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Crane flies (Diptera, Tipuloidea: Tipulidae, Limoniidae) of Wrangel Island (Chukotka AO, Russia). 2. Features of the faunal composition and spatial distribution

Типулоидные двукрылые (Diptera, Tipuloidea: Tipulidae, Limoniidae) острова Врангеля (Чукотский АО, Россия). 2. Особенности фаунистического состава и пространственного распределения

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Key words: Tipulidae, Limoniidae, Arctic, tundra zone, chorology, spatial distribution, abundance dynamics, climate warming.

Ключевые слова: Tipulidae, Limoniidae, Арктика, тундровая зона, хорология, пространственное распределение, динамика численности, потепление климата.

Abstract. Tipuloidea are an abundant and ecologically important group of tundra insects. In the insular Arctic, one of the richest faunas of crane flies (Tipulidae and Limoniidae) is represented on Wrangel Island, whose biota had a long successive development under conditions of high natural environment diversity and absence of glaciation. It is based on species of the genus *Tipula* Linnaeus, 1758 (13 species), the main part of whose range lies in the tundras of Siberia. In the material studied, they represent 63 % of the species composition and 98 % of all specimens collected. In most areas, two mesoxerophilic species dominate: the Siberian-Alaskan *Tipula* (*Pterelachisus*) *carinifrons carinifrons* Holmgren, 1883 (46 % of all specimens collected, found everywhere) and *T.* (*Vestiplex*) *wrangeliana* Stackelberg, 1944, the island subendemic (34 %, absent in areas with harshest climate). The remaining mesoxerophilic species (there are *Nephrotoma lundbecki lundbecki* (Nielsen, 1907) and four *Tipula* species from the subgenera *Lunatipula*, *Odonatisca*, *Pterelachisus* and *Vestiplex*) are only locally abundant; three of these species are restricted to the warmest areas of the island. Among the hydro- and hygrophilous (six species of Tipulidae and five of Limoniidae), only *Tipula* (*Savtshenkia*) *glaucocinerea* Lundström, 1915 has a high abundance (12 %, most common in climatically more severe areas of the island). The remaining species of this group occur sporadically, and the distribution of most of them does not show a close relationship with the climatic gradient on the island. In terms of species composition, the Tipuloidea fauna of Wrangel Island is most similar to that of Taymyr and, in the insular Arctic, to that of Novaya Zemlya. Compared to other areas belonging to the same bioclimatic subzone, mesoxerophilic species on Wrangel Island are significantly more diverse. In the 20th century (1980s–90s data), high abundances of Tipuloidea were recorded in almost all areas where quantitative surveys (using pitfall traps) were carried out. Data collected in the 21st century (mainly in 2010s) show a marked decline in the abundance of this group, which is particularly pronounced in the warmest inland areas of the island. This is due to declining abundance of some species (especially *Tipula carinifrons carinifrons* Holmgren, 1883), indicating the vulnerability of the High Arctic Tipulidae complex in the changing climate.

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Резюме. Типулоидные двукрылые (Tipuloidea) — многочисленная и экологически значимая группа насекомых в тундровой зоне. Одна из наиболее богатых фаун Tipuloidea (Tipulidae и Limoniidae) в островной Арктике представлена на острове Врангеля, биота которого имела длительное преемственное развитие в условиях высокого разнообразия природной среды и отсутствия покровного оледенения. Её основу составляют виды рода *Tipula* Linnaeus, 1758 (13 видов), основная часть ареала которых лежит в тундрах Сибири. В изученном материале они составляют 63 % видового состава и 98 % от всех собранных экземпляров. В большинстве районов доминируют два мезоксерофильных вида: сибирско-аляскинский *Tipula* (*Pterelachisus*) *carinifrons carinifrons* Holmgren, 1883 (46 % от числа всех собранных экземпляров, встречается повсеместно) и субэндемик острова *T.* (*Vestiplex*) *wrangeliana* Stackelberg, 1944 (34 %, отсутствует в климатически наиболее суровых районах). Остальные мезоксефильные виды (*Nephrotoma lundbecki lundbecki* (Nielsen, 1907) и четыре вида *Tipula* из подродов *Lunatipula*, *Odonatisca*, *Pterelachisus* и *Vestiplex*) только локально имеют высокое обилие; три из них ограничены наиболее тёплыми районами острова. Из видов, относящихся к гидро- и гигрофилам (шесть видов Tipulidae и пять Limoniidae) высокую численность имеет только *Tipula* (*Savtshenkia*) *glaucocinerea* Lundström, 1915 (12 %, наиболее обычен в климатически суровых районах острова). Остальные виды этой группы встречаются на острове спорадично, а распределение большинства из них не показывает тесной связи с климатическим градиентом. Сравнение с фаунами других регионов Арктики показало, что по видовому составу фауна Tipuloidea острова Врангеля наиболее близка к фауне Таймыра, а в островной Арктике — к фауне Новой Земли. По сравнению с другими районами, принадлежащими к той же биоклиматической подзоне, мезоксерофильные виды на острове Врангеля представлены заметно более разнообразно. В XX веке (данные 1980–90е гг.) почти во всех районах, где проводились количественные сборы (учёты почвенными ловушками) отмечены высокие показатели обилия Tipuloidea. Данные, полученные в XXI в. (преимущественно в 2010-е гг.), указывают на заметное снижение обилия этой группы, что особенно ярко проявляется в наиболее тёплых внутренних районах острова. Оно связано с сокращением численности ряда видов (особенно *Tipula carinifrons carinifrons* Holmgren, 1883), что свидетельствует об уязвимости высокоарктического комплекса типулид в меняющемся климате.

Introduction

Three families from superfamily Tipuloidea: Tipulidae, Limoniidae and Pediciidae, inhabit different regions of the tundra zone [MacLean, Pitelka, 1971; MacLean, 1975a; Chernov, 1978, 1985, 1995; Danks, 1981; Lantsov, Chernov, 1987]. The Tipulidae family is particularly important, especially in the northern tundra ecosystems, where this group is most abundant. Species with arctic, arcto-montane and hypoarctic distributions form the basis of the tundra fauna of the Tipulidae; the total number of such species is about 35 [Savchenko, 1983]. The other two families contain much fewer species with similar ranges [Lantsov, Chernov, 1987; Savchenko, 1989].

Information about the Tipuloidea of the Arctic islands is contained in a significant number of publications [Alexander, 1922, 1934; Curran, Alexander, 1927; Ǿkland, 1928; Lackschewitz, 1936; Savchenko, 1961, 1964, 1983; Oliver, 1963; Ryan, 1977; Danks, 1981; Brodo, 1987, 1990, 2000, 2009, 2012, 2017; Khruleva, 1987; Lantsov, Chernov, 1987; Stary, Brodo, 2009; Lantsov, 2011; Oosterbroek et al., 2007, 2015; Khruleva, Devyatkov, 2019; Pentinsaari et al., 2020; Brodo et al., 2022]. The available data indicate that this superfamily is extremely unevenly represented in the insular Arctic — from complete absence on Svalbard and Franz Josef Land [Coulson et al., 2014] to two dozen species on Novaya Zemlya and Wrangel Island [Lantsov, Chernov, 1987]. In the Arctic mainland, the highest latitude is occupied by the Taymyr Peninsula (Taymyr in the text below), from which about 25 species of Tipulidae, 16 Limoniidae and 1 species of Pediciidae are known [Lantsov, Chernov, 1987]. Despite a good knowledge of the species composition of Tipuloidea, studies of their ecology, distribution and population dynamics have only been carried out in Taymyr [Lantsov, Chernov, 1987] and in northern Alaska [MacLean, Pitelka, 1971; MacLean, 1973, 1975a].

Wrangel Island is one of the most important biogeographical areas with an unusually high diversity of flora and fauna [Yurtsev, 1987; Stishov, 2004; Khruleva, 2007] due to its location, landscape diversity and long-term evolution of its biota in the absence of glacial cover. The previously published information on crane flies of the island [Khruleva, 1987; Khruleva, Devyatkov, 2019; Brodo et al., 2022] has been significantly supplemented in recent years. On this basis, two articles have been prepared. The first paper, Comm. 1 [Khruleva et al., 2024], presents an annotated list of the Tipuloidea of Wrangel Island based on collections from 1966 to 1922. The present paper (Comm. 2) discusses faunal characteristics, spatial distribution of species and abundance dynamics of this group in seasons with different weather conditions and during Arctic climate warming. In addition, a comparative analysis of the Tipuloidea faunas of Wrangel Island and other Arctic regions has been carried out.

Materials and methods

A brief overview of Wrangel Island's natural environment and information on the material studied is given in Comm. 1 [Khruleva et al., 2024]. The subzonal differentiation of the island territory and the collection sites of Tipuloidea are shown in Fig. 1. The main quantitative material was collected in pitfall traps (Table 1), but only data from a few seasons in the 20th century have been identified. As in other Arctic regions [Alekseev et al., 2015; Box et al., 2019], climate warming was recorded on the island at the turn of the 21st century, manifested by increasing summer temperatures, longer frost-free periods and periodic autumn-winter thaws (based on data from the Rogers Bay weather station). When comparing the fauna of Wrangel Island with other areas of the Arctic, its boundaries are given by the Circumpolar Arctic Vegetation Map [CAVM Team, 2003]. The High Arctic

Table 1. Collections by pitfall traps: location, survey period, number of trap-days and Tipuloidea specimens collected in the 20th and 21st centuries

Таблица 1. Сборы почвенными ловушками: место, период исследования, количество отработанных ловушко-суток и собранных экземпляров Tipuloidea в XX и XXI вв.

