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Foraging dynamics of two bumblebee species (B. lucorum and B. lapidarius) during one summer

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Foraging dynamics of *Bombus lucorum* and *B. lapidarius* was followed during summer 1979 at Mekrijärvi, eastern Finland. These species are close in terms of proboscis length (*B. lucorum* 9.3 mm, queens; *B. lapidarius* 10.3 mm) and they are the two most abundant species (43 % and 38 % of observations) out of the total of 11 species present at the study area. Food niche overlap vs. proboscis length differences suggest that species in this community cluster to those utilizing flowers with intermediate corolla tube depths and to those frequenting flowers with short corolla tubes. This corresponds to the frequency distribution of available corolla tube depths for bumblebees. In the course of the summer food niche overlaps between queens of *B. lucorum* and *B. lapidarius* are smaller than expected on the basis of random foraging on available flowers, while in workers observed weekly niche overlaps are mostly larger than expected, or not distinguishable from random foraging. During the summer *B. lucorum* has two peaks of abundance while *B. lapidarius* peaks only once (in between *B. lucorum* peaks). These periods of abundance coincide with the activity times of workers. It follows that the temporal overlap between workers is low (0.34) whereas queens (0.73) and males (0.78) overlap more intensively.

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1. Introduction

In summer 1978 Ranta & Tiainen (1982) studied species composition and niche relationships of bumblebees in seven study areas in Mekrijärvi village, eastern Finland. Regionally they found 11 species, though only five of them were abundant. Out of these five the two most abundant species, found in all study sites, were *Bombus lapidarius,* 42 % of 1978 observations, and *B. lucorum,* 21 %. These two species, though very close in terms of proboscis length (*B. lapidarius* 10.3 mm, 6.7 mm, 7.2 mm; *B. lucorum* 9.3 mm, 6.3 mm, 7.0 mm; queens, workers and males, respectively) coexist in high numbers both locally and regionally (see table 2 in Ranta & Tiainen 1982). In fact, in terms of proboscis length differences the two species are closer to each other than any average two-species combination of the total of 11 species (Ranta 1984).

The present study was planned to shed more light on the within-season dynamics of the two species (*B. lapidarius* and *B. lucorum*) interaction. In particular, we were interested in the foraging behaviour of the two species relative to the pattern and dynamics of resource availability. This study is a one-summer description of the foraging dynamics of the two species and their changes in numbers in the frame of available resources and the foraging ecology of other bumblebee species present at the study area.

2. Material and methods

The data were collected at Mekrijärvi village, Ilomantsi, eastern Finland (62°, 46′N, 30°, 58′E). The study area (site A in Ranta & Tiainen 1982) comprises an abandoned meadow and the yard of the Mekrijärvi Reseach Station, University of Joensuu. In total the area is 8.4 ha, and it is surrounded by oat fields; in the south and south-west it borders on Lake Mekrijärvi. Field observations on flowers and bumblebees were made between May 15 and August 31, 1979. Field work was done daily during the whole study period with the following exceptions when no observations were made: May 17-20, June 21-24, July 3-5, August 5-11 and 14-18.

2.1. Flowers

We noted the beginning and end of flowering of each flowering plant species in our study area using daily observations. In May, when the vegetation was poor, we established a permanent grid system (ca. 20×40 m) all over the study area, including a permanent transect circling the field. Using the grid system the coverage of plant species in flower were recorded at the beginning of each week. These data were then compiled into flowering maps, and total coverage (m^2) of each plant species in flower was then estimated planimetrically. At the beginning of each week we also estimated the number of flowers per m^2 for the flowering plants. A 25×25-cm square was randomly thrown 40 times on the areas where plant species were in flower (stratified sampling with four strata). All individual flower heads were counted. Combining the data on the areas covered by flowering plant species and the numbers of flowers per m^2 we obtained weekly estimates of individual flowers in our study area. When these estimates are applied for the flower species visited by bumblebees we obtain estimates of the resources available for bumblebees during the season (henceforth called flower or resource availability). Our sampling period does not include the peak phase of flowering of early season flowers (*Salix* spp., *Tussilago farfara).*

2.2. Bumblebees

Twice a month we collected specimens of all bumblebee species encountered at our study site using a standarized working effort (fixed route, 30 min. sampling with an insect net, two collectors). Captured bumblebees were identified in the laboratory. The sampling was done during four consecutive days, and pooled four-day catches are used here as estimates of relative abundances of the 11 bumblebee species in our study area (Table 1).

Our study site coincides with the known area of distribution of *B. sporadicus* and *B. cingulatus* (Pekkarinen et al. 1981). These species, when identified in the field by habitus can be confused with *B. lucorum* and *B. hypnorum,* respectively. Also, difficulties arise in field identification of *B. lapidarius* and *B. ruderarius.* However, *B. lucorum* and *B. sporadicus* are easily distinguished by differences in their flying sound. Secondly, an examination of preserved material from the study area (571 individuals collected in summer 1978) included 115 individuals of *B. lucorum* and 19 individuals of *B. hypnorum,* but none of *B. sporadicus* or *B. cinculatus.* In the preserved material 39 individuals (7 %) belonged to *B. ruderarius* and 153 to *B. lapidarius.* Thus, it is likely that our data, in which all species were identified in the field, may include some misidentifications. However, instead of using combined species names, e.g., *B. lapidarius/hypnorum* (c.f. Teräs 1976), we prefer to use the name of the locally dominant species, and we are confident that the conclusions drawn from the data are not detrimentally sensitive to this usage.

The length of a bumblebee proboscis is certainly of importance to their flower choice in nectar foraging. We therefore measured proboscis lengths of the species encountered in our study area. Subsamples of the 1978 material were taken for the measurements. Mouthparts were pulled out of dry individuals with forceps, softened in water and measured under a 12× dissecting microscope to the nearest 0.1 mm. Proboscis length is defined as the total length of prementum and glossa (Table 1). All measurements were made by HM. Though our sample sizes are small, we prefer to use our own data instead of the figures reported in Pekkarinen (1979) for two reasons. Firstly, Pekkarinen's data do not include all species encountered in our study area. Secondly, the bumblebee proboscis is subject to geographical variation (see Macior 1978, 1979). A comparison between our data and Pekkarinen's (1979) figures shows differences in proboscis lengths of some species. Whether this is due to differences in measuring criteria and methods, or due to geographical variation is unclear. We prefer to use our local measures.

