Entomol. Gener.	13(1/2): 067—080	Stuttgart 1988-05	ISSN: 0171-8177

EGT-Nr 602 VIII

Co-phenology of Plants and Anthophilous Insects: a Historical Area-geographical Interpretation

Anselm Kratochwil

Received: 1987-10-21/1987-12-02 Accepted: 1987-12-04

Kratochwil, A. [Inst. Biol. II/Geobot., Univ.; D-7800 Freiburg]: **Co-phenology of Plants and Anthophilous Insects: a Historical Area-geographical Interpretation.** — Entomol. Gener. **13**(1/2): 067—080; Stuttgart 1988. ——— [Article].

Many dry grasslands (Mesobrometum) in SW' Germany are characterized by a high % of submediterranean and subcontinental plant and animal species. A phenological analysis (flowering times of entomophilous plants, flight activities of Hymenoptera: Apoidea and Lepidoptera) yields 4 seasonal periods named by the area-geographical centre of their species: eurosiberian period (III, IV); submediterranean period (V, VI); eurosiberian period (VII); eurosiberian period with subcontinental and submediterranean elements (VIII, IX). Vegetation, Apido- and Lepidofauna of the same area type correspond in their phenology (co-phenology). The flower-visiting insects of the studied area prefer plants of the same geoelement. The results are based on 1500 data of flower-visiting bees, 800 of butterflies and many references from bibliographical data. It is shown that the history of the flora and fauna is important for the interpretation of the flower-visiting communities.

Key words: Hymenoptera: Apoidea, Lepidoptera, Mesobrometum. — Flower visitor preferences, biogeography.

1 Introduction

Many dry grasslands in SW' Germany are characterized by a high % of submediterranean [smt][1] and subcontinental [sct][2] plant and animal species [Strohm 1933, Wilmanns 1977]. In the study area (Fig 1) 45% of all entomophilous plant species are part of the smt and 16% of the sct flora element (Fig 2). In the case of bees, 12% belong to the smt fauna element, 4% to the sct, in the case of butterflies 18% to the smt and 12% to the sct element (Fig 2); details in Kratochwil [1984a].

These species live here at the border of their area-geographical centre of distribution. The occurrence of smt and sct species in Central Europe can only be understood in the light of the history of flora and fauna of the postglacial period: in the late wuerm glacial period continental steppe species migrated to Central Europe; then in the postglacial warm period smt species followed. These smt and the sct species now exist in Central Europe only in some microclimatically favoured habitat islands.

The following 2 questions are considered:

(a) Do plant species and flower-visiting insects of different systematical rank but of the same area type have an analogous phenology, and is it possible to correlate this phenology with seasonal climatic conditions of their area of origin and area-geographical centre?

[1] submediterranean, in further text: smt — [2] subcontinental, in further text: sct

0171-8177/88/0013-0067 $ 3.50

(b) Are there any indications of a co-adaptive system where flowering plant species are visited by those insects which belong to the same geoelement and vice versa?

2 Methods and Materials

2.1 Study area

The study area has a size of 4000 m^2 and is situated in the centre of the "Kaiserstuhl", a volcanic loess-covered mountain island of about 100 km^2 lying in the plains of the Rhine near Freiburg (Fig 1, 2). The vegetation of the steep, southwards facing slope represents a fallow dry grassland complex surrounded by shrubbery ("coat") communities of the Rhamno-Prunetea and by oak-hornbeam woods (Querco-Carpinetum luzuletosum). Abandoned by farmers, these grasslands developed into a species-rich plant community composed of grassland species and — by succession — tall herb ("hem") species [Wilmanns 1975, Kratochwil 1983, Wilmanns & Kratochwil 1983]. Syntaxonomically the "hem" species belong to the Trifolio-Geranietea, Glechometalia and Epilobietea. Prior to the abandonment of the grasslands such "hem" species lived only on forest edges or inside thin forests. In phytosociological terminology the dry grasslands in this study area are called Mesobrometum globularietosum and Mesobrometum primuletosum, both with "hem" species [Kratochwil 1984 a, b]. At the base of the slope grows a fallow tall oatgrass meadow (Arrhenatheretum with "hem" species).

2.2 Flower visitors

In the course of 2 years 3600 flower-visiting insects (Hymenoptera, Lepidoptera, Diptera, Coleoptera) were observed visiting 71 different plant species. The high diversity of species is demonstrated by the fact that 128 bee species and 56 butterfly species (Rhopalocera, Hesperiidae, Zygaenidae) were recorded in an area only 4000 m^2.
We have analysed 1500 data of flower-visiting bees observed in the study area, and many references from bibliographical data. 800 flower visits of butterflies from the study area were evaluated and references to nectar plants, rare in the lepidopterological papers, were added.

3 Results and Discussion

3.1 Phenology of entomophilous plants, bees and butterflies

In the course of the year the entomophilous plant species reveal a continuous staggering of flowering times. Over the 2 years the sequence was largely constant. The same facts can be demonstrated concerning the phenology of bees and butterflies: The different genera of Hymenoptera: Apoidea, as well as their species, show special flight activities, staggered in the course of the year, too. Spring is characterized by the appearance of many solitary bees. For example, the genus *Andrena* is represented in the study area by 39 species, and the genus *Osmia* by 8 species. In summer social bee species dominate in very high individual numbers, for example, *Bombus* (10 species) and *Halictus/Lasioglossum* (30 species including solitary species). Most of the bees have their nesting sites within the study area or in the immediate neighbourhood. Their home range (except *Bombus*) is limited.
Analogous to the bees, the butterflies also show a seasonal staggering of the flight and flower-visiting activities.