Year	Area	Collection period, number of trap-days worked and surveys habitats *	Total specimens	Year	Area	Collection period, number of trap-days worked and surveys habitats *	Total specimens
1983	mNz	18.VII–29.VIII, 3540 (12)	294	2006	mNzh	10.VI–27. VII, 920 (4)	94
1984	IGs	28.VI–30.VIII, 7575 (17)	3976		SB	15.VI–16.VII, 600 (4)	106
1985	IGd	25.VI–17.VIII, 3435 (7)	224		SMM	15.VI–16.VII, 1800 (13)	23
	IKF	10.VII–10.VIII, 465 (3)	145		mM	19.VI–21.VII, 3075 (18)	216
1986	SB	24.VI–14.VIII, 1530 (3)	1393		uNz	4.VI–3.VIII, 1786 (9)	12
	SMM	5.VI–27.VIII, 2670 (7)	134	2011	mKF	16–27.VII.2011, 973 (10)	382
1988	ITn	24.VI–18.VIII, 1710 (4)	714		mM	26.VI–17.VII, 1006 (5)	51
	RB	24.VI–24.VII, 3790 (10)	274	2014	mM	2.VII–27.VII, 1785 (7)	712
1989	ITn	15.VI–19.VII, 2570 (10)	2370	2015	SB	15.VI–19.VII, 2105 (7)	520
	SB	9.VII–10.VIII, 775 (4)	183		SMM	12.VI–19.VII, 4959 (17)	120
	SMM	29.V–10.VIII, 2070 (4)	7		TnM	1–19.VII, 1080 (6)	58
1990	RB	5.VI–17.VII, 1660 (6)	1002		mM	29.VI–23.VII, 1095 (17)	75
	uNz	26.VI–27.VII, 930 (3)	100		uNz	21.VI–12.VII, 2726 (17)	236
1991	uNz	19–26.VII, 1557 (10)	318		PM	28.VI–13.VII, 600 (5)	7
1992	mM	20.VI–27.VII, 3550 (20)	1015	2016	uNzh	8.VII–1.VIII, 1200 (5)	16
	PM	18.VI–25.VII, 555 (3)	89		TmM	10–31.VII, 621 (3)	1
1993	mM	2.VI–30.VII, 3623 (19)	1228		Mb	11–31.VII, 800 (4)	47
	PM	13.VI–7.VII, 1636 (8)	661	2020	TnM	4–14.VII, 300 (3)	16
1994	mM	10–30.VII, 1800 (18)	262		WC	16–24.VII, 320 (4)	3
				2021	TnM	8–17.VII, 270 (3)	26
Total, 20th century		45621 trap-days (168 biotopes)	14389	Total, 21st century		29422 trap-days (161 biotopes)	2715
Total number of specimens identified			3369	Total number of specimens identified			2333
Of which, *Tipula carinifrons carinifrons* Holmgren, 1883			2091	Of which, *Tipula carinifrons carinifrons* Holmgren, 1883			718
T. wrangeliana Stackelberg, 1944			830	*T. wrangeliana* Stackelberg, 1944			1169
T. glaucocinerea Lundström, 1915			322	*T. glaucocinerea* Lundström, 1915			378

Note: * — collection dates and number of trap-days worked are given for the period when adults were caught in pitfall traps; the number of habitats surveyed is given in brackets. The abbreviations for area names are shown in Fig. 1.

Примечание: * — сроки сбора и количество отработанных ловушко-суток даны за период, когда в почвенные ловушки попадали имаго; количество изученных биотопов дано в скобках. Аббревиатура районов дана на рис. 1.

comprises bioclimatic subzones A-C, while the Low Arctic comprises subzones D and E. According to the classification used by Russian geobotanists [Matveyeva, 1998], subzone A corresponds to the polar desert zone, B to the arctic tundra subzone, C and D to the northern and southern variants of the typical tundra subzone, and E to the southern tundra subzone. We refer to arctic species as those restricted to the tundra zone or occurring outside this zone in some mountain regions. «Activity» refers to the ability of a species to colonize a given area using data on spatial distribution, frequency of occurrence and abundance. The abundance of Tipuloidea was mainly estimated on the basis of their catchability in pitfall traps. We divide the ecological groups (in relation to habitat humidity) based on literary data [Savchenko, 1961, 1964, 1983, 1989; Lantsov, Chernov, 1987]. Comparison of abundance data was performed using Statistica12 software; to compare the faunas of Arctic regions, PAST v. 3.06 [Hammer, 2015] was used. Abbreviations: ex/100t-d — specimens collected in pitfall traps and calculated per 100 trap-days. Abbreviations for area names and subzonal variants are shown in Fig. 1.

The present work is registered in ZooBank (www.zoobank.org) under urn:lsid:zoobank.org:pub:DFF016A2-8273-4465-ACDE-78EC8724650A

Results

Table 2 presents data on the geographical and ecological composition of Tipuloidea species and their abundance in different subzonal variants. The table excludes two species documented in the literature sources from Wrangel Island: *Tipula* (*Pterelachisus*) *crawfordi* Alexander, 1927 [Curran, Alexander, 1927] and *Limnophila* sp. [Makarchenko et al., 1980].

Taxonomic and arealogical composition of fauna

The taxonomic structure of the Tipulidae and Limoniidae families on Wrangel Island differs significantly, as demonstrated in Table 2. The family Tipulidae consists of three genera: *Nephrotoma* Meigen, 1803, *Prionocera* Loew, 1844, and *Tipula* Linnaeus, 1758, all of which belong to the subfamily Tipulinae. However, almost all species, 13 out of 15 (including *Tipula crawfordi* Alexander, 1927), belong to *Tipula* Linnaeus, 1758 and comprise species from seven subgenera: *Arctotipula*, *Lunatipula*, *Odonatisca*, *Pterelachisus*, *Savtshenkia*, *Vestiplex* and *Yamatotipula*. In the material studied, they represent 63 % of the species composition and 98.4 % of all specimens collected. In contrast, all the limoniid species collected on the island are represented by various genera from three subfamilies: Chioneinae (*Actoconopa* Alexander, 1955, *Symplecta* Meigen, 1830, *Ormosia* Rondani, 1856, and *Rhabdomastix* Skuse, 1890), Dactylolabinae (*Dactylabis* Osten Sacken, 1860) and Limnophilinae (*Limnophila* Macquart, 1834), each including a single species.

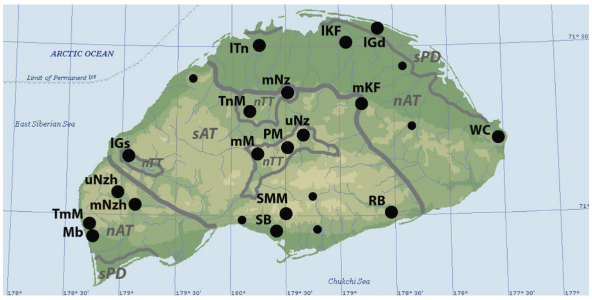


Fig. 1. Map of Wrangel Island showing localities where Tipuloidea were collected. Subzonal differentiation (according to Kholod [2013]): *sPD* — southern variant of polar desert zone; *nAT* — northern variant of Arctic tundra subzone; *sAT* — southern variant of Arctic tundra subzone; *nTT* — northern variant of typical tundra subzone. The bold line marks the boundary between the northern and southern zonal strips. Areas surveyed using pitfall trapping (big circles): **lGd** — lower reaches of the Gidrografov River; **lTn** — lower reaches of the Tundrovaya River; **TmM** — Thomas Mt.; **Mb** — Morzhovy brook; **uNzh** — upper reaches of the Neozhidannaya River; **mNzh** — middle flow of the Neozhidannaya River; **WC** — Cape Waring; **mKF** — middle reaches of the Krasnyi Flag River; **SB** — Somnitelnaya Bay environs, plain; **SMM** — Somnitelnaya Bay environs, mountainous part (Somnitelnye and Mineev Mts); **RB** — Rogers Bay environs; **lGs** — lower reaches of the Gusinaya River; **TnM** — environs of Tundrovaya Mt.; **mNz** — middle flow of the Neizvestnaya River; **mM** — middle flow of the Mamontovaya River; **PM** — spurs of Pervaya Mt.; **uNz** — upper reaches of the Neizvestnaya River. Small circles are other areas where Tipuloidea have been collected (see Comm. 1 [Khruleva et al., 2024]).

Рис. 1. Карта острова Врангеля с местами сборов Tipuloidea. Подзональная дифференциация (по Холоду [2013]): *sPD* — южный вариант зоны полярных пустынь; *nAT* — северный вариант подзоны арктических тундр; *sAT* — южный вариант подзоны арктических тундр; *nTT* — северный вариант подзоны типичных тундр. Жирная линия — граница между северной и южной зональными полосами. Районы, обследованные с помощью почвенных ловушек (большие кружки): **nGd** — нижнее течение р. Гидрографов; **TmM** — гора Томас; **Mb** — ручей Моржовый; **uNzh** — верхнее течение р. Неожиданная; **mNzh** — среднее течение р. Неожиданная; **lTn** — нижнее течение р. Тундровая; **WC** — мыс Уэринг; **mKF** — среднее течение р. Красный Флаг; **SB** — окрестности бухты Сомнительной, равнина; **SMM** — окрестности бухты Сомнительной, горная часть (горы Сомнительные и Минеева); **RB** — окрестности бухты Роджерса; **lGs** — нижнее течение р. Гусиная; **TnM** — окрестности горы Тундровая; **mNz** — среднее течение р. Неизвестная; **mM** — среднее течение р. Мамонтовая; **PM** — отроги горы Первая; u**Nz** — верхнее течение р. Неизвестная. Маленькие кружки — прочие районы, где были собраны Tipuloidea (см. Сообщ. 1).

