

Heat supply on the northern distribution limit of spiders (Arachnida: Aranei) living in xeromorphic habitats of the Kolyma River lower reaches, Northeastern Siberia

Теплообеспеченность на северной границе ареала пауков (Arachnida: Aranei) ксероморфных обитаний из низовий Колымы

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Ключевые слова: Araneae, Западная Чукотка, Неарктика, Палеарктика, северная граница ареала, теплообеспеченность.

Abstract. In this paper, we have analyzed the heat supply on the northern distribution limit of 65 spider species found in the warmest habitats of the lower reaches of Kolyma River. Kolyma River's mouth is the northernmost locality for 32 species with a Holarctic range and for nine species with a Palaearctic range. We found that among 39 species distributed in both Asia and the Nearctic, the demand for heat supply on the two continents is similar only for 1/3 of the species. Approximately half of the species with a Holarctic range found in the lower reaches of Kolyma River have been reported in North America from localities with a lower heat supply. This indicates that these species can be found in more northern and colder regions in Asia, where coastal areas are poorly studied.

Резюме. Проанализирована теплообеспеченность на северном пределе распространения 65 видов пауков, собранных в наиболее тёплых биотопах в низовье Колымы. Этот район оказался северным пределом распространения для 32 видов с голарктическим ареалом и для 9 видов-палаеарктов. Только у трети из 39 видов, распространённых и в Азии, и в Неарктике, требования к минимальной теплообеспеченности на обоих континентах совпадают. Примерно половина видов-голарктов, собранных в низовьях Колымы в Северной Америке заходит в область более низких температур, чем в Азии. Это обстоятельство позволяет рассчитывать на их обнаружение в более северных и холодных прибрежных районах Азии, которые пока плохо изучены.

Introduction

Spiders (Aranei) constitute one of the largest orders of animals. Unlike other mega- or hyperdiverse orders, all spiders are obligatory predators, and their distributions are not limited by host plants and animals or quality of the litter, as it is the case with phytophagous animals, parasites and detritophagous invertebrates. Most spiders living in the North are not

specialized. Accounting these and the fact that many spiders spread by air using gossamer, it becomes clear that the major limiting factor for their distribution in the North is summer temperatures or in other words, heat supply.

Conventionally, the impact of summer conditions on the distribution of terrestrial invertebrates can be divided into climatic and microclimatic. The latter factor is particularly important in the continental parts of northeastern Siberia [Alfimov, 1998]. For example, in the upper reaches of Kolyma River with continuously distributed permafrost, the heat supply of surface of the warmest soil is 1.9–2.0 times higher than air, and in the depth 10 cm this relation descends to 1.6. These differences are close to those observed between tundra and steppe zones [Berman et al., 2011]. However, in lowland tundra adjacent to the shore of the Arctic Ocean, the level on climate continentality is lower and the differences in heat supply between different habitats are not so pronounced. Because of this, the heat supply of the ground surface (on which most spiders live) is strongly correlated with the air temperature.

The goal of this research is to evaluate the impact of air temperature (as an indicator of heat supply) on the distribution of some species of spiders.

Material and methods

This study is based on the data of the summer temperatures in the northern distribution limit of 65 spider species collected in the warmest habitats of the lower reaches of Kolyma River [Marusik, Alfimov, 2012]. The mouth of Kolyma River is the northernmost locality in the entire range of 32 species, and for

nine species it is the northernmost locality in Asia. Among 65 species found, only two are specialized and feed on ants (*Micaria* and *Euryopis*). Indeed, the distribution of invertebrates, including spiders, is not limited by latitude but primarily by the heat supply, which varies in different localities on the same latitude [Khromov, Petrosyants, 1994].

The data on heat supply in Russia and North America were obtained from the Handbook on Climate in the USSR [1966a–c] and Canadian climate normals [1982], respectively. Corresponding information from Alaska, and Scandinavia is taken from NCEI database (<https://www.ncdc.noaa.gov>) and those from internal parts of the Wrangel Island is from Alfimov [2007].

The northern limit of distribution for most of the species considered in this paper is lying in regions where temperatures higher than 10 °C (considered biologically active) are not documented. Many invertebrates remain inactive in temperatures between 0 and 5 °C. Therefore, we decided to take the sum of temperatures during the growing season, or the sum of average daily temperatures above 5 °C as indicators of heat supply.

