

# Ecogeographical patterns in the incidence of brood parasitism in bees

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The percentage of cleptoparasitic species in a fauna of Apoidea decreases from 25–30% at high latitudes to 10–15% in the subtropics. We argue that this pattern should not be explained by an allegedly stronger seasonality at higher latitudes (that would enable parasites to better synchronize with their hosts), but rather by the unpredictability of the climate, and concomitantly host phenology and population size, in (sub)arid climates.

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## INTRODUCTION

The relative number of parasitic species of Hymenoptera is highest in high latitudes all over the world, and is minimal in the tropics and subtropics.

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This general pattern applies to various types of parasitism, and to various groups of Hymenoptera. The phenomenon is reviewed in detail by Wcislo (1981), who concentrated, like we do in the present paper, on bee cleptoparasitism. In high latitudes 25–30% of the bee species are cleptoparasites, against 10–15% or less in tropical and subtropical areas. The females of cleptoparasitic bees lay their eggs in the brood cells of their host species; their larvae kill their host's egg or larva and consume the stored food.

Wcislo (1981) explained the singular distribution of bee parasitism by the strong seasonality of high-latitude climates. This would have a twofold effect on the host-parasite interaction. First, the distribution over time of the host is squeezed into a relatively short period. This temporal concentration of the host would enable its parasites to build up high, stable, populations. Secondly, the brief season would effectively synchronize the ontogeny of host and parasite, permitting the parasite to penetrate optimally the window of susceptibility of the host.

A recent study on a pollinator community in Greece (Petanidou, 1991a, b) has revealed a surprisingly high diversity in Apoidea (Petanidou & Ellis, 1993). Like all mediterranean ecosystems, this one was strongly seasonal (Petanidou *et al.*, 1995), yet showed a relatively poor fauna of parasitic bees. This made us doubt the validity of Wcislo's argument. Moreover, we found that the few parasitic species were strongly concentrated at the start of the insect season, as opposed to what seems to be normal elsewhere. We will argue therefore that not weak seasonality, but rather the precipitation deficit and concomitant climatic unpredictability are the causative factors of the low contribution of cleptoparasites to the total bee fauna.

#### METHODS

Wcislo provided a list of 114 references to faunistic studies from all over the world, showing their provenance with estimated median latitude and the numbers of parasitic and non-parasitic bee species. We added some more studies that came to our attention, bringing the total to 148 bee faunas. Only faunas consisting of at least 70 species were accepted for addition.

Three faunas mentioned by Wcislo were removed from the analysis. A fauna originating from 'Australia and the South Pacific' (# 61 in the Appendix) had to be disregarded as too ill-defined geographically. We also chose to disregard as probably unrepresentative, at least for the purpose of ANOVA, a fauna consisting of two bumble bee species (one parasitic) from Ellesmere Island, high-Arctic Canada (# 1), and a fauna of 13 species (none parasitic) from Delaware, USA (# 6). For the 145 faunas that remained, the percentages of parasitic species (relative to the complete bee fauna), were approximately normally distributed, and were analysed by ANOVA. All faunas were assigned to a regional vegetation type, using the system in the *Times Atlas of the World* (1968, Table 1). Desert vegetations were grouped with steppe vegetations, and tropical rain forests with monsoon forests, leaving altogether ten vegetation classes. For a posteriori comparisons the Tukey-Kramer method was used with a cut-off level of 0.05.

We analysed the phenological pattern of the occurrence of parasitic species in four Palearctic faunas, viz, the one from Greece (Daphní), mentioned

above, another from The Netherlands (Nunspeet), and two on the basis of published data, *viz.*, from NW Germany (Bremen: Alfken, 1913) and Switzerland (Solothurn: Amiet, 1977). We calculated (separately for parasitic and non-parasitic species) the number of species present on any calendar day; the calculations are based on first and last dates of observation, irrespective of year, sex, or eventual caste. Species, observed for a period shorter than 14 days, were arbitrarily assigned a period of activity of 14 days. The resulting values were smoothed by taking the running average (over 14 days).