Field observations of flower visits by bumblebees were made daily during two periods (900-1100 hours, 1300-1600 hours) always with two persons walking at a slow pace through the fixed transect. We observed flower visits by all bumblebee species (sexes and castes separated) in our study area, but special attention was paid to *B. lapidarius* and *B. lucorum.*

Table 1. Proboscis length (mm) and abundance lists of the 11 bumblebee species caught at half-month intervals (pooled 4-day samples, see text) during the summer 1979 at Mekrijärvi. Nomenclature of species follows Løken (1973).

Bombus	Proboscis length						Individuals per sampling period (%)						Total number
	Queens			Workers			31.5–3.6	16–19.6	29.6–2.7	16–19.7	30.7–2.8	19–22.8	
	Mean	*SD*	*n*	Mean	*SD*	*n*							
lucorum (L.)	9.3	0.3	9	6.3	0.4	18	22.2	10.4	45.8	56.3	9.2	73.0	631
lapidarius (L.)	10.3	0.8	10	6.7	0.5	20	51.9	45.4	31.2	29.1	79.0	23.8	561
hypnorum (L.)	9.2	0.5	6	6.3	0.3	9	-	13.4	4.1	1.9	0.5	-	56
jonellus (Kirb.)	8.1	0.7	4	6.2	0.5	14	-	5.9	9.9	0.5	-	-	53
pratorum (L.)	9.5	0.4	8	6.6	0.4	10	-	11.9	3.3	2.3	0.5	0.3	51
hortorum (L.)	14.5	0.6	4	9.9	0.7	6	-	5.6	2.5	1.4	4.1	0.5	37
pascuorum (Scop.)	11.0	0.7	6	8.1	0.9	8	11.1	3.0	-	3.3	2.6	0.8	26
veteranus (Fabr.)	10.6	0.5	7	8.3	0.3	9	3.7	3.3	0.5	1.4	2.6	1.3	25
soroeensis (Fabr.)	9.4	0.2	5	6.2	0.4	11	-	2.7	2.7	2.8	1.0	0.5	22
ruderarius (Müll.)	10.1	0.2	4	6.4	0.5	9	7.4	0.4	-	0.9	0.5	-	6
sylvarum (L.)	12.0	0.6	5	9.3	0.3	4	3.7	-	-	-	-	-	1
						Sample size	27	269	365	213	195	400	1 469