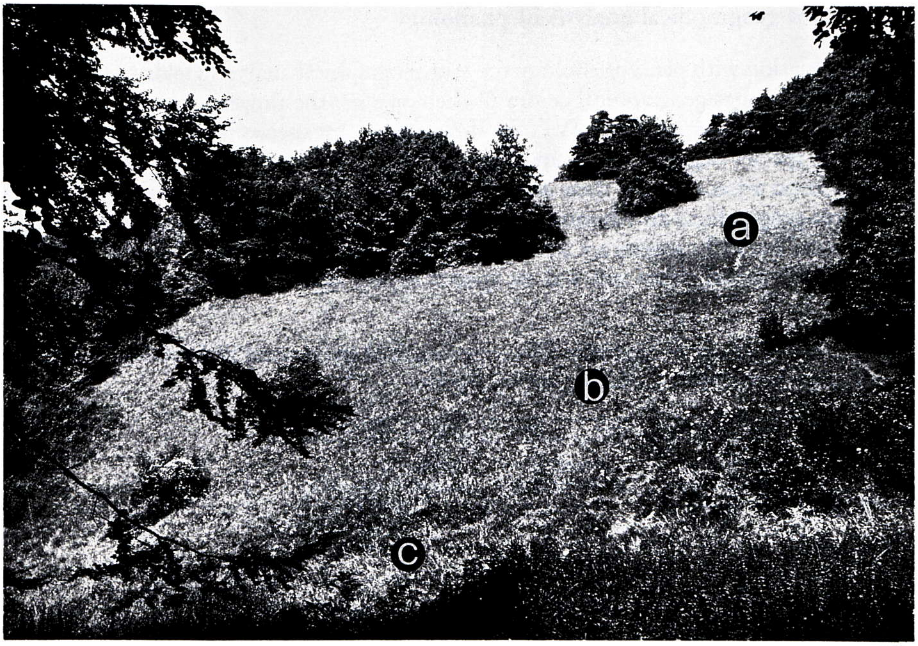

Fig 1: The study area, a dry grassland in the centre of the Kaiserstuhl (SW' Germany). — (a) Mesobrometum globularietosum, (b) Mesobrometum primuletosum, (c) Arrhenatheretum.

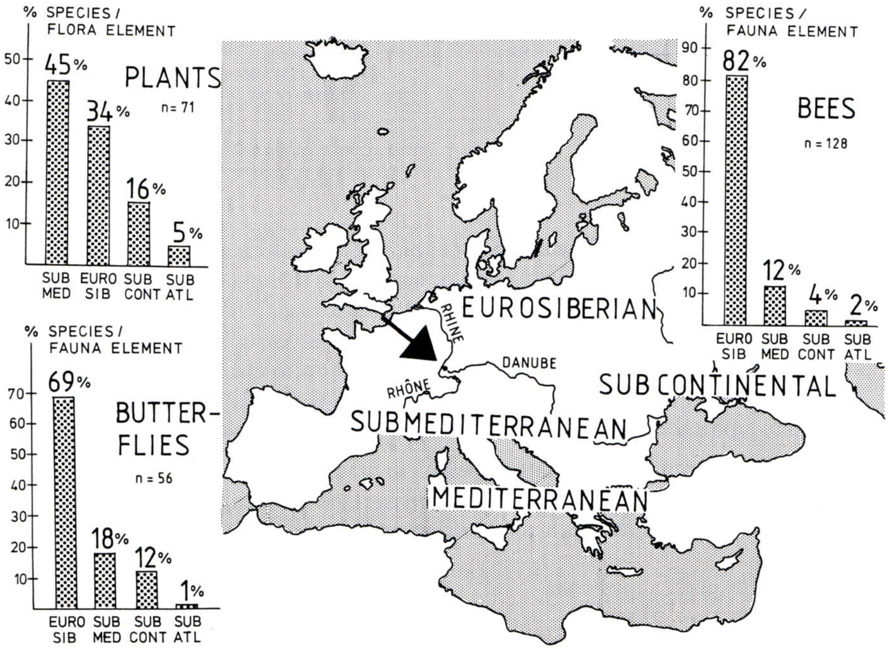

Fig 2: The localization of the study area in Central Europe and the % of entomophilous plant species and bee and butterfly species belonging to different geoelements [Hymenoptera: Apoidea/Lepidoptera]. — (The species and their area-geographical centre of distribution are recorded in Kratochwil 1984a).

3.2 Area-geographical analysis of phenology

In combination with plant phenology the area-geographical analysis yields 4 seasonal periods named by the area-geographical centre of their species: the flowering of eurosiberian [esb][3] species in March and April [III, IV][4], the flowering of smt species in VI. A flowering of other esb plant species begins in VII, supplemented by sct species in VIII and IX (Tab 1).
The question arises whether there are any correlations between the phenology of insects and their area-geographical distribution as can be noted in the case of plant species. In spring, only esb bee and butterfly species are active, in V and VI smt species. From VII till VIII the fauna elements are mixed, some smt and sct species appear aside esb species (Tab 1).

Tab 1: The phenology of vegetation (flowering time) and the seasonal flight activities of Apido- and Lepidofauna with respect to biogeographical aspects.

	MARCH	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER
VEGETATION	flowering of *EUROSIBERIAN* species		flowering of *SUBMEDITERRANEAN* species		flowering of *EUROSIBERIAN* species supplemented by *SUBCONTINENTAL* species		
APIDOFAUNA	*EUROSIBERIAN* fauna element		*SUBMEDITERRANEAN* fauna element		*EUROSIBERIAN* fauna element supplemented by *SUBMEDITERRANEAN* and *SUBCONTINENTAL* species		
LEPIDOFAUNA		*EUROSIBERIAN* fauna element	*SUBMEDITERRANEAN* fauna element		*EUROSIBERIAN* fauna element supplemented by *SUBMEDITERRANEAN* and *SUBCONTINENTAL* species		
	esb		smt		esb	esb+smt+sct	

The phenological analysis (flowering times of entomophilous plants, flight activities of bees and butterflies) yields 4 seasonal periods named by the area-geographical centre of their species: esb period (III, IV), smt period (V, VI), esb period (VII), esb period with smt and sct elements (VIII, IX) (Tab 1). Vegetation, Apido- and Lepidofauna of the same area type correspond in their phenology. It is a reasonable assumption to correlate these seasonal activities of different plant species and flower-visiting insects with the predominant climatic conditions in the geographical centre of their distribution area due to the:

- long vegetation period in the temperate esb area,
- limitation of the vegetation period in the smt and sct area to spring, early summer and autumn because of the high temperature and drought in the summer [Walter & Lieth 1960].

