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Communities of bumblebees: testing the core-satellite species hypothesis

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A recent model (Hanski 1982) asserts that communities consist of two kinds of species: *core species,* which are regionally common and usually locally abundant, and well spaced-out in niche space; and *satellite species,* which are regionally and locally rare and less well spaced-out in niche space. Published results on communities of bumblebees support this hypothesis. Abundance and distribution are positively correlated, and distribution of regional distributions appears to be bimodal, as predicted by the model. The difference in the lengths of proboscis in two species of bumblebees is negatively correlated with overlap in resource use, though only 25 % of the variance in the latter is accounted for. About seven core species usually occur in one region, and these are more spaced-out in proboscis length space than are species drawn randomly from the species pool.

The results suggest that core species richness is more constant than satellite species richness in northern European bumblebee communities. Other studies show that the niche relations in local communities of bumblebees are not distinguishable from those in randomly constructed communities. It is therefore suggested that interspecific competition is not strong enough to appreciably determine species composition in local communities, but it may structure the species pool itself: certain species are more likely to be or become core species than others, perhaps because of competition. These results resolve a controversy in the literature about bumblebee community structure.

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1. Introduction

Communities consist of abundant and rare species. Some species are widely distributed regionally but others occur patchily; and while species in some communities are well spaced-out in niche space, other communities are structured into guilds of similar yet coexisting species. A recent model (Hanski 1982a) purports to order this chaos by acknowledging that regionally common species tend to be locally abundant, and by predicting with this assumption that the distribution of species' regional distributions is bimodal, which leads to the distinction between core and satellite species. Finally, it is predicted that core species are better spaced-out in niche space than are equally many species randomly drawn from the species pool (= core + satellite species). These ideas are tested with published data on communities of bumblebees.

2. How to test the model?

A hypothesis about the pattern in species' regional distributions is generated by modelling regional population dynamics in one species. Let $p_i(t)$ be the distribution of species i at time t, defined as the fraction of population sites (habitat patches) in which a local population of species i is present at time t. It is assumed that the "region" is so small that individual movements from any one site to any other are possible (i.e. sites are within the dispersal distance of individuals). Perhaps the simplest model of changes in p_i is (Hanski 1982a):

$$\frac{dp_i}{dt} = s_i p_i(1-p_i), \qquad (1)$$

where s_i is a species-specific parameter. This model incorporates mere essentials of regional population dynamics, nothing more.

In the core-satellite species hypothesis (Hanski 1982a), s_i is assumed to be a random variable with mean $\bar{s}$ and variance $\sigma_{\bar{s}}^2$. If

$$\sigma_{\bar{s}}^2 > \bar{s} > 0, \tag{2}$$

the limit ($t \rightarrow \infty$) distribution of $\Phi\ (p_i, t)$, which is independent of $p_i(0)$, is bimodal, and during a long period of time species i is most of the time either common (p_i close to unity) or rare (p_i close to zero). (See also Hanski 1982b.) If stochasticity is unimportant, $p_i = 1$. One must assume that some outside dispersal exists to prevent regional, as opposed to local, extinction, and substantial stochasticity (large $\sigma_{\bar{s}}^2/\bar{s}$) is needed to keep p_i from being close to unity most of the time.

Result (2) may be extended to a community of species, for whatever differences there exist between the species, none of the species is expected to stay long at intermediate values of p (Hanski 1982a). At any given moment, most species are either widely distributed or rare, giving rise to a bimodal distribution of p values (or, if the distribution is unimodal, the peak is not near 0.5). The common species are termed core species and the rare ones are satellite species.

If a bimodal distribution of regional distributions is established in the community, classification of the species into core and satellite species may be used in various ways to develop and test hypotheses about community structure.

Unfortunately, there are several difficulties in testing the core-satellite species hypothesis itself (Hanski 1982a). In the multispecies context, we require that all species have similar habitat selection with respect to the population sites studied. If species that cannot occur in a subset of the sites are included, their distribution is constrained to be less than unity for reasons not studied in the model, and any patterns observed are difficult to interpret. If, on the other hand, all species can establish a local population in any of the sites, a meaningful analysis, in this context, becomes possible. The difficulty is in showing that the species have similar habitat selection.

