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Structure in bumblebee communities

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Overlap in flower visits by pairs of bumblebees (*Bombus*) in six communities in Europe and North America is inversely related to the difference in bumblebees' proboscis lengths. 'Corrected' proboscis lengths improve the correlation, and suggest niche shifts leading to tighter groups of species, similar in their flower visits. Complementary abundance changes attributable to interspecific competition were observed on geographical and regional scales but not on more local scales. Data from 12 communities in Europe and North America indicate that the core species (Hanski 1982) are better spaced out in proboscis length space than are randomly selected species from the respective species pools.

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1. Introduction

Bumblebees (*Bombus*) are characteristic and abundant insects in the northern hemisphere, buzzing about on meadows and other sites with sufficient numbers of flowers. In a region say 10 km^2 in size, up to 15 species may occur (Ranta & Vepsäläinen 1981), though many of them are usually rare (Hanski 1982a). On the continents of Europe and North America, the number of species is c. 50 (Løken 1973 and Heinrich 1979).

Hulkkonen (1928) was perhaps the first to suggest that proboscis length differences facilitate co-existence between sympatric species of bumblebees (Brian 1957, Heinrich 1976, Inouye 1980, Ranta & Lundberg 1980, Pyke 1982). In community studies, direct measurements of resource use are generally preferable to indirect morphological data, but it may be impossible to obtain direct data for rare species, which one may nonetheless wish to include in the analysis. In Section 2 I demonstrate that the difference in proboscis lengths of two species of bumblebees is in fact inversely related to their resource use overlap.

Hanski (1982a) applied the core-satellite species concept (Hanski 1982b) in an analysis of literature data on bumblebee communities, and found support for the theory. Here I extend the previous study to other sets of data, and subsequently focus on the core species — the species that are locally abundant and co-exist on most sites suitable for bumlebees. The theory predicts that interspecific competition increases the probability of a species being or becoming a satellite species — a regionally rare species. The question is not whether competition occurs in bumblebee communities — it does occur, and can be demonstrated experimentally (references below). The question is whether a good case can be made for interspecific competition structuring bumblebee communities.

2. Overlap in resource use vs. morphological similarity

Nectar is an essential resource for bumblebees, and often a scarce one, up to 90 % of the standing crop of nectar available per day being utilized (Heinrich 1976). One may establish the significance of proboscis length differences in nectar utilization by plotting the observed similarity in flower visits against the difference in bumblebees' proboscis lengths (Hanski 1982a). Results for six communities in Europe and North America are presented in Fig. 1.

I make a distinction in this paper between two spatial scales, and consequently differentiate between 'local' and 'regional' communities. Two of the data sets in Fig. 1 come from regional communities (Lublin and Mekrijärvi): these are sets of local communities situated within an area of say 10 km^2. A local community is the assemblage of species breeding in one meadow or some other relatively small area, say 1 ha, within which local populations may directly interact with each other. Two of the data sets in Fig. 1 cover a long transect along a mountain slope (Abisko and Colorado), whilst the remaining two sets represent local communities (Puumala and Maine).

