

Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes)

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Abstract. Meaningful ecological studies on insect communities require sampling protocols that take into consideration temporal fluctuations in abundance and species composition. Bees with their specific requirements for nutrition and nesting are good indicators of landscape structure and overall biodiversity, provided the ecological and seasonal patterns they show are taken into consideration. The present two year study traced the ecological and seasonal patterns on 2 km² of a southern slope in the Swiss Alps, ranging from 1150 to 1550 m above sea level. The study area consisted mainly of grassland under different regimes, mostly hay meadows and pastures. By direct netting at five monthly intervals in each year a total of 247 bee species were recorded. This comprehensive sampling scheme identified one of the most diverse bee faunas in Central and Northern Europe, consisting of a statistically estimated 280 species. Most species were rare with 14.6% represented by a single individual. Ecological analysis of the bee community showed that the primitively eusocial species were over represented among the abundant species and the parasitic species among the rarest.

Both abundance and species richness were subject to marked seasonal variations. A substantial turnover in species composition as well as changes in ecological patterns were observed. More than 25% of all species were recorded in only one of the two years, in particular many of the parasitic species. Singletons accounted for a higher proportion when individual years rather than the pooled data were analysed. All these findings underline the importance of season-long sampling and sampling over more than one year if bees are to be used as indicators in ecological and studies on bee communities.

INTRODUCTION

Meaningful ecological studies on insect communities require sampling protocols that take into consideration temporal fluctuations in abundance and species composition to avoid misleading results. The effects of sampling effort or seasonality on ecological patterns are only documented for a few insect groups. Sampling effort accounted for a large proportion of the variance in alpha-diversity in two of three guilds of a phytophagous insect community on Brassicaceae (Frenzel & Brandl, 1998). Furthermore, seasonal patterns depended on the level of specialization and the feeding habits of Auchenorrhyncha in a rain forest (Novotny & Basset, 1998).

Bees (Hymenoptera, Apiformes) with their high habitat requirements have recently been used as indicators of biodiversity or landscape structure in ecological studies (Tschardt et al., 1998; Steffan-Dewenter et al., 2002; Steffan-Dewenter & Leschke, 2003; Dauber et al., 2003). They are the best indicators of overall species richness in agroecosystems, together with Coleoptera and Heteroptera (Duelli & Obrist, 1998). Bees are characterized by complex life histories and have specific requirements for nutrition and nesting (Westrich, 1990). They need habitats rich in flowering plants, as a large proportion of the species only collect pollen from certain plants (Westrich, 1990; Müller, 1996; Wcislo & Cane, 1996). In addition, bees have specific nesting sites, such as dead wood, bare

soil, plant stems, or rock fissures. As bees are typical central-place foragers, which return to their nests after foraging, feeding and nesting sites must be close to one another (Westrich, 1996).

Several studies show that bee populations vary widely in abundance and species composition within and between years, but none of them included ecological patterns (Tepedino & Stanton, 1981; Pearson & Dressler, 1985; Wolda & Roubik, 1986; Ortiz-Sánchez & Aguirre-Segura, 1991; Banaszak & Cierzniak, 1994; Ortiz-Sánchez & Belda, 1994; Schmid-Egger, 1995; Banaszak & Krzysztofiak, 1996; Banaszak & Cierzniak, 1997; Minckley et al., 1999; Roubik, 2001; Banaszak & Wenzonka, 2002). Ecological patterns of bees are expected to vary during the season as in central Europe bee species have distinct phenologies. Therefore, a knowledge of the ecological, seasonal, and annual patterns shown by bee communities is crucial for the use of bees as bioindicators.

Bees were chosen as indicators of the overall species diversity in an extensive study of the effect of different agricultural practices on biodiversity in a grassland ecosystem in the Swiss Alps. A pilot study indicated that bee diversity in the area is exceptionally high. For the current study the data set was analysed to determine (i) the ecological and seasonal patterns in the bee community, and (ii) the variation between two subsequent years in the

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composition of the bee fauna and in the ecological patterns. Based on the findings, the sampling protocols needed for studying bee assemblages are discussed.

MATERIAL AND METHODS

Study area

The study was carried out on the southern slope of the Valais, a large valley in the southern part of Switzerland. The study area encompassed approximately 2 km² around the village of Erschmatt (46°19'18"N/7°41'30"E), at an altitude ranging from 1150 to 1550 m. Average annual precipitation was approximately 890 mm with the highest monthly precipitation in winter. The southern exposure, high insolation, and frequent winds result in a high rated evaporation (Budmiger, 1970). At the closest weather station at a comparable altitude and with similar exposure (Montana, 45°16'37"N/7°28'55"E) the mean daily maximum temperature ranges between 1.0°C in January and 19.4°C in July (MeteoSwiss, n.d.) and the absolute maximum in summer reach 30°C to 35°C. The average number of hours of sunshine per year at this station (2071 h) is surpassed by only four other weather stations in Switzerland.

Main vegetation types in the area are Arrhenaterion, Mesobromion, Stipo-Poion, Sedo-Scleranthion and Ononido-Pinion (Delarze et al., 1999). About 80% of the study area is used as hay meadows or pastures. Hay meadows are cut once or twice a year and are partly grazed in spring or autumn. Pastures are grazed either by sheep or Scottish Highland cattle and increasingly also horses.

Material examined and methods

The study was carried out between the end of March and the beginning of October in 2001 and 2002. Bees were collected by means of direct netting between 9.30 and 16.00 on sunny days when the temperature was above 15°C and there was little wind. Collecting was discontinued if either of these conditions was not fulfilled. Sampling followed standardized protocols: (1) fixed plots were sampled at intervals over the whole study, and (2) each area was sampled for the same period of time. Firstly, eight different land use types were defined: two types of meadows of two cuts differing in their landscape context, meadows of one cut, sheep pastures, cattle pastures, fallow land, steppic grassland, and pine forest. For each land use type four plots of 1600 m² each were marked out in the field. On these plots, bees were collected over a period of one hour per plot, five times per year between April and August 2001 and between May and September 2002. At each sampling the four plots of each land use type were sampled at different times of the day. Secondly, two plots of 2 ha each were selected, one consisting of a mosaic of different land use types and the other a homogeneous hay meadow of two cuts. Bees were collected over a period of five hours per plot, five times between April and August 2001. The third protocol was unstandardized regarding the duration of sampling per area: Bees were collected within the study area but outside the marked plots at potential nesting sites and pollen sources of oligolectic species on two days during each sampling period. The total time spent sampling amounted to approximately 500 h.

