NUPTIAL FLIGHT IN ANTS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Based on the collected data set (758 observations for the period 2007-2021) on the dates of the nuptial flight for 73 species of ants, an analysis of possible time shifts due to global climate changes has been carried out. It was found that for Eastern Europe and Asia, for most species of ants, the dates of nuptial flight were shifted by at least two weeks earlier in comparison with the data for Western Europe. In a cold climate, there are significant changes, towards earlier dates, in the phenology of nuptial flight for two species: *Lasius flavus* ($P<0.05$) and *Polyergus rufescens* ($P<0.01$). The corresponding rates of change are 3.9 and 6.25 days per year. In other types of climate, no significant changes in the phenology of the nuptial flight were found. Taking into account the boundaries of future climatic zones in temperate and arid zones, such changes were recorded for several species. *Solenopsis fugax* in temperate climates shows a tendency to delay flight at a rate of 6 days per year ($P<0.05$). Within the predicted boundaries of the arid climate, the flight phenology delay was recorded for *Lasius niger* (5.8 days per year; $P<0.01$) and *Messor* sp. (4.4 days per year; $P<0.05$). At the same time, for *Polyergus rufescens*, there is a tendency to an earlier flight at a rate of eight days per year ($P<0.05$). No connection was found between the date of nuptial flight and the geographic distance between populations (or locations).

Keywords: Nuptial flight, ants, climatic changes, phenology

ABSTRAK

Berdasarkan set data yang dikumpulkan (758 pemerhatian dalam tempoh 2007-2021) ke atas masa penerbangan untuk pengawanan bagi 73 spesies semut, analisis perubahan masa yang disebabkan oleh isu pemanasan global telah dijalankan. Didapati kebanyakkan masa untuk penerbangan pengawanan spesies semut dari Eropah Timur dan Asia telah berubah sekurang-kurangnya awal dua minggu berbanding dengan spesies dari Eropah Barat. Pada musim sejuk, terdapat perubahan signifikan terhadap tempoh masa awal ke atas fenologi untuk penerbangan pengawanan ke atas dua spesies; *Lasius flavus* (*P<0.05*) dan *Polyergus rufescens* (*P<0.01*). Kadar perubahan tersebut adalah 3.9 dan 6.25 hari per tahun. Pada musim lain, tiada perbezaan signifikan ke atas fenologi penerbangan pengawanan didapati. Dengan mengambil kira faktor sempadan pada zon iklim sederhana dan zon iklim gersang, beberapa perubahan direkodkan untuk beberapa spesies. *Solenopsis fugax* di zon iklim sederhana menunjukkan keupayaan untuk melewatkan penerbangan pada kadar enam hari per tahun (*P<0.05*). Dalam jangkaan sempadan pada zon iklim gersang, fenologi penerbangan direkodlan lewat ke atas *Lasius niger* (5.8 hari per tahun; *P<0.01*) dan *Messor* sp. (4.4 hari per tahun; *P<0.05*). Pada masa yang sama, *Polyergus rufescens*, berupaya untuk mempercepatkan penerbangannya pada kadar lapan hari per tahun (*P<0.05*). Tiada hubungan didapati di antara penerbangan pengawanan dan jarak geografi antara populasi (atau lokasi).

Kata kunci: Musim pengawanan, semut, penubahan cuaca, fenologi

INTRODUCTION

Nuptial flight is one of the key moments in the life cycle of ants (Hölldobler & Wilson 1990). To understand the nature of the nuptial flight, it is necessary to understand how it passes, what scenarios exist among the species of ants, and under what weather conditions it passes. After mating, the future queens shed their wings and look for shelter, or they themselves dig up chambers to found a nest. This is the most typical scenario for the beginning of colony development, which occurs in most ant species. Some of the ant species that have nuptial flight are parasites, for example, *Lasius umbratus*, *L. fuliginosus* (Radchenko 2016). If *L. umbratus* founds its colonies at the expense of *L. niger*, then *L. fuliginosus* - at the expense of *L. umbratus*, i.e. *L. fuliginosus* is a superparasite (Seifert 2018). *Solenopsis fugax* is a kleptobiont species that lives into colonies of other ant species - *L. niger*, *Tetramorium caespitum*, but *S. fugax* has a true nuptial flight (Radchenko 2016). Despite parasitism, the nuptial flight of *S. fugax*, *L. umbratus* is massive, as in *L. niger* and *Lasius flavus*. The *L. umbratus* queen who shed its wings kill the workers of *L. niger* in order to subsequently enter the nest of the host species, kill the local queen and take her place. Thus, mass nuptial flight can be both in ant species with a standard colony founding scheme, and in parasitic species, or kleptobiont species. A common feature of the nuptial flight in the above species is its massiveness, that is, it is carried out on a large scale simultaneously over large territories. For some other species of ants that found colonies on their own, the nuptial flight can be extended and not manifest en masse. These species include *Formica cunicularia*, *F. fusca* (Czechowski et al. 2012). Red wood ants can found their new colonies both due to daughter nests and due to the penetration of their queens shortly after the nuptial flight into the nests of some species of the subgenus *Serviformica*. Queens of some parasitic species, such as *Polyergus rufescens*, invade colonies of the host species during slave raids. The nuptial flight may not necessarily occur in the air; in desert ants of the genus *Cataglyphis*, it may also occur on the ground (Seifert 2018).

Thus, for the nuptial flight of ants, different features are characteristics that are massive and fit three to five times on year, or it can be extended over a long period of time. Depending on the way of founding a new colony, the nuptial flight may end with the independent founding, or with the penetration into the colony of the host species. The season of nuptial flight is significantly influenced by weather conditions. Typically, these are factors such as rainfall, high humidity, and suitable temperature conditions. The greatest influence is exerted by the air temperature and the intensity of insolation, since these factors can affect the body temperature of winged queens (Depa 2006). For larger queens *L. niger*, *L. flavus*, higher air temperatures are required than for small ones *Myrmica rubra*, *M. scabrinodis* (Boomsma & Leusink 1981). In addition, on the day of summer, as a rule, there was no preceding rain; precipitation was observed either after summer, as was shown for *Manica rubida* (Depa 2006). In general, nuptial flight is often timed to coincide with precipitation, since queens who have thrown off their wings find it easier to dig up the chambers of the future nest (Hölldobler & Wilson 1990). The first day suitable for weather conditions does not necessarily have to be accompanied by a nuptial flight, since at this moment not all winged queens can emerge from the brood (Depa 2006).

