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Original article

Comparison of pollen spectra collected by four different subspecies of the honey bee *Apis mellifera**

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Abstract – Colonies belonging to 4 subspecies of *Apis mellifera,* namely *A. m. capensis*, *A. m. ligustica*, *A. m. carnica* and *A. m. mellifera* were placed, one colony per subspecies, at 5 sites with a high floral diversity in the Taunus region in Germany. A total amount of 4008.3 g of pollen loads were trapped during 3 seasons and 214 different pollen types were identified. The comparison of pollen spectra did not result in a separation of the subspecies. Date of sampling and sampling site, however, had a major effect on the composition of pollen samples. Furthermore, subspecies were not significantly different in the structure of dominance, evenness and diversity of pollen types. We conclude that the investigated subspecies of *Apis mellifera* follow a generalist pollen foraging strategy which may be mainly shaped by natural selection to meet the nutritional and social requirements of populous colonies.

***Apis mellifera* / pollen sources / honey bee / subspecies / foraging strategy**

1. INTRODUCTION

Honey bee colonies can reach up to 30 000 individuals (Seeley, 1985, 1997) and such large insect societies need a fairly large amount of nutrients. Hence, honey bees show a typical polylectic and generalistic foraging strategy (e.g. Zander, 1931, 1935, 1937, 1941, 1949, 1951; Deans, 1957; Maurizio and Louveaux, 1965; Vorwohl, 1972; Kerkvliet and van der Putten, 1975; Maurizio and Schaper, 1994; Ricciardelli D'Albore, 1997, 1998). Many different plant species and families are used as pollen or/and nectar sources. Preferences for plant species appear to vary according to the quality and quantity of food reward (von Frisch, 1967; Schmidt, 1984; Seeley, 1985, 1986; Seeley et al., 1991) as well as to the needs of the colony (von Frisch, 1965; Seeley, 1997). The social foraging strategy and the ability to communicate about food sources are two of the most important requirements of *Apis mellifera* to colonize different ecosystems (Ruttner, 1988, 1992).

The natural distribution of *A. mellifera* extends across several climatic and vegetation zones. Within this huge area, considerable variability in genetically determined, quantitative characteristics arose among regional populations (Ruttner, 1988), resulting in 26 subspecies (Ruttner, 1988; Sheppard et al., 1997). The subspecies can be distinguished by morphological features (Ruttner et al., 1978; Ruttner, 1988), behavioural characteristics, such as learning ability, orientation mechanisms, and dance-language dialects (von Frisch, 1967; Lauer and Lindauer, 1971, 1973; Koltermann, 1973; Menzel et al., 1973; Ruttner, 1988, 1992), and biological features, such as the level and period of brood rearing, (Ruttner, 1988, 1992). These different characteristics in the biology and behaviour of the subspecies represent adaptations to the natural

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habitat (Ruttner, 1988; Hepburn and Crewe, 1991). Because a subspecies may be adapted to certain climatic conditions and vegetation types, local or regional adaptations in foraging strategy and the exploitation of food sources may also have evolved. Numerous studies have revealed subspecies differences in the tendency to forage on particular plant species (Michailov, 1930; Lunder, 1953), in the extent of flower constancy (Gasanov, 1967), in the pollen foraging activity (Danka et al., 1987) or in the amount of collected pollen (Malaspina et al., 1993). According to Hellmich et al. (1985), Hellmich and Rothenbuhler (1986), Calderone and Page (1988, 1992), Page and Fondrk (1995) or Page et al. (2000), European subspecies show genetically determined differences in the tendency to collect and store pollen. Villanueva (1994) and Basualdo et al. (2000) found differences between subspecies in nectar and pollen sources. However, comparatively little attention has been given to possible differences among subspecies of *A. mellifera* in colony-level foraging strategies, such as differences in the utilization of floral resources when occupying the same habitat. Here we present a comparison of 4 subspecies for pollen foraging in a multifloral environment. Colonies *of A. m. mellifera* (Flekkefjord, Norway), *A. m. carnica* (Lunz, Austria), *A. m. ligustica* (Toscana, Italy) and *A. m. capensis* (Cape Province, RSA) were placed side by side and the pollen types colleted by these colonies were monitored. Beside the question of a possible correlation of pollen sources in the natural habitat of the subspecies with pollen sources in the new multifloral environment, the investigations focused on different aspects of pollen collection. These were entire pollen spectra, factors influencing pollen sampling, comparison of pollen types and characteristics of pollen samples like dominant pollen, evenness or diversity.

