

The remarkable diversity of bumblebees (Hymenoptera: Apidae: *Bombus*) in the Eyne Valley (France, Pyrénées-Orientales)

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Abstract. Despite its small area (20.18 km²), the Eyne Valley, (France, E. Pyrenees) is known to be a place of great faunistic and floristic diversity. The authors have studied the bumblebee fauna of the valley for six years, gathering more than 5000 detailed observations. They observed 33 species, of the 46 living in continental France. For each species, the distribution and ecological preferences (altitude, vegetation type, CORINE biotopes, floral choices) were recorded. Floral resources may be the most important ecological factor. The altitude, the abundance, the diversity of food plants, and the heterogeneity of habitats seem to explain the survival and the coexistence of this great number of species of bumblebees with various ecological affinities.

Résumé. La remarquable diversité des bourdons (Hymenoptera : Apidae : *Bombus*) de la vallée d'Eyne (France, Pyrénées-Orientales). La Vallée d'Eyne (France, Pyrénées-Orientales) est bien connue pour la grande diversité de sa faune et de sa flore. Pendant six ans, les auteurs ont étudié les bourdons de cette vallée, accumulant plus de 5000 observations détaillées. Malgré la superficie réduite de la vallée (20,18 km²), 33 espèces de bourdons y ont été relevées sur les 46 espèces présentes en France continentale. Dans l'état actuel des connaissances, la vallée d'Eyne apparaît comme une des stations les plus riches au monde en espèces de bourdons. Pour chaque espèce, une carte de répartition et les préférendums écologiques (altitude, formations végétales, typologies CORINE, choix floraux) ont été établis. La caractérisation écologique de chaque espèce de bourdons indique que les ressources florales jouent un rôle important dans la structuration des communautés de bourdons de la vallée. L'altitude, l'abondance, la diversité des ressources florales et l'hétérogénéité en habitats permettent la survie et la coexistence de ce grand nombre d'espèces de bourdons aux affinités écologiques diverses.

Keywords: *Bombus*, Pyrenees, Biodiversity, Community structure, Floral resources, Altitude.

The very rich bumblebee (*Bombus* Latreille 1802) fauna of the West-Palaearctic region is well known (Appendix A) (Ranta 1983; Lavery & Harder 1988; Rasmont 1988; Pekkarinen & Teräs 1993; Rasmont *et al.* 1993; Williams 1994, 1996; Goulson 2004; Williams 2007).

Due to their endothermy, bumblebees play a large role in cold and temperate ecosystems, where they are the main pollinators of a wide diversity of plants (Heinrich 1979). For the last few decades, some bumblebee species have drastically regressed in large regions of western Europe (Pekkarinen *et al.* 1981; Williams 1982; Rasmont & Mersch 1988; Osborne *et al.* 1991; Osborne & Corbet 1994; Berezin *et al.* 1995; Rasmont 1995; Mänd *et al.* 1999; Peeters *et al.* 1999; Benton 2000; Carvell 2002; Goulson *et al.* 2005; Rasmont *et al.* 2005; Williams 2005; Benton 2006; Goulson *et al.* 2006). Most authors ascribe this decline to the evolution of modern agriculture. Intensive

farming has led to the fragmentation and reduction of the bumblebee habitats (Williams 1988; Osborne & Corbet 1994; Williams 2005). For Kevan (1999) and Goulson *et al.* (2006), the change in availability of nesting sites and food resources are both important. Potts *et al.* (2003), for their part, estimate that the local bumblebee fauna depends only on the diversity and abundance of floral resources.

A particular aspect of these changes is the drastic reduction of fodder crops and several authors (Rasmont & Mersch 1988; Rasmont 1995; Mänd *et al.* 1999; Goulson *et al.* 2005; Rasmont *et al.* 2005) stressed the connection between this reduction and that of bumblebee diversity.

A global understanding of bumblebee populations and of the regression or extension of some species is, indeed, very complex. Among the many ecological variables that have been taken in account, altitude has often been regarded as an essential parameter (e.g. Pittioni 1938; Pittioni & Schmidt 1942; Reinig 1970; Amiet 1977; Ornos Gallego 1984; Rasmont 1988; Williams 1991; Obeso 1992; Amiet 1996). On a very wider scale, the distribution of each bumblebee species

may be defined as an interval between two isotherms (Pekkarinen *et al.* 1981; Rasmont 1988), keeping in mind that these lines are strongly correlated, especially in central Europe, with altitude and latitude (Gorodkov 1986).

Many authors have described the vegetation types preferred by the various bumblebee species (e.g. Pittioni & Schmidt 1942; Móczár 1953; Dylewska 1957; Reinig 1970; Comba 1972; Ranta & Tiainen 1982; Pekkarinen 1984; Teräs 1985; Rasmont 1988; Williams 1988; Banaszak 1996; Benton 2000; Carvell 2002; Benton 2006; Goulson *et al.* 2006). However, as Brian (1957), Bowers (1985), Osborne *et al.* (1991), Carvell (2002), and Goulson (2004) have noted, the relation between vegetation type and bumblebee distribution is generally a loose one. Goulson (2004) and Goulson *et al.* (2006) suggest that most bumblebee species may be regarded as generalists, loosely associated with a particular environment.

Floral resources are the ecological factor most often mentioned as governing the structure of bumblebee communities (Brian 1957; Reinig 1970; Teräs 1976; Inouye 1977a; Pekkarinen 1979; Lundberg & Ranta 1980; Ranta & Vepsäläinen 1981; Pyke 1982; Ranta 1983; Pekkarinen 1984; Bowers 1985; Teräs 1985; Soltz 1987; Rasmont 1988; Osborne *et al.* 1991, 1999; Obeso 1992; Banaszak 1996; Benton 2000; Carvell 2002; Goulson 2004; Benton 2006).

It is important for plants to attract pollinators and, therefore, to invest in the production of nectar and pollen. However, the availability of this reward should be kept low enough to force bumblebees into visiting many flowers, to ensure their cross-pollination (Ranta *et al.* 1981). Bumblebees and flowering plants are bound in a co-evolutionary process (Leppik 1957; Banaszak 1983; Potts *et al.* 2003; Goulson 2004). As the availability of pollen and nectar resources puts a limit to the growth of bumblebee populations (Pelletier 2003), it also raises selective competition between them (Inouye 1978; Heinrich 1976; Ranta & Vepsäläinen 1981; Bowers 1985; Soltz 1987; Goulson 2004). This has caused the behavioural strategies of nectar gathering to become diversified among bumblebees (Heinrich 1979; Pekkarinen 1984; Goulson 2004; Benton 2006). The energy expenses of food gathering should be kept as low as possible (Heinrich 1979; Dafni 1992). Many elements, such as proboscis length, learning capacities, flight distance to the flowers and their richness in pollen and nectar play a role in the optimisation of food gathering (Goulson, 2004). Learning enables bumblebees to become familiar with the particular morphology of flowers, making food collecting more efficient (Heinrich 1979, Chittka *et al.* 1999).

Optimisation of nectar and pollen collecting may drive bumblebee species to food specialisation (Waser 1986; Chittka *et al.* 1999). Rasmont (1988) defined three levels of this specialisation: polytropic, mesotrophic and oligotrophic (or polylectic, mesolectic and oligolectic for pollen choices). Polytropic species exploit a wide variety of plants; examples mentioned by Ruskowski (1969, 1970a, 1970b) and Rasmont (1988) are: *Bombus hortorum*, *B. lucorum*, *B. pascuorum*, *B. pratorum*, *B. ruderarius*, and *B. terrestris*. On the contrary, an oligotrophic species exploits a restricted array of phylogenetically related plants. The more extreme cases are those of *Bombus consobrinus* Dahlbom and *B. gerstaeckeri* Morawitz, that strictly depend on the genus *Aconitum* L. *Bombus consobrinus* has been observed in Scandinavia, on *Aconitum septentrionale* Koelle, by Løken (1961, 1973) and Mjelde (1983). *B. gerstaeckeri* has been observed most often on *Aconitum vulparia* Reichenb. ex Sprengel, but also on *Aconitum napellus* L. and *A. anthora* L. (Pittioni 1937; Delmas 1976; Rasmont 1988; Osborne *et al.* 1991; Utelli & Roy 2000, Hagen & Aichhorn 2003; Ponchau *et al.* 2006), and *Delphinium dubium* (Rouy & Foucaud) (Mahé, 2007). Many species belong to an intermediary level of food specificity for which Rasmont (1988) coined the term “mesolectic” (or “mesotrophic”) (Pekkarinen 1998). Recently, taking into account the pollen gathering only, Cane & Sipes (2006) proposed a quantified definition of these categories.

The range of food choices of a bumblebee species is one dimension of its ecological niche (Hutchinson 1957). Many species may coexist within a given environment if their dietary niches only slightly overlap (Brian 1951, 1954; Leclercq 1960; Inouye 1977; Yalden 1983; Teräs 1976, 1985; Rasmont 1988; Goulson 2004). Another parameter of the dietary niche is the feeding speed that may vary widely according to species. It is optimal when the proboscis length is well suited to the depth of the visited corolla (Lundberg & Ranta 1980; Williams 1989; Benton 2006). Together with the food preferences, the proboscis length may explain how different species may share the resources of the same vegetation (Inouye 1978; Heinrich 1979; Pekkarinen 1984; Soltz 1987; Williams 1989; Carvell 2002).

Hobbs (1964), Osborne *et al.* (1991), Svensson *et al.* (2000), Potts *et al.* (2005), and Goulson (2004) stress that the complex distribution of bumblebees is to be explained not only by their dietary niches, but also by the availability of nesting places.

Williams *et al.* (2007) studied the interaction, on a continental scale, of the various parameters mentioned: altitude, latitude, climatic parameters,

and discussed also the habitat, floral resources, and availability of nesting sites. In Britain, they found that without climatic change, an interaction between climatic niche and food plant reduction can explain which bumblebees species have declined, where they have declined, and how they have declined. But for Williams *et al.* (2007), it would be better to evaluate reproductive success compared to climatic niches and resource levels according to the effects of altitude in mountainous regions than with the effect of latitude. It is allowed that a vertical rise in 200 m causes a fall of temperature of 1.1 °C, corresponding to a mean of 180 km towards north (Dendaletche 1997).

However interesting this far-reaching study may be, it may be easier to tackle the same problem at a local scale. In a mountain region, a climatic gradient corresponds to an altitudinal one. The mosaic of habitats and floral resources may be analysed in depth, through a sampling efficiency that cannot be achieved on a continental scale.

In the present contribution, the authors present the first results of a study, spanning several years, of the bumblebees of the Eyne valley (France, E. Pyrenees). A list is presented of all the species observed, compared with the bumblebee fauna of the rest of continental France (see tab. 1), of the West-Palaearctic region and of the world. For every species, the altitudinal range and the dietary and habitat preferences were recorded,

Table 1. Principal contributions to the knowledge of *Bombus* Latreille of the fauna of France

Authors	Studied area	Number of species
Benoist (1928) Tkalcú (1974)	Alpes françaises	22
Cavro (1950)	Nord – Pas de Calais	25
Gadoum <i>et al.</i> , 2005	Parc Naturel Régional du Vexin français	14
Gosselin <i>et al.</i> 2007	Réserve Naturelle de Nohèdes (Pyrénées-Orientales)	29
Iserbyt (<i>in lit.</i>)	Parc National des Pyrénées	30
Kruseman (1958) Delmas (1976) Rasmont (1988) Iserbyt <i>et al.</i> (2002)	Pyrénées-Orientales	36
Marion (1977)	Nièvre and Morvan	23
Pérez (1890)	Sud-Ouest	24
Rasmont (1988)	France	44
Rasmont (1989)	Larzac	24
Rasmont & Adamski (1995)	Corse	9
Rasmont & Parat (2002)	Limousin	26

allowing some inferences on the bearing of these parameters on community structure. The community structure and the food niche of bumblebees species will be studied in another paper.

Material and methods

Geography

Eyne is located in the S.-W. of the “Département des Pyrénées orientales” (E. Pyrenees) in France, at WGS84: 42°24'36" to 42°29'36"N and 2°04'16" to 2°08'53"E. Its valley extends between two crests, from the Spanish border, down to the Cerdagne plateau. The altitude near the village itself is 1450 m, it reaches 2850 m on the slopes (Torre d'Eina) (fig. 1). The area studied extends over 20.18 km² (fig. 2).

The mountain climate is strongly influenced by the Mediterranean region, with hot, dry summers. At a more local scale, the climate is influenced by altitude, snow, exposure to the sun, and winds: cold and dry northerlies, cold and moist easterlies, and from Spain (the S.-W.), warm and dry.

Microclimate and relief determine several vegetation zones (Braun-Blanquet 1948). Following the vegetation map of the CNRS (1970), the study area includes four main vegetation types: - Mountain meadows, around the village, at

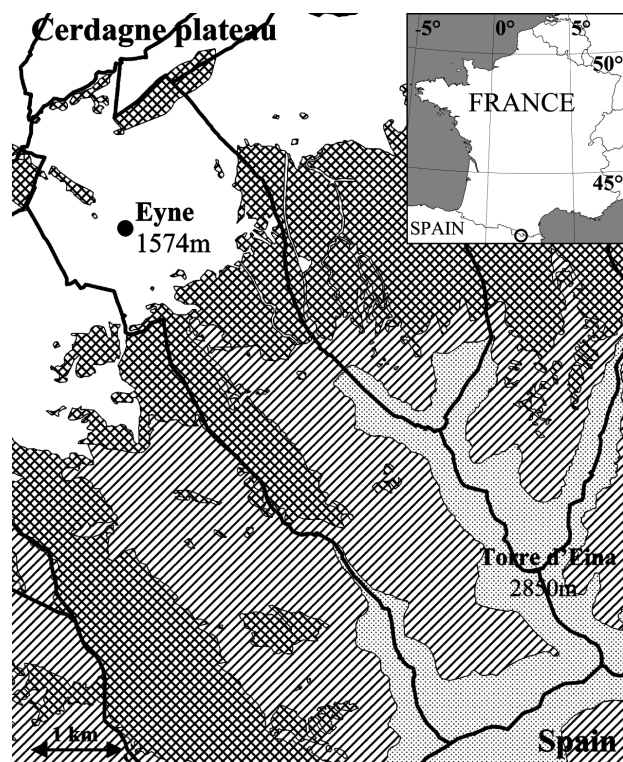


Figure 1 Localisation of Eyne. White: meadows; squared: woods; hatched: subalpine grasslands and moors; dotted: alpine grassland (after Centre National de la Recherche Scientifique 1970). Solid circle: the Eyne village (WGS84, 42°28'13"N, 02°05'06"E). Upper right corner: localisation of Eyne in France.