These families differ significantly in both their latitudinal and longitudinal structures. The fauna of the Limoniidae consists mainly of species with wide (including Holarctic) ranges, extending well beyond the Arctic. The family Tipulidae, on the other hand, is characterised by the predominance of arctic species. Many of these are restricted to Siberia (some also occur in north-eastern Europe or Alaska). Arctic species with such ranges are among the most abundant: *Tipula carinifrons carinifrons* Holmgren, 1883 (46.1 % of all collected specimens), *T. glaucocinerea* Lundström, 1915 (11.6 %) and the subendemic *T. wrangeliana* Stackelberg, 1944 (33.8 %). At the same time, some species with similar distributions (e.g. *Tipula oklandi* Alexander, 1922 and *T. lionota* Holmgren, 1883) are among the rarest. Among other species, the highest abundance was recorded for the arcto-montane *Tipula subrecticornis* Savchenko, 1964 (2.3 %).

Peculiarities of the spatial distribution of Tipuloidea

Most Tipuloidea species are very unevenly distributed across the island. This is particularly true for hygrophilic and hydrophilic taxa, represented by 11 species in our material (Table 3). Even the most abundant of them, *Tipula glaucocinerea* Lundström, 1915, was regularly found only in climatically rather harsh areas of the island (*sPD*, *nAT*), and its activity was significantly reduced in the southern zonal strip (*sAT*, *nTT*). On the whole, the highest number of hygrophilic species of Tipulidae has been collected in the well-watered (large number of lakes and wet relief depressions) but also colder northern part of the island. Only *Tipula convexifrons* Holmgren, 1883 and *T. oklandi* Alexander, 1922 were restricted to the warmest areas (*sAT*, *nTT*). Most of the limoniids were also quite widespread on the island, but they were even more sporadic in their occurrence (Tables 2, 3). Of these, *Dactylolabis novaezemblae* (Alexander, 1925) has the widest distribution and *Arctoconopa forcipata forcipata* (Lundström, 1915) is restricted to the warmest areas.

In general, the wet habitats are very incompletely occupied by hygrophilic taxa, although most of them have a fairly wide distribution on the island. The lack of a clear relationship with the climatic gradient is also evident in their occupation of the *nTT* enclaves. The activity of some hygrophiles is significantly higher in the northern enclave, which borders the *nAT* plain and where wet habitats occupy more extensive areas than in the southern enclave. It is suggested that landscape features of the area are probably more important than climatic conditions for the spatial distribution of hygrophilic species on the island.

On the contrary, the distribution of most mesoxerophilic taxa is clearly related to the climatic gradient (Table 3). Of the seven species in this group, only *Tipula carinifrons carinifrons* Holmgren, 1883 is ubiquitous on the island (including the *sPD*). The activity of this species is highest in the *nAT* and *sAT* plains, where it is occupy the full range of habitats (Fig. 2), and much lower in the mountains. *Tipula pribilofensis* Alexander, 1923 is the only species in this group found mainly in the *nAT*. This may be due to its confinement to vast sandy-pebble floodplains, which are most common in the lower reaches of large rivers on the northern plain. The

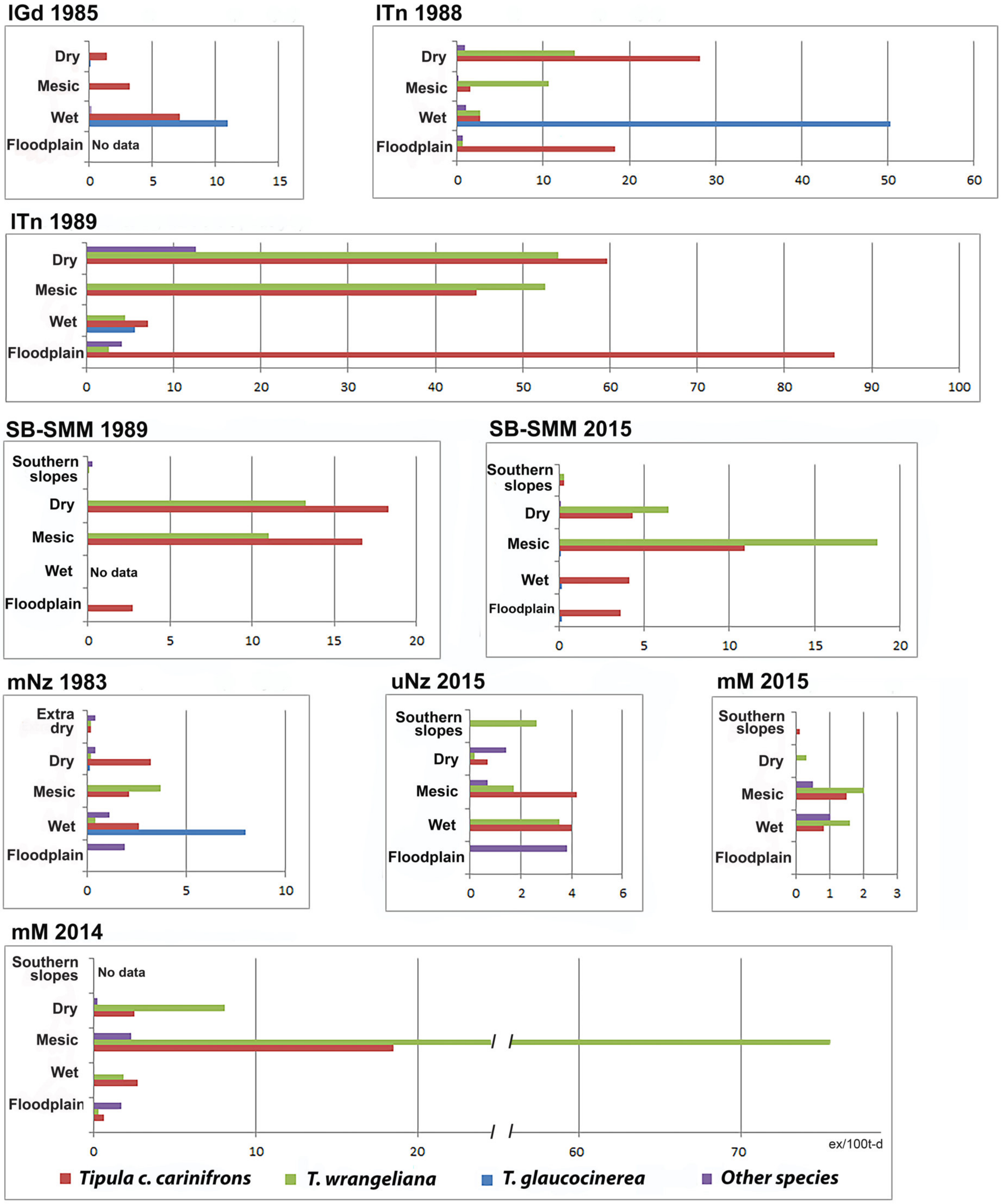


Fig. 2. Abundance of crane flies in pitfall traps (ex/100t-d) in habitats with different moisture contents in some of the most detailed study areas. The abbreviations for area names are shown in Fig. 1.

Рис. 2. Обилие Tipuloidea в почвенных ловушках (экз./100 ловушко-суток) в местообитаниях с различным увлажнением в наиболее подробно изученных районах. Аббревиатура районов дана на рис. 1.

