SITE CONSTANCY OF BUMBLEBEES (Hymenoptera: Apiformes: *Bombus* Latr.) IN THE HABITATS OF TWO FOREST SUCCESSIONAL SERIES OF THE WESTERN CARPATHIANS

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S u m m a r y

Site constancy of bumblebees in five habitat types of alder-swamp forest developmental (successional) series and six habitat types of Carpathian beech forest series in the Western Carpathians, NE Poland was studied. Bumblebees from the alder series were more constant in the foraging sites, where they were marked (7.0% of all marked bumblebees), and spread to other sites to a lesser extent (5.3%). A different pattern was observed in the beech series. The bumblebees were less constant to their original sites (5.6%) and spread to other sites (8.5%) to a higher extent. Quantitative contributions of bumblebees caught during the first day and those caught during the second and third days after marking were 2 : 6 : 1 in the alder series and 2 : 7 : 3 in the beech series. The higher percentage of dispersed bumblebees in the beech series indicated subordination of bumblebees to nutritional attractiveness (profusely blooming flowering vegetation) of those sites.

Keywords: *Bombus*, bumblebees, site constancy, alder-swamp successional series, beech successional series, Western Carpathians Mts.

INTRODUCTION

Habitat use of bumblebees was studied in two aspects of the habitats: nutritional attractiveness and attractiveness for nesting. The former aspect was indicated (mostly) as constancy in visiting the plant species (Osborne et al. 1999, Osborne & Williams 2001). In different habitat patches, very high fidelity (86-88% of all observed bumblebee individuals) to visited forage plants was found. Pollen analysis of pollen loads and direct observations of foraging showed high (1 species visited) or quite high (3-4 species visited) flower constancy, selected by 84% of the observed bumblebees (Pawlikowski 1992, 1993).

The latter aspect is correlated with the former through the spatial range of foraging flights from nesting sites. It was found that 70-100% of the observed bumblebee workers explored the environment within 1000 m from a nesting site. The rest of them did not fly any further than 1750 m away from a nest (Goulson 2003, Osborne et al. 1999, Walter-Hellwig & Frankl 2000, 2000a). Also Saville et al. (1997) and Dramstad (1996) demonstrated a considerable dispersion of marked bumblebees from their nests.

Less attention has been paid in the previous studies to the constancy of bumblebees to communities of forage plants in a

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Table 1

Study sites (200-400 m^2) of this study in the alder-swamp forest series and the Carpathian beech forest series in the Western Bieszczady Mts.

Location (Potential vegetation)	Site	Altitude [m]	Habitat
Wetlina (alder-swamp forest of *Circaea-Alnus*)	OG	700	alder-swamp forest *Alnus incana carpaticum*
	OK	700	ecotone between the alder-swamp forest and the meadow
	OM	700	wet meadow with *Valeriana*, *Carex* and *Petasites*
	OO	725	drained meadow with *Agrostis vulgaris* and *Centaurea jacea*
	OP	700	wet pasture with *Mentha* and *Juncus*
Przełęcz Wyżna (Carpathian beech forest of *Fagus carpaticum*)	BU	850	Carpathian beech forest *Fagus carpaticum* of poor variant
	BS	860	70-year-old pine monoculture
	BK	850	ecotone between the Carpathian beech forest and the meadow
	BN	930	dry meadow with *Stellaria*, *Deschampsia cespitosa*, *Agrostis vulgaris* and *Centaurea jacea*
	BM	950	mixed meadow with *Nardus stricta* and Fabaceae
	BP	880	pasture with *Festuca* and *Cynosurus*

complex of different neighbouring biocenoses. The aim of the present paper was to investigate the constancy of bumblebees to communities of forage plants from complexes of forest biocenoses representing typical developmental series, i.e. alder and beech wood in the Bieszczady range in the Polish part of the Western Carpathians.

MATERIALS AND METHODS

The research was carried out in the third week of August 1984 at 11 study sites of two succession series of plant communities: the alder series in Wetlin and the beech series in Brzegi Górne in the Wyżnia Mountain Pass (Fig. 1). The alder series included 5 study sites and the beech series included 6 study sites (Table 1). The sites of both series were selected within 1000-1500 m of each other due to the distance of optimal flights of bumblebees, as well as due to the short time required when visiting them during the observations. At the same time, sites of the alder series were scattered within 500 m, and sites of the beech series within 750 m. The distances between the sites are compared in the map (Fig. 1). This setup allowed unlimited flights of bumblebees between all sites within a series. Special care was taken to conduct the studies under similar meteorological conditions.