Figure 2
The Eyne Valley, seen from the N.-W. (Photo P. Rasmont).

1450 to 1650 m; - Forests of mountain pine (*Pinus uncinata* L.) climactic series, at the subalpine stage (1650 to 1800 m); - Grassland and moors of mountain pine (*Pinus uncinata* L.) climactic series, at the subalpine stage (1800 to 2500 m); - Short grassland on screes, at the alpine stage (2500 to 2850 m) (figs 1 and 2). Several transitional environments extend between these principal vegetation types.

Following the CORINE biotopes (Anonymous 1991; Bissardon *et al.* 1997) twenty habitat zones may be recognised over the study area (tab. 2).

Origin of the data

For the list of species and their relative abundance, we mainly resorted to our own collections and those of R. Delmas (tab. 3). These data are stored in the “Banque de Données Fauniques” at the University of Mons and the Faculty of Gembloux (Belgium).

For the distribution maps, we considered only the data for which the topographical location had been established by the most recent use of the Global Positioning System (GPS) (Rasmont 1999; Durieux 2000; Iserbyt 2000, Rasmont *et al.* 2001; Iserbyt *et al.* 2002; Ponchau 2002; Vandenberg 2002; Coppens *et al.* 2003; Viart *et al.* 2003). The precision of the topographical co-ordinates has increased through the years (Rasmont *et al.* 2003), with the technological advances in the GPS technology. In five years, the spatial resolution increased tenfold, from 30 to 50 m in 1998 to 3 to 5 m in 2002. For this reason, no data prior to 1998 has been figured in the maps or considered in the analyses.

Specimens were collected with a net or a pooter. Given the complexity of the terrain, the unpredictability of the weather and the lack of adequate traps, it has not been possible to devise an *a priori* collecting protocol. Whenever the specimens could be identified on the spot, the observations were performed without collecting.

For each observation, the collected data included the species, sex and number of specimens, the flower species on which they fed and the surrounding vegetation type, CORINE biotopes, the date, topographical co-ordinates and altitude.

During the months of July and August from 1998 to 2002, a total of 5020 observations were recorded.

Data processing and mapping

The data were computerised with the Data Fauna Flora software (Barbier *et al.* 2002) and mapped with the Carto Fauna Flora software (Barbier & Rasmont 2000).

Estimation of the species diversity

The species diversity of a location was quantified with the Shannon-Weaver index and the Hurlbert expectancy (Rasmont *et al.* 1990; Legendre & Legendre 1998). The mathematical expression of the Hurlbert expectancy (Hurlbert 1971) used in the present work is its simplified version by Rasmont *et al.* (1990). It expresses a number of species expected to be encountered in a random sample of 100 specimens.

The originality of the surroundings is expressed by the Cumulative rareness index computed by Rasmont *et al.* (1990):

$$R = \sum_i (1/N_i)$$

where N_i is the number of individuals of the species i observed in a reference area (France including Eyne and excluding Corsica).

This index expresses (in specimens⁻¹) the richness of a location in rare or endemic species in comparison with the reference area.

The ecological preferences

To study the factors relevant to the location (altitude, vegetation types, CORINE biotopes), we drew a matrix of 32 bumblebee taxa \times 457 locations.

For the study of flower preferences, we drew a matrix of 32 bumblebee taxa \times 120 plant taxa. For any given bumblebee taxon, we considered a flower taxon as a minor one if it supported less than 10% of the bees (i.e. the last decile).

Bumblebees have been allocated to thirteen 100 m altitude intervals with the K-Means method (R: *stats* package; MacQueen 1967). For each species, the symmetry of the altitudinal distribution has been tested with the Agostino test (R: *moments* package; Agostino 1970). In some relations, we

Table 2. CORINE biotopes characteristic of the habitat in the Eyne valley.

CORINE biotopes	Abbreviation used in this work
Montane <i>Calluna-Genista</i> heaths	Heaths- <i>Genista</i>
Pyrenean rusty alpenrose (<i>Rhododendron ferrugineum</i> L.) heaths	Heaths - <i>Rhododendron</i>
<i>Juniperus nana</i> Willd. scrub	Scrub- <i>Juniperus</i>
Pyrenean <i>Cytisus purgans</i> (L.) Boiss. fields	<i>Cytisus</i>
Willowherb (<i>Epilobium</i>) and foxglove (<i>Digitalis</i>) clearings	Clearings- <i>Epilobium</i>
Pyreneo-Catalonian Mesobromion	Mesobromion
Pyrenean Xerobromion	Xerobromion
Mesophile forest fringe grasslands	Forest fringe
Alpine and sub-alpine acidophilous grasslands	Sub and -alpine grasslands
Pyreneo-Alpine mesophile mat-grass (<i>Nardus stricta</i> L.) swards	grasslands - <i>Nardus</i>
<i>Festuca paniculata</i> (L.) Schinz & Thell. swards	grasslands - <i>Festuca paniculata</i>
<i>Festuca eskia</i> Ramond ex DC grasslands	grasslands - <i>Festuca eskia</i>
<i>Festuca airoides</i> Lam. grasslands	grasslands - <i>Festuca airoides</i>
Pyrenean naked-rush (<i>Elyna myosuroides</i> (Vill.) Fritsch and <i>Oxytropis balleri</i> Bunge ex Koch) swards	grasslands - <i>Oxytropis</i>
Bistort (<i>Polygonum bistorta</i> L.) meadows	Meadows - <i>Polygonum</i>
Mountain hay meadows	Meadows
Mountain pine (<i>Pinus uncinata</i> Miller ex Mirbel) forests	Pine forests
Pyrenean alpenrose (<i>Rhododendron ferrugineum</i> L.) mountain pine forests	Pine forests- <i>Rhododendron</i>
<i>Vaccinium</i> mountain pine forests	Pine forests - <i>Vaccinium</i>
Ruderal communities	Ruderal

Table 3. Principal contributors of the Eyne data. UMH: Université de Mons-Hainaut; ENSAM: Ecole Nationale Supérieure Agronomique de Montpellier; RNVE: Réserve Naturelle d'Eyne. *: Data not used because inaccurate coordinates.

Contributor	Periode of observation	Number of specimens
S. Iserbyt (UMH)	1999–2002	1389
E.-A. Durieux (UMH)	1999	1085
R. Delmas (ENSAM)	1960–1975	957 *
P. Rasmont (UMH)	1978–1997	98 *
P. Rasmont (UMH)	1998–2002	741
S. Viart (UMH)	2002	465
M. Terzo (UMH)	2002	396
J.-F. Godeau (UMH)	1999	259
F. Leclant (ENSAM)	1960–1970	180 *
M. Baracetti (RNVE)	1999–2000	156
P. Coppens (UMH)	2002	110
Autres		456

transformed the data logarithmically [$\ln(x+1)$] to ensure the normality. The best estimation of the relation between two variables has been obtained through linear regression (Legendre & Legendre 1998). The confidence interval has been estimated

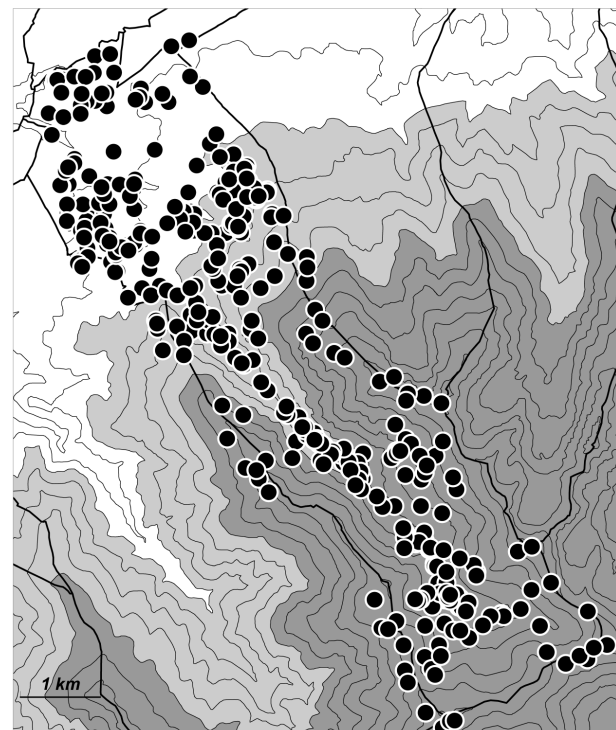


Figure 3

Position of the 457 observation points. Interval of the altitude lines: 100 m; light grey: below 1800 m; medium grey: 1800 to 2300 m; dark grey: above 2300 m.

Table 4. Species and numbers of specimens collected in France and in Eyne. *: Data of Delmas (1960–1975), Leclant (1960–1975) and Rasmont (1978–1997); **: autumn and winter data are not included.

Species	France	Eyne		Total
		before 1999*	since 1999	
<i>Bombus lucorum</i> (L. 1761)	5777	102	945	1047
<i>Bombus ruderarius</i> (Müller 1776)	4835	263	681	944
<i>Bombus soroensis</i> (Fabricius 1793)	5150	107	449	556
<i>Bombus monticola</i> Smith 1849	1660	15	537	552
<i>Bombus pyrenaicus</i> Pérez 1879	1659	75	402	477
<i>Bombus hortorum</i> (L. 1761)	3390	68	261	329
<i>Bombus mesomelas</i> Gerstaecker 1869	2086	91	195	286
<i>Bombus sylvorum</i> (L. 1761)	2774	22	210	232
<i>Bombus mendax</i> Gerstaecker 1869	1062	30	201	231
<i>Bombus sichelii</i> Radoszkowski 1859	2070	31	186	217
<i>Bombus humilis</i> Illiger 1806	3330	18	190	208
<i>Bombus pascuorum</i> (Scopoli 1763)	8379	32	120	152
<i>Bombus pratorum</i> (L. 1761)	3219	42	99	141
<i>Bombus sylvestris</i> (Lepeletier 1832)	1375	103	15	118
<i>Bombus subterraneus</i> (L. 1758)	1115	25	82	107
<i>Bombus bohemicus</i> Seild 1837	1519	69	35	104
<i>Bombus terrestris</i> (L. 1758)	5891**	3	98	101
<i>Bombus wurflenii</i> Radoszkowski 1859	2526	33	59	92
<i>Bombus lapidarius</i> (L. 1758)	6760	29	54	83
<i>Bombus mucidus</i> Gerstaecker 1869	775	20	51	71
<i>Bombus gerstaeckeri</i> Morawitz 1882	333	20	30	50
<i>Bombus rupestris</i> (Fabricius 1793)	1128	21	20	41
<i>Bombus flavidus</i> Eversmann 1852	273	18	20	38
<i>Bombus quadricolor</i> (Lepeletier 1832)	263	31	4	35
<i>Bombus hypnorum</i> (L. 1758)	682	10	13	23
<i>Bombus confusus</i> Schenk 1859	532	4	17	21
<i>Bombus norvegicus</i> (Sparre Schneider 1918)	135	-	9	9
<i>Bombus magnus</i> Vogt 1911	857	-	7	7
<i>Bombus ruderatus</i> (Fabricius 1775)	1898	1	5	6
<i>Bombus campestris</i> (Panzer 1801)	432	3	1	4
<i>Bombus cullumanus</i> (Kirby 1802)	95	3	1	4
<i>Bombus</i> (<i>Allopsithyrus</i>) <i>sp.</i>	423	1	-	1
<i>Bombus alpinus</i> (L. 1758)	94	-	-	-
<i>Bombus argillaceus</i> (Scopoli 1763)	434	-	-	-
<i>Bombus barbutellus</i> (Kirby 1802)	156	-	-	-
<i>Bombus brodmannicus</i> Vogt 1909	371	-	-	-
<i>Bombus cryptarum</i> (Fabricius 1775)	599	-	-	-
<i>Bombus distinguendus</i> Morawitz 1869	38	-	-	-
<i>Bombus inexpectatus</i> (Tkalcü 1963)	98	-	-	-
<i>Bombus jonellus</i> (Kirby 1802)	311	-	-	-
<i>Bombus maxillosus</i> Klug 1817	49	-	-	-
<i>Bombus mocsaryi</i> Kriechbaumer 1877	163	1	-	-
<i>Bombus muscorum</i> (L. 1758)	253	-	-	-
<i>Bombus pomorum</i> (Panzer 1805)	923	-	-	-
<i>Bombus vestalis</i> (Fourcroy 1785)	327	-	-	-
<i>Bombus veteranus</i> (Fabricius 1793)	299	-	-	-
Unspecified	114	1	3	4
Total number of specimens	76632	1292	5000	6292
Total number of species	46	31	31	33

on basis of the lower and upper confidence limits, with a risk of $\alpha = 0.99$ (R: stats package, *predict.lm*; Dalggaard 2002). The data have been processed with Microsoft Excel 2000 and the R software version 2.1.1 (<http://www.r-project.org/>).

