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HABITAT PREFERENCES OF APHIDOPHAGOUS COCCINELLIDS [*COLEOPTERA*]

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From May to July 1982 and 1983, coccinellids were sampled in habitats that differed in aphid density, insolation, and host plant type. The number of adults of *Coccinella 7-punctata* (CS), *C. 5-punctata* (CQ), *Propylea 14-punctata* (PQ), *Adonia variegata* (AV), *Adalia bipunctata* (AB), *A. 10-punctata* (AD), and *Calvia 14-guttata* (CA) were recorded. AB, AV and CS preferred high, while CQ tolerated low aphid density. CQ, CS, AB and AV preferred sunny, while AD and CA tolerated shaded conditions. CS and AV preferred herbaceous plants, AD and CA large plants, particularly trees, AB showed little specialization, CQ preferred trees early in the season and sparse herbaceous plants later. PQ appeared to be a generalist with a wide tolerance of all these factors, but with a tendency to move from trees to herbaceous plants as the season progressed. Habitats with a high abundance of a species were assumed to be those with on optimum combination of the preferred conditions. There were slight differences in the breadth of habitat preferences, and a little habitat overlap between species. The tendency to aggregate was greater in AB than in other species. Annual variations in species abundance influenced the number of habitats occupied, but not the abundance in the favoured places.

KEY-WORDS : *Coccinella 7-punctata, C. 5-punctata, Propylea 14-punctata, Adonia variegata, Adalia bipunctata, A. 10-punctata, Calvia 14-guttata,* aphid abundance, insolation, microclimate, host plant stature, migration, habitat overlap, multivariate statistical methods.

In Central Europe, 10 species of aphidophagous *Coccinellidae* commonly occur on agricultural crops stands, wild herbaceous plants, orchards and broad leaved forests. Although their larval development is influenced by the prey species (**Hodek,** 1966), the adults accept virtually all common aphid species. However, they are sensitive to aphid abundance, microclimate, and type of host plant (**Honěk,** 1979, 1981, 1982 ; **Honěk & Rejmanek,** 1982). In this study, the differences in the habitat preferences of 7 species were investigated and related to their requirements for environmental conditions.

MATERIAL AND METHODS

The abundance of adults of *Coccinella septempunctata* L. (CS), *C. quinquepunctata* L. (CQ), *Propylea quatuordecimpunctata* L. (PQ), *Adonia variegata* GOEZE (AV), *Adalia bipunctata* L. (AB), *A. decempunctata* L. (AD), and *Calvia quatuordecimguttata* L. (CA) was recorded in localities in Central Bohemia and Southwest Slovakia. Between May 1 and July 10, 1982 and 1983, 199 and 110 samples, respectively, were taken from different plants (table 1). The species of host plant and the number of samples were similar in both years. The coccinellids were collected by sweeping herbaceous plants and the low branches (below 3 m) of trees. The mean number of individuals per 100 sweeps (abundance) was calculated for each sample and coccinellid species. In very low and sparse plant stands (e.g. young beans or cereals) sweeping was supplemented by visual counts of coccinellids on the soil surface in the area previously sampled by sweeping. This method enabled a speedy comparison of coccinellid abundance on different plants. Every sample consisted from 50 to 500 sweeps (usually about 150).

These samples revealed the abundance of coccinellids in habitats that differed in at least 1 of 4 parameters referred to as environmental factors : date, aphid density, insolation, and type of plant cover. These environmental factors were further described by 9 quantitative variables (characteristics) :

Date : (1) Julian day from May 1. (2) Physiological time, i.e., the sum of mean daily temperatures from May 1.

Aphid density : (3) Number of aphids per cm^2 of leaf area. The leaf area from 20 to 50 plants or 50 to 100 randomly collected leaves was measured and the aphids were counted on 20 to 100 herbaceous plants, or on 100 to 500 tree leaves and adjacent twigs. (4) The size of the largest aphid colony observed on each plant stand.

Insolation : (5) Proportion of ground surface shaded from the sun. A scale with four values was used : 1) 0-10 % ; 2) 11-50 % ; 3) 51-90 % ; 4) 91-100 % surface shaded. In stands of herbaceous plants, these values were estimated visually. Ranks 2 and 4 were attributed to sunny and shaded shrub and tree stands, respectively. (6) Plant density. Characterised by a subjective scale with values of 1 for individual plants, 2 for patchy stands and 3 for dense stands.