2. MATERIALS AND METHODS

2.1. Pollen sampling

Pollen samples of *A. m. mellifera*, *A. m. carnica*, *A. m. ligustica* and *A. m. capensis* were taken between June/July till August/September in 7 to 14 days intervals for one day in each case with pollen traps (Carl Fritz Imkereitechnik, Mellrichstadt, Germany) fixed at the entrance of each hive in 1998, 1999 and 2000. In 1998 and 1999 5 colonies per subspecies were used. In 2000 5 colonies of each European race and 3 colonies of *A. m. capensis* were available. In each case, a group of 4 colonies, one per subspecies, was placed at 5 different sites at least 2 km apart, each characterized by a high diversity of flowering plants. In 2000, at 2 of 5 sites, only the European subspecies were monitored.

2.2. Pollen preparation and determination

The pollen pellets were sorted according to their colour, air-dried for at least 7 days and weighed per colour fraction. The weight of each colour fraction was expressed as a proportion of the total weight of the pollen sample. For each colour fraction, a pollen suspension was made in water and 1 to 3 microscope slides, number depending on number of pollen pellets in the colour fractions, were prepared. Slides were dried at 30 ˚C (Louveaux et al., 1978) and pollen embed and stained in glycerine gelatine with alkaline fuchsin (method of Kaiser, Romeis, 1948). A light microscope (400- to 1000-fold magnification) was used to classify the pollen types according to plant species, plant genera, plant families or forms and groups of pollen types. Pollen types were determined with the pollen collection of the "Landesanstalt für Bienenkunde" (University Hohenheim, Stuttgart, Germany) as well as pollen samples of flowering plants of the different sites of the Taunus region. Furthermore, different publications about pollen and plant determination (Armbruster and Oenike, 1929a,b; Armbruster and Jacobs, 1934/5; Zander, 1935, 1937, 1941, 1949, 1951; Beug, 1961; Eisenhut, 1961; Erdtmann, 1966; Kapp, 1969; Hodges, 1974; Graf, 1981; Sawyer, 1981; Rothmaler, 1987, 1988; Hesse, 1990; Brickel, 1994; Haberer, 1996) were consulted.

2.3. Analyses and comparison of pollen samples and types

To compare and analyse pollen samples, relative frequency of each pollen type within each sample was turned into account. The analysis of pollen

yield took place in different steps, by using multivariate analyses, comparing each pollen type separately as well as indices for each pollen sample per subspecies.

2.3.1. Multivariate analyses

Multivariate ordination methods (Jongman et al., 1987; Digby and Kempton, 1991; Ter Braak and Smilauer, 1998) were applied to show the entire pollen spectra of subspecies collected per year graphically. In addition, it offered a method to calculate the effect of different groups of variables independently (dates of sampling, sampling sites, subspecies in groups of variables in each case) by using partitioning of variance on base of multivariate ordination methods (Borcard et al., 1992). Because of a high number of small or zero frequency values of pollen types, for all multivariate models frequencies of pollen samples were ln-transformed with ln (p_i+1). This transformation was used to approximate data set to homogeneity of variance and to decrease the effects of single extreme values. Furthermore, unimodal models (correspondence analysis CA, detrended correspondence analysis DCA, canonical correspondence analysis CCA) were necessary, tested by a DCA and calculating the length of gradient. In all cases of pollen frequency data, the length of gradient was > 2.0, after what unimodal models are recommended (Ter Braak and Smilauer, 1998).

Graphical description of pollen spectra

The entire pollen spectra of each subspecies was ordinated and shown graphically by using a CA for 1998, 1999 and a DCA for 2000. CA or DCA result in graphical presentations of the relative arrangement of data to each other in space along theoretical variables (axes) and could lead to the separations of pollen type data according to subspecies. In 2000 the DCA was necessary, because of an effect, where the gradient of the 1st axis influences the 2nd axis (Ter Braak and Smilauer, 1998). By using a DCA this effect is eliminated.

Partitioning of variance

According to the method of partitioning of variance after Borcard et al. (1992), a CA was applied to detect the total inertia, i.e. 100% of variance of pollen samples (G), followed by a CCA with all significant variables to get their common variance (V) and by further stepwise CCA. With these stepwise CCA, the influence of groups of variables, date, site and subspecies, on pollen spectra were described. Each group of variables was composed by their single data sets: date (A, a) – all sampling dates, site (B, b) – all 5 sites and subspecies (C, c) – the 4 investigated subspecies. For calculating explained variance of each group of variables, in each case a CCA was conducted by including variables of that group, without (A, B, C) and with covariables (a, b, c), respectively. In CCA with one group of variable including covariables, variables of the remaining groups of variables were used as covariables in each case. With these analyses, for each CCA the sum of eigenvalues were calculated, what from the amount of variance for each group of variable (a, b, c in %) in relation to the total inertia resulted. Overlap (O) and not explainable variance (R) was calculated by using G, V, A, B and C (formula [1] and [2]). In all analyses only significant variables of the described groups of variables were considered ($P < 0.05$). Thereby, using a forward selection, the best explaining variables were selected. Afterwards, significance was tested with the Monte-Carlo Permutation test (N = 199 permutations) for each CCA-model.

