

Trophic links of bumble bees (Hymenoptera, Apidae: *Bombus* Latreille, 1802) on North-West Pacific islands, the Russian Far East

Трофические связи шмелей (Hymenoptera, Apidae: *Bombus* Latreille, 1802) на северо-западных островах Тихого океана Дальнего Востока России

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Abstract. The trophical links of 23 bumble bee species was studied on Karaginskiy Island (Bering Sea), Kuril Islands and Sakhalin (Sea of Okhotsk) during long-term surveys (1994–2011). Bumble bees visited 111 species of vascular plants from 28 families in the Kuril Islands (67 species from 22 families), Sakhalin (52 species from 18 families), and Karaginskiy Island (36 species from 15 families). The ranges of foraging for dominant bumble bee species are 26–28 vascular plant species for *Bombus lucorum* (Linnaeus) and 18–21 species for *B. jonellus* (Kirby). The bumble bees as pollinators of vascular plants dominate among the bees on the North of the Russian Far East, especially on the North-West Pacific islands.

Резюме. На основании многолетних исследований (1994–2011 гг.) изучены трофические связи 23 видов шмелей на Курильских островах, острове Сахалин в Охотском море и острове Карагинский в Беринговом море. Зарегистрировано посещение шмелями 111 видов сосудистых растений из 28 семейств: Курильские острова — 67 видов из 22 семейств, остров Сахалин — 52 вида из 18 семейств, остров Карагинский — 36 видов из 15 семейств. Наибольшее число видов растений посещают *Bombus lucorum* (Linnaeus) — 26–28 видов, и *B. jonellus* (Kirby) — 18–21 вид. Среди пчёл шмели являются основными опылителями сосудистых растений на севере Дальнего Востока России, особенно на островах.

Introduction

Karaginskiy Island (Bering Sea), Kuril Islands and Sakhalin Island (Sea of Okhotsk) are part of the Rus-

sian Far East island territories in the North-West Pacific. Owing to their geographical position and isolation from the mainland, these islands are unsuitable for the intensive human activities, and the natural habitat of these islands is less transformed in comparison with the mainland. The bumble bees (*Bombus* Latreille, 1802) are one of the well studied groups of the insects on these islands. Bumble bees number about 250 species worldwide, and are placed in a single genus *Bombus* with 15 subgenera [Williams et al., 2008]. They are important pollinators of many vascular plants, included cultivated ones. The bumble bees are distributed far in the North and in high mountains where the main pollinators of vascular plants became.

For more than a hundred years many papers on bumble bee taxonomy from these islands have been published, but foraging activity has been discussed only in several recent papers [Lelej, Kupianskaya, 2000; Proshchalykin et al., 2004; Berezin, Tkacheva, 2010]. Here we summarize and analyze floral preferences of bumble bees based on original long-term data.

Material and Methods

Russian Far East island territories in the North-West Pacific include the islands in the Bering Sea (Verkhoturova Island, Karaginskiy Island, Komandorskiye Islands) and Sea of Okhotsk (Shantarkiye Islands, Kuril Islands, Sakhalin Island, and Moneron Island). In this paper the data about foraging activity

are given for Karaginskiy Island, Kuril Archipelago, and Sakhalin Island (Fig. 1).

Karaginskiy Island is located in the central part of Karaginskiy Bay in the Bering Sea near the north-west coast of Kamchatka Peninsula, stretching for 111 km between south-western Cape Krasheninnikova and north-eastern Cape Golenishtsheva. The maximum width of the Karaginskiy Island is 45 km; its total area is 2404 km². Karaginskiy Island is separated from Kamchatka Peninsula by Litke Strait, which is 27 km wide at its narrowest point [Gerasimov, 2008].

The Kuril Archipelago is a chain of more than 56 islands covering an area of 10,200 km² and providing 2409 km of coastline (Fig. 2). Stretching 1200 km between Hokkaido, Japan, and the Kamchatka Peninsula of Russia (from 43° to 51° N latitude), the Kurils divide the Sea of Okhotsk from the Pacific Ocean and form the northern extension of an insular arc. It is composed of two main ridges: the Lesser Kuril Ridge and the Greater Kuril Ridge. The Lesser Kuril Ridge includes the Nemuro Peninsula of eastern Hokkaido, the Habomai Island group, and Shikotan, and continues to the northeast as the submarine Vityaz Ridge. The Greater Kuril Ridge includes the Shiretoko Peninsula of eastern Hokkaido, all of the remaining Kuril Islands, from Kunashir north to Shumshu, and the south-

ern tip of the Kamchatka Peninsula [Pietsch et al., 2003].

Sakhalin is one of the largest islands in the boreal zone of the Pacific Ocean (Fig. 1), stretching along the east coast of Asia for 948 km in a latitudinal direction between 45°54' N (Cape Kril'on) and 54°24' N (Cape Elizavety). The maximum width of the Sakhalin Island is about 157 km, while the narrowest point, on the Shmidt Peninsula in the north, is only about 6 km; its total area is 76,400 km². Its northern and eastern coasts are bounded by the Sea of Okhotsk, while the southern and western margins are bounded by the Sea of Japan. The northwestern margin of Sakhalin Island lies extremely close to the Russian mainland at the mouth of the Amur River, separated by the Amurskiy Firth and the shallow Nevelskogo Strait, which is only 7.5 km