Type of plant cover : (7) Type of plant : 1 for a herb, 2 for a tree. (8) Height of the stand. From ground surface to the top level of the canopy. (9) Type of plant stand on a subjective scale : 1 for a field, 2 for a hedge, garden, forest margin and 3 for the interior of a forest.

The variables (2), (3) and (8) were converted to a logarithmic form, and all variables were transformed to a number between 0 and 1 when 0 is the lowest and 1 the highest values for the variable in a given year.

These standardized variables were subjected to principal component analysis. The aim of this procedure (**Honěk,** in press) was to reduce the variation of the 9 primary variables to a smaller number of principal component (PCs). PCs are synthetic variables which could be interpreted as factors that determine coccinellid abundance. The position of each sample with respect to PCs was determined by calculating its factorial score (FS). In 1982, there were 3 PCs (with eigenvalue $>$ 1) : aphid density (PC 1, accounting for 27.8 % of variance in the original characteristics), plant cover (PC 2, 28.6 % var.), and insolation (PC 3, 22.6 % var.). In 1983, there were 4 PCs : date (PC 1, 25 % var.), plant cover (PC 2, 23.6 % var.), aphid density (PC 3, 23.1 % var.), and insolation (PC 4, 21.7 % var.). The habitat preferences of coccinellids with respect to PC 1 - PC 3 were studied in 1982, and to PC 2 - PC 4 in 1983.

For each species the samples were also ranked according to the species abundance, and divided into 4 quartils Q1 to Q4 (from low to high abundance). Samples of Q4 were considered to represent typical, i.e. the preferred habitat of a species. After their projection onto the planes of PC pairs, convex polygons circumscribing the Q4 points were constructed. These polygons represented "core areas" of species preference. The overlap of these "core areas" reveals the degree to which the preferred habitats are shared by the species. Also, the mean abundance of the species in samples from particular intervals of FS were calculated. The "habitat breadth" was calculated for 1982 data, as the arithmetic mean of the euclidean distances between samples of Q4. Habitat overlap was calculated according to the symmetrical method (**Pianka,** 1973) as :

$$\alpha_{ij} = \sum_{a}^{n} p_{ia}\, p_{ja} / \left[(\sum_{a}^{n} p_{ia}^2)(\sum_{a}^{n} p_{ja}^2) \right]^{\frac{1}{2}} \quad ; 0 \leqslant \alpha \leqslant 1$$

where p_{ia} and p_{ja} are proportions of i-th and j-th species in the a-th sample. According to **Slobodchikoff & Schulz** (1980), the index is a convenient measure of the degree to which 2 species use the same resource (habitat).

RESULTS

ANNUAL VARIATION IN SPECIES ABUNDANCE

Annual changes in the abundance of species affected the proportion of the samples in which a species occured. This proportion increased in years when a species was abundant. Proportion of the habitats occupied by the different species in 1982 & 1983 were :

	1982	1983		1982	1983
CS	52.7	58.8	AB	27.2	45.1
CQ	36.5	44.1	AD	12.8	24.5
PQ	68.2	43.1	CA	8.8	12.7
AV	6.8	11.8			

Thus, from 1982 to 1983, there was a decrease in PQ abundance (by 1/3), and an increase in AB and AD abundance (2-fold), while the changes in CS and CQ were not substantial. By contrast, there was no significant annual differences in the mean abundance of Q4 samples. Thus an increase in the population density of a species did not influence its abundance in the optimum (preferred) habitats, at least in 1982 and 1983, years in which there were relatively modest differences in coccinellid abundance.

DISTRIBUTION OF SPECIES ABUNDANCE

The species differed in their tendency to occur in high numbers (fig. 1). While the field species CS, CQ, and generalist PQ occured mostly at low densities ($\leqslant$ 5 individuals/100 sweeps), AB had a conspicuous tendency to occur in high numbers with 36 % of the populations being greater than or equal to 10 individuals/100 sweeps and sometimes even greated than 100 individuals/100 sweeps.

ABUNDANCE ON DIFFERENT HOST PLANTS

The mean species abundance on different host plant/aphid systems differed greatly (table 1) with AD most abundant on trees, AB on shrubs, CS and AV on herbs, and PQ evenly distributed on all plant growth types. However the variation in the abundance on different host species of similar growth type was large, and variation between samples from the same host species was still greater.