Table 2. Areal composition of Tipuloidea species and number of specimens collected on Wrangel Island in different subzonal variants

Таблица 2. Ареалологический состав видов Tipuloidea и число экземпляров, собранных на острове Врангеля в различных подзональных вариантах

Family, species, longitudinal and latitudinal group	Subzonal variants				Total number of locations detected and presence in the best studied local faunas	Total speci-mens*
	sPD	*nAT*	*sAT*	*nTT*		
Tipulidae						
Prionocera recta Tjeder, 1948; H, am	3	8	9	3	10: lGd, lTn, SB, SMM, RB, mNz, mM	22/1
Nephrotoma lundbecki lundbecki (Nielsen, 1907); H, ahm	–	–	–	29*	3: mM, uNz	4/25
Tipula (*Arctotipula*) *besselsoides* Alexander, 1919; N, a	–	7	24	7	6: lTn, RB, TnM, mNz	9/29
T. (*A.*) *oklandi* Alexander, 1922; S, A	–	–	2	7	4: SB, SMM, mM, uNz	2/7
T. (*Arctotipula*) sp.	–	1	–	1	2: lTn, mM	1/1
T. (*Lunatipula*) *subrecticornis* Savchenko, 1964; S, am	–	–	14	138	6: SMM, TnM, mNz, mM, uNz	19/133
T. (*Odonatisca*) *pribilofensis* Alexander, 1923; S-eB, h	–	41	–	15	5: lTn, mNz, mM	48/8
T. (*Pterelachisus*) *carinifrons carinifrons* Holmgren, 1883; S-eB, a	120	1912	550	497	20: lGd, lTn, SB, SMM, RB, TnM, mNz, mM, uNz	2245/824
T. (*Pt.*) *middendorffi middendorffi* Lackschewitz, 1936; Eu, am	–	–	4	47	4: SMM, TnM, mM, uNz	21/30
T. (*Savtshenkia*) *convexifrons* Holmgren, 1883; S, a	–	2	6	35	8: SB, SMM, TnM, mNz, mM	19/24
T. (*S.*) *glaucocinerea* Lundström, 1915; S, a	110	572	10	80	16: lGd, lTn, SB, SMM, RB, TnM, mNz, mM	369/403
T. (*Vestiplex*) *arctica* Curtis, 1835; H, am	–	57	15	29	11: lTn, SB, SMM, RB, TnM, mNz, mM, uNz	91/10
T. (*V.*) *wrangeliana* Stackelberg, 1944; Ch, a	–	837	550	865	13: lTn, SB, SMM, RB, TnM, mNz, mM, uNz	1003/ 1249
T. (*Yamatotipula*) *lionota* Holmgren, 1883;S-eB, a	–	3	2	2	4: SMM, TnM, mNz	6/1
Limoniidae						
Arctoconopa forcipata forcipata (Lundström, 1915); H, ah	–	–	–	6	2: mM	5/1
Ormosia (*Ormosia*) *fascipennis* (Zetterstedt, 1838); H, abm	–	–	1	–	1: RB	0/1
Rhabdomastix (*Rhabdomastix*) *borealis* Alexander, 1924: H, h	–	12	–	3	2: uNz	0/15
Symplecta (*Symplecta*) *sheldoni* (Alexander, 1955); eP-eB, hm	–	3	–	6	4: TnM, mM, uNz	6/3
Dactylolabis (*Dactylolabis*) *novaezemblae* (Alexander, 1925); Eu, a	–	16	1	8	7: lTn, RB, mNz, mM	14/11
Total specimens	233	3389	1188	1741		3884/ 2776
Total species	3	13	13	18		19

Note: * Before the line collection of the 20th century, after the line — collection of the 21st century. Longitudinal distribution: Ch — Chukotka AO; Eu — Eurasian; Eu-eB — Eurasian–East Beringian (Alaska); eP-eB — East Palearctic (Chukotka, Mongolia) – East Beringian (Alaska, Yukon); H — Holarctic; N — predominantly North American; S — Siberian (including Novaya Zemlya or Dolgiy Island); S-eB — Siberian – East Beringian. Latitudinal distribution: a — arctic; am — arcto-montane; abm — arcto-boreo-montane, ah — arcto-hypoarctic; ahm — arcto-hypoarcto-montane; h — predominantly hypoarctic, hm — predominantly hypoarcto-montane. The table contains all the material presented in Comm. 1 [Khruleva et al., 2024]. The abbreviations of subzonal variants and area names are given in Fig. 1; material from the mKF, located on the border of the *nAT* and *sAT*, is included in the *nAT* (according to Kholod [2013]).

Примечание: * перед чертой — сборы XX в., после черты — XXI в. Долготное распространение: Ch — Чукотский АО; Eu — евразийское; Eu-eB — евразийско–восточно-берингийское (Аляска); eP-eB — восточно-палеарктическое (Чукотка, Монголия) — восточно-берингийское (Аляска, Юкон); H — голарктическое; N — преимущественно северо-американское; S — сибирское (включая Новую Землю или остров Долгий); S-eB — сибирское–восточно-берингийское. Широтное распространение: a — арктическое, am — аркто-монтанное; abm — аркто-борео-монтанное; ah — аркто-гипоарктическое; ahm — аркто-гипоаркто-монтанное; h — преимущественно гипоарктическое; hm — преимущественно гипоаркто-монтанное. В таблицу включён весь материал, представленный в Сообщ. 1. Аббревиатура подзональных вариантов и названий районов приведена на рис. 1; материал из mKF, расположенного на границе *юАТ* и *сАТ*, включён в *сАТ* (согласно Холоду [2013]).

distribution of other mesoxerophilic species is clearly biased towards the southern zonal strip. Three species, *Nephrotoma lundbecki lundbecki* (Nielsen, 1907), *Tipula subrecticornis* Savchenko, 1964, and *T. middendorffi middendorffi* Lackschewitz, 1936 are restricted to the warmest areas of the island (mountains of the *sAT* and enclaves of the *nTT*). *Tipula arctica* Curtis, 1835 is also much more common in the southern zonal strip, but the highest abundance of this species was recorded in one season in the west of *nAT*.

The subendemic *Tipula wrangeliana* Stackelberg, 1944 has a distribution similar to that of most other mesoxerophilic species. In the northern zonal strip, it is completely absent in the north-east, but locally common in the drier western part of the northern plain (zonal positions here are occupied by plant assemblages with high participation of grasses and wormwoods). In the south-western part of the *nAT* it was collected in isolated habitats and only once in high abundance (at the foot of a south-facing slope). In contrast, in the southern zonal strip, *T. wrangeliana* Stackelberg, 1944 is almost ubiquitous (it was not found only in some mountainous areas where short-term collections were made), reaching its highest abundance in flat and slightly hilly landscapes.

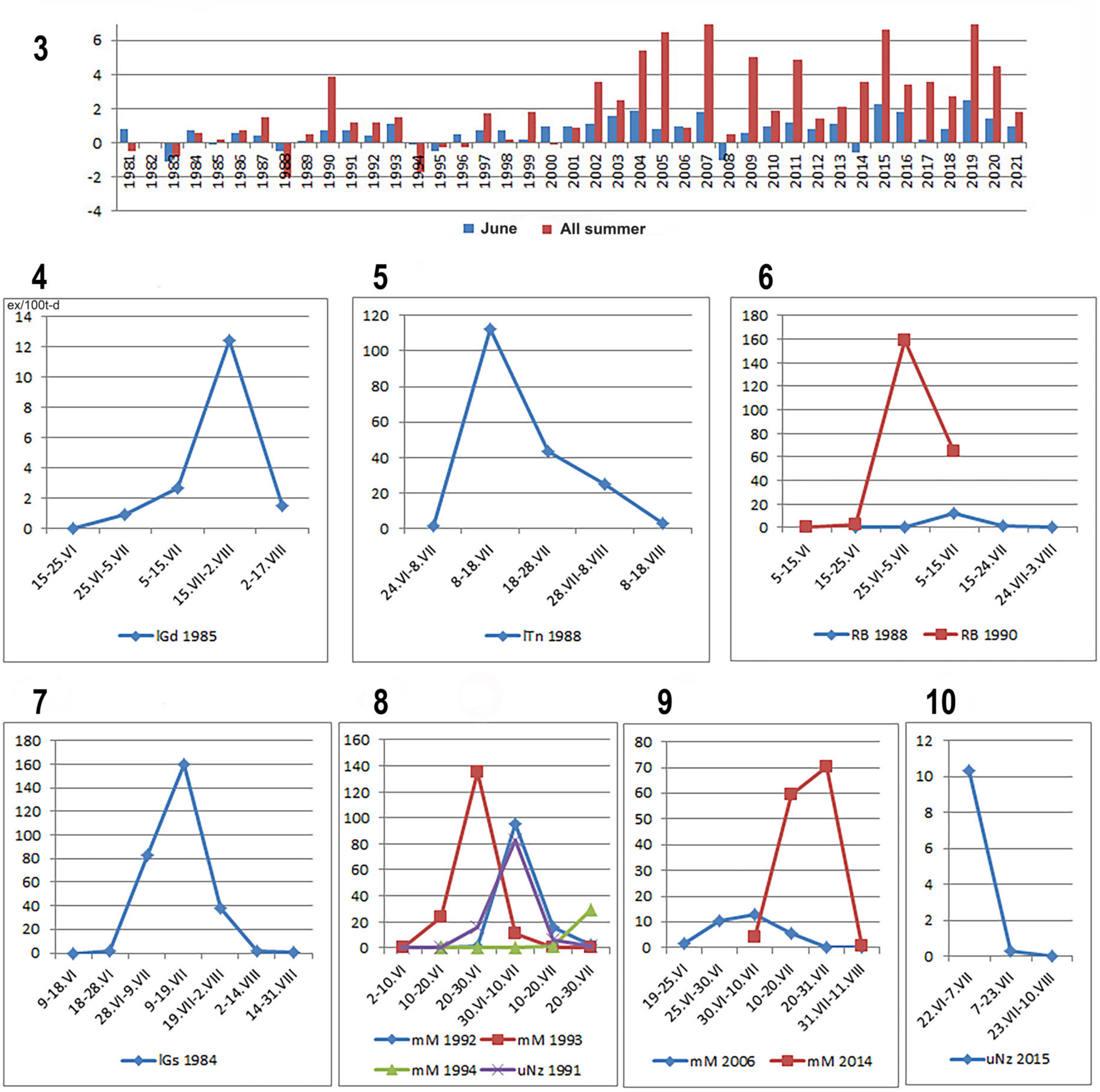
The two most abundant mesoxerophilic species, *Tipula carinifrons carinifrons* Holmgren, 1883 and *T. wrangeliana* Stackelberg, 1944, inhabit both dry and wet habitats on the island (Fig. 2). For the former, this is evident everywhere, whereas *Tipula wrangeliana* extends its topical spectrum only in the warmest areas of the island (*nTT*). At the quantitative level, the predominance of mesoxerophilic species in the most areas is very pronounced (Table 3). Only in the *sPD* are their proportions comparable due to the absence of almost all mesoxerophilic species and the high abundance of *Tipula glaucocinerea* Lundström, 1915. The proportion of mesoxerophilic species is particularly high in the *sAT* plain and in the southern *nTT* enclave (97–98 % of the total number of specimens collected). Of course, the figures obtained only show a general trend. For the northern part