---

3 eurosiberian; in further text: esb
4 March, April; names of months in further text: III, IV, V ... XII

It seems that even at the edge of their distribution area the phenological behaviour of the studied plant and insect species is similar to their behaviour in their area-geographical centre. The flowering period (V) of the following smt species is nearly identical in the study area and in the centre of the smt area, for example *Dianthus carthusianorum* L. (Caryophyllaceae), *Himantoglossum hircinum* (L.) Spreng. (Orchidaceae), *Hippocrepis comosa* L. (Fabaceae), *Onobrychis viciifolia* Scop. (Fabaceae), *Salvia pratensis* L. (Labiatae) (phenology in the smt area based on Pignatti 1982).

3.3 The flower-visiting behaviour of bees and butterflies with respect to biogeographical aspects

Phenological staggering of flowering periods and flight activities may be caused by climatic factors which restrict the phenological behaviour of species occurring in the same geoelement. However, in such species-rich communities, the phenology could also be conceivably caused by competition between species. Coexistence of many species of different area types is possible, provided there are special adaptations leading to competitive exclusion. Such features can be termed "preadaptations for coexistence". One preadaptation could be the preference of a plant species for a special group of flower-visiting insects of the same area type and vice versa. The following is a brief representation of some flower-ecological results with respect to biogeographical aspects and restricted to the esb, smt and sct element.

3.3.1 Eurosiberian element

The bee species as well as some butterfly species with esb distribution show a preference for esb plant species despite the fact that some smt and sct plant species are flowering in the same locality and at the same time. This does not only apply to stenanthic bees or butterflies, i e species which show a preference for only a few pollen and nectar plants, but also to some euryanthic species (species which visit a wide spectrum of plant species).
The esb entomophilous plant species which are visited by esb insects are (Tab 2):

(A) plant species living originally in river plains.

Some of the *Andrena* species (examples mentioned in Tab 2) are characterized by a preference for *Potentilla tabernaemontani* Aschers. (Rosaceae) which lived originally in drier parts of river plains, for example, as in plant communities of river banks, and *Veronica chamaedrys* L. (Scrophulariaceae) which lived for example in wetter parts of river plains [Zoller 1954]. Other *Andrena* species (Tab 2: examples) prefer willows (*Salix*). River plains are also the original habitats of many *Salix* species.
The preference of bees for plant species which live under natural conditions on river plains supports the conclusion, that the rivers Rhine, Rhône and Danube represented important migration paths during the postglacial recolonization of Central Europe [Stoeckhert 1954] (Fig. 2).

(B) plant species living originally in forests or in ecotones of forests (tall herb = "hem" communities, shrubbery = "coat" communities).

Andrena lathyri Alfken 1899 prefers to visit the flowers of *Lathyrus montanus* Bernh. (Fabaceae) growing in oak-hornbeam-woods (Querco-Carpinetum) but also in "hem" communities, or *Vicia sepium* L. (Fabaceae), a typical "hem" species. In beech-woods rich in *Lathyrus vernus* (L.) (Lathyri-Fagetum) *Andrena lathyri* Alfken 1899 visits this plant.
The preferred nectar source of *Leptidea sinapis* Linnaeus 1758 (Pieridae) is also *Lathyrus montanus* Bernh., or species of thin forests (e g *Viola riviniana* Rchb.) [Wiklund 1977]. In meadows this butterfly visits

usually yellow Fabaceae, e g *Lotus corniculatus* L. The larvae feed preferably on *Lathyrus pratensis* L., a species living in meadows but originally in ecotones of flood plain forests [Zoller 1954].
Many esb butterfly species (Tab 2: examples) visit tall herb ("hem") and shrubbery ("coat") species as sources of nectar. The original habitat of these plants are thin forests or the edges of woodland. The larvae of *Araschnia levana* Linnaeus 1758, but also some Nymphalidae widespread in Europe like *Inachis io* Linnaeus 1758 and *Aglais urticae* Linnaeus 1758 feed monophagously on *Urtica dioica* L., which lives originally in tall herb communities of river banks or in thin riparian alluvial forests. It could be possible, that — as in group (A) — the original habitat of such butterfly species was also a river plain.

Tab 2: Bee and butterfly species of the esb fauna element and their flower-visiting preferences [Hymenoptera: Apoidea/Lepidoptera] (area-geographical distribution of plant species in tab 2—6 according Meusel, Jäger & Weinert [1965 ff], Oberdorfer [1978] and Zoller [1964]). — a) examples of the study area, b) examples of other study sites and habitats in Central Europe (references are mostly bibliographical data).
1) occurs in Central and Western Europe,
2) occurs in Central Europe mainly, but also in the sct area (absent from the northern part of Europe),
3) widespread throughout Europe mainly Central Europe, its range not extending eastwards to Siberia,
4) grows in immediate neighbourhood of the dry grassland,
5) widespread throughout Europe mainly Central Europe, its range extending eastward to Siberia,
6) occurs in Central Europe mainly, but also in the smt area (absent from the northern part of Europe),
7) visits also some Compositae,
8) visits also Labiatae,
9) occurs also in the sct region.