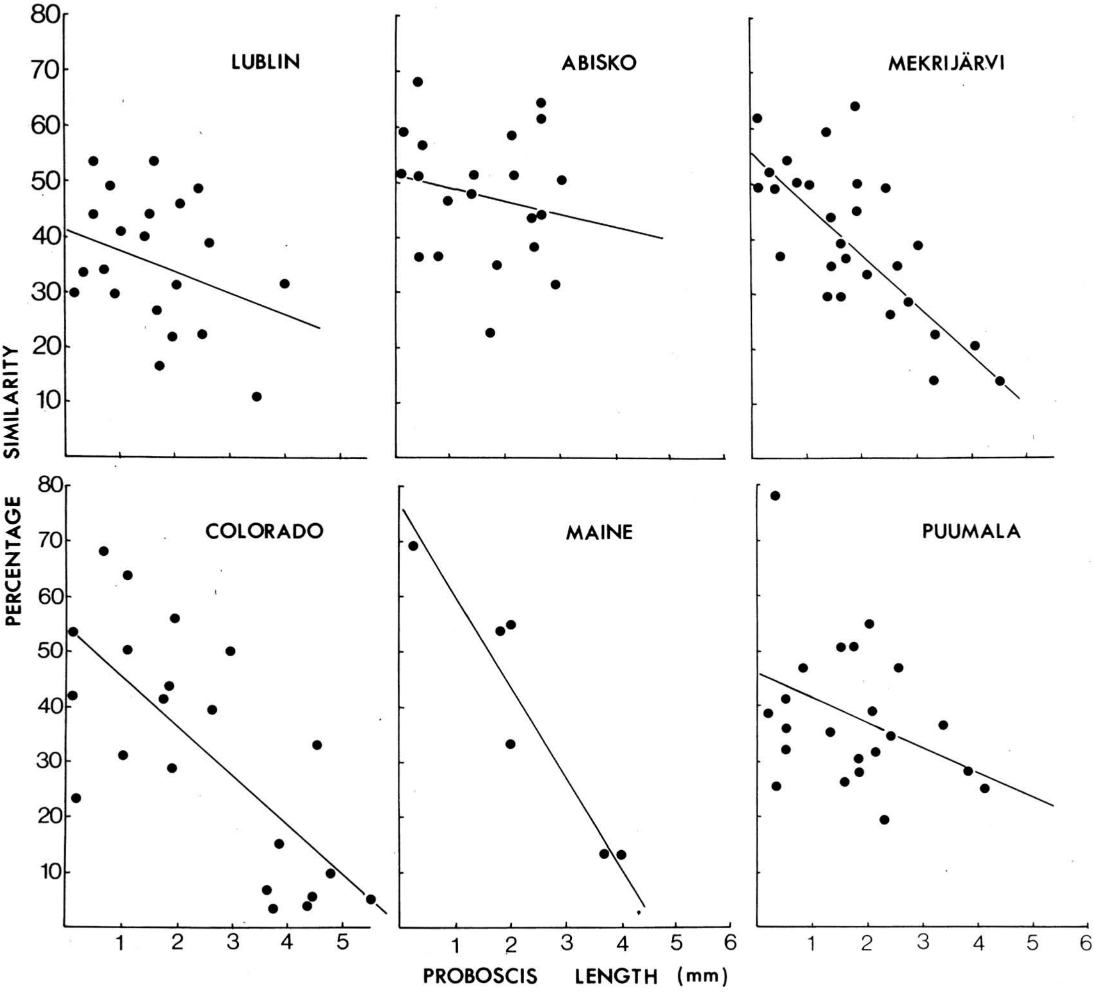

Fig. 1. Relationship between percentage similarity in flower visits and proboscis length difference in pairs of core species in six communities in Europe and North America. Percentage similarity (*PS*) was calculated as explained in Table 1. The amount of variation in the *PS* values accounted for by the regressions is given in Fig. 4 (except for Puumala, r^2=0.13). Data are from the following sources: Lublin (Poland), Anasiewicz (1971); Abisko (Sweden), Lundberg & Ranta (1980 and unpubl.); Mekrijärvi (Finland), Ranta & Tiainen (1982 and unpubl.); Colorado (USA), Pyke (1982); Maine (USA), Heinrich (1976); and Puumala (Finland), Teräs (1976) and Ranta et al. (1981 and unpubl.).

Bombus hortorum (a European species) has an exceptionally long proboscis (14.6 mm). The overlaps between it and the other species tend to be greater than other overlaps when allowance is made for the proboscis length differences, which suggests that *B. hortorum* behaves like a bumblebee with a somewhat shorter proboscis. I used the value 12.5 mm for *B. hortorum* in calculating the regressions and in the rest of the paper, which brings the European and North American results into good agreement, and incidentally 'normalizes' the distribution of proboscis lengths (Fig. 3). *Bombus hortorum* was a core species in all of the communities analysed; hence my tests in Section 3 concerning proboscis length relations are conservative.

The results shown in Fig. 1 confirm the importance of proboscis length in bumblebee ecology, and justify its use in analyses of resource partitioning. However, much of the variation in the overlaps remains to be explained. Whether or not a part of the residual variation is due to behavioural niche shifts will be studied in Section 4.

