

The effect of climatic variation on abundance and diversity of bumblebees: a ten years survey in a mountain hotspot

STÉPHANIE ISERBYT & PIERRE RASMONT

University of Mons (UMONS), Laboratory of Zoology, Place du Parc 23, B-7000 Mons, Belgium

Abstract. Even if climates play an evident role in the bumblebees distribution, at the present time, no research has been performed to test whether climatic parameters actually affect their abundance and diversity. For more than one decade (1999–2009), we monitored the bumblebee fauna of a mountain hotspot in the Eastern Pyrenees. We sampled each year, in July, the same hayfield habitat, resulting in the sampling of 28 species. We computed the correlation of the yearly abundance of the main species with several climatic parameters concerning temperature and precipitation. We separated the parameters measured during the bumblebee solitary phase and those measured during their social phase. Bumblebee fauna composition varied significantly over years. In the 13 species considered, the abundance of 9 was correlated with at least one climatic parameter. The lowest abundance of bumblebees was correlated with hot and dry conditions during the month of August the year before sampling (the nuptial time of the founders). The highest overall abundance of bumblebees was observed during the social phase in the rainy months. Across years, climatic parameters seem to have strongly affected the composition of bumblebee fauna. Our results seem to indicate that hot and dry weather represent serious threat for most bumblebee species. The potential effects of Global Warming are discussed: they may cause a severe reduction of the mountain bumblebee diversity.

Résumé. Les effets des variations climatiques sur l'abondance et la diversité des bourdons : une enquête de 10 ans dans une zone montagnarde riche en espèces. Même si les climats jouent un rôle évident dans la distribution des bourdons, aucune recherche n'a été menée jusqu'ici pour vérifier quels paramètres climatiques affectent réellement leur abondance et leur diversité. Durant plus d'une décennie (1999–2009), nous avons surveillé la faune de bourdons d'une zone montagnarde riche en espèces dans les Pyrénées-Orientales. Nous avons échantillonné le même habitat de prés de fauche en juillet de chaque année, ce qui a abouti à une liste de 28 espèces. Nous avons calculé la corrélation entre l'abondance annuelle des espèces principales et plusieurs paramètres liés à la température et aux précipitations. Nous avons séparé les paramètres mesurés durant la phase solitaire des bourdons de ceux mesurés durant leur phase sociale. La faune de bourdons varie significativement d'année en année. Parmi les 13 espèces prises en compte, l'abondance de 9 d'entre-elles était corrélée avec au moins un paramètre climatique. La plus faible abondance de l'ensemble des bourdons était corrélée avec les conditions chaudes et sèches durant le mois d'août de l'année qui précède l'échantillonnage (la période nuptiale des fondatrices). La plus forte abondance moyenne des bourdons a été observée les mois les plus pluvieux durant la phase sociale. D'année en année, les paramètres climatiques semblent avoir fortement influencé la composition de la faune de bourdons. Nos résultats semblent indiquer que les conditions chaudes et sèches représentent une menace sérieuse pour la plupart des espèces de bourdons. Les effets potentiels du Réchauffement Global sont discutés : ils peuvent provoquer une réduction sévère de la diversité des bourdons de montagnes.

Keywords: *Bombus*; Pyrenees; temperature; regression; Global Warming.

As main pollinators, the bees are a key component in most terrestrial ecosystems. Thanks to their endothermy and their life cycle alternatively solitary and social, the bumblebees are pollinators well suited to the Palaearctic mountain ecosystems (e.g. Williams 1991; Dylewska & Bak 2005; Xie *et al.* 2008).

Their nest growth and reproductive success could be affected by numerous factors depending on the cycle phases: queen's hibernation, foundation, colony growth, production of sexual castes, nuptial behaviours, mating (Alford 1975; Heinrich 1979). We know that insects are more or less affected by the temperature. Aside from their resistance to lethal high and low temperatures (Uvarov 1931), we also know that the endothermy of bumblebees conditions their life cycle (Heinrich 1979). The limitations are likely different for the colony or the individuals. On one hand, the colony itself clearly shows a high level of homeostasis that

E-mail: stephanie.iserbyt@umons.ac.be, stephanie.iserbyt@gmail.com,
pierre.rasmont@umons.ac.be
Accepté le 3 novembre 2012

could protect the individuals from the most extreme events (Richards 1973; Heinrich 1979). On the other hand, during their solitary life, the individuals can not rely on homeostasis and are exposed directly to the meteorological vicissitudes.

The solitary phase of the life cycle begins with the nuptial period. During this time, the males sleep outside the nest. They are thus exposed to rain, overheating and frost. Although virgin queens go back to their nest for the night during that period, they spend a lot of time searching for male pheromonal marks (Haas 1949; Cederberg *et al.* 1984). Once fertilized, queens also undergo exposure to weather conditions while they dig their hibernaculum (Alford 1975). After that time, the fertilized queens fall asleep at the bottom of their hibernaculum (1.5 to 19 cm deep; Hobbs 1965, 1968; Alford 1975), where they remain in diapause with an ectothermic metabolism. They are then exposed to extreme winter cold that could even reach lethal frost. In the spring, queens spend some time feeding on the first flower resources they find (Alford 1975; Nisbet 2005). At the beginning of the nest foundation, the queens take care of their brood and feed the first larvae after hatching. This requires a great deal of energy and thus a maximum foraging effort (Heinrich 1979).

The social part of the bumblebee cycle begins when the first workers emerge and replace the founding queen in her feeding task. This phase ends when young virgin queens and males fly out of the nest, generally four to ten weeks later (see Alford 1975; Goulson 2004). During this time, the individuals are protected against meteorological events by the homeostasis of the colony (i.e., collective thermoregulation, ventilation, food reserves). However, the colony needs considerable food intake and this could be a limiting factor (Heinrich 1979).

Except for the influence of resource availability, the great variability of the reproductive success of bumblebee colonies in the wild is still poorly understood (e.g. Pelletier 2003). Nonetheless, various studies have shown that wild bee populations could vary in composition and abundance yearly or even during a single season (e.g. Pérez 1879; Minckley *et al.* 1999; Oertli *et al.* 2005). Despite a very rich literature about bumblebees, few data are available about the effect of climatic factors on their fauna (e.g. Ranta & Vepsäläinen 1981; Rasmont *et al.* 2000; Evans *et al.* 2005; Williams *et al.* 2007, 2009; Williams & Osborne 2009).

In Eyne (France, Eastern Pyrenees), bumblebee diversity is extremely high (33 species in 20.18 km²)

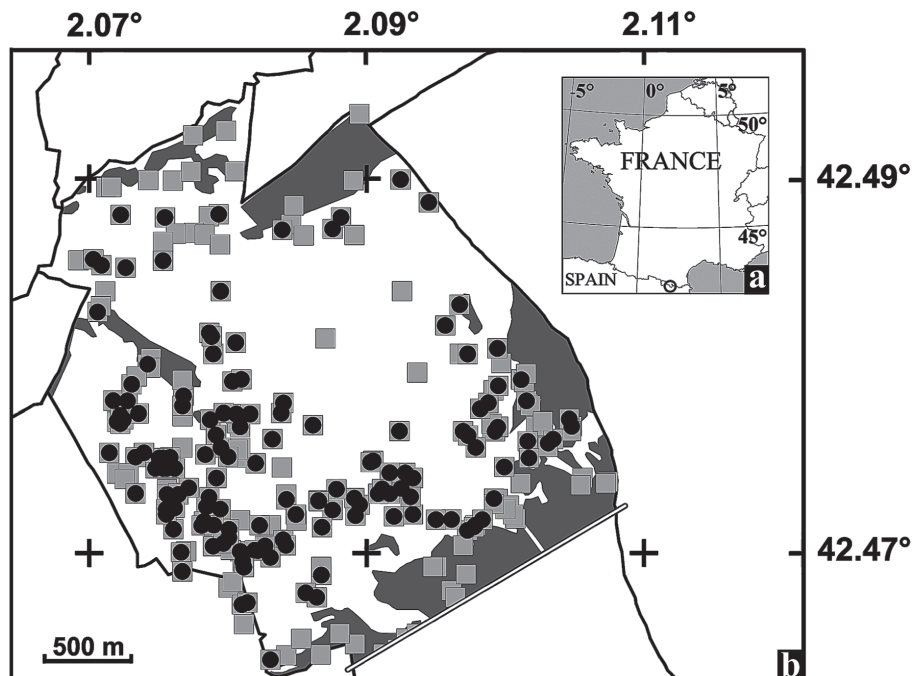


Figure 1

Localisation of the studied area in France: **a**, and in the hayfields and dry grasslands around the Eyne municipality; **b**, Grey faded: the woody area. Grey squares: all stations sampled between 1999 and 2009. Solid circles: sampled squares in grassland and hayfields rich in *Rhinanthus*, *Trifolium* and *Vicia* that were taken into account in the present study.