2.3.2. Comparison of frequencies of each pollen type

Frequencies of every pollen type per pollen sample and year of record was compared between the subspecies by using a non-parametric test (Kruskal and Wallis), after testing normality of data (Kolmogorov-Smirnov test for > 50 cases and with the Shapiro-Wilk test for < 50 cases, Sachs, 1984). Then, *P*-values were combined for 1998, 1999 and 2000 to one *P*-value for each pollen type (Fisher's combination procedure; [3], Sachs, 1984) and corrected (correction after Bonferroni [4]).

2.3.3. Indices and characteristics describing different aspects of pollen yield

Different indices and characteristics (structure of dominance, Müller, 1991, evenness after Buzas and Gibson [5], diversity after MacArthur [6] and [7],

Krebs, 1989) should describe different aspects of pollen yield. MacArthurs diversity index was applied to accommodate the varying number of pollen types per pollen sample and subspecies, because these varying number can cause problems in other indices, like the Shannon and Wiener diversity index. Buzas and Gibson evenness was calculated, which is based on the MacArthurs diversity index. To compare the indices between the subspecies, non-parametric analyse of variance (Kruskal and Wallis) was necessary, because of the distribution structure of data sets. Normality was tested again with the Kolmogorov-Smirnov test or the Shapiro-Wilk test (Sachs, 1984).

Calculation of overlap within variance partitioning
$O = (A+B+C)–V$ [1]

Calculation of not explainable variance within variance partitioning $R = G–V$ [2]

Fisher's combination procedure

$$\chi^2_{2n,\alpha} = -2 \sum_{n=1}^{i} \ln P_i \quad [3]$$

Correction after Bonferroni
$P_{corrected} = P^*N_{comparisons}$ [4]

E = Evenness after Buzas & Gibson $E = \frac{N1}{S}$ [5]

H' = Diversity after Shannon-Wiener

$$H' = \sum_{i=1}^{S} (p_i)(\ln p_i) \quad [6]$$

N_1 = Diversity after MacArthur $N_1 = e^{H'}$ [7]

O = overlap of variability of different groups of variables on pollen spectra;

A, B, C = variance explained by group of variable date of sampling, site and subspecies;

V = common variance of all groups of variables;

R = by included groups of variables not explainable variance;

P_i = P value after analysis of variance (Kruskal and Wallis) for 1998, 1999 or/and 2000 separately (depending on record of pollen type in 1998, 1999 and 2000);

χ^2 = χ^2-value after combination of P_i to get the one P value out of the χ^2-table (for all years, in which the pollen type was recorded);

P = P value after Fisher's combination procedure;

$N_{comparisons}$ = number of pollen types, which were compared in all three years or in an combination of two of the three years;

S = number of pollen types;

i = pollen type i;

p_i = frequency of pollen type i; (corresponding to (weight of pollen type i [g]) / (weight of pollen sample [g] = $\frac{w_i}{W}$)).

Table I. The most frequent pollen types of the four subspecies *A. m. capensis* (*cap*), *A. m. carnica* (*carn*), *A. m. ligustica* (*lig*) and *A. m. mellifera* (*mell*) of all data 1998, 1999 and 2000 (%).

Pollen type	subspecies			
	cap	*carn*	*lig*	*mell*
Zea mays	10.1	11.1	12.2	16.5
Filipendula ulmaria	8.0	5.9	5.8	2.3
Plantago sp.	6.9	8.2	6.8	8.0
Vitaceae	6.3	3.1	2.9	4.7
Castanea sativa	3.0	4.9	3.5	3.8
Asteraceae T	6.0	10.6	14.4	5,3
Rosaceae (small type)	5.9	6.9	4.2	4.8
Hedera helix	5.3	3.7	5.6	8.3
Epilobium angustifolium	3.3	2.2	9.5	2.8
Asteraceae A	1.5	2.3	3.0	2.0
Phacelia tanacetifolia	4.9	1.9	2.1	3.8
Brassicacceae (1)	3.6	2.4	1.6	1.7
Lycium sp.	7.0	2.3	1.8	3.0

For multivariate ordination procedures, Canoco for Windows 4.0 (Ter Braak and Smilauer, 1998) and for statistical analyses, SPSS 10.1 for Windows (SPSS Incorporation, USA) was applied.

3. RESULTS

3.1. Overview

In 1998, 1999 and 2000 all together 647 pollen samples, weighing 4008.3 g were collected. Overall 214 different pollen types (149 for *A. m. capensis*, 164 for *A. m. carnica*, 168 for *A. m. ligustica* and 166 for *A. m. mellifera*) from at least 70 plant families and 7 non-pollen-particles (e.g. spores of fungi and ferns) were determined. The most frequent pollen types for all subspecies were *Zea mays*, *Filipendula ulmaria*, *Plantago* sp., Vitaceae, *Castanea sativa*, Asteraceae form T, Rosaceae (small type) and *Hedera helix* (Tab. I). Further frequent pollen types are shown in Table I too.