Another difficulty is that models other than the core-satellite hypothesis may lead to a bimodal distribution of regional distributions (cf. McIntosh 1961 and Hanski 1982a, b and references therein about Raunkiaer's law of frequency). To discriminate between alternative explanations, one needs to study spatial processes (extinction, colonization) in detail, or to try to document changes in species' status from the core to the satellite class and vice versa. Such changes are predicted to take place, even if the pattern of environmental stochasticity is stationary (though these changes need not be frequent).

Bumblebees should satisfy the requirement of similar habitat selection. Bumblebees are generalists with respect to the species of flowering plants they visit (Anasiewicz 1971, Teräs 1976, Ranta et al. 1981, and many others), with rare exceptions (*Bombus consobrinus* which is associated with *Aconitum septentrionale* in Fennoscandia; Løken 1973), though individual bees may specialize on one or a few species at a time (Heinrich 1976a, 1979, Ranta & Lundberg 1981). Bumblebees are specialists, to some extent at least, with respect to the length of the corolla tube of flowers, because of constraints set by the length of their proboscis (Heinrich 1976b, Ranta & Lundberg 1980, and many others). We may nonetheless assume that the distribution of corolla tube lengths is sufficiently similar in reasonably large and heterogeneous stands of vegetation that any species of bumblebee may occur in any bumblebee community, within the limits of its geographical distribution and broad altitudinal zones (Svensson & Lundberg 1977, Pulliainen 1979, Lundberg & Ranta 1980, Inouye 1980).

3. Results

3.1. Bumblebees in Lublin, Poland

Anasiewicz (1971) recorded the numbers of bumblebees foraging in ten parks, squares, lawns, etc. in Lublin throughout the seasons 1964 and 1966. Her sampling sites were discrete habitat islands in and around the city (see fig. 1 in Anasiewicz 1971). Bumblebees were observed to breed within the sites, which suggests that the data consist of local breeding populations; and the intersite distances were within the flight powers of bumblebee queens moving from any one site to any other possible site, as required in the model. Altogether 1597 individuals of 15 species were captured while visiting 64 species of flowering plants.

Regionally common species tended to be locally abundant (Fig. 1), and the distribution of regional distributions was bimodal, as predicted (Fig. 2; $P < 0.01$ for the 6 largest sites). Seven species should be classified as core species.

Anasiewicz (1971) gives the frequency of bumblebees' visits to different kinds of flowers, which makes it possible to directly test the frequently-stated hypothesis that interspecific

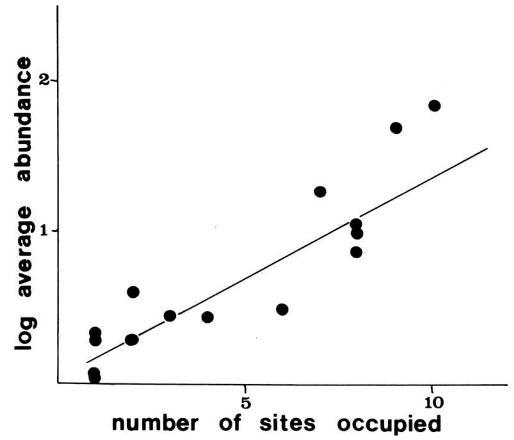

Fig. 1. Relationship between distribution (*p*, the proportion of sites occupied) and average local abundance (logarithmic transformation) in bumblebees in Lublin (Anasiewicz 1971).