Very rare species were released after the determination of species and sex, all other specimens were killed for determination. Members of the genus *Bombus* Latreille, 1802 were not collected before the middle of June in order to avoid killing queens. Voucher specimens of all species are deposited in the Entomological Collection of the Swiss Federal Institute of Technology (ETH). All bees were determined to species except for the few species pairs of uncertain taxonomy and the two groups

the females of which are difficult to distinguish: each of the pairs *Hylaeus gibbus* Saunders, 1850 and *H. confusus* Nylander, 1852, *Nomada succincta* Panzer, 1798 and *N. goodeniana* (Kirby, 1802), and *Andrena proxima* (Kirby, 1802) and *A. alutacea* Stöckert, 1942 was treated as a single species. Females of the *Bombus terrestris*-group, i.e. *B. terrestris* (Linné, 1758), *B. lucorum* (Linné, 1761), *B. magnus* Vogt, 1911 and *B. cryptarum* (Fabricius, 1775), were recorded as *Bombus terrestris*, and females of the *Halictus simplex*-group, i.e. *H. simplex* Blüthgen, 1923, *H. eurygnathus* Blüthgen, 1931 and *H. langobardicus* Blüthgen, 1944, were recorded as *Halictus simplex*. The honeybee, *Apis mellifera* Linné, 1758, was not recorded as its abundance and distribution depend more on the position of bee hives than on environmental factors. The nomenclature follows the catalogue of bees in Switzerland, Austria and Germany (Schwarz et al., 1996).

Data analysis

For the characterization of the bee community the data for both years were pooled. Species diversity was characterized by species richness and rank abundance distribution. The expected total species richness was calculated using the program EstimateS 6.0b (Colwell, 1997). The eight land use types, the two large plots and the data from outside the marked plots gave the 11 samples for the calculation. Following the criteria described in Chazdon et al. (1998), the two estimators chosen were those that gave values closest to the observed species richness when only two and six of the eleven samples were included in the calculation. In our case Chao2 and MMEan (Michaelis Menten estimator based on means) performed best.

Information on the following ecological aspects of the bees were extracted from Westrich (1990) and Müller et al. (1997), and included in the analyses: parasitic behaviour, nesting behaviour, floral relationships, and social behaviour.

The parasitic species were analysed separately against the non-parasitic species. Within the remaining aspects categories were formed:

To characterize nesting behaviour, species were divided into "endogeic" (nesting in the ground), "hyper-/endogeic" (nesting in the ground or close to the ground) and "hypergeic" (nesting in a variety of structures above ground). To characterize floral relationships, the species were divided into "polylectic" (gathering pollen from a variety of unrelated plant species) and "oligolectic" (specialized on a certain family or genus of plants). To characterize social behaviour, the species were divided into "solitary" (each female constructs her own nest and provisions it with food for the offspring) and "primitively eusocial" (forming temporary colonies with division of labour). Species for which details of a specific behavioural trait were unknown, were not included in the respective analysis.

The frequency of different ecological categories was related to the abundance of each species. For this purpose, four levels of abundance were recognized: singletons ($n = 1$), $1 < n < 0.1\%$ of all individuals, $0.1\% \leq n < 1\%$ and $n \geq 1\%$. A further division of the higher abundance categories was not possible, as expected values would have become too small. The number of species observed per ecological category and abundance class was compared with an even distribution of ecological categories over all abundance classes using a Chi-square test.

To illustrate the temporal turnover of species, the qualitative Soerensen index of similarity between the sampling periods was calculated (Magurran, 1988) and reproduced in a cladogram on ClustanGraphics (Version 5.27). To test for phenological effects on ecological patterns, observed proportions of ecological categories in each month were tested against the assumption that values remain constant throughout the season. Average values

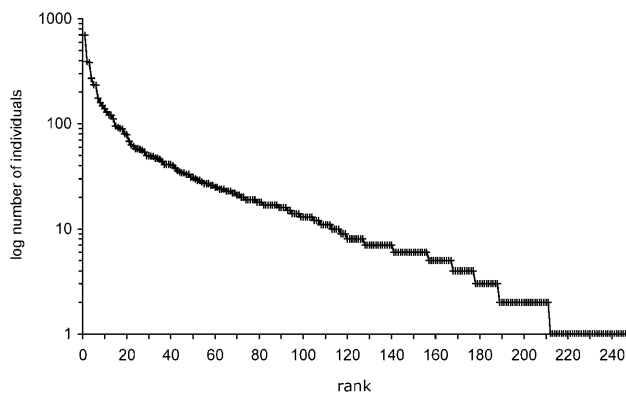


Fig. 1. Rank abundance distribution of the bee community based on data from both years.

were used for the months that were sampled in both years (May to August) and individual values for April 2001 and September 2002.

The data for each year were characterized with the same parameters as the pooled data. The expected species richness was calculated using the data for each year separately to investigate the effect of sampling intensity on the estimate. The proportions of singletons and ecological categories in each year and in the pooled data were compared by means of Chi-square tests.

RESULTS

Characterization of the bee fauna

Over the two years, a total of 6,888 bees were collected. They belong to 30 genera and 247 species (Appendix), which is 42.1% of the 587 species recorded in Switzerland. Very few species were abundant and a high proportion were rare (Fig. 1). Three species made up each more than 5% of the total number of the bees collected, namely 695 individuals (10.1%) of *Halictus simplex* Blüthgen, 1923, 392 (5.7%) of *Lasioglossum morio* (Fabricius, 1793), and 382 (5.5%) of *Bombus humilis* Illiger, 1806. These three species are primitively eusocial, polylectic and endogecic. Ten species made up from 1 to

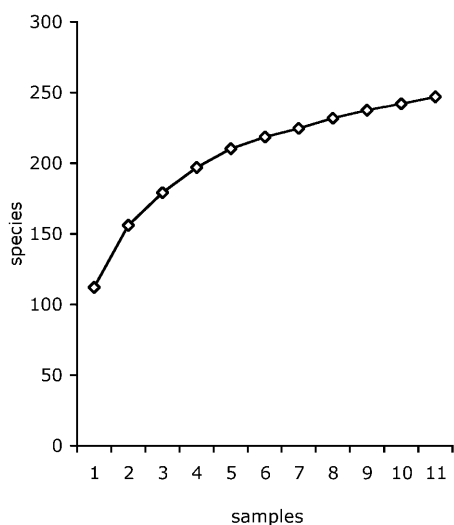


Fig. 2. Mean species accumulation curve for the pooled bee data based on 50 randomizations.

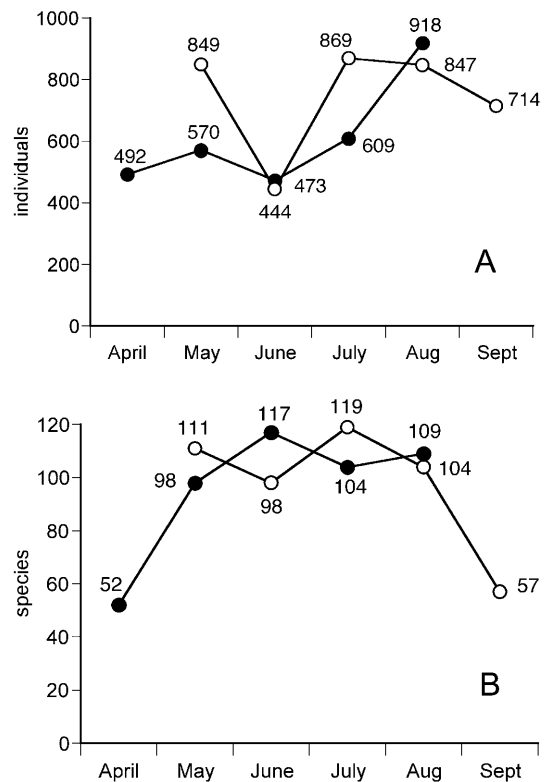


Fig. 3. Number of bee individuals (A) and species (B) collected each month in the two years of the study (filled circles = 2001, open circles = 2002).

