Long-distance dispersal of migrant butterflies to the Arctic Ocean islands, with a record of *Nymphalis xanthomelas* at the northern edge of Novaya Zemlya (76.95°N)

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http://zoobank.org/0F7FEE42-103C-4767-A870-69B5B307036B

Received 18 December 2020; accepted 9 February 2021; published: 17 March 2021
Subject Editor: David C. Lees.

Abstract. Although migrant butterflies are rare (or sporadically seen) guests on the Arctic Ocean islands, there is a slowly growing dataset on repeated occurrences of these insects in insular tundra and polar deserts. Altogether six long-distance migrant butterfly species were found to cross wide marine barriers north of the Arctic Circle (66.56°N), i.e. *Vanessa atalanta*, *V. cardui*, *Nymphalis antiopa*, *N. xanthomelas*, *Aporia crataegi*, and *Pieris napi*. Migrant individuals of *V. cardui* discovered on Svalbard (up to 78.27°N in 1978) reflect the farthest dispersal event of butterflies to the Arctic ever reported. Our record of *N. xanthomelas* at the northern margin of Novaya Zemlya (76.95°N) represents the northernmost finding of this species globally, reflecting the world's second farthest record of northern poleward immigration of butterflies. This occurrence coincides with an exceptionally warm summer season, when the third highest July and second highest August air temperature occurred (since global records began in 1880). Furthermore, the immigration into Novaya Zemlya coincides with a population explosion and massive expansion of *N. xanthomelas* in Siberia in 2019–2020. Our air current reconstructions indicate that this species most likely immigrated into Novaya Zemlya from mainland regions situated south-southeast (Polar Urals, Yugorsky Peninsula, and western Yamal) and east (Taymyr) of the archipelago. Overall, our findings reveal that long-distance dispersal events of butterflies to the Arctic islands are always linked to massive expansions of the corresponding species in mainland areas.

Introduction

It was shown that the faunas of Lepidoptera in Arctic polar deserts are characterised by low species richness and largely contain cold-tolerant, highly specialised species (Wolff 1964; Downes 1966; Tatarinov and Chernov 2006; Makarova et al. 2013; Coulson et al. 2014; Bolotov et al. 2015a; Kullberg et al. 2018). However, various long-distance migrant butterfly and moth species may also reach the High Arctic but could not establish permanent populations there, e.g. *Vanessa cardui* (Linnaeus, 1758), *V. atalanta* (Linnaeus, 1758), and *Plutella xylostella* (Linnaeus, 1758)

(Trybom 1877; Poppius 1906; Lokki et al. 1978; Korshunov et al. 1982, 1985; Chernov and Tatarinov 2006; Kozlov et al. 2006; Coulson et al. 2002, 2014). Studies on the immigration of southern insect species into the polar regions is a topic of great importance for further understanding of more general issues related to the patterns and pathways of global animal migrations (Williams 1925; Coulson et al. 2002; Hodkinson 2018).

A large body of historical and recent literature describes regular occurrences of migrant butterflies on subarctic islands situated in the North Atlantic such as Iceland (Wolff 1929, 1971; Downes 1966; Sømme 1993) and Faroes (Jacobson 1898; Jensen and Sivertsen 2010). Although many of these records were found to originate from human-mediated introductions with ships, goods, and plants, e.g. those of *Aglais io* (Linnaeus, 1758), *A. urticae* (Linnaeus, 1758), *Nymphalis antiopa* (Linnaeus, 1758), and *Pieris rapae* (Linnaeus, 1758) (Wolff 1971; Ólafsson and Björnsson 1997), several other species such as *Vanessa cardui* and *V. atalanta* arrived to the islands via natural dispersal events (Wolff 1929, 1971; Ólafsson and Björnsson 1997; Jensen 2001).

Individuals of a few migrant butterfly species repeatedly occurred even in extremely cold insular areas in the Arctic Ocean such as Greenland (Scott 1986; Karsholt et al. 2015), Svalbard (Lokki et al. 1978; Laarsonen 1985; Coulson 2015), Kolguev (Bolotov 2012), Vaygach (Vlasova et al. 2014), and Dolgiy (Kullberg et al. 2018). To the best of our knowledge, there were no reliable records of migrant butterflies from other Arctic islands and large archipelagoes, e.g. Novaya Zemlya, Franz Josef Land, Severnaya Zemlya, New Siberian Islands, Wrangel Island, and the Canadian Arctic Archipelago (Jacobson 1898; Wolff 1964; Scott 1986; Antonova and Khruleva 1987; Rydell et al. 2001; Makarova et al. 2013; Coulson et al. 2014). It is still unclear how many species of butterflies could reach the Arctic Ocean islands through natural migration events and how far north they can migrate globally.

This study (1) reports on the first occurrence of a migrant butterfly species on the Northern Island of Novaya Zemlya; (2) presents the most northern record of migrant specimens of *Nymphalis xanthomelas* (Esper, 1781) globally; (3) summarises available occurrences of long-distance migrant butterflies from the Arctic Ocean Islands; and (4) discusses possible causes and patterns of butterfly migrations to the High Arctic in a broader climate warming context.

Material and methods

Sampling of migrant butterfly occurrences on the Arctic Ocean islands

A body of available literature was collected via Google Scholar and Web of Science using keywords “migrant butterflies” and “migrant Lepidoptera” in combination with geographic names such as “Arctic islands”, “Svalbard”, “Vaygach”, “Greenland”, and “Iceland”. From these references, we collected the data on occurrences of migrant butterflies on the Arctic Ocean islands: species, sampling/observation locality, date, and number of recorded specimens. We selectively sampled records of migrant butterflies associated with natural long-distance dispersal events. Data on human-mediated introductions of butterflies to the Arctic islands and migrant butterfly occurrences on subarctic islands (e.g. Iceland and Faroes) were not included to the final dataset but used for the discussion.

All the selected occurrences were georeferenced using Google Maps and Google Earth v. 7.3.3 tools (Table 1). The estimated uncertainty of the co-ordinates was low (±1–2 km), because most of records were precisely linked to certain geographic locations. The shortest distance from a given locality to the mainland (km) was estimated with ESRI ArcGIS 10 software (www.esri.com/arcgis).

