influence on the distribution and selection of habitat by the Carabid beetles in the Sierra Morena Mountains.

INTRODUCTION

The distribution and density of the Carabid beetle in different habitats has been widely studied in the last 20 years (Laren, 1936; Krogerus, 1936, 1960; Lindroth, 1954, 1959, etc...). All these authors have concluded that both distribution and density of the populations are conditioned by the micro and macroclimatic characteristics of the habitat. Moreover, they have also demonstrated that distribution and density are dependent on the species.

More recent experiments carried out under controlled laboratory conditions (Kirchner, 1960; Lauterbach, 1964; Becker, 1975; Thiele, 1977 and Pietrazsko and De Clerq, 1980) have shown that the species studied preferred certain climatic factors such as temperature, humidity or degree of sunlight and physical-chemical ones like soil type and pH when selecting their habitat. However, these experiments have not answered such questions as why some species are widely associated to certain habitats and not to others apparently with similar characteristics or ... which factors are responsible for this selection, etc...

The purpose of this paper is to confirm the above laboratory experiments by field data and to try and find answers to the aforementioned questions.

THE AREA

This research was carried out in Hornachuelos, in the northwest of Córdoba (37°40' - 38°40'N and 5°11' - 5°20'W). This is a geologically and geographically natural region of the Bembazar Basin (Cabanas, 1962). The Bembazar is an important tributary of the Guadalquivir River.

Population density in the area is low and forestry is the main resource. The soil is chemically and physically homogeneous with a granular friable and porous structure. It has a clayey texture, a pH ranging between 5.2 and 7.7 and high levels of organic matter and carbon.

According to Marvizon's classification (1981) its climate corresponds to subindices $C_3a_3s_2s_2$, i.e., to a subtropical mediterranean climate, characterized by subtropical heat and mediterranean subdry relative humidity.

Vegetation in the area is typical of a mediterranean mixed forest and belongs to the Durillignose



Fig. 1. — Topographic map of the studied area. The sampling sites are indicated by numbers.

formation, represented in Spain by the *Quercetea ilicis* type. It is constituted by perennial leaf and phanerophyte communities where shrubs and bushes predominate. The most representative species are : *Quercus suber*, *Q. rotundifolia*, *Pistacia lentiscus*, *Asparagus albus* and different species of *Erica* and *Cistus*.

MATERIAL AND METHODS

The carabid beetle was studied between 1982 and 1984 with weekly sampling taken from 75 randomly distributed stations (Fig. 1). Collection was mainly done by hand and therefore selective. Albeit some non-selective methods such as pit-fall traps or Berlese Tulgren's techniques were sometimes used. A total of 300 samples were taken.

The 3 250 specimens collected were fixed and prepared following usual entomological techniques. After their determination, 117 species, 68 genera and 19 tribes were identified.

Four of these tribes belonged to the subfamily *Carabinae* and the others to the *Harpalinae* one. A list of species may be found at the end of this paper.

Air temperature, humidity and soil pH were recorded under the same conditions at each sampling station. Soil samples were also taken in order to analyse soil texture, structure, organic matter and carbon content.

Temperature and humidity were measured on a portable thermohydrometer and soil pH on a Crison pH-meter (ph/mv = 506) for solid samples.

Soil texture was determined by Bouyoucos' density method (Guitian and Carballas, 1975) and soil structure following C.E.B.A.C. criterion (1971).

Organic matter and carbon content were calculated by Walkey Black's $K_2Cr_2O_7$ oxidative method as described by Allison (1965).

The determination of the species was based on De la Fuente (1930), Jeannel (1941, 1942), Antoine (1955-62), Jeanne (1965-1980), Freude (1976), Novoa (1977) and Pérez Zaballos (1983).

The environmental parameters and species taken from each station were used to make up the initial quantitative and qualitative matrices from which the mathematical analyses were developed. Factorial Analysis of the BMDP series, selecting the 4M Ordination Analysis in Principal Components and the 6M Canonical Correlation Analysis (Dixon, 1981) were used.

The analyses were made on an IBM 5110 computer from the Calculus Center at the School of Veterinary Science, University of Córdoba and on the UNIVAC DCT 2000 terminal from the Calculus Center at the School of Mathematics, University of Sevilla.

RESULTS

1. Characterization of the sampling stations according to their physical-chemical variables

The following physical-chemical variables were determined in each of the sampling stations : temperature, environmental humidity, pH, organic matter and carbon contents, structure and texture (% of clay, lime and sand). The results are shown in tables I and II.

Some of the differences found between the sampling stations and the selection of habitat by the carabid beetles may be determined through the use of these parameters. Table III shows the variations in the number and percentage of captured species from one station to another. These ranged from 0 to 28 in stations 45-61 and 1, respectively.

A matrix of the data obtained from the physical-chemical variables was submitted to a Factorial Analysis of Principal Components with the 4M

Table I. — Day temperature (T°C) and humidity (% H.R.) for each station (P.M.).

P.M.	T °C	%H.r.	P.M.	T °C	%H.r.
1	26.2	38.8	39	18.0	46.2
2	20.5	41.0	40	16.0	48.3
3	27.5	34.5	41	25.5	38.5
4	27.2	35.5	42	23.0	41.5
5	27.7	34.5	43	21.0	45.5
6	23.5	36.5	44	24.3	37.0
7	19.2	41.0	45	24.3	40.9
8	20.7	49.0	46	29.0	26.5
9	21.0	34.2	47	29.5	25.2
10	23.2	33.2	48	28.2	38.0
11	27.7	36.7	49	26.4	30.3
12	25.5	33.4	50	26.0	34.0
13	25.0	33.3	51	23.3	38.3
14	24.5	31.5	52	21.0	42.3
15	20.4	39.0	53	18.8	39.3
16	21.4	36.0	54	28.3	30.3
17	26.4	35.8	55	20.5	42.5
18	23.0	38.0	56	26.9	31.5
19	23.2	38.5	57	25.5	35.7
20	23.2	35.4	58	23.8	39.3
21	22.2	35.5	59	21.8	38.7
22	21.5	36.2	60	19.5	40.7
23	20.2	36.0	61	20.8	43.3
24	19.1	34.8	62	25.5	31.5
25	16.2	37.5	63	25.5	33.3
26	17.8	39.5	64	27.0	38.5
27	17.5	40.5	65	27.0	29.0
28	18.2	40.5	66	15.5	51.4
29	19.5	39.0	67	17.8	38.9
30	18.8	31.1	68	20.0	46.3
31	22.2	40.2	69	21.0	40.5
32	19.3	34.7	70	18.8	42.0
33	24.4	36.7	71	19.2	44.5
34	20.8	40.5	72	22.3	45.5
35	23.5	29.2	73	20.0	44.0
36	22.8	41.8	74	25.0	36.0
37	20.8	44.1	75	25.0	25.6
38	17.5	47.9			