The material from Daphní, close to Athens, originated from a 30 ha large phrygana (eastern Mediterranean scrub, cf. garrigue or tomillares) plot that had partly been burnt in 1977, but has been protected from grazing and burning since then; it was studied intensely in the period 1983–1987 (Petanidou, 1991a). All material was hand-collected on flowers. A fuller description is given in Petanidou & Ellis (1993). A list of all bee species can be found in Petanidou (1991b).

The site at Nunspeet, in the central part of The Netherlands, consists of used and abandoned meadows, a garden, a large pond and a *Pinus sylvestris* stand (Ellis & Simon Thomas, 1994). By far the most material originated from five Malaise traps that were operated in the period 1975–1983.

We did not attempt to take eventual bivoltinism into account. Alfken (1913) meticulously segregated his observations into distinct generations, which enabled us to study the effect of disregarding this information. We calculated the daily number of species two times: first in the way described above, second while treating separate generations as distinct species. The distribution over time of the percentage of parasitic species turned out to differ significantly (Kolmogorov-Smirnov test,  $P < 0.01$ ), but the differences have no effect on what we wish to demonstrate in the present paper.

## RESULTS

The Appendix lists the raw data provided by Wcislo together with our additional data. As shown in Figure 1, the general correlation between latitude and percentage of parasitic species that was found by Wcislo is amply confirmed. This pattern remains the same when attention is focused on the Palearctic faunas only.

The percentage of parasitic species is not correlated with the total number of species in a fauna ( $r = -0.131$ ,  $P < 0.113$ ).

The distribution of the percentage of parasitic species over the ten climatic types mentioned above is significantly different (ANOVA,  $F = 9.674$ ,  $P < 0.000$ ; only faunas with  $\geq 70$  species included). Post-hoc comparisons showed that the faunas of the mountain vegetation, boreal forest, conifer forest, and broadleaved forest are all significantly different from that of the mediterranean scrub and the tropical rain forest; the fauna of the broadleaf forest moreover differs significantly from that of the steppe. Table 1 gives a list of the vegetation types and the average values of the percentage.

The phenological pattern of the daily percentage of parasitic species in Nunspeet, Bremen and Solothurn is very similar (Fig. 2): the percentage rises sharply to 25–30% as soon as the first non-parasitic species start to appear,

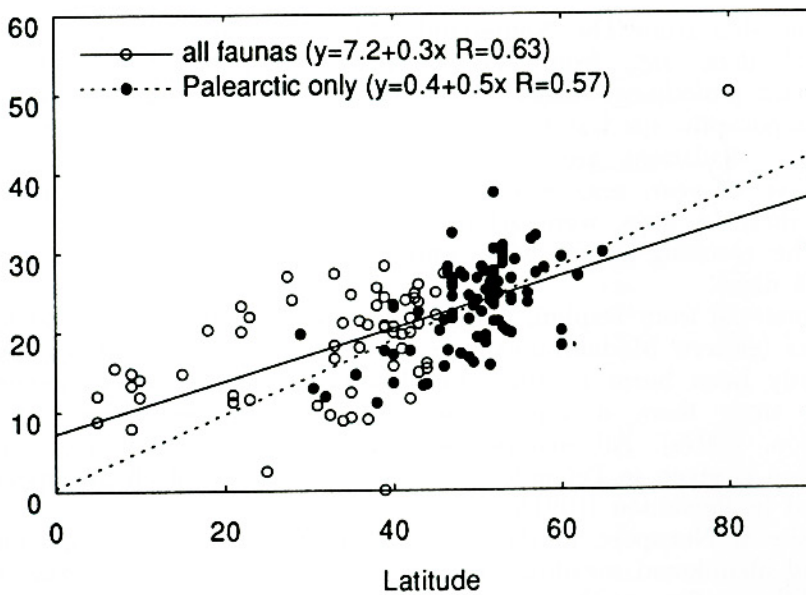


Figure 1. Scatter diagram of the percentages of parasitic species in all faunas and Palearctic faunas (closed circles only) against latitude, with linear regression.