(Rasmont *et al.* 2000; Iserbyt *et al.* 2008). The landscape mosaic of the municipality (topography, vegetation) seems to contribute to the coexistence of this very high number of species (Iserbyt *et al.* 2009). The bumblebee diversity in Eyne is persisting since more than half a century (Kruseman 1958; Delmas 1976; Iserbyt *et al.* 2008). Despite this high and long dated local faunistic diversity, we could expect some variation in abundance and species composition, year after year.

Pepin & Kidd (2006) already underlined the high variability of the East-Pyrenean climate. Taking into account this high local climatic variation, we could verify if the diversity, the abundance and the bumblebee species composition are more or less correlated with this variability. The aims of this study are (1) to point out the yearly variation of abundance of bumblebee species in such a mountain bumblebee hotspot; (2) to identify climatic parameters that could be correlated with these variations and (3) to discuss the climatic risks for the mountain bumblebee fauna.

Methods

Studied area

The study was performed in part of the territory of the municipality of Eyne (France, Eastern Pyrenees). The studied area is 5 km² with altitudes between 1450 and 1850 m and is near the village (WGS84: 42°28'13"N, 02°05'06"E; Fig. 1). The vegetation of the studied area includes quite xeric hayfields and pastures characterized by a high abundance of *Rhinanthus pumilus* (Sterneck) Soldano, *Trifolium pratense* L., *Trifolium ochroleucon* Hods, *Vicia cracca* L., *Stachys officinalis* (L.) Trévisan, with sparse *Pinus uncinata* Miller ex Mirbel and *Juniperus communis* L. var. *nana* Syme. Hay is cut once a year, at the end of July or at the beginning of August (R. Staats, pers. com.).

Climatic assessment

The nearest permanent meteorological station is situated in Sainte-Léocadie (WGS84: 42°26'07"N, 2°00'08"E; 1320 m), 5.8 km SW of the studied area. The meteorological data (monthly temperatures: minimum minimorum also called lowest minimum temperature, average of the minimum, average of the maximum, maximum maximorum also called highest maximum temperature and precipitations) registered between 1998 and 2009 were transmitted by Météo France. During this time, the mean annual precipitation varied from 342.6 mm to 682.3 mm; the mean of maximum temperatures from 3.5 °C to 27.7 °C, and the mean of minimum temperatures from -5.6 °C to 14.4 °C.

Data sampling

Bumblebees were collected yearly from 1999 through 2009 between 9 and 28 July (see Iserbyt *et al.* 2008, 2009a, 2009b). The present data were not collected specifically for the present study but they are the result of the compilation of different operations.

Out of the data collected during 11 years surveying Eyne, we only took into consideration for the present study the data restricted to the defined altitude interval (1450 to 1850m) and vegetation type, resulting in a focus on a total of 142 stations (Fig. 1). These restrictions also led us to exclude all data from 2003, 2005 and 2006 because the authors were then working in other places in the Eyne valley. In each station, all bumblebees were collected, killed and identified to the subspecies level in the laboratory. The material is now conserved in the collections of the University of Mons (UMONS, Belgium). The nomenclature conforms to that used by Rasmont *et al.* (1995) and Williams *et al.* (2008).

At the studied altitude, most species living in the area of interest undergo their social phase in June and July. The solitary phase begins with the nuptial period in August, continues with the entry into hibernation in September, and ends with pre-nesting and nesting in April-May. The separation of climatic factors in the August-May period, for the solitary phase, and the June-July period, for the social phase, fits with this general mountain life cycle. These two intervals of time include most of the parts of the life cycle, respectively solitary and social.

Statistical analysis

A rarefaction index, the Hurlbert formula (Hurlbert 1971; simplified by Rasmont *et al.* 1990) was used to put a figure on the species richness for each time interval: $E_s = \sum [1 - ((N_i - N_j)/N)]^S$ where N_i = number of specimens of the species i in the studied area, N = total number of specimens in the studied area and S = number of specimens in a random drawing. This index provides the number of species expected in a random drawing of S specimens (here, $S = 30$).

By assessing the null hypothesis that the populations are stable (Banaszak 1996), we have estimated that the expected frequency of the species during the year ($a+1$) is identical to the frequency of the year before (a). The χ^2 goodness-of-fit test was also used to estimate the differences in foraging resources (i.e., genera of plants foraged by bumblebees) between time intervals (Siegel & Castellan 1988).

Aridity was computed using the Emberger index (1930): $Q_e = 2000 \times P / (M^2 - m^2)$ where P = total rainfall (mm), M = mean maximum temperature of the hottest month and m = mean minimum temperature of the coldest month. Aridity is highest when the Emberger index is the lowest (Hufty 2001).

For each phase (solitary and social), we computed the Pearson correlation coefficients (Legendre & Legendre 1998) between the relative abundance of the species counting more than 25 specimens and the climatic parameters by intervals of time: (1) total rainfall in August-May and June-July, (2) mean of minimum temperatures in August-May and June-July, (3) mean of maximum temperatures in August-May and June-July, (4) mean of minimum minimorum (the mean of the lowest minimum temperatures) in August-May, December-February and June-July, (5) mean of maximum maximorum (the mean of the highest maximum temperatures) in August-September, August-May and June-July, (6) Emberger index for August-May and June-July.

We performed all these computations with R, Development Core Team 2005.

Table 1. Relative abundance of the number of specimens by species observed once a year between 1999 and 2009 in the study area of the low altitude of Eyme (according to Iserbyt *et al.* 2008), and value of the diversity indices and the originality for each period. *: Obligate inquiline species. In brackets, absolute abundance. -: species presents but in weak proportion. Nb: Number.