Table 1. Occurrences of long-distance migrant butterflies on the Arctic Ocean islands. Human-mediated introductions and data on subarctic islands (e.g. Iceland and Faroes) were not included. N/A – not available. †Dead specimen was found.

Family	Species	Locality	Latitude and Longitude	Shortest distance from the locality to the mainland (km)	Date	*N*	Reference
Nymphalidae	*Nymphalis xanthomelas* (Esper, 1781)	Russia: Cape Zhelaniya, Northern Island, Novaya Zemlya Archipelago	76.9481, 68.5400	450	23.vii.2020	1	This study
Nymphalidae	*N. xanthomelas* (Esper, 1781)	Russia: Cape Zhelaniya, Northern Island, Novaya Zemlya Archipelago	76.9481, 68.5400	450	23.viii.2020	1	This study
Nymphalidae	*N. antiopa* (Linnaeus, 1758)	Russia: shore of Lake Yangoto, Vaygach Island	70.2511, 59.0922	80	19.viii.2010	1†	Vlasova et al. (2014)
Nymphalidae	*Vanessa cardui* (Linnaeus, 1758)	Norway: NE slope of the Kolberget Mount at Grumantbyen, Svalbard	78.1667, 15.1167	850	02.vii.1978	1	Lokki et al. (1978)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Norway: Sassendalen Valley, Svalbard	78.2728, 17.1323	850	02.vii.1978	1	Lokki et al. (1978)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Russia: 1 km west of Bugrino village, Kolguev Island	68.7861, 49.3401	75	07.vii.2009	1	Bolotov (2012); this study
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Russia: Dolgiy Island	69.2730, 59.1010	30	2004	N/A	Kullberg et al. (2018)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Greenland: Qaqortoq (formerly Julianehåb)	60.7222, -46.0403	970	20.vii.1991	1	Karsholt et al. (2015)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Greenland: Upernaviarsuk	60.7493, -45.8902	970	20.vii.1991	1	Karsholt et al. (2015)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Greenland	N/A	N/A	7.vii–14.viii.1991	>2	Karsholt et al. (2015)
Nymphalidae	*V. cardui* (Linnaeus, 1758)	Southern Greenland	N/A	N/A	1992	>2	Karsholt et al. (2015)
Nymphalidae	*V. atalanta* (Linnaeus, 1758)	Greenland: Aasiaat (formerly Egedesminde)	68.7097, -52.8694	1,090	ix.1967	1	Karsholt et al. (2015)
Pieridae	*Aporia crataegi* (Linnaeus, 1758)	Russia: Cape Bolvanskij Nos, Vaygach Island	70.4464, 59.0900	90	09.vii.2013	1	Vlasova et al. (2014)
Pieridae	*A. crataegi* (Linnaeus, 1758)	Russia: Dolgiy Island	69.2730, 59.1010	30	2004	N/A	Kullberg et al. (2018)
Pieridae	*Pieris napi* (Linnaeus, 1758)	Russia: 5 km north of Bugrino village, Kolguev Island	68.8247, 49.2930	80	24.vii.2009	1	Bolotov (2012); this study

Field observations on adult migrant butterflies

The field observations on Novaya Zemlya were made around the research station "Cape Zhelaniya" of the Russian Arctic National Park [76.9481°N, 68.5400°E] during the period from 05 July to 18 October 2020 (observers: Vadim Zakhariin and Oleg Valkov, rangers of the National Park). This site is situated at the northern margin of the Northern Island of the Novaya Zemlya Archipelago (Fig. 1) and represents a flat polar desert area surrounded by a low mountain ridge with glaciers and perennial snowfields (Fig. 2A).