Results

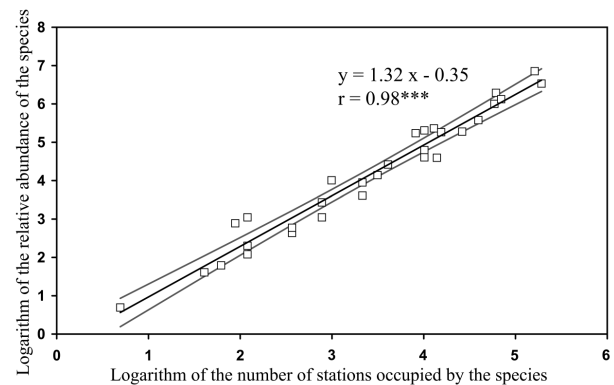
Species diversity

Since 1960, 6291 bumblebee have been observed within the limits of the Eyne commune (tab. 4). The observations were made over this whole territory, in 457 locations (fig. 3). The present fauna of the commune includes 33 bumblebee species.

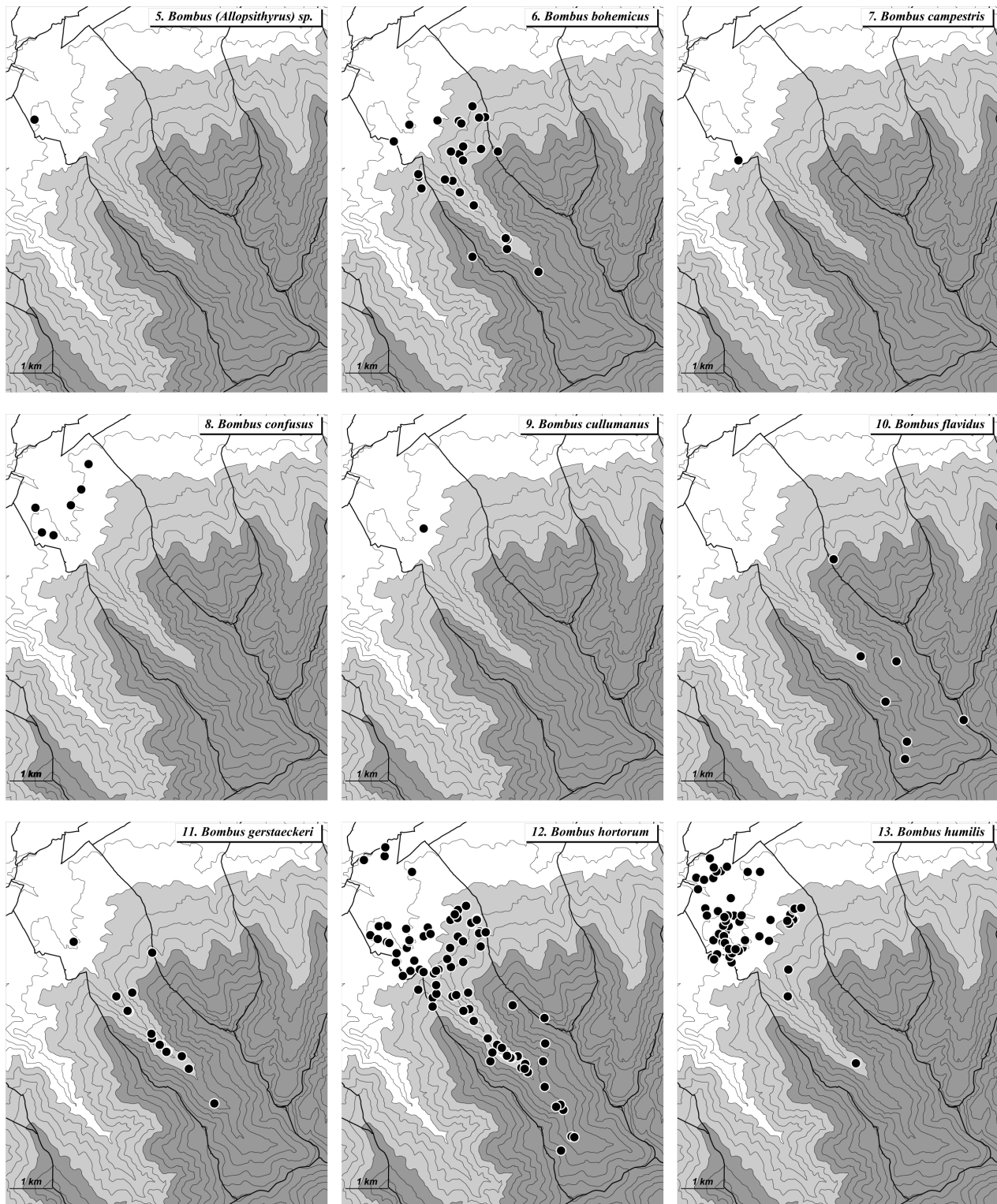
The lists of species observed before 1999 (31 species from 1292 specimens) and since (31 species from 5000 specimens) then are almost identical (tab. 4). We may therefore consider that our sampling is reproducible and that the fauna is relatively stable, without any noteworthy expansion or regression.

70% of the species present in continental France have been observed in Eyne. The most common species are *Bombus lucorum*, *B. ruderarius*, *B. soroensis*, *B. monticola*, and *B. pyrenaicus* (tab. 4). The local fauna also includes species that are uncommon or very rare elsewhere, such as *Bombus gerstaeckeri*, *B. confusus*, and *B. cullumanus*. *Bombus mocsaryi* was collected only once in the sixties by R. Delmas. Obligate inquiline species (*Bombus bohemicus*, *B. campestris*, *B. flavidus*, *B. norvegicus*, *B. quadricolor*, *B. rupestris* and *B. sylvestris*) are relatively uncommon (5.6 % of the observations).

The most common species (*Bombus ruderarius*, *B. lucorum*, *B. soroensis*, *B. monticola*, *B. pyrenaicus*) and those that occupy the largest number of locations, make up a very large proportion of the total observations (73.7 %, tab. 4). There is a very strong positive

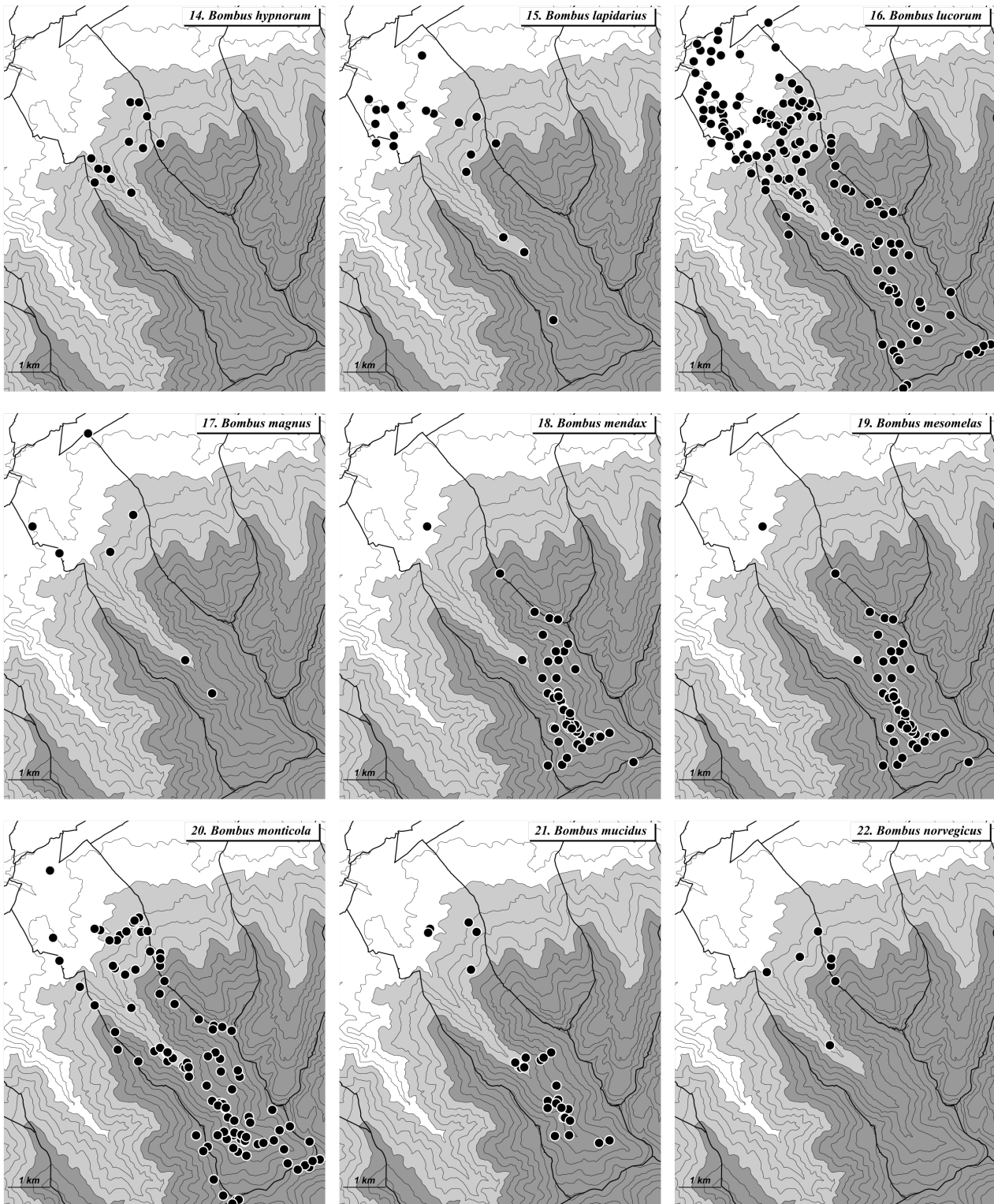
**Figure 4**

Log-log relation between the relative frequency of each species and the number of stations it occupies in the Eyne valley. Black: the regression line, grey: confidence intervals ($\alpha = 0.99$) of the regression.



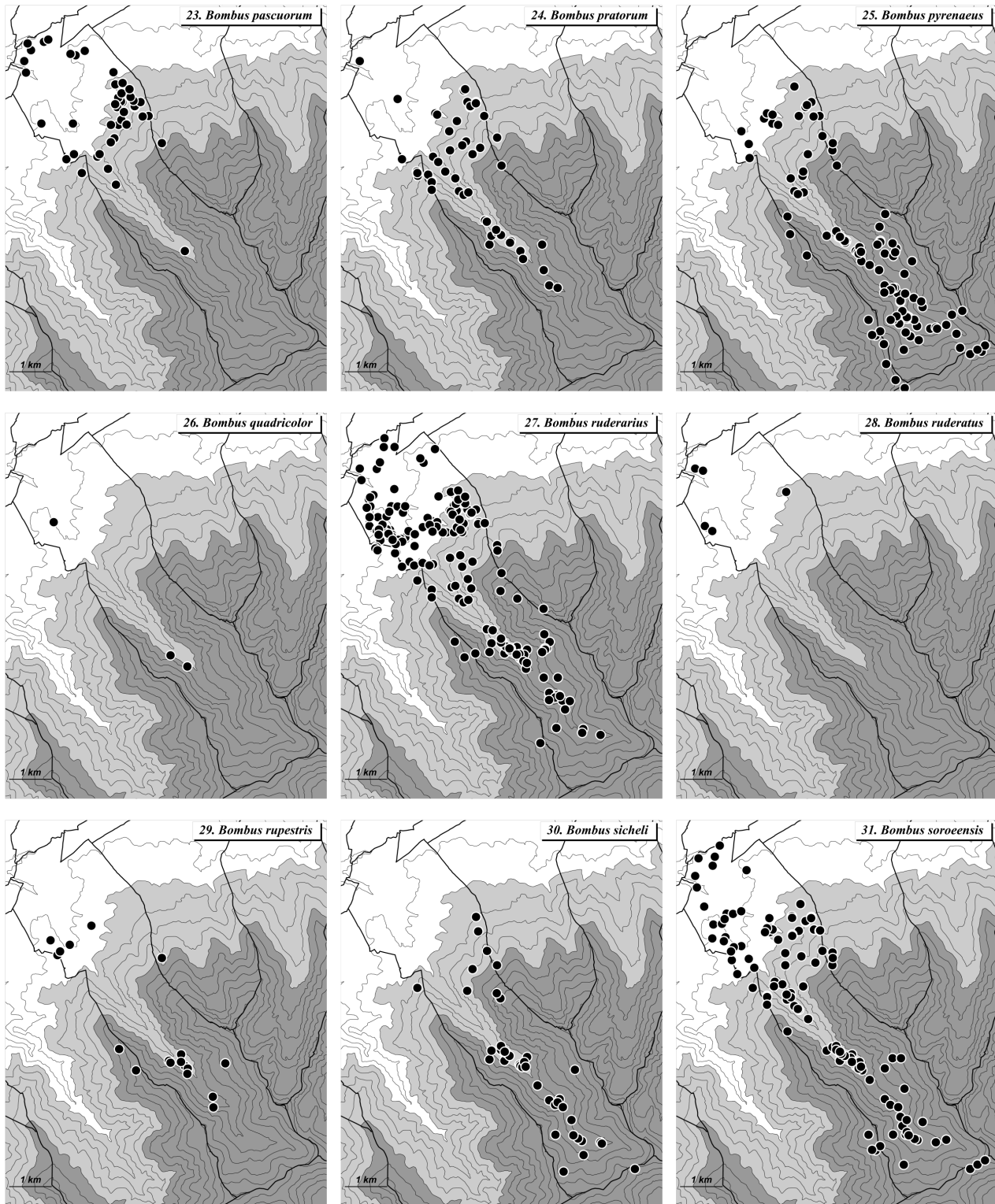
Figures 5–13

Distribution maps of the species. **5**, *Bombus (Allopsithyrus) sp.* * (1 specimen, 1 station); **6**, *B. bohemicus* * (110 specimens, 28 stations); **7**, *B. campestris* * (5 specimens, 1 station); **8**, *B. confusus* (23 specimens, 8 stations); **9**, *B. cullumanus* (4 specimens, 1 station); **10**, *B. flavidus* * (45 specimens, 10 stations); **11**, *B. gerstaeckeri* (46 specimens, 20 stations); **12**, *B. hortorum* (318 specimens, 101 stations); **13**, *B. humilis* (192 specimens, 67 stations).