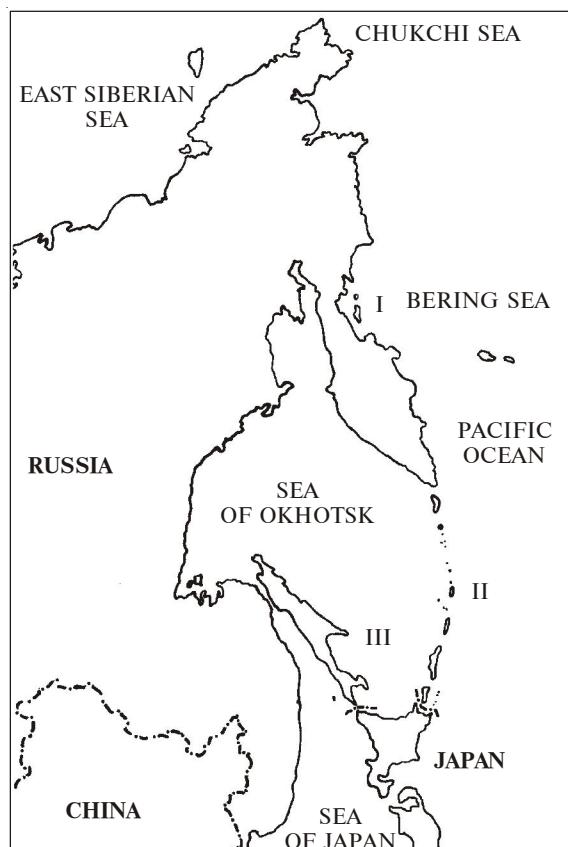


Fig. 1. Map of the Russian Far East. I — Karaginskiy Island; II — Kuril Islands; III — Sakhalin Island.

Рис. 1. Карта Дальнего Востока России. I — остров Карагинский; II — Курильские острова; III — остров Сахалин.

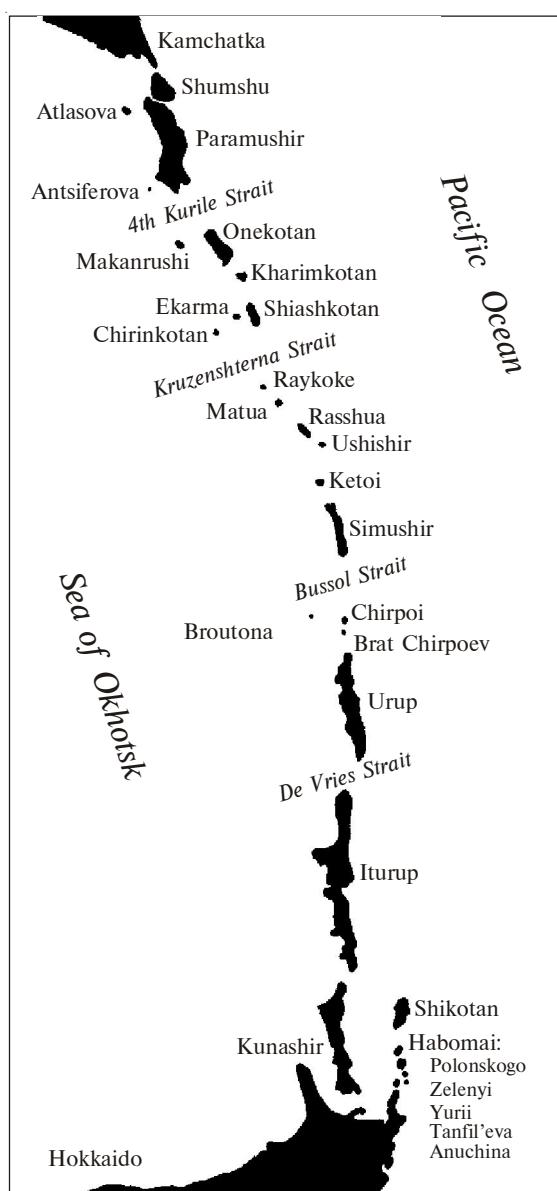


Fig. 2. Map of the Kuril Islands.

Рис. 2. Карта Курильских островов.

wide at its narrowest point. The 40-km-wide La Perouse Strait separates the southern end of Sakhalin from Hokkaido, the northernmost island of Japan. Because of its long, narrow shape, extending in a north-south direction, the habitat and biota of the island vary greatly with latitude [Bogatov, 2004].

Bumble bees were collected by teams of the International Kuril Island Project (IKIP) for each of the six

Table 1. Studied area and examined material
Таблица 1. Территория исследования и изученный материал

Islands	Area, km ²	Number of vascular plant species	Number of bumble bee species	Number of bumble bee specimens examined
Karaginskiy	2404	501	11	523
Sakhalin	76400	1521	20	1862
Kuril	10200	1411	16	3127
<i>Northern</i>	3242	605	8	670
Atlasova	150	248	3	41
Shumchu	388	450	8	179
Paramushir	2053	556	6	199
Antsiferova	7	23	2	3
Makanrushi	49	145	2	100
Onekotan	425	321	3	82
Kharimkotan	68	180	2	25
Ekarma	30	120	1	16
Shiashkotan	122	220	1	25
<i>Central</i>	550	393	3	294
Matua	52	214	2	115
Rasshua	67	264	2	57
Ushishir	5	230	2	28
Ketoi	73	272	2	20
Simushir	353	337	2	74
<i>Southern</i>	5521	1255	13	2161
Chirpoi	21	140	2	78
Brat Chirpoev	16	146	2	11
Urup	450	531	4	92
Iturup	3200	872	5	670
Kunashir	1490	1078	9	1034
Shikotan	250	724	5	177
Polonskogo	12	129	2	18
Zelenyi	51	187	2	18
Tanfil'eva	15	175	2	54
Iurii	13	212	2	7
Anuchina	3	103	1	3
Total		29	5512	