4.99% of the total. Among these, there are two oligolectic species [*Andrena proxima* (Kirby, 1802) and *Panurgus banksianus* (Kirby, 1802)] and two hypergeic species [*Osmia aurulenta* (Panzer, 1799) and *Anthidium oblongatum* (Illiger, 1806)]; the rest are polylectic or endogecic. Thirty-six species (14.6%) were represented by one individual (singletons). The species accumulation curve did not reach saturation (Fig. 2) indicating that some species remained undetected. The estimates of species richness obtained using Chao2 is 279 species, and using MMMMeans 275 species, which are respectively 47.5% and 46.8% of the bee fauna of Switzerland. Hence, by sampling over two consecutive seasons, nearly 90% of the estimated number of bee species present in the area was recorded.

Of the bees recorded 17.8% are parasites. Of the non-parasitic species 58.0% are endogecic, 32.5% hypergeic and 9.5% hyper-/endogecic nesting species. In terms of floral relationships 69.2% of the species are polylectic and 30.8% oligolectic. The most important plants for the oligolectic species were Asteraceae (n = 19), Fabaceae (n = 12) and *Campanula* (n = 8). In terms of social behaviour 83.2% of the species are solitary and 16.8% primitively eusocial.

Parasitic species made up a higher proportion of the singletons and lower proportions of the individual-rich classes than expected ($\chi^2 = 21.086$; $p < 0.001$). Primitively eusocial species were under-represented in the individual poor classes and over-represented in the

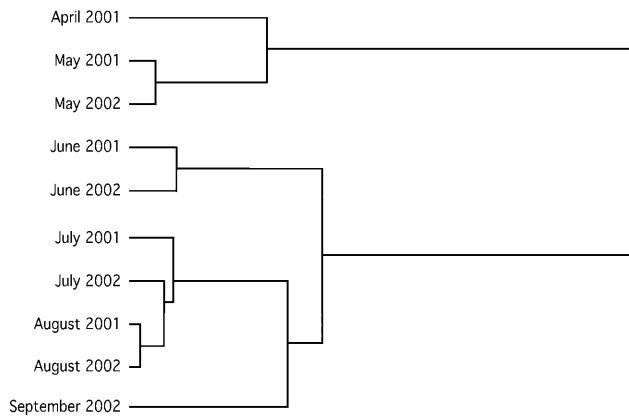


Fig. 4. Cladogram of the qualitative Soerensen indices of similarity of bee data collected in the different months. Cluster proximity = increase in sum of squares.

individual-richest class ($\chi^2 = 33.428$; $p < 0.001$). The proportions of the different nesting behaviours and floral relationships did not differ significantly among the abundance classes ($\chi^2 = 11.506$, $p = 0.074$ and $\chi^2 = 7.815$, $p = 0.080$, respectively).

Seasonal patterns

In terms of numbers of individuals least were collected in June of both years and most in August 2001 and July 2002, with nearly twice as many individuals (Fig. 3A). As for the numbers of species the seasonal minimum occurred in April 2001 and September 2002 and the peak of more than twice as many species in June 2001 and July 2002 (Fig. 3B).

The bee fauna showed a marked species turnover during a year with three clusters of species (Fig. 4): spring (April and May), early summer (June) and mid- to late summer clusters (July to September). Of the 247 species 22.3% were recorded only in one month and 38.5% in one cluster.