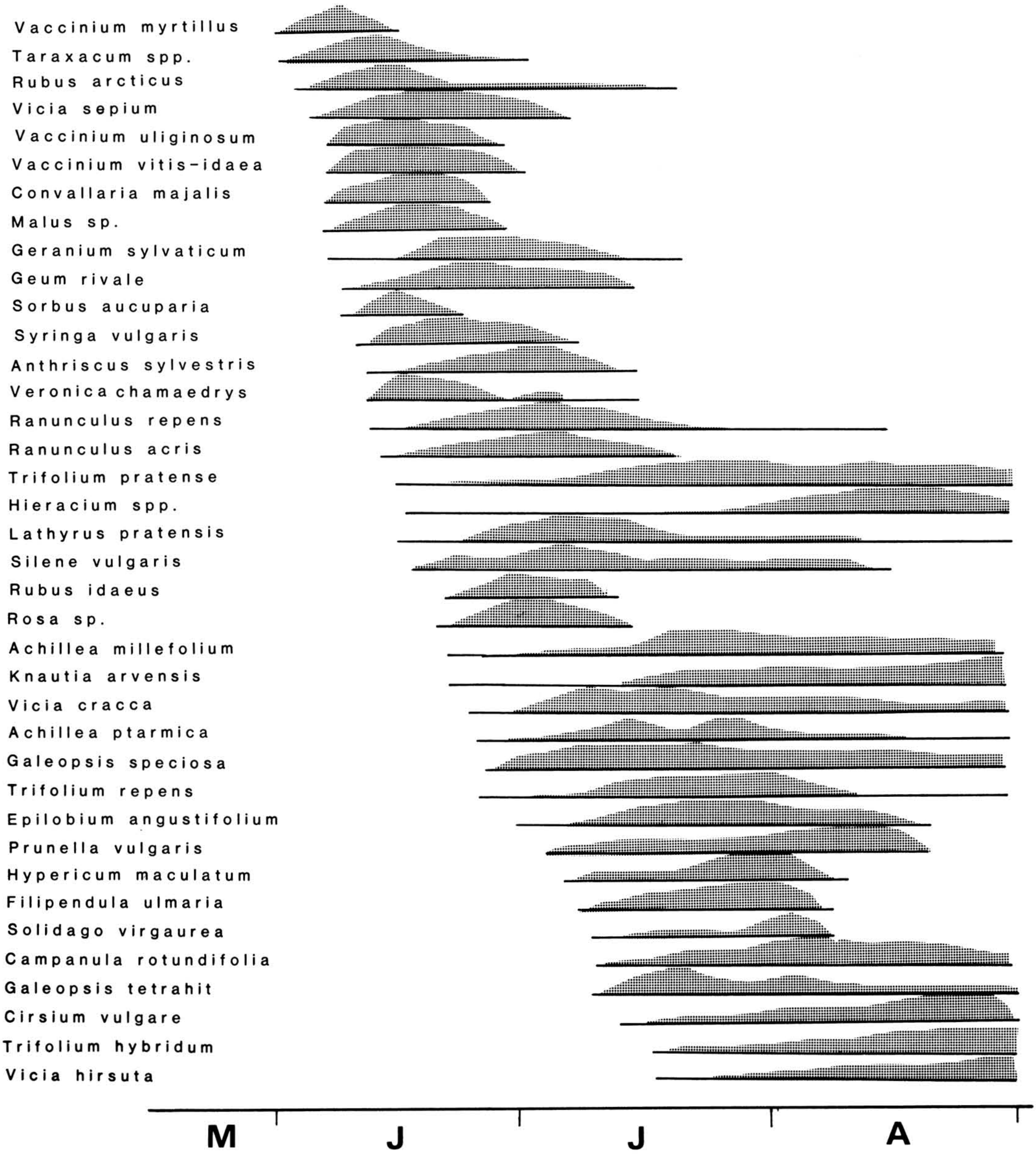

Fig. 1. Flowering phenology of bumblebee flowers at Mekrijärvi, 1979. The length of the flowering period and the daily intensity of flowering (maximum number of flowers per m^2 is scaled to 1.0 for each species) are shown for the flowering plant species (the early-season species, *Salix* spp., *Tussilago farfara,* are not shown).

3. Results

3.1. Phenology of flower resources

During the whole summer, 65 flowering plant species were observed in our study area; 41 of these species were observed to be visited by bumblebees (Fig. 1). The early season was characterized by a low number of species in flower, but after the first two weeks the number of plant species in flower increased rapidly (Fig. 2). A stable phase of 1.5 months began in the middle of June, having 21–23 "bumblebee flowers" in flower all the time. Though the number of bumblebee flowers decreased in August, it never fell below 15 species during the

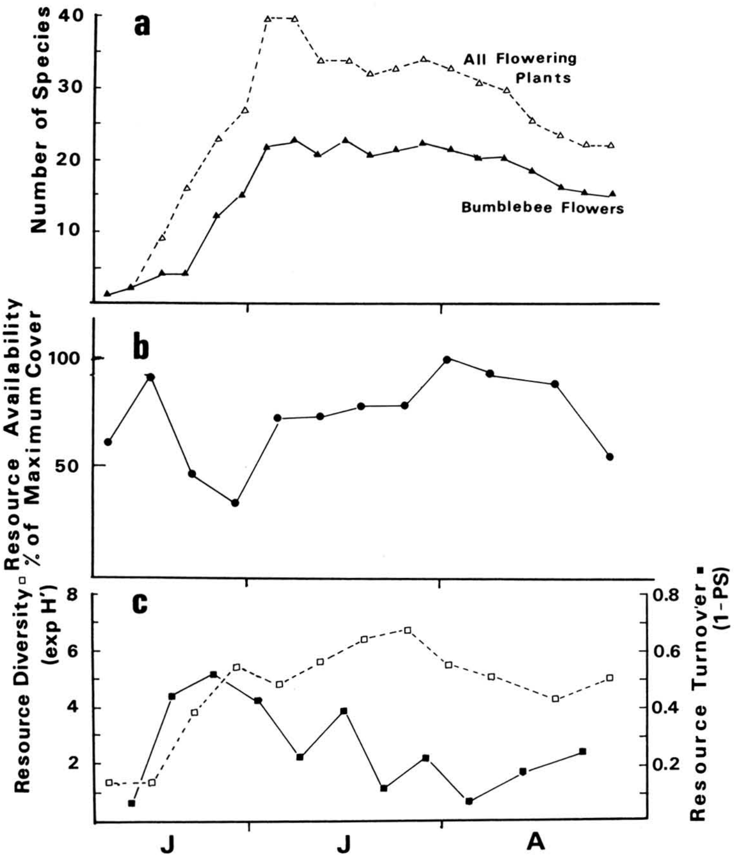

Fig. 2. Flower resource availability at the Mekrijärvi study site, 1979. (a) Seasonal changes in the total numbers of flowering plant species and bumblebee flower species at 5-day intervals. (b) Weekly abundance of all bumblebee flowers in the study area. The maximum number of flowers per m^2 (9th week) is scaled to 1.0 and the other observations are given as a fraction of this value. (c) Weekly diversity (open squares, diversity given as expH', where H' is the Shannon index) of bumblebee flowers. Black squares indicate turnover of flower resources (given as $1-PS$, where PS is the proportional similarity between consecutive weeks).

study period. Flowering phenologies of the bumblebee visited plants divide the summer clearly into two parts. Almost all early season species have a shorter period of flowering than those in flower in July and August (Fig. 1). The transition between the two periods takes place at the end of June, and it is also visible in the total numbers of flowers available, and the decreasing trend of resource turnover (Fig. 2). When the dominant early season flowers (especially *Taraxacum* spp.) wither away there is a low phase in the availability of resources. After the low phase the availability of flower resources recovered and remained at a fairly stable and high level to the end of the study period (Fig. 2).

Though the number of bumblebee flower species was 41, a few of them (*Taraxacum* spp., *Vicia sepium, Geranium sylvaticum, Vicia cracca, Lathyrus pratensis, Epilobium angustifolium, Trifolium repens, Trifolium pratense, Knautia arvensis* and *Hierachium* spp., in phenological order; all species rich in nectar, Käpylä 1978) had most visits by bumblebees.