	Eyme	Low altitude of Eyme	Study area							Total	
			1999	2000	2001	2002	2004	2007	2008		2009
<i>Bombus bohemicus</i> Seidl *	0.8 (36)	0.9 (21)			0.9 (3)	0.8 (2)				0.7 (1)	0.3 (6)
<i>Bombus campestris</i> (Panzer) *	- (1)	- (1)									
<i>Bombus confusus</i> Schenck	0.4 (18)	0.7 (18)			2.3 (8)	0.8 (2)	4.6 (8)				1.0 (18)
<i>Bombus cullmannus</i> (Kirby)	- (1)	- (1)			0.3 (1)						0.1 (1)
<i>Bombus flavidus</i> Eversmann *	0.3 (13)										
<i>Bombus gerstaeckeri</i> Morawitz	0.5 (22)	0.2 (4)		2.2 (3)							0.2 (3)
<i>Bombus hortorum</i> (L.)	4.7 (220)	5.1 (124)		1.5 (2)	6.1 (21)	2.7 (7)	0.6 (1)	14.7 (5)	0.7 (1)	3.5 (62)	
<i>Bombus humilis</i> Illiger	5.0 (238)	9.8 (237)		15.6 (21)	17.7 (61)	19.8 (52)	11.6 (20)	14.6 (15)	23.5 (8)	12.0 (216)	
<i>Bombus hypnorum</i> (L.)	0.5 (25)	0.7 (17)			0.3 (1)			1.9 (2)	5.9 (2)	4.5 (6)	
<i>Bombus lapidarius</i> (L.)	1.0 (49)	1.1 (27)		1.5 (2)	1.2 (4)	3.1 (8)	4.0 (7)	3.9 (4)		1.5 (27)	
<i>Bombus lucorum</i> (L.)	19.0 (897)	23.8 (578)		8.1 (11)	2.0 (7)	10.7 (28)	10.4 (18)	9.7 (10)	2.9 (1)	8.2 (11)	22.5 (405)
<i>Bombus magnus</i> Vogt	0.1 (5)	0.2 (4)		0.3 (2)							0.1 (2)
<i>Bombus mendax</i> Gerstaecker	3.9 (183)	0.1 (2)		0.3 (2)							0.1 (2)
<i>Bombus mesomelas</i> Gerstaecker	3.5 (167)	3.3 (81)		6.7 (9)	6.7 (23)	2.7 (7)	4.0 (7)	14.6 (15)	5.9 (2)	0.7 (1)	4.1 (74)
<i>Bombus monticola</i> Smith	10.1 (475)	1.4 (34)		2.9 (18)	2.3 (8)	0.8 (2)		1.0 (1)			1.6 (29)
<i>Bombus mucidus</i> Gerstaecker	1.1 (51)	0.2 (5)		0.2 (1)	0.9 (3)						0.2 (4)
<i>Bombus norvegicus</i> Sparre Schneider *	0.2 (8)	- (1)									
<i>Bombus pascuorum</i> (Scopoli)	2.4 (114)	4.4 (107)		8.9 (12)	1.2 (4)	4.6 (12)		5.8 (6)	5.9 (2)	3.7 (5)	2.6 (46)
<i>Bombus pratorum</i> (L.)	2.0 (93)	1.5 (36)		0.8 (5)	0.3 (1)	2.3 (6)				0.7 (1)	0.7 (12)
<i>Bombus pyrenaicus</i> Pérez	7.4 (348)	2.1 (52)		4.4 (27)	3.2 (11)	0.4 (1)				0.7 (1)	2.2 (40)
<i>Bombus quadricolor</i> (Lepeletier) *	- (2)	0.1 (2)		0.2 (1)							0.1 (1)
<i>Bombus ruderarius</i> (Müller)	13.9 (656)	19.5 (473)		9.6 (59)	26.5 (91)	25.2 (66)	38.7 (67)	7.8 (8)	8.8 (3)	15.7 (21)	20.1 (361)
<i>Bombus ruderatus</i> (Fabricius)	0.1 (3)	0.1 (3)		0.3 (2)	0.7 (1)						0.2 (3)
<i>Bombus rupestris</i> (Fabricius) *	0.3 (16)	0.2 (4)		0.7 (1)		0.4 (1)					0.1 (2)
<i>Bombus sichelii</i> Radoszkowski	3.3 (154)	0.1 (3)			0.6 (2)	0.4 (1)					0.2 (3)
<i>Bombus soroensis</i> (Fabricius)	10.3 (485)	9.8 (239)		12.1 (74)	1.5 (5)	11.5 (30)	1.2 (2)	11.7 (12)	26.1 (35)	26.1 (35)	9.0 (161)
<i>Bombus subterraneus</i> (L.)	2.3 (110)	4.3 (105)		0.5 (3)	14.8 (51)	3.1 (8)	12.7 (22)	2.9 (3)	1.5 (2)	1.5 (2)	5.5 (98)
<i>Bombus sylvaticus</i> (L.)	3.8 (178)	7.3 (177)		2.9 (18)	9.6 (33)	8.8 (23)	11.6 (20)	20.4 (21)	26.5 (9)	14.9 (20)	8.8 (158)
<i>Bombus sylvestris</i> (Lepeletier) *	0.2 (11)	0.2 (4)		5.4 (33)	1.2 (4)	0.4 (1)					0.1 (1)
<i>Bombus terrestris</i> (L.)	1.7 (80)	2.3 (57)		0.2 (1)	0.6 (2)	1.9 (5)	0.6 (1)	1.0 (1)	5.9 (2)	0.7 (1)	2.6 (47)
<i>Bombus wuelfenii</i> Radoszkowski	1.2 (58)	0.5 (11)		0.2 (1)	0.6 (2)						0.2 (4)
Number of specimens (N)	4717	2428		612	344	262	173	103	34	134	1797
Number of species (T)	31	30		20	21	19	11	13	9	13	28
Nb of stations with bumblebees (NSB)	449	244		31	17	35	12	12	10	17	142
Nb of sampled stations (NSS)	509	307		31	26	40	20	19	37	19	206
Expected number of species in a 30 specimen sample (Hurlbert)	12.7	10.8		8.2	8.9	9.9	7.7	9.7	7.9	7.7	10.5
Ratio Nb of specimens/ Nb of stations with bumblebees (N/NSB)	10.5	9.9		19.7	16.9	7.5	14.4	8.6	3.4	7.9	12.7
Ratio Nb of specimens / Nb of sampled stations (N/NSS)	9.3	7.9		19.7	9.6	6.6	8.7	5.4	0.92	7.1	8.7

Results

The bumblebee fauna of the studied area

In the studied area, 1797 specimens belonging to 28 bumblebee species were collected (Table 1). Only 6 species were abundant and include 77.8% of the total number (in decreasing order: *Bombus lucorum*, *B. ruderarius*, *B. humilis*, *B. soroensis*, *B. sylvarum*, and *B. subterraneus*; see Table 1). Aside from these locally abundant species, 19 of the remaining species each include less than 5% of the total number of specimens. The rarest species were observed only once (*B. cullumanus*, *B. quadricolor* and *B. sylvestris*).

Yearly variation

The total number of specimens collected in 1999 is larger than in subsequent years. The total number of species within the studied area is 28 from 1999 to 2009, but varies yearly from 9 (in 2008) to 21 species (in 2001) (Table 1). The Hurlbert expected number of species seems more or less constant between years: in a random drawing of 30 specimens, the number of species expected is estimated to 10 for the years 2001, 2002 and 2007, and a bit lower (8–9 species) for the remaining years (1999, 2000, 2004, 2008, 2009) (Table 1).

The annual species faunas are significantly ($p < 0.05$) to very highly significantly ($p < 0.001$) different (χ^2 goodness-of-fit test). Six species are always present (*B. hortorum*, *B. humilis*, *B. lucorum*, *B. mesomelas*,

B. ruderarius, *B. sylvarum*; Table 1). Four species are observed during 7 of the 8 studied years (*B. pascuorum*, *B. soroensis*, *B. subterraneus*, *B. terrestris*). Six species are observed during only one year (*B. cullumanus*, *B. gerstaeckeri*, *B. magnus*, *B. mendax*, *B. quadricolor*, *B. sylvestris*; Table 1).

The species composition changed greatly from one year to another. In fact, the dominant species one year was seldom dominant another year. *Bombus ruderarius* was generally the most abundant species, as it was the case in 2000, 2001, 2002 and 2004. *Bombus lucorum* was, by far, the dominant species in 1999, while this species was collected only once in 2008. *Bombus sylvarum* was the dominant species in 2007 and 2008, but quite rare in 1999. *Bombus soroensis* was the most abundant species in 2009, nearly *ex aequo* with *B. humilis*, but the former was rare in 2000, 2001 and 2004, and the latter even scarcer in 1999.

Climatic parameters

The annual climatic conditions vary substantially from one year to another (Table 2). Rainfall did not vary much during the solitary phases but varied greatly during the social phases. The weather during solitary phase was humid in 2000, 2002, 2003, 2004, 2005, 2006, 2009 and very humid in 1999, but dry in 2001, 2008 and very dry in 2007 (Table 2). This was also perceptible with Emberger's aridity index: it did not vary much during the solitary phases (although it was clearly damper in the 2002–2003 season) but was more variable in the social phases (damp in 2002, 2003; very

Table 2. Climatic parameters in Sainte-Léocadie for each year for 1998–2009.