EUROSIBERIAN ELEMENT

eurosiberian flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring:

1) eurosiberian plant species living originally in riverplains:

Potentilla tabernaemontani Aschers. / *Veronica chamaedrys* L.

a) *Andrena falsifica* Perkins 1915
Andrena saundersella Perkins 1914
(= *semilaevis* Pérez 1903)
Andrena strohmella Stoeckhert 1928 [1]
Andrena subopaca Nylander 1848
Andrena viridescens Viereck 1916 [2]

b) *Andrena labiata* Fabricius 1781 [3]

Salix sp. [4]

a) *Andrena gravida* Imhoff 1832 [2]
Andrena haemorrhoa (Fabricius 1781)
Andrena helvola (Linnaeus 1758)
Andrena jacobi Perkins 1921 [5]
(= *sabulosa* (Scopoli 1763))
Andrena strohmella Stoeckhert 1928 [1]
Andrena subopaca Nylander 1848

Polygonia c-album Linnaeus 1758 [5]
(s. also 2)

b) *Andrena apicata* Smith 1847
Andrena clarkella (Kirby 1802)
Andrena bimaculata morawitzi Thomson 1872 (1.Gen) [5]
Andrena nycthemera Imhoff 1866
Andrena praecox (Scopoli 1763)
Andrena ruficrus Nylander 1848
Andrena vaga Panzer 1799
Andrena ventralis Imhoff 1832
Colletes cunicularius (Linnaeus 1761) [5]

eurosiberian flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring:

2) eurosiberian plant species living in forests, in ecotones of forests or in fallow grasslands (tall herb = "hem" communities, shrubbery = "coat" communities)

Lathyrus montanus Bernh. (*Lathyrus vernus* (L.))

a) *Andrena lathyri* Alfken 1899 [3]

Leptidea sinapis Linnaeus 1758 [5] (s. also 3b)

Tab. 2. Eurosiberian Element (continued)

"coat" species: e.g. *Rubus, Crataegus, Prunus;*	"hem" species: e.g. *Origanum vulgare* L.
a) *Andrena fulva* (Müller 1766) [1]	b) *Andrena bucephala* Stephens 1846 [1]
	Andrena ferox Smith 1847 [6]
Aglais urticae Linnaeus 1758	*Andrena fucata* Smith 1847
Aphanthopus hyperanthus Linnaeus 1758	*Andrena fulvida* Schenck 1853
Araschnia levana Linnaeus 1758	*Andrena simillima* Smith 1851
Argynnis paphia Linnaeus 1758 [6]	*Andrena sabulosa trimmerana* (Kirby 1802) [5]
Coenonympha pamphilus Linnaeus 1758 [5,7]	*Andrena varians* (Rossi 1792)
Heodes tityrus Poda 1761 [6]	
Inachis io Linnaeus 1758	*Aporia crataegi* Linnaeus 1758
Maniola jurtina Linnaeus 1758 [5,7]	*Fabriciana adippe* Schiffermüller 1775 [5,7]
Pieris napi Linnaeus 1758 [5,7]	*Mesoacidalia aglaja* Linnaeus 1758 [5]
Polygonia c-album Linnaeus 1758 [5]	*Celastrina argiolus* Linnaeus 1758 [5]
Thymelicus sylvestris Poda 1761	*Pararge aegeria* Linnaeus 1758
	Thecla betulae Linnaeus 1758
	Vanessa atalanta Linnaeus 1758 [5]

eurosiberian flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring:
3) eurosiberian plant species living in meadows
a) with original distribution in forests (especially riverplains)

Cardamine pratensis L. (and *Alliaria petiolata* (M.B.)Cav.et Gr.)

a) *Anthocharis cardamines* Linnaeus 1758 [5]

Primula-, Viola-species (and "hem"-species)

a) *Gonepteryx rhamni* Linnaeus 1758 [5]

eurosiberian flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring:
3) eurosiberian plant species living in meadows:
b) which are polyploid species, originated before postglacial from diploid species

Campanula (Geranium)

a) *Andrena curvungula* Thomson 1870 [2]	b) *Dufourea dentiventris* (Nylander 1848)
Andrena pandelii Pérez 1895 [6]	*Dufourea inermis* (Nylander 1848)
Chelostoma campanularum (Kirby 1802) [3]	*Melitta haemorrhoidalis* (Fabricius 1775)
Chelostoma distinctum Stoeckhert 1929 [2] (= *cantabrica* Benoist 1936)	
Chelostoma fuliginosum (Panzer 1798) [4]	
Lasioglossum costulatum (Kriechbaumer 1873) [6]	
Osmia mitis Nylander 1852	

Knautia

a) *Andrena hattorfiana* (Fabricius 1775) [3]	b) *Andrena marginata* Fabricius 1776 [6]
Zygaena filipendulae Linnaeus 1758	

yellow Compositae (e.g. *Hieracium*)

a) *Andrena fulvago* (Christ 1791) [3]	b) *Andrena chrysopyga* Schenck 1853
Andrena humilis Imhoff 1832 [3]	*Andrena denticulata* (Kirby 1802)
Dufourea vulgaris (Schenck 1859)	*Dasypoda hirtipes* (Fabricius 1793) [5]

Tab 2. Eurosiberian Element (continued)