For most species in the temperate climatic zone of the Northern hemisphere, the nuptial flight season is associated with the summer period. Therefore, if it conditions change, a shift in the dates of the nuptial flight is also possible. According to B. Seifert, in the period 1990-2017, the nuptial flight of ant species in Central and Northern Europe moved on average 14.2 days earlier than in the previous period of 1845-1989 (Seifert 2018). Over the past decade, the average air temperature has steadily increased, which is associated with the increasingly manifested effect of global warming. For example, July 2021 was the hottest month on record since 1820. Therefore, shifts in the nuptial flight season in ants are quite possible, which can be noticeable during the last decade.

Research on the nuptial flight is usually rather incomplete. They usually focus on the nuptial flight of one or more species (Boomsma & Leusink 1981; Curtis 1985; Gómez & Abril 2012). The most detailed information (with dates for each species, arithmetic mean for days of summer, the earliest and latest dates of the nuptial flight) is given in the monograph by B. Seifert devoted to ants in Northern and Central Europe (Seifert 2018). In monographs devoted to ants in Poland and Ukraine, the dates of the nuptial flight are indicated as months (Czechowski et al. 2012; Radchenko 2016). At the same time, there are no publications with an analysis of the data set on the dates of nuptial flight in many ant species at once, at least for the Northern Hemisphere. It is known that the nuptial flight in closely related species can pass more intensively at close or coinciding dates (Dekoninck et al. 2004). Representatives of the subgenus *Chtonolasius* can spend nuptial flight approximately at the same time as their host species, *Lasius platythorax* (Dekoninck et al. 2004).

Seasonal development shift is one of the prominent responses of animal species to climate change and can further alter ecosystems integrity and species' ranges expansion or contraction. Recent studies analyzing phenological data at large scales have shown no uniform responses to climate change (Roslin et al. 2021). The uneven change in phenology's response relates to variability in patterns of climate change across regions and biomes. That means a need to investigate regional appearances of phenology's shift to better understand the consequences of ongoing global climate change.

We suggest that over the past decades, the dates of the nuptial flight have significantly shifted towards a temperature optimum. This is the first hypothesis of this study. The second hypothesis is that the dates of the nuptial flight will be shifted more in summer to an earlier period in the arid climatic zone and in spring to earlier periods in the cold zone. The aim of the study is to analyze whether there have been shifts in the timing of nuptial flight for ants in the Northern Hemisphere over the past decade. To do this, for the first time, we analyzed data on almost 750 observed cases of nuptial flight from 2007 to 2021 in the Northern Hemisphere, on the territory of 10 countries of Eastern Europe and Asia, for more than 70 species of ants belonging to five subfamilies. Among the secondary tasks of the study was the determination of optimal temperature optima and time of day for nuptial flight in a different species of ants.

MATERIALS AND METHODS

Samples

This study was made possible by the growing popularity of ant keeping among ant fanciers. This hobbies (keeping ants in captivity) has become especially popular among young people. In parallel with keeping ants, such amateurs are actively interested in the life of ants in nature, creating thematic sites and forums. Such forums may contain a significant amount of information about various aspects of the life of ants, including the nuptial flight of different species. This assumption has guided this study. The research material is based on data obtained as a result of the analysis of the Russian-speaking segment of the Internet, in particular the site www.antclub.org, in the forums of which there are topics related to the timing and geographical location of the nuptial flight of ant species.

The authors used the following work algorithm. a) Search for topics on the forums of the site www.antclub.org related to the nuptial flight (search by keywords: flight, nuptial flight, terms of the nuptial flight, alates). b) selection of messages and topics that are suitable for data analysis. This took into account the reports of experienced users who are able to identify ants to the species level. Authors used only those data from the site that reliably confirm the species of ants. To do this, authors used either data posted by professionals who are good at identifying ant species, or data confirmed by photos. Some of the users have been registered on the forum for 5 years, which served as the basis for determining the level of professional users. c) registration of the received data in the form of a database. The columns in the Excel table were filled in: 1) country; 2) region (region, city of the country); 3) date (year, month, day, separate column for each value); 4) species of ant; 5) geographical coordinates (latitude, longitude) of the place where the nuptial flight took place; 6) additional data (temperature, humidity, wind speed, if any). For species with a massive nuptial flight, the presence of a large number of winged queens and males or queens that had just shed their wings was noted on the ground or in the air. We took into account messages about the nuptial flight, carried out directly from the anthills. For species with an extended nuptial flight, the fact that individual winged females and males are on the ground (or flying from the nest) or in the air was taken into account.

In the generated data set, there are 758 cases of nuptial flight. In total, these data are given for 71 species of ants. The studied period covers 14 years, from 2007 to 2021 inclusive. The studies were carried out in 10 countries of Europe and Asia: Ukraine, Uzbekistan, Russian Federation, Kazakhstan, Belarus, Turkey, Moldova, Kyrgyzstan, Bulgaria, Azerbaijan.

Data Processing Methods

Forecasting the climate changes

The data on nuptial flight were distributed according to the updated climate classification given in the article by Beck et al. (2018). The article examines the period from 1980 to 2016 and the period from 2017 to 2100 (future). Climatic zones are considered within the framework of the Koppen-Geiger classification, taking into account the current situation. Geographical points corresponded to three climatic zones - arid, temperate, cold. The Cold zone includes the following climatic subzones: Dfb, Dfa, Dfc; Temperate - Cfb, Cfa, Csa; Arid: BWk, BSk. Belonging to a specific climatic subzone of a particular geographic point was established using the website www.climate.org. Points and climatic zones on the climate map until 2016 and in the period starting from 2017 are shown in Figure 1 (maps based on the article by Beck et al. 2018).