Table 3. Activity of crane fly species with different ecological preferences in the best studied areas of Wrangel Island
Таблица 3. Активность видов Tipuloidea с разными экологическими предпочтениями в наиболее хорошо изученных районах острова Врангеля

Family, species	Ecological group	*sPD*, northern plain	*nAT*, northern plain	*nAT*, south-western part	*sAT*, plain	*sAT*, mountain part	*nTT*, northern enclave	*nTT*, southern enclave
Tipulidae								
Prionocera recta Tjeder, 1948	g	2	3	–	1	1	1	1
Tipula glaucocinerea Lundström, 1915	g	5	5	3	1	2	3	1
T besselsoides Alexander, 1919	g	–	2	1	–	3	2	–
T. convexifrons Holmgren, 1883	g	–	1	–	1	2	3	3
T. oklandi Alexander, 1922	g	–	–	–	1	1	–	2
Tipula sp.	g	–	1	–	–	–	–	1
T. lionota Holmgren, 1883	m	–	1	–	–	1	1	–
T. pribilofensis Alexander, 1923	mx	–	3	–	–	–	2	2
T. carinifrons carinifrons Holmgren, 1883	mx	4	5	4	5	4	5	5
T. wrangeliana Stackelberg, 1944	mx	–	3	3	5	4	5	5
T. arctica Curtis, 1835	mx	–	3	1	2	2	2	3
T. subrecticornis Savchenko, 1964	mx	–	–	–	–	3	3	4
T. middendorffi middendorffi Lackschewitz, 1936	mx	–	–	–	–	2	3	3
Nephrotoma lundbecki lundbecki (Nielsen, 1907)	mx	–	–	–	–	–	–	3
Limoniidae								
Symplecta sheldoni (Alexander, 1955)	g	–	1	–	–	–	1	2
Rhabdomastix borealis Alexander, 1924	g	–	–	2	–	–	–	1
Ormosia fascipennis (Zetterstedt, 1838)	g	–	–	–	1	–	–	–
Arctoconopa forcipata forcipata (Lundström, 1915)	g	–	–	–	–	–	–	2
Dactylolabis novaezemblae (Alexander, 1925)	mg?	–	3	3	–	1	1	2
Total specimens		233	3297	174	541	293	356	1327
Proportion of meso-xerophilic taxa in the sample, %		52	83	63	98	84	69	97

Note: Ecological group: g — hygrophile (including hygro- and hydrophilous species); m — mesophile; mg — mesohygrophile; mx — mesoxerophile. Presence in suitable habitats: 1 — single specimens; 2 — rare; 3 — occurs quite regularly in some areas; 4 — occurs regularly in different areas (in some habitats in significant abundance); 5 — occurs everywhere. The abbreviations of the subzonal variants are given in Fig. 1.

Примечание: Экогруппа: g — гигрофил (включая гигро- и гидрофильные виды); m — мезофил; mg — мезогигрофил; mx — мезоксерофил. Присутствие в подходящих местообитаниях: 1 — единичные находки; 2 — редок; 3 — достаточно регулярно встречается в отдельных районах; 4 — регулярно встречается в различных районах (в отдельных биотопах — в значительном обилии); 5 — встречается повсеместно. Аббревиатура подзональных вариантов приведена на рис. 1.



Figs 3–10. The values of summer temperatures and the abundance of Tipuloidea in different seasons. 3 — deviation of average monthly temperatures in June and total positive temperatures in the summer months from the long-term average (1961–1990), data from the Rogers Bay weather station; 4–10 — seasonal dynamics of Tipuloidea abundance (ex/100 t-d) in pitfall traps on Wrangel Island during different summer seasons. The abbreviations and locations of the study areas are shown in Fig. 1.

Рис. 3–10. Значения летних температур и обилие типулоидов в различные сезоны. 3 — Отклонение среднемесячных температур июня и суммарных положительных температур летних месяцев от многолетних средних (1961–1990 гг.), данные метеостанции в бухте Роджерса; 4–10 — сезонная динамика обилия Tipuloidea (экз./100 ловушко-суток) в почвенных ловушках на острове Врангеля в различные летние сезоны. Аббревиатура и расположение районов даны на рис. 1.

of the *nAT*, the proportion of mesoxerophilic species is clearly greatly overestimated, since the main quantitative collections were carried out in the northwest, where their activity is significantly higher than in the northeast.

CHANGES IN TIPULOIDEA SPECIES RICHNESS ALONG A ZONAL GRADIENT

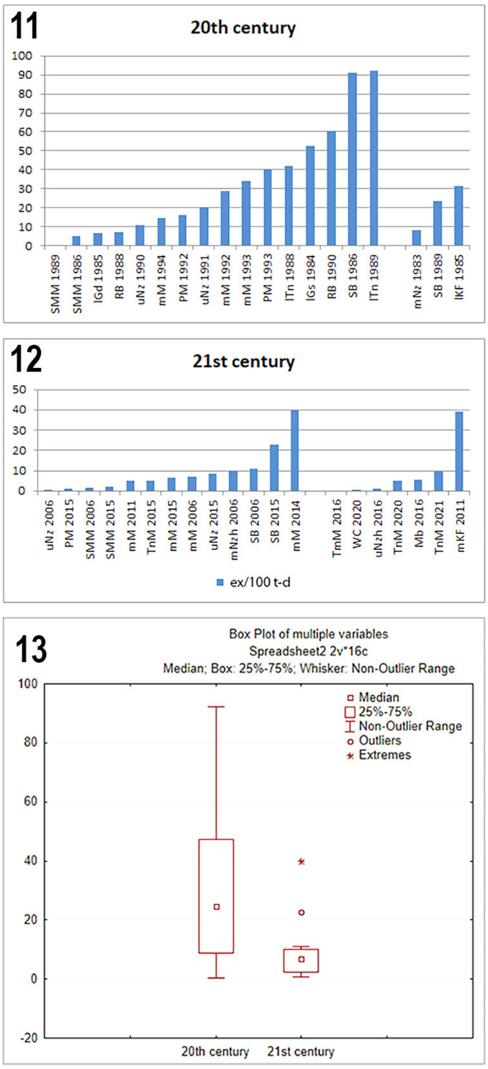
Table 2 shows the presence of crane fly species in the nine best-studied local faunas. In most of the studied local faunas, a close number of species have been collected, despite the fact that they belong to different subzonal variants. Thus, 9 species were collected in the *nAT* (lTn), 7 (SB), 8 (RB) and 10 (SMM) species in the *sAT*, 10 (TnM) and 11 (mNz) species in the northern enclave of the *nTT*, and 9 (uNz) and 15 (mM) species in the southern, warmest enclave. Only the fauna of *sPD* differs sharply from all others due to extreme poverty. During the entire summer season of 1985, only three species of Tipulidae were collected in the lGd (*sPD*), while in much shorter collections during the same season in the border areas belonging to the *nAT*, eight species (six of Tipulidae and two of Limoniidae) were collected. In the *sAT*, material was collected mainly in the vicinity of SB and RB. These areas turned out to be among the best studied: in addition to our studies, there are data on species collected here in the 1930s, as well as material from K.B. Gorodkov (see Comm. 1) [Khruleva et al., 2024]. The total number of species collected in this subzonal variant was similar to that of *nAT* (13 species in each), but the composition of the species was markedly different (Table 2). The greatest number of species was found in the *nTT*: almost all the species represented in our material (18 out of 19) were recorded here. Most of them were collected in the mM, where the longest studies were carried out (seven summer seasons).

Thus, there are no significant differences in species richness of Tipuloidea along the climatic gradient in most of the island's territory (with the exception of the *sPD*). Obviously, this is due both to the more frequent finds of some rare moisture-loving species in colder areas, and to the presence of species in the fauna that clearly tend to the warmest areas (see above).

INTER-ANNUAL DYNAMICS OF ABUNDANCE AND PECULIARITIES OF THE PHENOLOGY

The available data indicate significant inter-annual fluctuations in the abundance of tipulid species on Wrangel Island (Fig. 2). Comparative material was collected in pitfall traps in the lTn in 1988–1989, of which the first summer season was one of the coldest, and in 1989 summer temperatures were close to average (Fig. 3). Repeated surveys of the same habitats revealed significant multidirectional changes in the abundance of the most common species in pitfall traps. The abundance of the hygrophilic *Tipula glaucocinerea* Lundström, 1915 declined sharply in 1989, whereas the abundance of *T. carinifrons carinifrons* Holmgren, 1883 and *T. wrangeliana* Stackelberg, 1944 increased. An increase in abundance in 1989 was also observed for the two rarer species. The abundance of *Tipula arctica* Curtis, 1835 increased from 0.9 to 12.3 ex/100t-d (dry river terrace with forb-grass cover) and *T. pribilofensis* Alexander, 1923 from 0.7 to 2.9 ex/100t-d (sandy-pebble high floodplain). Significant differences in abundance were also recorded for *Tipula wrangeliana* Stackelberg, 1944 and *T. carinifrons carinifrons* Holmgren, 1883 in the mM in 2014–2015 (Fig. 2). These species were much more abundant in 2014 (especially *Tipula wrangeliana* Stackelberg, 1944), although the beginning of that summer season was significantly cooler than in 2015 (Fig. 3).