Year	Precipitations (mm)		Mean of minimum temperatures (°C)		Mean of maximum temperatures (°C)		Mean of minimum minimorum (°C)		Mean of maximum maximorum (°C)		Emberger Index	
	August–May	June–July	August–May	June–July	August–May	June–July	August–May	June–July	August–May	June–July	August–May	June–July
	August 1998–July 1999	429.8	193.0	3.0	10.8	13.5	22.9	–4.0	6.1	20.7	27.8	1346.5
August 1999–July 2000	468.5	115.0	3.2	10.1	14.2	22.6	–2.6	4.5	21.5	28.5	1461.2	478.5
August 2000–July 2001	419.5	92.5	3.7	10.7	13.9	23.9	–2.8	4.8	20.8	31.4	1284.1	384.8
August 2001–July 2002	372.0	163.5	2.9	11.0	14.0	23.8	–2.3	4.0	21.6	30.7	1105.2	699.0
August 2002–July 2003	485.5	144.8	3.0	12.8	12.9	25.8	–2.9	8.3	19.5	30.7	2110.7	554.2
August 2003–July 2004	496.8	110.4	3.2	11.2	13.4	23.6	–2.3	5.0	20.7	30.3	1297.8	466.0
August 2004–July 2005	345.1	101.2	2.8	11.6	13.8	25.1	–4.6	6.9	21.0	32.1	1162.7	366.1
August 2005–July 2006	432.9	153.0	3.0	12.2	13.6	26.3	–3.4	5.8	20.6	30.2	1601.3	481.7
August 2006–July 2007	368.9	34.5	4.0	10.8	14.9	24.0	–1.5	4.8	21.8	29.1	1425.5	121.1
August 2007–July 2008	467.1	84.3	3.1	10.3	14.3	23.2	–3.1	3.9	21.6	29.9	1615.6	300.8
August 2008–July 2009	387.8	101.4	2.8	11.3	13.5	24.8	–3.6	5.8	21.4	30.9	1166.1	328.0

damp in 1999; arid in 2001, 2005, 2008, 2009; and very arid in 2007; see Table 2).

Concerning temperatures, the highest means of maximum maximum were measured during the social phase in 2001 (31.4 °C) and 2005 (32.1 °C). The lowest mean of maximum maximum of the social phase was observed in 1999 (27.8 °C). The highest means of maximum temperature of social phase were in 2006 (26.3 °C) and 2003 (25.8 °C), the lowest were in 1999 (22.9 °C) and 2000 (22.6 °C). The mean of minimum minimum of the solitary phase was lowest during the winters of 2004–2005 (−4.6 °C) and 1998–1999 (−4.0 °C), but highest in the winters of 2006–2007 (−1.5 °C), 2001–2002 and 2003–2004 (−2.3 °C).

The remaining parameters were less contrasted.

Bumblebees in correlation to climatic parameters

Bombus magnus, *B. mendax*, *B. mucidus*, *B. sichelii* and *B. wurflenii* were the rarest species in the area of interest, and they were sampled during the most humid years (mainly 1999). *Bombus confusus* was a rare species only sampled during the hot and dry years (mainly 2001 and 2004).

Out of the 13 species represented by more than 25 specimens in 1999–2009, only 4 species were never correlated with any climatic parameters (i.e., *B. monticola*, *B. ruderarius*, *B. subterraneus*, and *B. terrestris*; $\alpha \geq 0.90$; Table 3). For the 9 remaining species, the abundance was correlated to rainfall, temperature or aridity.

Climatic parameters do not seem to influence in the same way bumblebees that are in the solitary phase (August–May) or in the social phase (June–July).

Considering the social phase, the abundance of 3 bumblebee species in the sampling is correlated with rainfall and aridity index (positively for *B. lucorum*, negatively for *B. sylvarum* and *B. mesomelas*), while other species are linked to low rainfall in the same phase (*B. soroensis*) and low aridity (*B. hortorum*) (Table 3).

As for temperatures, the abundance of 8 species is correlated with maximal or minimal temperature, during the social or solitary phase (Table 3). The abundance of several species is clearly correlated with hot and dry conditions. For *Bombus mesomelas*, 6 parameters are negatively correlated with rainfall and the Emberger index during the social phase but are positively correlated with mean minimal/maximal

Table 3. Correlation between the relative abundance of the species and the climatic parameters (Pearson's correlation coefficients).

Only correlation coefficient $r \geq 0.62$ are indicated ($\alpha \geq 0.90$). Bold, correlation coefficients significant in threshold $\alpha \geq 0.95$. Ratio N/NSB: Ratio Number of specimens / Number of stations with bumblebees. Ratio N/NSS: Ratio Number of specimens / Number of sampled stations.

Species	Precipitations (mm)		Mean of minimum temperatures (°C)		Mean of maximum temperatures (°C)		Mean of minimum minimorum (°C)			Mean of maximum maximorum (°C)			Emberger Index	
	August–May	June–July	August–May	June–July	August–May	June–July	August–May	December–February	June–July	August–September	August–May	June–July	August–May	June–July
<i>B. lucorum</i> (n = 406)		+0.70						−0.84	+0.67			−0.68		+0.65
<i>B. ruderarius</i> (n = 361)								+0.64			+0.62	+0.68		
<i>B. humilis</i> (n = 217)														
<i>B. soroensis</i> (n = 162)	−0.69			+0.62		+0.65								
<i>B. sylvarum</i> (n = 160)		−0.77						+0.70			+0.62			−0.81
<i>B. subterraneus</i> (n = 98)														
<i>B. mesomelas</i> (n = 74)		−0.77	+0.91		+0.87		+0.75	+0.69						−0.69
<i>B. hortorum</i> (n = 62)													+0.68	
<i>B. terrestris</i> (n = 47)														
<i>B. pascuorum</i> (n = 46)				−0.64	+0.68						+0.84			
<i>B. pyrenaicus</i> (n = 40)							−0.62	−0.81			−0.67			
<i>B. monticola</i> (n = 29)														
<i>B. lapidarius</i> (n = 27)							+0.86			−0.86				
Ratio N/NSB											−0.76			
Ratio N/NSS		+0.62						−0.82	+0.68		−0.75			+0.62
Number of species														

temperatures and mean of minimum minimum during the solitary phase (August-May and December-February). The abundance of *B. sylvarum* is correlated in the same way as the abundance of *B. mesomelas* but with fewer parameters (4). The abundance of *B. soroensis* is also correlated in a parallel way with three parameters (rainfall in the solitary phase, mean of minimal and maximal temperatures in the social phase). The abundance of *B. humilis* is correlated with hot climate because it is linked to hot mean minimum minimum temperature during the solitary phase (December-February) and hot mean of maximum maximum temperatures during both the solitary and social phases (positive correlation with continental temperature conditions). The abundance of *B. pascuorum* is linked to high mean of maximum temperatures and mean of maximum maximum during the solitary phase and to low mean of minimal temperatures during the social phase. The abundance of *B. lapidarius* is weakly linked to hot conditions when considering only two parameters: the mean of minimum minimum temperatures and the mean of maximum maximum temperatures (August-September) during the solitary phase.

The abundance of three species is correlated with cold and wet climatic factors. The abundance of *B. lucorum* is positively linked to 5 parameters during the social phase: rainfall, the Emberger index, cold maximum maximum and hot mean of minimum minimum (December-February and August-May) (positive correlation with oceanic conditions). The abundance of *B. pyrenaicus* is linked to high mean of minimum minimum (December-February and August-May) and low mean of maximum maximum during the solitary phase. The abundance of *B. hortorum* is linked to the Emberger index (more humid) during the solitary phase.

To summarize, the relative abundance of *B. mesomelas*, *B. sylvarum*, *B. soroensis*, *B. humilis*, *B. pascuorum*, and *B. lapidarius* are linked to dry and/or hot conditions, whereas the relative abundance of *B. lucorum*, *B. pyrenaicus*, and *B. hortorum* are correlated with wet and/or cold conditions.