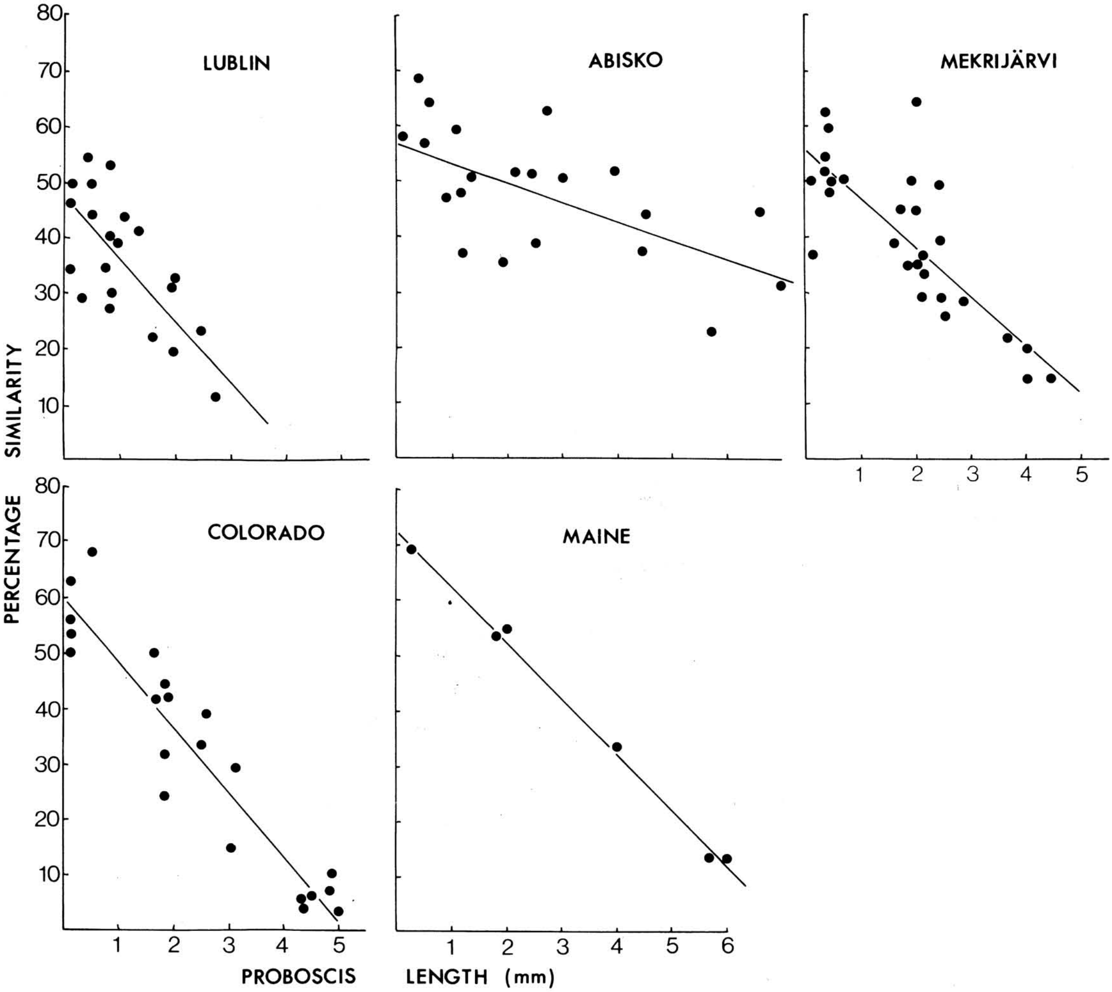

Fig. 2. As Fig. 1 but using the 'corrected' values of d_{ij} (see Section 3). For the amount of variation in the *PS* values explained by the regressions see Fig. 4. The two deviating points in Mekrijärvi are *Bombus ruderarius* x *B. pratorum* (the upper one) and *B. ruderarius* x *B. pascuorum.*