The seasonal dynamics of the catchability of adult Tipuloidea in pitfall traps are shown in Figures 4–10. In years with average weather conditions, adult activity in most areas peaked in the mid-July. Only in the climatically harshest area (*sPD*, 1985) the peak was shifted to the second half of July (Fig. 4), and in the warmest areas in the center (southern enclave of *nTT*) it was shifted to early July (Fig. 8). Importantly, the mass capture of Tipulidae in pitfall traps (from 84 to 99 % of all adults collected during the season) was limited to a narrow time period of 2 collections: approximately 20–30 days, depending on the exposure time of the traps. In areas where collections were made during two (RB, Fig. 6) or three (mM, Fig. 8) contrasting seasons, significant shifts in adult timing and abundance were found depending on seasonal weather conditions. In seasons with a warm June (1990 and 1993), abundance was high and the adult peak shifted earlier in the season. In contrast, during cold seasons (1988 and 1994), abundance in these areas was significantly lower, the peak shifted later and could be very short (RB data, 1988). However, in the same season of 1988, in another area (lTn, Fig. 5), a high abundance and a long period of collection of adults in pitfall traps were noted. In general, the available data for the 20th



Figs 11–13. Averaged data for Tipuloidea abundance in pitfall traps in different seasons in the 20th and 21st centuries (ex/100t-d). 11, 12 — ranked series of abundance (data for areas with a short survey period are shown separately at the end); 13 — box plots constructed from abundance data (areas with a short survey period are not included). The abbreviations and locations of the study areas are shown in Fig. 1.

Рис. 11–13. Усреднённые данные по обилию типулоидов в различные сезоны в почвенных ловушках в XX и XXI вв. (экз./100 ловушко-суток). 11, 12 — ранжированные ряды обилия (в конце отдельно приведены данные по районам с кратким периодом сбора). 13 — боксплоты, построенные на основе данных по обилию (районы с кратким периодом сбора не включены). Аббревиатура и местоположение районов даны на рис. 1.

century show considerable inter-annual variability in abundance, which tends to correspond well with seasonal weather conditions: increases in warm summer seasons and decreases in cold seasons.

Data from the Rogers Bay weather station indicate a marked warming of the island's climate since the 2002 (Fig. 3). Crane flies phenology data from 21st century are sparser due to the long exposure time of pitfall traps in most areas. The most detailed data are only available from the central part of the island (Figs 9–10). They support an earlier shift in the flight of crane flies in seasons with near-average (2006) and particularly warm (2015) weather conditions. However, in the season with an unusually cold June (2014), the peak of abundance occurred in mid to late July.

Changes in the abundance of crane flies during different climatic periods

All 20th century data (Fig. 11) indicate that there is no relationship between mean Tipuloidea abundance for a given area and its position on the climatic gradient. The only exception is perhaps the coldest area (*sPD*: lGd). In fact, one of the lowest values of abundance was recorded here, even though it was significantly higher in the neighbouring area of the *nAT* (lKF) during the same season 1985. The lowest abundance of crane flies on the island was recorded in the SMM (mountainous area with the steepest relief of all studied areas). Considering that in the adjacent plain (SB) the abundance was high in the same seasons (1986 and 1989), it is obvious that such sharp differences are related to landscape peculiarities rather than to the mesoclimate. Most of the rest of the lowest values of abundance were recorded in the coldest seasons (1983, 1988 and 1994). In contrast, the highest abundance was obtained in seasons following cold summers: 1984 (lGs), 1986 (SB) and 1989 (lTn). It is significant that the last two values are particularly out of line with the general series (Fig. 11). Both of them were obtained on the plains of the island and testify to the favourable conditions of existence created here for the most abundant species (which is confirmed by the above-mentioned fact of the high abundance of crane flies on the northern plain even in the unusually cold season of 1988). On the contrary, the abundance of these species in the mountain landscape was at a minimum.

In the 21st century, abundance data covering most of the adult activity period of crane flies (late June to mid-July) were obtained for four seasons (2006, 2011, 2014 and 2015), with collections from several areas simultaneously in 2006 and 2015 (Fig. 12). In these years, the abundance of Tipulidae in pitfall traps in most of the study areas was significantly lower than in the 20th century (Fig. 13). Interestingly, the highest abundance values were recorded in the only summer with a cold June (2014). It was only in this season that the abundance of Tipuloidea in the southern enclave of the *nTT* (mM) was comparable to that in the favourable seasons of the 20th century. All other values of abundance obtained here in the 21st century were significantly lower. During this period, relatively high abundance was observed in the flat *sAT* (SB) as well as in some areas of the *nAT* (mNzh, Mb, mKF). Thus, under conditions of climate warming, the trend of decreasing abundance was particularly evident in the climatically warmest areas of the island.

Tipula carinifrons carinifrons Holmgren, 1883 appears to have made the greatest contribution to the decline in catchability of crane flies in the 21st century. Its participation in pitfall trap material has declined dramatically both in terms of the number of specimens collected (Table 1) and its proportion of the total sample (from 62.1 to 30.8 %). *Tipula wrangeliana* Stackelberg, 1944 became the most abundant species in the 21st century sample (its proportion increased from 24.6 % to 42.9 %), but the total number of collected specimens increased insignificantly. Considering that only about a quarter of the collected specimens were identified in the 20th century (Table 1), this is rather indicative of its decreasing abundance on the island under conditions of climate warming. The number of collected specimens of the third most abundant species, *Tipula glaucocinerea* Lundström, 1915, remained at about the same level. As before, it was mainly found in the northern zonal strip, which is insufficiently studied in the 21st century, so we cannot judge the dynamics of its abundance.

Characteristically, the participation of other Tipuloidea species in pitfall traps remained very low in both collection periods (3–4 %). Considering all the available material (Table 2), it can be seen that, apart from *Tipula carinifrons carinifrons* Holmgren, 1883, the number of collected specimens of four other species decreased significantly in the 21st century. Thus, *Prionocera recta* Tjeder, 1948 and *Tipula lionota* Holmgren, 1883, previously recorded in different areas of the island, were represented by one specimen each in the 21st century. For *Tipula arctica* Curtis, 1835 and *T. pribilofensis* Alexander, 1923, the fact of a decline in abundance is difficult to interpret unambiguously, as most of the specimens were collected in an area (lTn) that has not been resurveyed in the 21st century. Only four species have become more abundant in collections in this period: *Nephrotoma lundbecki lundbecki* (Nielsen, 1907), *Tipula besselsoides* Alexander, 1919, *T. subrecticornis* Savchenko, 1964, and *Rhabdomastix borealis* Alexander, 1924. However, it is not possible to discuss changes in their abundance, as most specimens were collected in the 21st century using methods other than pitfall traps, including previously unused sweeping and yellow pan traps.

Discussion

Comparison of Tipuloidea faunas from Wrangel Island and other Arctic regions

As mentioned in the Introduction, the species richness of crane flies faunas varies considerably. They are completely absent from the highest latitude and most remote archipelagos, such as Svalbard and Franz Josef Land [Coulson et al., 2014]. In the Canadian Arctic Archipelago, crane flies are absent from islands with the

Table 4. The taxonomic composition of the Tipuloidea fauna of Wrangel Island in comparison with that of other Arctic regions
Таблица 4. Таксономический состав фауны Tipuloidea острова Врангеля в сравнении с другими регионами Арктики