The ratio of the number of specimens to number of collecting stations with bumblebees is negatively correlated with mean of maximum maximum during the solitary phase. The lowest ratio (3.4 specimens/station with bumblebees) is observed after a dry period (August 2008) succeeding another dry period, with the highest temperatures observed during the nuptial flight phase (August 2007). This is also perceptible for the ratio of the number of specimens to sampled stations, which is also correlated with high rainfall,

mean temperature and high Emberger index during the social phase. The ratio of the number of stations with bumblebees and the number of sampled stations is correlated with high rainfall, high mean minimum temperature and high mean minimum minimum during the social phase, but it is also correlated with low Emberger index during the solitary phase. The total number of species is not correlated with any parameter. All these correlations between climatic factors and faunistic ratio could be interpreted as follows: the number of bumblebee specimens is clearly lower after hot temperatures during the solitary phase (mainly nuptial time), but higher after rainy days (with higher night temperatures) during the social phase. Neither the total number of species and the rarefaction Hurlbert index are correlated with the climatic parameters in the studied area.

Discussion

The bumblebee fauna of the studied area

The studied area includes 28 bumblebee species. All species observed there in the past (Kruseman 1958; Delmas 1976) are still observed today, including some of the rarest species in France (e.g. *B. cullumanus*, *B. gerstaeckeri*, *B. confusus*; see Rasmont 1988; Rasmont *et al.* 2005; Iserbyt *et al.* 2008).

Yearly variations in bumblebee fauna

Unlike Oertli *et al.* (2005) in Wallis (Switzerland) and Kosior *et al.* (2008) in Krakow (Poland), we observed a quite constant diversity in Eyne year after year, with 8 to 10 registered species in a 30 specimens sampling (rarefaction Hurlbert index).

The very high species diversity in Eyne is still maintaining after 50 years (Kruseman 1958; Delmas 1976; Iserbyt *et al.* 2008). However, in the studied area, the relative abundance of the species seems to vary in an unpredictable way. The dominant species during one year could be completely different the year after and could even nearly disappear some years later. For example, the main species in 1999 were very different from those observed in 2008 (see Table 1).

Whereas bumblebees were found to be very abundant everywhere in all sampled stations in 1999 and 2001, they were found in less than one quarter of the sampled stations in 2008 (Table 1), just after the driest year of the decade. While Banaszak (1996) observed that the population density of bumblebees in mountain areas (including the Pyrenees) was high and stable, we see here that this was not the case in Eyne during the last decade. At the beginning of the decade

(1999 to 2001), we observed 16.9 to 20.2 specimens per sampled station with bumblebees, but this density fell to 3.4–14.4 after 2002. Despite their high and permanent diversity, we noted a clear decrease in bumblebee abundance after 2002. This decrease could be the result of the succession of hot and dry events in the region, as was the case in 2001, 2005, 2007, 2008, and 2009 (see Bessemoulin *et al.* 2004; “Météo France” 2009; Rasmont & Iserbyt 2012). It is remarkable that the total number of specimens seems especially low in the summer following a hot period during the solitary phase (in the month of August, the year just before).

Species observed in the present studied area, which are at the borders of their altitudinal range (e.g., *B. hypnorum*, *B. gerstaeckeri*, *B. magnus*, *B. mendax*, *B. mucidus*, *B. ruderatus*, *B. sichelii*, *B. wurflenii*; see Rasmont 1988; Iserbyt 2009b), show a higher sensitivity, disappearing from the sampling for several years. Only 22% of the total number of species, are always present during the whole survey. Such a low proportion of permanent species was already noticed by Cane *et al.* (2005) for the wild bees of South Arizona. According to Williams *et al.* (2007, 2009) and Williams & Osborne (2009), climatic factors and resource limitations could disturb the abundance of the species that are at the edge of their area and outside of their eco-climatological optimum. However, we see here in Eyne that even some species such as *B. lucorum* or *B. mesomelas*, which are clearly in their ranges and close to their eco-climatological optimum, show a considerable variability in abundance, being dominant one year and nearly absent another.

Correlation of bumblebee abundance during the solitary phase

The minimal temperature in the solitary phase is clearly linked to the coldest temperatures occurring during the winter, so it concerns the hibernation constraints. Only three species (*B. mesomelas*, *B. lapidarius*, *B. pyrenaicus*) have their abundance correlated with the minimal temperature of the solitary phase. As *Bombus pyrenaicus* inhabits only alpine and subalpine levels (Rasmont 1988; Amiet 1996), it is logical to think that it could benefit from extreme cold conditions. However, it is curious that the abundance of *B. mesomelas*, also a subalpine species, is correlated with the highest mean of minimum minimorum temperatures (Table 3). *Bombus lapidarius* is a lowland species (see Alford 1975; Løken 1973; Rasmont 1988), reaching its highest altitude in Eyne. Quite logically, it is also the species with the strongest correlation with the highest mean of minimum minimorum temperatures. Hobbs (1964, 1968) measured the resistance to lethal

low temperatures of several bumblebee species in the Rocky mountains (North America). He found very low lethal temperatures (e.g. $-14\text{ }^{\circ}\text{C}$ for *B. rufocinctus* and $-19\text{ }^{\circ}\text{C}$ for *B. nevadensis*), much lower than the mean of minimum minimorum registered in our studied area in January ($-8.5\text{ }^{\circ}\text{C}$). Hobbs (l.c.) also hypothesized that the hibernaculum's depth could influence the resistance of the species to the cold. Alford (1969) showed that different bumblebee species search for subtle microclimatic conditions to dig their hibernaculum. Unfortunately, no data are available about the hibernaculum of the Pyrenean bumblebees.

The highest temperature of the solitary phase is linked to the nuptial time in August and the abundance of 7 species are positively or negatively correlated with this parameter.

More interestingly, the correlations of abundance ratios (N/NSB, N/NSS; Table 3) are maximal with a low mean of maximum maximum in August, a low mean of maximum maximum in December-February, but also with high aridity (low Emberger index) during the solitary phase. For the first time, we show that climatic conditions occurring during the nuptial and hibernation times are very important for bumblebees. This was never reported before.

Correlation of bumblebee abundance during the social phase

The abundance of 6 species is positively or negatively correlated with temperatures in June-July while three species are correlated with rainfall.

The abundance ratios (N/NSB, N/NSS) are linked to high rainfall, high mean temperature and a high mean of minimum minimorum temperatures during the social phase, all parameters well known to be linked to high plant production.

Solitary versus social phase

While the abundance of 6 species is linked to some climatic parameters during the social phase, the abundance of 8 was correlated to the climatic parameters that occurred during the solitary phase the year before the sampling. This is consistent with the protective and buffering role played by the colony thermoregulation (Richards 1973; Heinrich 1979). It is very difficult to differentiate the direct effects of the climatic factors on the bumblebees themselves from the indirect effects on their flower resources (Williams & Osborne 2009). During drought, we observed that the vegetation was clearly less abundant and that there were much less flowering plants (Fig. 2). Therefore, we suggest that resource scarcity was a main factor of local bumblebee abundance, as was already observed

by many authors (see Carvell *et al.* 2006; Goulson *et al.* 2008a, b; Lye *et al.* 2009).

From correlation to relation

In the present study, we only concentrated our analyses on correlations, which do not allow us to conclude that these climatic parameters are the direct causes of the variations in bumblebee fauna.

A late spring could delay the foundation of the colony, thus reducing the time available for development and leading to smaller colonies (Alford 1975; Pelletier 2003). Low temperatures could also slow the growth of the brood, despite the existence of nest thermoregulation (Cartar & Dill 1991). Bumblebees do not fly when the temperature outside the nest exceeds 32 °C to 35 °C (see Velthuis & van Doorn 2006), but such high temperatures were barely reached in the studied area, except in microclimatic conditions.