Table II. — Physical-chemical variables tested in the sampling stations (P.M.). C : carbon, M.O. : organic matter, A : clay, L : lime, Ar : sand, Tex : texture, F : loamy.

P.M.	pH	% C	% M.O.	% A	% L	% Ar	Tex.
1	7.4	2.6	4.4	11	43	46	FL
2	7.2	1.8	1.8	11	45	44	FL
3	6.9	1.3	2.3	4	50	46	FL
4	6.5	3.9	6.8	7	47	46	FA
5	7.6	3.9	6.8	10.8	42.2	47	FL
6	7.4	2.0	4.1	3	50	47	FL
7	7.7	3.9	6.8	4	52	43	FA
8	6.7	1.0	1.8	8	30	62	FA
9	6.7	7.6	13.1	9	39	52	FA
10	5.8	7.9	13.6	7	43	50	FA
11	6.7	7.8	13.5	9	25	66	FA
12	5.4	7.8	13.5	7	39	54	FA
13	5.4	5.7	9.8	12	23	65	FA
14	5.8	7.8	13.9	7	33	60	FA
15	6.0	7.9	13.6	4	25	71	AF
16	5.6	7.7	13.3	5	26	69	FA
17	5.6	1.6	2.8	3	30	67	FA
18	5.5	1.7	2.9	5	43	52	FA
19	5.9	2.2	3.8	5	37	58	FA
20	6.0	1.3	2.2	3	40	57	FA
21	5.6	2.1	3.7	8	44	48	FA
22	6.0	0.8	1.4	5	52	43	FL
23	5.6	3.3	5.7	8	44	56	FA
24	6.0	5.1	8.7	8	50	42	FL
25	5.7	3.8	6.5	3	31	66	FA
26	6.1	7.2	12.3	6	32	62	FA
27	5.2	6.1	10.4	5	40	52	FA
28	5.7	7.3	12.6	7	30	63	FA
29	5.7	3.2	5.6	11	52	37	FA
30	5.3	1.2	2.1	13	54	32	FL
31	6.3	1.0	1.8	12	24	64	FL
32	5.7	4.7	8.1	8	30	62	FA
33	6.9	2.4	4.3	14	53	33	FL
34	7.1	0.8	1.4	4	36	50	FA
35	6.3	1.6	2.9	6	29	65	FA
36	6.5	6.8	11.1	8	50	42	FL
37	5.9	6.3	10.8	10	28	62	FA
38	7.6	8.0	13.7	10	38	52	FA
39	6.0	3.6	6.1	7	39	54	FA
40	5.6	2.1	3.6	9	67	24	FL
41	6.6	7.4	12.7	7	24	69	FA
42	6.0	3.5	6.1	9	48	43	F
43	5.9	3.7	6.3	10	38	52	F/FA
44	5.7	6.4	11.0	10	54	36	FL
45	6.0	5.2	5.5	8	47	45	F
46	5.2	3.7	6.3	0	48	52	FA
47	6.7	7.9	13.7	4	29	67	FA
48	6.9	2.8	4.8	7.5	38.5	54	FA
49	6.7	7.7	13.2	4	35	61	FA
50	6.9	8.0	13.7	14	30	56	FA
51	7.2	7.6	13.3	8	42	50	FA
52	7.3	7.3	12.6	10	42	48	FA
53	7.4	5.2	8.8	9	53	38	FL
54	7.2	2.6	4.6	9	24	67	FA
55	5.3	2.7	4.6	9	49	42	F
56	6.4	6.8	11.7	5	48	47	F
57	7.1	2.8	4.9	5	38	57	FA
58	5.2	7.8	12.1	4	34	62	FA
59	5.4	7.9	13.7	4	37	59	FA
60	7.5	5.8	10.0	3	55	42	FL
61	6.3	6.0	10.4	8	50	42	FL
62	6.2	1.5	2.5	7.5	16.5	76	AF
63	6.0	4.6	7.9	5	32	63	FA
64	5.6	7.9	13.7	5	12.5	82.5	AF
65	6.6	3.0	5.2	15	46	39	F
66	6.9	1.9	3.5	7	35	58	FA
67	6.4	2.3	4.0	0.9	39	52	F/FA
68	5.7	4.8	4.2	6	48	46	F
69	5.7	4.5	7.7	12	33	55	FA
70	6.8	4.0	7.0	14	36	60	FA
71	6.7	7.9	13.7	11	50	39	FL
72	5.5	3.4	6.8	13	48	39	FL
73	5.4	6.8	4.0	13	35	52	FA
74	5.5	5.7	9.8	13	30	57	FA
75	6.4	6.6	11.3	9	15	76	FA

program of the BMDP series previously described by Frane and Hill (1975) in order to demonstrate the aforementioned results. Table IV shows the correlation matrix between the variables analysed. A

Table III.— Number of species caught (n° sp.) and their overall percentage (% sp) at each sampling station (P.M.).