Family, genera, subgenera	Arctic islands										Mainland Arctic					
	Wrangel	Dolgiy [1]	Vaigach [2]	Novaya Zemlya [3]	New Siberian [2, 3]	Victoria [4–7]	Devon [8]	Southampton [4, 6, 9, 10]	Ellesmere [5, 6, 11,12]	Greenland [12]	Yugorsky Pen. [2]	Taymyr Pen. (AT)** [2, 6, 13]	Taymyr Pen. (TT)** [2, 14]	Northern Yakutia [2, 14, 15]	Northern Chukotka [2, 4, 10, 14, 16–21]	Northern Alaska [4, 10, 14, 22–24]
Tipulidae																
Prionocera Loew, 1844	1	1/1	1/1	2/1	2/1	2/1	–	2/1	–	1	2/1	3/1	2/1	4/1	1	3/1
Nephrotoma Meigen, 1803	1	–	–	–	–	1/1	1/1	1/1	1/1	2/1	–	–	–	–	1/1	1/1
Tipula (*Arctotipula*) Alexander, 1934	3	–	1	2/1	1	2/1	1	1	1	2/1	1	2/1	2/1	2/1	–	2
T. (*Lunatipula*) Edwards, 1931	1	1	–	–	–	–	–	–	–	–	–	–	1/1	–	1	–
T. (*Odonatisca*) Savchenko, 1956	1	–	–	–	–	–	–	–	–	–	–	–	1/1	2/1	1	1/1
T. (*Pterelachisus*) Rondani, 1842	3	1/1	1/1	3/1	1/1	2	–	2	–	–	2/1	2/2	4/2	7/2	4/2	3/1
T. (*Savtshenkia*) Alexander, 1965	2	4/1	–	2/1	2/2	–	–	–	–	–	2	1/1	2/2	1/1	2/1	–
T. (*Vestiplex*) Bezzi, 1924	2	1	1/1	3/1	–	1/1	1/1	1/1	1/1	1/1	1	–	3/1	2/1	5/2	2/1
T. (*Yamatotipula*) Matsumura, 1916	1	2	–	1/1	–	–	–	–	–	–	1/1	1/1	3/1	4/1	2/1	2/1
Other taxa*	–	–	–	1	1	1	–	1	–	–	1	–	–	1	1	1
Limoniidae																
Arctoconopa Alexander, 1955	1	–	1/1	–	–	–	–	–	–	–	1/1	–	2	1/1	3/1	2/1
Ormosia Rondani, 1856	1	–	–	1/1	–	–	–	–	1/1	3/1	1/1	1/1	–	–	1/1	–
Rhabdomastix Skuse, 1890	1	–	–	–	–	–	–	–	–	1		–	–	–	1/1	–
Symplecta Meigen, 1830	1	1	–	2	1	4	–	2	2	2	1	2	2	–	4/1	–
Dactylolabis Osten Sacken, 1860	1	–	–	1/1	–	–	1	–	1	1	–	1/1	–	1/1	1	–
Limnophila Macquart, 1834	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Other taxa*	–	1	1	1	–	1	–	–	–	2	3	2	3	3	7	–
Pediciidae*	–	–	–	2	–	–	–	–	–	–	2	–	1	1	5	1
Total Tipuloidea / species common to Wrangel Island	21	12/3	6/4	21/8	8/4	14/4	4/2	10/3	7/3	15/4	18/5	15/8	26/10	29/10	40/11	19/7
Bioclimatic subzones	B	D	BC	ABC	B	BCD	B	CD	ABC	A–E	D	B	CD	CD	CD	C

Note: * Taxa absent from Wrangel Island are represented by single species from *Tipula* (*Acutipula*) Alexander, 1924, *T.* (*Beringotipula*) Savchenko, 1961 and *Angarotipula* Savchenko, 1961 (Tipulidae), *Molophilus* Curtis, 1833, *Neolimnophila* Alexander, 1920, *Austrolimnophila* Alexander, 1920, *Phylidorea* Bigot, 1854, *Dicranomyia* Stephens, 1829, *Limonia* Meigen, 1803, *Metalimnobia* Matsumura, 1911, *Rhipidia* Meigen 1818 (Limoniidae), *Dicranota* Zetterstedt, 1838, *Pedicia* Latreille, 1809, *Tricyphona* Zetterstedt, 1837 (Pediciidae). ** For Taymyr, species collected in the arctic (AT) and typical (TT) tundra subzones are listed separately. The bioclimatic subzones are given after CAVM Team [2003]. Sources of data: [[1] Lantsov, 2011; [2] Lantsov, Chernov, 1987; [3] Oosterbroek, 2025; [4] Brodo, 1987; [5] Brodo, 1990; [6] Stary, Brodo, 2009; [7] Pentinsaari et al., 2020; [8] Ryan, 1977; [9] Alexander, 1934; [10] Brodo, 2017; [11] Oliver 1963; [12] Oosterbroek et al., 2015; [13] Devyatkov, 2025; [14] Brodo, 2009; [15] Verves et al., 1990; [16] Savchenko, 1964, 1977, 1978, 1979, 1980; [17] Savchenko, Parchomenko, 1980; [18] Pilipenko 2011; [19] Starkevich, Paramonov, 2016; [20] Devyatkov, 2024; [21] Paramonov, Khruleva, 2024; [22] Alexander, 1918; [23] MacLean, 1975a; [24] Brodo, 2012].

Примечание: * Отсутствующие на острове Врангеля таксоны представлены единичными видами *Tipula* (*Acutipula*) Alexander, 1924, *T.* (*Beringotipula*) Savchenko, 1961 и *Angarotipula* Savchenko, 1961 (Tipulidae), *Molophilus* Curtis, 1833, *Neolimnophila* Alexander, 1920, *Austrolimnophila* Alexander, 1920, *Phylidorea* Bigot, 1854, *Dicranomyia* Stephens, 1829, *Limonia* Meigen, 1803, *Metalimnobia* Matsumura, 1911, *Rhipidia* Meigen 1818 (Limoniidae), *Dicranota* Zetterstedt, 1838, *Pedicia* Latreille, 1809, *Tricyphona* Zetterstedt, 1837 (Pediciidae). ** Для Таймыра отдельно указаны виды, собранные в подзонах арктических (AT) и типичных (TT) тундр. Биоклиматические подзоны приведены по: CAVM Team [2003]. Литературные источники: см. выше.

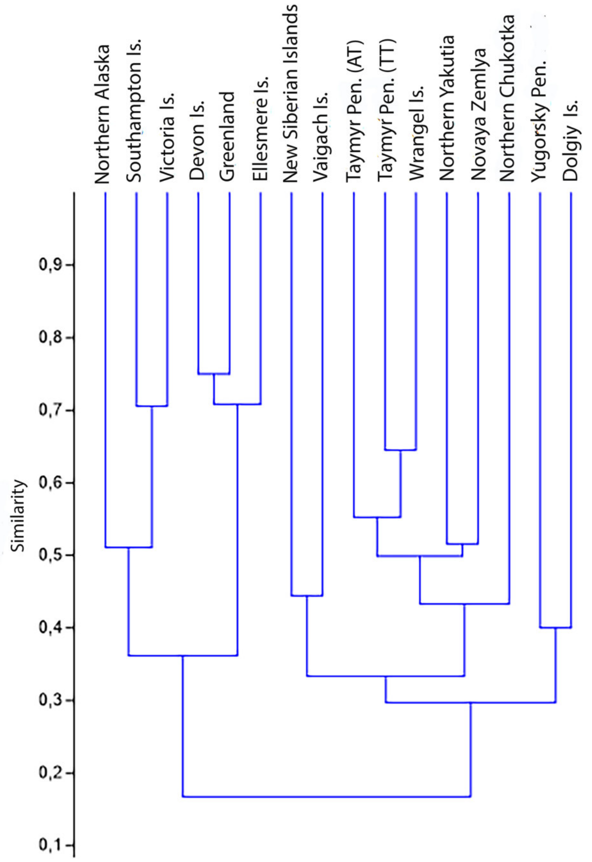


Fig. 14. Dendrogram of species similarity of Tipulidae faunas from different Arctic regions (*Algorithm*: Paired groups; *Similarity measure*: Dice). Subzonal differentiation and literature sources used, see Table. 4. Data on species of the group *Tipula salicetorum* Siebke, 1870 are not included because material from most Arctic regions has to be redefined.

Рис. 14. Дендрограмма сходства видового состава фаун Tipulidae различных регионов Арктики (алгоритм: Paired groups, мера сходства: Dice). Подзональную дифференциацию и использованные литературные источники см. в табл. 4. Данные по видам группы *Tipula salicetorum* Siebke, 1870 не включены в связи с необходимостью переопределения материала из большинства регионов Арктики.

harshest climate [Brodo 1990], such as Ellef Ringnes (subzone A) and Bathurst (subzones A and B according to the CAVM Team [2003]). On Severnaya Zemlya (subzone A), only *Tipula glaucocinerea* Lundström, 1915 was collected [Lantsov, Chernov, 1987].

Table 4 presents data on the taxonomic composition of the fauna of Wrangel Island in comparison with other Arctic regions, mainly located in subzones B to D. Despite the relatively small size and harsh climatic conditions of Wrangel Island, its fauna includes most of the taxa of Tipuloidea inhabiting in the insular Arctic, and is one of the richest. In terms of species richness and the number of identical species, it is closest to the fauna of Novaya Zemlya. The faunas of the Canadian Arctic Archipelago is much poorer; the fauna of Wrangel Island is brought closer to them by the presence of two species common only in the High Arctic of North America. These are *Nephrotoma lundbecki lundbecki* (Nielsen, 1907) (in Eurasia this species occurs mainly in the southern part of the tundra zone) and *Tipula besselsoides* Alexander, 1919, known in the Palearctic only from Wrangel Island. About a quarter of the species collected on Wrangel Island are not known from other Arctic islands. These include species that inhabit predominantly hypoarctic landscapes (*Tipula pribilofensis* Alexander, 1923, *Symplecta sheldoni* (Alexander, 1955), and *Rhabdomastix borealis* Alexander, 1924), as well as species known in large numbers only from Wrangel Island (*Tipula subrecticornis* Savchenko, 1964 and *T. wrangeliana* Stackelberg, 1944). The species richness of the Tipulidae fauna of Wrangel Island is comparable to that of mainland Arctic areas such as northern Taymyr and Yakutia (Table 4). Most Arctic species are distributed in tundra landscapes with significant disjunctions (see maps in Brodo [1987, 2009], Lantsov, Chernov [1987], and Brodo et al. [2022]). In this regard, it is interesting to note that almost all the species most common to the Siberian tundras are found on the island [Lantsov, Chernov, 1987]. Only *Prionocera ringdahli* Tjeder, 1948 and *Tipula* (*Pterelachisus*) *trisrtiata* Lundström, 1915 were not collected here.