Another explanation of the role played by hot and dry conditions, leading to the drastic decrease in the total number of bumblebees, could be linked to disease sensitivity. It is well known that control of temperature and humidity are of key importance in the rearing of bumblebees (Velthuis & van Doorn 2006): outside of narrow temperature and humidity intervals, the whole colony suffers from increased disease sensitivity. In normal weather conditions, most bumblebees could likely maintain the homeostatic conditions of the nest inside its limits, but probably not if heat waves or extreme droughts occur. The increased sensitivity of the fauna stressed by climatic events was proposed by Pounds *et al.* (2006) to explain the regression of Amphibian species. These authors suggested, for example, that 80% of the regressing of the toad species of the genus *Atelopus* Duméril & Bibron were last seen following a hot year that triggered their fungal sensitivity.

These climatic parameters could also act in another very indirect way, by modifying vegetation productivity as well as nectar and pollen availability. It is clear that from dryer to damper episodes, the state of the vegetation can vary dramatically. There are clearly less flowers available during dry periods (Fig. 2). This may explain why the low rainfall and the high temperatures in June-July could alter the abundance of the whole bumblebee fauna. The nights are sometimes very cold during the summer in the studied area, even with frost. These cold episodes could increase the need for food intake by the colony but they could also decrease the growth of the brood and at the same time, reduce plant productivity (which may lead to a resource crisis for bumblebees).

Some authors (e.g., Dennis 1993; Thomas *et al.* 1999, 2004, 2006) already hypothesized that the variation of climatic factors could explain the expansion/regression episodes of insects in general and sometimes bumblebees in particular (e.g., the recent expansion of *B. terrestris* and *B. lapidarius* to the North; MacDonald 2001). Other authors (Williams 1986, 1989; Goulson *et al.* 2005; Williams *et al.* 2007) noticed that some bumblebee species regress even near the centrum of their apparent climatic optimum. We see here that even a very abundant species like *B. lucorum* could drastically decrease in number, and even nearly disappear locally, when climatic factors are unfavourable. We also noticed that the total number of bumblebees observed in Eyne could decrease by more than one order of magnitude the year following a warm, dry summer (e.g., 0.9 bumblebees per sampled station in 2008 against 19.7 in 1999). Nevertheless *B. sylvarum* and *B. pascuorum* could be more resistant to hot weather than are all other bumblebees, as these species remain in relative high abundance even in the worst years.

This reduction in the total number of bumblebees does not seem connected to a decrease in the perceptible diversity. However, we have to keep in mind that such events could possibly lead to a local extinction of some rare species. If the local extinction concerns the last remaining populations of a considerably rarefied bumblebee species like *Bombus cullumanus* (Rasmont *et al.* 2005), this could lead to the definitive extirpation of the species.

For several high altitude species (e.g., *B. mendax*, *B. monticola*, *B. mucidus*, *B. wurflenii*) workers were observed in the studied area only in 1999, which corresponds to the coldest and dampest year of the decade. It is known that foragers do not fly far away from their nest, generally up to a few meters (Butler 1951; Saville *et al.* 1997; Ponchau *et al.* 2006), which implies that the alpine queens should have founded their nest in 1999 at lower altitudes than they did the following years. It may be questioned whether if that phenomenon was an exceptional situation or if it was the norm before the drying and warming period starting in 2002.

Role of climatic heterogeneity in maintaining bumblebee diversity

Ranta & Vepsäläinen (1981) and Teräs (1985) already noticed that the dynamics of the bumblebee species in Finland could be partly dependent on climatic events. In the same way, Obeso (1992) also hypothesized that unstable climatic conditions in the Cantabrian Mountains induce year-to-year variations in the bumblebee fauna, increasing the spatial

heterogeneity of the species assemblages. Veech & Crist (2007) also presented a similar hypothesis to explain the diversity of species assemblages of birds.

Differential use of diversified floral resources and various nesting sites mostly explains the coexistence of a high number of bumblebee species (Pekkarinen 1979, 1984; Bowers 1985; Kneitel & Chase 2004; Evans *et al.* 2005; Westphal *et al.* 2006; Iserbyt *et al.* 2009). According to Ranta & Vepsäläinen (1981), Rasmont (1989) and Rasmont *et al.* (2000), a high local diversity could also be maintained thanks to a decrease in competition for limited resources. In other words, the number of specimens drops off after harsh climatic conditions and this could maintain the population size below a given competition threshold. The study presented here, which concentrates on a yearly survey in a small but diversified area, leads to discredit the validity of such an explanation in the present case. For instance, the highest species richness was observed when the total number of specimens was the highest, thanks to favourable climatic factors, while the lowest richness occurred after the worst conditions. If damp and arid years closely alternate, these climatic conditions could balance the population levels of different pools of bumblebee species. However, several dry years could follow one another, leading to a considerable regression of some sensitive species.

Potential effects of global warming on mountain bumblebees

The IPCC (2007) estimated that a global warming of 0.74 °C already occurred during this last century (1906–2005), and is expected to reach 2 °C to 3 °C more in the next hundred years.

It is well known that the temperature decreases by 0.5 °C (saturated air) to 1 °C (unsaturated air) for each 100 m rise in altitude (Hufty 2001). According to this rule, the increase in temperature due to global warming (i.e., 0.74 °C that occurred during the last century) should have driven to a shift of +75 to +150 m in altitude for the mountain-inhabiting fauna.

Since 1970, Franco *et al.* (2006) observed an uphill shift of 150 m for the butterfly *Erebia epiphron* (Knoch 1783) in Britain. In Sierra de Guadarrama (centre of Spain), Wilson *et al.* (2005) observed an isothermic uphill shift of +225 m between 1967 and 2004, where the climatic and faunistic conditions are close to those of the Pyrenees. The estimation of this uphill shift corresponds to an increase of +1.3 °C in 30 years, which led to a distribution change towards the top of the mountains for 16 mountain butterfly species (considering an average altitude of +212 m). The study of Wilson *et al.* (2005) gives a clearly more dramatic

figure than the simple extrapolation of the uphill shift of 75 m to 150 m estimated based on the temperature increase of 0.74 °C (see IPCC 2007). The reproductive success of insect populations is not only driven by temperature but also by water exchanges, by resource availability and by microclimatic considerations (e.g., slope effects increasing with altitude). The temperature increase could also lead to abnormal heat waves and drought (Rasmont & Iserbyt 2012).

The future warming estimated to 2–3 °C by Thomas *et al.* (2004, 2006) could lead to a 200–500 m uphill shift for the whole ecosystem during the current century. If these projections are validated in the future, a local extinction of all subalpine and alpine species of bumblebees (e.g. *B. flavidus*, *B. gerstaeckeri*, *B. mendax*, *B. monticola*, *B. mucidus*, *B. pyrenaicus*, *B. sichelii*, *B. wurflenii*; see Iserbyt *et al.* 2008) could be foreseeable in the Eastern Pyrenees. Even currently plentiful bumblebee species (e.g., *B. lucorum*) could be drawn to scarcity or local extinction. In conclusion, the perspectives of a further temperature increase of 2–3 °C is worrying as it could represent a major cause of extinction of mountain fauna in the next decades (Thomas *et al.* 1999, 2004, 2006; Manino *et al.* 2007). The creation of nature reserves could be useless in this context, even if the policy of their delimitation is changed as suggested by Araújo *et al.* (2004). Despite the robustness of plant-pollinator assemblages against disturbances caused by global warming (Hegland *et al.* 2009), it would be impossible to avoid major disruptions in the future.