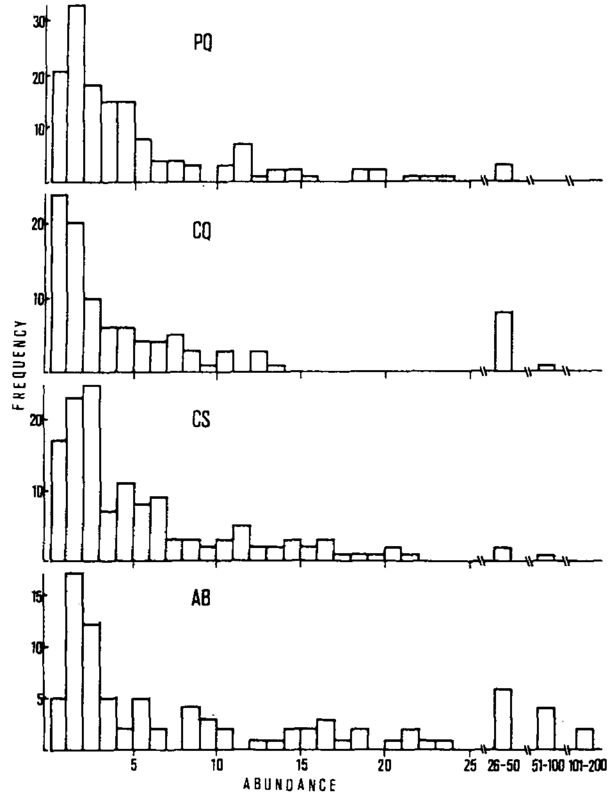

Fig. 1. The frequency distribution of samples with different abundance (no. of adults/100 sweeps) in 4 coccinellid species (abbreviations - see Methods).

ABUNDANCE IN RELATION TO ENVIRONMENTAL FACTORS

The abundance of different species in relation to 3 environmental factors (represented by different PCs) was determined for 2 years (figs 2, 3).

Aphid density

CA, AV and particularly AB strongly preferred habitats with a high aphid density. CS revealed a less marked preference for dense aphid populations, while PQ and AD were tolerant of low aphid densities. CQ was in both years more abundant in habitats with low aphid densities.

Insolation

CS, AB and CQ preferred sunny habitats. AV also showed this tendency, which was obscured, in 1983, by its occurence on dense evenly developed bean stands. By contrast, AD (and perhaps CA) preferred shaded habitats, while PQ tolerated the whole range of insolation conditions investigated.

TABLE 1

Mean abundance of adults of 7 coccinellid species on different host plants (a)

Host plant	N (b)	CS	CQ	PQ	AV	AB	AD	CA
Trees								
Acer sp.	12	1.45	3.23	4.29	0.00	8.90	1.81	0.48
Betula sp.	21	1.67	8.52	4.57	0.00	6.53	1.14	1.21
Carpinus sp.	77	0.00	0.77	1.06	0.00	0.89	4.71	0.00
Fagus sp.	8	0.75	0.30	9.25	0.00	0.00	0.51	0.35
Malus sp.	4	2.45	11.48	4.23	0.00	10.35	0.68	0.95
Pirus sp.	4	0.00	11.85	2.87	0.00	1.93	0.00	0.00
Prunus sp.	10	0.45	0.84	0.63	0.00	4.54	0.46	0.10
Quercus sp.	18	0.71	0.23	2.12	0.00	0.90	1.81	0.74
Tilia sp.	8	0.00	0.20	0.79	0.00	3.53	0.77	0.00
Others	3	0.00	0.00	0.35	0.00	2.00	0.00	0.00
Mean (weighed)	95	0.89	3.47	3.23	0.00	4.14	1.43	0.55
Shrubs								
Corylus sp.	5	0.00	0.00	1.70	0.00	6.42	1.18	0.54
Crataegus sp.	5	1.46	0.70	3.68	0.00	1.44	0.28	0.76
Padus sp.	12	1.23	1.43	5.63	0.17	6.17	1.18	0.66
Sambucus sp.	10	0.64	1.08	0.44	0.00	30.24	0.50	0.00
Mean (weighed)	32	0.89	0.98	2.95	0.06	12.99	0.83	0.45
Herbs								
Anthriscus sp.	2	7.40	7.40	0.00	0.00	8.55	0.00	1.00
Avena sp.	19	7.22	7.73	1.22	0.00	0.00	0.00	0.00
Beta sp.	5	5.80	0.50	0.00	0.00	3.20	0.00	0.00
Brassica sp.	6	0.88	0.82	1.60	0.00	0.00	0.00	0.00
Faba sp.	16	8.14	1.56	1.13	2.04	3.55	0.00	0.00
Hordeun sp.	31	5.26	4.19	1.77	0.08	0.00	0.00	0.00
Medicago sp.	28	4.15	0.09	4.88	0.21	0.00	0.00	0.00
Tripleurospermum sp.	9	11.70	4.72	1.79	5.44	4.48	0.00	0.00
Triticum sp.	20	0.61	0.04	0.88	0.00	0.00	0.00	0.00
Urtica sp.	21	1.61	0.63	3.06	0.00	9.06	0.04	0.39
Others	15	1.78	1.18	1.09	0.00	4.26	0.03	0.25
Mean (weighed)	172	4.48	2.32	2.07	0.57	2.25	0.01	0.08