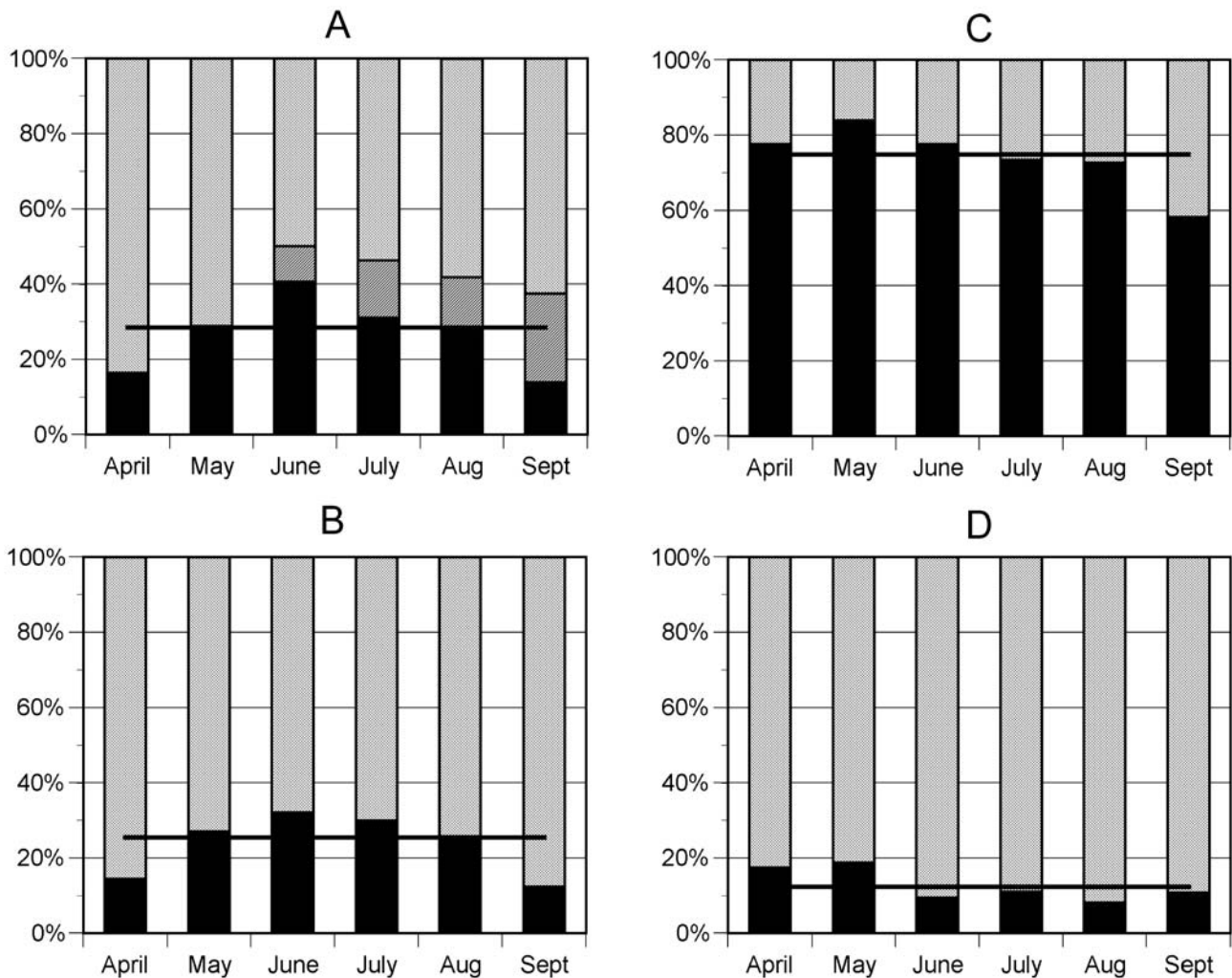


Fig. 5. Proportion of bee species in each ecological category in each month. The black lines indicate the expected value for the first category based on constant proportions. A – Nesting behaviour (black = hypergeic species, hatched = hyper-/endogeic species, grey = endogeic species); B – Floral relationships (black = oligolectic species, grey = polylectic species); C – Social behaviour (black = solitary species, grey = primitively eusocial species); D – Parasitic (black) versus non-parasitic species (grey).

The proportions of species in the different nesting categories deviate significantly from constant over the season ($\chi^2 = 42.922$, $p < 0.001$; Fig. 5A). In April and May there were more endogeic (dominated by *Andrena* spp.) and in June more hypergeic species than expected (maximum activity period of Megachilidae). Hyper-/endogeic species (mostly bumblebees) were more frequent in July and September, and in August the observed values deviated little from the expected values. A marginally significant phenological effect was observed in the floral relationships ($\chi^2 = 10.602$, $p = 0.060$; Fig. 5B) and social behaviour ($\chi^2 = 10.426$, $p = 0.064$; Fig. 5C). The proportion of parasitic species did not vary significantly ($\chi^2 = 8.11$, $p = 0.150$; Fig. 5D).

Comparison between years

The quantitative comparison of the two years (2001 and 2002) yields 3075 versus 3813 specimens belonging to 209 versus 222 species, respectively. A total of 63 species were collected only in one of the two years, which corresponds to 25.5% of the 247 species recorded. The proportion of singletons was significantly higher in the single years (19.6% in 2001 and 20.3% in 2002) than in the pooled data (14.6%; 2001 versus pooled data: $\chi^2 = 4.220$, $p = 0.040$; 2002 versus pooled data: $\chi^2 = 5.725$, $p = 0.017$).

The total species richness estimates obtained using the data for 2001 were 250 for the Chao2 estimator and 242 for the MMMeans estimator. These values are considerably lower than those obtained using the 2002 data (Chao2 = 276 and MMMeans = 280), and are close to the observed species number of the pooled data.

The differences in the proportions of ecological categories between the single years and the pooled data were not significant (Chi-square tests, p-values between 0.262 and 1.000). However, more parasitic species were recorded than expected in one year and more non-parasitic species in both years ($\chi^2 = 11.219$, $p < 0.001$). The phenology based on individual numbers and species numbers recorded each month differed between the two years (Spearman's rho = -0.700, $p = 0.188$ and Spearman's rho = 0.100, $p = 0.873$).

However, the species composition of the samples collected in the same month in the two years was more similar than that of samples collected in different months within a year (Fig. 4).

DISCUSSION

Characterization of the bee fauna

During sampling over two years, to trace ecological and seasonal patterns, 247 species of bees were recorded on a small study area. This is nearly 90% of all the predicted native bee species in the area. Sampling significantly larger areas in Central and Northern Europe, using a wide range of methods and protocols, yielded 236 species in extensively used vineyards in northwestern Baden-Wuerttemberg (Schmid-Egger, 1995), 233 in the Principality of Liechtenstein (Bieri, 2002), 92 on the East Friesian island of Norderney (Haeseler, 1990) and 91 in

semi-natural habitats in a Danish agricultural landscape (Calabuig, 2000). Although the different methods used prevent direct comparison, the data indicate that the study area harbours one of the most diverse bee faunas in Central and Northern Europe.

Factors favouring the high bee diversity in this area are climate, range in altitude and diversity of land use. (i) The warm-temperate, xeric climate typical of the inneralpine valley of the Valais is similar to that of the Mediterranean region, which is known to be one of the global hotspots of bee diversity (Michener, 1979). (ii) The large range in altitude in the area covers a transition zone, where both lowland and subalpine species co-exist. Typical lowland species, such as *Anthidium septemdentatum* Latreille 1809, *Ceratina chalybaea* Chevri r, 1872 and *Lasioglossum euboense* (Strand, 1909), were recorded along with species known from the subalpine zone including for example *Bombus monticola* Smith, 1849, *Bombus sicheli* Radoszkowski, 1859 and *Lasioglossum cupromicans* P rez, 1903. (iii) The co-existence of different habitat types and the low intensity of land use are crucial for the high biodiversity in the study area. This is shown by a detailed analysis of the correlations between landscape characteristics, resource abundance, and species richness (Oertli et al., in prep.).

Singletons usually have to be treated as noise in ecological studies. Intensive sampling keeps the proportion of singletons low, as the number of bee specimens collected and the percentage of singletons are negatively correlated (Williams et al., 2001). The proportion of singletons in the current study is low (14.6%) and compares favourably with the 15 to 40% singletons reported for ten studies in which more than 2000 specimens were collected (Williams et al., 2001).

In the present study, parasitic species were over represented among the singletons and more often recorded in only one year than expected. Similarly, a lower persistence of parasitic than non-parasitic species is reported in a three-year study on the bee fauna in southern Baden-Wuerttemberg (Herrmann & M ller, 1999). Parasitic species are recorded less efficiently by direct netting than non-parasitic species due to their low densities and tendency to visit flowers only for nectar. An assessment of the number of parasitic species therefore requires a greater sampling effort.

The high proportion of hypergeic species indicates that suitable above-ground nesting sites are abundant and there is no shortage of open soil, which could cause an under representation of endogeic species. The abundance of primitively eusocial species in the individual-richest abundance class indicates the size and density of their colonies. This life history strategy seems to be very successful in the study area.

Seasonal patterns

The seasonal peak in individual numbers in August 2001 and July 2002 is due to the bumblebee colonies being at their maximum size then and the emergence of a new generation of halictid species. The seasonal maximum in the numbers of species in June 2001 and

July 2002 might reflect the differing phenology of the bee taxa resulting in the coexistence of late spring and early summer species at this time.