Acknowledgements. We thank a lot R. Thorp (Davis, California) and R. Shelby (Mons, Belgium) for their help in English edition. We thank the students and colleagues who helped us with the bumblebee sampling: K. Belkheir, L. Blondiau, M. Bouzin, A. Coppée, P. Coppens, E. Delattre, E.-A. Durieux, L. Ghoul, C. Marchetti, D. Michez, R. Moerman, B. Namur, C. Parys, O. Ponchau, A. Séché, M. Terzo, M. Vandenberg, and S. Viart. We thank X. Simon for his help in the composition of the article. We thank the “Centre Départemental des Pyrénées-Orientales de Météo France” (Miss C. Bonay) who gave us access to the climatic data of the Sainte-Léocadie meteorological station. This research was funded by the Mairie d’Eyne (Mayor A. Bousquet), the Réserve Naturelle d’Eyne (M. Baracetti, R. Staats) and the National Funds for Scientific Research in Belgium (F.R.S.-FNRS). We also thank Prof. F.J. Ortiz-Sanchez (Almeria, Spain) and two anonymous referees for constructive comments. This paper is a contribution to the European Community’s Seventh Framework Programme (FP7/2007-2013) under grant agreement no 244090, STEP Project (Status and Trends of European Pollinators, www.step-project.net).

References

- Alford D.V. 1969. A study of the hibernation of bumblebees (Hymenoptera: Bombidae) in Southern England. *Journal of animal Ecology* **38**: 149–170.

Alford D. V. 1975. *Bumblebees*. Davis-Poynter, London.

Amiet F. 1996. *Insecta Helvetica*, 12: *Hymenoptera Apidae*, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, die Gattungen *Apis*, *Bombus* und *Psithyrus*. Schweizerischen Entomologischen Gesellschaft, Neuchatel.

Araújo M. B., Cabeza M., Thuillier W., Hannah L., Williams P. H. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10: 1618-1626.

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.

Bessemoulin P., Bourdette N., Courtier P., Manach J. 2004. La canicule d'août 2003 en France et en Europe. *La Météorologie* 46: 25-33.

Bowers M. A. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66: 914-927.



Figure 2

The first author collecting in a hayfield rich in *Rhinanthus pumilus*, near Eyne. **A**, Mid July 1999 during a damp year; **B**, Mid July 2006 during a hot, dry year (Photos P. Rasmont).

- Butler C.G. 1951.** *Annual Report*, Bee Department, Rothampstead Experimental Station, Rothampstead.
- Cane J.H., Minckley R., Kervin L., Roulston T. 2005.** Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: the bees of *Larrea tridentate*. *Biological Journal of the Linnean Society* **85**: 319-329.
- Cartar R.V., Dill L.M. 1991.** Costs of energy shortfall for bumble bee colonies: predation, social parasitism, and brood development. *Canadian entomologist* **123**: 283-293.
- Carvell C., Roy D.B., Smart S.M., Pywell R.F., Preston C.D., Goulson D. 2006.** Declines in forage availability for bumblebees at a national scale. *Biological Conservation* **132**: 481-489.
- Cederberg B., Svensson Bo G., Bergström G., Appelgren M., Groth I. 1984.** Male marking Pheromones in North European Cuckoo Bumble Bees *Psithyrus* (Hymenoptera, Apidae). *Nova Acta Regiae Societatis Scientiarum Upsaliensis* **3**: 161-166.
- Delmas R. 1976.** Contribution à l'étude de la faune française des Bombidae (Hymenoptera, Apoidea, Bombidae). *Annales de la Société entomologique de France (N.S.)* **12**: 247-290.
- Dennis R.L.H. 1993.** *Butterflies and climate change*. Manchester University Press, Manchester.
- Dylewska M., Bak J. 2005.** Apiformes (Hymenoptera, Apoidea) of the Eysogóry Mountains and adjacent area. *Acta zoologica cracoviensis*, **48B**(1-2): 145-179.
- Emberger L. 1930.** Sur une formule applicable en géographie botanique. *Comptes rendus à l'Académie des Sciences* **191**: 389-390.
- Evans K.L., Warren P.H., Gaston K.J. 2005.** Species-Energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* **80**: 1-25.
- Franco A.M.A., Hill J.K., Kitschke C., Collingham Y.C., Roy D.B., Foxs R., Huntley B., Thomas C.D. 2006.** Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12**: 1545-1553.
- Goulson D. 2004.** *Bumblebees. Their Behavior and Ecology*. Oxford University Press, New York.
- Goulson D., Hanley M.E., Darvill B., Ellis J.S., Knight M.E. 2005.** Causes of rarity in bumblebees. *Biological Conservation* **122**: 1-8.
- Goulson D., Lye G.C., Darvill B. 2008a.** Decline and conservation of bumblebees. *Annual review of entomology* **53**: 191-208.
- Goulson D., Lye G.C., Darvill B. 2008b.** Diet breadth, coexistence and rarity in bumblebees. *Biodiversity and Conservation* **17**: 3269-3288.
- Haas A. 1949.** Arttypische Flugbahnen von Hummelmännchen. *Zeitschrift für vergleichende Physiologie* **31**: 281-307.
- Hegland S.J., Nielsen A., Lázaro A., Bjerknes A.-L., Totland Ø. 2009.** How does climate warming affect plant-pollinator interactions? *Ecology Letters* **12**: 184-195.
- Heinrich B. 1979.** *Bumblebee economics*. Cambridge University Press, Cambridge MA.
- Hobbs G.A. 1964.** Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. I. Subgenus *Alpinobombus* Skorikov. *Canadian Entomologist* **96**: 1465-7470.
- Hobbs G.A. 1965.** Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. II. Subgenus *Bombias* Robt. *Canadian Entomologist* **97**: 120-128.
- Hobbs G.A. 1968.** Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. VII. Subgenus *Bombus*. *Canadian Entomologist* **100**: 150-164.
- Hufy A. 2001.** *Introduction à la climatologie*. De Boeck Université, Bruxelles.
- Hurlbert S.H. 1971.** The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-586.
- IPCC 2007.** *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. (eds Pachauri R.K., Reisinger A.), IPCC, Geneva, Switzerland.
- Iserbyt S. 2009a.** La faune des bourdons (Hymenoptera : Apidae) du Parc National des Pyrénées occidentales et des zones adjacentes. *Annales de la Société entomologique de France (N.S.)* **45**: 217-244.
- Iserbyt S. 2009b.** *Ecologie des bourdons montagnards (Hymenoptera, Apidae) : topographie, biotopes, climat*. Thèse de doctorat, Université de Mons, Mons, 274 p.
- Iserbyt S., Dufrière M., Rasmont P. 2009.** Les facteurs explicatifs de la structure de la communauté des bourdons (Hymenoptera : Apidae) de la vallée d'Eyne (France, Pyrénées-Orientales) in: **Iserbyt S. 2009b.** *Ecologie des bourdons montagnards (Hymenoptera, Apidae) : topographie, biotopes, climat*. Thèse de doctorat, Université de Mons, Mons, 274 p.
- 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 (N.S.)* **44**: 211-241.
- Kneitel J.M., Chase J.M. 2004.** Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**: 69-80.
- Kosior A., Celary W., Solarz W., Rasmont P., Fijał J., Król W., Witkowski Z., Iserbyt S. 2008.** Long-term changes in the species composition and distribution of Bombini (Apidae) in Cracow since the mid 1850s. *Annales de la société entomologique de France (N.S.)* **44**: 393-407.
- Kruseman G. 1958.** Notes sur les bourdons pyrénéens du genre *Bombus* dans les collections néerlandaises. *Beaufortia* **6**: 161-170.
- Legendre P., Legendre L. 1998.** *Numerical Ecology*. Second English edition, Elsevier Science BV, Amsterdam.
- Løken A. 1973.** Studies on Scandinavian Bumble Bees (Hymenoptera, Apidae). *Norsk entomologisk Tidsskrift* **20**: 1-218.
- Lye G.C., Park K., Osborne J., Holland J., Goulson D. 2009.** Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation* **142**: 2023-2032.
- MacDonald M.A. 2001.** The colonization of northern Scotland by *Bombus terrestris* (L.) and *B. lapidarius* (L.) (Hym., Apidae), and the possible role of climate change. *Entomologist's Monthly Magazine* **137**: 1-13.
- Manino A., Patetta A., Porporato M., Quaranta M., Intoppa F., Piazza M., Frilli F. 2007.** Bumblebees (*Bombus* Latreille, 1802) distribution in high mountains and global warming. *Redia* **90**: 125-129.
- Météo France 2009.** *Statistiques inter-annuelles de 1998 à 2008 – Ste-Léocadie (66)*. Météo France, Perpignan.
- Minckley R.L., Cane J.H., Kervin L., Roulston T.H. 1999.** Spatial predictability and resource specialization of bees (Hymenoptera : Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society* **67**: 119-147.
- Nisbet G.E. 2005.** A comparison of the phenology and ecology of bumblebees, *Bombus* spp., (Hym., Apidae) in the Central Highlands of Scotland. *Entomologist's Monthly Magazine* **141**: 69-92.
- Obeso J.R. 1992.** Geographic distribution and community structure of bumblebees in the northern Iberian peninsula. *Oecologia* **89**: 244-252.
- Oertli S., Müller A., Dorn, S. 2005.** Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera : Apoidea : Apiformes). *European Journal of Entomology* **102**: 53-63.