Lasioglossum parvulum (Schenck 1853) [2]	*Heriades truncorum* (Linnaeus 1758) [3]
(= *minutum* Schrank 1781)	*Lasioglossum leucozonium* (Schrank 1781) [5]
Lasioglossum villosulum (Kirby 1802) [5]	*Lasioglossum lucidulum* (Schenck 1859) [5]
Osmia spinulosa (Kirby 1802) [3]	*Osmia leaiana* (Kirby 1802) [3]
Panurgus calcaratus (Scopoli 1763) [3]	(= *ventralis* Panzer 1798)
	Panurgus banksianus (Kirby 1802) [3]
Fabaceae (e.g. *Lotus*, *Trifolium*)	
a) *Megachile circumcincta* (Kirby 1802)	b) *Andrena gelriae* van der Vecht 1927 [5]
Megachile versicolor (Smith 1844)	*Andrena intermedia* Thomson 1870 [5]
Trachusa byssina (Panzer 1798)	*Andrena labialis* (Kirby 1802) [5]
	Andrena wilkella (Kirby 1802) [5]
Cyaniris semiargus Rottemburg 1775	*Anthidium punctatum* Latreille 1809 [5]
Cupido minimus Fuessli 1775 (?)	*Anthidium strigatum* (Panzer 1805) [5]
Erynnis tages Linnaeus 1758 [5] (?)	*Eucera longicornis* (Linnaeus 1758) [5]
Leptidea sinapis Linnaeus 1758 [5]	*Lasioglossum punctatissimum* (Schenck 1853) [3]
Papilio machaon Linnaeus 1758 [5]	*Megachile leachella* Curtis 1828 [6]
Polyommatus icarus Rottemburg 1775 [5]	*Lasioglossum lativentre* (Schenck 1853) [7]
	Lasioglossum punctatissimum (Schenck 1853) [3]
	Megachile leachella Curtis 1828 [6]
	(= *argentata* Fabricius 1793)
	Megachile nigriventris Schenck 1768
	Megachile willughbiella (Kirby 1802)
	Melitta leporina (Panzer 1799)
	Meliturga clavicornis (Latreille 1806)
	Everes argiades Pallas 1771 [6]
3) eurosiberian plant species living in meadows: combination group a and b (original distribution in forests, polyploid species)	
Fabaceae (e.g. *Lotus*, *Trifolium*), *Primula*- and *Viola*-species	
a) *Osmia aurulenta* (Panzer 1799) [6]	b) *Osmia claviventris* (Thomson 1872)
(= *funensis aurulenta* (Panzer 1799))	*Osmia coerulescens* (Linnaeus 1758) [5]
Osmia bicolor (Schrank 1781)	*Osmia leucomelana* (Kirby 1802) [5]
	Osmia parietina Curtis 1828
	Osmia xanthomelana (Kirby 1802)

(C) plant species living in meadows.
(a) species with original distribution in forests

Some plant species which live today in meadows are derived from woodland species. This is proved by cytotaxonomical examinations, for example, in the case of *Cardamine pratensis* L. (Cruciferae) [Dersch 1969]. Insects which prefer flowers of *Cardamine* should originally be woodland species, such as *Anthocharis cardamines* Linnaeus 1758 (Pieridae).
This assumption is corroborated by the observation of Wiklund & Åhrberg [1978], that the preferred nectar source in Sweden is the woodland and "hem" species *Lathyrus montanus* Bernh. Further indications that this butterfly is originally a woodland species are provided by the other nectar plants of *Anthocharis cardamines* Linnaeus 1758 and by the fact that the caterpillars feed preferably on *Cardamine pratensis* L. and on "hem" species like *Alliaria petiolata* (M.B.) Cav. et Gr. [Wiklund & Åhrberg 1978, Dennis 1982, Courtney & Duggan 1983]. According to Dennis [1982] *Anthocharis cardamines* Linnaeus 1758 represents in its N' part of distribution a riverside butterfly (Tab 2: group 1).

Similar preferences are shown by other butterflies, for example *Gonepteryx rhamni* Linnaeus 1758. In the study area this species visits *Primula veris* L. by preference, which is originally distributed in European woodlands [Zoller 1954] (Tab 2).

(b) plant species wich are polyploid and widespread and which originated prior to the postglacial period from diploid species.

Many oligolectic esb bee species visit meadow species, which are polyploid and widespread and which originated prior to the postglacial period from diploid plant species, for example the polyploid *Knautia arvensis* (L.) Coult. (Dipsacaceae), *Campanula* (Campanulaceae) and *Hieracium* species and many other yellow Compositae [Ehrendorfer 1962a, b, 1970] (Tab 3). These plant species, which have existed only since the postglacial period, are derived from plant species (diploid, entomogamic) which represent relict species living in the mountains of the mediterranean area (Tab 3). In the glacial period these mountains were the most important refuges and residua of Central European plant and animal species. We assume that the above mentioned bee species — today with a Central European distribution — preferred the diploid ancestors in the glacial period. In the postglacial period many plant species originated from different diploid mediterranean species by allopolyploidy and hybridization. These plant species are characterized by a wide ecological amplitude.
Plant species derived from diploid species in the postglacial period are frequently characterized by apomixis. Contrary to their diploid ancestors they need no insect pollination. The stenanthic behaviour of the bee species, which in the postglacial period followed these plant species into Central Europe, can be interpreted as a relict of a former coevolution.

3.3.2 Submediterranean element

The oligolectic bees of the study area (including references of other study sites and habitats in Central Europe), which exhibit a smt distribution, prefer blue and violet Compositae, Cruciferae, Labiatae or Cistaceae (Tab 4). These familiae include many plant species widespread in the smt area. There many Cruciferae, for example, live in coastal regions, on riversides or rock and ruderal habitats. Many oligolectic bee species have found an abundance of such feeding sites in the old landscape of the Rhine plain which gives some indications of the migratory possibilities in the postglacial period.
Bees, showing a preference for a particular plant family, visit within this family especially those plant species of the same geoelement. All investigated bee and butterfly species with smt distribution avoid "hem", "coat" and woodland species when collecting pollen and/or sucking nectar. These flower visitors prefer smt grassland species. They are furthermore typical insects of open habitats.

3.3.3 Subcontinental element

Sct bee species prefer e g Boraginaceae (Tab 5). This plant family is represented by many species in the sct region. In their flower-visiting behaviour, the sct bee and butterfly species resemble esb species in that they also visit "hem" species.
With regard to the spectrum of visited plant species, it seems that the vegetation of riversides and rocky valley walls are of special importance. Therefore, the valley of the Danube could have served as a migratory path for such sct species.
Lasioglossum lineare (Schenck 1868) widespread in the sct region prefers in the study area *Pulsatilla vulgaris* Mill. (Ranunculaceae) which has its area of origin in the sct geoelement.

