文 (Original article) 論

Pollen utilization by Bombus hypocrita sapporoensis colonies in fragmented forest landscapes in Hokkaido, Japan

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Abstract

Pollen utilization by three colonies of Bombus hypocrita sapporoensis nesting in fragmented forests was investigated in Hokkaido, Japan. The colonies in different landscapes used pollen of wild plants, crops, and garden plants in different proportions. The fraction of pollen volume of garden plants was highest in a landscape where the residential area was largest among the three nest sites. The fraction of pollen volume of wild plants was highest in a landscape in which the relative area of natural vegetation was smallest and that of the agricultural area was largest, probably because wild trees in the forest inhabited by the colony supplied sufficient pollen. The fraction of the pollen volume of crops was highest in a landscape in which the agricultural area was intermediate, possibly because entomophilous crops were abundant in this area. These results suggest that bumblebees nesting in fragmented forests use pollen of cultivated plants around the nest sites corresponding to the landscape structure.

Key words : Bombus hypocrita sapporoensis, habitat fragmentation, landscape structure, pollen diet

Introduction

Bumblebees are important pollinators of many wild and cultivated plants (Corbet et al., 1991). Thus, pollination of these plants is potentially affected by both a decrease in the density of bumblebees and a change in their foraging behavior. Small and isolated plant populations in fragmented habitats may suffer from few flower visits by bumblebees because such habitats harbor few bumblebees and/or because the flowers in such habitats are less attractive to bumblebees (Matsumura & Washitani, 2000). The fruit set of an understory perennial, Corydalis ambigua, mainly pollinated by bumblebees, was lower in more isolated forests, and the low fruit set was caused by pollinator limitation (Yasaka et al., 1994). In order to understand the effects of habitat fragmentation on pollination systems of plants and bumblebees, the utilization of flowers by bumblebees should be examined in fragmented habitats.

Habitat fragmentation caused by agriculture and urbanization may lead to a reduction in the abundance of bumblebees due to declines in suitable foraging and nesting sites. In recent decades, the density of bumblebees has declined in Europe and North America, which is probably linked to increases in agricultural

fields and changes in farm management (Buchmann & Nabhan, 1996). The spatial and temporal distributions of flower patches in such farmlands are likely to make floral resource dynamics unstable in a foraging range for bumblebees. Discontinuous flowering phenology due to loss of natural vegetation results in temporal shortages of floral resources (Walther-Hellwig & Frankl, 2000). Because bumblebees require a continuous food supply throughout the period of colony growth, such unstable floral resources may arrest the colony growth. The effects of farm management schemes on bumblebee colony growth have not been demonstrated in field experiments (Goulson et al., 2002), probably because bumblebees foraged over a larger spatial scale than that of the experiments (Cresswell et al., 2000; Osborne et al., 1999). Although distribution of foragers has been investigated in various vegetations of arable fields (Pywell et al., 2005), floral resources of colonies have rarely been studied in farmlands that consist of natural and artificial vegetations.

Bombus hypocrita sapporoensis Cockerell is a common bumblebee species in Hokkaido, Japan. This species has a shorter tongue than other Japanese bumblebee species and prefers shallow flowers to deep flowers (Inoue & Kato, 1992). This species tends to

原稿受付:平成16年11月5日 Received Nov. 5, 2004 原稿受理:平成17年2月8日 Accepted Feb. 8, 2005

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inhabit forests in the mountain outskirts (Sakagami & Katayama, 1977) and is abundant at the high elevation in the northern Tokachi district, Hokkaido (Saito, 1995; Usui et al., 1976) although its nests have been found outside of forests in lowlands (Nakajima et al., 2004). If *B. hypocrita* prefers forests as foraging habitats, forest fragmentation in farmlands may affect floral resource utilization of this species.

In this study, we tested the hypothesis that the landscape structure of vegetation around nests of *B*. *hypocrita* affects its pollen utilization. First, we surveyed and collected *B*. *hypocrita* nests in fragmented forests and described the landscape structure around the nests using GIS analysis on a vegetation map. Next, we observed pollen diets of colonies of the collected nests and tested whether the pollen assemblages differed among the nests. Finally, we examined correspondences between the habitats of pollen source plants that were unique among the nests and the vegetation that characterized landscapes around the nests.