P.M.	n° Sp.	% Sp.	P.M.	n° Sp.	% Sp.
1	28	0.26	39	6	0.05
2	5	0.04	40	9	0.07
3	14	0.11	41	11	0.09
4	8	0.06	42	11	0.09
5	7	0.05	43	14	0.12
6	7	0.05	44	1	0.01
7	10	0.08	45	0	0.00
8	5	0.04	46	17	0.14
9	8	0.06	47	22	0.19
10	4	0.03	48	7	0.06
11	4	0.03	49	5	0.04
12	16	0.15	50	12	0.10
13	19	0.18	51	2	0.02
14	10	0.08	52	10	0.08
15	3	0.02	53	7	0.06
16	5	0.04	54	4	0.03
17	11	0.09	55	5	0.04
18	17	0.16	56	17	0.16
19	18	0.16	57	12	0.11
20	6	0.05	58	7	0.06
21	10	0.08	59	11	0.09
22	8	0.06	60	4	0.03
23	6	0.05	61	0	0.00
24	6	0.05	62	23	0.20
25	5	0.04	63	20	0.17
26	2	0.02	64	18	0.16
27	17	0.16	65	6	0.05
28	7	0.06	66	17	0.16
29	9	0.07	67	17	0.16
30	8	0.07	68	12	0.10
31	11	0.09	69	5	0.04
32	7	0.06	70	4	0.03
33	6	0.05	71	13	0.11
34	7	0.06	72	3	0.02
35	12	0.12	73	3	0.02
36	9	0.07	74	11	0.09
37	5	0.04	75	14	0.12
38	8	0.06			

relationship between the following parameters was found : temperature/humidity, organic matter/carbon content and clay/lime.

The variance absorbed by the first four axes was 0.72, 0.61, 0.46 and 0.27, respectively. The M.S.A. value was 0.52. The loaded factors after the axes were turned are shown in table V. In the graph obtained with axes I and II (fig. 2,1), the stations corresponding to a wet environment and to cultivated lands are separated according to clay and lime content. The latter is obviously greater in the first environment than in the second one. However, when the stations were represented according to organic matter and carbon content no separation was found. Moreover, no differences in clay and lime content were found in the forest stations.

When the temperature and humidity variables (axis III) were compared to organic matter and carbon contents (axis I), the 75 sampling stations were scattered over the four quadrants (Fig. 2,2).

However, only forest stations appeared in the quadrant with the highest percentage of organic

Table IV. — Correlation matrix for the variables tested in the area.

	T.	H.	pH	C.	M.O.	A.	L.	Ar.	Est.	Sp.
T.	1.000									
H.	-0.729*	1.000								
pH	0.090	0.046	1.000							
C.	0.009	-0.055	-0.046	1.000						
M.O.	0.032	-0.112	0.007	0.965*	1.000					
A.	0.016	0.151	0.133	0.019	-0.009	1.000				
L.	-0.177	0.236	0.123	-0.240	-0.248	0.030	1.000			
Ar.	0.176	-0.278	-0.151	0.224	0.240	-0.301	-0.955*	1.000		
Est.	-0.138	0.017	0.137	0.140	0.118	-0.023	-0.042	0.044	1.000	
Sp.	0.258	-0.206	-0.178	-0.103	-0.068	-0.177	-0.219	0.238	-0.078	1.000

Table V. — Loaded factors once the axes had been turned. Key of shortened forms like Table II.

VARIABLE	FACTOR			
	1	2	3	4
T	0.002	0.072	<u>0.920</u>	0.156
H	-0.088	-0.166	<u>-0.897</u>	0.100
pH	0.011	-0.090	0.043	<u>0.731</u>
C	<u>0.961</u>	0.133	0.007	-0.021
MO	<u>0.953</u>	0.146	0.056	-0.010
A	0.100	-0.166	-0.115	0.570
L	-0.158	<u>-0.954</u>	-0.095	0.016
Ar	0.128	<u>0.951</u>	0.131	-0.164
Est	0.291	-0.144	-0.109	-0.533
Sp	-0.266	0.302	0.376	-0.316

matter and carbon content as well as the highest temperatures and lowest humidity indices.

In the plane defined by the clay/lime and temperature/humidity variables (axes II and III, respectively) the sampling stations which are on the positive side of both axes correspond to the more humid and temperate habitats (Fig. 2,3). These habitats also have a greater percentage of lime than clay. The cultivated fields with more clayey soils are found on the negative side of axis II (Fig. 2,1). There were no significant differences in the distribution of the forest stations with respect to these variables.

The graphs obtained for axes I-IV, II-IV and III-IV show that soil pH (associated with factor 4) does not influence the distribution of the sampling stations (Fig. 2,4 and 3 respectively). The separation found in fig. 3,6 is due to soil texture.

The results show that there are significant differences between the sampling stations when some physical-chemical variables such as soil texture, temperature and humidity are analysed. This determines that different groups of species can colonize them, as will be shown in the following sections.

2. Analysis of the abiotic factors as possible agents in the selection of habitat

In order to analyse the possible influence of the abiotic factors on the distribution of the carabid beetle, an overall matrix of quantitative and dichotomic qualitative data (0 and 1) was developed. The quantitative data correspond to the physical-chemical variables (environmental and edaphic) tested at each station and the qualitative one to the presence or absence of the species.

A Canonical Correlation Analysis was carried out with data from the matrix using the BMDP Program (Dixon, 1982). This program establishes the degree of dependence between the variables from the data of the first set (environmental parameters) and the second one (species). This dependence may be inferred from the following information :

First, a linear correlation matrix between all the variables themselves relating them to the level of probability $\geq 90\%$ ($n = 73, p \leq 0.2$).

a) variables corresponding to the sampling stations themselves :

- temperature and humidity (negative correlation)
- clay and lime percentage (negative correlation)
- organic matter and carbon content (positive correlation)

b) variables corresponding to the sampling station and the species present :

- humidity is correlated to the species *Chlaenius vestitus*, *Stenolophus teutonius*, *Ocydromus maroccanus*, *O. coeruleus*, *O. dalhi* and *Tachyura inaequalis*.
- structure is correlated to the species *Licinus granulatus*, *Synechostictus elongatus*, *Bemdidium quadripustulatum*, *Ocydromus coeruleus*, *O. ustulatus*, *O. genei*, *Tachyura inaequalis*, *Ocys harpaloides* and *Asaphidion stierlini*.