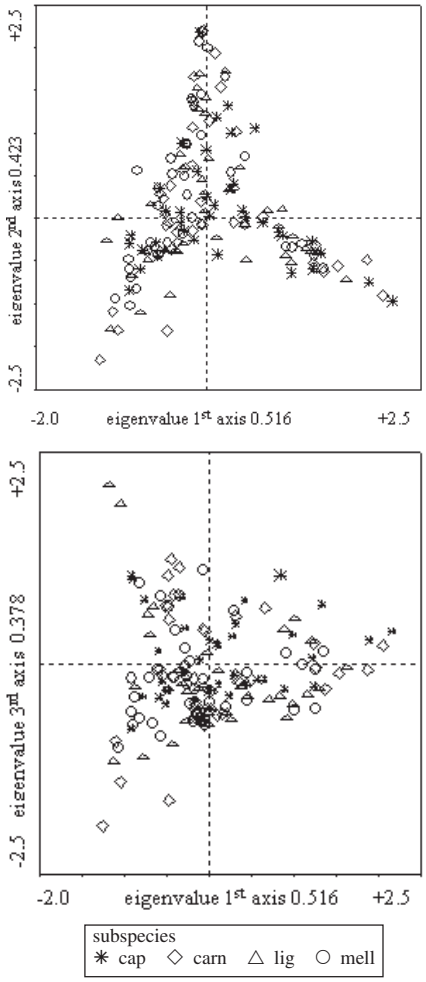

Figure 1. Correspondence analysis (CA) of pollen types and pollen samples, ranks of pollen samples classified by subspecies and suppression of ranks of pollen types 1998.

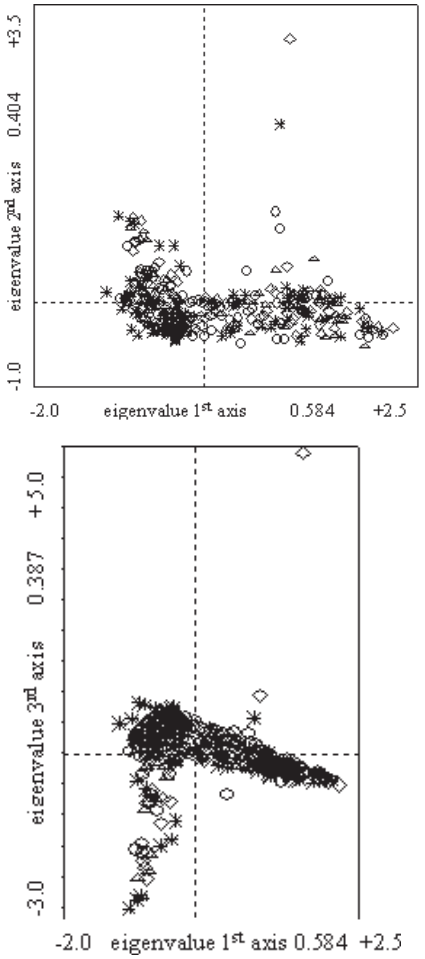

Figure 2. Correspondence analysis (CA) of pollen types and pollen samples, ranks of pollen samples classified by subspecies and suppression of ranks of pollen types 1999.

3.2. Graphical description of pollen spectra by using multivariate analyses

Figures 1 and 2 show the ordinated ranks of frequencies of ln-transformed pollen samples at axis 1 and 2 (a), respectively, and 1 and 3 (b) after the correspondence analysis (CA) for 1998 and 1999. For the data of 2000 the detrended correspondence analysis (DCA) was applied (Fig. 3). Eigenvalues and cumulative variance of pollen type frequencies of the analyses are shown in Table II. There is no grouping of ranks according to the subspecies. A concentration of rank values of *A. m. mellifera* at axis 1 and 3 is obvious only in 1999. However, it does not lead to a separation of the ranks of pollen frequencies and hence, there is no clear separation of the pollen spectrum of this subspecies compared to the others. Following, there is no clear graphical differentiation of pollen spectra of the different subspecies (Figs. 1–3).

Table II. Parameters of CA (1998, 1999) and DCA (2000): eigenvalues of the first 4 axes and cumulative variance of pollen type frequencies (%).