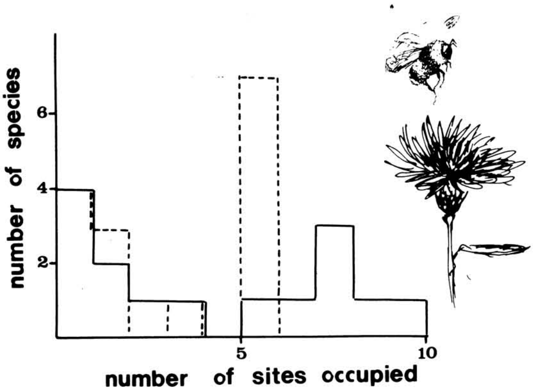

Fig. 2. The distribution of regional distributions of bumblebees among 10 sites in Lublin (Anasiewicz 1971). The broken line histogram gives the result for the six largest samples (sites). The null hypothesis of uniform distribution is rejected for the six largest sites (distribution classes 1 and 6, 2 and 5, and 3 and 4 pooled, $\chi^2 = 11.2$, $df = 2$, $P < 0.01$) but cannot be rejected with this test for all 10 sites (classes 1, 2, 9, and 10; 3, 4, 7, and 8; and 5 and 6 pooled, $\chi^2 = 2.0$, $df = 2$). See Table 2 for the names of the species.

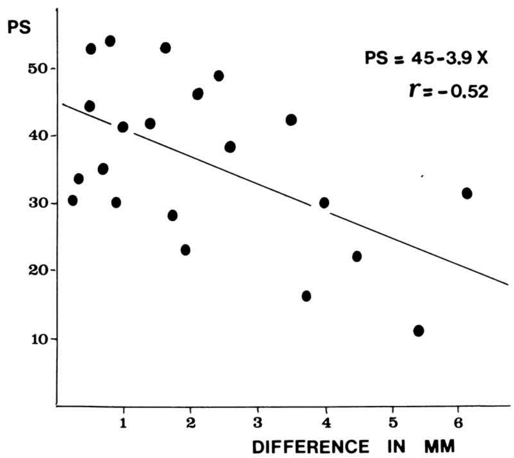

Fig. 3. Relationship between the percentage similarity *(PS)* in the utilization of 25 common species of flowers and the difference in proboscis lengths in pairs of core species in Lublin (data from Anasiewicz 1971). There is a tendency towards a negative relationship, but for two reasons it is not possible to give the probability of a significant correlation: the distribution is not quite normal (while there are ecological reasons *not* to use the logarithmic transformation), and the points in the figure are not independent of each other, as they represent all possible pairs of species from among the seven core species.

differences in proboscis length determine the degree of similarity in resource use (Hulkkonen 1928, Heinrich 1976b, Inoye 1977, 1978; these authors used other, indirect evidence to support the hypothesis). As there are no Polish measurements available, Pekkarinen's (1979) results on the lengths of proboscis in Fennoscandian bumblebees were used (with some measurements from other sources as indicated in Table 2). I have restricted the analysis to the queens. Results for males and workers are expected to be qualitatively similar (cf. Pekkarinen 1979).

Pair-wise overlap in resource use *(PS)* tends to decrease with increasing difference in proboscis length (Fig. 3). This result directly supports the importance of proboscis length in bumblebee ecology, though it should be noted that *all* species overlap to some extent, *no* species overlap totally, and only c. 25 % of the variance in *PS* is accounted for by the regression; much of the variation which remains may be due to random spatial variation in resource use (cf. Ranta & Vepsäläinen 1980). Similar results have recently been reported by Ranta & Tiainen (1982) from eastern Finland.

The core-satellite species hypothesis predicts (Hanski 1982a, Section 8) that the seven core species are more spaced-out in niche space than are seven species drawn randomly from the species pool. Because the relationship between overlap *(PS)* and morphological difference is linear (Fig. 3), it is sufficient to study spacing of the species in the morphological space of proboscis length; these results map corresponding niche overlaps in the niche space of flower species.

Table 1. Average difference in proboscis lengths (in mm) between two species from among the core species and in a group of equally many species selected randomly from the species pool. Three spatial scales are analysed. On the scale of northern Europe (large scale), the first comparison is for the three species which were core species in each of the seven regions in Table 2; and the next three lines are for species present in 7, 6, and 5 of the regions. In the analysis of each data set from small and medium scales, calculations were repeated for species other than those with very long proboscis (second line).