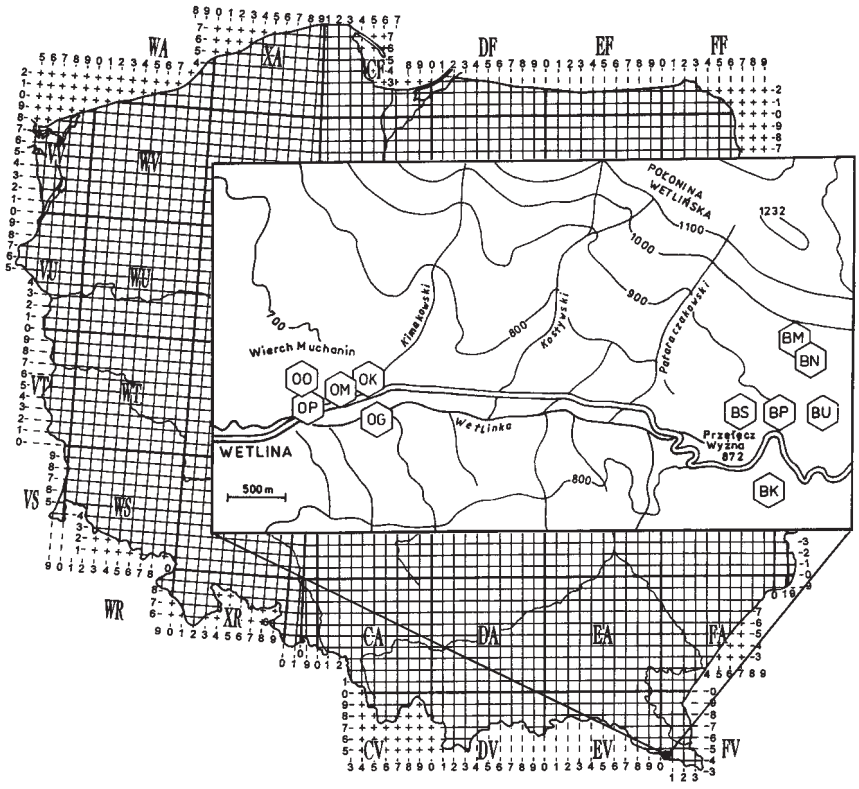

Fig. 1. Study sites in NE Poland, Western Carpathians (with the UTM grid system).

The research in the beech series was conducted over 4 days (21-24.08.1984) and in the alder series over 3 days (25--27.08.1984). The research team consisted of 4-5 persons, which enabled the continuation of studies simultaneously in two groups. In order to investigate the penetration by bumblebees into substitute communities of a given series, flights of wild-caught individuals from respective species were registered three times during the day: at 10.00-11.00 a.m., 1.00--2.00 p.m. and 4.00-5.00 p.m. MET, with an air temperature of 14-20°C, air humidity of 65-94% and changeable cloudiness and wind. Bumblebees were caught on the first day from flowers during a walk of about 20 minutes. Captured bumblebees were identified by species level, their gender was recorded as well as the trapping region and the forage plants on which they were caught. Each specimen was then marked on the thorax and/or abdomen (according to Osborne & Williams 2001) with red nitro paint and was released. Altogether, 901 bumblebees were marked; 398 at the sites from the alder series and 503 at the sites from the beech series (Table 2). Marked bumblebees were recaptured (together with other non-marked bumblebees) during repeated observations at subsequent dates. At the same site, at which bumblebees were marked, three classes of repeated observations were considered: on the first day (5-10 hours from the moment they were marked and released), on the second day and on the third day. Differences between bumblebee frequency values in habitat

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Table 2

Bumblebees recorded and marked at each study site of the alder-swamp forest series and the Carpathian beech forest series (according to Table 1) and the plants that the bees visited.