TABLE 1. Major vegetation types (as recognized by the *Times Atlas of the World*, 1968), their corresponding code numbers, and the average percentage of parasitic species in its bee faunas ( $\pm$ SE). (Faunas with <70 species and # 61 excluded; cf. Appendix)

vegetation type	code	av. parasites
mountain vegetation	1	27.0 $\pm$ 5.4
boreal forest ("taiga")	3	22.6 $\pm$ 2.0
conifer forest	4	22.3 $\pm$ 1.7
mixed forest, mid-latitudes	5	24.8 $\pm$ 1.6
broadleaf forest (deciduous)	6	23.5 $\pm$ 0.6
mediterranean scrub	7	14.9 $\pm$ 1.0
prairie (long grass)	8	19.8 $\pm$ 2.8
steppe (short grass) + desert (code 16)	9	17.7 $\pm$ 1.8
tropical rain forest + monsoon forest (code 12)	11	13.6 $\pm$ 1.3
dry tropical forest	13	15.6 $\pm$ 4.4

remains more or less at a constant level, and declines steeply at the end of the season. By contrast, at Daphní (Fig. 2) the initial rise stops at about 20%, then declines somewhat more gradually, and is followed by a later smaller rise. Even more clearly than in the other three faunas, the percentage of parasite species reaches its top level well before the total bee faunal diversity is at its peak.

The maximal values of the daily number of species differ strongly between the four faunas, although the total numbers of species differ much less (Fig. 2). This is caused by a significant difference in the average duration of activity of the bee species in these four faunas ( $F=28.901$ ,  $P < 0.000$ ). These averages are as follows: Bremen 90.6; Solothurn 69.9; Nunspeet 59.9; Daphní 50.7 days; the average of Bremen differs significantly from that of the three

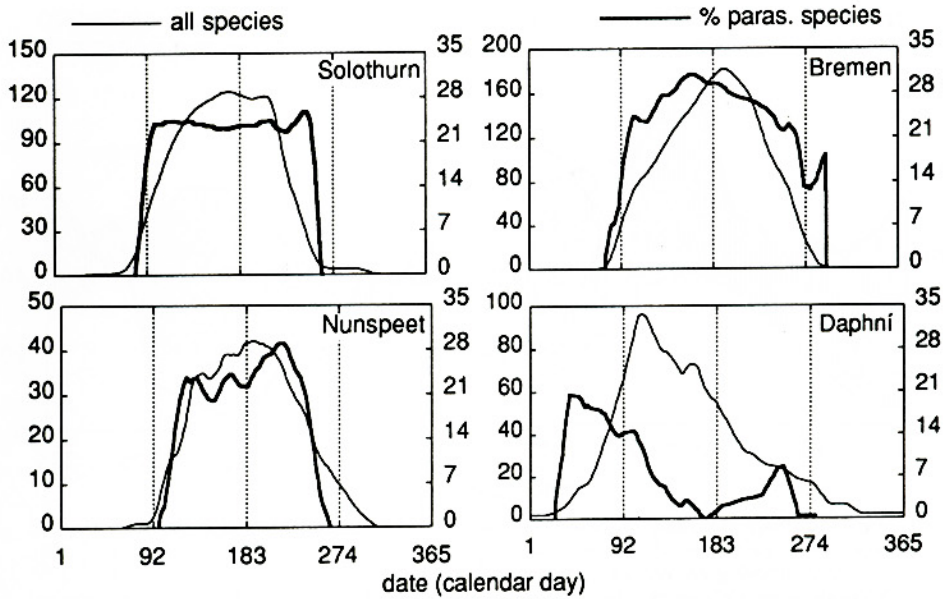


Figure 2. Number of bee species present on any calendar day (thin lines, left axes), and percentage of this value attributable to parasitic species (bold lines, right axes) in Solothurn (Switzerland, total bee fauna 238 species), Bremen (Germany, 273), Nunspeet (The Netherlands, 84) and Daphni (Greece, 262). Data based on Amiet (1977), R.T. Simon Thomas (in prep.), Alfken (1913), and Petanidou (1991b), respectively.

other faunas, and moreover the one from Solothurn is significantly different from that of Daphni. (When the calculation is limited to the non-parasitic species, precisely the same pattern emerges.) Differences like this could result from inadequate sampling of a fauna (too few records per species will lead to underestimation of its period of activity), but because of the size of the faunas (273, 238, 84, and 262 species, respectively) we assume that the differences are essentially genuine.