Region	Number of species		Observed core spp.	Random		$\frac{obs-x}{SD}$	*P*
	core	satellite		*x*	*SD*		one-tailed
Small scale							
Lublin, Poland	7	8	2.18	1.43	0.46	1.63	0.05
	6a	7b	1.24	0.92	0.29	1.10	0.14
E. Finland	8	3	2.32	1.87	0.44	1.02	0.15
	7a	3	1.45	1.33	0.12	1.00	0.16
	5	5a	1.54	1.29	0.22	1.14	0.13
Medium scale							
S. England	7	8	2.22	2.27	0.66	—0.08	
	6a	7c	1.22	1.30	0.29	—0.28	
N. England	6	7	2.39	1.94	0.58	0.78	
	5a	7	1.22	1.37	0.26	—0.58	
S. Sweden	8	10	2.05	2.17	0.47	—0.26	
	7a	9c	1.17	1.28	0.24	—0.46	
Large scale							
3 core species	3	18	4.07	2.18	1.16	1.62	0.05
present in 7 of 7	4	17	3.27	2.02	0.94	1.33	0.09
present in 6 of 7	9	12	2.08	2.06	0.48	0.04	
present in 5 of 7	12	9	1.84	2.01	0.39	—0.44	

Species omitted are: a) *B. hortorum*, b) *B. pomorum*, and c) *B. ruderatus*. The line 5+5 from eastern Finland was constructed by assuming that the 5 clearly most abundant species are core species (see table 2 in Ranta & Tiainen 1982; *B. hortorum* has moreover been omitted). Note that the length of proboscis of *B. cullumanus* is unknown (Table 2), and hence this species has been omitted from the calculations for S. England and S. Sweden.

See Table 2 for the proboscis lengths.

Spacing-out amongst the seven core species is better than in a randomly selected group of seven species from the species pool ($P = 0.05$, Table 1). The result is substantially affected by the long-tongued species, and especially by *B. hortorum.* Another set of calculations was carried out for species other than it and *B. pomorum,* a long-tongued satellite species (12.5 mm, Table 2). The predicted difference is again observed, though it is not significant ($P = 0.14$, Table 1). Naturally, the reason for *B. hortorum* being a core species may well have something to do with its long proboscis, and there is no good reason to exclude it from the analysis. The small number of species in the community is a problem in the statistical analysis of this and other questions (below).

3.2. Bumblebees in eastern Finland

Ranta & Tiainen (1982) have recently studied seven local communities in one (rural) locality in eastern Finland throughout one summer. Four of the seven sites were comparable abandoned fields. Ten species of *Bombus* were recorded from 4, 4, 4, 4, 4, 4, 4, 4, 2, and 1 sites, respectively. Another species, *B. soroeensis,* was known to be present in the species pool though not recorded from the four fields. The data suggest a classification of the eleven species into eight core and three satellite species (Table 2). Local abundances averaged 119 and five individuals (collected) in the core and satellite species, respectively.

Although one would wish for more than four fields in the data, the number of core species is unlikely to be overestimated by more than one or two species at most. In Lublin, for example, just one satellite species was recorded at four out of ten sites.

Ranta & Tiainen (1982) failed to find differences in the distribution of proboscis length between local communities and random ones of the same size, drawn from the species pool. Here I test the core-satellite species hypothesis: Are core species better spaced-out than equally many randomly selected species from the species pool? Three sets of calculations were carried out as explained and presented in Table 1; the core species are better spaced-out than randomly

Table 2. The status of the species in the five large regions in Fig. 4, in Lublin (Anasiewicz 1971), and in one locality in eastern Finland (Ranta & Tiainen 1982). The length of the proboscis is taken from Pekkarinen (1979) unless stated otherwise. c = core species and s = satellite species.