Plant species	Study site										
	OG	OK	OM	OO	OP	BU	BS	BK	BN	BM	BP
Campanula patula L.	-	-	-	-	-	-	-	-	1	-	-
Carduus acanthoides L.	-	-	1	-	-	-	-	-	-	-	-
Carduus personata (L.)	5	-	-	-	-	-	-	-	-	-	-
Centaurea jacea L.	-	5	9	44	8	-	1	3	21	16	9
Cirsium arvense (L.)	-	-	-	-	-	-	-	-	6	20	16
Cirsium oleraceum (L.)	21	1	-	-	-	-	-	-	-	-	-
Cirsium palustre (L.)	-	27	-	-	-	-	10	-	-	37	7
Cirsium vulgare (Savi)	-	1	1	-	-	-	-	-	-	2	-
Epilobium angustifolium L.	-	-	-	-	-	-	6	-	-	-	-
Euphrasia rostkoviana Hayne	-	2	2	8	22	-	-	4	29	6	64
Filipendula ulmaria (L.)	1	1	-	-	-	-	-	-	-	-	-
Galeopsis speciosa Mill.	1	-	-	-	-	-	-	-	-	-	-
Gentiana asclepiadea L.	-	-	-	-	5	-	7	22	4	3	-
Hypericum maculatum Crantz	-	-	2	1	2	-	28	5	1	5	1
Hypericum perforatum L.	-	-	-	-	-	-	-	-	-	2	-
Impatiens noli-tangere L.	20	-	-	-	-	-	-	1	-	-	-
Knautia arvensis (L.)	-	1	4	-	1	-	1	-	1	1	-
Lathyrus pratensis L.	-	3	-	-	-	-	-	-	-	-	-
Leontodon hispidus L.	-	-	-	2	-	-	-	-	-	-	-
Lotus corniculatus L.	-	-	-	7	-	-	-	-	1	-	10
Mentha arvensis L.	-	-	2	-	-	-	-	-	-	-	-
Mentha longifolia (L.)	-	-	4	-	-	-	-	-	-	-	-
Odontites serotina (Lam.)	-	27	4	-	-	-	-	-	-	-	-
Ononis arvensis L.	-	-	5	7	2	-	-	-	-	-	-
Prenanthes purpurea L.	1	-	-	-	-	-	-	-	-	-	-
Prunella vulgaris Huds.	-	-	-	-	-	-	-	3	-	-	-
Rubus idaeus L.	-	-	-	-	-	-	1	-	-	-	-
Rubus sp.	-	-	-	-	-	8	21	-	1	1	-
Salvia glutinosa L.	19	-	-	-	-	-	-	-	-	-	-
Satureja vulgaris L.	-	3	8	53	31	-	-	-	-	-	-
Stachys palustris L.	-	2	8	-	-	-	5	-	-	1	-
Stachys sylvatica L.	2	-	-	-	-	-	2	-	-	-	-
Thymus pulegioides L.	-	-	-	-	1	-	-	7	22	4	1
Trifolium hybridum L.	-	2	3	-	-	-	-	-	-	-	-
Trifolium medium L.	-	1	1	5	1	-	-	1	6	-	1
Trifolium pratense L.	-	-	4	4	-	-	-	-	-	-	2
Trifolium repens L.	-	1	-	-	-	-	-	2	-	1	1
Vaccinium myrtillus L.	-	-	-	-	-	-	-	-	1	-	-
Vicia sepium L.	-	-	-	-	-	-	1	-	-	-	-
Others	-	4	-	4	1	36	-	2	7	-	14
The total numbers of bumblebee specimens	70	61	58	135	74	44	83	50	101	99	126
The number of visited plant species	8	15	15	10	10	2	11	10	13	13	11
	31					25					

Table 3

Site constancy of the marked bumblebees (according to Table 1).

Species (No. of individuals)	Study site										
	OG	OK	OM	OO	OP	BU	BS	BK	BN	BM	BP
Bombus lucorum (L.) (618)	3Mx 1Myc 20Wx 1Wya	1Mx 22Wx 3Wyb 2Wz	1Mx 22Wx 3Wz	21Mx 1Myb 1Mz 41Wx 1Wya 3Wz	2Mx 34Wx 1Wz	1Qx 7Mx 1Mz 26Wx 1Wya 4Wyb 1Wz	7Mx 55Wx 1Wya 3Wz	13Mx 1Mz 28Wx 2Wz	1Qx 29Mx 3Mya 6Myc 5Mz 43Wx 6Wz	34Mx 2Myb 3Mz 38Wx 9Wz	6Mx 3Myb 2Mz 82Wx 2Wya 2Wyb 7Wz
Bombus terrestris (L.) (124)	2Mx 5Wx 1Wya 1Wyb 1Wz	8Wx 3Wyb	1Mx 9Wx	2Mx 2Myb 30Wx 3Wyb 3Wz	18Wx 1Wyb 1Wz	-	2Wx 1Mx 1Mz	-	2Wx 1Wz	9Wx 1Mx	14Wx 1Mx 1Myb
Bombus pascuorum (Scop.) (55)	1Mx 5Wx 1Wz	15Wx	15Wx 1Wyb	5Wx 2Wz	3Wx	-	6Wx	-	-	1Wx	-
Bombus hortorum (L.) (38)	15Wx 3Wya 2Wyc 1Wz	-	5Wx	4Wx 1Wz	5Wx 1Wyb	-	-	-	1Wx	-	-
Bombus mastrucatus Gerst. -31	5Wx	-	-	10Wx 1Wyb 1Wz	1Wx	-	2Wx 1Wyb	2Mx 3Wx	1Wx	-	3Wx 1Wz
Bombus lapidarius (L.) (11)	-	4Wx 1Wyb	Mx	2Wx	1Mx 2Wx	-	-	-	-	-	-
Bombus pratorum (L.) (11)	1Mx	-	-	-	-	2Wx	1Mya 1Wyb	1Wx	-	1Wx	1Wx
Bombus hypnorum (L.) (7)	1Mx	-	-	-	-	-	2Wx	-	1Wx 1Mx	1Mx	1Mx
Bombus ruderarius (Mûll.) (5)	-	-	-	1Wx	3Wx 1Wyb	-	-	-	-	-	-
Bombus humilis Ill. (1)	-	-	-	-	-	-	-	-	1Mx	-	-
Marked specimens	58x 9y 3z	52x 7y 2z	54x 1y 3z	116x 8y 11z	69x 8y 11z	37x 5y 2z	75x 4y 4z	47x 0y 3z	80x 9y 12z	85x 2y 12z	108x 8y 10z
(Total number)	(70)	(61)	(58)	(135)	(74)	(44)	(83)	(50)	(101)	(99)	(126)
	(398)					(503)					