Materials and Methods

Nests

We found three nests (denoted as A, B, and C) of *Bombus hypocrita sapporoensis* in Obihiro, Hokkaido (Fig. 1). We collected these nests from the fields and preserved them at 4°C.

Nest A was located in a spruce (*Picea jezoensis*) plantation (4.0 ha) between a university campus and a river surrounded by farms and residential areas (42°52.4' N, 143°10.4' E, altitude 76 m). This nest was found in a wooden birdhouse 3 m above the ground. The nest, which was collected on 1 August 2000, contained about 80 cocoons.

Nest B was located in an old secondary forest (1.6 ha) dominated by *Quercus dentata* with 20-30 cm in diameter at breast height, near an agricultural experimental station surrounded by farms (42°53.1' N, 143°5.3' E, altitude 87 m). This nest was made in a rat-hole 30 cm below the ground beside roots of an oak tree. This nest was collected on 2 August 2000 and consisted of about 500 cocoons.

Nest C was located in a young secondary forest (1.0 ha), which was dominated by *Betula platyphylla, Ulmus davidiana, Quercus dentata,* and *Salix sachalinensis* with 5-20 cm in diameter at breast height. Farms, windbreak forests, and a river with riparian forests surrounded the nest site (42°43.2' N, 143°9.4' E, altitude 165 m). This nest was found in a rat-hole 50 cm below the ground beside the roots of a birch tree. The nest, which was collected on 31 August 2001, contained about 300



Fig. 1. Vegetation map around three sampled nests of *Bombus hypocrita sapporoensis* in Obihiro, Hokkaido. Natural vegetation (black), tree plantation (dark gray), agricultural area (medium gray), residential area (light gray), and other areas (white) are shown. The locations of nests and circles within a 4 km radius from the nests are also shown.

cocoons.

Landscapes

In order to describe the landscapes around these nests, we created a vegetation map (Fig. 1). The Third Vegetation Survey, a part of the National Survey on the Natural Environment of Japan (Environment Agency of Japan, 1988), provided this vegetation map, which consisted of 24 plant communities and other lands in the study area (Table 1). These plant communities were classified based on flora lists recorded from several plots investigated from 1983 to 1986. We categorized 11, 3, 5, and 5 plant communities into four vegetation types: natural vegetation, tree plantation, agricultural area, and residential area, respectively (Table 1). We drew 20 concentric circles within a 0.2-4.0 km radius from the nests at intervals of 0.2 km. We calculated the

Table 1. Vegetation types and plant communities in circles with a 4 km radius from three Bombus hypocrita sapporoensis nests.

Vegetation type		Area (km ²) around nest					
Plant community	Codea	А	В	С	Total		
Natural vegetation		5.93	4.59	5.25	15.78		
Acer mono and Tilia community	42	0.02	0.04		0.06		
Ulmus davidiana community	47	1.10	1.00	1.21	3.31		
Tall Salix commnity	48			0.08	0.08		
Short Salix community	51	0.18	0.92	1.79	2.89		
Alnus japonica and Fraxinus mandshurica community	54			0.03	0.03		
Quercus community	66	0.40	0.38	1.08	1.87		
Betula platyphylla and Sasa community	70		0.01		0.01		
Logged area	78	0.37	0.27	0.91	1.55		
Secondary forest after logging	81	0.13	0.59	0.11	0.84		
Various grassland	82	3.71	1.36	0.04	5.11		
Phragmites communis grassland	87	0.01	0.02		0.03		
Tree plantation		2.06	2.08	3.83	7.97		
Deciduous conider plantation	103	1.62	2.08	3.77	7.47		
Exotic conifer plantation	104	0.02			0.02		
Deciduous broad-leaved tree plantation	105	0.42		0.06	0.48		
Agricultural area		27.45	40.15	37.46	105.05		
Nursary	109	0.32			0.32		
Farm	110	23.56	38.54	36.58	98.68		
Abandoned farm	111	0.18	0.21		0.39		
Pasture	112	3.39	1.21	0.88	5.47		
Paddy field	115		0.18		0.18		
Residential area		12.91	2.86	1.44	17.22		
Golf cource	113	0.01			0.01		
Airport	114	0.55			0.55		
Urban area	119		0.11		0.11		
Suburban area	120	11.66	2.14	1.17	14.96		
Industrial area	121	0.69	0.62	0.28	1.59		
Others		1.91	0.58	2.28	4.78		
Developed tract	122	0.35	0.11	0.33	0.79		
Water area	123	0.69	0.19	1.16	2.04		
Bare land	124	0.87	0.29	0.79	1.95		
Unknown area		0.00			0.00		
Total		50.27	50.27	50.27	285.82		

a: plant community codes in the Report of the Third Vegetation Survey in Hokkaido (Environment Agency of Japan, 1988).