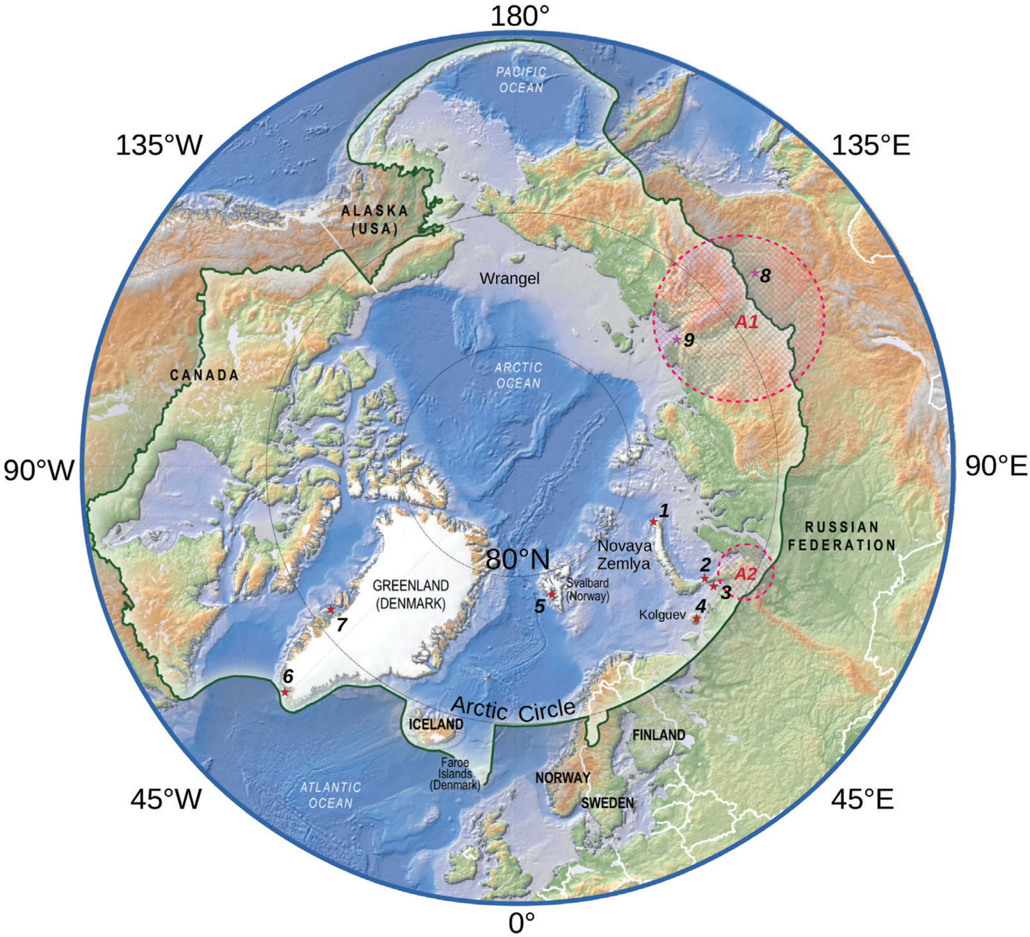

Figure 1. Occurrences of long-distance migrant butterflies on the Arctic Ocean Islands. The red stars indicate insular occurrences of migrant butterflies: *1* – Cape Zhelaniya, Northern Island, Novaya Zemlya, Russia (*Nymphalis xanthomelas*, 2020); *2* – north of Vaygach Island [shore of Lake Yangoto and Cape Bolvanskij Nos], Russia (*Nymphalis antiopa*, 2010, and *Aporia crataegi*, 2013); *3* – Dolgiy Island, Russia (*Vanessa cardui* and *A. crataegi*, 2004); *4* – Bugrino village, Kolguev Island (*V. cardui* and *Pieris napi*, 2009); *5* – Svalbard [Grumantbyen and Sassendalen], Norway (*V. cardui*, 1978); *6* – Southern Greenland [Qaqortoq and Upernaviarsuk] (*V. cardui*, 1991); *7* – Aasiaat, Greenland (*V. atalanta*, 1967). The pink stars indicate localities in mainland Eastern Siberia (Yakutia), in which a population explosion of *N. xanthomelas* was registered in 2020: *8* – Yakutsk; and *9* – Tiksi, east of the Lena River delta. The circles hatched with pink lines indicate approximate areas of massive expansion of *N. xanthomelas* throughout Eastern Siberia in 2020 (*A1*) and of regular occurrence of this species in the Polar Urals and adjacent areas since 1970s (*A2*) (see discussion section for detail). The CAFF Map No. 14 (Arctic Council; http://library.arcticportal.org/id/eprint/1336) was used as the topographic base of this image.

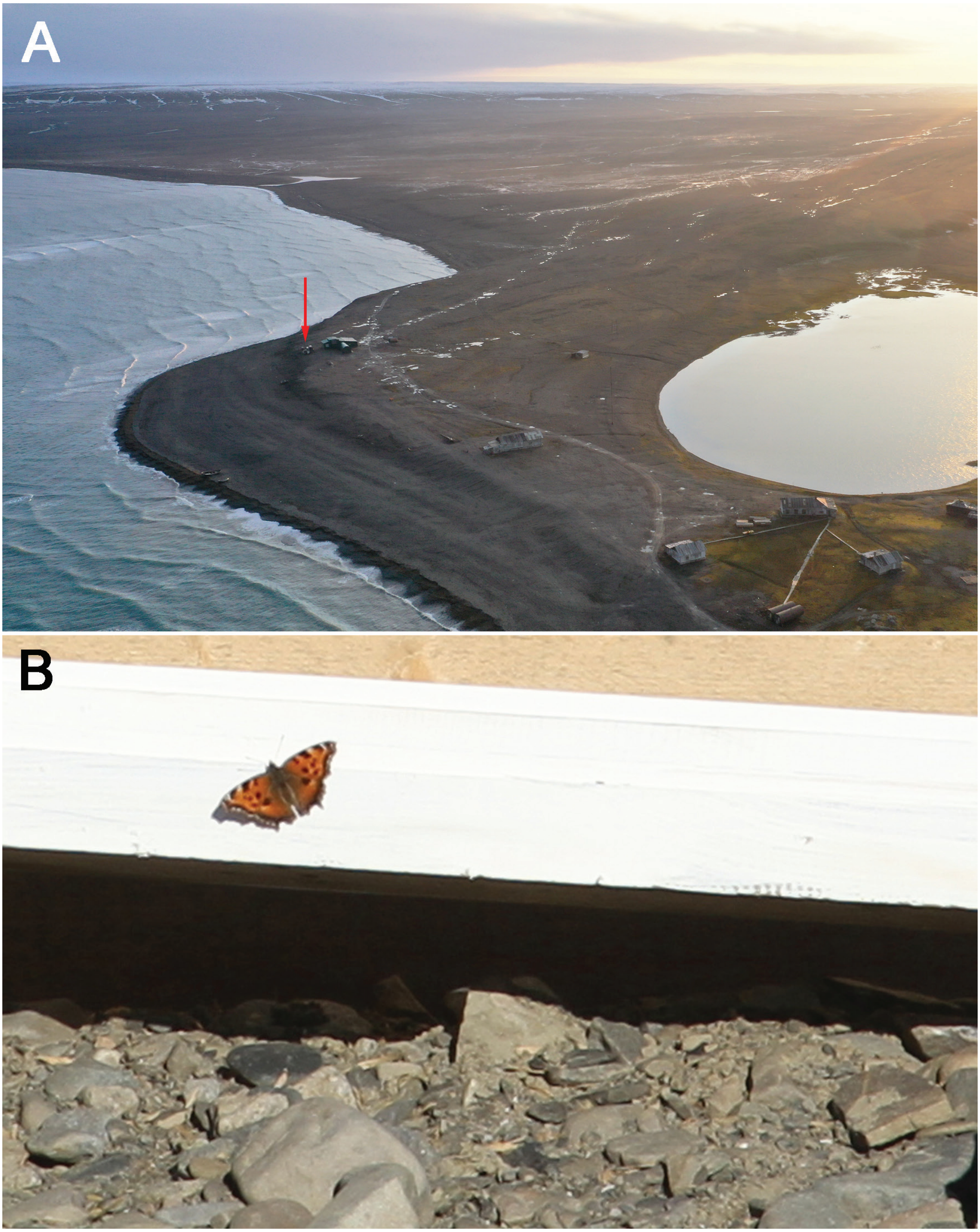

Figure 2. Scarce Tortoiseshell *Nymphalis xanthomelas* on Cape Zhelaniya, Northern Island, Novaya Zemlya. (**A**) General view of the northern extremity of Novaya Zemlya. The red arrow indicates the field observation site [76.9481°N, 68.5400°E]. In the front is the research station "Cape Zhelaniya" of the Russian Arctic National Park. In the background is a mountain range covered by glaciers and perennial snowfields. (Photo: Steffen Graupner). (**B**) Living butterfly near the research station on 23 August 2020. (Photo: Vadim Zakhariin).