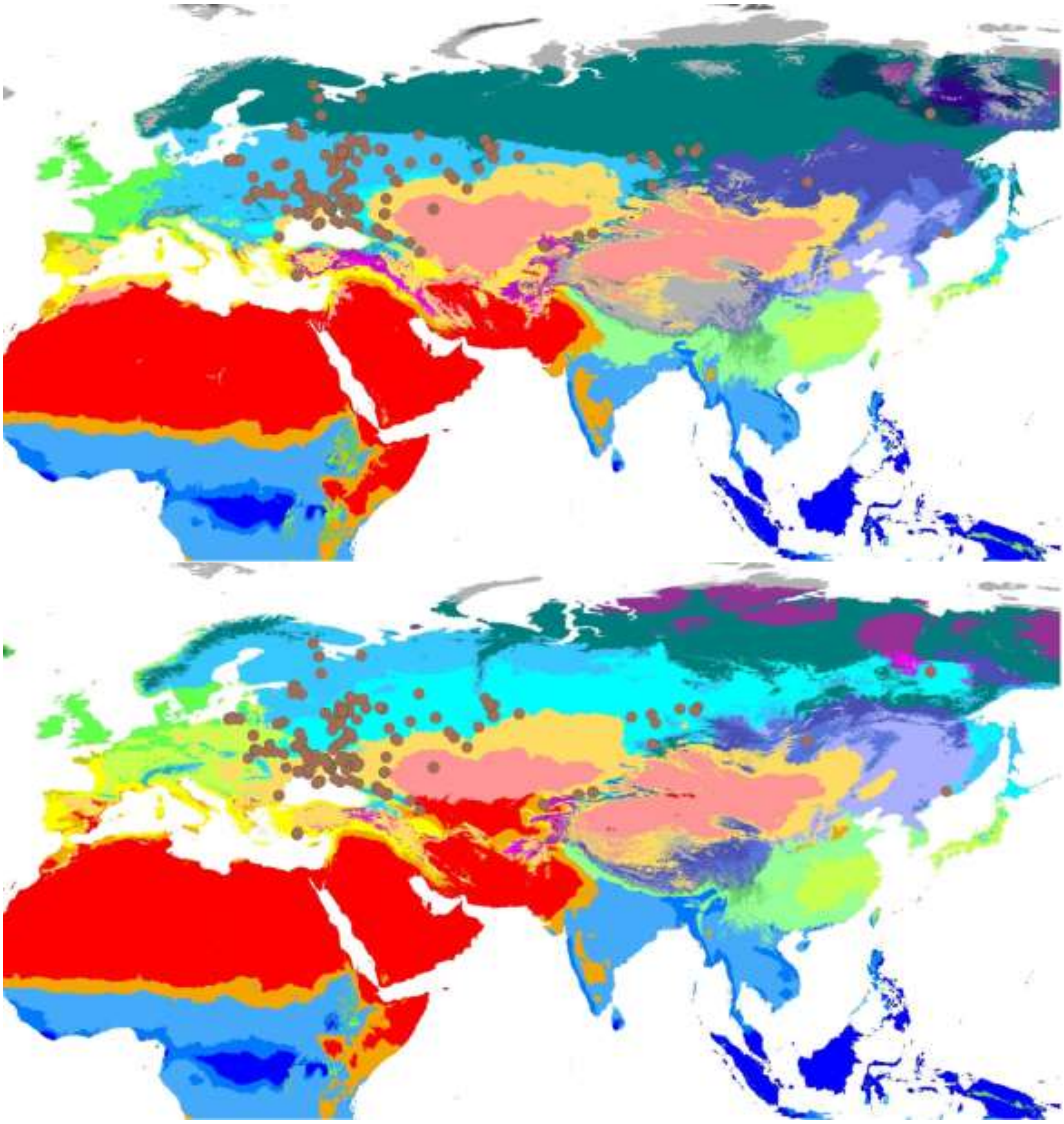

Figure 1. Map of research points of nuptial flight in ants in 2007-2021 under climatic conditions 1980-2016 (A, above) and 2017-2100 (B, below) (according to Beck et al. 2018)

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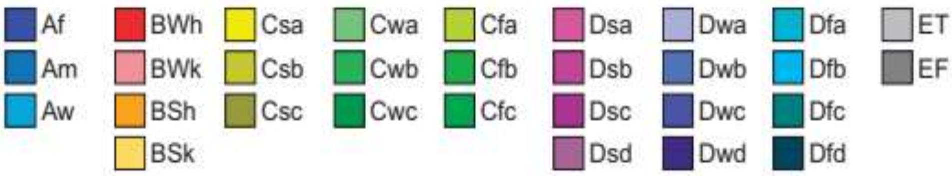

Processing of information
The nuptial flight date was translated into the day of the year corresponding to its ordinal number (DOY). To measure the effect of distance on the simultaneity of the nuptial flight, geographic coordinates (latitude, longitude) were used for each of the points. When measuring changes in the dates of the nuptial flight that occur between years, the day was taken as an average for all species in a given climatic zone. We also considered it possible to calculate the average nuptial flight day for all ant species, since separately for each species of such data may not be enough for statistical analysis. A similar method was previously applied by B. Seifert, who also calculated the average for all species (Seifert 2018). To assess shifts in nuptial flight phenology we applied linear regression for DOY and year for each species and then tested whether the 'trend', i.e. slope, was significant.

Study Design
In order to analyze the changes in the dates of the nuptial flight, it is necessary to break down the existing data by species into dates corresponding to reliably different periods. To do this, we applied cluster analysis, which made it possible to establish which species of ants most often fly at a certain time. Some ant species are present in different clusters as they have two mating terms, with approximately equal numbers of reported cases. This allowed us to associate the terms of summer of ant species with certain seasons of the year - spring, summer and autumn. This fact is known for some species, for example, for *Manica rubida*, whose nuptial flight season can occur in May and September, months with similar climatic conditions (Depa 2006). Changes in the timing of nuptial flight by seasons were compared for ant species with different climatic zones.