areas of the four vegetation types within a circle with a 0.2 km radius and 19 doughnut-shaped areas with a 0.2 km width between the concentric circles using ArcView GIS software. We plotted the relative areas of the four vegetation types against the distance from the nests.

Pollen analysis

Bumblebees store food both in cocoons after pupae have emerged and in pots made entirely from wax (Sakagami & Katayama, 1977). Post-emergence (old) cocoons used for food storage are usually coated with wax. In order to collect pollen samples from nests, we selected both old cocoons coated with wax and pots made from wax in the three nests. These cocoons and pots were scattered in multi-layered nests. We sampled 10 cocoons or pots randomly from each of the three nests that had been preserved after collection from the fields. We collected walls (about 20 mm^2 area) at the base of the sampled cocoons or pots with debris inside of them.

We acetolysed these samples and mounted pollen grains from the samples in silicon oil on slides (Erdtman, 1960). Fifty pollen grains randomly selected from each slide were examined under a light microscope, and the plant taxa of the pollen grains were identified according to the literature (Nagamitsu & Nagamasu, 1994; Nakamura, 1980a, b). The Kruskal-Wallis test was used to determine whether the number of pollen grains of each plant taxon differed among the nests. These tests were conducted for plant taxa of which more than nine pollen grains were observed. The levels of statistical significance of multiple tests were corrected by the Bonfferoni method.

Pollen source plants

The pollen source plants identified at the genus or species level were classified into four categories: wild plants, crops, garden plants, and others (Table 2).

This classification was based both on the presence

in flora lists of plant communities and on the cultivation status in the study site. First, we counted the number of plant communities in each of the three vegetation types: natural vegetation, tree plantation, and agricultural area, in which each pollen source plant was recorded in the flora lists (Environment Agency of Japan, 1988). The flora lists of plant communities in the residential area

Table 2. Plant taxa of pollen grains found in three *Bombus hypocrita sapporoensis* nests. Most plant taxa are classified into four categories based on the number of plant communities for which the flora lists consist of the plant taxa and the cultivation status of the plant taxa. Differences in the number of pollen grains among the three nests are tested in several plant taxa (Kruskal-Wallis test). The mean pollen volume of each plant taxon is also shown.