Figures 14–22

Distribution maps of the species. **14.** *B. hypnorum* (25 specimens, 21 stations); **15.** *B. lapidarius* (118 specimens, 26 stations); **16.** *B. lucorum* (1069 specimens, 200 stations); **17.** *B. magnus* (7 specimens, 7 stations); **18.** *B. mendax* (224 specimens, 59 stations); **19.** *B. mesomelas* (285 specimens, 94 stations); **20.** *B. monticola* (548 specimens, 129 stations); **21.** *B. mucidus* (69 specimens, 29 stations); **22.** *B. norvegicus* * (9 specimens, 7 stations).



Figures 23–31

Distribution maps of the species. **23**, *B. pascuorum* (157 specimens, 64 stations); **24**, *B. pratorum* (146 specimens, 63 stations); **25**, *B. pyrenaicus* (458 specimens, 128 stations); **26**, *B. quadricolor** (43 specimens, 5 stations); **27**, *B. rupestris** (45 specimens, 20 stations); **28**, *B. ruderarius* (906 specimens, 212 stations); **29**, *B. ruderatus* (7 specimens, 6 stations); **30**, *B. sicheli* (194 specimens, 47 stations); **31**, *B. soroensis* (541 specimens, 135 stations).

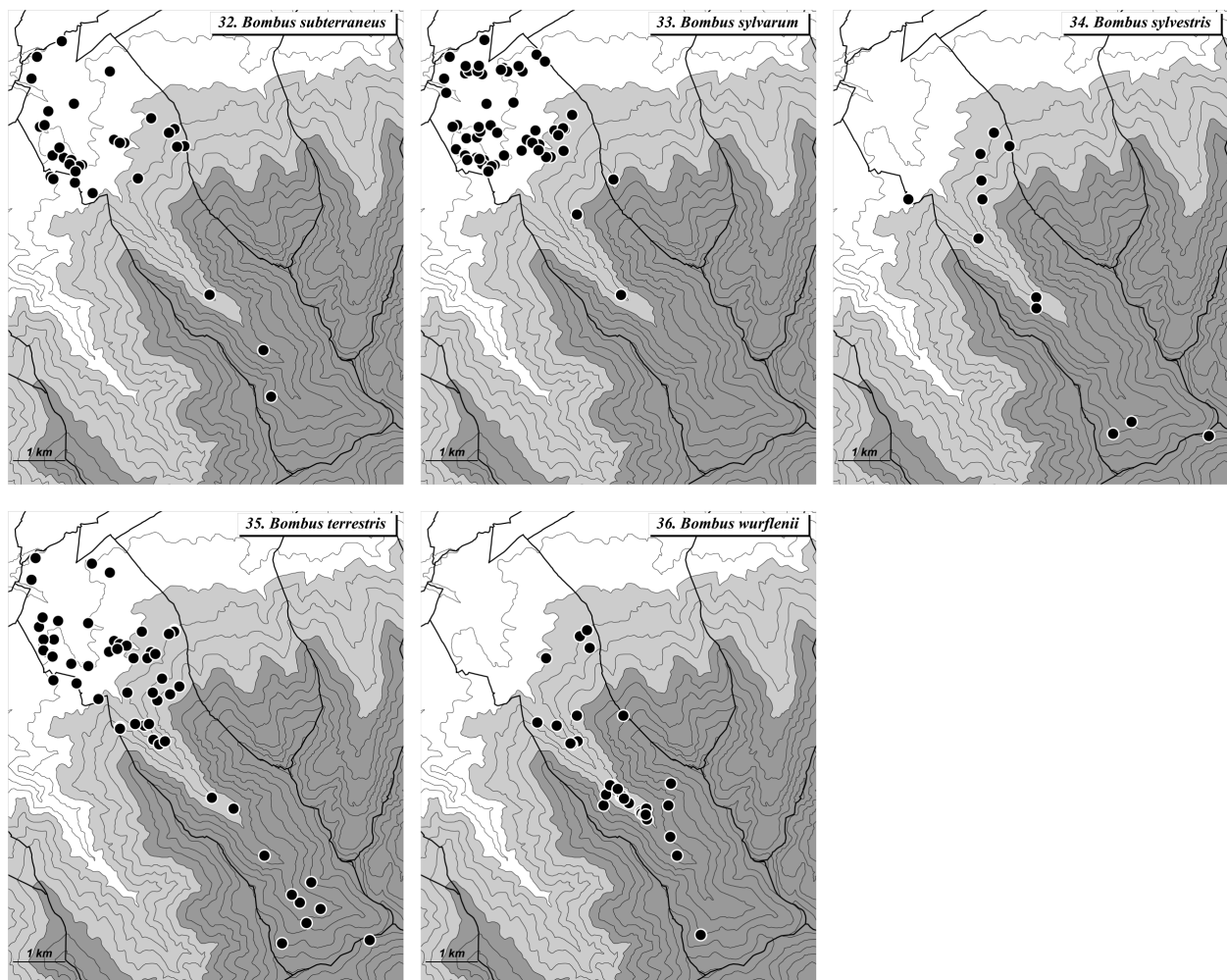
correlation between the abundance of each species and the number of stations occupied by them ($r = 0.98$, $p < 0.001$, fig. 4). However, two species: *Bombus rupestris* and *B. subterraneus*, deviate notably from the regression line.

Local distribution of species

A distribution map has been drawn for every species (figs. 5–36). *Bombus (Allopsithyrus) sp.* (fig. 5), *B. campestris* (fig. 7), *B. confusus* (fig. 8, 44), *B. cullumanus* (fig. 9), *B. humilis* (fig. 13), *B. ruderatus* (fig. 28), *B. subterraneus* (fig. 32) and *B. sylvarum* (fig. 33) live below 1700 m. *Bombus bohemicus* (fig. 6), *B. gerstaeckeri* (fig. 11), *B. hortorum* (fig. 12), *B. hypnorum* (fig. 14), *B. magnus* (fig. 17), *B. pratorum* (fig. 24),

B. pascuorum (fig. 23), *B. quadricolor* (fig. 26), *B. sylvestris* (fig. 34) and *B. wurflenii* (fig. 36), live mainly between 1700 and 2100 m. *Bombus flavidus* (fig. 10), *B. mendax* (fig. 18), *B. mucidus* (fig. 21), *B. norvegicus* (fig. 22) and *B. sichelii* (fig. 30) stay rather at the higher altitudes, beyond 2100 m. *Bombus lapidarius* (fig. 15), *B. lucorum* (fig. 16), *B. mesomelas* (fig. 19, 41), *B. ruderarius* (fig. 27), *B. rupestris* (fig. 29), *B. soroensis* (fig. 31) and *B. terrestris* (fig. 35) are found all over the Eyne commune. This is true also for *Bombus monticola* (fig. 20, 42) and *B. pyrenaicus* (fig. 25, 43) but with populations that increase with the altitude.

As expected, the overlapping of their distribution maps shows that the inquiline species and their hosts live mostly in the same surroundings (*B. bohemicus* fig.



Figures 32–36

Distribution maps of the species. 32, *B. subterraneus* (110 specimens, 39 stations); 33, *B. sylvarum* (233 specimens, 65 stations); 34, *B. sylvestris* * (119 specimens, 13 stations); 35, *B. terrestris* (100 specimens, 63 stations); 36, *B. wurflenii* (105 specimens, 39 stations). Captions: see fig. 3. The «*» indicate obligate inquilines. *B. mocsaryi* is not mapped because of the imprecision of the original data (1 ♀ „Cambre d’Aze“ leg. R. Delmas, likely in the 1960)

6 inquiline of *B. lucorum* fig. 16; *B. campestris* fig. 7 inquiline of *B. pascuorum* fig. 23 and *B. humilis* fig.13; *B. flavidus* fig. 10 inquiline of *B. monticola* fig. 20 or *B. pyrenaicus* fig. 25; *B. norvegicus* fig. 22 inquiline of *B. hypnorum* fig. 14; *B. quadricolor* fig. 26 inquiline of *B. soroensis* fig.31; *B. rupestris* fig. 29 inquiline of *B. lapidarius* fig. 15 and *B. sichelii* fig.30; *B. sylvestris* fig. 34 inquiline of *B. pratorum* fig. 24).

Ecological preferences

Altitudinal preferences

The altitudinal distribution is presented in table 5.

Four groups of species can be distinguished by the cluster reallocation procedure (K-means).

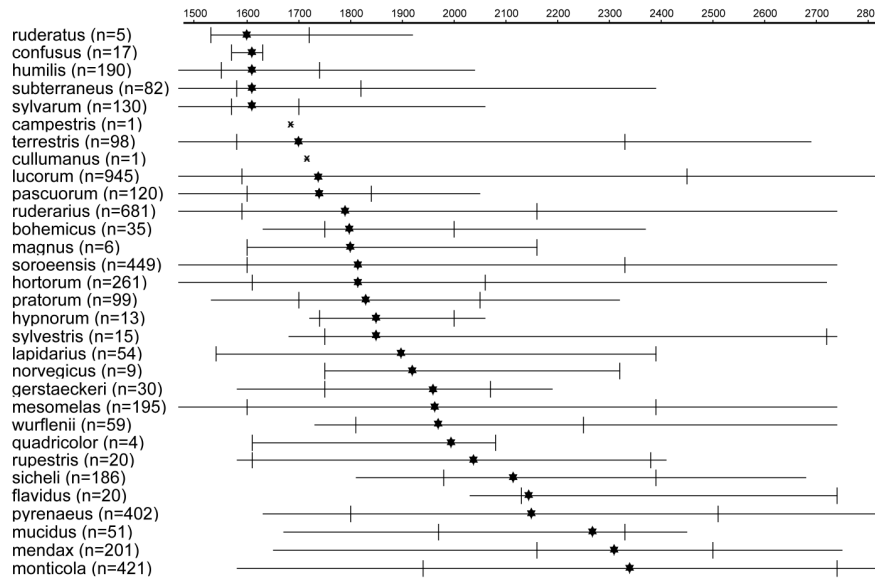
In the group of lower altitudes, we find species

for which the median of altitudinal distributions is below 1700 m. For the intermediate altitude group, this median is between 1700 and 2100 m. The higher altitude group has median over 2100 m. We left in a last group the ubiquitous species and the very rare ones (*Bombus campestris*, $n=1$; *B. cullumanus*, $n=1$ and *B. magnus*, $n=6$).

In the most widespread species (*Bombus lucorum*, *B. ruderarius*, *B. soroensis*, and *B. hortorum*), with the exception of *B. monticola*, the distribution is skewed towards the low altitudes (fig 37, tab. 5). The same is true for the common low-altitude species (*B. humilis*, *B. subterraneus*, and *B. sylvarum*): their altitude distribution is also highly significantly skewed towards the lower altitudes. On the contrary, two high-altitude species (*B. mucidus* and *B. monticola*) have an

Table 5. Altitudinal distribution of bumblebee species. Skew: Skewness or asymmetry. *: Obligatory inquiline species. NS: symmetrical distribution. *, **, ***: asymmetrical distribution with critical value: $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ (Agostino test).

Species	Minimum	First decile	Mediane	Last decile	Maximum	Skew	Symmetry
<i>ruderatus</i> (n=5)	1530	1530	1600	1720	1925	-	-
<i>confusus</i> (n=17)	1570	1570	1610	1630	1630	-0,16	NS
<i>humilis</i> (n=190)	1480	1555	1610	1740	2050	1,87	***
<i>subterraneus</i> (n=82)	1480	1570	1610	1815	2390	2,41	***
<i>sylvarum</i> (n=210)	1480	1570	1610	1700	2060	3,55	***
<i>campestris</i> (n=1) *	1680	-	-	-	-	-	-
<i>terrestris</i> (n=98)	1480	1570	1700	2335	2685	1,43	**
<i>cullumanus</i> (n=1)	1715	-	-	-	-	-	-
<i>lucorum</i> (n=945)	1480	1580	1740	2450	2830	1,46	***
<i>pascuorum</i> (n=120)	1480	1600	1740	1840	2050	-0,17	NS
<i>ruderarius</i> (n=681)	1480	1585	1790	2160	2740	0,91	***
<i>bohemicus</i> (n=35) *	1630	1750	1800	2005	2385	1,30	*
<i>magnus</i> (n=6)	1600	1600	1800	2160	2160	-	-
<i>hortorum</i> (n=261)	1480	1610	1815	2060	2725	1,33	***
<i>soroensis</i> (n=449)	1480	1600	1815	2330	2740	1,17	***
<i>pratorum</i> (n=99)	1530	1700	1830	2050	2320	0,59	NS
<i>hypnorum</i> (n=13)	1720	1740	1850	2000	2050	0,56	NS
<i>sylvestris</i> (n=15) *	1680	1750	1850	2720	2740	0,98	NS
<i>lapidarius</i> (n=54)	1555	1555	1865	2390	2390	0,38	NS
<i>norvegicus</i> (n=9) *	1750	1750	1930	2320	2320	0,49	NS
<i>gerstaeckeri</i> (n=30)	1580	1750	1970	2060	2180	-0,57	NS
<i>mesomelas</i> (n=195)	1480	1600	1975	2390	2740	0,32	NS
<i>wurflenii</i> (n=59)	1740	1800	1980	2255	2740	1,56	**
<i>quadricolor</i> (n=4) *	1610	1610	2005	2075	2075	-	-
<i>rupestris</i> (n=20) *	1580	1610	2050	2385	2410	-0,46	NS
<i>sichelii</i> (n=186)	1815	1975	2125	2390	2685	0,47	NS
<i>flavidus</i> (n=20) *	2040	2135	2155	2740	2740	1,29	NS
<i>pyrenaicus</i> (n=402)	1630	1800	2160	2500	2830	0,17	NS
<i>mucidus</i> (n=51)	1670	1975	2270	2330	2450	-1,10	*
<i>mendax</i> (n=201)	1650	2160	2310	2500	2750	0,08	NS
<i>monticola</i> (n=537)	1580	1940	2340	2740	2830	-0,36	*

**Figure 37**

Altitudinal distribution of the species. The horizontal line indicates the complete distribution, the star indicates the median value; the vertical dashes, the first and last deciles of the distribution.

altitude distribution significantly skewed towards the higher altitudes (fig. 37). In the other species, the altitude distribution, either uni- or plurimodal, is symmetrical.