3. The core-satellite species hypothesis

In the previous paper (Hanski 1982a), only two of the communities in Fig. 1 were analysed (Lublin and Mekrijärvi). As these are the only regional communities from which data are available, the relevant analysis of species' site occupancy distribution (Hanski 1982b) is possible only in their case (Hanski 1982a). But assuming that the core species are more abundant than the satellite ones (Hanski 1982a, b), one can do an extended analysis of niche (proboscis length) relations in 12 communities, including the ones in Fig. 1 and six other large samples from more local communities: the core species are predicted to be better spaced out in proboscis length space than are species in a random collection of equally many species from the species pool. The dichotomy between 'common' and 'rare' species is usually clear in the original papers, whose authors often omit the rare (satellite) species from their analyses. The uncertainty which remains about the allocation of the species into the two groups does not affect the null hypothesis: in any case one expects there to be no difference between the two sets of species. Figure 3 gives the data on which the following analysis is based.

Average 'overlap' amongst the core species was calculated as

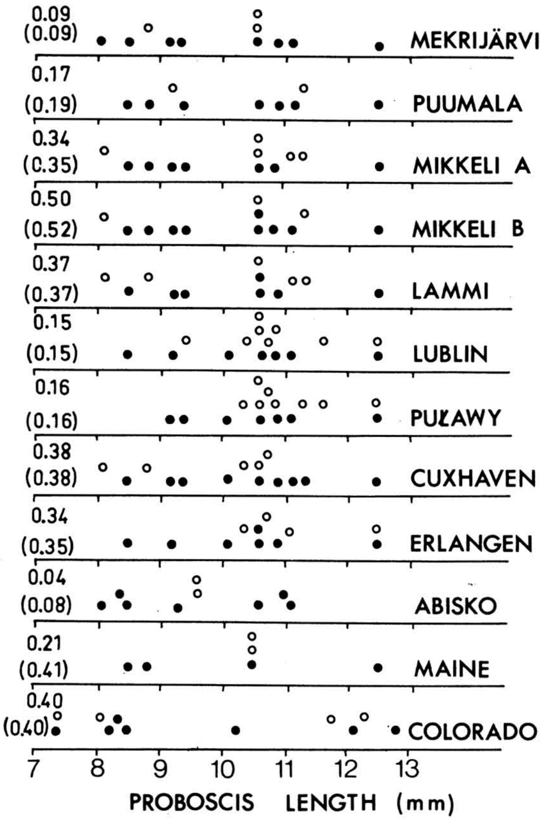

Fig. 3. Proboscis lengths of the queens (in mm) in 12 communities in Europe and North America. Proboscis lengths are from the sources given in Hanski (1982a) and Inouye (1980). Solid symbols are core (abundant) species and open symbols refer to satellite (rare) species. The proboscis length of *Bombus centralis* (a satellite in Colorado) is not known. The figures on the left give the proportion of 1000 randomizations in which the species were spaced out better or equally as well as the core species (the cases of equal spacing were halved; when all of them were counted the conservative figures in brackets were obtained). See the text for further explanations. Data not appearing in Fig. 1 are from the following sources: Mikkeli A (Finland), Teräs (unpubl.); Mikkeli B (Finland), Teräs (unpubl.); Lammi (Finland), Pekkarinen et al. (1981); Puławy (Poland), Ruszkowski et al. (1981); Cuxhaven (Germany), Wagner (1971); and Erlangen (Germany), Postner (1951).

$$OL=\sum_{i=1}^{s-1}\sum_{j=i+1}^{s}\max(2-d_{ij},0)/[s(s-1)/2],$$

where s is the number of species and d_{ij} is the difference in proboscis lengths of species i and j. Random sets of species were created by randomly drawing s species from the species pool (=core+satellite species) 1000 times, and OL was calculated for each draw. The number of random collections in which OL was smaller than or equal to the observed value in the core species is given in Fig. 3 for each community (conservative figures are obtained if all (and not half) of the equal cases are counted; see Fig. 3).

There is a definite trend in the results, in the direction predicted, though the individual values are not significant (12 values < 0.5, $P=0.0002$). Using Fisher's method to combine probabilities gives $\chi^2=36.8$ ($df=24$), which is significant at the 5 % level (the conservative estimate is $\chi^2=33.7$, $P<0.10$).