Additional field observations were performed in Eastern Siberia (Yakutia Republic), i.e. in the vicinity of Yakutsk [62.0371°N, 129.6131°E; 26.vii and 07.viii.2020] and near Tiksi airport [71.7064°N, 128.8843°E; 30.vii–05.viii.2020] (Fig. 3A) (observer: Olga Aksenova).

Climate data and air current reconstruction

The data on mean air temperature anomalies for the summer season of 2020 was obtained from free open sources such as the NOAAGlobalTemp v.5.0.0 database and NOAA's Global Climate Reports (NOAA/OAR/ESRL PSL, Boulder, Colorado, USA; https://www.ncdc.noaa.gov; Vose et al. 2012). The Ventusky web application (https://www.ventusky.com; InMeteo, Pilsen, Czech Republic) was used to reconstruct air currents and weather conditions in Northern Siberia and Novaya Zemlya at the dates corresponding to the butterfly migrations.

Results

Occurrences of long-distance migrant butterflies on the Arctic Ocean islands

Overall, our dataset contains 15 occurrences of long-distance migrant butterflies on six Arctic Ocean islands, i.e. Svalbard, Kolguev, Vaygach, Dolgiy, Novaya Zemlya (Northern Island), and Greenland (Table 1). The occurrence covers the period from 1967 to 2020. In most cases, two migrant butterfly species per island were recorded, while on Svalbard and Novaya Zemlya only one species was discovered so far. These occurrences correspond to six species belonging to two families: *Vanessa atalanta*, *V. cardui*, *Nymphalis antiopa*, *N. xanthomelas* (Nymphalidae), *Aporia crataegi* (Linnaeus, 1758), and *Pieris napi* (Linnaeus, 1758) (Pieridae). The most northern record of migrant butterflies (*Vanessa cardui*) in the world was made on Svalbard (up to 78.27°N). Our occurrences of *N. xanthomelas* on Novaya Zemlya are the world's second farthest record of migrant butterflies on the Arctic islands (76.95°N). Furthermore, it seems to be the most northern finding of this species globally. The shortest distance from an insular butterfly occurrence to the mainland shoreline in our dataset varies from 30 (Dolgiy) to 1,090 km (Greenland) (Table 1).

Records of *Nymphalis xanthomelas* north of the Arctic Circle in 2020

The first imago of *N. xanthomelas* was recorded at Cape Zhelaniya near the research station of the Russian Arctic National Park [76.9481°N, 68.5400°E] (Fig. 1) on 23 July 2020 (visual observation by Oleg Valkov) (Table 1). The second butterfly was photographed there on 23 August 2020 by the park ranger Vadim Zakhariin (Fig. 2A, B). These findings are representing natural migration events, because the butterfly occurrences do not correspond to the dates of ship calls and aircraft arrivals. There were five ship calls at Cape Zhelaniya: 05 and 28 July, 04, 21, and 24 August 2020. Additionally, a helicopter from the town of Naryan-Mar (Nenets Autonomous Okrug) arrived on 13 July 2020.

In mainland Siberia (Yakutia), *N. xanthomelas* was found to be abundant around the city of Yakutsk [62.0371°N, 129.6131°E] on 26 July and 07 August 2020 and near the Tiksi settlement [71.7064°N, 128.8843°E] on 30 July–05 August 2020 (Fig. 3A, B).

The occurrences of *N. xanthomelas* in the High Arctic in 2020 coincide with an extremely warm summer season. Based on the NOAAGlobalTemp v.5.0.0 database and NOAA's Global Climate Reports, the third highest July and second highest August air temperature since global records began in 1880 were registered during this period. Our reconstructions revealed that a warm air