(a) Abundance - no. of individuals/100 sweeps. Abbreviations of species names - see Methods.

(b) N - no. of samples investigated ; pooled data of 1982 and 1983.

Plant cover

CS and AV preferred herbaceous plants and AD trees. AB was apparently an opportunist, and preferred the plant stands which supported high aphid densities, irrespective of plant species with a preference for low and medium height plants. CQ has a peculiar bimodal preference for both small and tall plants. PQ showed no clear preference for any type of plant. In both the latter species, the bimodality (or apparent even distribution) was caused by a shift in the species preference from trees to herbaceous plants in the course of the season. In successive 10 days periods from May 1, the following average (1982 plus 1983) abundances for CQ and PQ were observed.

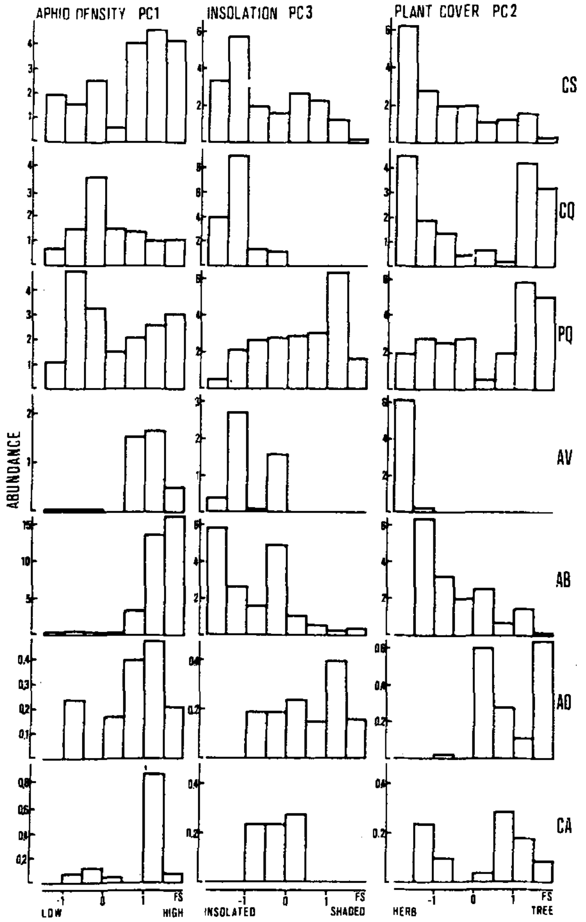

Fig. 2. The mean abundance (no. of adults/100 sweeps) of coccinellid species (horizontal series, abbreviations - see Methods) in relation to 3 environmental factors (vertical series) : aphid density, insolation and plant cover, scaled according to factorial scores (FS) at principal component axes (PC). Aphid density : LOW - sparse aphid populations, aphids scattered or in small colonies, HIGH - dense aphid populations, large colonies. Insolation : INSOLATED - habitats with high proportion of soil surface insolated, or directly insolated tree stands, SHADED - habitats with shaded soil surface or shaded trees. Plant cover : HERB - herbaceous field stands, TREE - tree forest stands. Results of 1982.