The limited number of weather stations in the North and strong sea-land temperature gradients during the warm season [Zhang et al., 1996] led us to make some extrapolations. This fact, as well as inaccurate data about some northernmost localities of spiders, reduced the accuracy of our analysis. It should be accounted that spiders have been collected in the warmest habitats and represent only a fraction of the entire fauna. The number of collected wolf spiders and thomisids is the same as in other faunas lying at the same latitudes in Fennoscandia, while the numbers of species of Gnaphosidae, Philodromidae and Salticidae are higher [Marusik, Alfimov, 2012]. The number of species of Linyphiidae collected by pitfall traps only is very low, apparently comprising only 10 % of the species occurring in the region.

Results and discussion

Heat supply on the northern limit of distribution of species with Palaearctic and Holarctic ranges in Eurasia. Among 65 species found in the lower reaches of Kolyma River, 26 are restricted to the Palaearctic

and 39 have either Circumholarctic or Siberio-Nearctic ranges. An analysis of the distribution of all these species revealed that the species distributed in both parts of the Holarctic penetrate regions of Eurasia with lower heat supply in comparison to those occurring only in Eurasia (see Table 1). The average minimum sum of temperatures at the northern limit of distribution for the exclusively Palaearctic species is 755 °C, whereas such sum for the species with Holarctic ranges is 634 °C.

Heat supply in the northern limit of distribution of the species with Holarctic distribution in Eurasia and North America. The northernmost localities of most of the species collected in the lower reaches of Kolyma River lie on the same distance from the Arctic Ocean both in Eurasia and North America; however, the sum of positive temperatures differ significantly (Fig. 1).

Differences in the location of weather stations, i.e. on cape, in the bay, on flat shore, determine significant variations in the heat supply conditions on the shore parts of Asia and North America [Zhang et al., 1996]. Regardless, the heat supply in the Asian part of the Arctic coast is higher than in North American one (the average values for 18 and 17 weather stations are 262° and 190°C, respectively).

Nevertheless, about one third of the species minimal heat supply demand in Eurasia and North America is similar (Fig. 2). This circumstance with a high degree of probability indicates that heat supply that limits distribution of these species to the North. Such species belong to all families with the exception of Tetragnathidae and Theridiidae. The deviations from the “balance line” can most likely be explained by the insufficient knowledge of the distribution of species and the rarity of weather stations, the data of which make it possible to estimate the heat supply in the places where species are found with relatively low accuracy.

Minimal heat supply in 12 Holarctic species in the Nearctic is lower in comparison with those in the Eurasia (Fig. 2). For example the northern limit of distribution of *Araniella displicata* and *Ohlertidion ohlerti* (Fig. 2, Nos 1 and 58) in the Nearctic is Mackenzie River mouth (69°27' N), and in Asia northern limit is somewhat more southern (68°30'–69°00' N)

Table 1. Average of the minimum sums of temperatures above 5 °C at the northern limit of distribution in Eurasia for the species collected in the lower reaches of Kolyma River

Таблица 1. Средние из минимальных сумм температур выше 5 °C на северной границе ареала пауков, собранных в низовьях Колымы

Family	Dictynidae	Gnaphosidae	Linyphiidae	Lycosidae	Philodromidae	Theridiidae	Thomisidae	Total (M±SE)
N of species	3	12	10	14	12	4	5	65
Species of Palaearctic distribution (°C)	600	865	794	698	774	947	580	755±34
Species of Holarctic distribution (°C)	319	586	720	544	753	649	609	634±36

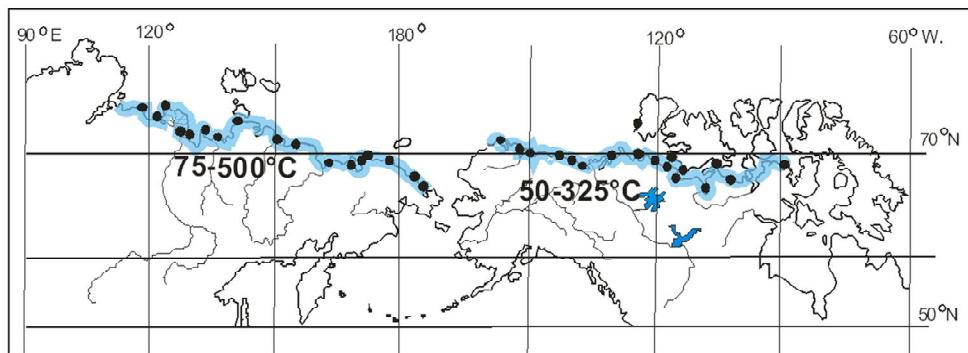


Fig. 1. The range of variation of the sum of temperatures above 5°C on the shore lands of northern Asia and North America according to weather stations. Dark dots refer to the position of weather stations.