The marked turnover of species during the course of a season is due to the activity spans which are limited to a few weeks in most bee species (Westrich, 1990). In fact, Minckley et al. (1999) report a median of similarity of only about 35% between the bee assemblages present at different times during a study only lasting a few weeks (modified data presented in Williams et al., 2001). Therefore, season-long sampling is essential for the complete assessment of a bee community.

A significant phenological effect was observed in the frequency of the different nesting behaviours and a marginal effect on floral relationships and social behaviour. Parasitic species as well as hypergeic, oligolectic and solitary species were present in lower proportions in most months than in the entire data set. This can only be explained by a greater species turnover in these ecological categories than in the others. These findings indicate that only sampling over a whole season will reveal the ecological structure of a bee community.

Comparison between years

The orders of magnitude by which bee abundances may vary between consecutive years can be as high as five (Pearson & Dressler, 1985; Cane & Payne, 1993; Frankie et al., 1998; Roubik, 2001). Values can be much higher when non-consecutive years in long-term studies are compared (Roubik, 2001). Large differences in the abundance of bees between years are caused by several factors such as large- and small-scale climatic conditions, weather conditions during the census and during the activity span of the parental generation, vegetation phenology and land use.

The studies quoted above on the variation in the abundance of bees between consecutive years were confined to a taxonomic section of the local bee fauna. As abundances of different species do not fluctuate synchronously, variation in the complete bee fauna – as presented in our study – will be smaller than in single taxa.

The species richness varied little between the two years of this study. However, species richness is increasingly recognised as too rough a measure of biodiversity and species composition is gaining in importance (Jeanneret et al., 2003; Su et al., 2004). Indeed, species composition was different in the two years. As many as 25% of all species recorded were collected in only one of the two years. This stresses the importance of long-term studies for the detailed assessment of bee faunas.

The decrease in the percentage of singletons with increased sampling effort – represented by the number of individuals collected – conforms to the conclusions of a recent review (Williams et al., 2001). A high percentage of singletons in bee studies is postulated to be due to (i) low sampling intensities, (ii) rarity of species, or (iii) transient species (Williams et al., 2001). Most of the parasitic species in the current study are probably rare, while some

of the lowland and subalpine species could be transient due to the weather conditions changing from year to year.

An underestimate of the total species richness resulted from using the data set for 2001, as one value was smaller than the total number of species recorded in both years together. In contrast, the estimates were almost identical when the data set for 2002 and the pooled data were used. Fluctuations between years in the abundance structure of communities led to estimates varying by more than 10%, despite the comparable sampling efforts in an identical study area.

The proportions of the ecological categories in each year did not differ significantly from the proportions in the pooled data. However, parasitic species were more often recorded than non-parasitic species in only one of the two years. Therefore, one year of sampling might be sufficient if only the proportion of ecological categories is of interest. However, if the objective is to determine the presence or absence of single species (e.g. in the analysis of change in community structure), several years of sampling are necessary.

CONCLUSIONS

The species composition of a bee assemblage differed in subsequent years. Together with a significant reduction in singletons in the pooled data set compared to that for single years, this result emphasises the importance of biodiversity studies being done over two complete seasons.

The estimate of total species richness in the area suggests that only a few species remained undetected. This indicates that recording an entire bee fauna is possible by intensive collecting over two seasons.

Our findings show that changes in the season have a marked effect on the ecological patterns shown by a bee assemblage. Therefore, sampling over only part of a season will not only underestimate the diversity, but will also affect the proportions of species in the different ecological categories.

Thus, the timing, duration and frequency of sampling will significantly influence the results of ecological studies on bee communities and the conclusions drawn.

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APPENDIX.

Species	2001	2002	total	nesting behaviour	floral relationships	social behaviour
<i>Andrena afrensensis</i> Warncke 1967	1		1	en	po	?
<i>Andrena albofasciata</i> Thomson 1870	17	32	49	en	?	?
<i>Andrena barbareae</i> Panzer 1805	43	6	49	en	po	so
<i>Andrena bicolor</i> Fabricius 1775	14	15	29	en	po	so
<i>Andrena coitana</i> (Kirby 1802)		1	1	en	po	so
<i>Andrena combinata</i> (Christ 1791)	15	26	41	en	po	so
<i>Andrena congruens</i> Schmiedeknecht 1883		4	4	en	po	so
<i>Andrena curvungula</i> Thomson 1870	8	4	12	en	<i>Campanula</i>	so
<i>Andrena falsifica</i> Perkins 1915	74	21	95	en	po	so
<i>Andrena flavipes</i> Panzer 1799		1	1	en	po	so
<i>Andrena floricola</i> Eversmann 1852	5	1	6	en	Brassicaceae	so
<i>Andrena fulva</i> (Müller 1766)	2	2	4	en	po	so
<i>Andrena fulvago</i> (Christ 1791)	3	3	6	en	Asteraceae	so
<i>Andrena haemorrhoa</i> (Fabricius 1781)	158	17	175	en	po	so
<i>Andrena hattorfiana</i> (Fabricius 1775)	8	5	13	en	Dipsacaceae	so
<i>Andrena humilis</i> Imhoff 1832	27	13	40	en	Asteraceae	so
<i>Andrena jacobii</i> Perkins 1921	1	1	2	en	po	so
<i>Andrena labiata</i> Fabricius 1781	28	19	47	en	po	so
<i>Andrena lathyri</i> Alfken 1899	1	3	4	en	<i>Lathyrus/Vicia</i>	so
<i>Andrena minutula</i> (Kirby 1802)		1	1	en	po	so
<i>Andrena minutuloides</i> Perkins 1914	41	22	63	en	po	so
<i>Andrena nana</i> (Kirby 1802)	1	1	2	en	po	so
<i>Andrena nigroaenea</i> (Kirby 1802)	9	8	17	en	po	so
<i>Andrena polita</i> Smith 1847	4	1	5	en	Asteraceae	so
<i>Andrena praecox</i> (Scopoli 1763)	5		5	en	<i>Salix</i>	so
<i>Andrena probata</i> Warncke 1973	17	17	34	en	Brassicaceae	so
<i>Andrena propinqua</i> Schenck 1853	1		1	en	po	so
<i>Andrena proxima</i> (Kirby 1802)	73	48	121	en	Apiaceae	so
<i>Andrena ranunculorum</i> Morawitz 1878	1		1	en	Brassicaceae	so
<i>Andrena rufizona</i> Imhoff 1834	6		6	en	<i>Campanula</i>	so
<i>Andrena similis</i> Smith 1849	6	11	17	en	Fabaceae	?
<i>Andrena strohmella</i> Stöckhert 1928	15	6	21	en	po	so
<i>Andrena thoracica</i> (Fabricius 1775)	5	2	7	en	po	so
<i>Andrena tibialis</i> (Kirby 1802)	7	5	12	en	po	so
<i>Andrena wilkella</i> (Kirby 1802)	8	9	17	en	Fabaceae	so
<i>Anthidium byssinum</i> (Panzer 1798)	19	25	44	en	Fabaceae	so
<i>Anthidium laterale</i> Latreille 1809	3	3	6	en	po	so
<i>Anthidium manicatum</i> (Linné 1758)	1	7	8	hy	po	so
<i>Anthidium montanum</i> Morawitz 1864	1		1	hy	Fabaceae	so
<i>Anthidium oblongatum</i> (Illiger 1806)	44	36	80	hy	po	so
<i>Anthidium punctatum</i> Latreille 1809	17	19	36	en	po	so
<i>Anthidium scapulare</i> Latreille 1809	6	10	16	hy	Asteraceae	so
<i>Anthidium septemdentatum</i> Latreille 1809	1		1	hy	po	so
<i>Anthidium strigatum</i> (Panzer 1805)	6	4	10	hy	po	so
<i>Anthophora aestivalis</i> (Panzer 1801)	29	17	46	en	po	so
<i>Anthophora balneorum</i> Lepeletier 1841		1	1	en	po	so
<i>Anthophora crassipes</i> Lepeletier 1841	1	1	2	en	po	so
<i>Anthophora plumipes</i> (Pallas 1772)	3	6	9	en	po	so
<i>Anthophora quadrimaculata</i> (Panzer 1798)	4	3	7	en	po	so
<i>Bombus argillaceus</i> (Scopoli 1763)	18	12	30	hy/en	po	pe
<i>Bombus barbutellus</i> (Kirby 1802)	1	2	3	pa	—	—
<i>Bombus bohemicus</i> Seidl 1838	3	5	8	pa	—	—
<i>Bombus campestris</i> (Panzer 1801)		1	1	pa	—	—
<i>Bombus hortorum</i> (Linné 1761)	15	5	20	hy/en	po	pe
<i>Bombus humilis</i> Illiger 1806	167	215	382	hy/en	po	pe
<i>Bombus hypnorum</i> (Linné 1758)	1	1	2	hy	po	pe
<i>Bombus lapidarius</i> (Linné 1758)	104	54	158	hy/en	po	pe