3.2. Niche relationships

Only eight of the 11 species (*B. lucorum, B. lapidarius, B. hypnorum, B. pascuorum, B. jonellus, B. hortorum, B. pratensis* and *B. veteranus*) were so abundant that weekly observations of their flower visits are available for the whole season. Our particular interest in this connection is the development of interspecific niche relationships during the summer. Weekly data matrices (8 bumblebee species, 12 weeks, n_i flower species) were ordinated with the detrended correspondence analysis (Gauch 1982). Eigenvalues of the 1st axis ranged from 0.25 to 0.99, and those of the 2nd axis were considerably lower (0.02-0.12). Consequently, ordination scores on the 1st axis for the 8 species were assumed to reflect sufficiently well the position of the species' niches in the resource space of flowers visited. To analyse the significance of proboscis length as a niche segregating factor we proceeded as follows. The eight species were arranged in order of increasing proboscis length and their

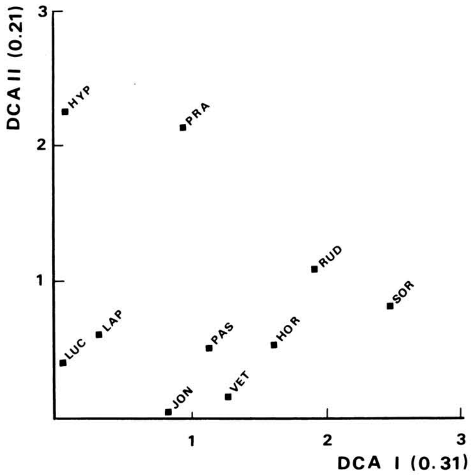

Fig. 3. Detrended correspondence analysis ordination of the pooled whole season flower visits (41 flower species) of the 10 most abundant bumblebee species (for full names of the species, see Table 1). Identification of the 1st DCA-axis (eigenvalues in parentheses) is: high negative scores for the following plant species (*indicates deep corolla tube) *Rubus idaeus, Vaccinium vitis-idaea,* * *Vicia cracca, Achillea millefolium, Ranunculus acris* and *Anthriscus sylvestris,* species with high positive scores are *Campanula rotundifolia, Hierachium* spp., * *Trifolium hybridum,* * *T. pratense,* * *Vicia sepium, Knautia arvensis* and * *Lathyrus pratensis.* Correspondingly * *Prunella vulgaris, Vaccinium myrtillus, V. uliginosum* and *Solidago virgaurea* scored high negative values on the 2nd axis, while *Sinapis arvensis,* * *Galeopsis tetrahit, Convallaria majalis, Epilobium angustifolium* and *Taraxacum* spp. scored high positive values.

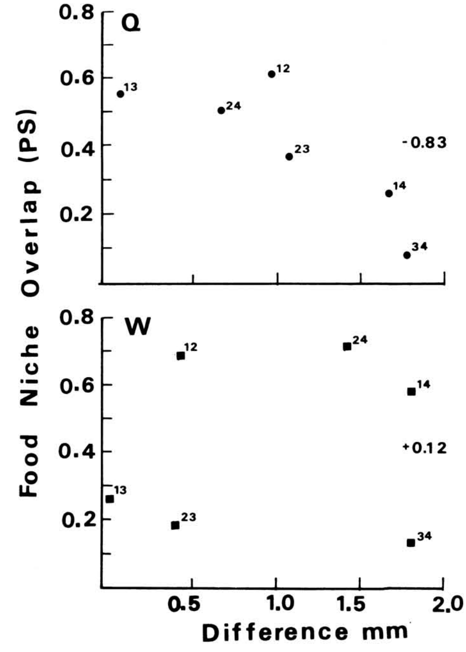

Fig. 4. Relationship between niche overlap and proboscis length differences of species pairs in queens (Q) and workers (W) of the species (1) *B. lucorum,* (2) *B. lapidarius,* (3) *B. hypnorum* and (4) *B. pascuorum.*

corresponding DCA scores on the 1st axis were ranked for each week. We then compared the agreement among the 12 weekly rankings with the nonparametric Kendall's coefficient of concordance (W), thus calculated $W = 0.13$, which is not statistically significant (queen proboscises $\chi^2 = 11.42$, worker proboscises $\chi^2 = 8.39$, $df = 11$). The analysis suggests that on a weekly basis there are no good indications of the role of proboscis length differences as a niche segregating factor among the eight bumblebee species.

Our next task was to discover whether the pooled whole-season data on flower visits of the eight bumblebee species gave any indication of proboscis length related foraging patterns. We ordinated the pooled data (41 flower species, 8 bumblebee species) with the detrended correspondence analysis. The first axis has an eigenvalue of 0.31 and the second one of 0.21. As shown in Fig. 3 both axes include flower species with both short and long corolla tubes. Furthermore, the species with the longest proboscis (*B. hortorum*) scored in a very similar way to the species having either a short or intermediate proboscis length (*B. jonellus, B. pascuorum, B. veteranus*). Thus, again most of the species locations in the ordination space do not clearly support foraging similarities (or dissimilarities) related to proboscis length.

To illustrate foraging niches of bumblebees related to proboscis length in more detail we studied flower visits by queens and workers of the species *B. lucorum, B. lapidarius, B. hypnorum* and *B. pascuorum,* for which there were enough data. Niche overlaps between these species were calculated separately for queens and workers using the index of proportional similarity as a measure of niche overlap. The significance of proboscis length differences in flower selection among queens and workers is given in Fig. 4, where observed niche overlaps between species pairs are given against differences in their proboscis lengths.

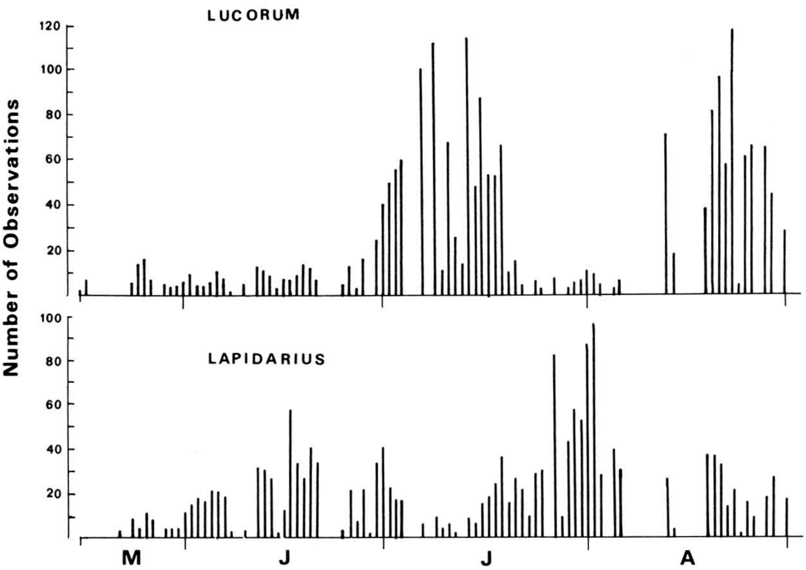

Fig. 5. Daily numbers of observations of *B. lucorum* and *B. lapidarius* during summer 1979 at Mekrijärvi.