The number of vascular plant species is taken from [Kharkevich, 1979; Barkalov, Taran, 2004; Barkalov, 2009]. The number of bumble bee species is taken from [Lelej, Kupianskaya, 2000; Proshchalykin et al., 2004; Proshchalykin, Kupianskaya, 2005; Berezin, Tkacheva, 2010].

annual summer expeditions (1995–2000), International Sakhalin Island Project (ISIP) for each of three annual summer expeditions (2001–2003), and by M.V. Berezin and E.Yu. Tkacheva on Karaginskiy Island (2008). During IKIP expeditions all large and almost all small islands of the Kuril Archipelago have been investigated. Sakhalin Island was studied from Southern Capes to Northern Capes. The bumble bees were observed on flowers and identified in field conditions, with part of them being captured for precise identification. Forage plant species were identified in the field and in laboratories with the help of botanists who were participants of expeditions.

All material collected during IKIP and ISIP expeditions are deposited in the collections of the Institute of Biology and Soil Science, Russian Academy of Sciences, Vladivostok (IBSS). The bumble bees (including data about forage plants) from the collections of Zoological Institute Russian Academy of Sciences, St. Petersburg (ZISP), Zoological Museum of the Moscow State University (ZMM), and private collection of M.V. Berezin, Moscow (PCMB) have been examined also. The total number of examined bumble bee specimens is 5512 including more than 2000 specimens with the data about forage plants (Tab. 1). The classification of bumble bees follows Williams et al. [2008].

Results and discussions

It is known that bumble bees select flowers according to the length of their tongues [Ranta, Lundberg, 1980; Goulson, 2003]. Besides, there exists a preference for particular plant species for each bumble bee species [Inouye, 1978; Pekkarinen, 1984] and in individual foragers as well [Heinrich, 1976]. These preferences change during the season, depending on plant phenology, stage of the bee colony development, the diversity of forage plants, and on competition in insect communities for feeding resources [Pyke, 1978; Goulson, 2003]. The foraging activity for 23 of 29 recorded species on the North-West Pacific islands has been studied (Tab. 2). Bumble bees visited 111 species of vascular plants from 28 families in the Kuril Islands (67 species from 22 families), Sakhalin Island (52 species from 18 families), and Karaginskiy Island (36 species from 15 families) (Fig. 3). Among 111 species of vascular plants visited by bumble bees, 33 species from 13 families are common for these islands, from them only ten species from seven families are visited by bumble bees on the North-West Pacific islands (Tab. 3). Most forage-plant species on North-West Pacific islands belong to the families Asteraceae (28 species), Fabaceae (12), Rosaceae (11), and Scrophulariaceae (10). Twenty bumble bee species visited 28 plant species of Asteraceae, but most of them visited *Senecio pseudoarnica* (15 species), *Cirsium kamtschaticum* (14), and *Tanacetum boreale* (10), other species of Asteraceae were visited by one to five bumble bee species. Three former species of Asteraceae are common and abundant on the islands in the differ-

Table 2. Distribution of bumble bees on the North-West Pacific Islands of the Russian Far East
 Таблица 2. Распространение шмелей на северо-западных островах Тихого океана Дальнего Востока России

No	Species	Islands				
		Karaginskiy	Southern Kuril	Central Kuril	Northern Kuril	Sakhalin
1.	<i>B. (Alpinobombus) balteatus</i> Dahlbom, 1832	+	-	-	+	-
2.	<i>B. (Bombus) florilegus</i> Panfilov, 1956	-	+	+	+	-
3.	<i>B. (Bombus) hypocrita</i> Pérez, 1905	-	+	-	-	+
4.	<i>B. (Bombus) lucorum</i> (Linnaeus, 1761)	+	+	+	+	+
5.	<i>B. (Bombus) patagiatus</i> Nylander, 1848	-	-	-	-	+
6.	<i>B. (Bombus) sporadicus</i> Nylander, 1848	+	-	-	-	+
7.	<i>B. (Megabombus) consobrinus</i> Dahlbom, 1832	-	-	-	-	+
8.	<i>B. (Megabombus) diversus</i> Smith, 1869	-	+	-	-	+
9.	<i>B. (Megabombus) pseudoligusticus</i> (Skorikov, 1926)	+	-	-	+	-
10.	<i>B. (Megabombus) yezoensis</i> Matsumura, 1932	-	+	-	-	-
11.	<i>B. (Melanobombus) sichelii</i> Radoszkowski, 1859	-	-	-	+	+
12.	<i>B. (Psithyrus) bohemicus</i> Seidl, 1838	+	+	-	+	+
13.	<i>B. (Psithyrus) flavidus</i> Eversmann, 1852	+	-	-	+	+
14.	<i>B. (Psithyrus) norvegicus</i> (Sparre-Schneider, 1918)	-	-	-	-	+
15.	<i>B. (Psithyrus) sylvestris</i> (Lepeletier, 1832)	-	-	-	-	+
16.	<i>B. (Pyrobombus) ardens</i> Smith, 1879	-	+	-	-	-
17.	<i>B. (Pyrobombus) beaticola</i> Tkalcù, 1968	-	+	-	-	-
18.	<i>B. (Pyrobombus) cingulatus</i> Wahlberg, 1854	+	-	-	-	+
19.	<i>B. (Pyrobombus) hypnorum</i> (Linnaeus, 1758)	+	+	-	+	+
20.	<i>B. (Pyrobombus) joneillus</i> (Kirby, 1802)	+	-	-	-	+
21.	<i>B. (Pyrobombus) karaginius</i> Skorikov, 1912	+	-	-	-	-
22.	<i>B. (Pyrobombus) lapponicus</i> (Fabricius, 1793)	+	-	-	-	-
23.	<i>B. (Pyrobombus) modestus</i> Eversmann, 1852	-	-	-	-	+
24.	<i>B. (Pyrobombus) oceanicus</i> Friese, 1909	-	+	+	+	-
25.	<i>B. (Subterraneobombus) distinguendus</i> Morawitz, 1869	-	-	-	-	+
26.	<i>B. (Thoracobombus) deuteronymus</i> Schulz, 1906	-	-	-	-	+
27.	<i>B. (Thoracobombus) pascuorum</i> (Scopoli, 1763)	-	-	-	-	+
28.	<i>B. (Thoracobombus) pseudobaicalensis</i> Vogt, 1911	-	+	-	-	+
29.	<i>B. (Thoracobombus) schrencki</i> Morawitz, 1881	-	+	-	-	+
Total (in the parentheses the number of species distributed on this islands only)		11(2)	12(3)	3(0)	9(0)	20(8)