Value	Year	1st axis	2nd axis	3rd axis	4th axis	Total inertia
eigenvalue	1998	0.516	0.423	0.378	0.349	8.832
	1999	0.584	0.404	0.387	0.348	9.833
	2000	0.463	0.382	0.286	0.239	6.427
Cumulative variance of pollen	1998	5.80	10.60	14.90	18.90	
type frequencies (%)	1999	5.90	10.00	14.00	17.50	
	2000	7.20	13.20	17.60	21.30	

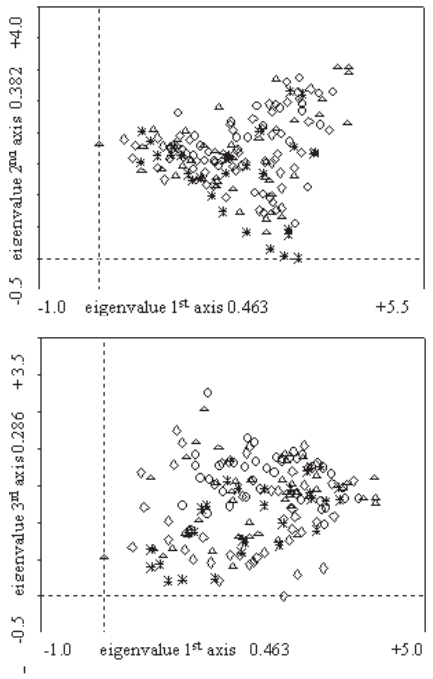

Figure 3. Detrended correspondence analysis (DCA) of pollen types and pollen samples, ranks of pollen samples classified by subspecies and suppression of ranks of pollen types 2000.

3.3. Partitioning of variance by using multivariate analyses

For calculating the proportion of variance of each group of variables, consisting of significant single variables, CA and CCA models were run stepwise as described in the methods. The results of the significance tests of the whole models by the Monte-Carlo-Permutation test are listed in Table III and demonstrate the significance of all tests. The proportions of variance of pollen spectra, described by the different variables are shown in Table IV. The results of the separated years 1998, 1999 and 2000 are similar. Dates of sampling, i.e. the phenology of flowering plants, is of most importance for the composition of pollen yield within the explainable variance and accounts for 11.5 to 15.9% of the observed variance. A further important factor for pollen spectra is the site of sampling. The site of collection accounts for 4.9 to 8.5% of the variability observed among the different subspecies. Within the compared variables the subspecies is of less importance. The subspecies of bee did not have a strong effect on the observed results and explained only 2.0 to 4.5% of the variance in pollen yield in different years. The overlap of variables is very low in 1998, 1999 and 2000, shown in Table IV. In contrast, the proportion of variance, which is not explained by date of sampling, site and subspecies, resulted in higher values of 73.3 to 76.9% (Tab. IV).

3.4. Comparison of frequencies of each pollen type

For further characterization of pollen foraging, the frequency of each pollen type per sample was compared between the subspecies. Only those pollen types differing in at least two of three years were considered. The results of the comparisons are shown in Table V (Kruskall and Wallis, Fisher‘s combination procedure, formula [3], Sachs, 1984, correction after Bonferroni [4]). The examined subspecies collected 11 of 214 pollen types within

Table III. Results the Monte-Carlo-Permutation test for different CCA runs (N = 199) involved in the partitioning of variance (F-values and level of significance *P*).

Model/Year	1998		1999		2000	
CCA with:	F-value	*P*	F-value	*P*	F-value	*P*
All significant variables	3.274	0.005	3.990	0.005	3.781	0.005
Significant dates of sampling	3.218	0.005	3.717	0.005	3.387	0.005
Significant sites	2.949	0.005	4.364	0.005	3.668	0.005
Significant subspecies	2.322	0.005	3.928	0.005	2.619	0.005
Significant dates as variables and sites and subspecies as covariables	3.528	0.005	3.919	0.005	3.816	0.005
Significant sites as variables and dates and subspecies as covariables	3.330	0.005	4.916	0.005	4.221	0.005
Significant subspecies as variables dates and sites as covariables	3.732	0.005	2.870	0.005	2.973	0.005

Table IV. Proportions of variance of the groups of variables (date of sampling, site, subspecies, for every year), the overlap of the groups of variables and the not explainable variance in pollen yield (%).

Year/group of variables	date	site	subspecies	overlap	not explainable variance
1998	11.5	7.3	4.4	0.0	76.8
1999	15.9	4.9	2.2	0.2	76.9
2000	13.5	8.5	4.5	0.2	73.3

Table V. Pollen types with significant differences between subspecies in at least two of three years of investigation (n.s. = no significant differences).