The altitudinal distribution of the inquiline species is more restricted than that of their hosts (e.g.: *B. bohemicus* 1630–2385 m is inquiline of *B. lucorum* 1480–2830 m), with the remarkable exception of *Bombus sylvestris* (1680–2740 m), that lives at higher

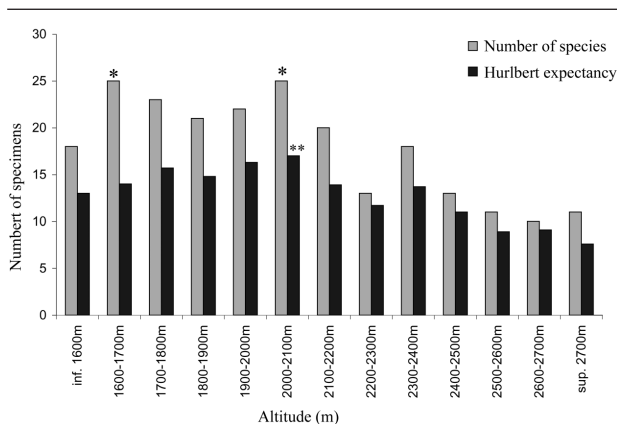
altitudes than its host *B. pratorum* (1530–2320 m). This could be the result of a significant presence of *Bombus sylvestris* queens which seems to be more erratic than males.

When the species numbers are ranked by altitude, in 100 m-intervals, two peaks appear: from 1600 to 1700 m and from 2000 to 2100 m. The number of species strongly decreases beyond 2400 m (fig. 38).

Computing the Hurlbert expectancy as a function of altitude gives one maximum, in the 2000–2100 interval. The difference between the observed and expected numbers of species is very large in the 1600–1700 m, 1700–1800 m and 2000–2100 m intervals. This could suggest that these intervals have been over-sampled.

Distribution of the bumblebees as a function of other environmental factors

Computing the correlation's between bumblebee species and the environmental factors (vegetation types and CORINE biotopes) brings to light the optimal surroundings for each species (tab. 6). For instance, the species *B. confusus*, *B. humilis*, *B. ruderatus*, *B. sylvarum*, and *B. subterraneus* are correlated by the vegetation types and the “meadow” CORINE biotope (fig. 45); *B. mendax*, *B. mucidus*, *B. pyrenaicus*, and *B. sichelii*, however, are characteristic of the subalpine grassland vegetation types and of the “subalpine and

**Figure 38**

Numbers of species and Hurlbert expectancy as a function of altitude. Black: the number of species observed; grey, the number of species expected in a random sample of 100 specimens (Hurlbert expectancy). *: species diversity peaks, **: maximal Hurlbert expectancy.

Table 6. Pearson correlation coefficients between the species distributions and the characteristics of the stations. Only the significant values ($p \leq 0.05$) are indicated. The underlined values are very highly significant in $P \leq 0.001$.

	<i>Number of species</i>	<i>Number of specimens</i>	<i>wurflenii</i> (n=59)	<i>terrestris</i> (n=98)	<i>sylvestris</i> (n=15)	<i>sylvarum</i> (n=210)	<i>subterraneus</i> (n=82)	<i>soroensis</i> (n=449)	<i>sichelii</i> (n=186)	<i>rupestris</i> (n=20)	<i>runderatus</i> (n=5)	<i>runderarius</i> (n=681)	<i>quadricolor</i> (n=4)	<i>pyrenaenus</i> (n=402)	<i>pratorum</i> (n=99)	<i>pascuorum</i> (n=120)	<i>norvegicus</i> (n=9)	<i>mucidus</i> (n=51)	<i>monticola</i> (n=537)	<i>mesomelas</i> (n=195)	<i>mendax</i> (n=201)	<i>magnus</i> (n=6)	<i>lucorum</i> (n=945)	<i>lapidarius</i> (n=54)	<i>hypnorum</i> (n=13)	<i>humilis</i> (n=190)	<i>hortorum</i> (n=261)	<i>gerstaeckeri</i> (n=30)	<i>flavidus</i> (n=20)	<i>cullumanus</i> (n=1)	<i>confusus</i> (n=17)	<i>campestris</i> (n=1)	<i>bohemicus</i> (n=35)				
Heaths - <i>Genista</i>																																					
Heaths - <i>Rhododendron</i>																																					
Scrub - <i>Juniperus</i>					<u>0.43</u>																																
<i>Cytisus</i>																																					
Clearings - <i>Epilobium</i>								<u>0.33</u>																													
Mesobromion								<u>0.28</u>																													
Xerobromion								<u>0.19</u>																													
Forest fringe																																					
Sub- and alpine grassland																																					
Grasslands - <i>Nardus</i>																																					
Grasslands - <i>Festuca paniculata</i>																																					
Grasslands - <i>Festuca eskia</i>																																					
Grasslands - <i>Festuca atrovirens</i>																																					
Grasslands - <i>Oxytropis</i>																																					
Meadows - <i>Polygonum</i>																																					
Meadows																																					
Pine forests																																					
Pine forests- <i>Rhododendron</i>																																					
Pine forests- <i>Vaccinium</i>																																					
Ruderal																																					
Forests																																					
Forest fringe / Meadows																																					
Forest fringe / Subalpine Heaths																																					
Meadows																																					
Subalpine grasslands																																					
Alpine grasslands																																					

alpine grassland” CORINE biotope. The species *B. hypnorum*, *B. norvegicus*, and *B. pratorum* are characteristic of wooded surroundings, but more specially of the CORINE biotopes related to the pine forests (*Vaccinium-*

pine forests, *Rhododendron*-pine forests). Other species (*Bombus lucorum*, *B. ruderarius*, and *B. soroensis*) are clearly ubiquitous and not specially related to a given vegetation type nor to any CORINE biotope.

Table 7. Genera of the visited plant. In bold, main genera of the visited plant (more than 100 observations).

Genera	Number of specimens	Relative abundance	Genera	Number of specimens	Relative abundance
<i>Trifolium</i>	648	13.10	<i>Helianthemum</i>	17	0.34
<i>Rhinanthus</i>	566	11.44	<i>Teucrium</i>	17	0.34
<i>Vicia</i>	372	7.52	<i>Sempervivum</i>	16	0.32
<i>Epilobium</i>	329	6.65	<i>Anthyllis</i>	15	0.30
<i>Eryngium</i>	266	5.38	<i>Delphinium</i>	15	0.30
<i>Rhododendron</i>	249	5.03	<i>Senecio</i>	14	0.28
<i>Aconitum</i>	220	4.45	<i>Armeria</i>	10	0.20
<i>Centaurea</i>	189	3.82	<i>Digitalis</i>	9	0.18
<i>Phyteuma</i>	166	3.36	<i>Symphytum</i>	9	0.18
<i>Thymus</i>	144	2.91	<i>Lamium</i>	8	0.16
<i>Carduus</i>	143	2.89	<i>Scabiosa</i>	8	0.16
<i>Gentiana</i>	135	2.73	<i>Crepis</i>	7	0.14
<i>Prunella</i>	123	2.49	<i>Galeopsis</i>	6	0.12
<i>Sideritis</i>	110	2.22	<i>Lupinus</i>	4	0.08
<i>Echium</i>	90	1.82	<i>Ononis</i>	3	0.06
<i>Potentilla</i>	87	1.76	<i>Scutellaria</i>	3	0.06
<i>Knautia</i>	81	1.64	<i>Astragalus</i>	2	0.04
<i>Geranium</i>	76	1.54	<i>Carlina</i>	2	0.04
<i>Pedicularis</i>	70	1.42	<i>Dianthus</i>	2	0.04
<i>Stachys</i>	68	1.37	<i>Geum</i>	2	0.04
<i>Lotus</i>	63	1.27	<i>Solidago</i>	2	0.04
<i>Adenostyles</i>	57	1.15	<i>Antennaria</i>	1	0.02
<i>Taraxacum</i>	52	1.05	<i>Ballota</i>	1	0.02
<i>Allium</i>	47	0.95	<i>Biscutella</i>	1	0.02
<i>Jasione</i>	46	0.93	<i>Cynoglossum</i>	1	0.02
<i>Minuartia</i>	46	0.93	<i>Euphrasia</i>	1	0.02
<i>Lathyrus</i>	36	0.73	<i>Filipendula</i>	1	0.02
<i>Rubus</i>	34	0.69	<i>Heracleum</i>	1	0.02
<i>Melampyrum</i>	31	0.63	<i>Hieracium</i>	1	0.02
<i>Cirsium</i>	30	0.61	<i>Malva</i>	1	0.02
<i>Linaria</i>	27	0.55	<i>Melilotus</i>	1	0.02
<i>Genista</i>	26	0.53	<i>Orchis</i>	1	0.02
<i>Campanula</i>	25	0.51	<i>Plantago</i>	1	0.02
<i>Chamaespartium</i>	23	0.47	<i>Polygala</i>	1	0.02
<i>Alchemilla</i>	22	0.44	<i>Polygonum</i>	1	0.02
<i>Sedum</i>	21	0.42	<i>Silene</i>	1	0.02
<i>Hypericum</i>	20	0.40	<i>Veratrum</i>	1	0.02
<i>Oxytropis</i>	20	0.40	<i>Viola</i>	1	0.02
Number of foraging specimens					4946
Number of specimens flying or seeking a nest					74

The inquiline species are found in less diversified surroundings, rather different from those of their hosts. *Bombus bohemicus* seems to prefer the CORINE biotope “Scrub - *Juniperus*” and the vegetation type “Forest fringe/Meadows” whereas its host potential *B. lucorum* prefers CORINE biotopes “Mesobromion, Clearing - *Epilobium*” and the vegetation types of edges (Forest fringe / Meadows, Forest fringe / Subalpine heaths) and Meadows (tab. 6). *Bombus sylvestris* seems to prefer CORINE biotopes “Scrub- *Juniperus*, Pine forests” and the vegetation type “Forest fringe / Meadows” whereas its host potential *B. pratorum* seems to prefer CORINE biotopes “Clearing - *Epilobium*, Mesobromion”, and the habitats related to edges and the vegetation type “Forest fringe / Meadows” (tab. 6).

All together, more than ten species co-exist in most of the vegetation types studied (tab. 6).

Flower choices

Table 7 lists the plant genera on which bumblebees were seen feeding. In our 5020 observations, 4997 bumblebees were seen feeding on 120 floral species, distributed in 76 genera. Fourteen genera, with more than 100 visits, are regarded as principal. They account for 74 % of the observations.

The most visited flower families are: Fabaceae (*Trifolium*, *Vicia*), Scrophulariaceae (*Rhinanthus*), Asteraceae (*Centaurea*, *Carduus*), Lamiaceae (*Sideritis*, *Thymus*, *Prunella*), Onagraceae (*Epilobium*), Apiaceae (*Eryngium*) and Ericaceae (*Rhododendron*).

Appendix B lists the visited plant species for each bumblebee species. From this list, we can draw the more or less narrow flower preferences of each species. For six species (*B. campestris*, *B. cullumanus*, *B. magnus*, *B. norvegicus*, *B. quadricolor*, and *B. ruderatus*) however, observations are too few to allow such conclusions to be drawn.

Bombus ruderarius, *B. lucorum*, *B. soroensis*, *B. monticola*, and *B. pyrenaicus* are among the most common species and among the most broadly generalist (polytropic) as well, with more than 40 flower taxa visited (fig. 39). Some species, as *Bombus lapidarius*, *B. mucidus*, *B. wurflenii*, *B. mendax*, *B. subterraneus*, *B. sichelii*, *B. pascuorum*, and *B. pratorum* are more specialised. However, even for these species, the spectrum of visited flowers remains large: 13 taxa for *Bombus lapidarius* and 28 for *B. pratorum*. The sole narrowly specialized (oligotropic) species is *Bombus gerstaeckeri* that is restricted to two taxa of the genus *Aconitum*. In fig. 39, this species is located farthest from the regression line. From the same graph, it appears that *B. confusus* and *B. subterraneus* are more

broadly polytropic than expected while *B. ruderarius* is less so.

Most species feed on two to seven favourite flowers during the sampling season. These support 10 to 60 % of the population of the species. Beside these preferred plants, each species may visit “second choice” ones, the diversity of which may be very large: 62 taxa in the case of *Bombus lucorum*.

In most cases, inquiline bumblebees and their hosts feed on different flower species (Appendix B). *Bombus bohemicus* seems to prefer *Eryngium bourgatii*, *Knautia sp.*, and *Rubus idaeus* whereas its host potential *B. lucorum* mainly prefers *Rhinanthus pumilus* and *Vicia cracca*.

Bombus flavidus seems to prefer *Carduus carlinoides* and *Adenostyles alliariae* whereas these two supposed hosts *B. monticola* mainly prefers *Potentilla nivalis*, *Rhododendron ferrugineum* and *B. pyrenaicus* mainly prefers *Eryngium bourgatii*, *Gentiana burseri*, *Epilobium angustifolium*, *Rhododendron ferrugineum*, and *Phyteuma hemisphaericum*.

Some flower taxa are favoured by many bumblebee species. For instance, *Rhinanthus pumilus*, *Epilobium angustifolium*, *Eryngium bourgatii*, *Trifolium pratense*, *Vicia cracca*, *Trifolium repens*, and *Centaurea jacea* are visited by more than fifteen species (Appendix B). Some flower taxa, on the contrary, are visited by very few bumblebees.