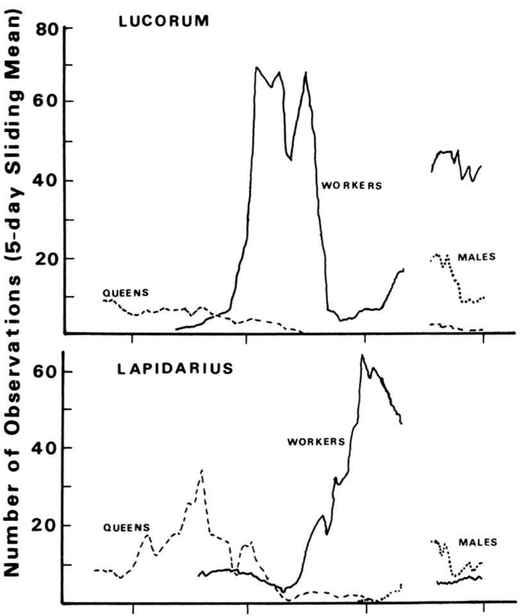

Fig. 6. Numbers of observations of queens (broken line), workers (solid line) and males (dotted line) of *B. lucorum* and *B. lapidarius* during the summer 1979 at Mekrijärvi (the lines are drawn on the basis of 5-day moving averages).

In queens there is a decreasing trend in niche overlap with increasing difference in proboscis length, while no such correlation is to be seen in workers (Fig. 4). In other words, queens with similar proboscises tend to converge in their flower choice. This is, in fact, what is expected for simple mechanical reasons in foraging (long proboscis for deep corollas, short proboscis for short corollas). Possible competitive interactions between species should distort the trend. Whether this is the explanation in the case of workers remains unclear with the present data.

3.3. Bombus lucorum and Bombus lapidarius

Seasonal changes in numbers

We used the daily total numbers of observed bumblebees as an index of the abundance of the two species in the study area (Fig. 5). Usually, the numbers were low at the beginning of the summer, but they soon increased above 30 observations per day, and the maximum numbers were seen from the beginning of July onwards (Fig. 5). Because of rains and cold or windy periods the numbers of bees observed daily varied somewhat. In general, *B. lapidarius* observations were more evenly distributed over the whole observation period (Fig. 5). This

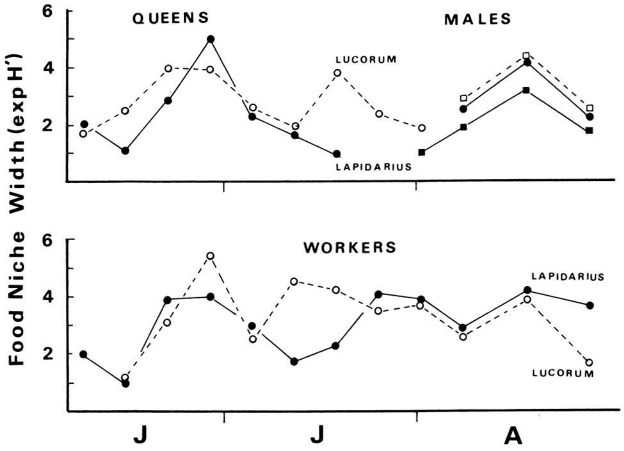

Fig. 7. Weekly food niche widths of queens, workers and males of *B. lucorum* (open symbols) and *B. lapidarius* (closed symbols). The niche width is given as expH', where H' is the Shannon function.

species dominated in numbers until the end of June when the first generation of *B. lucorum* workers emerged. The period of numerical dominance by *B. lucorum* was short and intensive (between July 1 and July 18) after which *B. lapidarius* again became numerically dominant. The second peak of *B. lucorum* activity coincided with the second half of August (Fig. 5).

When the seasonal changes in the numbers of the two species are examined at the level of sexes and castes (Fig. 6), it becomes obvious that the proportion of queens in *B. lucorum* was much lower (11 % queens, 82 % workers, 7 % males) than in *B. lapidarius* (36 %, 58 %, 6 %). At the level of sexes and castes the temporal segregation of the two species was very pronounced, i.e., when *B. lapidarius* decreased in numbers *B. lucorum* increased, and vice versa. The temporal overlaps between *B. lucorum* and *B. lapidarius* was 0.73 in queens, 0.34 in workers and 0.78 in males. When the temporally shifting abundance pattern of the two species was first noted in the study area we increased our surveys in the nearby fields. Our surveys confirm that the temporal abundance pattern of the two species was similar in a large number of fields at least within the area of Mekrijärvi village.

Foraging dynamics

In the analysis of weekly niche widths of queens, workers and males of *B. lucorum* and *B. lapidarius,* two different measures were applied. Firstly, the niche width for each week was calculated as the exponential form of the Shannon index of diversity (expH'). This measure indicates the numbers of flower species the bumblebees visit in "equal proportions", and thus expH' is a better index of niche width than a direct number of flower species visited weekly, as it also takes into account the frequencies of visits to different flower species. In general, niche widths calculated in this way varied between 1 and 5 (Fig. 7). Of course there were changes in the expH' values during the season but no clear trends were to be seen, and the difference between queens, workers and males both within and between species are not statistically significant.

Secondly, as we have weekly data on the availability of different flower species at our study area, we also estimated niche widths by using the index of proportional similarity

$$PS_i = \Sigma \min (Ph_i, Ph),$$

where PS_i is the niche width of the *i*th species, and Ph_i is the proportion of the *h*th flower species in the diet of the *i*th bumblebee species. Correspondingly, *Ph* is the proportion of the *h*th flower species of all flower species available in that week. Low values of the index (range 0–1) indicate specialization on a certain subset of flowers, and high values indicate that the bees foraged indiscriminately on the flowers, in the proportions in which they were available in the field. The two measures of niche width certainly indicate different things, both providing information on how bumblebees behave while foragin.