Рис. 1. Диапазон варьирования суммы температур выше 5°C в Северной Азии и Северной Америке по данным метеостанций. Тёмные точки — расположение метеостанций.

in environs of Cherski Village, while sum of temperatures differs in 2.4 times.

Pardosa lapponica (Fig. 2, No. 37) reaches almost the same latitude in the Nearctic (ca. N72°, Banks

Island) and in Asia (N71.4°, Taimyr Peninsula) but heat supply in Asia is 3–4 times higher.

Three more species *Philodromus alascensis*, *Tha-*
natus arcticus and *Tetragnatha extensa* (Fig. 2, Nos

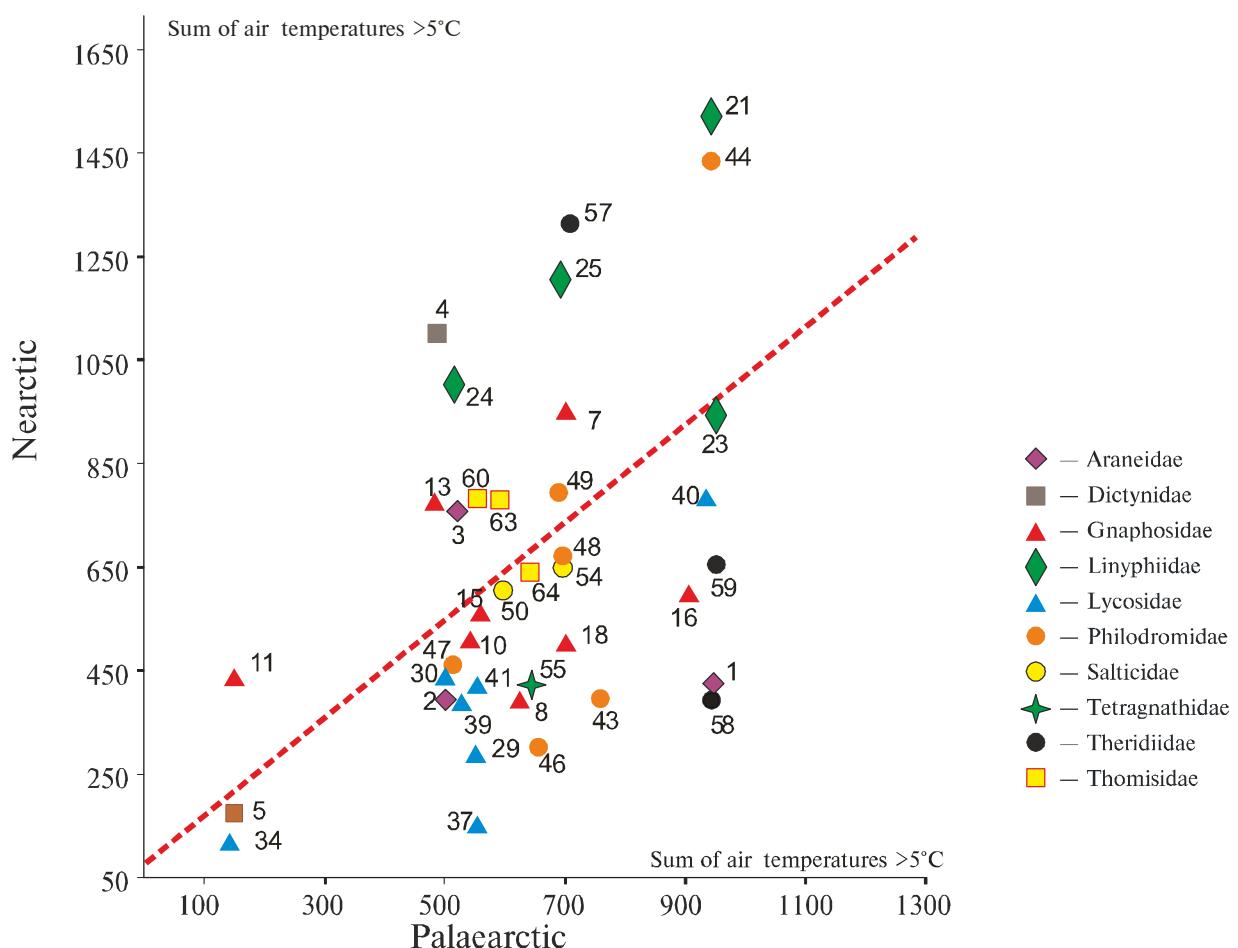


Fig. 2. Minimal heat supply of species with the Holarctic distribution in Eurasia and North America. Numbers corresponds to those in the Tables 2 and 3 (Supplement).