Statistical Analysis
To process the data by calculating the arithmetic mean (and mean error, SE), the Paleontological Statistics Software (PAST) program (v.4.03) was used. One-way ANOVA (Kruskal-Wallis test (KW), Welch F test in the case of unequal variances (W), Mann-Whitney pairwise test (M-W)). Regression analysis was used to analyze trends in the change in the average dates of the nuptial flight. To classify species by terms of nuptial flight into clusters, the Wards cluster method was used. All other calculations were performed in the R software environment (R Core Team 2020).

To confirm or refute the hypothesis that the dates of nuptial flight of ants of the same species change with the distance between populations (locations), we used the Mantel test (1967). The significance of the test results was checked by the Monte Carlo method with 1000 replicates. To detect temporal trends in the variation of the calendar day of nuptial flight, we used linear regression analysis, in which a positive value of the slope indicates a delay in phenology with time, and a negative one, respectively, its shift to earlier dates.

RESULTS

Table 1 shows data on the dates of nuptial flight for 73 species of ants belonging to 5 subfamilies ie., Formicinae (46 species), Myrmicinae (19 species), Dolichoderinae (4 species), Ponerinae (3 species), and Dorylinae (1).

Table 1. List of ant species, number of measurements, data by country and by climatic zone of the original study in comparison with the data of B. Seifert (2018)

Species	**Country**	**Number of original observations**	**Median (DOY)**	**Number of Seifert (2018) observations**	**Median (day, DOY)**	**Earliest (day, DOY)**	**Latest (day, DOY)**
Camponotus aethiops	Ru, Uk, Uz	6	174	30	17 Jul (198)	15 Jun (166)	15 Sept (258)
Camponotus baldaccii	Tu	2	174	n/a			
Camponotus fallax	Ru, Uk	12	173	16	10 May (130)	26 Apr (116)	1 Jun (152)
Camponotus herculeanus	Ru, Uk	6	190	34	12 Jun (163)	18 May (138)	3 Aug (215)
Camponotus fedtschenkoi	Uz	1	155	n/a			
Camponotus interjectus	Uz	3	120	n/a			
Camponotus lameerei	Uz	2	106	n/a			
Camponotus ligniperda	Ru	2	186	26	5 Jun (156)	3 May (123)	26 Jun (177)
Camponotus piceus	Ru	1	212	10	10 May (130)	25 Apr (115)	22 May (142)
Camponotus pilicornis	Uz	1	240	n/a			
Camponotus reihardti	Uz	3	157	n/a			
Camponotus saxatilis	Ru	2	247	n/a			
Colobopsis truncata	Tu, Ru	4	172	21	21 Jul (202)	15 Jun (166)	9 Sept (252)
Camponotus turkestanicus	Uz	3	117	n/a			
Camponotus vagus	Uk, Ru	11	180	36	2 May (122)	3 Apr (93)	15 Jun (166)
Camponotus xerxes	Uz	1	109	n/a			
Camponotus sp	Ru	1					
Cardiocondyla sp	Ru	1	107	1	n/a		
Cataglyphis aenescens	Uk, Uz, Az	11	141	n/a		20 May (140)	10 Jun (130)
Cataglyphis cinnamomea	Uz	1	145	n/a			
Cataglyphis nodus	Uz	1	120	10	29 Jun (180)	31 May (151)	27 Aug (239)
Cataglyphis pallida	Uz	1	145	n/a			
Cataglyphis setipes	Uz	1	145	n/a			
Crematogaster subdentata	Uz	4	284	n/a			

Dolichoderus quadripunctatus	Ru, Uk	3	144	22	27 Jul (208)	17 May (137)	2 Sept (245)
Formica cinerea	Ru	1	147	1			
Formica cunicularia	Uk, Ru, Uz	41	149	22	4 Jul (185)	8 Jun (159)	5 Aug (217)
Formica fusca	Uk, Ru	8	188	20	27 Jul (208)	21 Jun (172)	10 Sept (253)
Formica gagatoides	Ru	1	190	n/a		earl Jul	mid Sept
Formica polyctena	Ru	25	181	34	9 May (129)	29 Mar (88)	22 Jun (173)
Formica pratensis	Uk, Mo	1	145	95	10 Jun (161)	15 Apr (105)	24 Jun (175)
Formica rufa	Ru	2	149	25	30 May (150)	20 Apr (110)	10 Jul (191)
Formica rufibarbis	Uk, Ka, Bu, Ru	7	179	25	8 Jul (189)	16 Jun (167)	3 Aug (215)
Formica sanguinea	Uk, Be, Ru, Mo	7	189	60	18 Jul (199)	25 May (145)	15 Sept (258)
Formica truncorum	Uz	1	163				
Hypoponera eduardi	Uz	6	265	n/a			
Lasius brunneus	Uk, Ru	4	205	33	17 Jun (168)	19 May (139)	4 Aug (216)
Lasius emarginatus	Uk, Ru	2	176	57	24 Jul (205)	10 Jun (161)	4 Sept (247)
Lasius flavescens	Uz	1	238				
Lasius flavus	Uk, Ru	38	199	40	19 Aug (231)	11 Jul (192)	21 Oct (294)
Lasius fuliginosus	Uk, Ru, Be, Mo	30	177	52	7 Jun (158)	3 May (123)	1 Jul (182)
Lasius mixtus	Uk, Ru	2	222	n/a			
Lasius neglectus	Uz	3	147				
Lasius niger	Uk, Ru, Be, Ka	218	199	67	25 Jul (206)	26 Jun (177)	6 Sept (249)
Lasius paralienus	Uk	2	241				
Lasius umbratus	Uk, Ru, Mo	49	191	136	5 Aug (217)	5 Jun (156)	31 Oct (304)
Lasius uzbeki	Uz	1	97	n/a			
Lepisiota semenovi	Uz	1	107	n/a			
Liometopum microcephalum	Uk	1	170				