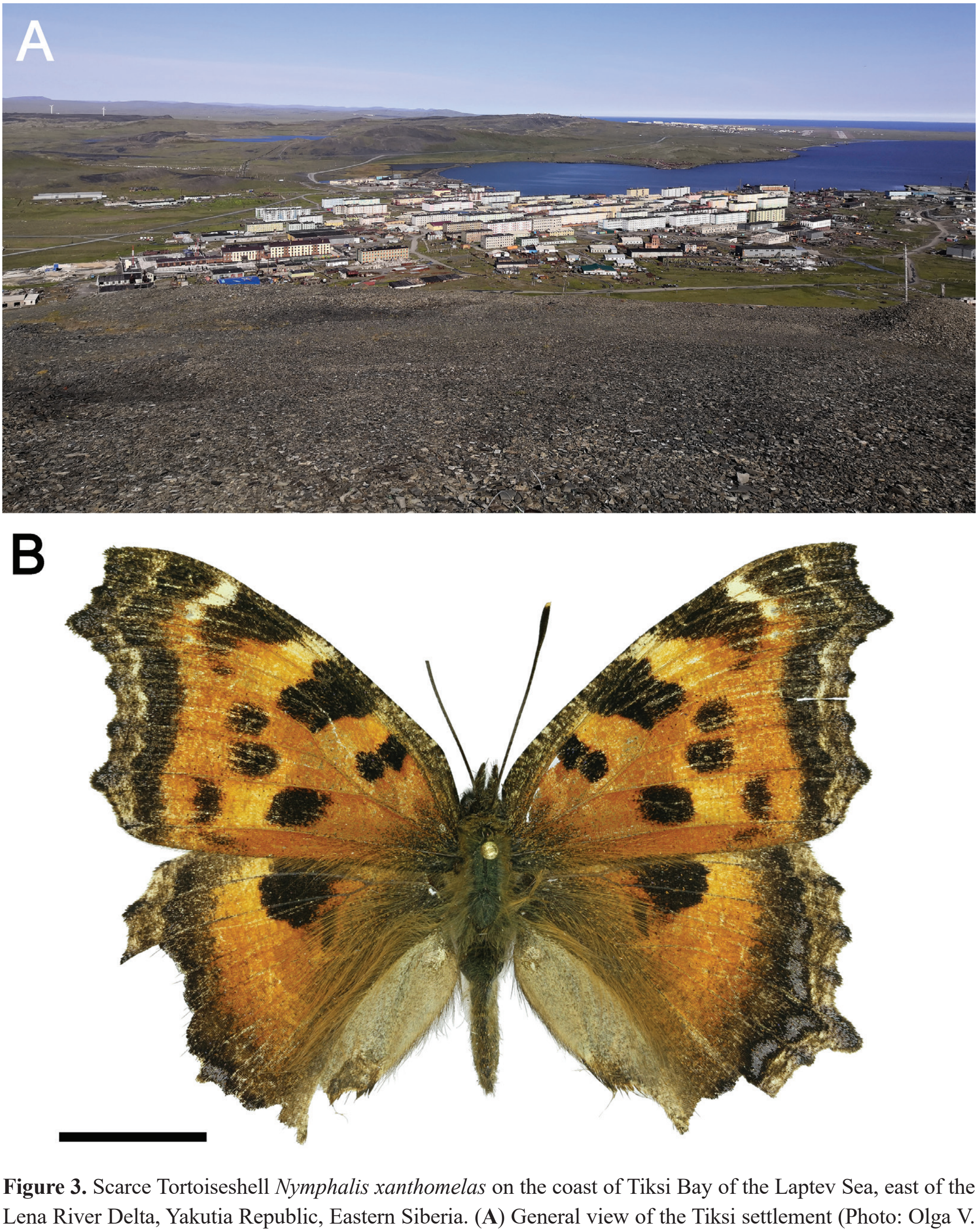

Figure 3. Scarce Tortoiseshell *Nymphalis xanthomelas* on the coast of Tiksi Bay of the Laptev Sea, east of the Lena River Delta, Yakutia Republic, Eastern Siberia. (**A**) General view of the Tiksi settlement (Photo: Olga V. Aksenova). (**B**) Specimen collected near Tiksi on 05 August 2020. Scale bar: 10 mm. (Photo: Vitaly M. Spitsyn).

mass from the Polar Urals, Yugorsky Peninsula, and western Yamal moved along the eastern coast of Novaya Zemlya to the northern edge of the archipelago during the period of 21–23 July 2020 (approximate direct distance 650 km) (Fig. 4A). Furthermore, there was an intense movement of