- Pekkarinen A. 1979.** Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica* **158**: 1-60.
- Pekkarinen A. 1984.** Resource partitioning and coexistence in bumblebees (Hymenoptera, Bombinae). *Annales Entomologici Fennici* **50**: 97-107.
- Pelletier L. 2003.** *Facteurs affectant le succès reproducteur des bourdons en milieu naturel*. Thèse de doctorat, Université Laval, Faculté des Sciences et Génie, Québec, 170 p.
- Pepin N., Kidd D. M. 2006.** Spatial temperature variation in the Eastern Pyrenees. *Weather* **61**: 300-310.
- Pérez J. 1879.** Contribution à la faune des Apiaires de France. *Actes de la Société Linnéenne de Bordeaux* **33**: 119-229.
- Ponchau O., Iserbyt S., Verhaeghe J.-C., Rasmont P. 2006.** Is the caste-ratio of the oligolectic bumblebee *Bombus gerstaeckeri* Morawitz (Hymenoptera: Apidae) biased to queens? *Annales de la Société entomologique de France* (N.S.) **42**: 207-215.
- Pounds J. A., Bustamante M. R., Coloma L. A., Consuegra J. A., Fogden M. P. L., Foster P. N., La Marca E., Masters K. L., Merino-Viteri A., Puschendorf R., Ron S. R., Sánchez-Azofeifa G. A., Still C. J., Young B. E. 2006.** Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**: 161-167.
- R, Development Core Team R 2005.** *A language and environment for statistical computing 2.1.1*, R Foundation for statistical computing (<http://www.r-project.org>), Vienna, Austria.
- Ranta E., Vepsäläinen K. 1981.** Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos* **36**: 28-34.
- Rasmont P. 1988.** *Monographie écologique et zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae)*. Thèse de doctorat, Faculté des Sciences agronomiques de Gembloux, 309 p. + LXII
- Rasmont P. 1989.** Centres de richesse et centres de pauvreté de la faune des Bourdons de France (Hymenoptera, Apidae). Théorie d'Inouye contre théorie de Ranta & Vepsäläinen, p. 215-225 in: **de Beaufort J., Maurin H. (eds.)**. *L'utilisation des Inventaires informatisés d'Invertébrés pour l'Identification et la Surveillance d'Espaces de grand Intérêt faunistique*. Secrétariat de la Faune et de la Flore, Paris.
- Rasmont P., Barbier Y., Pauly A. 1990.** Faunistique comparée des Hyménoptères Apoïdes de deux terriils du Hainaut occidental. *Notes fauniques de Gembloux* **21**: 39-58.
- Rasmont P., Durieux E.-A., Iserbyt S., Baracetti M. 2000.** Why are there so many bumblebees species in Eynne (France, Pyrénées-Orientales, Cerdagne)? p. 83-92 in: **Sommeijer M. J., de Ruijter A. (eds.)**. Proceedings of the first Specialists' Meeting on "Insect Pollination in Greenhouses", Universiteit Utrecht, Soesterberg.
- Rasmont P., Ebmer A., Banaszak J., Zanden G. van der 1995.** Hymenoptera Apoidea Gallica. Liste taxonomique des abeilles de France, de Belgique, de Suisse et du Grand-Duché de Luxembourg. *Bulletin de la Société Entomologique de France* **100**: 1-98.
- Rasmont P., Iserbyt S. 2012.** The Bumblebees Scarcity Syndrome: Are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: *Bombus*)? *Annales de la société entomologique de France* (N.S.) **48(3-4)**: 369-374.
- Rasmont P., Pauly A., Terzo M., Patiny S., Michez D., Iserbyt S., Barbier Y., Haubruge E. 2005.** *The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France*. Food and Agriculture Organisation, Roma, 18 p.
- Richards K. W. 1973.** Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schönherr at Lake Hazen, Northwest Territories (Hymenoptera: Bombini). *Quaestiones Entomologicae* **9**: 115-157.
- Saville N. M., Dramstad W. E., Fry G. L. A., Corbet S. A. 1997.** Bumblebees movement in a fragmented agricultural landscape. *Agriculture, Ecosystems & Environment* **61**: 145-154.
- Siegel S., Castellan N. J. 1988.** *Nonparametric statistics for the Behavioral Science*. McGraw-Hill Book Company, Singapore.
- Teräs I. 1985.** Food plants and flower visits of bumblebees (*Bombus*: Hymenoptera, Apidae) in southern Finland. *Acta Zoologica Fennica* **179**: 1-120.
- Thomas C. D., Franco A. M. A., Hill J. K. 2006.** Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution* **21**: 415-416.
- Thomas J. A., Rose R. J., Clarke R. T., Thomas C. D., Webb N. R. 1999.** Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology* **13**: 55-64.
- Thomas C. D., Cameron A., Green R. E., Bakkenes M., Beaumont L. J., Collingham Y. C., Erasmus B. F. N., de Siqueira M. F., Grainger A., Hannah L., Hughes L., Huntley B., van Jaarsveld A. S., Midgley G. F., Miles L., Ortega-Huerta M. A., Peterson A. T., Phillips O. L., Williams S. E. 2004.** Extinction risk from climate change. *Nature* **427**: 145-148.
- Uvarov B. P. 1931.** Insects and climate. *Transactions of the Royal Entomological Society of London* **79**: 1-247.
- Veech J. A., Crist T. O. 2007.** Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology & Biogeography* **16**: 650-656.
- Velthuis H. H. W., van Doorn A. 2006.** A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie* **37**: 421-451.
- Westphal C., Steffan-Dewenter I., Tscharntke T. 2006.** Bumblebees experience landscape at different spatial scales: possible implications for coexistence. *Oecologia* **149**: 289-300.
- Williams P. H. 1986.** Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* **67**: 50-61.
- Williams P. H. 1989.** Why are there so many species of bumblebees at Dungeness. *Botanical Journal of the Linnean Society* **101**: 31-44.
- Williams P. H. 1991.** The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum Natural History - Entomology* **60(1)**: 1-204.
- Williams P. H., Araújo M. B., Rasmont P. 2007.** Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation* **138**: 493-505.
- Williams P. H., Cameron S. A., Hines H. M., Cederberg B., Rasmont P. 2008.** A simplified subgeneric classification of the bumblebees (genus *Bombus*). *Apidologie* **39**: 46-74.
- Williams P. H., Colla S., Xie Z. 2009.** Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents. *Conservation Biology* **23(4)**: 931-40.
- Williams P. H., Osborne J. L. 2009.** Bumblebee vulnerability and conservation world-wide. *Apidologie* **40**: 367-387.
- Wilson R. J., Gutiérrez D., Gutiérrez J., Martínez M. D., Agudo R., Monserrat V. J. 2005.** Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* **8**: 1138-1146.
- Xie Z., Williams P. H., Tang Y. 2008.** The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation* **12**: 695-703.