	$P_{corrected}$	higher frequencies by		
Pollen type/year		1998	1999	2000
Asteraceae S	0.005	*carn, lig*	*carn*	*carn, lig*
Asteraceae T	0.005	*lig*	*cap, carn, lig*	n.s.
Begonia sp.	0.0002	*mell*	mell	n.s.
Bryonia sp.	0.00155	*cap*	n.s.	*cap, carn*
Cornus sp.	3×10^{-7}	*mell*	*mell*	*mell*
Datura sp.	1.8×10^{-6}	*mell*	*cap, mell*	*mell*
Ericaceae	0.0004	*mell*	*mell*	*mell*
Malva sp.	6.9×10^{-6}	*mell*	*mell*	n.s.
Oenothera sp.	1.9×10^{-8}	*mell*	*mell*	*mell*
Rosaceae (small type)	3×10^{-7}	*mell*	*mell*	*mell*
Trifolium repens	2.1×10^{-5}	n.s.	*cap, carn*	*cap, carn, lig*

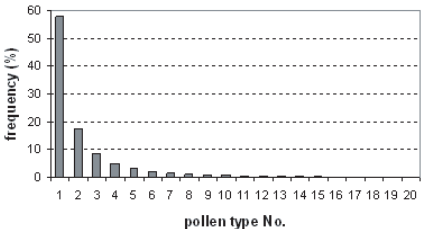

Figure 4. Average structure of dominance combining data of all four subspecies, *A. m. capensis*, *A. m. carnica*, *A. m. ligustica* and *A. m. mellifera* as well as 1998, 1999 and 2000.

three years in significantly different frequencies. In *A. m. mellifera* samples, more pollen of *Begonia* sp., *Cornus* sp., Ericaceae, *Malva* sp., *Oenothera* sp. and Rosaceae (small type) could be detected. *Datura* sp. was found more frequently in *A. m. mellifera* as well as *A. m. capensis* samples. The two subspecies *A. m. carnica* and *A. m. ligustica* collected more Asteraceae form S-pollen than the other subspecies. Furthermore, these two subspecies and *A. m. capensis* foraged more pollen of Asteraceae form T and *Trifolium repens* than did *A. m. mellifera*. *Bryonia* sp. could be found more frequently in *A. m. capensis* pollen samples.

3.5. Indices and characteristics describing different aspects of pollen yield

In all three successive years of investigation, 157 to 174 different pollen types could be determined depending on subspecies. The mean structure of dominance for the 4 subspecies combined, is shown in Figure 4, including the 20 most frequent pollen types of every subspecies in 1998, 1999 and 2000. When comparing the different pollen types that in combination accounted for approximately 90% of total pollen weight per sample, no significant difference between subspecies could be found (Kruskal and Wallis, Mann-Whitney, Bonferrroni correction, $P > 0.05$). On average, 90% of total pollen weight per sample was accounted by 4 to 5 different pollen types, i.e. 23% to 28% of pollen types per sample.

Table VI. Average evenness E (Buzas & Gibson) and diversity N_1 (MacArthur) for the subspecies *A. m. capensis* (*cap*), *A. m. carnica* (*carn*), *A. m. ligustica* (*lig*) and *A. m. mellifera* (*mell*) with standard error (SE).

Subspecies	evenness E ± SE	diversity N_1 ± SE
cap	0.30 ± 0.0002	4.08 ± 0.05
carn	0.31 ± 0.0002	4.63 ± 0.05
lig	0.27 ± 0.0001	4.26 ± 0.04
mell	0.28 ± 0.0006	5.22 ± 0.09

To compare the frequency distributions of pollen types per sample between the subspecies, the index of evenness (after Buzas and Gibson, formula [5], Krebs, 1989) was calculated. This allows the inclusion of all pollen types per sample, whereas in using the structure of dominance, only the most frequent pollen types are shown. The analysis of evenness of the four subspecies of all three years per pollen sample did not show a significant difference between the subspecies (Kruskal and Wallis, $\chi^2 = 7.55$, $P > 0.05$).

A further index to describe pollen yield is the diversity of pollen types, calculated by using MacArthurs diversity index (formula [7], Krebs, 1989). For the comparison of the subspecies, diversity per pollen sample of 1998, 1999 and 2000 was included. Using these data, no significant difference between the subspecies could be found (Kruskal and Wallis, $\chi^2 = 7.79$, $P > 0.05$). In Table VI average values of evenness and diversity are shown.

4. DISCUSSION

The analysis and comparison of pollen types of four subspecies of *A. mellifera* in one area and on different sites with a high diversity of pollen sources was made on different levels. The entire pollen spectra, single pollen types, spectra of dominance, evenness and diversity were considered. The main pollen sources were almost the same in all subspecies, and on average 90% of pollen per sample originated from 23 to 28% of pollen types per sample without significant differences between the subspecies. Similar results

were shown in Wille et al. (1985), where 90% of pollen came from 21% of pollen types and in Stimec et al. (1997), where 99% originated from one pollen source. These results suggest that the subspecies of *A. mellifera* concentrate pollen collection not on specific plant types, also confirmed in this study by foraging 214 pollen types (between 149 and 168 for single examined subspecies) and all together 70 plant families with differing flower types.