At the beginning of the summer queens forage quite widely on what is available, but the breadths of the niches of queens of the two species decrease with time (Fig. 8). The trend indicates that queens tend to become more selective in

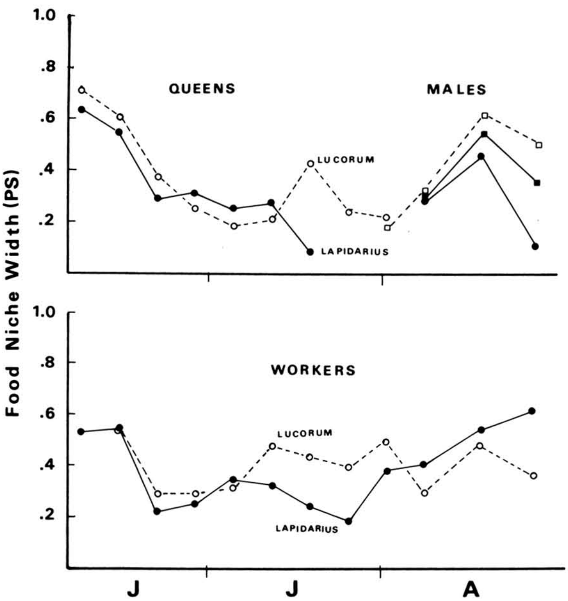

Fig. 8. Weekly food niche widths of queens, workers and males of *B. lucorum* (open symbols) and *B. lapidarius* (closed symbols). The niche width is given with the index of proportional similarity as compared to the availability of resources (see text).

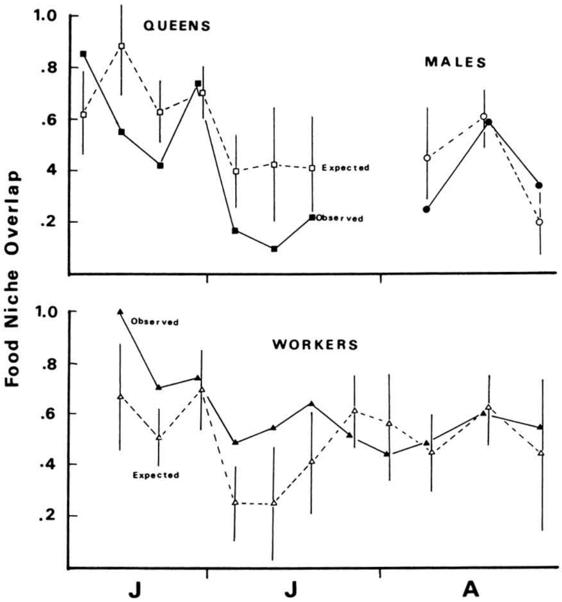

Fig. 9. Observed (closed symbols, solid line) and randomized (open symbols, broken line; vertical bars indicate ± one standard deviation) niche overlaps between queens, workers and males of *B. lucorum* and *B. lapidarius.*

their flower visits as the summer proceeds. No such trend is to be seen in workers of the two species. With a few exceptions *B. lapidarius* workers have a wider spectrum of utilized flowers than *B. lucorum* workers in relation to the availability of the flowers, though the between species differences were prominent only for a short period in July. Note that this phase coincides with the part of the summer when *B. lapidarius* was low in numbers (Figs. 8 and 6). Otherwise this analysis of niche widths suggests that the two species (both queens and workers) are fairly selective in their flower usage (niche widths frequently less than $PS = 0.5$).

Niche overlaps between the sexes and castes of the two species were calculated by using the index of percentage similarity as a measure of niche overlap. The availability of different flower species was taken into account by weighting for different resource categories, as suggested by Sale (1974). From the weekly matrices of weighted observations we calculated observed niche overlaps between the two species. Matrix cell randomizations were done 100 times and expected niche overlaps (with standard deviations) were then computed. These computations were made separately for sexes and castes for all the 12 weeks we have observations of flower visits (Fig. 9). In the analyses flower species with such deep corolla tubes that were not observed to be visited by queens, workers or males, respectively were excluded from the corresponding "availability" matrices.

For the most of the season workers of the two species tend to forage on the flowers more similarly than expected on the basis of the "random" model of foraging. In other words, workers of *B. lucorum* and *B. lapidarius* tend to converge towards each other while foraging. In queens the differences between "random" foraging and observed foraging were the opposite when compared to workers. Only a few of the differences between observed and expected niche overlaps are statistically significant (Fig. 9). In the late season workers of *B. lucorum* and *B. lapidarius* foraged as expected on the basis of the "random" model of foraging, thus suggesting that the species do not avoid the resource flowers utilized by one of them.

The data collected on resource availability and resource utilization provide a possibility to study in closer detail how bumblebees utilize flowers of