Lioponera desertorum	Uz	1	125				
Manica rubida	Uk, Ru	2	196		30 May (150)	29 Apr (119)	1 Jul (182)
Messor denticulatus	Uz	2	160				
Messor laboriosus	Uz	4	77				
Messor lamellicornis	Uz	1	108				
Messor sp.	Uk, Ka, Ki, Ru, Uz	52	179	n/a		early Apr	mid Jun
Myrmica sp.	Uk, Ru	32	163	62	24 Aug (236)	8 Jul (189)	2 Oct (275)
Myrmica salina	Uz	3	293				
Myrmica bergi	Uz	1	214	n/a			
Pheidole koshewnikovi	Uz	1	149	n/a			
Pheidole sp.	Uz	1	239	n/a			
Plagiolepis pallescens	Uz	2	228	n/a			
Plagiolepis pygmaea	Uz	1	215	7	24 Jul (205)	28 Jun (179)	22 Aug (234)
Polyergus rufescens	Uk, Ru, Ka, Uz	13	201	60	6 Aug (218)	25 Jun (176)	6 Sept (249)
Ponera coarctata	Ru	1	96	18	2 Sept (245)	15 Jul (196)	26 Sept (269)
Ponera testacea	Uz	1	231				
Solenopsis fugax	Uk, Ru, Ka, Tu, Uz	35	208	51	14 Sept (257)	10 Aug (222)	13 Oct (286)
Stenamma sp.	Ru	1	121	39	26 Sept (269)	1 Sept (244)	5 Nov (309)
Strongylognathus sp.	Ru	1	125	32	19 Jul (200)	23 Jun (174)	28 Aug (240)
Tapinoma erraticum	Uk, Uz	4	181	14	21 Jun (172)	5 Jun (156)	7 Jul (188)
Tapinoma karavaievi	Uz	1	142				
Temnothorax sp.	Uk	1	191	18	14 Jul (195)	10 Jun (161)	14 Sept (257)
Tetramorium armatum	Uz	1	163				

Tetramorium caespitum	Uk, Ru, Ka, Uz, Mo	30	189	86	27 Jun (178)	28 May (148)	19 Aug (231)
Trichomyrmex destructor	Uz	2	135				

Note: Uk – Ukraine, Ru – Russian Federation, Uz – Uzbekistan, Ka – Kazakhstan, Mo – Moldova, Tu – Turkey, Ki – Kirgizstan, Be – Belarus, Bu – Bulgaria, Az – Azerbaijan.

For nine species in some locations, dates are presented for the first time (*Crematogaster subdentata*, *Lasius neglectus*, *Tetramorium schneideri*, *T. armatum*, *Messor lamellicornis*, *Myrmica salina*, *Camponotus reihardti*, *Lasius flavescens*, and *Trichomyrmex destructor* in Uzbekistan). For 36 species living in Northern and Central Europe, Seifert (2018) provides detailed data, which are displayed in Table. 1. When comparing our data with the data of Seifert (2018), it can be seen that the average indicators of nuptial flight days in a number of species do not coincide. Thus, for the genus *Camponotus* and *Colobopsis*, in some species the dates of nuptial flight were shifted in two weeks or earlier (*Camponotus aethiops*, *Colobopsis truncata*), while in others, on the contrary, later (*Camponotus vagus*, *C. fallax*, *C. herculeanus*). Moreover, this is true not only for species with a small number of observations, but also for species with a comparable number with the data of B. Seifert (2018). *Cataglyphis aenescens* received the same period of nuptial flight. For species of the genus *Formica*, the main number of species (*F. cunicularia*, *F. fusca*, *F. sanguinea*, *F. rufibarbis*) flies earlier than in Central and Northern Europe, while others, on the contrary, later (*F. polyctena* - almost 50 days). Among the species of the genus *Lasius*, most have earlier dates of nuptial flight (*L. flavus*, *L. niger*, *L. umbratus*), some have later dates (*L. fuliginosus*). Among the genus *Myrmica*, we obtained averaged data, except for two species (*M. bergi*, *M. salina*). *Polyergus rufescens*, on average, also has an earlier nuptial flight (by 17 days, Table 1). At the same time, *Tetramorium caespitum* has a later term of nuptial flight (by 11 days). Based on this, it can be concluded that most ant species in Eastern Europe and Asia are characterized by earlier nuptial flight periods compared to Central and Northern Europe, and only some species fly later.

In most of the regions included in the study, significant climatic changes have occurred over the past 20 years (Figure 1A-B). So, if in the period 1980-2016 most of Ukraine and the entire west of Russia belonged to the Dfb climatic zone (Figure 1A), then after 2016 these territories move into the Dfa zone, and the southeastern part of Ukraine goes into the Bsk zone, corresponding to semi-deserts. The eastern (Asian) part of Russia is also undergoing significant changes - instead of the subarctic climate Dfc, Dfa, Dfb will dominate here. In Central Asia, the Bwk, Bsk zone will expand (Figure 1B). In connection with these significant climatic changes, one should expect significant shifts in the timing of the nuptial flight in ants, even within 10 years.

The investigated species can be conditionally divided into three clusters corresponding to different periods of the nuptial flight (Figure 2). The first cluster included 12 species of ants, the nuptial flight of which falls on autumn (Figure 3). The second cluster comprised half of all species (36) in which the nuptial flight was in summer, the third - 27 species with the spring period of nuptial flight. There are significant differences between the dates of the nuptial flight in the species from the three clusters (K-W: $P = 1.41E-37$, W: $F = 189.2$, $df = 66.42$, $P = 3.751E-28$). In species from the first cluster, nuptial flight are on average 63 days later than in species from the second (MW: $P = 1.96E-11$), and in species from the second cluster - 53 days later than in species from the third (MW: $P = 1,45E-28$). The difference between the species from the first and third clusters is thus 116 days (M-W: $P = 1.00E-14$) (Figure 3). Conventionally, the species from the first cluster can be attributed to the autumn, the second to the summer, the third to the spring. It can be expected that, in the event of sharp climatic changes in summer, for most ant species, the dates of nuptial flight will shift.