	CQ		PQ	
Julian day	Herb	Tree + Shrub	Herb	Tree + Shrub
1 - 10	0.0	23.6	0.3	6.3
11 - 20	1.6	5.1	1.2	5.7
21 - 30	3.4	0.7	0.8	2.9
31 - 40	7.7	0.5	2.6	0.6
41 - 50	2.2	0.0	4.5	0.3
51 - 60	3.9	0.0	2.0	0.1
61 - 70	4.1	–	3.8	0.0

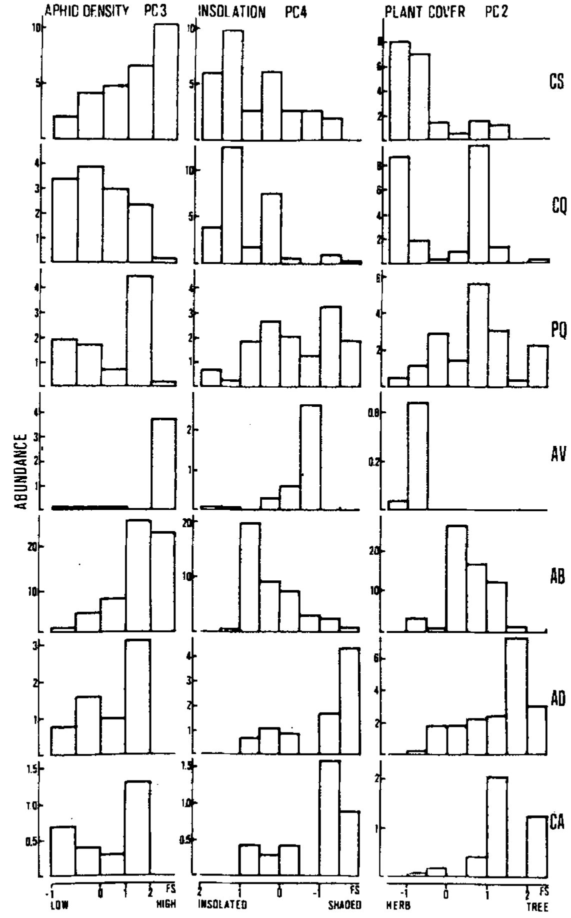

Fig. 3. See fig. 2 for explanation. Results of 1983.

For CQ only the records for sunny habitats were considered.

Thus only PQ appeared to be a generalist with a broad range of preferences. The other species had specific requirements with respect to at least 1 factor. Species with a similar biology, CS and CQ differed in their requirements for aphid density, while AB and AD in their requirements for insolation and host plant type.

DIFFERENCES IN HABITAT UTILIZATION

The different species preferences for the various environmental factors determined their typical habitat. The ranking of the preferred habitats based on the PCs (figs 4 - 5) revealed the same trends as that based on average species abundances. The trends in the results for both years were similar, though the "core areas" in 1982 were greater than in 1983.

The habitat preferences may be summarized as follows : CS tended to prefer herbaceous plants in sunny places. It showed a wide tolerance to differences in aphid abundance. CQ