Q = queen
W = worker
M = male
x = not reobserved in the area after marking
y = reobserved in the area after marking: a = first day (5-10 h), b = second day, c = third day
z = reobserved in another area after marking (Tab. 3)

types of developmental series were tested by a Pearson test (χ^2).

RESULTS

In both series, bumblebees visited 33 flowering plant species, of which 31 were in the alder series, and 25 were in the beech series. In both habitat types, plant species from the families *Asteraceae*, *Lamiaceae* and *Fabaceae* were particularly favoured (Table 2). In total 10 bumblebee species were recorded, the most common ones be-

Table 4

Bumblebees reobserved in another area after marking at the study sites of the alder-swamp forest series and the Carpathian beech forest series (according to Table 1). Habitats where specimens were marked are in bold.

Species	Alder-swamp forest series	Carpathian beech forest series
Bombus lucorum (L.)	1W OK –› OMa 1W OK –› OOb 1W OM –› OGb 1W OM –› OPa 1W OM –› OPb 1W OO –› OOab –› OGc 1W OO –› OPa 1W OO –› OPa –› OMbc 1W OP –› OOab 1M OO –› OGa	1W BK –› BMb 1W BK –› BSab 2W BN –› BMab 1W BN –› BPab 2W BN –› BUb 2W BM –› BKab 1W BM –› BNb 1W BM –› BPab 5W BM –› BSabc 1W BP –› BNa 4W BP –› BMab 1W BP –› BSab 1W BP –› BUb 1W BS –› BNab 1W BS –› BPa 1W BU –› BNa 1M BK –› BNab 2M BN –› BNab –› BKac 1M BN –› BKb 3M BN –› BMab 2M BM –› BNab 1M BM –› BUab 1M BP –› BNab 1M BP –› BUa –› BKb 1M BU –› BNab
Bombus terrestris (L.)	1W OG –› OMab 1W OO –› OKab –› OOc 1W OO –› OMb 1W OO –› OPb 1W OP –› OOab	1W BN –› BUa –› BPab 2W BS –› BPa –› BSab
Bombus pascuorum (Scop.)	1W OG –› OKab 2W OO –› OKa	
Bombus hortorum (L.)	1W OG –› OMa 1W OO –› OGbc	
Bombus mastrucatus Gerst.	1W OO –› OPb	1W BP –› BSb
Marked specimens	21	43

W = worker
M = male
–› reobserved in another area after marking (original site in bold):
a = 1st day, b = 2nd day, c = 3rd day

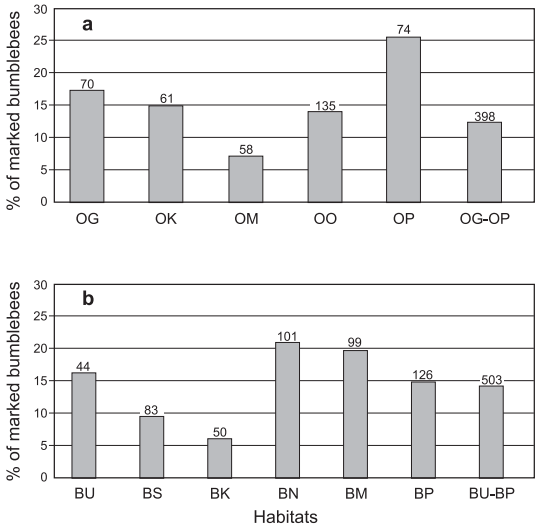

Fig. 2. Percentages of reobserved bumblebees marked at each study site of alder-swamp forest series (a) and the Carpathian beech forest series (b) (as in Table 1). Figures above the bars show the numbers of marked bumblebees. Differences between bumblebee frequency values in habitat types of two forest successional series with the significance level P 0.01 (according to Pearson test).