	Proboscis length in queens (mm)	S. England	N. England	Scotland	Ireland	S. Sweden	Lublin, Poland	Eastern Finland
B. lucorum (L.)	8.5	c	c	c	c	c	c	c
B. terrestris (L.)	10.1	c	c	c	s	s	c	-
B. pratorum (L.)	9.3	c	c	c	s	c	s	c
B. lapidarius (L.)	10.9	c	c	-	c	c	c	c
B. hortorum (L.)	14.6	c	c	c	c	c	c	c
B. ruderadius (Müller)	11.1	c	s	-	s	s	c	c
B. pascuorum (Scop.)	10.6	c	c	c	c	c	c	c
B. soroeensis (F.)	8.8	s	s	s	-	c	-	s
B. cullumanus (Kirby)	?	s	-	-	-	s	-	-
B. jonellus (Kirby)	8.1[1]	s	s	s	s	s	-	c
B. humilis Ill.	10.7	s	-	-	-	c	s	-
B. muscorum (L.)	10.4	s	s	s	s	s	s	-
B. sylvarum (L.)	10.6	s	-	-	s	c	s	s
B. distinguendus Mor.	11.2	s	s	s	s	s	-	-
B. subterraneus (L.)	11.6	s	-	-	-	s	s	-
B. ruderatus (F.)	15.3[2]	s	-	-	-	s	-	-
B. magnus Vogt[5]	8.7	-	s	s	c	s	-	-
B. monticola Smith	8.3[3]	-	s	s	-	-	-	-
B. hypnorum (L.)	9.2	-	-	-	-	s	c	c
B. veteranus (F.)	10.6	-	-	-	-	s	s	s
B. confusus Schenc.	10.9[2]	-	-	-	-	-	s	-
B. pomorum Pz.	12.5[4]	-	-	-	-	-	s	-

[1] Esa Ranta (unpubl.).
[2] Medler 1962b.
[3] *B. lapponicus scandinavicus* = *B. monticola*, and the length of proboscis is taken from Pekkarinen (1979, for *lapponicus*).
[4] Medler 1962a.
[5] Possibly conspecific with *B. lucorum* (Pekkarinen 1979).

selected species, though the difference is not significant ($P \sim 0.15$). In any case, there is no great difficulty in explaining why our results might differ (Section 4).

3.3. Patterns of distribution in the U.K. and Scandinavia

Bumblebee distributions in larger regions are documented in the distribution maps of Alford (1975) for the United Kingdom and of Løken (1973) for Scandinavia. From these maps, I delimited five large regions that are relatively homogeneous in topography: southern and northern England, Scotland, southern Ireland, and southern Sweden (Fig. 4). Although the core-satellite species hypothesis does not directly apply to large regions (Section 2), patterns emerging have some relation to patterns in small regions (Section 4), and are worth comparing.

The distribution of regional distributions appears to be bimodal in southern ($P < 0.01$) and northern England ($P < 0.1$), and in Sweden ($P < 0.1$), while in Scotland and Ireland it is not (Fig. 5). Note that the "exceptional" patterns are from the geographically extreme regions. There are seven and six core species in southern and northern England, respectively, *B. ruderadius* having changed status. In southern Sweden, there is no clear-cut difference but I have classified eight of the 19 species as core species (see Fig. 5).

The status of the species in the five regions has been summarized in Table 2. The two small regions studied in Sections 3.1 and 3.2 have been included (for their locations see Fig. 4), though they are clearly not strictly comparable.

No significant differences were found in spacing between core species and a random set of equally many species from the species pool of southern and northern England, or of southern Sweden (each region is analysed separately; Table 1). Returning to Table 2, there were three species that were core species in each of the seven regions: *Bombus lucorum* (proboscis 8.5 mm), *Bombus pascuorum* (10.6 mm), and *Bombus hortorum* (14.6 mm). One cannot fail to note how well spread out these species are from each other in terms of proboscis length (for its distribution see Table 2 and Ranta 1982: table 1). This degree of separation is unlikely to be due to chance ($P = 0.05$, Table 1). Four species, including the above-mentioned ones, were present in each of the seven

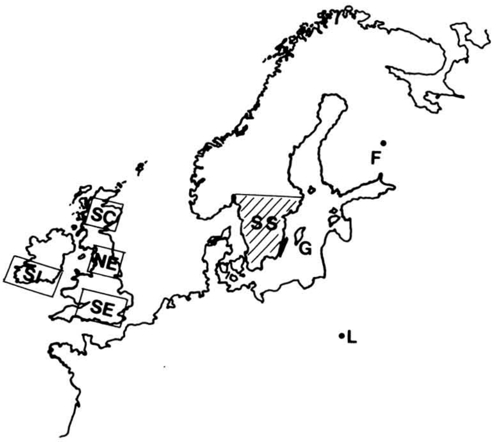

Fig. 4. A map showing the five regions in northern Europe for which bumblebee distributions were analysed (Fig. 5). The symbols are: SE = southern England, NE = northern England, SC = Scotland, SI = southern Ireland, and SS = southern Sweden. The locations of three other places are shown: L = Lublin (Anasiewicz 1971), F = a locality in eastern Finland (Ranta & Tiainen 1982), and G = the island of Gotland.