The distribution data of bumble bee species are taken from [Lelej, Kupianskaya, 2000; Proshchalykin et al., 2004; Proshchalykin, Kupianskaya, 2005; Berezin, Tkacheva, 2010].

ent biotopes [Barkalov, 2009] and very attractive for pollinators. Twenty-one bumble bee species visited 12 plant species of Fabaceae, but most of them were registered on *Trifolium repens* (13 species) and *Lathyrus japonicus* (9) which are common Fabaceae species on the islands [Barkalov, 2009]. Sixteen bumble bee species visited eleven plant species of Rosaceae, and nine species were registered on *Rosa rugosa*. This bush is abundant on the Kuril Islands and Sakhalin and very often forms the belt along sandy seashores [Barkalov, 2009]. *Geranium erianthum* is a single forage-plant species of family Geraniaceae was visited by ten bumble bee species (Fig. 4). This very common Geraniace-

ae species is distributed on the North West Pacific islands from seashore to 1600 m in different kinds of meadows.

On the Kuril Islands the most visited plants are *Cirsium kamtschaticum*, *Senecio* spp. (Asteraceae), *Trifolium* spp., *Hedysarum* spp., *Lathyrus japonicus* (Fabaceae), *Geranium erianthum* (Geraniaceae), *Rosa rugosa* (Rosaceae), *Pedicularis* spp., and *Pennellianthus frutescens* (Scrophulariaceae) which are more common and abundant everywhere [Barkalov, 2009]. Thirty-nine forage-plant species from 15 families are registered for *Bombus florilegus* and 26 plant species from ten families are registered for *B. lucorum*. These

bumble bees are widely distributed and the most abundant species on the Kuril Islands. When several bumble bee species coexist in one habitat they usually visit different plants. On the small volcanic island Chirpoi (without forest) both bumble bee species (*Bombus florilegus* and *B. oceanicus*) which inhabit this island occur from the seashore to the volcano summit (691 m). Near seashore both species visited seven grass species (mainly *Cirsium kamtschaticum*) but became more abundant in tundra zone. Upper island part and volcano top occupied by volcanic pebbles where the «pioneer» plants of *Pennellianthus frutescens* (Scrophulariaceae) and *Campanula lasiocarpa* (Campanulaceae) are growing. The first plant visited by *B. oceanicus*, the second plant by *B. florilegus*.

On Sakhalin Island the most visited plants are *Angelica ursina* (Apiaceae), *Senecio* spp., *Tanacetum boreale* (Asteraceae), *Lathyrus japonicus*, and *Trifolium* spp. (Fabaceae). Twenty-seven forage-plant species from 11 families are registered for *Bombus lucorum* and 15 plant species from seven families are registered for *B. schrencki*. These bumble bees are widely distributed and the most abundant species on Sakhalin Island (Figs 5, 7).

All studied bumble bees on the North-West Pacific islands are polylectic species. The eight medium-tongued bumble bee species (subgenus *Pyrobombus*) visited 69 forage-plant species from 21 families, but

prefer *Oxycoccus palustris*, *Rhododendron aureum*, *Vaccinium vitis-idaea*, *Comarum palustre*, *Rubus arcticus*, and *Spiraea beauverdiana* in particular (Tab. 3). The four long-tongued bumble bee species (subgenus *Megabombus*) visited 24 forage-plant species from 11 families and everywhere preferred deep-corolla flowers of plants from the families Lamiaceae, Fabaceae, and Ranunculaceae. For example, *B. (Megabombus) pseudoligusticus* has a very long tongue and uses the pollen and nectar from *Iris setosa* (Iridaceae), *Delphinium brachycentrum* (Ranunculaceae), *Thermopsis lupinoides*, and *Lathyrus japonicus* (Fabaceae) flowers, which are rarely visited by other *Bombus* species. The four short-tongued bumble bees (nominotypical subgenus *Bombus*) have the largest range of forage-plant species: 86 species from 23 families. Only bumble bees from this subgenus visited the forage-plants from the families Caryophyllaceae (*Dianthus repens*, *Honckenya oblongifolia*), Clusiaceae (*Hypericum kamtschaticum*), Salicaceae (*Salix* spp.), but most of them have been registered on the forage-plants from the family Asteraceae (21 plant species) with short-corolla flowers.