Tab 3: Polyploid and in some cases apomictic plant species derived from diploid ancestors by allopolyploidy or hybridization and examples of stenanthic flower visitors [Hymenoptera: Apoidea].

stenanthic bee species	*Andrena falsifica* Perkins 1915, *Andrena saundersella* Perkins 1914 (= *semilaevis* Pérez 1903), *Andrena strohmella* Stoeckhert 1928, *Andrena subopaca* Nylander 1848, *Andrena viridescens* Viereck 1916	
preferred polyploid plant species	*Potentilla tabernaemontani* Aschers. (polyploid, apomictic)	*Veronica chamaedrys* L. (polyploid, entomogamic)
diploid (tetraploid) ancestors	*Potentilla cinerea* Chaix, *Potentilla tommasiana* F.W.Schulz (di-/tetraploid, entomogamic); submed. mountain species, submed./subcont. species	*Veronica prostrata* L. (diploid, entomogamic) and other submed./subcont. species
	relict species, species of glacial refuges	

stenanthic bee species	*Andrena curvungula* Thomson 1870, *Andrena pandellei* Pérez 1895, *Chelostoma campanularum* (Kirby 1802), *Chelostoma distinctum* Stoeckhert 1929 (= *cantabrica* Benoist 1936), *Chelostoma fuliginosum* (Panzer 1798), *Lasioglossum costulatum* (Kriechbaumer 1873), *Osmia mitis* Nylander 1852
preferred polyploid plant species	*Campanula rotundifolia* agg. (tetraploid, entomogamic)
diploid ancestors	"Lanceolatae" (thin forests, grasslands) (Pyrenees etc.) "Saxicolae" (submed. rock-/grassland communities) "Pusillae" (virgin soil pioneer species of mountains) relict species, species of glacial refuges

stenanthic bee species	*Andrena fulvago* (Christ 1791), *Andrena humilis* Imhoff 1832, *Dufourea vulgaris* (Schenck 1851), *Lasioglossum parvulum* (Schenck 1853) (= *minutulum* Schrank 1781), *Lasioglossum villosulum* (Kirby 1802), *Panurgus calcaratus* Scopoli 1763, *Osmia spinulosa* (Kirby 1802)
preferred polyploid plant species	*Hieracium* (polyploid, apomictic)
diploid ancestors	frequently diploid species of mediterranean mountains (diploid, entomogamic) relict species, species of glacial refuges

stenanthic bee species	*Andrena hattorfiana* (Fabricius 1775)
preferred polyploid plant species	*Knautia arvensis* ssp. *arvensis* L. (tetraploid, entomogamic)
diploid ancestors	*Knautia drymeia* agg. (SE-European deciduous mixed forests) *Knautia longifolia* agg. (tall herb community, mountain grasslands) *Knautia arvensis* agg. (submed. mountained rock-/grassland communities) (diploid, entomogamic) relict species, species of glacial refuges

Tab 4: Bee and butterfly species of the smt fauna element and their flower-visiting preferences [Hymenoptera: Apoidea/Lepidoptera]. — (a) examples of the study area, (b) examples of other study sites and habitats in Central Europe (references are mostly bibliographical data) (footnotes see in text Tab 2).

SUBMEDITERRANEAN ELEMENT

submediterranean flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring mainly grassland species, avoiding "hem", "coat" or forest species

blue/violet Compositae (e.g. *Centaurea*)

a) *Lasioglossum albocinctum* (Lucas 1849)
Lasioglossum major (Nylander 1852) [8]

b) *Anthidium lituratum* (Panzer 1801)
Heriades crenulatus Nylander 1856
Lasioglossum scabiosae (Rossi 1790)
Lasioglossum smaragdulus Vachal 1895

in combination with Labiatae, Dipsacaceae and/or Boraginaceae

a) *Halictus simplex* Blüthgen 1923 [6] (?)
(= *marchali* Vachal 1891)

b) *Ceratina cucurbitina* (Rossi 1792)
Lasioglossum quadrisignatum (Schenck 1853)
Nomia femoralis (Pallas 1773)

Melitaea parthenoides Keferstein 1851

Cruciferae

b) *Andrena agilissima* (Scopoli 1770)
Andrena distinguenda Schenck 1871
(= *obsoleta spongiosa* Warncke 1967)
Andrena hypopolia Schmiedeknecht 1883 (1.Gen.)
(= *numida hypopolia* Schmiedeknecht 1883)
Andrena nana (Kirby 1802) (1.Gen.)
Andrena niveata Friese 1887 [9]
Andrena pusilla Pérez 1903
(= *spreta pusilla* Pérez 1903)
Andrena suerinensis Friese 1884 [6]
Andrena tscheki Morawitz 1872 [9]

Labiatae

a) *Rophites trispinosus* Pérez 1903 [6]
(= *algiricus trispinosus* Pérez 1903)

b) *Lasioglossum clypeare* (Schenck 1853)
Lasioglossum convexiusculum (Schenck 1853) [6]
Osmia andrenoides Spinola 1808

Cistaceae

a) *Andrena enslini* Alfken 1921
(= *granulosa enslini* Alfken 1921)

Tab 5: Bee species of the sct fauna element and their flower-visiting preferences [Hymenoptera: Apoidea]. — (a) examples of the study area, (b) examples of other study sites and habitats in Central Europe (references are mostly bibliographical data) (footnotes see in text Tab 2).

SUBCONTINENTAL ELEMENT

subcontinental flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) preferring "hem" species or tall herbs of ruderal habitats, for example:

Boraginaceae

a) —

b) *Andrena nasuta* Giraud 1863
Andrena symphyti Schmiedeknecht 1883
Colletes nasutus Smith 1853

3.3.4 Submediterranean/subcontinental element

Bee and butterfly species of the study area (including references to other study sites and habitats in Central Europe), which have a smt as well as a sct distribution, visit preferably grassland species for pollen and nectar foraging and in some cases also "hem" species. Some bee and butterfly species exhibit stenanthy for Dipsacaceae and Umbelliferae (Tab 6). In their preference for blue Compositae and Labiatae they resemble smt flower visitors. For example the preference of the butterfly *Melitaea phoebe* Schiffermüller 1775 (Nymphalidae) for blue/violet Compositae is remarkable. The larvae feed preferably on *Centaurea* and the adults suck its nectar [Weidemann 1985].