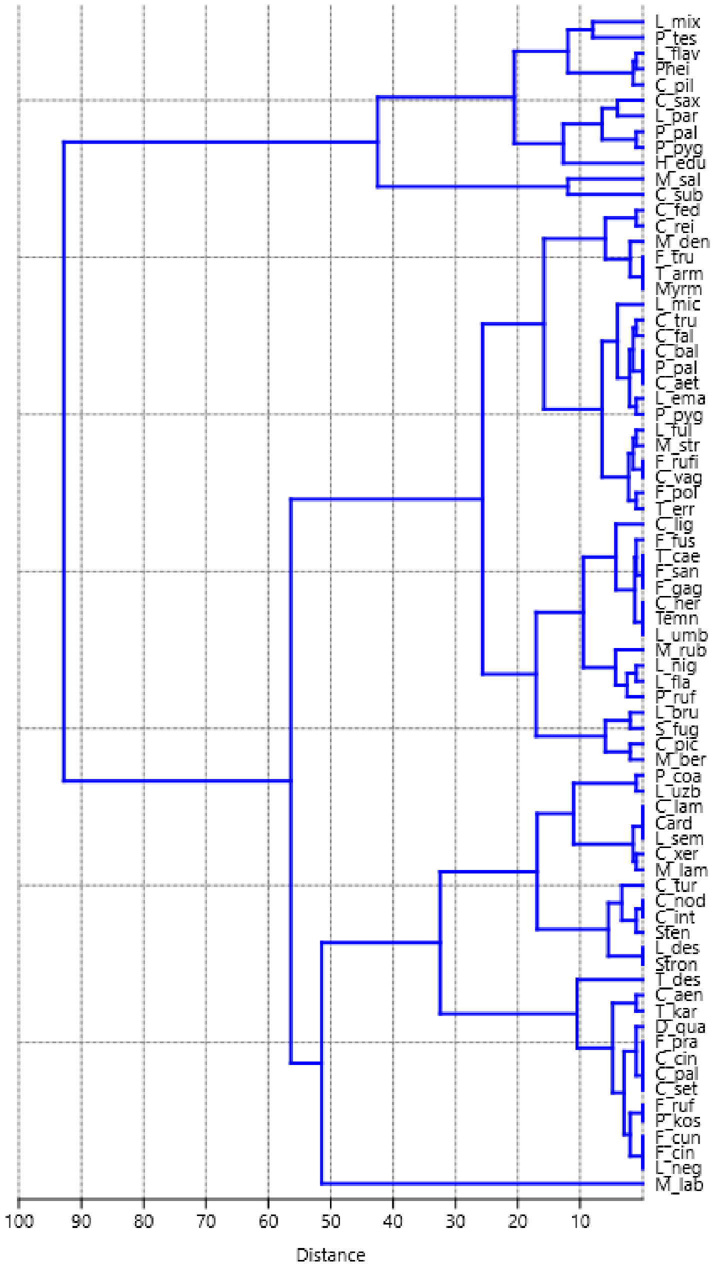

Figure 2. Results of cluster analysis of nuptial flight dates for all ant species (Similarity Index – Euclidean, Algorithm – Paired Group (UPGMA))

Note: C_aet - *Camponotus aethiops*; C_bal - *Camponotus baldaccii*; C_fal - *Camponotus fallax*; C_her - *Camponotus herculeanus*; C_fed - *amponotus fedtschenkoi*; C_int - *Camponotus interjectus*; C_lam - *Camponotus lameerei*; C_lig - *Camponotus ligniperda*; C_pic - *Camponotus piceus*; C_pil - *Camponotus pilicornis*; C_rei - *Camponotus reihardti*; C_sax - *Camponotus saxatilis*; C_tru - *Colobopsis truncata*; C_tur - *Camponotus turkestanicus*; C_vag - *Camponotus vagus*; C_xer - *Camponotus xerxes*; Card - *Cardiocondyla* sp.; C_aet - *Cataglyphis aenescens*; C_cin - *Cataglyphis cinnamomea*; C_nod - *Cataglyphis nodus*; C_pal - *Cataglyphis pallida*; C_set - *Cataglyphis setipes*; C_sub - *Crematogaster subdentata*; D_qua

- *Dolichoderus quadripunctatus*; F_cin - *Formica cinerea*; F_cun - *Formica cunicularia*; F_fus - *Formica fusca*; F_gag - *Formica gagatoides*; F_pol - *Formica polyctena*; F_pra - *Formica pratensis*; F_ruf - *Formica rufa*; F_rufi - *Formica rufibarbis*; F_san - *Formica sanguinea*; F_tru - *Formica truncorum*; H_edu - *Hypoponera eduardi*; L_bru - *Lasius brunneus*; L_ema - *Lasius emarginatus*; L_flav - *Lasius flavescens*; L_fla - *Lasius flavus*; L_ful - *Lasius fuliginosus*; L_mix - *Lasius mixtus*; L_neg - *Lasius neglectus*; L_nig - *Lasius niger*; L_par - *Lasius paralienus*; L_umb - *Lasius umbratus*; L_uzb - *Lasius uzbeki*; L_sem - *Lepisiota semenovi*; L_mic - *Liometopum microcephalum*; L_des - *Lioponera desertorum*; M_rub - *Manica rubida*; M_den - *Messor denticulatus*; M_lab - *Messor laboriosus*; M_lam - *Messor lamellicornis*; M_sp - *Messor* sp.(*muticus*); Myrm - *Myrmica sp.*; M_sal - *Myrmica salina*; M_ber - *Myrmica bergi*; P_kos - *Pheidole koshewnikovi*; Phei - *Pheidole sp.*; P_pal - *Plagiolepis pallescens*; P_pyg - *Plagiolepis pygmaea*; P_ruf - *Polyergus rufescens*; P_coa - *Ponera coarctata*; P_tes - *Ponera testacea*; S_fug - *Solenopsis fugax*; Sten - *Stenamma sp.*; Stro - *Strongylognathus sp.*; T_err - *Tapinoma erraticum*; T_kar - *Tapinoma karavaievi*; Temn - *Temnothorax sp.*; T_arm - *Tetramorium armatum*; T_cae - *Tetramorium caespitum*; T_des - *Trichomyrmex destructor*.