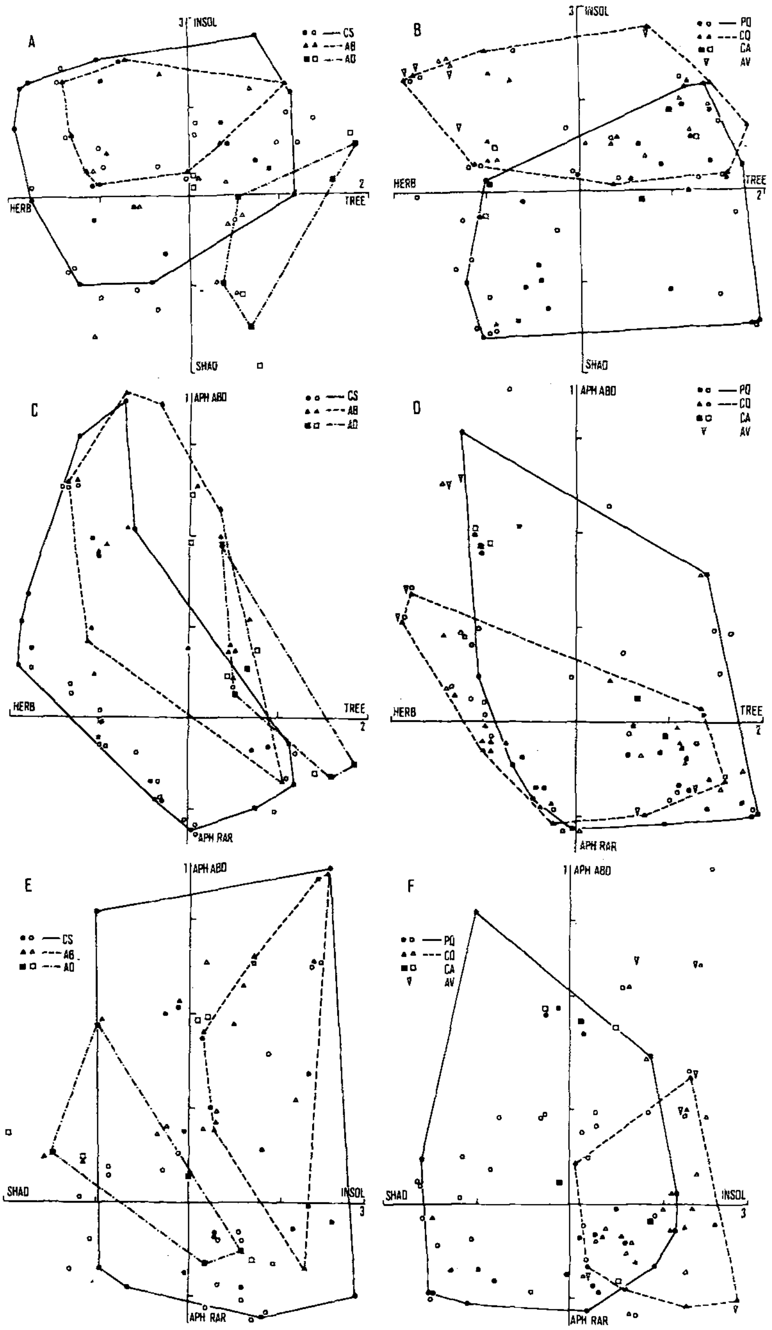

Fig. 4. The distribution of preferred habitats (of Q3 and Q4, i.e. with above median abundance of adults) of coccinellid species (abbreviations - see Methods) with respect to 3 environmental factors represented by PC axes. PC1 - aphid density : APH RAR - sparse aphid populations, scattered individuals or small colonies, APH ABD - dense aphid populations, large colonies. PC 2 - plant cover : HERB - herbaceous field stands, TREE -forest tree stands. PC3 - insolation : INSOL - insolated sparse stands, SHAD - shaded dense stands. PC axes scaled in units of FS. Horizontal pairs of figures indicate the relation of different species to the same combinations of PC. Heavy symbols - Q4 habitats, open symbols - Q3 habitats. Polygons indicate the areas where Q4 samples of a particular species occur "core areas". Results of 1982.