Species	2001	2002	total	nesting behaviour	floral relationships	social behaviour
<i>Bombus lucorum</i> (Linné 1761)	6	6	12	hy/en	po	pe
<i>Bombus mesomelas</i> Gerstaecker 1869		17	17	hy/en	po	pe
<i>Bombus monticola</i> Smith 1849	1		1	hy/en	po	pe
<i>Bombus pascuorum</i> (Scopoli 1763)	34	20	54	hy/en	po	pe
<i>Bombus pratorum</i> (Linné 1761)	7	4	11	hy/en	po	pe
<i>Bombus quadricolor</i> Lepeletier 1832	4	2	6	pa	—	—
<i>Bombus ruderarius</i> (Müller 1776)	21	6	27	hy/en	po	pe
<i>Bombus rupestris</i> (Fabricius 1793)	2		2	pa	—	—
<i>Bombus sichelii</i> Radoszkowski 1859	1	1	2	hy/en	po	pe
<i>Bombus soroeensis</i> (Fabricius 1776)	57	82	139	hy/en	po	pe
<i>Bombus subterraneus</i> (Linné 1758)	2	3	5	hy/en	po	pe
<i>Bombus sylvarum</i> (Linné 1761)	43	46	89	hy/en	po	pe
<i>Bombus terrestris</i> (Linné 1758)	60	51	111	hy/en	po	pe
<i>Bombus vestalis</i> (Geoffrey 1785)	9	14	23	pa	—	—
<i>Bombus wurflenii</i> Radoszkowski 1859	6	23	29	hy/en	po	pe
<i>Ceratina chalybaea</i> Chevrier 1872	4	3	7	hy	po	so
<i>Ceratina cucurbitana</i> (Rossi 1792)	1	5	6	hy	po	so
<i>Ceratina cyanea</i> (Kirby 1802)	9	4	13	hy	po	so
<i>Chelostoma campanularum</i> (Kirby 1802)	6	18	24	hy	<i>Campanula</i>	so
<i>Chelostoma distinctum</i> Stöckhert 1929	12	5	17	hy	<i>Campanula</i>	so
<i>Chelostoma florisomne</i> (Linné 1758)	22	28	50	hy	<i>Ranunculus</i>	so
<i>Chelostoma grande</i> (Nylander 1852)	10	3	13	hy	Dipsacaceae	so
<i>Chelostoma rapunculi</i> (Lepeletier 1841)	16	17	33	hy	<i>Campanula</i>	so
<i>Coelioxys conoidea</i> (Illiger 1806)		1	1	pa	—	—
<i>Coelioxys elongata</i> Lepeletier 1841		1	1	pa	—	—
<i>Coelioxys quadridentata</i> (Linné 1758)	3	3	6	pa	—	—
<i>Colletes fodiens</i> (Geoffroy 1785)	1	1	2	en	Asteraceae	so
<i>Colletes marginatus</i> Smith 1846		1	1	en	po	so
<i>Colletes nigricans</i> Gistel 1857	3	4	7	en	po	so
<i>Colletes sierrensis</i> Frey-Gessner 1903	17	24	41	en	<i>Odontites</i>	so
<i>Dasypoda argentata</i> Panzer 1809	2	3	5	en	Dipsacaceae	so
<i>Dasypoda hirtipes</i> (Fabricius 1793)		5	5	en	Asteraceae	so
<i>Dioxys cineta</i> (Jurine 1807)		1	1	pa	—	—
<i>Dioxys tridentata</i> (Nylander 1848)		2	2	pa	—	—
<i>Dufourea dentiventris</i> (Nylander 1848)	1		1	en	Campanulaceae	so
<i>Dufourea inermis</i> (Nylander 1848)		1	1	en	Campanulaceae	so
<i>Dufourea minuta</i> Lepeletier 1841	8	17	25	en	Asteraceae	so
<i>Eucera interrupta</i> Baer 1850	4	2	6	en	Fabaceae	so
<i>Eucera longicornis</i> (Linné 1758)	16	12	28	en	Fabaceae	so
<i>Eucera nigrescens</i> Pérez 1879	3	4	7	en	Fabaceae	so
<i>Halictus eurygnathus</i> Blüthgen 1931		1	1	en	po	?
<i>Halictus leucaheneus</i> Ebmer 1972	12	21	33	en	po	?
<i>Halictus maculatus</i> Smith 1848	31	61	92	en	po	pe
<i>Halictus quadricinctus</i> (Fabricius 1776)	24	17	41	en	po	so
<i>Halictus rubicundus</i> (Christ 1791)	7	20	27	en	po	pe
<i>Halictus scabiosae</i> (Rossi 1790)	10	21	31	en	po	pe
<i>Halictus seladonius</i> (Fabricius 1794)		1	1	en	po	?
<i>Halictus sexcinctus</i> (Fabricius 1775)		3	3	en	po	so
<i>Halictus simplex</i> Blüthgen 1923	224	471	695	en	po	pe
<i>Halictus smaragdulus</i> Vachal 1895	27	29	56	en	po	pe
<i>Halictus subauratus</i> (Rossi 1792)	14	12	26	en	po	pe
<i>Halictus tumulorum</i> (Linné 1758)	67	167	234	en	po	pe
<i>Heriades crenulatus</i> Nylander 1856	1	6	7	hy	Asteraceae	so
<i>Heriades truncorum</i> (Linné 1758)	4	11	15	hy	Asteraceae	so
<i>Hylaeus angustatus</i> (Schenck 1861)	3	8	11	hy	po	so
<i>Hylaeus annularis</i> (Kirby 1802)	1	6	7	hy	po	so
<i>Hylaeus brevicornis</i> Nylander 1852	1	2	3	hy	po	so
<i>Hylaeus clypearis</i> (Schenck 1853)	2	1	3	hy	po	so
<i>Hylaeus communis</i> Nylander 1852	19	22	41	hy	po	so
<i>Hylaeus difformis</i> (Eversmann 1852)		1	1	hy	po	so
<i>Hylaeus duckei</i> (Alfken 1904)	5		5	?	po	so
<i>Hylaeus gibbus</i> Saunders 1850	4	16	20	hy	po	so
<i>Hylaeus gredleri</i> Förster 1871	4		4	hy	po	so
<i>Hylaeus hyalinatus</i> Smith 1842	4	7	11	hy	po	so