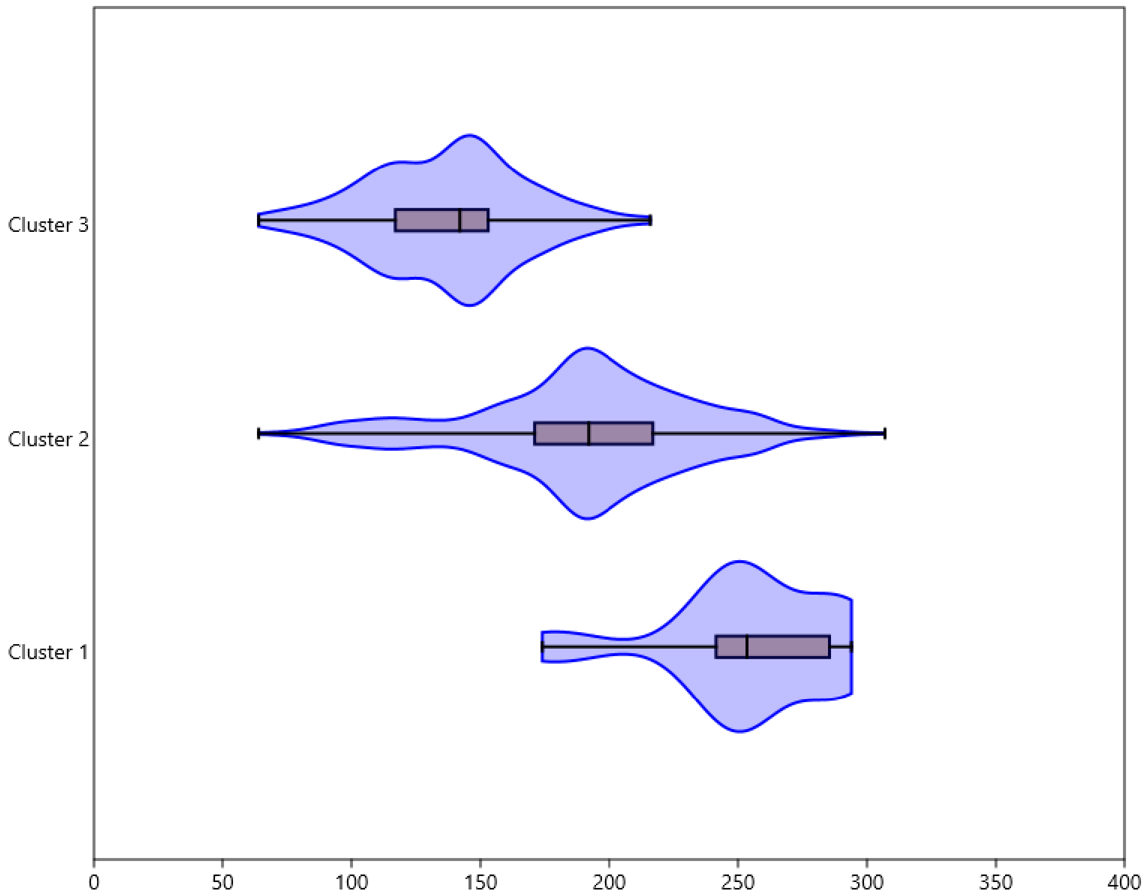

Figure 3. Mean and error of the mean (SE) for ant species grouped into three clusters

According to the results of the location of species by geographic points, the majority are assigned to those living in regions with a cold climate (41), 2 times less with a temperate (20), and arid (23) (Figure 4). Consequently, most ant species will be most affected by changes in cold climates. After climatic changes, most ant species in the study area will moved in a zone with a temperate climate (37), followed by arid (29) and cold (27) climatic zones (Figure 5).