Discussion

Species diversity

The exhaustive study of the bumblebee fauna of

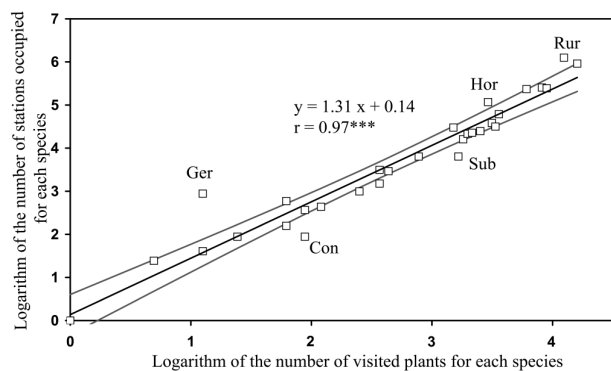


Figure 39

Log-log relation between the numbers of stations occupied by each species and the number of plant species on which it feeds in the Eyne valley. Black: the regression line; grey: confidence intervals ($\alpha = 0.99$) of the regression. Con, *Bombus confusus*; Ger, *B. gerstaeckeri*; Hor, *B. hortorum*; Rur, *B. ruderarius*; Sub, *B. subterraneus*.

the Eyne valley during the summers 1998 to 2003 confirmed the presence of 31 species. This diversity is very high in comparison with the fauna of other regions of France (tab. 1). The diversity and originality indices are very high in comparison with other studied locations (tab. 8). Compared with similar studies on areas 10 (Larzac; Rasmont 1989) to 22 times (Parc National des Pyrénées; Iserbyt *in lit.*) greater in area, the species diversity in Eyne is much larger. The cumulated rareness index, clearly higher for the Eyne location, indicates the presence of more uncommon species (tab. 8).

The comparison of the species diversity of Eyne with that of the nearby Nohèdes valley (29 species; Gosselin *et al.* 2007) and of the Pyrenees National Park (Parc National des Pyrénées; 30 species) makes it a reasonable guess that could be extrapolate over the entire Pyrenees ridge. As Banaszak (1996) showed for the Pyrenees and the Alps, the population density of the bumblebees in Eyne is especially high, compared with the other European mountain ranges.

For the whole of the West-Palaeartic region (Appendix A), there is a strong correlation between the areas of the studied zones and their species diversity (fig. 42). The species diversity in Eyne appears clearly greater than expected from the area of the location.

From the review of the zones of greater species diversity established by Pekkarinen & Teräs (1993), it may be concluded that the diversity encountered in Eyne is not matched anywhere else in such a small area. The only West-Palaeartic regions where the species diversity is as large are these of Erzurum (Özbek 1990), the Asturias (Obeso 1992) and Moscow (Berezin *et al.* 1995). These three regions, however, are far more extended than the Eyne valley. The region of Erzurum, in Turkey, harbours 30 bumblebee species on 25 000 km². In the Asturias Province (Spain) 31 species were discovered in an area of about 10 600 km². In the Moscow region, 34 species were discovered in an area of 47 000 km². Obeso (1992) states that the species di-

versity in the Asturias is larger than that in any area of the same size, either in the rest of Europe (Ranta 1983) or in North America (Lavery & Harder 1988). With a larger number of bumblebee species for a much smaller area, the Eyne valley may now be considered as the most diversified location in the West-Palaeartic region.

Rasmont *et al.* (2000) compared the species diversity of the Eyne bumblebees with that of other regions known for their large species diversity. In the Dombai reserve (Teberda valley, W. Caucasus), Dathe (1981) lists 19 species. In the Kashmir, Williams (1991) finds 29 bumblebee species. In the New World, the diversity is highest in California, where 26 species live (Thorp *et al.* 1983). The only regions where the species diversity is higher than in Eyne are the Sichuan and the Altai, with respectively 60 and 54 species, although on areas much larger than Eyne (Williams 1994, 1998). To our present knowledge, the species diversity in Eyne is quite exceptional.

For some uncommon species, the valley accounts for a large proportion of the specimens collected in France (tab. 5). *Bombus gerstaeckeri* Morawitz is one of the less common species in France, as in the whole West-Palaeartic region (Rasmont *et al.* 2003; Rasmont *et al.* 2005; Ponchau *et al.* 2006). *B. confusus* Schenck still well represented in the Eyne fauna, is regressing elsewhere throughout Europe (Rasmont & Mersch 1988; Berezin *et al.* 1995; Rasmont 1995; Söderman 1999; Goulson *et al.* 2005; Rasmont *et al.* 2005; Williams 2005). *Bombus cullumanus* (Kirby) has strongly regressed or even disappeared from the northern part of its former geographical extension (Rasmont *et al.* 2005). The species is presently restricted to a few locations in the E. Pyrenees, the Massif Central (France), and Navarra (Spain).

Eyne is interesting, not only for its species diversity, but also for the presence of very uncommon species. As this situation has remained unchanged for a half

Table 8. Estimation of the diversity and the originality for the studied sites.

Country, Area (ref)	Number of specimens	Number of species	Superficie km ²	Shannon-Weaver Bit	Hurlbert Number of species expected in a 100 specimens sample	Cumulative rareness specimens ⁻¹
France, Larzac (Rasmont 1989)	1723	24	200.00	3.45	14.58	0.036
France, Parc National des Pyrénées (Iserbyt <i>in lit.</i>)	4385	30	456.40	3.91	18.90	0.039
France, Nohèdes (Gosselin <i>et al.</i> 2007)	3092	29	28.93	3.45	17.15	0.034
France, Eyne	6288	33	20.18	4.04	21.14	0.054

century (Kruseman 1958; Delmas 1976), it may be presumed that its origin lies in some permanent structures and relationships.

Ecological preferences

Altitude

The mapping data (figs. 5–36) clearly indicate that the distribution of the species is not uniform over the whole territory of the commune. These discrepancies may be explained by the altitude, the vegetation and the floral resources.

The altitudinal ranges of the various species overlap in a way that suggests the complexity of their ecological requirements. Despite this overlapping, these ranges fall into four categories: lower, intermediate and higher altitudes, the fourth category containing the ubiquitous or very uncommon species. This subdivision is consistent with the observations of many authors (Pittioni 1937; Dylewska 1966; Comba 1972; Svensson 1979; Lundberg & Ranta 1980; Dathe 1981; Rasmont 1988; Williams 1991; Obeso 1992; Gosselin *et al.* 2007).

The study of species diversity as a function of altitude shows two frequency peaks: 1600 to 1700 m and 2000 to 2100 m and a decrease at higher altitudes (above 2400 m). In the Eyne valley, these altitudes correspond respectively to the meadows and to the transition between woods and subalpine grassland.

The most common species present an asymmetric distribution according to altitude. These species seem, however, to prefer the higher altitudes.

The curves of altitudinal range are mostly flattened out towards the higher altitudes. Svensson & Lundberg (1977) explain it by the consideration that bumblebees tend to forage along the flowering periods of their favourite plants. However, Teräs (1985) stresses that bumblebees may forage on their favourite plants away from their preferred habitat. Rasmont (1988) explains the asymmetric distribution by a better resistance of bumblebees to lower than to higher temperatures.

Habitats

By classifying the observations along the vegetation types and the CORINE biotopes, it has been possible to determine, for some bumblebee species, one or more favourite habitats. However, most species cannot be regarded as forest, wood edge or open field ones, along an ecological classification advocated e.g. by Pittioni & Schmidt (1942), Reinig (1970) and Rasmont (1988). Furthermore, the favourite habitat of a given species may differ from region to region. *Bombus lucorum*, e.g. is an ubiquitous species at Eyne, whereas elsewhere, it is regarded as a forest species (Pekkarinen 1984;

Rasmont 1988), as a wood edge species (Pittioni & Schmidt 1942; Móczár 1953; Dylewska 1957; Reinig 1970; Teräs 1985; Benton 2000, 2006), as an open field one (Løken 1973; Delmas 1976; Svensson 1979; Ornoza Gallego 1984) or as ubiquitous (Ranta & Tiainen 1982). In the Eyne valley, as in most places, *Bombus hypnorum* is characteristic of the forest habitat (Pérez 1890; Pittioni & Schmidt 1942; Móczár 1953; Dylewska 1957; Reinig 1970; Delmas 1976; Ranta & Tiainen 1982; Rasmont 1988) but elsewhere, it is an open field species (Løken 1973; Ornoza Gallego 1984), or an ubiquitous one (Teräs 1985), or characteristic of human habitats (Benton 2006) suburban areas.

As suggested by Teräs (1985), Osborne *et al.* (1991), Goulson (2004) and Goulson *et al.* (2006), most bumblebee species live in more than one habitat. According to Lundberg & Ranta (1980), Teräs (1985) and Benton (2000, 2006), the spatial heterogeneity of the resources forces the bumblebees to visit a succession of foraging sites and of new habitats through the seasons.

In the Eyne region, the vegetation types that support a large diversity of bumblebees are also rich in visited flower species (72 taxa in the meadows and 65 in the subalpine grassland). As stated by Banaszak (1996) and Goulson (2004) the species diversity of bumblebees is positively correlated with the floral diversity ($r = 0.89$, $p < 0.001$; fig. 40)

Floral resources

According to many authors (Alford 1975; Rasmont 1988; Benton 2000; Carvell 2002; Goulson 2004; Benton 2006), bumblebees mostly feed on the following families: Fabaceae, Scrophulariaceae,

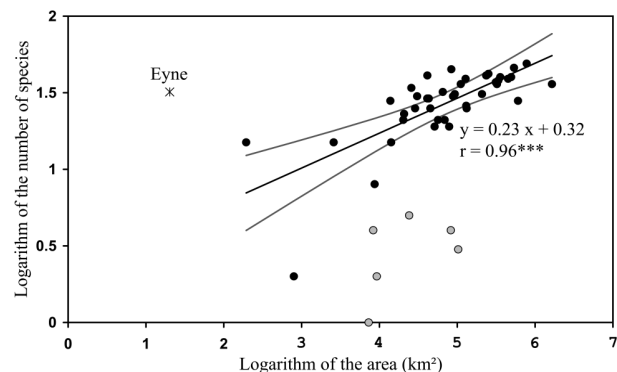


Figure 40

Log-log relation between the numbers of bumblebee species and the area of countries in the West-Palaeartic region. The solid circle indicates the European countries (Appendix A). The grey dots indicate the islands (Appendix A). The cross indicates the Eyne valley. Black: the regression line; grey: confidence intervals ($\alpha = 0.99$) of the regression.

Lamiaceae, Onagraceae, Asteraceae, Ericaceae and Ranunculaceae. However, the list of plants on which a given bumblebe species forages may differ from one region to another. For instance the genus *Aconitum* L., which is an important flower resource for *Bombus mendax* in Eyne, is also important elsewhere in France (Rasmont 1988) and in Austria (Hagen & Aichhorn 2003). On the other hand, in Austria (Pittioni 1937; Aichhorn 1976), the genus *Rhododendron* is favoured by the species (e.g. fig. 42, 43). In the Eyne valley, as in many regions, a general preference for some plant genera (*Trifolium*, *Vicia*, *Centaurea*, and *Epilobium*) has been described in many studies (e.g. Brian 1957; Dylewska 1958, Elfving 1968; Ruzskowski 1969a, 1969b, 1969c, 1970a, 1970b, 1970c, 1970d; Løken 1973; Teräs 1976; Pekkarinen *et al.* 1981; Steffny *et al.* 1984; Teräs 1985; Rasmont 1988; Corbet *et al.* 1991; Fussell & Corbet 1992; Macior 1994; Monsevicius 1995; Benton 2000; Carvell 2002; Benton 2006). Most bumblebee species feed on 2 to 7 favoured plants and on various numbers of minor taxa. Most favoured species are visited by more than 10 bumblebee species. As Rasmont (1988), Fussell & Corbet (1993), and Benton (2006) stated, a restricted number of plant taxa pool the preferences of the bumblebees. The fact that so many bumblebee species feed on so few flower species raises the question of the competition for resources. This could be explained by the plenty of flower resources and by the use of many minor resources.

In the present study, no distinction has been made between visiting plants for nectar or for pollen. It is therefore impossible to rely upon the criteria of Cane & Sipes (2006) to determine a scale of dietary specialisation. Indeed, the same bumblebee species may be specialist for pollen and generalist for nectar.

With the exceptions of *Bombus lucorum* and *B. ruderarius*, the list of generalist species in Eyne is different from those established by Rasmont (1988) for the whole Languedoc-Roussillon region (France) and by Benton for Essex (England) (2000, 2006). Three species (*Bombus pascuorum*, *B. pratorum*, *B. terrestris*), regarded as generalist in these studies appear to be less so in the Eyne valley where they feed on a score of flower species. It is true that these species are less plentiful. In a given region, the more or less restricted dietary choice of a bumblebee species appears to result from the interspecific competition for the resources. The most broadly generalist species are among the most common (fig. 40). It may be asked whether the observed polytropy reflects only the abundance of specimens or if polytropy is, in itself, a factor of commonness? Rasmont (1988) established that in

France there is a very strong correlation between the diversity of plants visited and the number of UTM grid cells in which the species was observed, whereas there is no significant correlation between the diversity of visited plants and the number of bumblebee specimens in each UTM grid cell. This means that it is the geographical distribution of a species, rather than its commonness, that is related with polytropy. Rasmont (1988) concluded that prosperity is an outcome of polytropy, rather than the reverse proposition. A more recent study by Pekkarinen (1998) points to the same conclusion. Goulson *et al.* (2005) concluded that the regression of some bumblebee species in England is the result of their dietary specialisation. The disruption of plant communities by modern agriculture may cause the restriction of the distribution of the more specialised species, as *Bombus sylvarum*, *B. ruderatus*, *B. subterraneus*, and *B. cullumanus*. Discussing the problem on a European scale, Williams (2005) does not find an obvious relation between the regression of a bumblebee species and its dietary specialisation. He would rather consider climatic or environmental specialisation as potential regression factors (Williams 2005; Williams *et al.* 2007).

In the Eyne valley, most (77 %) of the plants visited by bumblebees are perennial, some (20 %) are biennial, very few (3 %) annual (Appendix B). This preference for perennial plants has already been observed (Fussell & Corbet 1991; Corbet *et al.* 1994; Calabuig 2000; Ortwine-Boes & Silbernagel 2003). Osborne & Corbet (1994) concluded that: “*The most important factor in management for pollinators on farmland is to safeguard and extend areas of perennial herbaceous vegetation*”. On their side, Dramstad & Fry (1995) stressed that the maintenance of a perennial herbaceous vegetation depends on periodical perturbations to avoid its evolution into a forest environment.