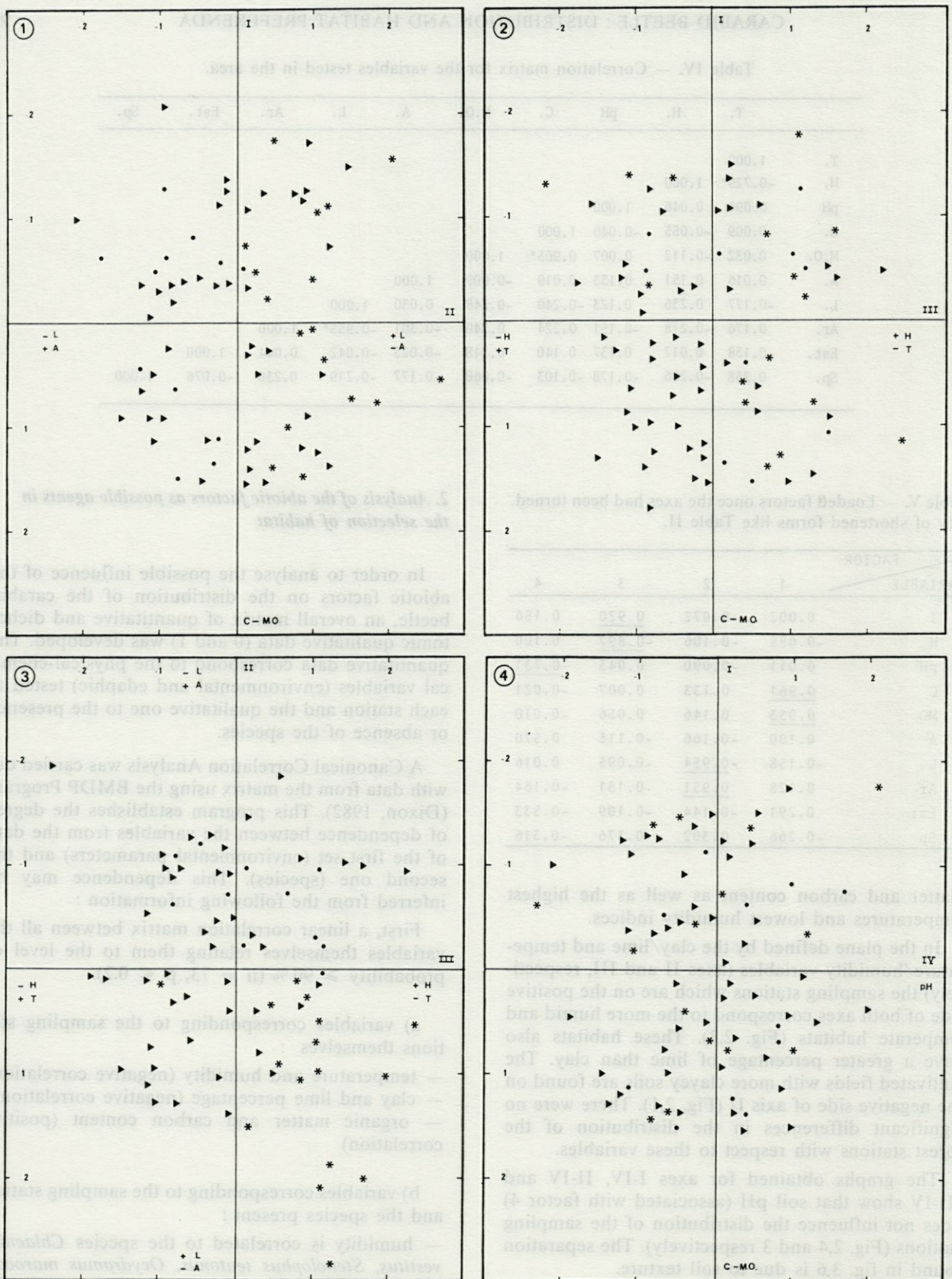


Fig. 2. — 1, representation in the plane defined by I and II axes of the sampling stations. forest stations; \blacktriangle wet stations; \bullet cultivated land; C : carbon content; M.O. : organic matter; T : temperature; H : humidity. 2, representation in the plane defined by I and III axes of the sampling stations. Symbol key like fig. 2,1. 3, representation in the plane defined by II and III axes of the sampling stations. Symbol key like fig. 2,1. 4, representation in the plane defined by I and IV axes of the sampling stations. Symbol key like fig. 2,1.