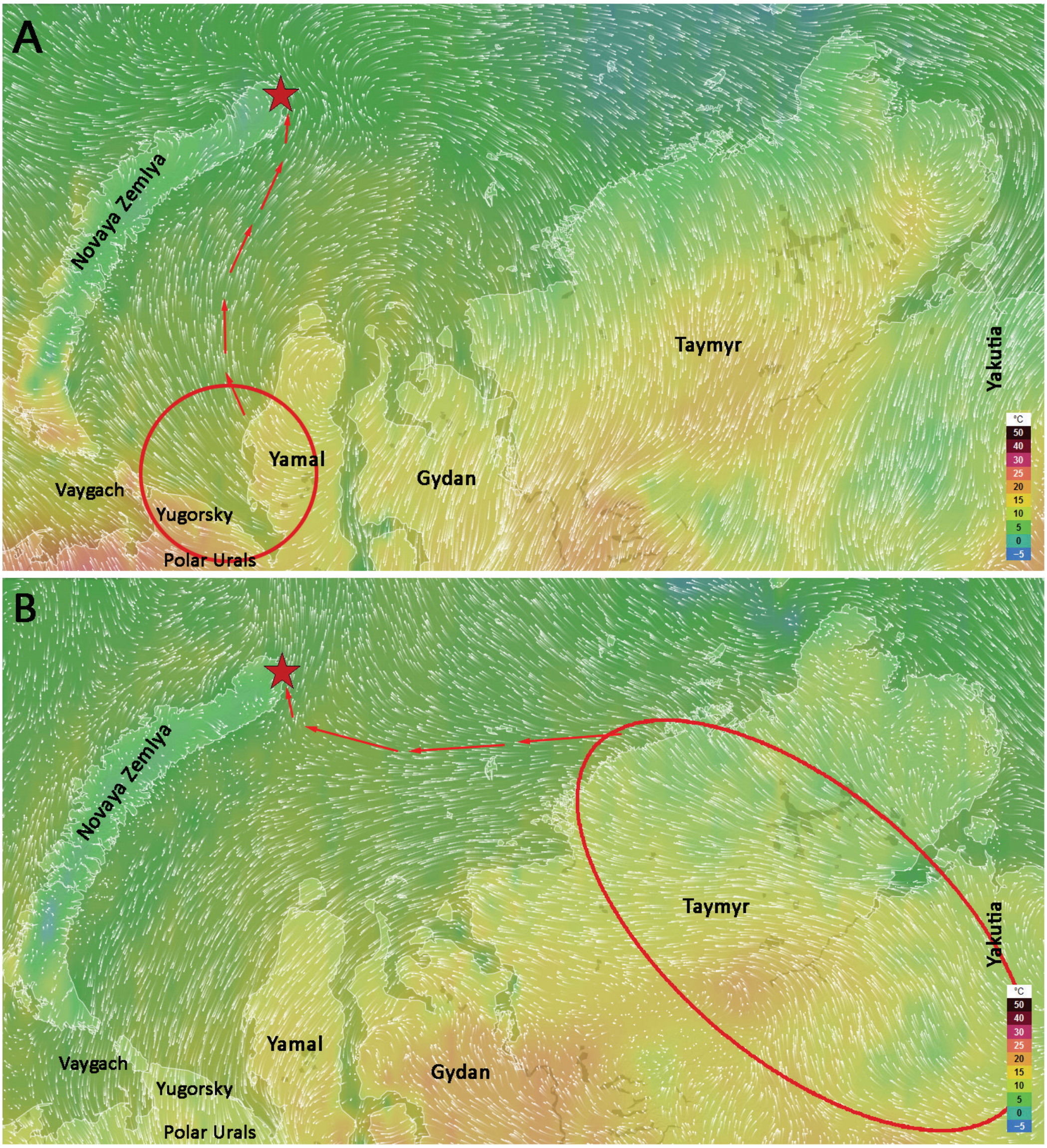

Figure 4. Reconstruction of air currents and air temperatures throughout Northern Siberia and Novaya Zemlya at the dates corresponding to *Nymphalis xanthomelas* migrations in 2020. In each case, the weather conditions were reconstructed on a day before the butterfly occurrence on Novaya Zemlya. The white arrows indicate air mass movements. The red stars indicate the butterfly occurrences. The red contours indicate possible source mainland areas for the butterfly immigration into Novaya Zemlya. The red arrows indicate possible migration routes of the butterflies on moving warm air masses from the mainland areas. The images were created using the Ventusky web application (https://www.ventusky.com; InMeteo, Pilsen, Czech Republic). (**A**) 22 July 2020, 12:00 PM (this pattern was constant during the period of 21–23 July 2020). (**B**) 22 August 2020, 12:00 PM (this pattern was constant during the period of 17–23 August 2020).

warm air mass from Taymyr towards Novaya Zemlya during the period of 17–23 August 2020 (approximate direct distance 580 km) (Fig. 4B). Because the daily patterns of air current movements and temperatures were similar within each period, we illustrated the situation on 22 July and 22 August 2020 (both at 12:00 PM, i.e. on a day before the butterfly occurrence on Novaya Zemlya) (Fig. 4A and 4B, respectively) as examples.

Discussion

Occurrences of migrant butterflies on the Arctic Ocean Islands are linked to regional expansions in the mainland

In total, six migrant butterfly species were recorded on the Arctic Ocean islands (Svalbard, Kolguev, Vaygach, Dolgiy, Novaya Zemlya, and Greenland) so far (see Table 1). Records of *N. xanthomelas* from Novaya Zemlya correspond to the recent expansion of this species throughout mainland Siberia and Europe, the patterns and timing of which are discussed in a special section (see below). We show that this species crossed 580–650 km wide marine barriers on warm air currents from the mainland (see Fig. 4).

Nymphalis antiopa is a widespread forest species, with occasional migrations to subarctic areas (Bogacheva and Olschwang 1978; Olschwang 1980; Korshunov et al. 1985; Chernov and Tatarinov 2006) and the British Isles (Williams 1935; Van Swaay et al. 2008). A dead specimen of this species was found on the shore of Lake Yangoto in the northern part of Vaygach Island [70.2511°N, 59.0922°E] (Vlasova et al. 2014) that appears to be the most northern occurrence of this species globally. This record coincides with expansion of *N. antiopa* towards the Polar Urals (Kara River basin) in 2010 (Tatarinov and Kulakova 2017), where it can sometimes establish temporary local populations (Chernov and Tatarinov 2006). Its imago was recorded in the Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 06.viii.2012] (Vlasova et al. 2014). Conversely, a single visual observation of *N. antiopa* on Svalbard (Sømme 1993; Coulson 2015) reflects rather a human-mediated introduction event with imported wood than a natural expansion event, as those in Iceland (Ólafsson and Björnsson 1997).

Vanessa atalanta and *V. cardui* are well-known seasonal long-distance migrant species that may successfully breed in boreal and subarctic areas (Bolotov 2002, 2004; Bolotov et al. 2013; Brattström et al. 2018) with a subsequent backward autumnal migration of newly emerged adults to the lower latitudes (Williams 1935; Stefanescu 2001; Mikkola 2003a, b; Stefanescu et al. 2017). *V. cardui* appears to be one of the most widespread and mobile butterflies globally (Shields 1992; Talavera and Vila 2017), which shows low genetic diversity and no clear phylogeographic structure (Pfeiler and Markow 2017). The African continent seems to be both the starting and the final area for its seasonal circulating migrations to Europe and back (Stefanescu et al. 2011, 2012, 2017). Migrations of both species regularly reached subarctic islands such as Faroes and Iceland (Wolff 1929, 1971; Ólafsson and Björnsson 1997; Jensen 2001). Among the Arctic Ocean islands, *V. atalanta* was found only on Greenland (Karsholt et al. 2015), while migrant individuals of *V. cardui* were recorded from Svalbard, Kolguev, Dolgiy, and Greenland (Lokki et al. 1978; Laarsonen 1985; Bolotov 2012; Karsholt et al. 2015; Kullberg et al. 2018). Exact source areas for the immigration of *V. atalanta* and *V. cardui* into Greenland are unclear, although these arrivals can clearly be linked to massive expansions and population dynamics in more southern continental regions of North America (Scott 1992, 2020; Swanson and Monge-Nájera 2000; Vandenbosch 2003). Records of *V. cardui* from Svalbard in 1978, Dolgiy in 2004, and Kolguev in 2009 coincide with its massive migrations to the North (Korshunov et al. 1982; Bolotov and Tikhomirov 2000; Tatarinov and Kulakova 2005, 2010, 2013; Bolotov et al. 2013; Stefanescu et al. 2013). In 1978, this species was recorded across Finland up to Lapland (Lokki et al. 1978), as well as from Northern European Russia (Bolotov and Tikhomirov 2000) and Taymyr (Korshunov et al. 1982). In 2004, it commonly occurred in the eastern part of the Bolshezemelskaya Tundra (Tatarinov and Kulakova 2005). In 2009, there was an enormous expansion event of *V. cardui* from North Africa and the Mediterranean Region towards northern Europe and the Urals (Stefanescu et al. 2011, 2013; Bolotov et al. 2013; Tatarinov and Kulakova 2010, 2013; Tatarinov 2016). For example, this butterfly was found on 87.5% of observation sites surveyed around the Padimey Lakes in the eastern part of the Bolshezemelskaya Tundra [67.5711°N, 62.1616°E; 24.vi–17.vii.2009] (Tatarinov and Kulakova 2010). Some number of migrant individuals arrived to Iceland [07.vi–02.vii.2009] (Elzerman 2009; Goethals 2009).