	Cat- No. of			Cultiva-	No. of pollen grains			Pollen		
Plan taxa	egory	communities ^b		tion	Nest				volume	
	a	Ν	Т	А	status ^c	А	B	C	Total	10 ³ µm ³
Trifolium repens	0	1	0	3	с	105	90	33ns	228	15
Actinidia spp.	W	5	2	0		68	13	89ns	170	3
Polvgonatum odoratum	W	6	3	0		35	84	46ns	165	21
Solanum tuberosum	с	0	0	1	с	17	4	117**	138	5
<i>Ouercus</i> spp.	W	5	2	0		1	109	0ns	110	9
Syringa vulgaris	g	0	0	0	g	70	5	0**	75	22
Fagopyrum esculentum	c	0	0	0	c	3	3	63*	69	34
Lespedeza spp.	0	3	3	1		23	17	21ns	61	3
Rhodorendron dauricum	g	0	0	0	g	52	6	2**	60	45
Sorbus spp.	w	7	1	0	g	6	47	0ns	53	8
Castanea crenata	W	0	1	0	g	4	43	0ns	47	1
Polygala spp.	g	0	0	0	g	44	0	0**	44	13
Rumex spp.	0	1	1	3	C	0	4	37ns	41	11
Thalictrum minus	W	8	3	0		0	0	33**	33	5
10 unknown pollen types						16	2	4	22	5
Lupinus spp.	g	0	0	0	g	0	14	0ns	14	26
Rubus spp.	0	3	2	1		2	12	0ns	14	5
Euonymus spp.	W	7	3	0	g	10	0	3ns	13	8
Hydrangea spp.	W	6	2	0	g	5	7	0ns	12	2
Zea mays	с	0	0	1	c	1	11	0ns	12	230
Tilia spp.	W	4	1	0		6	1	4ns	11	15
Angelica spp.	W	7	1	0		0	0	10*	10	2
Rosaceae sp.1						3	0	7ns	10	7
Trifolium pratense	0	1	0	3	с	8	1	1ns	10	73
Cucurbita moshchata	с	0	0	0	с	1	2	4	7	905
Plantago asiatica	0	3	1	2		0	7	0	7	4
Swida controversa	W	2	1	0		1	6	0	7	18
Prunus spp.	W	6	3	0	g	1	5	0	6	24
Umbelliferae sp.2						0	0	6	6	3
Visia spp.	W	1	1	0		5	0	1	6	8
Commelina communis	0	0	0	1		0	0	4	4	25
Rosaceae sp.4						4	0	0	4	3
Salicaceae spp.	0	8	1	2		0	2	1	3	4
Viburnum spp.	W	3	2	0	g	3	0	0	3	8
Cirsium spp.	0	9	3	1		0	0	2	2	47
Compositae sp.2						0	0	2	2	15
Leguminosae sp. I						0	1	1	2	/
Rosaceae sp.2		~	2	0		0	0	2	2	11
Vitis coignetiae	W	6	3	0		0	2	0	2	5
Weigela spp.	W	1	0	0	g	1	0	1	2	51
Anemone spp.	W	1	0	0		0	1	0	1	11
Compositae sp. 1						1	0	1	1	0
Compositae sp.5						0	1	0	1	11
Lilium spp	W	4	1	0	σ	0	0	1	1	74
Monotronastrum globosum	vv	0	0	0	B	0	0	1	1	13
Oenothera hiennis	0	1	2	2		1	0	0	1	1/137
Patrinia spp	w	0	1	0		0	0	1	1	48
Pinaceae spp.	w	2	1	ŏ	g	ĭ	ŏ	0	1	235
Ranunclus spp.	w	3	0	Ũ	0	0	Ő	1	1	11
Rosaceae sp.3		-	-			0	Ő	1	1	5
Spiraea spp.	W	4	1	0	g	1	0	0	1	4
Staphylea bumalda	g	0	0	0	g	1	0	0	1	22
Total						500	500	500	1500	

a: wild plants (w), crops (c), garden plants (g), and others (o); b: natural vegetation (N), tree plantation (T), and agricultural area (A); c: crops (c) and garden plants (g); P > 0.05 (ns), P < 0.05 (*), P < 0.01 (**).



Fig. 2. Relative area of natural vegetation (a), tree plantation (b), agricultural area (c), and residential area (d) at distances in 200 m increments from three nests. Descriptions of the categories are shown in text.

were unavailable. Next, we determined whether these plants were cultivated as garden plants or crops in the study site. We defined wild plants as those present in natural vegetation and/or tree plantations and absent in agricultural areas regardless of the cultivation status. We defined garden plants as those cultivated exclusively in gardens and not occurring in natural vegetation, tree lantations, or agricultural areas. Crops were defined as plants that do not occur in natural vegetation or tree plantations. Other taxa of pollen source plants, most of which occurred in a variety of vegetation, fell under other categories.

In order to compare the compositions of the four categories of pollen source plants, the fraction of pollen volume in the four plant categories was calculated for each of the 30 samples because pollen size differed among different plant taxa. The mean volume of pollen grains in each taxon of pollen source plants was measured according to the method of O'Rourke & Buchmann (1991). The Kruskal-Wallis test was used to determine whether the fraction of pollen volume in each of the four plant categories differed among the three nests.



Fig. 3. Variation in the fraction of pollen volume of four plant categories (wild plants, crops, garden plants, and others) among three nests (A, B, and C). Central lines, boxes, bars, and circles indicate median, 25 and 75 percentiles, 10 and 90 percentiles, samples out of the range, respectively. Differences in the fraction of pollen volume in each habitat type among the three nests (n = 10) are tested by Kruskal-Wallis test.