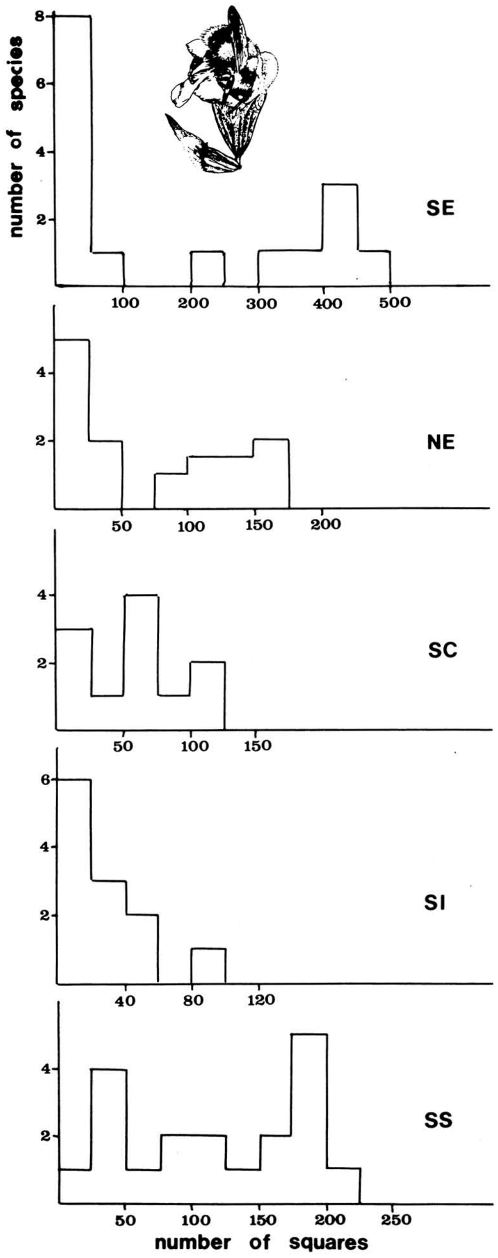

Fig. 5. Distributions of regional distributions in the five regions shown in Fig. 4. The symbols are the same as in Fig. 4. "Distribution" is the number of 10 km^2 squares from which the species has been recorded since 1960, except southern Sweden, where distribution is the number of observations on the map. Data are from Alford (1975) for the U.K. and from Løken (1973) for Sweden. The statistics are as follows (pooled distribution classes in brackets, cf. Fig. 2): SE (1+2+9+10, 3+4+7+8, and 5+6), $\chi^2 = 11.3$, $df = 2$, $P < 0.01$; NE (1+7, 2+6, and 3+4+5), $\chi^2 = 4.7$, $df = 2$, $P < 0.1$; SS (1+9, 2+8, 3+7, and 4+5+6), $\chi^2 = 7.2$, $df = 3$, $P < 0.1$.

regions, and these too are relatively well spaced-out ($P = 0.09$, Table 1). There were no significant differences when species present in six and five regions were finally examined (Table 1).

3.4. Island communities

Hanski (1982a) suggested that as satellite species occur in small local populations, their regional existence should hinge on the size of the region, and hence the proportion of satellite species in island communities should decline with area.

Records for five islands, or groups of islands, around the British Isles are given in Table 3. These data are mostly from Alford's (1975) distribution maps and have the inevitable drawback that they do not necessarily represent the actual situation at any given moment, as data for many years have been pooled. The number of species increases from the small islands of Cara, Lundy, and Scilly (6 or 7 species) to the Channel Islands (9 species) and to the Isle of Man (11 species); in other words, the number of species increases with island size, up to 14 species in Ireland and 19 species in the whole U.K. This observation is, of course, universal (e.g. Connor and McCoy 1979).