Species	2001	2002	total	nesting behaviour	floral relationships	social behaviour
<i>Hylaeus kahri</i> Förster 1871	1	6	7	hy	po	so
<i>Hylaeus nigritus</i> (Fabricius 1798)	8	14	22	hy	Asteraceae	so
<i>Hylaeus punctulatus</i> Smith 1842	2	6	8	hy	<i>Allium</i>	so
<i>Hylaeus signatus</i> (Panzer 1798)	6	1	7	hy	<i>Reseda</i>	so
<i>Hylaeus sinuatus</i> (Schenck 1853)		4	4	hy	po	so
<i>Hylaeus styriacus</i> Förster 1871		2	2	hy	po	so
<i>Lasioglossum aeratum</i> (Kirby 1802)	18	20	38	en	po	?
<i>Lasioglossum albipes</i> (Fabricius 1781)	23	67	90	en	po	?
<i>Lasioglossum albocinctum</i> (Lucas 1849)	4	4	8	en	po	so
<i>Lasioglossum brevicorne</i> (Schenck 1870)	9	17	26	en	po	?
<i>Lasioglossum breviventre</i> (Schenck 1853)	2		2	en	po	so
<i>Lasioglossum calceatum</i> (Scopoli 1763)	62	210	272	en	po	pe
<i>Lasioglossum convexiusculum</i> (Schenck 1853)	9	4	13	en	po	?
<i>Lasioglossum costulatum</i> (Kriechbaumer 1873)	7	4	11	en	po	so
<i>Lasioglossum cupromicans</i> Pérez 1903	1	5	6	en	po	?
<i>Lasioglossum euboense</i> (Strand 1909)	1	12	13	en	po	?
<i>Lasioglossum fulvicorne</i> (Kirby 1802)	31	16	47	en	po	so
<i>Lasioglossum interruptum</i> (Panzer 1798)	1	2	3	en	po	pe
<i>Lasioglossum laeve</i> (Kirby 1802)	1	4	5	en	?	so
<i>Lasioglossum laevigatum</i> (Kirby 1802)	45	23	68	en	po	so
<i>Lasioglossum laticeps</i> (Schenck 1870)	25	10	35	en	po	pe
<i>Lasioglossum lativentre</i> (Schenck 1853)	4	5	9	en	po	so
<i>Lasioglossum leucopus</i> (Kirby 1802)	2	8	10	en	po	so
<i>Lasioglossum leucozonium</i> (Schränk 1781)	59	90	149	en	po	so
<i>Lasioglossum lissonotum</i> (Noskiewicz 1926)	7	7	14	en	po	?
<i>Lasioglossum marginatum</i> (Brullé 1832)		2	2	en	po	pe
<i>Lasioglossum minutulum</i> (Schenck 1853)	5	1	6	en	po	so
<i>Lasioglossum morio</i> (Fabricius 1793)	127	265	392	en	po	pe
<i>Lasioglossum nigripes</i> (Lepelletier 1841)	46	76	122	en	po	pe
<i>Lasioglossum nitidulum</i> Fabricius 1804	6	5	11	en	po	so
<i>Lasioglossum nitidusculum</i> (Kirby 1802)	1	3	4	en	po	so
<i>Lasioglossum pallens</i> (Brullé 1832)		1	1	en	po	so
<i>Lasioglossum parvulum</i> (Schenck 1853)	3	4	7	en	po	so
<i>Lasioglossum pauxillum</i> (Schenck 1853)	22	57	79	en	po	pe
<i>Lasioglossum punctatissimum</i> (Schenck 1853)	7	8	15	en	po	?
<i>Lasioglossum quadrisignatum</i> (Schenck 1853)	2		2	en	po	?
<i>Lasioglossum rufitarse</i> (Zetterstedt 1838)	1	1	2	en	po	so
<i>Lasioglossum subfasciatum</i> (Imhoff 1832)	19	6	25	en	po	so
<i>Lasioglossum tricinctum</i> (Schenck 1874)	12	6	18	en	po	?
<i>Lasioglossum villosulum</i> (Kirby 1802)	7	9	16	en	po	so
<i>Lasioglossum xanthopus</i> (Kirby 1802)	47	14	61	en	po	so
<i>Lasioglossum zonulum</i> (Smith 1848)	11	10	21	en	po	so
<i>Megachile alpicola</i> Alfken 1924	1	1	2	hy/en	po	so
<i>Megachile analis</i> Nylander 1852	15	8	23	en	po	so
<i>Megachile circumcincta</i> (Kirby 1802)	8	9	17	en	po	so
<i>Megachile leachella</i> Curtis 1828	3	4	7	hy/en	po	so
<i>Megachile maritima</i> (Kirby 1802)		1	1	en	po	so
<i>Megachile melanopyga</i> Costa 1863	8	11	19	?	po	so
<i>Megachile nigriventris</i> Schenck 1870	1		1	hy	Fabaceae	so
<i>Megachile parietina</i> (Geoffroy 1785)	3	1	4	hy	po	so
<i>Megachile pilidens</i> Alfken 1924	6	3	9	hy/en	po	so
<i>Megachile pyrenaica</i> Pérez 1890	3	5	8	hy	po	so
<i>Megachile pyrenaica</i> Lepelletier 1841	10	9	19	hy	po	so
<i>Megachile versicolor</i> Smith 1844		7	7	hy	po	so
<i>Megachile willughbiella</i> (Kirby 1802)	6	18	24	hy	po	so
<i>Melecta luctuosa</i> (Scopoli 1770)	7	1	8	pa	—	—
<i>Melitta dimidiata</i> Morawitz 1876		3	3	en	<i>Onobrychis</i>	so
<i>Melitta haemorrhoidalis</i> (Fabricius 1775)	30	27	57	en	<i>Campanula</i>	so
<i>Melitta leporina</i> (Panzer 1799)	16	34	50	en	Fabaceae	so
<i>Melitta tricincta</i> Kirby 1802	20	14	34	en	<i>Odontites</i>	so
<i>Nomada conjungens</i> Herrich-Schäffer 1839	2	4	6	pa	—	—
<i>Nomada emarginata</i> Morawitz 1877	2	4	6	pa	—	—
<i>Nomada fabriciana</i> (Linné 1767)	1	2	3	pa	—	—
<i>Nomada facilis</i> Schwarz 1967	1	1	2	pa	—	—