There are two groups of polylectic bumble bee species (Tab. 4). 1, *Wide polylectic bumble bee species* visited forage-plant species from eight to 19 families (eight bumble bee species). *Bombus lucorum* is a single species which inhabits all North-West Pacific

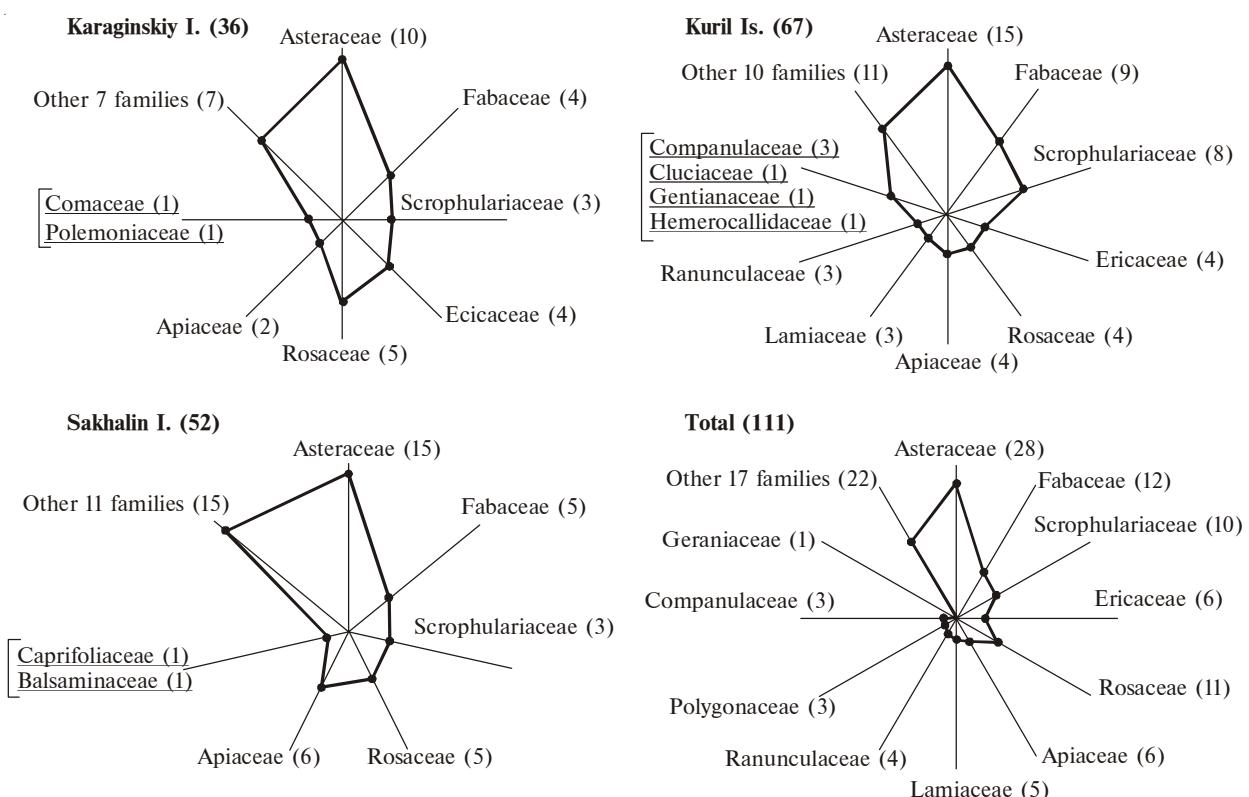


Fig. 3. The ratio of vascular plant families in trophic range of bumble bees (number of plant species in parentheses).
Рис. 3. Соотношение семейств сосудистых растений в диапазоне шмелей (в скобках указано число видов растений).

Table 3. Food plants of bumble bees on North-West Pacific Islands of the Russian Far East
 Таблица 3. Кормовые растения шмелей на северо-западных островах Тихого океана Дальнего Востока России