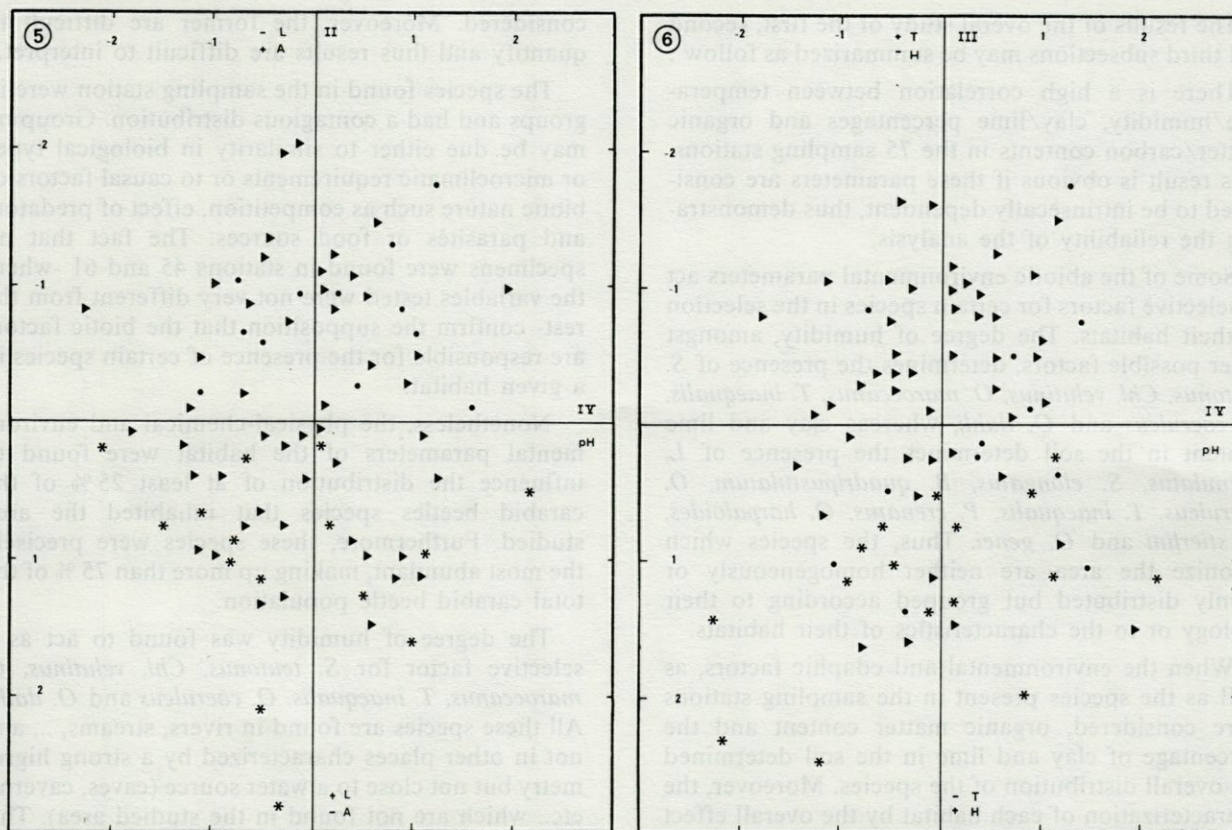


Fig. 3. — 5, representation in the plane defined by II and IV axes of the sampling stations. Symbol key like fig. 2,1. 6, representation in the plane defined by III and IV axes of the sampling stations. Symbol key like fig. 2,1.

c) variables corresponding to the species themselves.

Second, a canonical correlation matrix between each variable from the first group (physical-chemical) with all those from the second one (species), basing the canonical values on the last one. Data were obtained from this correlation for the values of the statistical parameter « F » (Ostle, 1965). This parameter was significant only for organic matter content (75 % probability and 71 degrees of freedom) and texture (90 % probability and 3 degrees of freedom).

These « F » values were not significant in any of the other variables. Thus it may be inferred that they do not influence or influence minimally in the distribution of the species (Table VI).

Third, a correlation matrix of the each variable in the second group (species) with all those from the first group (physical-chemical) basing the canonical values on the last one.

The « F » test was significant (with 10 and 64 degrees of freedom at 99 % ($p \geq 0.01$, $F = 0.380$) for *Steropus globosus*, at 95 % ($p \geq 0.05$, $F = 0.502$) for *Perileptus areolatus*, at 90 % ($p \geq 0.1$, $F = 0.586$) for *Dyschirius chalybaeus*, *Orthomus barbarus*, *Platysma nigrita*, *Calathus granatensis*, *Carierus tricuspis-*

Table VI. — Statistical parameter « F » values and their significance for the physical-chemical variables.

VARIABLE	STATISTIC "F"
T	2.34
H	5.26
pH	2.11
C	3.82
MO	0.75 *
A	0.63 **
L	6.52
Ar	2.04
Est	1.70

atus, *Lebia cyanocephalus*, *Microlestes corticalis*, *M. luctuosus*, *M. nigrita* and *M. abeillei*; at 75 % ($p \geq 0.025$, $F = 0.770$) for *L. fulvibarbis*, *Trepanes articulatus*, *O. hispanicus*, *Odontonyx fuscatus*, *Platyderus* sp., *Calathus circumseptus* and *Amara anthobia* ; at 50 % ($p \geq 0.50$, $F = 1.060$) for *Phyla tethys*, *O. maroccanus*, *A. ruficornis*, *Harpalus distinguendus*, *L. granulatus*, *Zabrus ignavus*, *Z. rotundatus*, *Bradycellus verbasci* and *Callistus lunatus*.

This last matrix is included in the annex at the end of the paper.

The results of the overall study of the first, second and third subsections may be summarized as follow :

There is a high correlation between temperature/humidity, clay/lime percentages and organic matter/carbon contents in the 75 sampling stations. This result is obvious if these parameters are considered to be intrinsically dependent, thus demonstrating the reliability of the analysis.

Some of the abiotic environmental parameters act as selective factors for certain species in the selection of their habitats. The degree of humidity, amongst other possible factors, determines the presence of *S. teutonius*, *Chl. velutinus*, *O. maroccanus*, *T. inaequalis*, *O. coeruleus* and *O. dahli*, whereas clay and lime content in the soil determines the presence of *L. granulatus*, *S. elongatus*, *B. quadripustulatum*, *O. coeruleus*, *T. inaequalis*, *P. crenatus*, *O. harpaloides*, *A. stierlini* and *O. genei*. Thus, the species which colonize the area are neither homogeneously or evenly distributed but grouped according to their biology or to the characteristics of their habitats.

When the environmental and edaphic factors, as well as the species present in the sampling stations were considered, organic matter content and the percentage of clay and lime in the soil determined the overall distribution of the species. Moreover, the characterization of each habitat by the overall effect of the physical-chemical parameters determined that the habitat could be colonized (at different probability levels) by a given group of species. The following species were the ones most influenced by the characteristic of the habitat : *S. globosus*, *P. aerolatus*, *D. chalybaeus*, *O. barbarus*, *P. nigrita*, *C. granatensis*, *C. tricuspidatus*, *L. cyanocephala*, *M. corticalis*, *M. negrita* and *M. abeillei*.