Results

The landscapes around nests A, B, and C differed in terms of the areas and distributions of three vegetation types: natural vegetation, agricultural area, and residential area (Fig. 2). We identified 52 plant taxa of 29 families and 10 unknown pollen types in 30 samples from the three nests (Table 2). Of 23 plant taxa, from which more than nine pollen grains were observed, the number of pollen grains of seven taxa was significantly different among the three nests (Kruskal-Wallis test, P < 0.016; Table 2). Twenty-two, 4, 5, and 10 plant taxa were classified into four categories, wild plants, crops, garden plants, and others, respectively. The mean volume of pollen grains varied about 1,000-fold among the 52 plant taxa. The fraction of pollen volume of plants in three categories, wild plants, crops, and garden plants, was significantly different among the three nests (Kruskal-Wallis test, P < 0.032; Fig. 3). The landscape structure and pollen utilization of each nest were described as follows.

Both the largest residential area and the smallest agricultural area among the three nests characterized the landscape around nest A (Fig. 2). The relative area of natural vegetation around nest A was similar to that around nest C and larger than that around nest B at a distance from 0.2 to 3.0 km from the nest. The number of pollen grains of three taxa of garden plants, *Syringa*

vulgaris, Rhododendron dauricum, and *Polygala* spp., was significantly larger in nest A than in nests B and C (Table 2). Of the three nests, the fraction of pollen volume of garden plants was largest in nest A (Fig. 3). On the other hand, that of wild plants and crops was smallest in nest A.

From 0.2 to 2.6 km from nest B, the agricultural area was largest, and the natural vegetation area was smallest among the three nests (Fig. 2). As long as the distance from nest B ranged from 3.0 to 3.8 km, the natural vegetation area was largest among the three nests, and the agricultural area was intermediate between nests A and C. The residential area around nest B was similar to that around nest C but larger at both less than 1.0 km and more than 3.0 km. Although the number of pollen grains of three woody taxa, *Quercus* spp., *Sorbus* spp., and *Castanea crenata*, was largest in nest B, these differences were not significant due to variation among samples within the nest (Table 2). The fraction of pollen volume of wild plants was largest in nest B, and that of garden plants and crops was intermediate between nests A and C (Fig. 3).

A mosaic of natural vegetation and agricultural areas without a residential area characterized the landscape around nest C within a distance of 1.6 km (Fig. 2). At a distance of about 3 km from nest C, the natural vegetation area was smallest, and the agricultural area was largest among the three nests. The residential area increased slightly at a distance of 3 km. The number of pollen grains of two crops, *Solanum tuberosum* and *Fagopyrum esculentum*, and two wild herbs, *Thalictrum minus* and *Angelica* spp., was significantly larger in nest C than in nests A and B (Table 2). In nest C, the fraction of pollen volume of crops was largest among the three nests A and B, and that of garden plants was smallest among the three nests (Fig. 3).

Discussion

Bumblebees are thought to forage over several km based on radar tracking (Osborne et al., 1999), mark and recapture (Walther-Hellwig & Frankl, 2000), and homing experiments (Goulson & Stout, 2001). Circles with a 4 km radius seem to include the main foraging ranges of bumblebee colonies.

The landscapes in the foraging range of the examined nests showed differences in the composition of vegetation types. The available pollen sources also differed among the nests, assuming that vegetation types provided different taxa of pollen source plants. Most taxa of the pollen source plants used by the examined colonies showed distinctive habitats. Wild plants occurred in natural vegeta-

tion, crops were cultivated in agricultural areas, and garden plants were planted in residential areas. However, 10 out of 22 wild plant taxa were occasionally planted as garden plants, which potentially occurred in residential areas. The flora lists of the National Vegetation Survey showed that most of these taxa, such as Sorbus spp., Euonymus spp., Hydrangea spp., and Prunus spp., were abundant in plant communities of natural vegetation. Thus, the pollen resources of these taxa seemed to be more abundant in natural vegetation than in residential areas in spite of their occasional occurrence in residential areas. Our results suggest a correspondence between the habitats of pollen source plants and the vegetation types in landscapes. However, only a single nest was examined in each landscape, and thus variation in pollen diets among nests in the same landscape should be evaluated in the future study.

In the landscapes with large residential areas, the fraction of pollen from garden plants was high. This result suggests that garden plants in residential areas attract foragers from colonies that inhabit fragmented forests. Nests of *B. terrestris* gained weight more quickly when placed in suburban gardens than when in farmlands (Goulson et al., 2002). Genetic analysis also demonstrated that foragers at flower patches of about 1 ha in an urban site came from more than 50 colonies (Chapman et al., 2003). These findings support the idea that suburban residential areas provide a good foraging habitat for bumblebees.