Рис. 2. Соотношение минимальной теплообеспеченности на границе палеарктической и неарктической частей ареалов голарктических видов. Номера значков соответствуют номеру вида в таблицах 2 и 3 (см. Supplement).

43, 46, 55) have heat supply in Lena River lower reaches (ca. N72°) about 2–3 times higher than in Mackenzie River mouth or Disko Island (both ca. N69.5°).

Six species have a higher heat supply in their northern limit of distribution in North America than in the Palaearctic. The northern range boundaries of *Dictyna alaskae*, *Cnephalocotes obscurus*, *Microlinyphia pusilla*, *Minurioloides trifrons*, *Philodromus histrio*, and *Euryopis saukea* (Fig. 2, Nos 4, 21, 24, 25, 44, 57) lie in Eurasia, close the Arctic Ocean on the latitudes ranging from 69.5 to 71.5° N. Of them only *M. pusilla* has a similar range limit in the interior part of Alaska (69°22' N) with much higher temperatures in comparison to those in the coastal part of Asia. The other five species are not known north of 65° N in the Nearctic. The reason for such differences in distribution remains unclear: it could be caused by an inadequate level of studies in North America, an interspecific competition, or other, non-climatic factors. In case of the insufficient studies, it is expectable that some of the species will be found in more northern regions as well. In case of *Euryopis saukea*, a myrmecophagous spider, its distribution is most likely limited by the distribution of its prey.

Conclusions

An analysis of heat supply on the northern limit of distribution of 65 spider species in the warmest habitats of the lower reaches of Kolyma River revealed that a high latitude does not necessarily correspond to a lower demand for heat supply. The lower reaches of Lena River (lying on N 72°) have a higher heat supply than 2–3° south in the central part of Eastern Chukotka or in near coastal parts of Canadian Arctic.

A comparison of heat supply on the northern boundaries of distribution in Siberia and North America for 39 species with Circumholarctic or Siberio-Nearctic distributions clarified that half of the species do not reach their potential (temperature) limit of distribution in Siberia. Judging from their demand for heat supply, they can occur in shorelands of East Siberian and Chukchi seas, where the weather condition of growing period is harsher in comparison to the lower reaches of Kolyma and Lena rivers. However, the lack of collections from these regions does not allow us to assess the reliability of this speculation.

The presence of a «reserve» of heat supply sufficient for an expansion to the north in a significant number of species found in the xeromorphic habitats of Kolyma River's mouth could have been an important factor during the cold periods of the Pleistocene. The depression of the sea level by 120 m a.s.l. associated with the last glaciation led to the retreat of the coastline of the Arctic Ocean along the shelf of the modern Laptev, East Siberian, and Chukchi seas by 400–600 km [Clark, Mix, 2002]. Dry landscapes inhabited by tundra- and steppe-dwelling animals and

Table 2. List of species found in Kolyma River lower reaches (1) and number of specimens collected (2)

Таблица 2. Список видов, собранных в низовьях Колымы (1) и количество экземпляров (2)