#### DISCUSSION

The faunas of Nunspeet, Bremen and Solothurn belong to the biomes of broad-leaf forests (type 6) and conifer forests (type 4), i.e. to landscapes with a rather high incidence of parasitism (see Table 1). The Daphni fauna, in contrast, belongs to the low-incidence mediterranean scrub biome (type 7). If indeed the Daphni fauna is representative of the bee faunas of that biome, then the observed phenological patterns may demonstrate how the low percentage of parasitic species comes about. At the start of the season the incidence of parasitism is close to what we see elsewhere, but further in the season the parasitic species are few or none. The period of maximal occurrence of parasite species coincides with the end of the winter-rain period.

Towards the end of spring both the quantity and the regularity of the precipitation decline while the rising temperatures soon start to create an

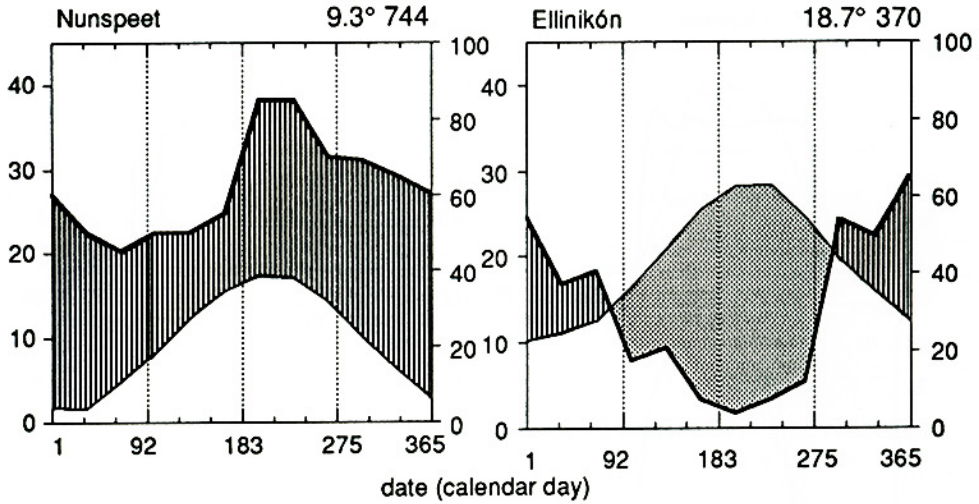


Figure 3. Climate diagrams of Nunspeet, The Netherlands and Ellinikón, close to Daphni, Greece. Data based on the *Climate atlas of The Netherlands* (1972) and Maheras (1983), respectively; drawing conventions according to Walter, Harnickell & Mueller-Dombois (1975), with temperature ( $^{\circ}\text{C}$ ) on the left, and precipitation (mm/month) on the right axis; average yearly temperature and total precipitation on top right.

evaporation excess (Fig. 3). At the peak of the diversity of all bees together (which coincides with the peak of flowering of the vegetation, cf. Petanidou *et al.*, 1995) there is already a distinct rainfall deficit. The majority of the vegetation consists of annual plants that thrive on the rapidly decreasing soil moisture. Variations in precipitation may lead to big differences in abundance of the vegetation and of the flower-visiting fauna; in fact, the coefficient of variation of the monthly rainfall over the last 50 years is above 100 from May to September, and only in December is it less than 50 (based on Maheras, 1983). We hypothesize that the emergence of the parasitic bees is concentrated at the very start of the period of flowering because this is the only period with a relative high degree of predictability of the phenological conditions of the host bee fauna. That bee parasites can indeed have synchronization problems, despite physical proximity to their host, is exemplified by the observation by Wcislo *et al.* (1994) that a climate-induced delay in emergence of a halictid bee caused its parasites to emerge too early.