There is one pitfall in this analysis. Several of the communities are situated in the same geographical regions, and are perhaps not independent of each other. For this reason I repeated the analysis for the following six communities, representing different geographical areas and hence more independent communities: Maine, Colorado, Abisko, Mekrijärvi, Lublin and Cuxhaven (the latter three were randomly selected from the three sets (Mekrijärvi, Puumala, Mikkeli A, Mikkeli B, Lammi), (Lublin, Puławy), and (Cuxhaven, Erlangen)). The result, however, is the same as in the case of all the 12 communities: the combined probability, $\chi^2=21.9$ ($df=12$), is significant at the 5 % level (the conservative estimate is $\chi^2=19.2$, $P<0.10$).

4. Niche shifts?

A possible explanation of deviations from the regression lines in Fig. 1 is niche shifts. For example, a species in a certain community may utilize flowers with a 'too' deep corolla tube because of interspecific competition or some other reason.

Let us arrange the species in order of decreasing proboscis length, and denote by d_{ij} the difference in the proboscis lengths of species i and j, and by PS_{ij} the percentage similarity in their flower visits. The following regression model was fitted to the six data sets in Fig. 1 (using the stepwise multiple regression technique):

$$PS_{ij} = a_0 + a_1 d_{ij} + \sum_k b_k T_k,$$

$$\text{where } T_i=1;\ T_j=-1;\ T_{\substack{k\neq i\\ k\neq j}}=0.$$

Large values of b_k (usually the ones which were significantly different from zero) were used to calculate 'correction coefficients' b_k/a_1, by which bumblebees' proboscis lengths were changed. The number of species affected varied from one to four. The above model was then applied to the corrected data. The second set of b_k values did not differ significantly from zero, except in one case (Puumala). The method does not necessarily yield 'optimal' results, but should indicate the pattern

Table 1. Relative abundances (x100) of the core species in 9 bumblebee communities in Europe (the first 9 communities in Fig. 3). The species have been divided into 4 groups according to their method of foraging and proboscis length (for *Bombus terrestris* see Alford 1975). The proboscis lengths of the queens are given (in mm; from the sources given in Hanski 1982a). Satellite species have been marked by + and absent species by —.

Species	Proboscis	Relative abundances								
	length	Mek	Puu	MiA	MiB	Lam	Lub	Pul	Cux	Erl
Robbers										
B. jonellus	8.1	11	-	+	+	-	-	-	+	-
B. lucorum	8.5	21	17	23	25	28	1	-	7	8
B. terrestris	10.1	-	-	-	-	-	30	22	24	23
Total		32	17	23	25	28	31	22	31	31
Short proboscis										
B. soroeensis	8.8	+	1	8	7	+	-	-	+	-
B. hypnorum	9.2	2	+	9	3	5	8	18	16	7
B. pratorum	9.3	8	14	21	3	6	+	1	10	-
Total		10	15	38	13	11	8	19	26	7
Intermediate proboscis										
B. sylvarum	10.6	+	-	+	+	+	+	+	-	3
B. veteranus	10.6	+	-	+	12	4	+	+	+	-
B. pascuorum	10.6	12	59	34	15	27	5	27	12	10
B. lapidarius	10.9	43	5	4	28	24	46	16	14	38
B. ruderarius	11.1	2	1	+	4	+	6	6	4	+
B. distinguendus	11.2	-	+	+	+	+	-	+	4	-
Total		57	65	38	59	55	57	49	34	51
Long proboscis										
B. hortorum	14.6	1	3	2	3	6	4	10	5	4
Sample size		5291	7257	13249	3391	13972	1560	27955	4430	8654

of changes.

Figure 2 gives the new regressions. The method did not work properly with the data set from Puumala, but in all other communities much of the remaining variance in Fig. 1 could be accounted for. In the data set from Lublin, the original regression explained 10 % whilst the 'corrected' one explained 67 % of the variance in the *PS* values. Apparently, for some reason the overlaps in Puumala cannot be well predicted from the proboscis lengths only, whether real or modified.

In which way has the distribution of proboscis lengths changed? One clear — and expected — change is an increase in the proboscis lengths of the robber species — *Bombus lucorum* in Europe and *B. occidentalis* in North America — by c. 2 mm (this shift is apparent in the original data and was applied before using the regression model). An exception, however, was the community in Mekrijärvi, where *B. lucorum* did not shift.