Species	2001	2002	total	nesting behaviour	floral relationships	social behaviour
<i>Nomada femoralis</i> Morawitz 1869		2	2	pa	—	—
<i>Nomada flavoguttata</i> (Kirby 1802)	4	4	8	pa	—	—
<i>Nomada guttulata</i> Schenck 1861		2	2	pa	—	—
<i>Nomada integra</i> Brullé 1832	5	9	14	pa	—	—
<i>Nomada lathburiana</i> (Kirby 1802)	3		3	pa	—	—
<i>Nomada marshamella</i> (Kirby 1802)	1		1	pa	—	—
<i>Nomada melathoracica</i> Imhoff 1834	2	3	5	pa	—	—
<i>Nomada obtusifrons</i> Nylander 1848		1	1	pa	—	—
<i>Nomada ruficornis</i> (Linné 1758)	10	4	14	pa	—	—
<i>Nomada signata</i> Jurine 1807		1	1	pa	—	—
<i>Nomada similis</i> Morawitz 1872	1		1	pa	—	—
<i>Nomada striata</i> Fabricius 1793		1	1	pa	—	—
<i>Nomada succincta</i> Panzer 1798	2	1	3	pa	—	—
<i>Nomia diversipes</i> Latreille 1806		1	1	en	po	?
<i>Osmia adunca</i> (Panzer 1798)	8	9	17	hy	<i>Echium</i>	so
<i>Osmia anceyi</i> Pérez 1879	2	4	6	hy	Asteraceae	so
<i>Osmia andrenoides</i> Spinola 1808	6	10	16	hy	po	so
<i>Osmia anthocopoides</i> Schenck 1853	3	3	6	hy	<i>Echium</i>	so
<i>Osmia aurulenta</i> (Panzer 1799)	113	123	236	hy	po	so
<i>Osmia brevicornis</i> (Fabricius 1798)		2	2	hy	Brassicaceae	so
<i>Osmia caerulescens</i> (Linné 1758)		1	1	hy	po	so
<i>Osmia claviventris</i> (Thomson 1872)	4	6	10	hy	po	so
<i>Osmia cornuta</i> (Latreille 1805)	2	1	3	hy	po	so
<i>Osmia dalmatica</i> Morawitz 1871	9	9	18	hy	Dipsacaceae	so
<i>Osmia gallarum</i> Spinola 1808	7	11	18	hy	Fabaceae	so
<i>Osmia labialis</i> Pérez 1879	1	3	4	hy	Asteraceae	so
<i>Osmia lepeletieri</i> Pérez 1879		5	5	hy	<i>Echium</i>	so
<i>Osmia leucomelana</i> (Kirby 1802)	2	4	6	hy	po	so
<i>Osmia loti</i> Morawitz 1867	2	4	6	hy	Fabaceae	so
<i>Osmia mitis</i> Nylander 1852	15	43	58	hy	<i>Campanula</i>	so
<i>Osmia mustelina</i> Gerstaecker 1841	9	4	13	hy	po	so
<i>Osmia niveata</i> (Fabricius 1804)	2		2	hy	Asteraceae	so
<i>Osmia parietina</i> Curtis 1828	1	1	2	hy	po	so
<i>Osmia praestans</i> Morawitz 1894		2	2	?	<i>Campanula</i>	so
<i>Osmia rufa</i> (Linné 1758)	11	12	23	hy	po	so
<i>Osmia spinulosa</i> (Kirby 1802)	12	12	24	hy	Asteraceae	so
<i>Osmia submicans</i> Morawitz 1870	3		3	hy	po	so
<i>Osmia tergestensis</i> Ducke 1897	6	21	27	hy	po	so
<i>Osmia uncinata</i> Gerstaecker 1869	1		1	hy	po	so
<i>Osmia villosa</i> (Schenck 1853)	1	1	2	hy	Asteraceae	so
<i>Osmia xanthomelana</i> (Kirby 1802)	11	8	19	hy	Fabaceae	so
<i>Panurgus banksianus</i> (Kirby 1802)	37	93	130	en	Asteraceae	so
<i>Panurgus calcaratus</i> (Scopoli 1763)	2	14	16	en	Asteraceae	so
<i>Panurgus dentipes</i> Latreille 1811	7	15	22	en	Asteraceae	so
<i>Rophites algirus</i> Pérez 1903	12	7	19	en	Lamiaceae	so
<i>Sphecodes crassus</i> Thomson 1870	7	7	14	pa	—	—
<i>Sphecodes ephippius</i> (Linné 1767)	23	35	58	pa	—	—
<i>Sphecodes ferruginatus</i> Hagens 1882	1	4	5	pa	—	—
<i>Sphecodes geofrellus</i> (Kirby 1802)	4	6	10	pa	—	—
<i>Sphecodes gibbus</i> (Linné 1758)	5	26	31	pa	—	—
<i>Sphecodes longulus</i> Hagens 1882		1	1	pa	—	—
<i>Sphecodes monilicornis</i> (Kirby 1802)	6	13	19	pa	—	—
<i>Sphecodes niger</i> Hagens 1874	1		1	pa	—	—
<i>Sphecodes pellucidus</i> Smith 1845	3	1	4	pa	—	—
<i>Sphecodes puncticeps</i> Thomson 1870	4	3	7	pa	—	—
<i>Sphecodes reticulatus</i> Thomson 1870	5		5	pa	—	—
<i>Sphecodes rufiventris</i> (Panzer 1798)	3	5	8	pa	—	—
<i>Stelis punctulatissima</i> (Kirby 1802)		1	1	pa	—	—
<i>Stelis signata</i> (Latreille 1809)		1	1	pa	—	—
<i>Tetralonia dentata</i> (Germar 1839)	1	1	2	en	Asteraceae	so
<i>Thyreus hirtus</i> (De Beaumont 1939)	1		1	pa	—	—
<i>Xylocopa valga</i> Gerstaecker 1872	4		4	hy	po	so

pa = parasitic; en = endogeic; en/hy = endo-/hypergeic; hy = hypergeic; po = polylectic; for oligolectic species the plant family or genus is mentioned; so = solitary; co = communal; pe = primitively eusocial; ? = unknown.