The strong unpredictability of arid and semi-arid ecosystems has often been described (e.g. Beadle, 1959; Walter, 1968–1973) and we think that we may extend the interpretation of the low incidence of parasitic species in the Mediterranean to that in all more or less xeric ecosystems. Under these circumstances the population sizes of the host species will tend to be erratic in size and time. Moreover, these types of ecosystems are generally the richest in bee species (Michener, 1979; O'Toole & Raw, 1991; Petanidou & Ellis, 1993). This dense species packing will entail small population sizes in general. It may well be that often a potential host population would be simply too small to sustain a parasite population.

In a parallel, yet opposite reasoning, the high species-richness of tropical herbivorous insects has been explained by the stability in time and the diversity of food items (Janzen, 1973). Of course, such explanations are valid only when there is a high degree of specialization; in the case of bee cleptoparasites this is amply indicated (see, for instance, Tengö & Bergström, 1976, 1977; Westrich, 1989). Yet, if species packing would have a very strong effect, this would be difficult to reconcile with the total absence of correlation we found between fauna size and incidence of parasitism, even while allowing for the fact that our data contain much noise.

Mediterranean vegetations are prone to frequent fires, resulting in a strong dynamism of their biotas. It might be argued therefore that the low incidence of cleptoparasitism in the Daphní fauna could rather be attributable to insufficient time of recovery after fire. We rejected this explanation because the time that had elapsed since the last fire (maximally 10 years) was not very short. Margaris (1976) mentions 25–70 years as the interval between natural fires in phrygana. Sabaté & Gracia (1993) stress (albeit for plants) that recovery of the diversity is a fast process; they found that after 33 months the diversity in a French garrigue was at its maximum. In accord with this, the bee fauna of Daphní is, with 262 species on 30 hectares, exceptionally rich. These facts are difficult to reconcile with undersaturation of parasites, although it cannot be excluded that these come in when the diversity is already past its peak. Anyhow, as shown above, the low number of parasites in Daphní fits in with a large-scale pattern.

The unpredictability of the Daphní ecosystem is exacerbated by the relatively short duration of the activity of the individual species; this increases the difficulties for parasites to attack their hosts at the right moment.

It is an interesting speculation that non-parasitic bee species of semi-arid habitats may be subject to a selective pressure to shift their period of activity towards the summer, because this may free them from cleptoparasitic relatives.

Our explanation does not cover the low percentage of parasitic species in tropical regions. The bee faunas of tropical ecosystems are dominated by social species; this is very different from the situation at temperate latitudes, where, at least in terms of species number, solitary species dominate by far. We agree with Roubik (1989) that it might be unjustified to look for a single explanation of the geographical patterns in cleptoparasitism that covers both tropical and temperate regions.

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## APPENDIX

Apoidea faunas with climax vegetation type (according to the *Times Atlas of the World*, cf. Table 1), latitude, total number of Apoidea species and percentage of parasitic species.