We should not conclude too much from the shifts of the long-tongued species upwards in Maine and Abisko (Fig. 4). These shifts may be artefacts of the method. Note also that *Bombus hortorum* has been 'shifted' from 14.6 to 12.5 mm for reasons explained in Section 2.

The three communities which showed the most 'regular' shifts and with which the regression model worked well are Lublin, Mekrijärvi, and Colorado. The interesting point about the shifts in these communities is that they tend to make tighter groups of species rather than to spread the species better in proboscis length space (Fig. 4).

Niche shifts in bumblebees have been demonstrated experimentally in the field (Heinrich 1976, Inouye 1978), but a community-wide study addressing possible grouping of species, such as suggested by Fig. 4, has not yet been undertaken.

5. Abundance relations

Table 1 gives the relative abundances of the core species in nine European communities with a roughly similar species composition. The species have been divided into four groups: robbers, short-tongued, intermediate-tongued and long-tongued species (inevitably there is an exception: the workers of *B. lapidarius* have a disproportionately short proboscis (Pekkarinen 1979) and are occasional robbers).

The distribution of corolla tube depths in the flowers utilized by bumblebees is frequently, though not always, unimodal (e.g. Ranta & Tiainen 1982), on the basis of which the standard competition theory (e.g. Roughgarden 1979) predicts that abundances are not randomly distributed amongst the species. In the case of matching distributions of proboscis lengths and corolla tube depths, the pooled abundance of the intermediate-tongued species is expected to be disproportionately high. Ranta & Tiainen (1982) found that the distribution of bumblebees' proboscis lengths peaks later than the distribution of corolla tube depths. But apart from the difficulty of knowing exactly how a bumblebee's proboscis should be compared with the depth of a flower's corolla tube, a correction should be made for the higher rate of nectar production by larger flowers (Zimmerman & Pleasants 1982), which should bring the two distributions into better agreement.

The pooled relative abundances of the four groups in Table 1 mostly vary from 25 to 30 % in the robbers, from 10 to 20 % in the short-tongued species, from 50 to 60 % in the intermediate-tongued species, and from 3 to 5 % in *Bombus hortorum,* the only long-tongued core species in these communities. These data suggest a non-random distribution of abundances amongst the species, but such a conclusion cannot be drawn without further analyses, as the number of species in the four groups varies in the same way as pooled abundance.

I hypothesize that the above distribution of abundances amongst the four groups is a structural property of bumblebee communities, at least partly independent of the species that happen to occur in any particular community. To test this hypothesis I first calculated the percentage similarity in the species and group composition in the nine communities in Table 1. The latter figure is necessarily greater than the former one.

I then once randomized the abundances amongst the species in the nine communities, and repeated the above calculations. Results in Table 2 indicate that at the species level there is little, if any, similarity beyond the random expectation, but at the group level the observed similarity is higher than predicted by the random model. Interspecific interactions have affected the distribution of species abundances in these communities.

Let us then move to a smaller spatial scale and study species co-existing in local communities situated close to each other. Two data sets, from Lublin and Mekrijärvi, allow us to repeat the above analysis at this spatial scale. The results (Table 2) diverge in the sense that the species composition is 'random' in Mekrijärvi whilst relatively constant in Lublin, but in neither regional community is the group composition more constant than the species composition. My interpretation of these figures is that at the lowest spatial level, where the numbers of colonies per local community (and hence sample) are small, random factors cause much variation and the pattern apparent in larger samples is less clear. The sample size was less than 500 per local community in Lublin, mostly less than 1000 per local community in Mekrijärvi, but mostly much greater than 1000 in the communities in Table 1.

Table 2. The observed and expected (randomized) similarity in the species and group composition in the 9 communities in Table 1 and in the local communities in Mekrijärvi and Lublin. The four groups are given in Table 1. The measure of similarity used is $PS=\Sigma \min(p_{ik},p_{jk})$, where p_{ik} is the relative abundance of species k in community i. The expected figures were calculated after once randomizing the observed abundances amongst the species independently for each community.