Vascular plant families and species	Location (I, II, III) (see fig.1)	Number of bumble bee species	Bumble bee species
Apiaceae			
<i>Angelica gmelinii</i> (DC.) M. Pimen.	I-III	7	1,2,4,12,13, 20,22
<i>Angelica ursina</i> (Rupr.) Maxim.	III	6	3,4,6,7,8,12
<i>Cicuta virosa</i> L.	III	1	4
<i>Glenia littoralis</i> Fr. Schmidt ex Miq.	II, III	2	2,4
<i>Heracleum lanatum</i> Michx.	II, III	1	2
<i>Ligusticum scoticum</i> L.	I-III	3	2,4
Alliaceae			
<i>Allium maximowiczii</i> Regel	III	1	19
<i>Allium ochotense</i> Prokh.	II	3	2,24,29
Araliaceae			
<i>Aralia cordata</i> Thunb.	II, III	4	4,6,17,19
Asteraceae			
<i>Arctanthemum arcticum</i> (L.) Tzvel.	I, III	2	2,4
<i>Arctium lappa</i> L.	III	4	4,6,23,29
<i>Arnica sachalinensis</i> (Regel) A.Grey	III	4	7,19,20,28
<i>Artemisia arctica</i> Less.	I	1	4
<i>Cacalia hastata</i> L.	I, III	5	4,8,18,23,29
<i>Cacalia robusta</i> Tolm.	II	3	2,19,24
<i>Cirsium kamtschaticum</i> Ledeb.ex DC.	I-III	14	2,3,4,7,8,10, 12,17,18,19, 20,24,25,29
<i>Cirsium schantarensse</i> Trautv. et Mey.	III	1	19
<i>Cirsium setosum</i> (Willd.) Bess.	I	1	18
<i>Eupatorium glehnii</i> Fr. Schmidt et Trautv.	II	3	3,17,19
<i>Hieracium umbellatum</i> L.	III	1	20
<i>Inula britannica</i> L.	III	1	13
<i>Lagedium sibiricum</i> (L.) Sojak	III	3	4,19,20
<i>Leontodon autumnalis</i> L.	II	2	2,4
<i>Ligularia hodgsonii</i> Hook. fil.	II	3	2,24,29
<i>Mulgedium tataricum</i> DC.	III	1	6
<i>Picris kamtschatica</i> Ledeb.	II	1	2
<i>Pilosella aurantiaca</i> (L.) F.Schultz et Sch.Bip.	III	2	3,4
<i>Ptarmica macrocephala</i> (Rupr.) Kom.	II	1	2
<i>Saussurea kuriensis</i> Tatew.	II	2	24,29
<i>Saussurea riederi</i> Herd.	II	1	24
<i>Senecio cannabifolius</i> Less.	I-III	9	2,4,6,7,12, 13,19,20,29 1,2,4,6,7, 8,18,19,20, 22,23,24,25, 28,29
<i>Senecio pseudoarnica</i> Less.	I-III	15	

Table 3. (Continuation)
 Таблица 3. (Продолжение)

Vascular plant families and species	Location (I, II, III) (see fig.1)	Number of bumble bee species	Bumble bee species
<i>Solidago spiraefolia</i> Fisch. ex Herd.	I, III	4	2,19,20,29
<i>Solidago paramuschiensis</i> Barkalov	II	1	29
<i>Tanacetum boreale</i> Fisch. ex DC.	I, III	10	1,4,6,12,13, 19,20,23, 25,29
<i>Taraxacum ceratoforum</i> (Ledeb.) DC.	II	2	2,4
<i>Taraxacum ketojense</i> Tatew. et Kitam.	II	1	2
Balsaminaceae			
<i>Impatiens noli-tangere</i> L.	III	1	8
Boraginaceae			
<i>Mertensia maritima</i> (L.) S.F. Gray	I-III	9	2,4,7,18,19, 20,22,24,29
<i>Mertensia pubescens</i> (Roem. et Schult.) DC.	II	1	4
Campanulaceae			
<i>Adenophora triphylla</i> Thunb.	II	2	2,24
<i>Campanula chamissonis</i> Fed.	II	3	4,19,24
<i>Campanula lasiocarpa</i> Cham.	II	1	2
Caprifoliaceae			
<i>Lonicera chamaedrys</i> Bunge ex P.Kir.	III	1	19
Caryophyllaceae			
<i>Dianthus repens</i> Willd.	III	2	4,2
<i>Honckenya oblongifolia</i> Torr. et Gray	I	1	4
Clusiaceae			
<i>Hypericum kamtschaticum</i> Ledeb.	II	1	2
Cornaceae			
<i>Chamaepericlymenum suecicum</i> (L.) Aschers. et Graebn.	I	4	4,12,18,20
Ericaceae			
<i>Oxycoccus palustris</i> Pers.	I	3	4,18,20
<i>Rhododendron aureum</i> Georgi	I, II	3	4,18,19
<i>Rhododendron camtschaticum</i> Pall.	II	3	2,4,19
<i>Pyrola minor</i> L.	I	1	18
<i>Vaccinium uliginosum</i> L.	II	2	3,4
<i>Vaccinium vitis-idaea</i> L.	I, II	4	4,12,18,20
Fabaceae			
<i>Astragalus alpinus</i> L.	I	2	2,18
<i>Astragalus frigidus</i> (L.) A. Gray	II	1	4
<i>Hedysarum nonnae</i> Roskov	II	3	2,4,24
<i>Hedysarum hedysaroides</i> (L.) Schinz et Thell.	I	6	1,4,18,20, 22,24
<i>Hedysarum sachalinense</i> B.Fedtsch.	II	3	18,24,29
<i>Lathyrus japonicus</i> Willd.	III	9	1,4,7,8,9,11, 20,28,29
<i>Oxytropis revoluta</i> Ledeb.	I	2	1,2
<i>Thermopsis lupinoides</i> (L.) Link	II, III	2	4,7

Table 3. (Continuation)
Таблица 3. (Продолжение)