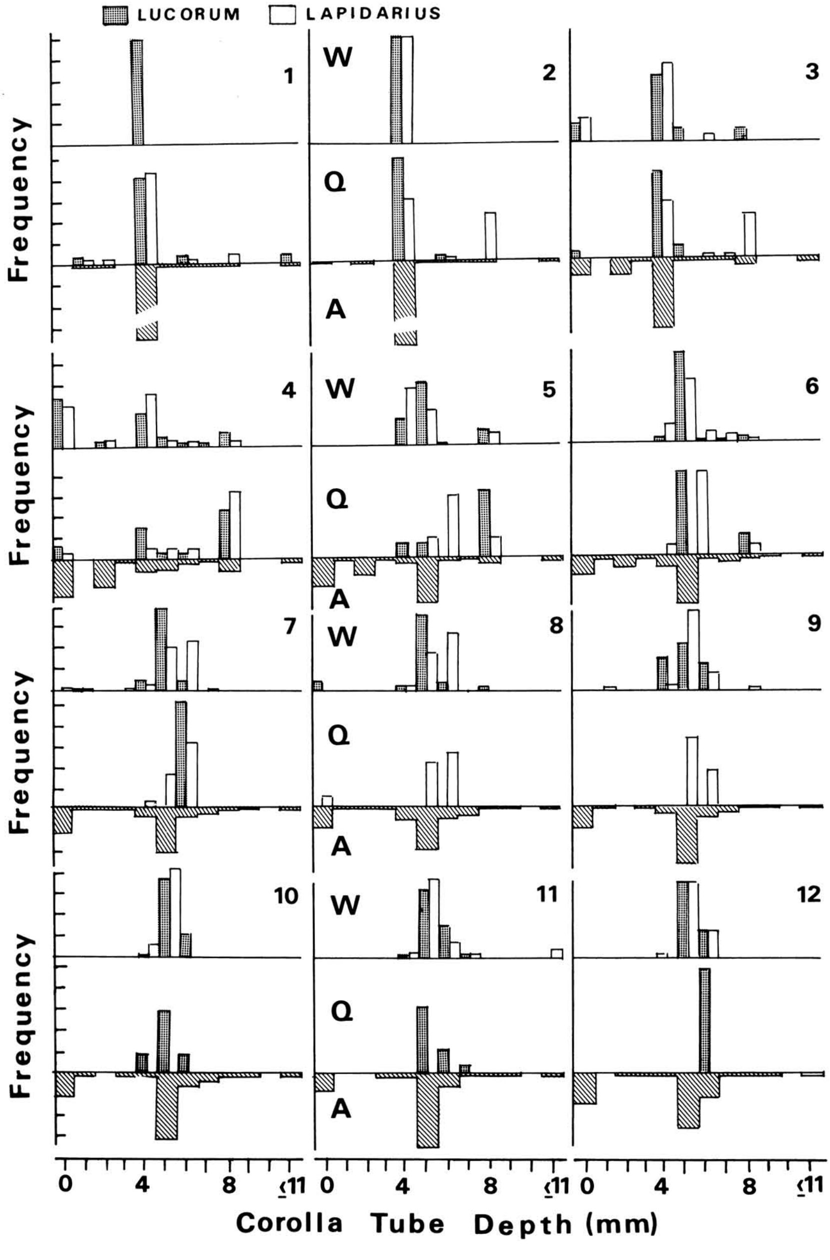

Fig. 10. Corolla tube depths available (A) and utilized by queens (Q) and workers (W) by the two bumblebee species, *B. lucorum* and *B. lapidarius*, at weekly intervals in summer 1979, Mekrijärvi.

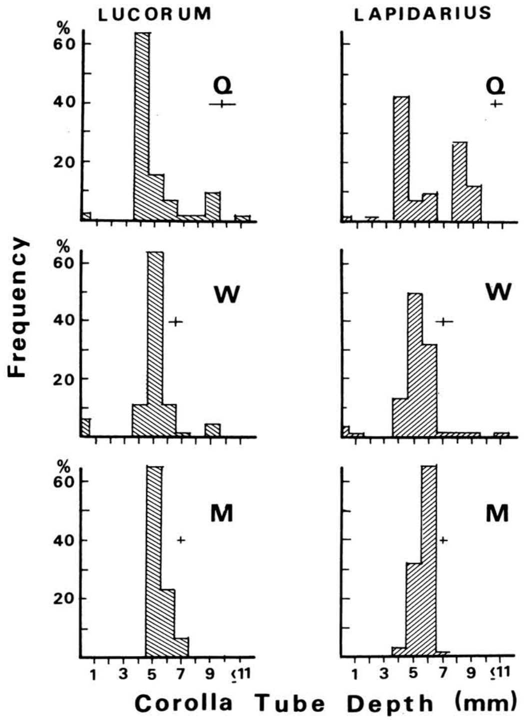

Fig. 11. Frequency distribution of utilized corolla tube depths (pooled whole-season data) by queens (Q), workers (W) and males (M) of *B. lucorum* and *B. lapidarius* (mean and range of proboscis lengths are indicated)

different corolla tube depths. For the species pair *B. lucorum* and *B. lapidarius* the dynamics of corolla tube depth utilization during the 12 study weeks is depicted in Fig. 10. There were no very pronounced differences in the availability of flowers (in terms of corolla tube depths) during the course of the season. Though the diversity was highest in the middle of the season, the corolla tube depth classes from 4 to 6 mm were predominant throughout the summer (Fig. 10). Queens and workers of the two species, irrespective of proboscis lengths, reflected the availability fairly well. In other words, bumblebees are opportunists that utilize what is available, and so shifts in foraging patterns occur.

Pooled histograms of the utilized corolla tube depths are given for queens, workers and males of the two species (Fig. 11). Although bumblebee species and castes differ in terms of proboscis lengths (especially queens vs. others), the corolla tube depths of resource flowers are not deeper in early summer, when only queens forage, than in the middle or late summer when workers and males, with shorter proboscises, are foraging. In fact, most of the flowers with deep corollas flower in the middle and late summer (Fig. 10). Neither queens nor workers of either species differed much in the ranges of corolla tube depths utilized. The mode depth class was 4 mm in queens and 5 mm in workers. Males of both species show a much closer match between proboscis lengths and utilized corolla tube depths than queens or workers (Fig. 11). These data suggest that within-species (i.e., between sexes and castes) differences in proboscis lengths have little or nothing to do with the avoidance of intraspecific competition for resources in bumblebees. Furthermore, they raise a question: Why do bumblebee queens have such long proboscises?