Tab 6: Bee and butterfly species of the smt/sct fauna element and their flower-visiting preferences [Hymenoptera: Apoidea/Lepidoptera]. — (a) examples of the study area, (b) examples of other study sites and habitats in Central Europe (references are mostly bibliogeographical data) (footnotes see in text Tab 2).

SUBMEDITERRANEAN / SUBCONTINENTAL ELEMENT

flower visitors (Hymenoptera Apoidea, Lepidoptera/imagines) with submediterranean and subcontinental distribution preferring grassland species, "hem" species or tall herbs of ruderal habitats, for example:

	a)	b)
Dipsacaceae / blue or violet Compositae		
	Melanargia galathea Linnaeus 1758	*Dasypoda argentata* (Panzer 1809)
	Melitaea phoebe Schiffermüller 1775	*Andrena morio* Brullé 1832
Labiatae / Fabaceae		
	Eucera tuberculata (Fabricius 1793) [3]	*Megachile rotundata* (Fabricius 1787) [3]
	Megachile pilidens Alfken 1924	
	Hipparchia fagi Scopoli 1763	
in combination with Boraginaceae		
	Osmia adunca (Panzer 1798)	*Eucera interupta* Baer 1850
		Nomia femoralis (Pallas 1773)
Umbelliferae		
	Andrena combinata (Christ 1791)	
	Andrena nitidiuscula Schenck 1853	

3.4 The area-geographical subsystems of the studied flower-visiting community

Many examples indicate that flower-visiting insects (here bees and butterflies) of special area types prefer those plant species for collecting pollen or sucking nectar which occur in the same geoelement. Different area-geographical subsystems with distinct entomophilous plant species and flower-visiting insects can be distinguished in the study area (Fig 3). In many cases the flower-ecological coincidences are based on interrelations and coevolutionary processes developed in the biocoenosis of the area of origin. The area type spectrum of plants and insects of the study area can only be understood with regard to the history of flora and fauna of the postglacial period. Inborn foraging preferences of flower visitors (stenanthy) presuppose synchronization with distinct plant species. The scope of mutual phenology (co-phenology) is fixed by the seasonal climatic conditions in the area of origin and area of main distribution. The composition of the floral and faunal species in the study area (dry grassland with "hem" species), their phenologies, and the different interrelationships between the entomophilous plants and the flower-visiting insects are perhaps best understood in light of their histories.

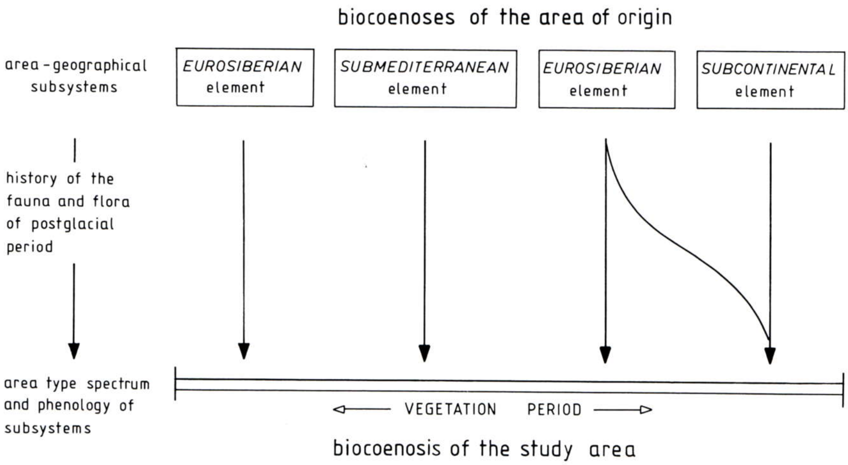

Fig 3: The area-geographical subsystems of the plant/flower visitor community in the study area and their phenology.

4 Acknowledgements

Thanks are due to Dr O. Kudrna (Bonn) and to Dr K. Warncke (Dachau) for useful advice regarding the area geographical distribution of butterflies and bees.

5 References

Courtney, S. P., & Duggan, A. E. [1983]: The population biology of the Orange Tip butterfly Anthocharis cardamines in Britain. — Ecol. Entomol. **8**: 271—281; Oxford.

Dennis, R. L. H. [1982]: Observations on habitats and dispersion made from oviposition markers in North Cheshire Anthocharis cardamines (L.) (Lepidoptera: Pieridae). — Entomol. Gaz. **33**: 151—159; Faringdon.

Dersch, G. [1969]: Über das Vorkommen von diploidem Wiesenschaumkraut (Cardamine pratensis L.) in Mitteleuropa. — Ber. Dtsch. Bot. Ges. **82**: 201—207; Stuttgart.

Ehrendorfer, F. [1962a]: Cytotaxonomische Beiträge zur Genese der mitteleuropäischen Flora und Vegetation. — Ber. Dtsch. Bot. Ges. **75**: 137—152; Stuttgart.

Ehrendorfer, F. [1962b]: Beiträge zur Phylogenie der Gattung Knautia (Dipsacaceae). I. Cytologische Grundlagen und allgemeine Hinweise. — Österr. Bot. Z. **109**: 276—343; Heidelberg.

Ehrendorfer, F. [1970]: Mediterran-mitteleuropäische Florenbeziehungen im Lichte cytotaxonomischer Befunde. — Feddes Report. **81**: 3—32; Berlin.