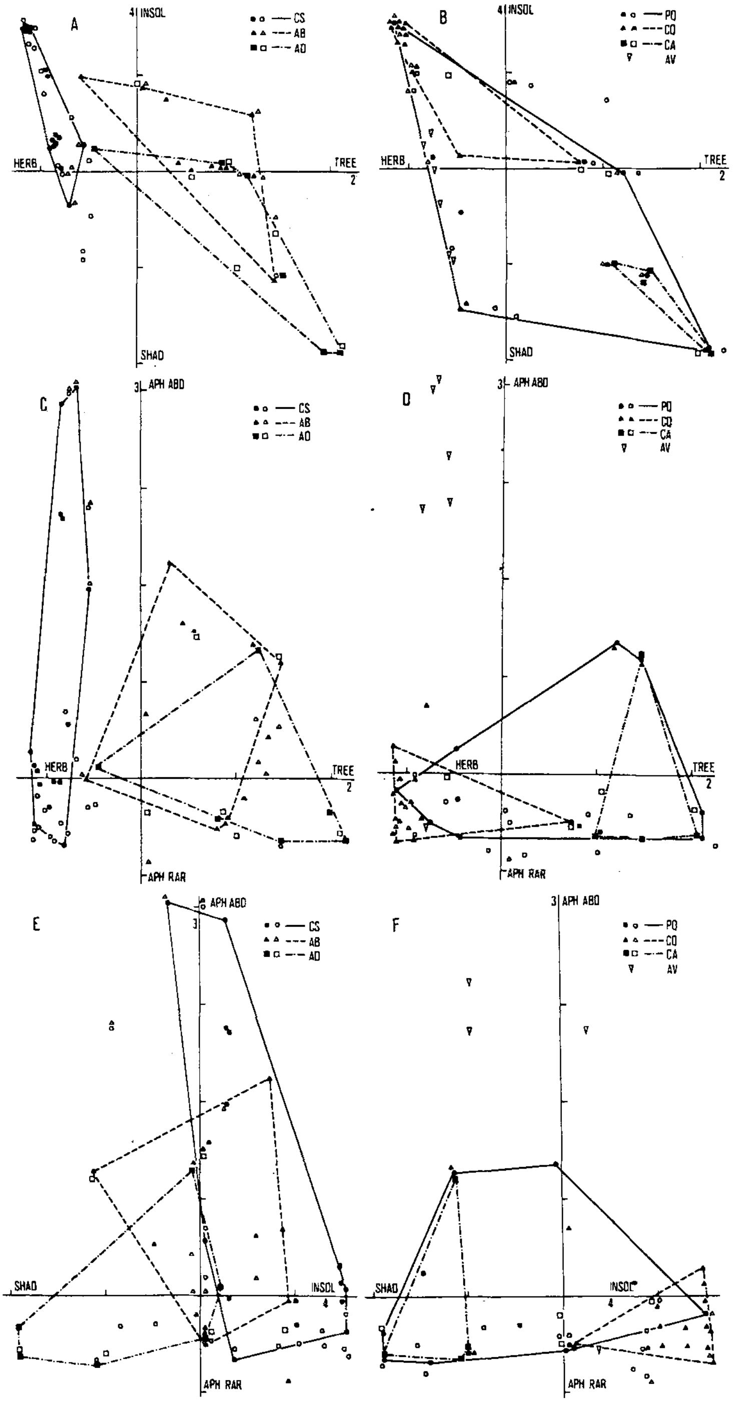

Fig. 5. See fig. 4 for explanation. Results of 1983.

strongly preferred sunny places, but its preference for particular plants changed in the course of the season and it tolerated low aphid densities. PQ was a generalist, which tolerated a wide range of environmental conditions, with some preference for shaded areas. AB preferred sunny habitats with a abundance of aphids, but some apparently favourable habitats were sparsely occupied (fig. 4C, E) and at low aphid densities it showed some preference for shrub and trees. AD preferred shaded trees and tolerated low aphid densities.

In 1982, habitat breadth (for Q4 samples) did not substantially differ between species. Mean euclidean distances between the Q4 samples were 3.23 ± 1.18 ; 3.80 ± 1.59 ; 3.88 ± 1.62 and 4.21 ± 1.63 for CQ, PQ, AB and CS, respectively. Thus there was no difference in the range of preferred habitats between the generalist (PQ) and the specialists (CQ, AB). The core areas (see Methods) for the different species never completely overlapped. The habitat overlap was generally low, in most cases $< 0{,}3$ (table 2). The high values, e.g. AV × CS in 1982 or PQ × CQ in 1983, were apparently spurious, due to the small number of Q4 habitats for both species.

TABLE 2

Habitat overlap in 7 coccinellid species, in 1982 and 1983

				Habitat overlap (α) - 1982				
		CS	CQ	PQ	AV	AB	AD	CA
Habitat overlap (α) - 1983	CS	–	.388	.348	.728	.236	.017	.205
	CQ	.352	–	.214	.312	.033	.172	.033
	PQ	.110	.677	–	.078	.148	.122	.190
	AV	.269	.009	.007	–	.018	.000	.000
	AB	.093	.144	.204	.114	–	.019	.587
	AD	.103	.049	.234	.077	.278	–	.131
	CA	.079	.232	.496	.000	.169	.512	–

DISCUSSION

There are many records of the habitats of aphidophagous coccinellids in faunistic, taxonomic and applied works. **Hodek** (1973) revealed the need for quantification and causal study of habitat diversification. Little attention, however, has been paid to this type of investigation. **Iperti** (1965, 1978) demonstrated the effect of plant type on coccinellid abundance. Other studies have revealed that, in different species, abundance may be influenced by prey availability (**Neuenschwander** *et al.*, 1975 ; **Radcliffe** *et al.*, 1976 ; **Tamaki & Long,** 1978 ; **Capinera & Roltsch.,** 1981) or microclimate, chiefly insolation (**Smith,** 1971). Effects of the above factors on central European species in agricultural landscape were demonstrated earlier by **Honěk** (1981, 1982).