Can the floristic richness and the juxtaposition of many micro-habitats explain the particularly complex structure of the bumblebees communities of Eyne?

Inquilinism

Two species: *Bombus bohemicus* and *B. sylvestris*, make up 63 % of the observations of inquiline bumblebees. *Bombus bohemicus* and its host *Bombus lucorum* are the most common species. Conversely, *Bombus sylvestris* seems as abundant and more widespread as its host *B. pratorum*. Alford (1975) and Benton (2006) mentioned a study of Awram (1970) which stating that the invasion ratio of the *Bombus pratorum* nests by *B. sylvestris* (50 %) is greater than in any other inquilinism relation. The invasion ratio of *Bombus lapidarius* by *B. rupestris* is 20 to 40 %, (Sladen

1989) and that of *B. lucorum* by *B. bohemicus* is 30 % (Müller & Schmid-Hempel 1992). This difference in the invasion ratios suggests that some ecological factors favour the reproductive success of *B. sylvestris*. Many aspects of bumblebee social life, foraging behaviour and mating strategies may have impact and can be one element of response to the risk of infestation (Benton 2006). As Pekkarinen *et al.* (1981), Rasmont (1988), Pekkarinen & Teräs (1993), and Benton (2006) already stated, we found that the inquiline species, however less common than their hosts, have the same or a more restricted distribution. In the Eyne valley as in other regions, the distribution maps of the inquiline species and of their hosts do not completely coincide. In the Eyne valley as in England, the ecological preferences appear to be more restricted for the inquiline species than for their hosts (Alford 1975). Few comparative study of the ecological preferences of the inquiline species and their hosts has yet been published. According to Benton (2000, 2006), the flower preferences of the inquiline species may be more restricted than those of their hosts and their habitats somewhat different. In Eyne, *Bombus bohemicus* seems to prefer transition vegetation (CORINE biotope “Scrub - *Juniperus*”) whereas its potential host *B. lucorum* seems especially to prefer pioneer vegetation (CORINE biotopes “Mesobromion”). For Rasmont (1988), the inquilines and their hosts live in the same vegetation types. However, he showed differences between their altitudinal ranges and their flower preferences. In the Eyne valley, the altitudinal ranges and the environmental preferences of the inquilines are more restrictive than those of their hosts. Furthermore, the flower preferences of the inquiline species and of their hosts are different (they forage just for nectar). Within sight of the relatively low number of specimens of *Psithyrus*, one can understand that the ecological preferences presented in this study do not account for reality completely. From the point of view of diversity, it seems probable that inquilinism has a negligible effect on the species composition of local bumblebees assemblages.

Competition

It may be wondered how more than ten bumblebee species may coexist in the same altitudinal range, in the same surroundings or within a single vegetational type. The spatio-temporal heterogeneity of the flower resources must play a role in the complex Eyne communities. A continuous supply of nectar and pollen is essential for the survival of bumblebee colonies (Pelletier 2003). For many authors, competition for resources is one of the main mechanisms of resource

division and the main factor that could explain the local structure of the bumblebee fauna (Inouye 1977a, 1977b; Pekkarinen 1984; Soltz 1987; Obeso 1992). Inouye (1977a) explained the bumblebee fauna of the Colorado Rocky Mountains by the hypothesis that only four species may coexist: a short-tongued one, a medium-tongued one, a long-tongued one, and a nectar robber. According to Rasmont (1989), this hypothesis is valid only in some regions as in Corsica while it is falsified on other places, like the Massif Central or Pyrenees. The diversity described in Eyne also falsifies this hypothesis (Rasmont *et al.* 2000): at any time, in any place, the number of co-existing species is obviously greater than four.

Several factors may explain this co-existence. Species competing for the same resources may differ in their altitudinal and environmental preferences. Other factors may also be taken in account: the nesting site, the time of hibernation ending, the size of the colony, competitors and predators, feeding strategies and resistance to bad weather (Pekkarinen 1984; Osborne *et al.* 1991; Obeso 1992; Svensson *et al.* 2000; Carvell 2002; Pelletier 2003; Potts *et al.* 2005). As Ranta (1982) and Ranta & Vepsäläinen (1981) imagined, resources may be plenty in regard of the needs of bumblebee populations. The natural increase of these populations would gradually restrain the possibility of co-existence until accidental events; mainly climatic (thunderstorms, out-of-season frost or snow) but also epizootic periodically diminish the population densities. To quote Ranta & Vepsäläinen (1981): “*Effects of competitive relaxation may be studied in two following ways: (1) When resources are superabundant [...] (e.g. on large clover fields in full blossom), even monocultures are able to maintain a diverse assemblage of bumblebees species. This should provide a good test for the behavioural flexibility of individuals with different proboscis lengths, but also for the functional flexibility of tongue morphology. [...]. (2) Due to the harsh climate, an average northern community should include a higher proportion of the geographical species pool, as populations are kept below competitive interactions by physically stressing and even catastrophic environmental vicissitudes*”. As the Eyne valley includes nearly all the bumblebees of the regional pool, Ranta & Vepsäläinen hypothesis may afford a good explanation of the exceptional species diversity in Eyne (Rasmont *et al.* 2000).

The traditional mixed agriculture, still in use at Eyne, contributed to the floral diversity of the place, known since the seventeenth century (Marage 2004). As in the National Reserve of Mt Carmel (Israël) (Potts *et al.* 2003), the diversity of floral resources, as well

as the altitudinal diversity of habitats may explain the co-existence of species with diversified ecological requirements.

Conclusion

The great diversity of the bumblebee fauna in the Eyne valley and the presence of many uncommon or even very rare species stress the exceptional character of this location. Four groups of species may be distinguished by their altitudinal range. On the other hand, it was not possible to draw a clear-cut distinction based on the vegetation types. Some CORINE biotopes look very attractive for bumblebees. A total of 120 flower species are visited, among which 14 genera are specially favoured. Each bumblebee species has favourite plants species (this might vary during season). The altitudinal diversity of habitat and flower resources may play a role in the complex structure of this fauna.

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Appendix A. Relation between the area and the number of species of bumblebees per area. *: according to The Times Atlas of the World (1993). **: does not appear in figure 40. ***: islands.

Studied area	Area km ² *	Number of species	References
Albania	28750	25	Tkalcù 1969
Germany	356840	40	Westrich 1984; Smissen & Rasmont, 2000
England	130360	26	Alford 1975; Osborne <i>et al.</i> 1991; Williams 1998
Austria	83855	45	Schwarz <i>et al.</i> 1996
Belgium	30520	30	Rasmont 1988
Belorussia	208000	31	Prishchepchik 1996
Bosnia	51130	19	Reinig <i>in lit.</i> and original data
Bulgaria	110910	36	Atanassov 1972a, 1972b, 1974
Croatia	56540	22	Original data
Denmark	43075	29	Calabuig 2000
Scotland	78750	19	Alford 1975
Eire	68895	21	Alford 1975
Spain	492590	40	Ornosa Gallego 1984
Estonia	45100	25	Mänd <i>et al.</i> 1999
Finland	337030	38	Pekkarinen <i>et al.</i> 1981; Söderman 1999
France	535285	46	Rasmont <i>et al.</i> 1995
Luxembourg	2585	15	Rasmont <i>et al.</i> 1995
Greece	131985	25	Reinig <i>in lit.</i> and original data; Anagnostopoulos 2005
Hungary	93030	31	Móczár 1953
Iran	1648000	36	Baker 1996 and original data
Northern Ireland	14150	15	Alford 1975
Israel**	20770	1	Dafni & Shmida 1996
Italy	251445	42	Intoppa <i>et al.</i> 1995
Lebanon**	10400	3	Original data
Lithuania	65200	32	Monsevicius 1995
Macedonia	25715	34	Reinig & Rasmont 1988
Moldavia**	33700	8	Osytschnyuk <i>in lit.</i>
Montenegro	13810	28	Reinig <i>in lit.</i> and original data
Norway	323895	36	Løken 1973, 1984
Wales	20760	23	Alford 1975
Netherlands	41160	29	Peeters <i>et al.</i> 1999
Poland	312685	39	Banaszak 2000
Portugal	91630	6	Reinig <i>in lit.</i> and original data
Romania	237500	41	Lehrer & Ciurdarescu 1979
Serbia - Kosovo	88360	30	Reinig <i>in lit.</i> and original data
Slovenia	20250	21	Gogala 1999
Sweden	449790	39	Løken 1973, 1984
Switzerland	41285	41	Amiet 1996; Schwarz <i>et al.</i> 1996
Syria**	185680	3	Mavromoustakis 1956 and original data
Former Czechoslovakia	127899	39	May 1959
Turkey	779450	49	Özbek 1990; Rasmont & Flagothier 1996
Ukraine	603700	28	Osytschnyuk <i>in lit.</i>
Yugoslavia	235555	41	Gogala 1999
Corsica***	8680	9	Rasmont & Adamski 1995
Canary Islands***	7275	1	Lieftinck 1958
Cyprus***	9250	2	Mavromoustakis 1957a, 1957b
Crete***	8330	4	Alfken 1927
Channel Islands***	194	15	Richards 1978
Madeira***	796	2	Original data
Novaya Zemlya***	82620	4	Friese 1923
Sardinia***	24090	5	Rasmont 1983

Appendix B. Visited plants for each bumblebee species ⁽¹⁾; Nomenclature based on Kerguelén (1993). In bold, relative abundance higher than 10%; -, plant not visited by the species; +, less than 1% of the choices of this bumblebee species. Phenology according to Coste (1927): *, perennial; **, annual; ***, bisannual.

Family, Species ⁽¹⁾	Phenology	bohemicus (n=34)	campestris (n=1)	confusus (n=17)	cullumanus (n=1)	flavidus (n=20)	gerstaeckeri (n=30)	hortorum (n=261)	humilis (n=190)	hypnorum (n=11)	lapidarius (n=54)	lucorum (n=937)	magnus (n=7)	mendax (n=201)	mesomelas (n=190)	monticola (n=536)	mucidus (n=50)	norvegicus (n=9)	pascuorum (n=119)	pratense (n=99)	pyrenaicus (n=402)	quadricolor (n=4)	runderarius (n=654)	runderatus (n=5)	rupestris (n=14)	sichelii (n=186)	soroensis (n=449)	subterraneus (n=82)	sylvarum (n=209)	sylvestris (n=14)	terrestris (n=92)	wurflenii (n=59)	Number of species																					
Apiaceae																																																						
<i>Eryngium bourgatii</i> Gouan																																																						
<i>Heracleum sphondylium</i> L.																																																						
Asteraceae																																																						
<i>Adenostyles alliariae</i> (Gouan) Kerner																																																						
<i>Antennaria carpatica</i> (Wählemb.) Bluff & Fingerh.																																																						
<i>Carduus carlinifolius</i> Lam.																																																						
<i>Carduus carlinoides</i> Gouan																																																						
<i>Carduus nutans</i> L.																																																						
<i>Carduus sp.</i>																																																						
<i>Carlina acutis</i> L.																																																						
<i>Centaurea jacea</i> L.																																																						
<i>Centaurea scabiosa</i> L.																																																						
<i>Centaurea sp.</i>																																																						
<i>Cirsium acule</i> Scop.																																																						
<i>Cirsium eriophorum</i> (L.) Scop.																																																						
<i>Cirsium foax</i> (L.) DC.																																																						
<i>Cirsium palustre</i> Scop.																																																						
<i>Crepis sp.</i>																																																						
<i>Hieracium sp.</i>																																																						
<i>Senecio leucophyllus</i> DC.																																																						
<i>Senecio pyrenaeus</i> L.																																																						
<i>Senecio sp.</i>																																																						
<i>Solidago virgaurea</i> L.																																																						
<i>Tanacetum pyrenaicum</i> Reuter																																																						
<i>Tanacetum sp.</i>																																																						
Borraginaceae																																																						
<i>Gynoglossum officinale</i> L.																																																						
<i>Echium vulgare</i> L.																																																						
<i>Symphytum officinale</i> L.																																																						

Appendix B. Visited plants for each bumblebee species ⁽¹⁾: Nomenclature based on Kerguelén (1993). In bold, relative abundance higher than 10%; -, plant not visited by the species; +, less than 10% of the choices of this bumblebee species. Phenology according to Coste (1927): *, perennial; **, annual; ***, bisannual. (Continued)

Family, Species ⁽¹⁾	<i>bohemicus</i> (n=34)	<i>campestris</i> (n=1)	<i>confusus</i> (n=17)	<i>cullumanus</i> (n=1)	<i>flavidus</i> (n=20)	<i>gerstaeckeri</i> (n=30)	<i>hortorum</i> (n=261)	<i>humilis</i> (n=190)	<i>hypnorum</i> (n=11)	<i>lapidarius</i> (n=54)	<i>lucorum</i> (n=937)	<i>magnus</i> (n=7)	<i>mendax</i> (n=201)	<i>mesomelas</i> (n=190)	<i>monticola</i> (n=536)	<i>mucidus</i> (n=50)	<i>norvegicus</i> (n=9)	<i>pascuorum</i> (n=119)	<i>pratense</i> (n=99)	<i>pyrenaicus</i> (n=402)	<i>quadricolor</i> (n=4)	<i>runderarius</i> (n=654)	<i>runderatus</i> (n=5)	<i>rupestris</i> (n=14)	<i>sichelii</i> (n=186)	<i>soroensis</i> (n=449)	<i>subterraneus</i> (n=82)	<i>sylvarum</i> (n=209)	<i>sylvestris</i> (n=14)	<i>terrestris</i> (n=92)	<i>wurflenii</i> (n=59)	Number of species																
Brassicaceae																																																
<i>Biscutella laevigata</i> L.																																																
Campanulaceae																																																
<i>Campanula glomerata</i> L.																																																
<i>Campanula rotundifolia</i> L.																																																
<i>Campanula</i> sp.																																																
<i>Jasione crispa</i> (Poult.) Samp.																																																
<i>Phyteuma hemisphaericum</i> L.																																																
<i>Phyteuma orbiculare</i> L.																																																
<i>Phyteuma spicatum</i> L.																																																
Caryophyllaceae																																																
<i>Dianthus lysiofolius</i> L.																																																
<i>Minuartia recurva</i> (All.) Schinz et Thill.																																																
<i>Minuartia</i> sp.																																																
<i>Silene ciliata</i> Pourr.																																																
Cistaceae																																																
<i>Helianthemum mammillarium</i> (L.) Mill.																																																
Crassulaceae																																																
<i>Sedum montanum</i> Perrier & Song.																																																
<i>Sedum rupestre</i> L.																																																
<i>Sedum</i> sp.																																																
<i>Sempervivum atrachnoides</i> L.																																																
<i>Sempervivum montanum</i> L.																																																
<i>Sempervivum</i> sp.																																																
Dipsacaceae																																																
<i>Scabiosa</i> sp.																																																
<i>Knautia arvensis</i> (L.) Coult.																																																
<i>Knautia dipsacifolia</i> Kreutzer																																																
<i>Knautia</i> sp.																																																
Ericaceae																																																