DISCUSSION

From our study, it is possible to differentiate the randomly distributed sampling stations in an apparently uniform geographical, edaphic, climatic and vegetative area according to physical-chemical and edaphic variables.

Amongst the different factors which can be registered in a given area, the ones chosen were used for the following reasons :

a) most of them had been studied under laboratory conditions as was already mentioned. Results from these works has shown a preference or non preference to them by certain species and thus we wanted to confirm these data with field studies for other species.

b) these factors are easily measurable and quantifiable and can thus be submitted to analysis and,

c) other factors such vegetation, type of habitat, slope, etc..., are indirectly determined by the ones

considered. Moreover, the former are difficult to quantify and thus results are difficult to interpret.

The species found in the sampling station were in groups and had a contagious distribution. Grouping may be due either to similarity in biological types or microclimatic requirements or to causal factors of biotic nature such as competition, effect of predators and parasites or food sources. The fact that no specimens were found in stations 45 and 61 -where the variables tested were not very different from the rest- confirm the supposition that the biotic factors are responsible for the presence of certain species in a given habitat.

Nonetheless, the physical-chemical and environmental parameters of the habitat were found to influence the distribution of at least 25 % of the carabid beetles species that inhabited the area studied. Furthermore, these species were precisely the most abundant, making up more than 75 % of the total carabid beetle population.

The degree of humidity was found to act as a selective factor for *S. teutonius*, *Chl. velutinus*, *O. maroccanus*, *T. inaequalis*, *O. coeruleus* and *O. dahli*. All these species are found in rivers, streams, ... and not in other places characterized by a strong hygrometry but not close to a water source (caves, caverns, etc.. which are not found in the studied area). This implies that the water source indirectly determines the presence of these species.

On the other hand, soil structure (with respect to clay and lime content is highly correlated to the presence or absence of certain species (*L. granulatus*, *S. elongatus*, *B. quadripustulatum*, *O. coeruleus* ...). This feature probably acts as a physical obstacle in the burial of the eggs or of the species themselves.

In short, from this study and in accordance with Thiele (1977) it may be concluded that the microclimatic factors have a decisive influence on the ecological distribution of most Carabid species. Moreover, in our case in which these factors, isolated or jointly, were related to environmental (climatic) and edaphic (physical-chemical) variables, they were also found to determine in part the distribution and selection of habitat in the Sierra Morena Mountains.

LIST OF SPECIES

CARABIDAE - CARABINAE - Carabini : *Calosoma (Campalita) maderae indagator* (Fabricius, 1787); *Hadrocarabus (Hadrocarabus) lusitanicus latus* (Dejean, 1826); *Hygrocarabus (Rhabdotocarabus) melancholicus costatus* (Germar, 1824); *Macrothorax rugosus* (Fabricius, 1792).

Nebriini : *Nebria (Nebria) salina* Fairmaire and Laboulbène, 1854; *Leistus (Leistus) fulvibarbis* Dejean, 1826.

Notiophilini : *Notiophilus geminatus* Dejean, 1831; *Notiophilus biguttatus* (Fabricius, 1779); *Notiophilus quadripunctatus* Dejean, 1826.

Scartini : *Dyschirius (Dyschirius) punctatus* (Dejean, 1825); *Dyschirius (Dyschirius) hispanus* Putzey, 1866.

HARPALINAE - Trechini : *Perileptus areolatus* (Creutzer, 1799); *Trechus (Trechus) fulvus* Dejean, 1831; *Trechus (Trechus) quadristriatus* (Schrank, 1781); *Trechus (Trechus) obtusus* Erichson, 1837.

Bembidiini : *Typhlocharis baetica* Ehlers, 1883; *Eotachys bistriatus* (Duftschmid, 1831); *Tachyura parvula* (Dejean, 1831); *Tachyura lucasi* (Jacquelin-Duval, 1852); *Tachyura inaequalis* (Kolenati, 1845); *Tachyta nana* (Gyllenhal, 1810); *Ocys harpaloides* (Serville, 1821); *Asaphidion stierlini* (Heyden, 1880); *Asaphidion curtum* (Heyden, 1870); *Asaphidion rosii* (Schaum, 1857); *Metallina lampros* Herbst, 1784; *Metallina (Neja) ambiguus* Dejean, 1831; *Phyla tethys* (Netolitzky, 1926); *Notaphus varius* (Olivier, 1795); *Emphanes (Emphanes) latiplaga* Chaudoir, 1850; *Trepanes (Trepanes) maculatus* (Dejean, 1831); *Philochthus iricolor* (Bedel, 1879); *Philochthus lunulatus* (Fourcroy, 1785); *Bembidion quadripustulatum* Serville, 1823; *Princidium (Testedium) laetum* Brullé, 1838; *Princidium (Actedium) paulinoi* Heyden, 1870; *Ocydromus (Ocydromus) decorus* (Zenker, 1801); *Ocydromus (Nepha) genei* (Küster, 1847); *Ocydromus (Nepha) lateralis* (Dejean, 1831); *Ocydromus (Peryphus) ustulatus* (Linné, 1758); *Ocydromus (Peryphus) hispanicus* (Dejean, 1831); *Ocydromus (Bembidionetolitzkya) coeruleus* (Serville, 1826); *Ocydromus (Peryphanes) maroccanus* Antoine, 1923; *Synechostictus elongatus* (Dejean, 1831); *Synechostictus cribrum* (Jacquelin-Duval, 1851); *Synechostictus dalhi* (Dejean, 1831).