As information about Limoniidae is clearly incomplete in many Arctic areas, the dendrogram of species composition similarities has been constructed using data for Tipulidae only (Fig. 14). The dissimilarity in the composition of the Tipulidae faunas of the Eurasian and North American tundra regions is due to a limited number of species with extensive Holarctic ranges (these include *Prionocera recta* Tjeder, 1948 and *Tipula arctica* Curtis, 1835). In the single Eurasian cluster, the fauna of Wrangel Island is closest to that of the typical tundra subzone of Taymyr (C and D according to [CAVM Team, 2003]). They have similar levels of species richness (15 and 18 respectively), and the core of both faunas is a common set of arctic species. The fauna of the arctic tundras of Taymyr, located in closer climatic conditions (subzone B according to CAVM Team [2003]), is significantly poorer than the fauna of Wrangel Island.

The dendrogram clearly shows that the similarity of faunas within the Eurasian cluster is in most cases weakly related to their geographical location. In the insular Arctic, this is compounded by the lack of relationship between zonal position and faunal species richness (Table 4). For example, the high-latitude fauna of Novaya Zemlya is much richer in species than the southern faunas of the neighboring islands (Dolgiy and Vaigach), and its composition is more similar to the fauna of Wrangel Island, which is the furthest away. It can be assumed that this is due to the presence of a mountainous relief, which is absent on the other Eurasian islands compared. The high diversity of the natural environment of Novaya Zemlya and Wrangel Island has apparently helped to maintain populations of arctic species through repeated climate changes during the Quaternary [Velichko, 1973]. The bumblebee *Bombus glacialis* Friese 1902 clearly demonstrates that conditions here are particularly favourable for such long-term survival. It is a relict species that appears to have once been widespread along the Eurasian continental margin, but is now only known from Novaya

Zemlya and Wrangel Island [Potapov et al., 2021]. On these islands, it is represented by different subspecies, the separation of which, according to genetic data, occurred in the Middle Pleistocene.

PECULIARITIES OF THE TIPULIDAE TAXA ON WRANGEL ISLAND

According to Savchenko [1983], over half of the tipulid species residing in the Arctic and sub-Arctic regions, are young taxa by evolutionary measures. These are species of the subgenera *Pterelachisus*, *Vestiplex*, *Odonatisca* and *Lunatipula* of the genus *Tipula* Linnaeus, 1758. They have morphological adaptations of the xerophytic type, which allow them to develop in soils with a lack of moisture during a certain part of the growing season. In the insular Arctic, they are most abundant on Wrangel Island and Novaya Zemlya, with 7 and 6 species respectively (Table 4). Their numbers are significantly lower not only on other Arctic islands, but also on the most climatically severe continental margins. For example, near Dikson (northwestern Taymyr), the basis of the fauna consists of hygrophilic species (seven out of nine, including three species of *Prionocera* Loew, 1844), and mesoxerophilic taxa are represented by two species of the subgenus *Pterelachisus* [Lantsov, Chernov, 1987]. On the contrary, even in the *nAT* on the Wrangel Island, they are represented by three subgenera: *Pterelachisus*, *Vestiplex* and *Odonatisca*, and in the *sAT* — by four (*Lunatipula* is added). The abundance of some species also varies considerably: hygrophilic *Prionocera recta* Tjeder, 1948 and mesophilic *Tipula* (*Yamatotipula*) *lionota* Holmgren, 1883 are rare on Wrangel Island, but are among the most common species in the arctic tundra of Taymyr [Lantsov, Chernov, 1987].

A similar situation occurs in the area of Cape Barrow area of northern Alaska. Of the six species collected, only *Tipula carinifrons carinifrons* Holmgren, 1883 belong to mesoxerophilic taxa. This species and the hygrophilic *Prionocera recta* Tjeder, 1948 are abundant here [MacLean, Pitelka, 1971]. In addition to these two, single specimens of *Prionocera mannheimsi* Savchenko, 1983, *Tipula* (*Angarotipula*) *tumidicornis* (Lundström, 1907), *T.* (*Yamatotipula*) *aleutica* Alexander, 1923, and *T.* (*Y.*) *lionota* Holmgren, 1883 are reported for this area in a number of other publications [Alexander, 1918; Brodo, 2009, 2012, 2017]. Such significant differences in the ecological composition of tipulids in these regions cannot be explained by the summer thermal conditions. Thus, the temperature of July, the warmest month (20th century data), is higher on Dikson (5 °C [Isachenko, 1985]), and on Cape Barrow it is close to that on the coast of Wrangel Island: 3.7 °C [Bunnell et al., 1975] and 2.4–3.6 °C [Svatkov, 1970], respectively.

The marked decline in the activity of hygrophilic tipulids and the success of mesoxerophilic species on Wrangel Island cannot be explained by current landscape and climatic conditions alone. Probably, other factors, including historical ones, also influence this phenomenon. Increased diversity of xerophilic species (including those that are not usually found in high latitudes) occurs in various taxonomic groups [Yurtsev, 1987; Stishov, 2004; Khruleva, 2007]. An important role in this process may have been played by the long-term development of the island's biota in the Pleistocene as part of the tundra-steppe hyperzone, as well as relatively weak transformations of its landscape environment and climate in the Holocene [Yurtsev, 1986; Alfimov, Berman, 2004; Alfimov, 2007; Vartanyan, 2007]. These features of the history of the island's biota are clearly reflected in its composition. In the flora this is manifested by the presence of numerous continental species of Asian origin, including meadow-steppe and even steppe plants [Petrovsky, Yurtsev, 1970; Yurtsev, 1982, 1987]. Among terrestrial arthropods, there are also species whose close relatives live in the arid regions of southern Siberia. These include both species with disjunctive distribution, as well as endemic and subendemic species inhabiting the driest and warmest biotopes on the island [Khruleva, Korotyaev, 1999; Khruleva, 2007, 2009; Khruleva et al., 2021, 2022].

Of the Tipulidae, the arcto-montane *Tipula* (*Lunatipula*) *subrecticornis* Savchenko, 1964 has such disjunctive distribution [Savchenko, Theischinger, 1978]. It range has much in common with that of two herbivorous beetles, the weevil *Coniocleonus astragali* Ter-Minasian, Korotyaev, 1977 [Alfimov et al., 2003], and the leaf beetle *Chrysolina brunnicornis* (Weise, 1883) [Khruleva, 2004]. All three species are known from isolated mountainous areas of southern Siberia and extreme northeast Asia, where they only occur together on Wrangel Island. Both beetle species were common in deposits in Northeast Asia dating back to the cryoarid phases of the Pleistocene [Kiselev, Nazarov, 2009; Kuzmina, 2015]. In the extreme northeast (northern Yakutia), they are known from sediments dated to early Pleistocene [Elias et al., 2006], indicating significant age of xerophilic insect complexes in this region. Both beetles are currently very sporadic in northeast Asia, but on Wrangel Island, like *Tipula subrecticornis* Savchenko, 1964, they are widespread and even abundant in some habitats [Khruleva, Korotyaev, 1999; Khruleva, 2004].

The fact that one of the most abundant and widespread tipulid species on Wrangel Island is *Tipula wrangeliana* Stackelberg, 1944, a subendemic species of Angara origin (i.e. the mountainous regions of eastern Siberia) [Savchenko, 1983], also supports the long evolution of the island's tipulid fauna in cryoarid conditions. The fact that *Tipula wrangeliana* Stackelberg, 1944 is clearly located here in the zone of its ecological optimum suggests that it was formed in close natural conditions, apparently on the territory of Wrangel Island or adjacent shelf areas.

ON THE QUESTION OF TIPULIDAE ABUNDANCE CHANGES ON WRANGEL ISLAND

As in other areas of the Arctic [MacLean, Pitelka, 1971; MacLean, 1973; Lantsov, Chernov, 1987], crane flies on Wrangel Island show significant inter-annual fluctuations in abundance. According to these authors, non-pupating older larvae were always present in the populations studied, and the dynamics of adult hatching was related to the temperature regime during the pupation period, as well as in the previous season. Data collected on the Wrangel Island in the 20th century also confirm that inter-annual fluctuations in tipulid abundance are highly characteristic of Arctic ecosystems. Data collected in the 21st century clearly indicate a decline in Tipuloidea abundance on the island under warming Arctic climatic conditions. This fits well with the suggestion of Bale et al. [2002] that climate warming has a negative effect on insects with long life cycles and low developmental rates, which is exactly what characterizes arctic crane flies [MacLean, 1973; 1975b; Lantsov, Chernov, 1987].

Tipula carinifrons carinifrons Holmgren, 1883 seems to have contributed most to the decline of this group on the island, but a number of some other arctic species have also become rarer on the island in the 21st century. The data obtained suggest a rather high vulnerability of the High Arctic complex of Tipulidae under climate warming conditions. This assumption explains well the significant disjunctions in the ranges of many arctic species. It also agrees well with the narrowness of the zone of their ecological optimum, as well as with the fact of a significant decrease in the cenotic importance of this group along the climatic gradient from the northern part of the tundra zone to the southern one [Lantsov, Chernov, 1987]. Obviously, for a group with such ecological peculiarities, the landscape and climatic diversity of Wrangel Island is very important for the long-term stable existence of tipulid populations under conditions of cyclical polar climate fluctuations.

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