Vascular plant families and species	Location (I, II, III) (see fig.1)	Number of bumble bee species	Bumble bee species
<i>Trifolium pacificum</i> Bibr.	II	1	29
<i>Trifolium pratense</i> L.	II, III	5	2,7,12,25,29 2,3,4,6,7,8, 10,12,16,19, 23,24,29
<i>Trifolium repens</i> L.	II, III	13	
<i>Vicia cracca</i> L.	II, III	4	2,19
Gentianaceae			
<i>Swertia stenopetala</i> (Regel et Til.) Pissjauk.	II	4	2,17,24,29
Geraniaceae			
<i>Geranium erianthum</i> DC.	I-III	10	2,3,4,9,12, 18,19,20, 24,29
Hemerocallidaceae			
<i>Hemerocallis esculenta</i> Koidz.	II	1	29
Iridaceae			
<i>Iris setosa</i> Pall. ex Link	I, II	7	1,4,7,9,18, 20,24
Lamiaceae			
<i>Galeopsis bifida</i> Boenn.	III	2	7,24
<i>Lamium barbatum</i> Siebold et Zucc.	II	2	7,1
<i>Prunella asiatica</i> L.	II	1	2
<i>Scutellaria strigillosa</i> Hemsl.	II	1	2
<i>Thymus japonicus</i> (Hara) Kitag.	III	4	4,7,20,23
Liliaceae			
<i>Cardiocrinum cordatum</i> (Thunb.) Makino	II, III	2	4,29
Lobeliaceae			
<i>Lobelia sessifolia</i> Lamb.	II, III	3	19,24,29
Lythraceae			
<i>Lythrum salicaria</i> L.	II	1	29
Onagraceae			
<i>Chamaenerion angustifolium</i> L.	I-III	10	1,2,4,6,9,13, 18,20,23,29
<i>Epilobium amurense</i> Hausskn.	II	2	6,24
Polemoniaceae			
<i>Polemonium acutiflorum</i> Willd. ex Roem. et Schult.	I	3	4,18,20
Polygonaceae			
<i>Bistorta vivipara</i> (L.) Delarbre	I	1	18
<i>Fagopyrum esculentum</i> Moench	III	4	3,4,6,24
<i>Reynoutria sachalinensis</i> (Fr.Schmidt) Nakai	III	2	4,28
Ranunculaceae			
<i>Aconitum sachalinense</i> Fr. Schmidt	III	2	8,29
<i>Corydalis ambigua</i> Cham. et Schlecht.	II	2	2,29
<i>Delphinium brachycentrum</i> Ledeb.	II	1	9
<i>Trollius miyabei</i> Sipl.	II	1	2

Table 3. (Continuation)
Таблица 3. (Продолжение)

Vascular plant families and species	Location (I, II, III) (see fig.1)	Number of bumble bee species	Bumble bee species
Rosaceae			
<i>Comarum palustre</i> L.	I, III	4	4,13,18,20
<i>Filipendula camtschatica</i> (Pall.) Maxim.	II, III	4	2,4,6,24
<i>Potentilla egedii</i> Wormsk.	I	2	2,18
<i>Rosa amblyotis</i> C.A. Mey.	I	3	4,18,20
<i>Rosa rugosa</i> Thunb.	II, III	9	2,3,4,6,17, 19,20,24,29
<i>Rubus arcticus</i> L.	I	5	4,12,16,18,20
<i>Rubus sachalinensis</i> Lévl.	III	3	19,23,29
<i>Sanguisorba tenuifolia</i> Fisch. ex Link	II	3	2,24,29
<i>Sorbaria sorbifolia</i> (L.) A.Br.	III	3	4,8,13
<i>Sorbus sambucifolia</i> Cham. et Schlecht.	II	5	4,12,19,24,29
<i>Spiraea beauverdiana</i> Schneid.	I	4	1,4,18,20
Salicaceae			
<i>Salix arctica</i> Pall.	I	1	4
<i>Salix udensis</i> Trautv. et Mey.	II	2	4,12
Scrophulariaceae			
<i>Linaria japonica</i> Miq.	II, III	3	3,4,20
<i>Pedicularis chamissonis</i> Stev.	II	4	2,4,9,19
<i>Pedicularis labradorica</i> Wirsing	I, III	7	1,3,4,18, 19,23
<i>Pedicularis oederi</i> Vahl	II	1	4
<i>Pedicularis resupinata</i> L.	I-III	8	2,4,6,17,18, 19,20,29
<i>Pedicularis verticillata</i> L.	I, II	3	4,18,20
<i>Pennellianthus frutescens</i> (Lamb.) Crosswhite	II	3	4,19,24
<i>Rhinanthus minor</i> L.	II	2	2,29
<i>Scrophularia grayana</i> Maxim. et Kom.	II	1	2
<i>Veronica sachalinensis</i> Yamazaki	III	2	4,2

The names of vascular plant species are taken from [Kharkevich, 1979; Barkalov, Taran, 2004; Barkalov, 2009].

islands. This abundant species visits most forage-plants: 62 species from 19 families (Tab. 4), but mainly Asteraceae (13 species), Rosaceae (8), Scrophulariaceae (8), and Fabaceae (6). 2. *Narrow polyleptic species* visited forage-plant species from one to seven families (16 bumble bee species including *Bobmus sichelii*, recorded on *Lathyrus japonicus* only). The number of bumble bees strongly depends of climatic patterns. In 1998 (Aug. 22), when August was cold with high humidity, we saw hundreds of bumble-bees of seven species near hot springs (Kunashir, 17 km south of Yuzhno-Kurilsk). In 1999 (Aug. 17) at the same place, when August was warm and dry, we collected four bumble-bee specimens of two species only.