The proportion of core species is slightly but consistently higher on small islands than on the mainland: 57 to 67 % on the smaller islands than the Isle of Man, where 45 % of the species were core species, as on the mainland (there were 4 small islands, hence $P = 0.5^4 = 0.06$). There is one

Table 3. Presence of bumblebees on five islands/groups of islands around the British Isles. Data are from the distribution maps in Alford (1975), except those for the Cara Island (off Gigha, Scotland), which are from Richards (1936).

	Cara Island	Lundy	Scilly	Channel Islands	Isle of Man
B. lucorum	*	*	*	*	*
B. lapidarius	*	*	*	*	*
B. hortorum	*	*	*	*	*
B. terrestris			*	*	*
B. pascuorum	*	*		*	*
B. ruderadius				*	
B. magnus					*
B. jonellus	*	*	*		*
B. monticola					*
B. ruderatus				*	
B. humilis					*
B. muscorum	*	*	*	*	*
B. sylvarum				*	
B. distinguendus					*
B. soroeensis	*				
Total species	7	6	6	9	11
core species	4	4	4	6	5
% core species	57	67	67	67	45

clearly exceptional species — *Bombus pratorum* (9.3 mm), a core species on the mainland, which did not occur on any of the five islands. Three core species, *B. lucorum* (8.5 mm), *B. lapidarius* (10.9 mm), and *B. hortorum* (14.6 mm), and one satellite, *B. muscorum* (10.4 mm), were present on each island (Table 3; the latter is something of an island specialist, see Alford 1975). One should note that the three core species are distinct in their proboscis length.

Other evidence exists to confirm that *B. pratorum,* though common on the mainland, is a poor island colonizer. Its occurrence in Ireland is due to a recent invasion (Alford 1975), and it is still absent from the large Baltic island of Gotland, unlike any other core species in southern Sweden (Løken 1973). The proportion of core species is 58 % on Gotland, which is greater than the corresponding figure (42 %) on the mainland (a nonsignificant difference, but see above).

It can be mentioned here that three species are known from Iceland: *Bombus lucorum, B. jonellus,* and *B. hortorum* (E. Olafsson unpubl.). *B. lucorum* and *B. hortorum,* which are very different in proboscis length, are both core species in the U.K. but *B. jonellus* is not.

4. Discussion

Let us collate results with direct bearing on the validity of the core-satellite species hypothesis:

1) Local abundance and regional distribution are positively correlated, as assumed in the model.

2) The distribution of species' regional distributions was bimodal in a set of data from a small region (Lublin), as predicted by the model, but in large regions the distribution appeared bimodal in only three out of five cases.

3) In bumblebee communities in two small regions (Lublin and eastern Finland), core species were better spaced-out in niche space than were species in random selections from the species pool; no such differences were found in three large regions, but on the scale of northern Europe, species present in each of the regions studied were better spaced-out than randomly selected species.

The core-satellite model is an "island model", as opposed to a "stepping stone" model, because movements from any one site to any other are assumed to be possible and equally likely (Eq. 1). Of the three spatial scales in Section 3, only the smallest is strictly appropriate for testing the model, though geographically widespread but rare species are likely to become classified as satellite species on many spatial scales. Encouragingly, results for the smallest scale confirmed the model prediction about niche relations. Distribution maps are problematic for the present purpose because their data, pooled for tens or even hundreds of years, misrepresent instantaneous distributional patterns. Taylor & Woiwod (1980) have shown that ecologically significant, year-to-year changes in distribution and abundance of moths and aphids take place in the scale of Great Britain.

Naturally, one would wish to be able to present more conclusive results than those possible here. Definite conclusions must wait until data that simultaneously cover spatial and temporal variation have been analysed. With such data, one could test the validity of model (l) directly. Nonetheless, as shown below, the present results already suggest new ways of looking at communities of bumblebees.