Kratochwil, A. [1983]: Zur Phänologie von Pflanzen und blütenbesuchenden Insekten (Hymenoptera, Lepidoptera, Diptera, Coleoptera) eines versaumten Halbtrockenrasens im Kaiserstuhl (Südbaden) — ein Beitrag zur Erhaltung brachliegender Wiesen als Lizenz-Biotope gefährdeter Tierarten. — Beih. Veröff. Naturschutz Landschaftspfl. Bad.-Württ. **34**: 57—108; Karlsruhe.

Kratochwil, A. [1984a]: Pflanzengesellschaften und Blütenbesucher-Gemeinschaften: biozönologische Untersuchungen in einem nicht mehr bewirtschafteten Halbtrockenrasen (Mesobrometum) im Kaiserstuhl (Südwestdeutschland). — Phytocoenologia **11**: 455—69; Stuttgart, Braunschweig.

Kratochwil, A. [1984b]: Quelques observations sur la phénologie des plantes à fleurs et des insectes butinants dans un Mesobrometum avec des espèces d'ourlets au Kaiserstuhl (Allemagne). — In: Géhu, J.-M. (ed): La vegetation des pelouses calcaires — Strasbourg 1982. — Colloques phytosociologiques **XI**: 421—456; Vaduz.
Meusel, H., Jäger, E., & Weinert, E. [1965ff.]: Vergleichende Chorologie der zentraleuropäischen Flora. 2 Bde. — Jena.
Oberdorfer, E. [1978]: Süddeutsche Pflanzengesellschaften. — 4. A. — Stuttgart.
Pignatti, S. [1982]: Flora d'Italia. Vol. 1—3. — Bologna.
Stoeckhert, F.K. [1954]: Fauna Apoideorum Germaniae. — Abh. Bayer. Akad. Wiss. Math.-naturw. Kl. N.F. **65**: 01—87; München.
Strohm, K. [1933]: Die Insekten. Tiergeographische Charakterisierung des Kaiserstuhls. — In: Bad. Landesver. Naturk. (ed): Der Kaiserstuhl: 285—466, 384—402; Freiburg i. Br.
Walter, H., & Lieth, H. [1960]: Klimadiagramm Weltatlas. — Jena.
Weidemann, H. J. [1985]: Ökologisch orientierte Lepidopterologie als Grundlage für Konzeption und Durchführung von Lepidopterenschutzprogrammen. — Entomol. Z. **95**: 49—64; Stuttgart.
Wiklund, C. [1977]: Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of Leptidea sinapis (Lepidoptera). — Oikos **28**: 56—68; Copenhagen.
Wiklund, C., & Åhrenberg, C. [1978]: Hostplants, nectar source plants, and habitat selection of males and females of Anthocharis cardamines (Lepidoptera). — Oikos **31**: 169—183; Copenhagen.
Wilmanns, O. [1975]: Junge Änderungen der Kaiserstühler Halbtrockenrasen. — In: Univ. Hohenheim (ed): Vortr. Tagung "Umweltforschung": 15—22; Stuttgart-Hohenheim.
Wilmanns, O. [1977]: Vegetation. — In: Wilmanns, O., Wimmenauer, W., Fuchs, G., Rasbach, H. u. K. (eds): Der Kaiserstuhl. Gesteine und Pflanzenwelt. — Natur- u. Landschaftsschutzgeb. Baden-Württ. **8**: 33—71; Karlsruhe.
Wilmanns, O., & Kratochwil, A. [1983]: Naturschutz-bezogene Grundlagen-Untersuchungen im Kaiserstuhl. — Beih. Veröff. Naturschutz Landschaftspfl. Bad.-Württ. **34**: 39—56; Karlsruhe.
Zoller, H. [1954]: Die Arten der Bromus erectus-Wiesen des Schweizer Juras. — Veröff. Geobot. Inst. Eidg. techn. Hochsch. Stift. Ruebel **28**: 001—289; Zürich.

Author's address — Anschrift des Verfassers: Dr Anselm Kratochwil, Institut für Biologie II (Geobotanik), Albert-Ludwigs-Universität, Schänzlestraße 1, D-7800 Freiburg/Breisgau; Bundesrepublik Deutschland — F.R. Germany.

Slobodda, S.: **Pflanzengemeinschaften und ihre Umwelt. — Plant Societies and their Environment.** — [254 pages, numerous figures and colour photographs, size 175 x 245 mm, balacron hard cover, jacket]. — Publisher: Quelle & Meyer GmbH, Heidelberg-Wiesbaden 1985; ISBN: 3-494-01135-4; price: DM 29,80. --- [EGR-Nr 1183].

Ein schönes und ein gutes Buch liegt hier vor: reich bebildert mit instruktiven zweifarbigen Strichzeichnungen und Farbfotos sowie einem leicht verständlichen, aber durchweg wissenschaftlich fundierten Text. Jeder, der sich mit Umweltproblemen und dem Schutz der noch verbliebenen Lebensgemeinschaften befaßt, sollte dieses Buch nicht übersehen. Angefangen von Themen wie „Die Pflanzendecke und ihre Beziehungen zum Menschen im Blickfeld der Geschichte", „Der sommergrüne Laubwald – Vergesellschaftung verschiedener pflanzlicher Lebensformen", „Sind Unkräuter nur unnütze Kräuter?", „Pflanzenleben im Hochmoor – Anpassung und Auslese am extrem feuchten und nährstoffarmen Standort", „Wohin entwickeln sich unsere Seen? – Pflanzengesellschaften geben Auskunft", „Pflanzengemeinschaften als Basisglieder von Ökosystemen" bis zur Problematik der „Erhaltung der biologischen Mannigfaltigkeit – ein humanistisches Anliegen" werden hier Wissensgebiete und Fragenkomplexe aufbereitet, die heute jeden angehen sollten, und aus deren gründlich durchdachter Behandlung jeder, der sich aktiv mit Naturschutzfragen befassen möchte, reichen Gewinn ziehen kann.