Patrobini : *Penetretus rufipennis* (Dejean, 1828)

Pterostichini : *Abacetus salzmanni* (Germar, 1824); *Poecilus (Poecilus) kugelanni* (Panzer, 1797); *Poecilus (Poecilus) cupreus* (Linné, 1758); *Poecilus (Poecilus) quadricollis* (Dejean, 1828); *Poecilus (Angoleus) crenatus* (Dejean, 1838); *Poecilus (Angoleus) baeticus* (Rambur, 1838); *Orthomus barbarus* (Dejean, 1828); *Argutor (Omaseus) aterrimus nigerrimus* (Dejean, 1828); *Percus (Pseudopercus) politus* (Dejean, 1831); *Platysma (Melanius) nigrita* (Fabricius, 1792); *Steropus (Corax) globosus* (Fabricius, 1792); *Odontonyx elongatus* (Wollaston, 1854); *Odontonyx fuscatus* (Dejean, 1828); *Anchomenus dorsalis* (Pontoppidan, 1763); *Anchus ruficornis* (Goeze, 1777); *Platyderus saezi* Vuillefroy, 1868; *Calathus (Calathus) circumseptus* Germar, 1824; *Calathus (Calathus) piceus* (Mars-

ham, 1802); *Calathus (Calathus) ambiguus* (Paykull, 1790); *Calathus (Calathus) granatensis* Vuillefroy, 1866; *Calathus (Calathus) baeticus* Rambur, 1824; *Pristonychus (Laemosthenus) complanatus* Dejean, 1828.

Amarini : *Amara (Amara) aenea* (De Geer, 1774); *Amara* sp., *Amara (Amara) anthobia* (Villa, 1833); *Amara (Amara) eurynota* (Panzer, 1797).

Zabrini : *Zabrus (Zabrus) ignavus* Csiki, 1907; *Zabrus (Iberozabrus) rotundatus* (Rambur, 1842).

Harpalini : *Carterus tricuspis* (Fabricius, 1792); *Ditonus clypeatus* (Rossi, 1790); *Ditonus sphaerocephalus* (Olivier, 1795); *Ophonus (Pseudophonus) griseus* (Panzer, 1787); *Harpalus (Harpalus) tenebrosus* (Dejean, 1829); *Harpalus (Harpalus) distinguendus* (Duftschmid, 1812); *Bradycellus verbasci* (Duftschmid, 1812); *Acupalpus brunneipes* (Sturm, 1828); *Egadroma marginatum* (Dejean, 1829); *Stenolophus skrimshiranus* Stephens, 1828; *Stenolophus teutonius* (Schrank, 1781); *Stenolophus abdominalis* Gene, 1836.

Licinini : *Licinus punctatulus granulatus* Dejean, 1826.

Oodini : *Lonchosternus hispanicus* (Dejean, 1826).

Callistini : *Chlaenius (Chlaenius) velutinus* (Duftschmid, 1812); *Chlaenius (Chlaeniellus) vestitus* (Paykull, 1790); *Chlaenius (Chlaeniellus) olivieri* Crotch, 1870; *Callistus lunulatus* (Fabricius, 1775).

Masoreini : *Masoreus wetterhalli* (Gyllenhal, 1813).

Lebiini : *Lebia (Lamprias) cyanocephala* (Linné, 1758); *Singilis soror* Rambur, 1839; *Singilis bicolor* Rambur, 1839; *Trymosternus onychinus plicipennis* Chaudoir, 1837; *Demetrius atricapillus* (Linné, 1758); *Lionychus albonotatus* (Dejean, 1825); *Apristus europaeus* Mateu, 1980; *Mesolestes scapularis* (Dejean, 1829); *Microlestes corticalis* (Dufour, 1820); *Microlestes* sp.; *Microlestes negrita* Wollaston, 1854; *Microlestes luctuosus* Holdhaus, 1904; *Microlestes ibericus* Holdhaus, 1912; *Microlestes abeillei* (Brisout, 1885); *Syntomus fuscumaculatus* (Motschoulsky, 1844); *Syntomus foveatus* (Fourcroy, 1785); *Syntomus obscurouguttatus* (Duftschmid, 1812); *Metadromius ramburi* La Brulerie, 1867; *Polystichus connexus* (Fourcroy, 1785);

Pheropsophini : *Pheropsophus hispanicus* (Dejean & Latreille, 1823).

Brachinini : *Brachinus (Brachinus) sclopeta* (Fabricius, 1792); *Brachinus (Pseudaptinus) bellicosus* Dufour, 1826.

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Annex. — Squared multiple correlations of each variable in the second set with all variables in the first set.