The present study has revealed that the habitat diversification shown by the adults of 7 common species may be explained in terms of different preferences for only 3 environmental factors : aphid abundance, insolation, and type of plant cover. The preferences may also determine the amount of between habitat movement (cf. **Ives,** 1981). As the tendency to leave the preferred habitats is low, the coccinellids aggregate in these places. Further determinants (cf. **Ruzicka & Hodek,** 1978 ; **Horn,** 1981) and finer within habitat diversification of specific preferences (cf. **Ewert & Chiang,** 1966 ; **Cosper** *et al.*, 1983) may increase the separation and facilitate the coexistence of different species.

The concept of niche is defined in terms of different patterns of resource utilization (**Price,** 1975 ; **Pianka,** 1976). Habitat separation indicate that the different species of adult coccinellids show niche separation. Although the vagility of the adults enable them seek out habitats with the maximum aphid abundance, differences in habitat utilization nevertheless exist (cf. **Stechmann,** 1982). The monovoltine CS is more specialized in field herbaceous plants than is the bivoltine opportunistic AB. **Obrycki & Tauber** (1981) and **Obrycki** *et al.*, (1983) demonstrated that both CS and AB, because of their different thermal requirements, are specialized for speedy development in the warm periods of the year or slower development over a wide range of temperatures, respectively. Therefore CS is found in warm, xeric, steppe-like field habitats, supporting a temporary abundance of aphids. As a specialist, in some years, it may tolerate a low prey abundance. AB is capable of developping in a wider range of temperatures, and is opportunistic in selecting dense prey populations on a wide range of host plants. Thus AB can make use of early spring outbreaks of aphids on trees (e.g. *Rhopalosiphum padi* on bird-cherry), as well as of later aphid infestations on herbaceous weeds (cf. **Honěk,** 1981).

An important characteristic of a species specific use of its environments is its breeding place. A study of larval habitats is now needed to complement the results presented here for adults. This will improve our understading of habitat utilization by the sympatric central european species of aphidiphagous coccinellid.

RÉSUMÉ

Choix des habitats chez les Coccinelles aphidiphages (*Coleoptera*)

En 1982 et 1983, de mai à juillet, on a procédé à des échantillonnages de Coccinelles dans des habitats différents par la densité d'Aphides d'insolation et le type de plante-hôte. On enregistra le nombre d'adultes de *Coccinella 7-punctata* (CS), *C. 5-punctata* (CQ), *Propylea 14-punctata* (PQ), *Adonia variegata* (AV), *Adalia bipunctata* (AB), *A. 10-punctata* (AD) et *Calvia 14-guttata* (CA). AB, AV et CS préféraient une forte densité de pucerons, tandis que CQ en tôlérait une faible. CQ, CS, AB et AV préféraient les conditions ensoleillées, tandis que AD et CA tôléraient les ombragées. CS et AV préféraient les plantes herbacées, AD et CA les plantes volumineuses, particulièrement les arbres, AB manifestait une faible spécialisation, CQ préférait les arbres en début de saison et les plantes herbacées clairsemées plus tard. PQ apparaissait comme étant un généraliste largement tolérant vis-à-vis de tous ces facteurs, mais ayant tendance à migrer des arbres vers les plantes herbacées au fur et à mesure que la saison s'avance. Les habitats qui hébergent le plus grand nombre d'individus d'une espèce semblent correspondre à la combinaison optimale des conditions préférées par cette espèce. Mais l'ampleur des préférences d'habitat est faible et un petit habitat peut être partagé entre plusieurs espèces. La tendance à l'agrégation était plus grande chez AB que chez les autres espèces. Les variations annuelles de l'abondance des espèces influençaient le nombre d'habitats occupés, mais non l'abondance des espèces au sein des habitats favorables.

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