The similarity of pollen spectra in ordination graphs corresponds with the above described findings. The main factor influencing pollen foraging was not the subspecies, but the date of sampling. This result indicates the ability of honey bees to explore many different food sources in the course of the vegetation period, which are available subject to plant phenology. In spite of different sampling sites with different vegetation structure, sites did not influence the pollen choice of the subspecies as much as the sampling date in the presented study. Sites were located at least 2 km apart from each other. According to the results of Vissher and Seeley (1982), 95% of foraging occurs within 6 km with a median of 1.7 km. This suggests an overlap of foraging areas of honey bee colonies of the different sites, which can be confirmed by the overlap in the main pollen sources for the studied subspecies.

Within the results only a negligible influence (2.2 to 4.4%) of the subspecies could be found in pollen samples in 1998, 1999 and 2000. Comparing the frequencies of single pollen types, significant differences ($P < 0.01$) got obvious in 11 of 214 pollen types. Within these few pollen types, very frequent (e.g. Asteraceae form T, *Trifolium repens*) and less frequent (e.g. *Malva* sp., *Begonia* sp.) pollen types are present. Telleria (1993) assumed a correlation between the use of pollen types in a new habitat and the origin of subspecies. But, the hypothesis, that the pollen sources, which are common in the natural habitat, might be preferred by each subspecies in the new location, can not be confirmed in this study. Most pollen types, which were found in significantly higher percentages in pollen samples of one of the subspecies, were not mentioned as main pollen sources of these subspecies in the literature (Köttner, 1991; Persano Oddo and Piana, 2001; Fossel, 1956, Maurizio, 1979), i.e. *Begonia* sp., *Bryonia* sp., *Cornus* sp., *Datura* sp., *Malva* sp. or *Oenothera* sp. Only the plant familiy Asteraceae is described in the mentioned articles as a frequent pollen type for the subspecies, except for *A. m. mellifera*. The two forms of Asteraceae pollen, form S (e.g. *genera Serratula*, *Cirsium*, *Carduus*, Zander, 1935) and T (e.g. genera *Taraxacum*, *Leontodon*, *Hieracium*, *Crepis*, Zander, 1935), found in the present study, were not mentioned separately. But, these forms were significantly more often used by *A. m. carnica* and *A. m. ligustica* and partly by *A. m. capensis*. The significantly higher percentage of collected pollen of Ericaceae only by *A. m. mellifera* confirms the results of Maurizio (1979), but not of Fossel (1956), who found this pollen also very frequently in *A. m. carnica* pollen samples. According to the literature, the plant family Rosaceae is an important pollen source for all investigated subspecies. In this study Rosaceae (small type, e.g. *Spirea*, *Cotoneaster*, pers. comm. Vorwohl) was more frequently foraged by *A. m. mellifera*. Pollen of *Trifolium repens*, a widespread native plant species (Strasburger et al., 1971) is mentioned for the European subspecies (Fossel, 1956; Persano-Oddo and Piana, 2001; Maurizio, 1979), but not for *A. m. capensis*, which collected this pollen together with *A. m. carnica* and *A. m. ligustica* more frequently than *A. m. mellifera* in the present study.

Especially introduced or partly introduced plant genera, like *Begonia*, *Cornus*, *Datura* or *Oenothera*, which originated from the tropics, northern extra tropical regions of America, Asia, Europe or from Northern America (Hegi, 1924/25, 1965; Haberer, 1996; Schmeil-Fitschen, 1958) do not support the hypothesis of a correlation of pollen collection in the natural and new habitats. This hypothesis is also not supported by Stimec et al. (1997), who mentioned 75% of pollen yield of honey bees originating from introduced plant taxa. Also Köttner (1991) described the introduced plant species *Plantago lanceolata* and *Hypochoeris radicata* as main pollen sources for *A. m. capensis* in the cape region of South Africa. The few pollen preferences of

subspecies observed in this study do not relate to dominant pollen sources in the natural habitat of the tested subspecies and are not explainable with the findings of this study. Instead, pollen collection suggests that the subspecies are highly polylectic and generalist foragers in all habitats, and pollen spectra are not distinguishable between subspecies. Further, the homogeneity of the structure of dominance, the evenness and diversity of pollen sources indicate the uniformity of the foraging strategy of the studied subspecies of *A. mellifera.*

The high geographical variability of the honey bee according to morphological characteristics is connected with genetic variability (Badino et al., 1985; Sheppard and McPheron, 1986; Ruttner, 1988) as well with variability in physiology and behaviour (Ruttner, 1988). Only some of these specific features can be seen as adaptions to the natural habitats (Ruttner, 1988). According to this study, foraging strategy and foraging behaviour refered to collected pollen types do not belong to these habitat specific characteristics. The results support the concept of a uniform and flexible exploitation of pollen for all investigated subspecies, which is classified as having a generalistic and opportunistic foraging strategy (Zander, 1931; Seeley, 1997). Schneider and Hall (1997) found no differences in the pollen foraging behaviour of African and European-African hybrid honey bees and suggested that pollen collection was influenced more by environmental factors than genetics. This is an expression of the described flexibility in foraging behaviour.