Contrary to that from garden plants, pollen utilization from wild plants and crops did not show clear associations with the relative area of natural vegetation and agricultural area, respectively. As long as the distances from two nests (B and C) ranged from 3.0 to 3.8 km, the pollen utilization from wild plants and crops showed a positive correspondence with the relative area of natural vegetation and agricultural area, respectively. However, it is not likely that pollen from distant foraging sites were dominant in pollen diets (Cresswell et al., 2000). Within a distance of 2.6 km, the pollen of wild plants was more widely used in a landscape with a larger agricultural area, and the pollen of crops was more widely used in a landscape with a larger natural vegetation area.

This inconsistency may result from different pollen availability per unit area in agricultural areas around nests and/or in forests that harbored the nests. The more abundant pollen grains of potatoes (*Solanum tuberosum*) and buckwheat (*Fagopyrum esculentum*) in nest C than in nest B suggest a difference in the compositions of cultivated crops between the two sites. Based on reports of Obihiro Statistics and Information Center, Ministry of Agriculture, Forestry, and Fisheries of Japan, we compared the fraction of cultivated area of various crops in 2000 between Memuro-cho, where nest B was located, and Nakasatsunai-mura, where nest C was located. The fraction of the cultivated area of wheat (Triticum aestivum) and corn (Zea mays) was larger in Memuro-cho, and that of potatoes, beans (Glycine max), sugar beets (Beta vulgaris), and other vegetables was larger in Nakasatsunai-mura. Thus, entomophilous crops were more abundant around nest C than around nest B, and the pollen availability of crops in agricultural areas was likely to be higher around nest C than around nest B. Furthermore, a secondary forest inhabited by colony B was older than that inhabited by colony C. This difference in the forest age may affect the pollen availability of wild plants. Old secondary forests may consist of more diverse taxa of trees in a larger size and are more likely to supply a larger amount of pollen than young secondary forests (Saito et al., 1989). The pollen of the woody taxa of wild plants tended to be more abundant in nest B in an old secondary forest, whereas the pollen of wild herbs was more abundant in nest C in a young secondary forest. This result may reflect quantitative and qualitative differences in pollen resources between the inhabited forests.

In conclusion, our results suggest that cultivated plants affect pollen utilization by bumblebees nesting in fragmented forests depending on landscape structure around the nests. Garden plants in residential areas are likely to contribute to pollen diets. Because the contribution of crops in arable fields seems to vary as crop species change, the pollen supply from wild plants in inhabited forests may be potentially important.

Acknowledgements

We would like to thank Mitsuhiro Iwasa and Yoshitaka Nakajima (Obihiro University of Agriculture and Veterinary Medicine), Masato Ono (Tamagawa University), and Shoko Sakai and Yukihiko Toquenaga (Tsukuba University) for their helpful suggestions and Fumito Miura and staff members of the Memuro Agricultural Experimental Station and Manabe Garden for their permission to use the land and their assistance with the fieldwork.

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北海道の断片化した森林の景観におけるエゾオオマルハナバチコロニーに よる花粉利用

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要旨

北海道の断片化した森林に営巣したエゾオオマルハナバチ3コロニーの花粉利用を明らかにした。これ らのコロニーは異なる景観において野生植物と農作物、園芸植物の花粉を異なる比率で利用した。園芸植 物の花粉の体積比率は、住宅地の相対面積が最も大きい景観で最も高かった。野生植物の花粉の体積比率 は、自然植生の相対面積が最も小さく、農耕地の相対面積が最も大きい景観で最も高かった。この理由は、 営巣した断片林の野生樹木が十分な花粉をコロニーに供給したためだと考えられる。農作物の花粉の体積 比率は、3つの営巣地のなかで農耕地の相対面積が中程度の景観で最も高かった。この理由は、この地域 で多く栽培されていた農作物が虫媒であるためだと思われる。これらの結果は、断片林に営巣したマルハ ナバチが営巣場所周辺の栽培植物の花粉を景観構造に応じて利用していることを示唆する。

キーワード:エゾオオマルハナバチ、花粉利用、景観構造、生息地の断片化

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