VARIABLE	R-SQUARED	ADJUSTED R-SQUARED	F STATISTIC	DEGREES OF FREEDOM	P-VALUE	VARIABLE	R-SQUARED	ADJUSTED R-SQUARED	F STATISTIC	DEGREES OF FREEDOM	P-VALUE		
11 (x)11	0.160818	0.029696	1.23	10	64	0.2917	60 (x)60	0.079474	-0.064358	0.55	10	64	0.8458
12 (x)12	0.198871	0.073695	1.59	10	64	0.1303	61 (x)61	0.235222	0.115725	1.97	10	64	0.0517
13 (X)13	0.107263	-0.032228	0.77	10	64	0.6577	62 (x)62	0.204192	0.079847	1.64	10	64	0.1149
14 (x)14	0.154146	0.021981	1.17	10	64	0.3298	63 (x)63	0.075985	-0.068392	0.53	10	64	0.8653
15 (x)15	0.366661	0.267702	3.71	10	64	0.0006	64 (x)64	0.153961	0.021768	1.16	10	64	0.3309
16 (x)16	0.070896	-0.074276	0.49	10	64	0.8916	65 (x)65	0.040681	-0.109213	0.27	10	64	0.9853
17 (x)17	0.119025	-0.018627	0.86	10	64	0.5700	66 (x)66	0.105482	-0.034287	0.75	10	64	0.6708
18 (x)18	0.101779	-0.038568	0.73	10	64	0.6979	67 (x)67	0.115877	-0.021110	1.85	10	64	0.5860
19 (x)19	0.133134	-0.002314	0.98	10	64	0.4672	68 (x)68	0.455808	0.370777	5.36	10	64	0.0000
20 (x)20	0.215591	0.093027	1.76	10	64	0.0867	69 (x)69	0.073198	-0.071615	0.51	10	64	0.8001
21 (x)21	0.063538	-0.081784	0.43	10	64	0.9243	70 (x)70	0.087144	-0.055490	0.61	10	64	0.7989
22 (x)22	0.243161	0.124904	2.06	10	64	0.0415	71 (x)71	0.316107	0.209248	2.96	10	64	0.0041
23 (x)23	0.132353	-0.003217	0.98	10	64	0.4727	72 (x)72	0.148656	0.015633	1.12	10	64	0.3633
24 (x)24	0.046220	-0.102808	0.31	10	64	0.9759	73 (x)73	0.184447	0.057017	1.45	10	64	0.1805
25 (x)25	0.195290	0.069554	1.55	10	64	0.1416	74 (x)74	0.150822	0.018138	1.14	10	64	0.3499
26 (x)26	0.157644	0.026026	1.20	10	64	0.3095	75 (x)75	0.255189	0.138812	2.19	10	64	0.0294
27 (x)27	0.111336	-0.027518	0.80	10	64	0.6274	76 (x)76	0.064007	-0.082242	0.44	10	64	0.9224
28 (x)28	0.143269	0.009405	1.07	10	64	0.3980	77 (x)77	0.218215	0.096061	1.79	10	64	0.0811
29 (x)29	0.181099	0.053146	1.42	10	64	0.1940	78 (x)78	0.100436	-0.040121	0.71	10	64	0.7076
30 (x)30	0.175189	0.046313	1.36	10	64	0.2196	79 (x)79	0.089465	-0.052806	0.63	10	64	0.7837
31 (x)31	0.142655	0.008694	1.06	10	64	0.4020	80 (x)80	0.103362	-0.036738	0.74	10	64	0.6864
32 (x)32	0.169969	0.040276	1.31	10	64	0.2442	81 (x)81	0.316107	-0.023122	0.83	10	64	0.5990
33 (x)33	0.353046	0.251959	3.49	10	64	0.0010	82 (x)82	0.071520	-0.073556	0.49	10	64	0.8885
34 (x)34	0.131251	-0.004492	0.97	10	64	0.4806	83 (x)83	0.131973	-0.003656	0.97	10	64	0.4754
35 (x)35	0.100720	-0.039792	0.72	10	64	0.7856	84 (x)84	0.109341	-0.029824	0.79	10	64	0.6422
36 (x)36	0.251429	0.134465	2.15	10	64	0.0328	85 (x)85	0.148117	0.015011	1.11	10	64	0.3667
37 (x)37	0.139041	0.004516	1.03	10	64	0.4262	86 (x)86	0.142900	0.008984	1.07	10	64	0.4004
38 (x)38	0.057654	-0.089587	0.39	10	64	0.9458	87 (x)87	0.307920	0.199783	2.85	10	64	0.0054
39 (x)39	0.214190	0.091407	1.74	10	64	0.0899	88 (x)88	0.280583	0.168174	2.70	10	64	0.0135
40 (x)40	0.088217	-0.054249	0.62	10	64	0.7919	89 (x)89	0.300960	0.191735	2.76	10	64	0.0069
41 (x)41	0.214088	0.091289	1.74	10	64	0.0901	90 (x)90	0.258066	0.142139	2.23	10	64	0.0270
42 (x)42	0.121314	-0.015980	0.88	10	64	0.5530	91 (x)91	0.373221	0.275286	3.81	10	64	0.0005
43 (x)43	0.130148	-0.005767	0.96	10	64	0.4885	92 (x)92	0.181391	0.053483	1.42	10	64	0.1928
44 (x)44	0.234933	0.115391	1.97	10	64	0.0522	93 (x)93	0.245683	0.127821	2.08	10	64	0.0387
45 (x)45	0.286413	0.174915	2.57	10	64	0.0112	94 (x)94	0.077526	-0.066610	0.54	10	64	0.8569
46 (x)46	0.060228	-0.086611	0.41	10	64	0.9369	95 (x)95	0.188696	0.061930	1.49	10	64	0.1644
47 (x)47	0.187325	0.060344	1.48	10	64	0.1695	96 (x)96	0.140150	0.005798	1.04	10	64	0.4187
48 (x)48	0.281971	0.169779	2.51	10	64	0.0129	97 (x)97	0.244899	0.126914	2.08	10	64	0.0395
49 (x)49	0.258932	0.143130	2.24	10	64	0.0263	98 (x)98	0.292340	0.181768	2.64	10	64	0.0092
50 (x)50	0.255335	0.138981	2.19	10	64	0.0292	99 (x)99	0.113241	-0.025315	0.82	10	64	0.6132
51 (x)51	0.147807	0.014652	1.11	10	64	0.3687	100 (x)100	0.107263	-0.032228	0.77	10	64	0.6577
52 (x)52	0.209889	0.086434	1.70	10	64	0.1000	101 (x)101	0.129004	-0.007089	0.95	10	64	0.4967
53 (x)53	0.092311	-0.049516	0.65	10	64	0.7647	102 (x)102	0.211908	-0.088769	1.72	10	64	0.0951
54 (x)54	0.174422	0.045426	1.35	10	64	0.2231	103 (x)103	0.214527	0.091797	1.75	10	64	0.0891
55 (x)55	0.116877	-0.021110	0.85	10	64	0.5860	104 (x)104	0.188471	0.061669	1.49	10	64	0.1652
56 (x)56	0.158682	0.027226	1.21	10	64	0.3036	105 (x)105	0.067919	-0.077719	0.47	10	64	0.0056
57 (x)57	0.311272	0.203659	2.89	10	64	0.0048	106 (x)106	0.353755	0.252780	3.50	10	64	0.0010
58 (x)58	0.161132	0.030058	1.23	10	64	0.2900	107 (x)107	0.258024	0.142090	2.23	10	64	0.0270
59 (x)59	0.268698	0.154432	2.35	10	64	0.0196	108 (x)108	0.238475	0.119487	2.00	10	64	0.0473