The record of *Aporia crataegi* on Vaygach Island coincides with a population explosion and intense expansion of this species in European Russia and Western Siberia in 2012–2013 (Tatarinov and Kulakova 2013; Vlasova et al. 2014). In 2012, this butterfly was abundant around Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 17–20.vii.2012] (Vlasova et al. 2014), and in the Pechora River delta relatively close to Kolguev (Tatarinov and Kulakova 2013). Although successful development of *A. crataegi* larvae on creeping willows, the dwarf birch, and blueberry were observed in the Polar Urals (Kara River basin) (Chernov and Tatarinov 2006) and on the Kanin Peninsula (Bolotov 2012), its breeding on the Arctic Ocean islands such as Vaygach is next to impossible. Our records from Vaygach and Amderma seem to be the farthest northern occurrences of this species globally. Other examples of *A. crataegi* observations beyond the Arctic Circle are as follows: near Igarka, Taymyr [67.4594°N, 86.6119°E; 15.vii.1955] (Korshunov et al. 1982), Khadyta River valley, southern Yamal [67.0°N, 69.5°E; 1976–1979] (Olschwang 1980), and several records throughout the Bolshezemelskaya Tundra [up to 68.17°N; 1997–2004] (Tatarinov and Kulakova 2005). This migrant species shares a shallow phylogeographic structure throughout Northern Eurasia, including extinct populations in the United Kingdom and Korea (Todisco et al. 2020).

Pieris napi commonly occurred in subarctic and arctic areas of Eurasia such as the Finnish Lapland (Marttila et al. 2001), Bolshezemelskaya Tundra (Tatarinov and Kulakova 2005), Polar Urals (Korshunov et al. 1985; Bogacheva 1986; Tatarinov and Kulakova 2005), Yamal (Korshunov et al. 1985), and Taymyr (Korshunov et al. 1982). However, its native long-distance dispersal events to the Arctic Ocean islands are rather rare, with a single available occurrence from Kolguev (Bolotov 2012). A *P. napi* specimen recorded from Svalbard was accidentally imported (Kaisila 1973; Lokki et al. 1978).

Usually, air currents support long-distance dispersal in insects (Mikkola 1986; Stefanescu et al. 2007; Chapman et al. 2015). Wind-borne dispersal processes could explain cases of extremely long migrations such as the arrivals of the American Painted Lady butterfly *Vanessa virginiensis* (Drury, 1773) to the Azores, Canary Islands, Madeira, mainland Spain and Portugal, France, and Britain (Vieira 2017). It was shown that lepidopterans could be carried to the Arctic and Sub-Antarctic islands by air masses (Lokki et al. 1978; Sømme 1993; Coulson et al. 2002; Convey 2004; Hawes and Greenslade 2013). For example, the immigration of *Plutella xylostella* into Svalbard in 2000 was associated with a warm southeasterly air mass movement from Russia (Coulson et al. 2002). This invasion coincides with the arrival of multiple dipteran and lepidopteran species to the Faroes and Iceland (Jensen 2001), revealing a possible concatenated aerial dispersal of various invertebrates from continental Europe through the North Atlantic-Arctic Ocean marine barriers. Similar observations on weather-dependent aerial arrivals of migrant butterflies and moths were made on Svalbard (Lokki et al. 1978) and in Iceland (Wolff 1971). In the present study, we show that *N. xanthomelas* migrated to the northern margin of Novaya Zemlya on warm air masses moving from the mainland (see Fig. 4 and discussion below).

The recent expansion of *Nymphalis xanthomelas*: timing, geographic coverage, and success

The distribution of *N. xanthomelas* covered Central and Eastern Europe and temperate Asia up to Korea and Japan (Kudrna et al. 2011). The most northern findings of this species in Europe were from southern Finland (Kaisila 1962; Kudrna et al. 2011). In European Russia, it was seen rarely as far north as the Kirov, Vologda, and Saint Petersburg provinces (Ershov 1884; Tatarinov and Kulakova 2013). There were a few more northern records, e.g. near Kotlas [61.25°N, 46.64°E; vi.1906] (Krulikovsky 1909), Ukhta [63.67°N, 53.32°E; 1998] (Tatarinov and Kulakova 2013), and Petrozavodsk [61.78°N, 34.33°E; 25.iv.2005] (Kutenkova 2006; Gorbach 2013). In contrast, *N. xanthomelas* was more widespread and common throughout the Ural Mountains (Gorbunov and Olschwang 1997; Tatarinov 2016), where it occurred up to the Polar Urals, e.g. in the Kara River basin [68.87°N, 64.57°E; vii.2010] (Tatarinov and Dolgin 1999; Tatarinov and Kulakova 2013). Additionally, there were multiple occurrences from the eastern part of the Bolshezemelskaya Tundra, i.e. Vorkuta [67.49°N, 64.05°E; 1970s], Chum Station [67.0914°N, 63.1831°E; 23.vi.2001], Shapkina River [67.0°N, 55.0°E; 5–29.vii.2003], and Khalmer-Yu River [68.1654°N, 64.5783°E; 7–9.vii.2004] (Tatarinov and Kulakova 2005, 2007, 2013). In the Polar Urals, successful development of this species on dwarf willows (e.g. *Salix reticulata* L.) was registered (Tatarinov 2016).