# country, locality, etc.	veg. type	latitude	nr. spec.	percent paras.
Nearctic				
1 Canada, Ellesmere Island	2	80	2	50
2 USA, Alabama	4	33	78	17
3 USA, California	7	36	1920	18
4 USA, California, Channel Islands	7	34	91	9
5 USA, Connecticut	6	41.5	205	24
6 USA, Delaware	6	39	13	0
7 USA, Florida	4	28	258	24
8 USA, Florida, Archbold Biological Station	4	27.5	74	27
9 USA, Georgia	4	33	361	18
10 USA, Illinois	8	40	277	23
11 USA, Illinois, Carlinville	8	39	296	24
12 USA, Illinois, Chicago	8	42	171	20
13 USA, Indiana	6	40	206	20
14 USA, Kentucky	6	38	51	25
15 USA, Maine	3	45	199	22
16 USA, Maine, Mount Desert	3	44	111	15
17 USA, Maryland	6	39	135	21
18 USA, Massachusetts	5	42.5	278	25
19 USA, Michigan	5	43	405	24
20 USA, Michigan, George Reserve	5	42.5	174	24
21 USA, Mississippi	6	32.5	116	9
22 USA, Mississippi, Hattiesburg	6	31	102	11
23 USA, Nevada Test Site	9	37	67	9
24 USA, New England, New York & E Canada	6	46	411	27
25 USA, S New England (Mass., Rhode I, Conn.)	6	42	254	22
26 USA, New Hampshire	3	43	143	21
27 USA, New Jersey	6	40	185	16
28 USA, New York	6	43	320	26
29 USA, North Carolina	6	35	520	25
30 USA, Ohio	6	40	189	21
31 USA, Pennsylvania	5	41	183	20
32 USA, Rhode Island	6	41	123	18
33 USA, S Carolina	6	34	71	21
34 USA, Tennessee	6	36	164	21
35 USA, Utah & Idaho, Curlew Valley	9	42	130	12
36 USA, Vermont	3	44	100	16
37 USA, Virginia	6	38	262	23
38 USA, Washington DC	6	39	99	28
39 USA, W Virginia	6	39	112	21
40 USA, Wisconsin	5	45	169	25
41 USA, Wyoming	9	43	653	15
Neotropic				
42 Argentina	9	37	230	21
43 Argentina, Mendoza	9	33	231	27
44 Brasil, Ribeirão Preto	8	21	207	12
45 Chile	7	35	349	9
46 Chile	7	35	73	12
47 Costa Rica	11	10	76	12
48 Cuba	13	22	43	23
49 Cuba	13	22	105	20
50 Jamaica	11	18	69	20
51 Mexico, Estación Biológica Chamela	13	21	241	11
52 Panamá	11	9	353	13
53 Panamá, Barro Colorado Island	11	9	76	8
Oriental region				
54 India, Barrackpore	11	23	73	22

APPENDIX—*continued.*

# country, locality, etc.	veg. type	latitude	nr. spec.	percent paras.
55 India, Burma, Sri Lanka	11	23	287	11
56 Indonesia, Java	11	7	116	16
57 Philippine Islands	11	15	251	15
58 Sri Lanka	11	9	47	15
Afrotropic				
59 Congo Basin	11	5	68	9
60 Nigeria	11	10	135	14
Australian region				
61 Australia & South Pacific	—	25	1920	2
62 New Guinea	11	5	183	12
Palaearctic				
63 Belgium	6	50.5	121	28
64 Belgium	6	51.5	205	24
65 Croatia, Dalmatia	7	43.5	279	13
66 Croatia, Istria	7	45.5	373	20
67 Czech Republic, Erzgebirge	6	50.5	98	22
68 Denmark	6	56	218	25
69 Denmark	6	56	216	24
70 Denmark, Laesø Island	6	57	44	27
71 Finland	3	65	231	30
72 France	6	46	435	16
73 France	6	46	767	21
74 France, N region	6	49.5	362	23
75 France, SW region	6	43	516	22
76 Germany, Baden-Württemberg	6	49	514	25
77 Germany, Berlin	6	52.5	47	21
78 Germany, Bienwald	6	49.5	210	23
79 Germany, Brandenburg	6	52.5	243	25
80 Germany, Bremen	6	53	273	29
81 Germany, E region	6	47	311	24
82 Germany, E region	6	48	274	27
83 Germany, Franken	6	50	407	27
84 Germany, Hiddensee Island	6	54.5	62	29
85 Germany, Kaiserstuhl	6	48	99	17
86 Germany, Klagenfurt I	6	46.5	281	28
87 Germany, Klagenfurt I,II,III	6	46.5	306	27
88 Germany, Klagenfurt II	6	46.5	182	18
89 Germany, Kölner Bucht	6	47	266	27
90 Germany, Leudelsbachtal	6	49	176	22
91 Germany, Lower Harz	6	51.5	152	16
92 Germany, Lower Saxony	6	52	72	38
93 Germany, Mittenwalde	6	52	151	26
94 Germany, Nassau	6	50	224	19
95 Germany, Nassau	6	50	348	27
96 Germany, Oldenburg	6	53	77	29
97 Germany, Pommern	6	54	259	27
98 Germany, Rheinland	6	50	343	24
99 Germany, Tübingen	6	48.5	186	27
100 Germany, Tuniberg	6	49.5	143	16
101 Germany, Uesen & Baden	6	53	146	31
102 Germany, W region	6	51.5	568	26
103 Germany, W region	6	51.5	517	26
104 Greece, Crete	7	35.5	82	15
105 Greece, Daphní	7	38	262	11
106 Iran	9	32	227	12
107 Ireland	6	53	123	30
108 Israel	7	30.5	162	13
109 Italy, Latium	7	42	455	18
110 Italy, Sardinia	7	40	162	14
111 Yugoslavian Macedonia	7	44	224	13