Appendix B. Visited plants for each bumblebee species ⁽¹⁾: Nomenclature based on Kerguelén (1993). In bold, relative abundance higher than 10%; -, plant not visited by the species; +, less than 10% of the choices of this bumblebee species. Phenology according to Coste (1927): *, perennial; **, annual; ***, bisannual. (Continued)

Family, Species ⁽¹⁾	Phenology	bobemicus (n=34)	campestris (n=1)	confusus (n=17)	cullumanus (n=1)	flavidus (n=20)	gerstaeckeri (n=30)	hortorum (n=261)	humilis (n=190)	hypnorum (n=11)	lapidarius (n=54)	lucorum (n=937)	magnus (n=7)	mendax (n=201)	mesomelas (n=190)	monticola (n=536)	mucidus (n=50)	norvegicus (n=9)	pascuorum (n=119)	pratorum (n=99)	pyrenaicus (n=402)	quadricolor (n=4)	rudivarius (n=654)	rudiveratus (n=5)	rupestris (n=14)	sichelii (n=186)	soroensis (n=449)	subterraneus (n=82)	sylvarum (n=209)	sylvestris (n=14)	terrestris (n=92)	wurflenii (n=59)	Number of species		
<i>Rhododendron ferrugineum</i> L.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	
Fabaceae																																			
<i>Anthyllus vulneraria</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Astragalus penduliflorus</i> Lamk	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Chamaespartium sagittale</i> (L.) Gibbs	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Genista tinctoria</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	
<i>Lathyrus pratensis</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	
<i>Lotus alpinus</i> Schleich.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	
<i>Lotus corniculatus</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	
<i>Lupinus</i> sp.	***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Melilotus officinalis</i> Lam.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Ononis cristata</i> Miller	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Oxytropis balleri</i> Bunge ex Koch	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	
<i>Trifolium alpinum</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	
<i>Trifolium montanum</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	
<i>Trifolium ochroleucon</i> Huds.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	
<i>Trifolium pratense</i> L.	*	3	-	-	-	-	-	-	13	-	4	7	-	2	11	+	6	-	12	-	1	+	-	-	-	-	-	-	-	-	-	-	-	-	18
<i>Trifolium repens</i> L.	*	-	-	-	-	-	-	-	1	-	2	2	-	+	+	6	4	-	2	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	16
<i>Trifolium</i> sp.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	
<i>Vicia cracca</i> L.	*	-	-	-	-	-	-	-	17	-	8	13	14	-	1	+	-	-	9	-	7	+	3	5	8	-	8	2	18	-	-	-	-	18	
<i>Vicia onobrychioides</i> L.	*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
<i>Vicia pyrenaica</i> Pourr.	*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
<i>Vicia sativa</i> L.	**	-	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Vicia sepium</i> L.	***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Vicia</i> sp.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
Gentianaceae																																			
<i>Gentiana buseri</i> Lap.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
<i>Gentiana lutea</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Geraniaceae																																			
<i>Geranium pratense</i> L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9

Appendix B. Visited plants for each bumblebee species ⁽¹⁾; Nomenclature based on Kerguelén (1993). In bold, relative abundance higher than 10%; -, plant not visited by the species; +, less than 1% of the choices of this bumblebee species. Phenology according to Coste (1927): *, perennial; **, annual; ***, bisannual. (Continued)

Family, Species ⁽¹⁾	<i>bohemicus</i> (n=34)	<i>campestris</i> (n=1)	<i>confusus</i> (n=17)	<i>cullumanus</i> (n=1)	<i>flavidus</i> (n=20)	<i>gerstaeckeri</i> (n=30)	<i>hortorum</i> (n=261)	<i>humilis</i> (n=190)	<i>hypnorum</i> (n=11)	<i>lapidarius</i> (n=54)	<i>lucorum</i> (n=937)	<i>magnus</i> (n=7)	<i>mendax</i> (n=201)	<i>mesomelas</i> (n=190)	<i>monticola</i> (n=536)	<i>mucidus</i> (n=50)	<i>norvegicus</i> (n=9)	<i>pascuorum</i> (n=119)	<i>pratense</i> (n=99)	<i>pyrenaicus</i> (n=402)	<i>quadricolor</i> (n=4)	<i>runderarius</i> (n=654)	<i>runderatus</i> (n=5)	<i>rupestris</i> (n=14)	<i>sichelii</i> (n=186)	<i>soroensis</i> (n=449)	<i>subterraneus</i> (n=82)	<i>sylvarum</i> (n=209)	<i>sylvestris</i> (n=14)	<i>terrestris</i> (n=92)	<i>wurflenii</i> (n=59)	Number of species		
<i>Geranium sylvaticum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	
Hypericaceae																																	10	
<i>Hypericum</i> sp.	-	-	-	-	-	-	-	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Lamiaceae																																		1
<i>Balboa nigra</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
<i>Galeopsis pyrenaica</i> Bart	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
<i>Lamium album</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
<i>Prunella grandiflora</i> (L.) Jacquin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	
<i>Scutellaria alpina</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Sideritis lysopifolia</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Stachys officinalis</i> Trev.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	
<i>Teucrium polium</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	
<i>Thymus nervosus</i> Willk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
<i>Thymus praecox</i> Opiz	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Thymus serpyllum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Thymus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	
Liliaceae																																		11
<i>Allium schoenoprasum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
<i>Veratrum album</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Malvaceae																																		1
<i>Malva moschata</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Onagraceae																																		20
<i>Epilobium angustifolium</i> Lamk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Orchidaceae																																		1
<i>Orchis mascula</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Plantaginaceae																																		1
<i>Plantago media</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Plumbaginaceae																																		5
<i>Armeria maritima</i> Willd.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Polygalaceae																																		

Appendix B. Visited plants for each bumblebee species ⁽¹⁾: Nomenclature based on Kerguelén (1993). In bold, relative abundance higher than 10%; -, plant not visited by the species; +, less than 1% of the choices of this bumblebee species. Phenology according to Coste (1927): *, perennial; **, annual; ***, bisannual. (Continued)

Family, Species ⁽¹⁾	bohemicus (n=34)	campestris (n=1)	confusus (n=17)	cullumanus (n=1)	flavidus (n=20)	gerstaeckeri (n=30)	hortorum (n=261)	humilis (n=190)	hypnorum (n=11)	lapidarius (n=54)	lucorum (n=937)	magnus (n=7)	mendax (n=201)	mesomelas (n=190)	monticola (n=536)	mucidus (n=50)	norvegicus (n=9)	pascuorum (n=119)	pratense (n=99)	pyrenaicus (n=402)	quadricolor (n=4)	runderarius (n=654)	runderatus (n=5)	rupestris (n=14)	sichelii (n=186)	soroensis (n=449)	subterraneus (n=82)	sylvarum (n=209)	sylvestris (n=14)	terrestris (n=92)	wurflenii (n=59)	Number of species		
<i>Polygala</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Polygonum bistorta</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Ranunculaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
<i>Aconitum anabara</i> L.	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
<i>Aconitum lycoctonum</i> (Reichenb. & Sprengel) Nyman	-	-	-	-	-	90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Aconitum napellus</i> L.	-	-	-	-	-	-	6	1	-	-	-	-	-	37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	
<i>Delphinium montanum</i> DC.	-	-	-	-	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
Rosaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	
<i>Alchemilla</i> sp.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Filipendula vulgaris</i> Moench	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Genem rivale</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
<i>Potentilla nitida</i> Lap.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	
<i>Rubus idaeus</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	
<i>Rubus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
Scrophulariaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
<i>Melampyrum pratense</i> L.	-	-	-	-	-	-	-	-	-	-	2	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
<i>Melampyrum sylvaticum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Digitalis lutea</i> L.	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Euphrasia minima</i> Jacq ex DC.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Linaria repens</i> Mill.	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
<i>Pedicularis comosa</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Pedicularis pyrenaica</i> Gay	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Rhinanthus punilus</i> (Sterneck) Soldano	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Violaceae	-	-	-	-	-	-	35	5	9	6	21	14	-	-	8	+	-	17	11	4	-	19	60	7	+	4	16	2	-	14	17	22	22	
<i>Viola tricolor</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Number of plants species visited	14	1	6	1	6	2	30	32	7	12	62	7	23	33	50	13	4	26	28	42	2	57	3	11	26	48	24	33	8	29	18	18		



Figures 41–45

41, *Bombus mesomelas* Gerstaecker foraging on *Trifolium pratense* L.; 42, *Bombus monticola rondoui* Vogt foraging on *Rhododendron ferrugineum* L.; 43, *Bombus pyrenaicus pyrenaicus* Pérez on the same plant; 44, *Bombus confusus* Schenck male in nuptial activity; 45, the first author in a typical landscape of the Cerdagne plateau: a very diversified meadow rich in leguminous plants.

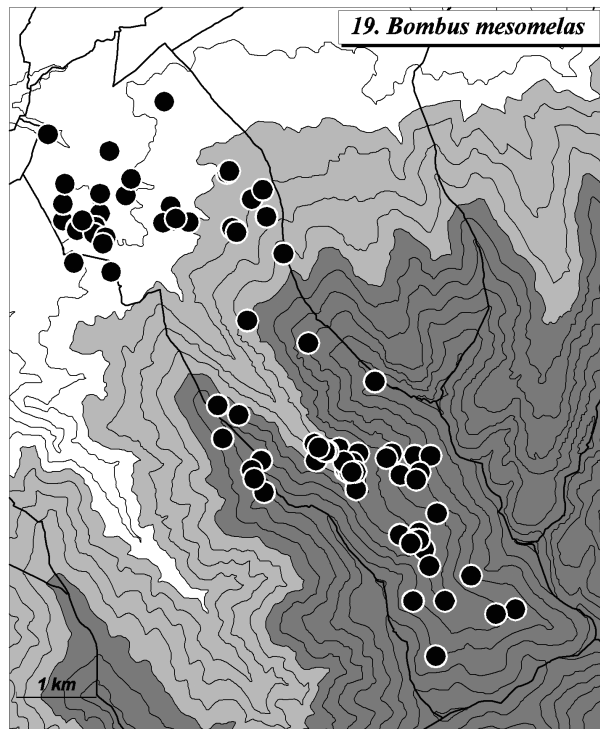
Erratum

Volume 44, fascicule 2 (avril-juin 2008)

Iserbyt S., Durieux E.-A., Rasmont P. 2008. The remarkable diversity of bumblebees (Hymenoptera: Apidae: *Bombus*) in the Eyne Valley (France, Pyrénées-Orientales). *Annales de la Société entomologiques de France* 44(2) : 211-241.

Page 215, Figure 3, under “light grey: below 1800 m; medium grey: 1800 to 2300 m; dark grey: above 2300 m.”, read “light grey: below 1700 m; medium grey: 1700 to 2100 m; dark grey: above 2100 m.”

Page 218, replace the Figure 19 by this figure:



Page 219, Figure 30, under „30. *Bombus sicheli*“, read „30. *Bombus sicheli*“

Page 221, Table 5, under „Altitude distribution“, read „Altitudinal distribution“

Page 227, in place of „As stated by Banaszak (1996) and Goulson (2004) the species diversity of bumblebees is positively correlated with the floral diversity ($r = 0.89$, $p < 0.001$; fig. 40).“, read “As stated by Banaszak (1996) and Goulson (2004) the species diversity of bumblebees is positively correlated with the floral diversity ($r = 0.89$, $p < 0.001$).”

Avec toutes nos excuses pour ces erreurs.

We apologize for these errors.

Pierre Rasmont
 Rédacteur-en-Chef
 Editor-in-Chief

Erratum

Volume 45, fascicule 2 (avril-juin 2009)

Iserbyt S. 2009. La faune des bourdons (Hymenoptera: Apidae) du Parc National des Pyrénées occidentales et des zones adjacentes. *Annales de la Société entomologique de France* 45(2) : 217-244.

Page 241, à la place de «Comme Banaszak (2000) l'a montré pour les Pyrénées, le PNPO», **lire** «Comme Banaszak (1996) l'a montré pour les Pyrénées, le PNPO»

Page 242, à la place de «**Banaszak J. 2000.** Effects of habitat heterogeneity on the diversity and density of pollinating insects. p.123-140 in: **Ekbom B., Irwin M.E., Robert Y. (eds)**, *Interchanges of Insects between agricultural and surrounding landscapes*, Kluwer Academic Publishers, Dordrecht, 239 p.», **lire** «**Banaszak J. 1996.** Effects of habitat heterogeneity on the diversity and density of pollinating insects. p.123-140 in: **Ekbom B., Irwin M.E., Robert Y. (eds)**, *Interchanges of Insects between agricultural and surrounding landscapes*, Kluwer Academic Publishers, Dordrecht, 239 p.»

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