Table 4. Trophical links of bumble bee species on the North-West Pacific Islands of the Russian Far East

Таблица 4. Трофические связи шмелей на северо-западных островах Тихого океана Дальнего Востока России

No	Species	Number of vascular plant	
		Family	Species
1.	<i>B. (Alpinobombus) balteatus</i> Dahlbom, 1832	7	10
2.	<i>B. (Bombus) florilegus</i> Panfilov, 1956	15	39
3.	<i>B. (Bo.) hypocrita</i> Pérez, 1905	8	11
4.	<i>B. (Bo.) lucorum</i> (Linnaeus, 1761)	19	62
5.	<i>B. (Bo.) patagiatius</i> Nylander, 1848	-	-
6.	<i>B. (Bo.) sporadicus</i> Nylander, 1848	8	14
7.	<i>B. (Megabombus) consobrinus</i> Dahlbom, 1832	5	10
8.	<i>B. (Mg.) diversus</i> Smith, 1869	7	15
9.	<i>B. (Mg.) pseudoligusticus</i> (Skorikov, 1926)	6	6
10.	<i>B. (Mg.) yezoensis</i> Matsumura, 1932	3	3
11.	<i>B. (Melanobombus) sichelii</i> Radoszkowski, 1859	1	1
12.	<i>B. (Psithyrus) bohemicus</i> Seidl, 1838	7	13
13.	<i>B. (Ps.) flavidus</i> Eversmann, 1852	4	7
14.	<i>B. (Ps.) norvegicus</i> (Sparre-Schneider, 1918)	-	-
15.	<i>B. (Ps.) sylvestris</i> (Lepeletier, 1832)	-	-
16.	<i>B. (Pyrobombus) ardens</i> Smith, 1879	2	2
17.	<i>B. (Pr.) beaticola</i> Tkalcu, 1968	4	5
18.	<i>B. (Pr.) cingulatus</i> Wahlberg, 1854	12	26
19.	<i>B. (Pr.) hypnorum</i> (Linnaeus, 1758)	12	28
20.	<i>B. (Pr.) jonellus</i> (Kirby, 1802)	14	35
21.	<i>B. (Pr.) karaginus</i> Skorikov, 1912	-	-
22.	<i>B. (Pr.) lapponicus</i> (Fabricius, 1793)	4	4
23.	<i>B. (Pr.) modestus</i> Eversmann, 1852	6	9
24.	<i>B. (Pr.) oceanicus</i> Friese, 1909	14	25
25.	<i>B. (Subterraneobombus) distinguendus</i> Morawitz, 1869	2	4
26.	<i>B. (Thoracobombus) deuteronymus</i> Schulz, 1906	-	-
27.	<i>B. (Th.) pascuorum</i> (Scopoli, 1763)	-	-
28.	<i>B. (Th.) pseudobaicalensis</i> Vogt, 1911	3	5
29.	<i>B. (Th.) schrencki</i> Morawitz, 1881	13	34

Among the bees of the Northern Russian Far East, bumble bees are the dominant pollinators of vascular plants, especially on the North-West Pacific islands (on the North Kuril Islands bumble bees is the only group of bees present, including endemic subspecies [Proshchalykin, 2011] (figs. 5, 6)). There are some evident patterns regarding bumble bee foraging on the islands. 1, the islands are inhabited by polylectic bumble bee species only; 2, bumble bees collect pollen and nectar during the whole season by visiting forage-plants in different habitats; 3, according to our long-term observation on the Kuril Islands and Sakhalin,

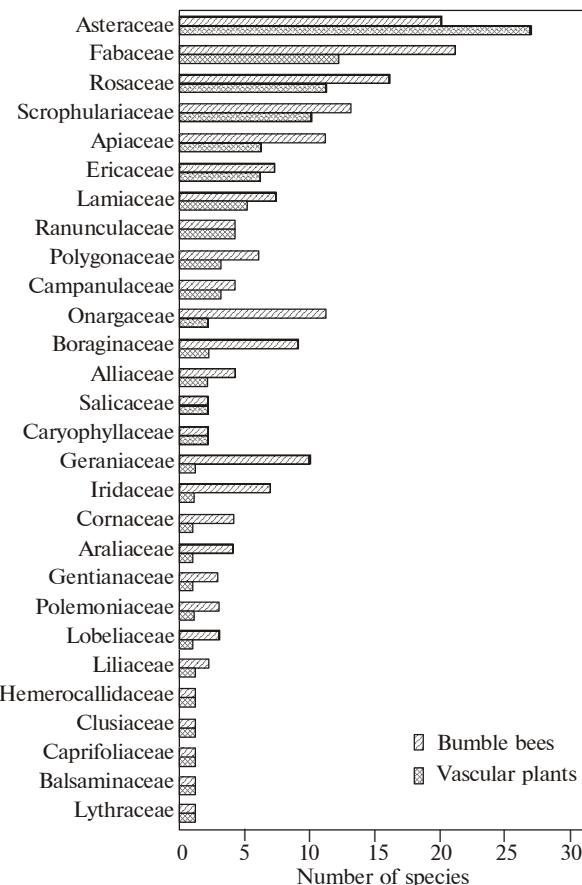


Fig. 4. The trophic links of bumble bees with vascular plants on North-West Pacific Islands (Russian Far East).

Рис. 4. Трофические связи шмелей с сосудистыми растениями на северо-западных островах Тихого океана (Дальний Восток России).

bumble bees visit forage-plants from early morning to late evening not only during sunny days, but also during cloudy and foggy days also (in the latter cases the number of bumble bees is decreased).

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