4. Discussion

The modern theory on competition and coexistence of species is well elaborated (e.g., MacArthur 1972, Pianka 1981, Pontin 1982). However, we frequently encounter field observations that are inconsistent with the theory. For example, there are no doubts that the length of a bumblebee proboscis affects the rewards obtained in foraging from flowers with different corolla tube depths. Thus, bumblebees with similar proboscis length are expected to forage on flowers with corresponding corolla tube depths (Morse 1978, Inouye 1980, Ranta 1983, Harder 1983). On the other hand, competition arguments suggest that no two similarly foraging bumblebee species are expected to coexist. In the nature the opposite seems rather to be true as abundant species in most bumblebee communities are, on average, more close in terms of proboscis length than a corresponding number of species drawn randomly from the species pool (Ranta 1984). Thus, to proceed we examined in closer detail the ways of coexistence of the two abundant and sympatric bumblebee species (*B. lucorum* and *B. lapidarius*) during one summer in a single study area.

4.1. Evidence for interspecific competition?

Wide spacing in morphological characters between species is generally evoked as evidence for competition (see Wiens 1982 and Simberloff

1983 for critical reviews). However, in this community the two most abundant species, *B. lucorum* and *B. lapidarius,* fit the non-competitive trend in niche overlap vs. proboscis length difference graphs (especially workers), while on the basis of their high abundances and small proboscis length difference the expectation should be for intensive competition (Connell 1980, Hanski 1982a, b) and niche differentation. However, observed niche overlaps between workers of the two species as compared to the randomized overlaps (Fig. 9) support, if anything, the non-competitive argumentation.

Another conceivable mechanism enabling the coexistence of two otherwise similar species would be temporal difference in colony cycles. It would be tempting to suggest that phenological differences in population dynamics of *B. lucorum* and *B. lapidarius* as reported here are due to interspecific competition. However, not much can be concluded on the basis of a single observation. To establish whether or not this mode of seasonal segregation is a result of competition, a study should be carried out with replicated observations and varying species composition. Besides our data, a temporal difference (though considerably weaker) in activity between *B. lucorum* and *B. lapidarius* is shown in Teräs (1976) at Puumala, central Finland (in his data *B. lucorum* has a similar and clear bimodality in numbers as in our data while *B. lapidarius* has a single population peak). Teräs (pers. comm.) has studied seasonal changes in bumblebee numbers with mark-recapture methods at Lammi, southern Finland, for two years. Although his data include these species, even in abundance, no such differentation in time was observed. Nor do we find this type of temporal differentation among the six most abundant species in a northern Swedish bumblebee community at Abisko, where the observation period also covered the whole summer (Ranta & Lundberg 1981).

B. lucorum is widely distributed all over Fennoscandia, while *B. lapidarius* is more restricted to the southern parts of the area (Løken 1973, Pekkarinen et al. 1981). One can suspect that the range of different climatological conditions encountered by *B. lucorum* has a bearing on the observed bimodality in numbers. Perhaps the species is better adapted to northern conditions than *B. lapidarius,* and this is reflected as a production of the second peak of workers in the late summer. Due to lack of data the question remains open, however.

4.2. Coexistence of bumblebees with similar proboscis lengths

Aggregation of bumblebee species with proboscises of intermediate length is commonplace (8 out of 11 species here are between 9 and 11 mm; Ranta 1984, and references there). Our data on the availability of resources (in terms of corolla tube depths) demonstrate that most of the flowers utilized by bumblebees had intermediate corolla tube depths (4-6 mm). The frequency distribution of corolla tube depths was fairly stable throughout the summer (Fig. 10). As resources are not evenly distributed, one would expect the majority of bees to be clustered around the dominant resource category. It is unclear to us why none of the species was competitively able to monopolize the dominant intermediate (4-6 mm) corolla tube depths. Spatio-temporal unpredictability of resources is evoked as a tentative explanation for the high species richness of bumblebees with similar proboscises in northern and temperate bumblebee communities (see Ranta & Vepsäläinen 1981, Ranta 1982 for further discussion of the topic).

Bumblebees with similar proboscises can coexist if they prefer a subset of flowers "available" to them. In workers of the two species no diet differentation was documented, while in queens this mode of resource partitioning was observed during the first half of the season. This provides modest support for ecological segregation between the species. However, as workers do most of the foraging for sexual offspring of queens, the reproductive output of a queen bumblebee depends on how well her workers find nectar and pollen. Recall that the temporary overlap between *B. lucorum* and *B. lapidarius* workers was 0.34. If no good competitive differentation between foraging niches of *B. lucorum* and *B. lapidarius* workers are to be seen, it might be a result of the temporal differences in timing of the worker generation activities, or that resources were in abundance. Unfortunately, we lack the data to demonstrate how much nectar and pollen was available daily to the bumblebees. Heinrich (1976) suggests that up to 92 % of the daily nectar crop is depleted by bumblebees, thus indicating a shortage of resources. An indirect evidence of scarcity of nectar is the short time bumblebees spent per a single flower while foraging (Inouye 1980, Ranta 1983). If the amount of nectar available is experimentally increased, bumblebees spent considerably longer times on flowers while emptying the nectar volume (Heinrich 1978, own observations).

Bumblebees are typical "central place foragers" (Orians & Pearson 1979) where foraging bees leave and return to the nest. Energetic costs of flying set the constraints on how far it pays to fly for nectar. Good nectar sources are worth long-distance flights, but nectar-poor flowers are worth visiting only at short distances. If most of the flowers are low in nectar (as is the case with most of the flowers in temperate areas) the distribution of foraging flights is expected to be skewed on short distances. It follows that each nest depletes nectar and pollen from a certain area surrounding the nest, i.e., no bee from far-away nests gains in foraging these areas. Furthermore, if no obvious species specific differences exist in nest site selection, nests of different species are randomly scattered in the flower fields. It follows that different species are observed to visit more or less the same flower species (in the extreme cases "random processes" in nest foundation might determine the forthcoming diet of the colony), i.e., observed foraging niches between species overlap considerably. If correct, the reasoning above suggests that small scale studies (viz., areas around bumblebee nests) on bumblebee foraging, together with field experiments, would improve our understanding of species coexistence and of possible competition among bumblebees.

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