	Observed $PS \pm SD$	Expected $PS \pm SD$	n	t	P*
Nine communities in Table 1					
13 species	51±51	32±32	36	1.88	NS
4 groups	83±8	54±19	36	8.29	0.001
Mekrijärvi					
8 species	53±21	38±19	10	1.67	NS
4 groups	71±15	52±26	10	2.00	NS
Lublin					
7 species	66±16	30±17	15	6.10	0.001
4 groups	76±10	43±25	15	4.78	0.001

*Because the observations are not independent of each other, these are only approximately correct significance levels

If competition strongly affects abundances in local communities, one would expect that positively associated species (correlation coefficient positive) were better spaced out in proboscis length space than are positively associated species in the corresponding randomized data. There were fewer than expected positively associated pairs of species in Mekrijärvi (in 100 randomizations, three cases were equally or more extreme), but on the other hand such pairs were more numerous than expected in Lublin (2/100; note the related difference in Table 2). In neither regional community were the species pairs with $r>0$ unexpectedly well spaced out in proboscis length space. This suggests lack of *strong* competition affecting species' abundances in relation to their proboscis lengths.

6. Discussion

The core-satellite species hypothesis (Hanski 1982b) predicts that interspecific competition increases the probability of a species being or becoming a satellite species. The observed proboscis length relations in 12 bumblebee communities support this prediction, but other observations on niche shifts and abundance

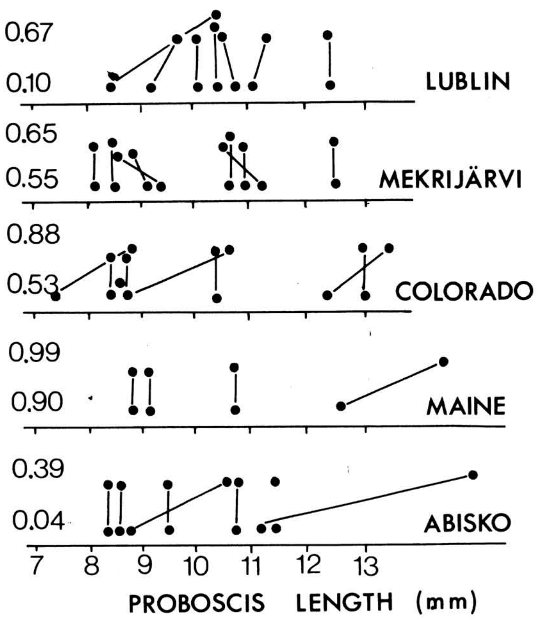

Fig. 4. Niche shifts suggested by the regression model in Section 3. The lower symbols are the original and the upper ones the 'corrected' proboscis lengths. The r^2 values refer to the corresponding regressions in Figs. 1 and 2.

relations may appear difficult to reconcile with this conclusion.

Results in Fig. 3 show relatively good spacing out of the core species in proboscis length space, but results in Fig. 4 suggest that the core species have shifted to form two or three relatively tight groups of species foraging on the same species of flowers. Nonetheless, these two results are not necessarily contradictory, because both the environment and competitors must affect a bumblebee's foraging decisions. In a certain local community, the short-tongued species may overlap 'too' much because one or a few of the flower species present is so profitable that it pays many individuals in each species to utilize it, notwithstanding interspecific competition. It is the average outcome over many local environments and many assemblages of competitors that determine species' probabilities of being or becoming a satellite species.

Ranta & Tiainen (1982) found that species in the local communities in Mekrijärvi were not better spaced out in proboscis length space than were randomly selected species. Local competition is not strong enough here to mould the structure of local communities quantitatively (species composition), thought I would expect competition to mould abundance relations qualitatively. The evidence (Section 5) does not support this exceptation, but more critical observations and experiments are needed.

Geographical and altitudinal replacements have been reported (or suggested) in *Bombus* (Løken 1950, Hänninen 1962, Thomson 1979, Inouye 1980, Lundberg & Ranta 1980, Pyke 1982). Complementary abundance changes found here (Tables 1 and 2) on geographical and regional scales support these earlier observations. Three interesting pairs of species in this respect are *Bombus lucorum- B. terrestris, B. hypnorum- B. pratorum*, and *B. lapidarius- B. pascuorum.*

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