It was also known to occur throughout the forest zone of Siberia, with a few records in forest-tundra and tundra of the Taymyr Peninsula (Korshunov et al. 1982, 1985; Kozlov et al. 2006). The downstream of the Verkhnyaya Taymyra River [74.15°N, 99.40°E; 17.viii.1983] appears to be the most northern locality in Asia, in which a migrant specimen of this species was collected (Korshunov et al. 1985). There were additional earlier findings on Taymyr, i.e. from Dudinka [69.40°N, 86.18°E; 1–12.vii.1915], Talnakh [69.48°N, 88.40°E; 5–6.viii.2001], Lake Lama [69.42°N, 90.71°E; 28.vii.2002] (Kozlov et al. 2006), and the middle reaches of the Rybnaya River [55.77°N, 94.80°E; 12.vii.1976] (Korshunov et al. 1982). Massive population explosions of *N. xanthomelas* were registered in Eastern Siberia (Yakutia) in 1958, 1967–1968, 1994, and 2002 (Ammosov 1971; Kaymuk et al. 2005).

Overall, this butterfly was seen rarely throughout Europe before the 2010s, i.e. for over one and a half centuries (Ershov 1884; Kaisila 1962; Anikin et al. 1993; Manil and Cuvelier 2014; Dennis and Hardy 2018). In Russia, the recent massive expansion of *N. xanthomelas* started in the 2010s. An extensive migration of *N. xanthomelas* (mean counts = 900–2700 individuals per hour) was observed on 24–25.vi.2012 in the Chuvashia and Mary-El republics (Lastukhin et al. 2016). The butterflies flying westward were recorded along the road from the Yakanzasy village [57.2947°N, 65.0805°E] to Lake Karas' [56.3996°N, 47.7974°E] (Lastukhin et al. 2016). The species became abundant throughout the boreal zone of European Russia (Arkhangelsk Region and Komi Republic), the Urals, and Western Siberia (Tyumen Region) (Tatarinov and Kulakova 2013; Vlasova et al. 2014; Bolotov et al. 2015b; Tatarinov 2016). In the Arctic, it was common in the Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 18–19.vii.2012] (Vlasova et al. 2014), as was in several other localities of the Nenets Autonomous Okrug, including the town of Naryan-Mar

[67.63°N, 53.05°E] (Tatarinov 2016; Kozlov et al. 2019). Successfully overwintered adults were recorded in Arkhangelsk [64.5308°N, 40.6264°E] in April 2014 (Bolotov et al. 2015b), and in the Subpolar and Polar Urals in 2013–2017 (Tatarinov 2016; Morgun 2017; Vlasova and Potapov 2018).

In 2019–2020, another population explosion of *N. xanthomelas* was recorded in Yakutia, Eastern Siberia. In 2019, the abundance of this species had increased so much that its massive expansion throughout Yakutia attracted full attention of regional mass media (News.Ykt.Ru 2019). Vagrant individuals of this species occurred east of the Lena River delta (Tiksi settlement; 71.6995°N, 128.8791°E) in late July-early August 2020. These data indicate that the arrival of migrants to Novaya Zemlya coincided with a massive expansion of *N. xanthomelas* in Eastern Siberia. Based on our air current reconstructions, we propose that the butterflies migrated to Novaya Zemlya from two source areas, i.e. the Polar Urals, Yugorsky Peninsula, and western Yamal (the occurrence on 23 July), and Taymyr (the occurrence on 23 August) (see Fig. 4A and 4B, respectively).

In European countries, the range of *N. xanthomelas* shifted northward since 2009–2010, and its settlements appeared in Finland and southeastern Sweden in 2011–2013 (Manil and Cuvelier 2014). In 2012–2013, this species was found to be highly abundant throughout Ukraine (Martynov and Plushtsch 2013). In Estonia, a series of striking immigration events of *N. xanthomelas* was registered in 2012–2015 (Tiitsaar et al. 2019). In July 2014, the butterfly was abundant throughout Scandinavia, northern Germany, the Netherlands and northern Belgium, while a flock of migrants crossed the Channel and immigrated into eastern England (Manil and Cuvelier 2014; Fox et al. 2015; Hensle and Seizmair 2015; Dennis and Hardy 2018). These observations coincide with intense dispersal processes in Western Siberia, the Urals, and European Russia (Tatarinov and Kulakova 2013; Vlasova et al. 2014; Bolotov et al. 2015b; Lastukhin et al. 2016; Tatarinov 2016). It is clear that its expansion in Western Europe resulted from the population explosion and massive westward migration of *N. xanthomelas* in Russia (Tatarinov and Kulakova 2013; Vlasova et al. 2014; Bolotov et al. 2015b; Lastukhin et al. 2016) and Ukraine (Martynov and Plushtsch 2013). The abundance of *N. xanthomelas* in mainland Western Europe and the United Kingdom during the summer of 2015 decreased abruptly, most likely due to very scarce offspring of overwintered migrant butterflies caused by unfavourable weather conditions (Manil and Cuvelier 2015). Conversely, in Estonia it was still a common species in 2016–2017 (Tiitsaar et al. 2019).

Finally, we assume that the recent expansion of *N. xanthomelas* to Western Europe and to the Arctic areas in Siberia and Europe was triggered by global climate warming during the period of 2012–2020. The European distribution of this species can be explained well by climatic variables, while its range shift to Scandinavia was predicted under climate warming scenarios (Settele et al. 2008). It was shown that the long-term trends in the range shifts, abundance, and phenology of migrant butterflies in continental Europe and Britain correlate with seasonal weather conditions and rising air temperatures (Mikkola 1986; Parmesan et al. 1999; Warren et al. 2001; Burton and Sparks 2003; Sparks et al. 2005, 2007; Dennis and Hardy 2018).

Acknowledgements

We are thankful to the Editor David Lees, and to our reviewers John Tennent, Niklas Wahlberg, and Martin Wiemers for their kind comments on an earlier version of this paper. This study was partly supported by the Ministry of Science and Higher Education of the Russian Federation (projects 0409-2019-0042 to Y.S.K. and 0793-2020-0005 to I.N.B.), Russian Science Foundation (project 19-14-00066 to O.V.A.), and Russian

Foundation for Basic Research (projects 18-44-292001 to M.Y.G. and 19-34-90012 to V.M.S.). We are grateful to Steffen Graupner, Vadim Zakhariin, and Oleg Valkov for their kind help during this study. Special thanks goes to Mikhail Kozlov (University of Turku, Finland) who kindly provided pdfs of several literature sources.

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