No	1	2
Araneidae		
1	<i>Araniella displicata</i> (Hentz)	1
2	<i>Larinoides cornutus</i> (Clerck)	2
3	<i>Larinoides patagiatus</i> (Clerck)	1
Dictynidae		
4	<i>Dictyna alaskae</i> Chamberlin et Ivie	1
5	<i>Dictyna major</i> Menge	33
6	<i>Dictyna t. tyshchenkoi</i> Marusik	5
Gnaphosidae		
7	<i>Drassodes neglectus</i> (Keyserling)	1
8	<i>Gnaphosa borea</i> Kulczyński	11
9	<i>Gnaphosa gracilior</i> Kulczyński	2
10	<i>Gnaphosa microps</i> Holm	4
11	<i>Gnaphosa orites</i> Chamberlin	2
12	<i>Gnaphosa similis</i> Kulczyński	10
13	<i>Haplodrassus hiemalis</i> (Emerton)	1
14	<i>Haplodrassus pugnans</i> (Simon)	3
15	<i>Haplodrassus signifer</i> (C.L. Koch)	4
16	<i>Micaria alpina</i> L. Koch	8
17	<i>Micaria lenzi</i> Bösenberg	108
18	<i>Micaria rossica</i> Thorell	31
Linyphiidae		
19	<i>Agyneta affinisoides</i> (Tanasevitch)	1
20	<i>Agyneta pseudosaxatilis</i> (Tanasevitch)	1
21	<i>Cnephalocotes obscurus</i> (Blackwall)	1
22	<i>Incestophantes incestoides</i> (Tanasevitch et Eskov)	2
23	<i>Kaestneria pullata</i> (O. Pickard-Cambridge)	1
24	<i>Microlinyphia pusilla</i> (Sundevall)	26
25	<i>Minurioloides trifrons</i> (O. Pickard-Cambridge)	1
26	<i>Procerocymbium sibiricum</i> Eskov	21
27	<i>Tmeticus tolli</i> Kulczyński	27
28	<i>Walckenaeria tyschenkoi</i> Eskov et Marusik	2
Lycosidae		
29	<i>Arctosa alpigena</i> (Doleschall)	40
30	<i>Alopecosa aculeata</i> (Clerck)	12
31	<i>Alopecosa borea</i> (Kulczyński)	182
32	<i>Alopecosa sibirica</i> (Kulczyński)	242
33	<i>Pardosa adustella</i> Roewer	36
34	<i>Pardosa algens</i> (Kulczyński)	2
35	<i>Pardosa atrata</i> (Thorell)	15
36	<i>Pardosa eiseni</i> (Thorell)	9
37	<i>Pardosa lapponica</i> (Thorell)	143
38	<i>Pardosa lyra</i> (Odenwall)	7
39	<i>Pardosa podhorskii</i> (Kulczyński)	1

Table 2. (continuation)
Таблица 2. (продолжение)

No	1	2
40	<i>Pardosa sodalis</i> Holm	3
41	<i>Pardosa tesquorum</i> (Odenwall)	46
42	<i>Sibricosa subsolana</i> (Kulczyński)	18
	Philodromidae	
43	<i>Rhysodromus alaskensis</i> (Keyserling)	4
44	<i>Rhysodromus histrio</i> (Latrelle)	3
45	<i>Thanatus albomaculatus</i> Kulczyński	10
46	<i>Thanatus arcticus</i> Thorell	9
47	<i>Thanatus bungei</i> (Kulczyński)	3
48	<i>Tibellus asiaticus</i> Kulczyński	1
49	<i>Tibellus maritimus</i> (Menge)	2
	Salticidae	
50	<i>Chalcoscirtus glacialis</i> (Caporiacco)	8
51	<i>Dendryphantes czechanowskii</i> Prószyński	4
52	<i>Euophrys proszynskii</i> Logunov et al.	10
53	<i>Pellenes ignifrons</i> (Grube)	2
54	<i>Sittix ranieri</i> (Peckham et Peckham)	8
	Tetragnathidae	
55	<i>Tetragnatha extensa</i> (Linnaeus)	8
	Theridiidae	
56	<i>Enoplognatha serratospinata</i> (L. Koch)	1
57	<i>Euryopis sauvea</i> Levi	5
58	<i>Ohlertidion ohlerti</i> (Thorell)	3
59	<i>Phyloneta impressa</i> (L. Koch)	1
	Thomisidae	
60	<i>Ozyptila arctica</i> Kulczyński	5
61	<i>Psammitis albidus</i> (Grese)	42
62	<i>Spiracme balticana</i> (Caporiacco)	10
63	<i>Xysticus britcheri</i> Gertsch	25
64	<i>Xysticus emertoni</i> Keyserling	11
	Titanoecidae	
65	<i>Titanoeeca sibirica</i> L. Koch	63

plant were formed in the southern part of the drained shelf [Sher, 1990; Yurtsev, 1974].

Despite a global decrease in temperatures, due to the increase of continentality, the heat supply of these landscapes was higher compared to the modern conditions on the coast of the Arctic Ocean [Alfimov, Berman, 2004; Bartlein et al., 2015]. However, even without taking this circumstance into account, the tundra-steppe landscapes on the drained shelf turned out to be available (at least to the latitude of the Wrangel Island) for the settlement of those species of spiders, the northern distribution limit of which is

currently the xeromorphic habitats of the lower reaches of Kolyma River.

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