Ranta (1982) and Ranta & Tiainen (1982) have found that local communities in Anasiewicz's (1971) study from Lublin, in Løken's (1949) study from Norway, and in their own study (Ranta & Tiainen 1982) from eastern Finland consisted of species which were not better spaced-out in proboscis length space than were species randomly selected from the respective species pools. This result is different from the one in this paper, but the questions asked were different, too: in their case, *local communities* were compared with randomly constructed communities from the species pool; in my case, *one set of species (core species) in the species pool* was compared with randomly constructed selections from the species pool. While Ranta (1982) and Ranta & Tiainen (1982) test possible *local effects* of (strong) competition, I test possible *regional effects* of (possibly weaker) competition. The questions are different, though it is true that most core species occur in any given community, and that only a few satellite species can be found from a given community. Our results together suggest that competition in bumblebee communities is not strong enough to determine species composition in local communities, but competition appears to structure the species pool itself, i.e. to select, to some extent at least, certain species to become or to be core species more likely than others (cf. Hanski 1982a: Section 8).

This observation is of wider interest. Recent critics (Connor & Simberloff 1979, Simberloff 1980, Rotenberry & Wiens 1980, Wiens & Rotenberry 1981) of the "competition paradigm" in community ecology have shown that local communities are, in many cases, indistinguishable from random draws from the species pool.

Less attention has been paid to developing hypotheses about the structure of the species pool itself. My results should encourage more work in this potentially rewarding direction.

In the bumblebee communities that covered a small region, the numbers of core species were seven and eight in Lublin and eastern Finland, respectively, while the corresponding numbers of satellite species were eight and three; core species richness was more constant than satellite species richness. Results from the larger regions support a hypothesis that about seven core species is a maximum in any one region.

A plausible hypothesis is that a ceiling to the numbers of core species in one region is set by interspecific competition. Satellite species richness is affected by factors other than competition, and it may reflect increasing (total) species richness from north (eastern Finland here) to south (Lublin), as observed in most organisms (see Ranta 1982 for a map of bumblebee species richness in Finland, Scandinavia, and England). I do not mean to imply that core species richness would not generally increase from north to south — it may or may not. In bumblebees it perhaps does not because there is no great change in resource availability or dimensionality of the niche space influencing coexistence of abundant (core) species in the same community. Studies on latitudinal diversity gradients might bring new insights if the distinction between core and satellite species is made whenever possible.

There is a controversy in the literature about species richness in bumblebee communities. Heinrich (1979, see also 1976b) has suggested that "only three or four species of bumblebees are likely to be abundant in a small locale, such as a meadow, bog, or mountaintop, although a dozen or more may be present in the larger surrounding area. Generally, one of the abundant species is short-tongued, another is long-tongued, and a third has a tongue of intermediate length." Inouye (1977, see also 1978) has added the possibility of a 4th 'robber' species, such as *B. lucorum* in Europe, able to bite holes in the corolla tube and thereby able to obtain nectar from practically any flower.

The views of these American workers have been challenged by Ranta & Vepsäläinen (1981), who point out that many (European) bumblebee communities are much richer in species, up to 15 species having been recorded from one community. Though the cause for the disagreement about species richness may simply be that Heinrich and Inouye did not count the rare species, Ranta et al. (1981) have demonstrated that many (5) similar bumblebee species may coexist in the same community, which appears to refute Heinrich's (1979) hypothesis (quoted above).

The present results throw much light on these questions. The key is the explicit analysis of the community structure at the regional level (= species pool), and especially the distinction between core and satellite species. There *exists* support for the hypothesis that bumblebees are well spaced-out in proboscis length space, though not necessarily amongst species in a local community with respect to the species pool, but amongst the core species in the species pool. Indeed, the three core species present in each of the seven regions studied here (Table 2) fit exactly Heinrich's hypothesis, and if all the species present in each of the seven regions are counted, Inouye's hypothesis is found to be correct: there are four species, three of which are well separated in proboscis length (*B. pratorum,* 9.3 mm — *B. pascuorum,* 10.6 mm — *B. hortorum,* 14.5 mm), and one of which is a robber species (*B. lucorum,* 8.5 mm). From the point of view of the community structure, the above suggestion about approximately seven core species being present in one region is an equally important — and testable — generalization.

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