ing *Bombus lucorum*, *Bombus terrestris* and *Bombus pascuorum*. From among all species, as many as 9 of the species were encountered in both succession series (Table 3). In the alder series 12.3% of the 398 marked bumblebees and in the beech series 14.1% of the 503 marked bumblebees were re-observed.

The way the bumblebees spread within the sites of the alder and beech series is shown in Table 4. Bumblebees spreading to different sites in the alder series belonged to 5 species and in the beech series to 3 species. In the former, 48% of the individuals were *Bombus lucorum* and 91% in the latter.

Bumblebees from the alder series were more constant to their sites, where they were marked (7.0% of all marked bumblebees), and spread to other sites to a lesser extent (5.3%). A different pattern was observed in the beech series. The bumblebees were less constant to their original sites (5.6%) and spread to other sites of this series (8.5%) to a higher extent.

Site-constant bumblebees were observed most frequently during the second day after marking. Quantitative contributions of bumblebees caught during the first day and those caught during the second and third days after marking were 2 : 6 : 1 in the alder series and 2 : 7 : 3 in the beech series.

DISCUSSION

The research to date indicates high constancy of bumblebees to foraging sites, particularly with profusely flowering plants. Saville and others (1997) re-observed up to 50% of marked bumblebees at the same site and in quest for nutritionally attractive sites the bees covered a distances of up to two kilometres. The tendency of bumblebees to travel relatively long distances from their nests in search for food was also observed by Dramstad (1996).

The results of the present study also confirm this tendency. They indicate that the spreading of bumblebees between nutritionally unequal sites depended on the

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degree of dispersion of those sites and is irrespective of their nutritional attractiveness. The studied developmental series had different nutritional attractiveness, which was reflected by the different numbers of marked bumblebees (398 in the alder series and 503 in the beech series) and the percentages of recaptured bumblebees (Fig. 2). At the sites of the beech series, the percentage of recaptured bumblebees (14.1%) was found to be significantly (P 0.01) higher than at the sites of the beech series (12.3%). The percentage was particularly high in meadow habitats. The higher number of dispersed bumblebees observed at more scattered sites of the beech series in relation to the smaller number of dispersed bumblebees at less scattered sites of the alder series would indicate subordination to the above-mentioned relationship.

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WIERNOŚĆ SIEDLISKOWA TRZMIELI (Hymenoptera: Apiformes: *Bombus* Latr.) W DWÓCH LEŚNYCH SUKCESYJNYCH SERIACH Z KARPAT ZACHODNICH

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S t r e s z c z e n i e

Badano rozpraszanie się trzmieli na 5 powierzchniach siedliskowych typów sukcesyjnej serii olszynowej i 6 powierzchniach siedliskowych typów serii buczynowej w Karpatach Zachodnich (Bieszczady Mts, NE Poland). Trzmiele z serii olszynowej były bardziej przywiązane do swoich powierzchni, na których były znakowane (7,0% ogółu znakowanych) i w mniejszym stopniu rozpraszały się na inne powierzchnie siedliskowe (5,3%). Zupełnie odmiennie zachowywały się trzmiele z serii buczynowej. Były one mniej przywiązane do swych powierzchni (5,6%) i w większym stopniu rozpraszały się na inne powierzchnie z tej serii (8,5%). Udziały ilościowe trzmieli odłowionych podczas pierwszego dnia do odłowionych drugiego dnia oraz do odłowionych trzeciego dnia miały się jak 2 : 6 : 1 w serii olszynowej, a 2 : 7 : 3 w serii buczynowej. Zaobserwowana większa liczba rozproszonych trzmieli na bardziej rozproszonych powierzchniach serii buczynowej, a mniejsza liczba rozproszonych trzmieli na mniej rozproszonych powierzchniach serii olszynowej, wskazywała na podporządkowywanie się trzmieli atrakcyjności pokarmowej (obficie kwitnącej roślinności kwiatowej) tych powierzchni.

Słowa kluczowe: *Bombus*, trzmiele, wierność siedliskowa, siedliska serii olszynowej, siedliska serii buczynowej, Karpaty Zachodnie.