APPENDIX—*continued*

# country, locality, etc.	veg. type	latitude	nr. spec.	percent paras.
112 Latvia	5	58	—	28
113 Netherlands	6	52	322	28
114 Netherlands, Limburg	6	51	261	28
115 Netherlands, Maastricht 1	6	51	86	19
116 Netherlands, Maastricht 2	6	51	111	25
117 Netherlands, Maastricht 3	6	51	77	19
118 Netherlands, Nunspeet	6	52.5	84	26
119 Poland	6	52	377	23
120 Poland, Kampinos National Park	6	52	180	27
121 Poland, NW region	6	54	182	20
122 Poland, Pieniny Mountains	6	54	172	24
123 Poland, Poznan	6	52	132	21
124 Poland, W region	6	47	253	26
125 Poland, W region	6	52	256	24
126 Poland, Wolin National Park	6	53.5	75	20
127 Portugal	7	40	146	17
128 Russia, 'Volgo-Uralensis'	9	60	253	18
129 Russia, Bashkir	9	53	328	20
130 Russia, St. Petersburg	3	60	170	20
131 Scandinavia	3	60	211	29
132 Spain	7	40	1009	23
133 Spain, Canary Islands	7	29	147	20
134 Spain, Ibiza	7	39	74	18
135 Sweden	3	62	212	27
136 Sweden	3	62	—	27
137 Sweden, Aledal	6	57	—	32
138 Sweden, Öland	5	56.5	79	32
139 Switzerland	4	47	—	26
140 Switzerland, Neuchâtel	4	47	261	22
141 Switzerland, National Park	1	47	199	22
142 Switzerland, Solothurn	4	47	238	26
143 Switzerland, Suisse Romande (Alps)	1	47	111	32
144 UK	6	54	285	24
145 UK, Bedfordshire	6	52	158	30
146 UK, Chobham Common	6	51.5	126	24
147 UK, Woking area	6	51.5	126	25
148 Ukraine, Suma, Chernigov & Kiev	9	49	245	17

## Notes

Unless specified, all data are derived from Wcislo (1981). 24, 25: Stubblefield *et al.* (1993). 51: cf. Addendum to Wcislo (1981). 65: Maidl (1922). 66: Graeffe (1902). 67: Müller & Sieber (1929). 76: Westrich (1989). 77: Dathe (1969). 78: Brechtel (1986). 79: Schirmer (1912). 80: Alfken (1913, 1935). 83: Stoeckhert (1933). 85: Kratochwil (1984). 86, 87, 88: Warncke (1981). 90: Westrich (1983). 91: Rudow (1872). 92: Riemann (1988). 93: Hedicke (1922). 95: Wolf (1955). 96: Haeseler (1978). 97: Blüthgen (1919). 98: Aerts (1960). 100: Klug (1965). 101: Höppner (1901). 105: Petanidou (1991b). 109: Comba & Comba (1991). 110: Alfken (1938). 111: Friese (1922). 115, 116, 117: Lefebvre (1983–84). 118: R.T. Simon Thomas (in prep.). 122: Dylewska (1962), Dylewska & Noskiewicz (1963); no data on Apidae. 133: Hohmann *et al.* (1993; incl. subsp.). 134: Hohmann (1984). 142: Amiet (1977). 144: Fitton *et al.* (1978). 146, 147: Guichard (1977); 5 *Bombus* spp., 'probably present', included.