Reasons for this uniformity in pollen sources and foraging strategy can be found in life strategy of *Apis mellifera*. The honey bee is a eusocial insect species, whose colonies survive for several years. They show highly developed abilities to communicate and to orientate in their habitat (Ruttner, 1988; Winston, 1987), which allows an effective exploitation of food sources during the whole vegetation period. This does not allow a specification to pollen or nectar sources. The honey bee colonies are highly flexible in pollen collection, i.e. depending on the amount of brood and available pollen in the hive (Seeley, 1985). This flexibility in food collection becomes especially clear in colonization of new habitats, where originally no honey bees occurred. According to Ruttner (1992), the main features for a successful colonization of new regions are not the specific utilization of food sources, but the swarming tendency or climatic conditions in the natural habitat.

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Comparaison des spectres polliniques de quatre sous-espèces d'abeilles domestiques *Apis mellifera*.

***Apis mellifera* / sous-espèce / pollen / stratégie de butinage / analyse multivariée / indice de diversité / indice de similarité**

Zusammenfassung – Vergleich der Pollenspektren von vier verschiedenen Unterarten der Honigbiene *Apis mellifera*. 1998, 1999 und 2000 wurde der Polleneintrag von 4 Unterarten der Honigbiene *Apis mellifera* auf 5 Standplätzen am Südostrand des Taunus (Deutschland) jeweils von Juni bis September untersucht. Die Standplätze waren durch eine hohe Diversität an Blütenpflanzen gekennzeichnet. In diese Untersuchung wurde die nordeuropäische *A. m. mellifera*, die südosteuropäische *A. m. carnica* und die italienische *A. m. ligustica* sowie die südafrikanischen Unterart *A. m. capensis* einbezogen. Die Pollenprobennahme erfolgte mittels Pollenfallen am Flugloch der Bienenstöcke alle 7 bis 14 Tage jeweils an einem Tag.
Die Auswertung des Polleneintrags und dessen Vergleich zwischen den Unterarten fand auf verschiedenen Ebenen statt. Es wurden Ordinationsverfahren innerhalb der multivariaten Statistik zur Gesamtanalyse und graphischen Darstellung aller Pollenproben sowie zur Ermittlung des Einflusses von Datum, Standort der Probennahme sowie Unterart angewandt. Weiterhin erfolgte der Unterartenvergleich anhand verschiedener Aspekte, wie anhand des Einzelvergleichs der Pollentypen, der Dominanzstruktur, Diversität und Evenness der einzelnen Pollenproben.
In 647 Pollenproben mit einem Gesamtgewicht von 4008,3 g wurden 214 verschiedene Pollentypen und

7 weitere Nicht-Pollen-Bestandteile (z.B. Farn- und Pilzsporen) nachgewiesen. Die häufigsten Pollentypen waren *Zea mays*, *Filipendula ulmaria*, *Plantago* sp., Vitaceae, *Castanea sativa*, Asteraceae Form T, Rosaceae (Kleinform) und *Hedera helix*. 90 % des Eintrags pro Pollenprobe stammte von 23 bis 28 % der in den Proben jeweils insgesamt nachgewiesenen Pollentypen, wobei sich die Unterarten hierbei nicht unterschieden.

Die gesamten Pollenspektren stimmten zwischen den Unterarten weitgehend überein. Nur in einzelnen Pollentypen waren Unterschiede zwischen den Unterarten festzustellen, wobei sich die europäischen Unterarten entsprechend ihrer verwandtschaftlichen Beziehungen absetzten. Der Einfluss der Unterart auf die Variabilität des Polleneintrags lag in den einzelnen Untersuchungsjahren zwischen 2,2 und 4,5 % Ein Zusammenhang zwischen Ursprungsgebieten der Unterarten und dem Mehreintrag einzelner Pollentypen im Untersuchungsgebiet ließ sich nicht herstellen. Innerhalb der ermittelten Faktoren wurde der Polleneintrag im Wesentlichen vom Angebot an Pollen beeinflusst, der an den verschiedenen Standorten und im Verlauf der Vegetationsperiode variierte. Aus dem Vergleich der Dominanzstruktur, Diversität und Evenness konnte keine unterschiedliche Sammelstrategie der Unterarten abgeleitet werden.

Sowohl die europäischen Unterarten als auch die südafrikanische Unterart wiesen ein einheitliches Sammelverhalten auf. Sie zeigten die Art-typischen Eigenschaften der Honigbiene, wie polylektische, generalistische und opportunistische Sammelweise sowie die Konzentration auf wenige ergiebige Pollenquellen.

***Apis mellifera* / Pollenquellen / Honigbiene / Unterarten / Sammelstrategie**

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