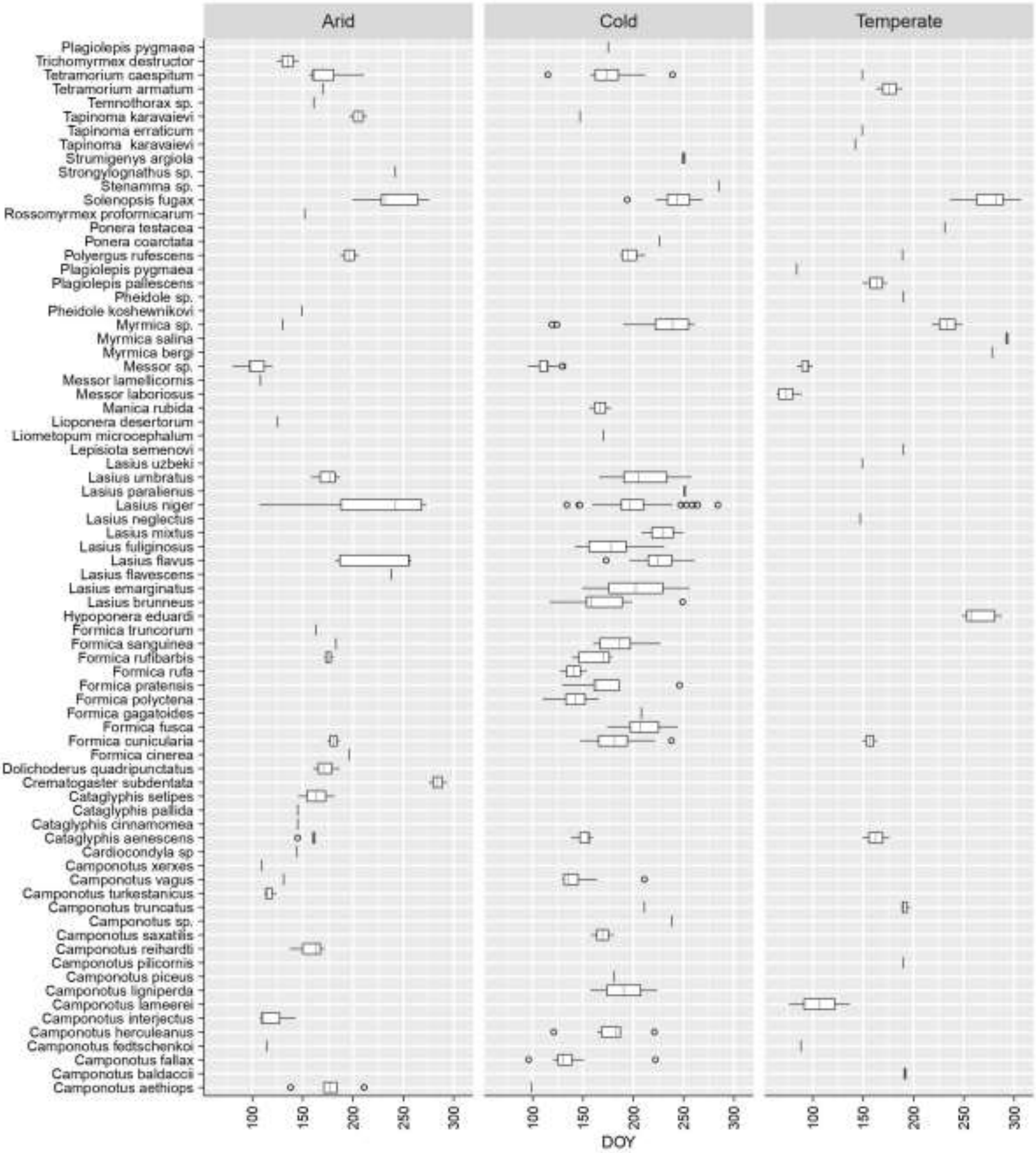

Figure 4. Distribution of all species of ants by phenology and by types of climate

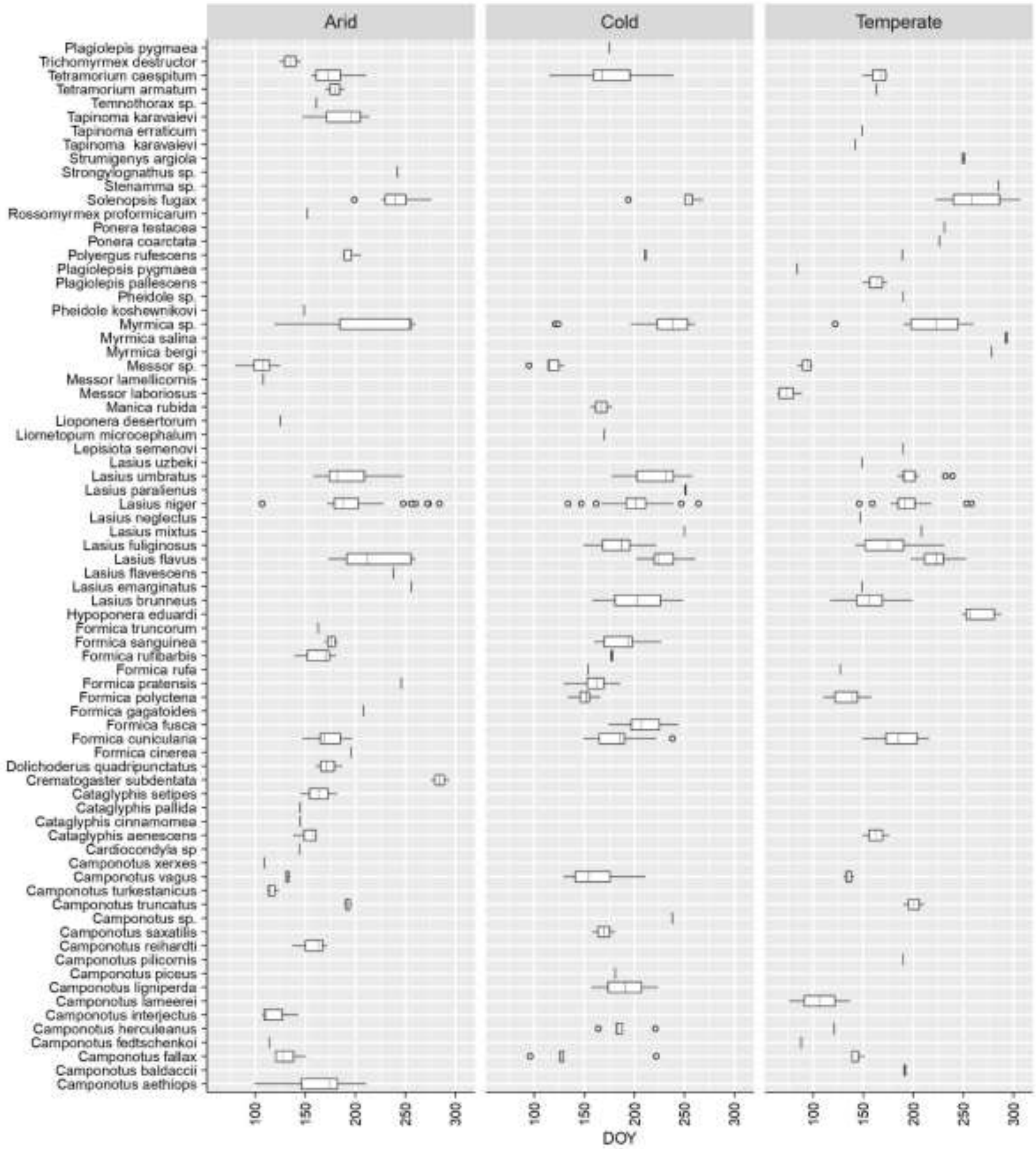

Figure 5. Expected distribution of all ant species by phenology and by climate types

The dates of nuptial flight in ant species also differ, depending on the climatic zone. So, in the arid zone there are practically no species in which nuptial flight in autumn (except *Crematogaster subdentata*), in summer there are nuptial flight in 16 species, and in spring in 8 species. In the temperate zone in autumn nuptial flight in 5 species, in summer in 11 species, and in the spring in 4 species. In the cold climatic zone, in the autumn nuptial flight in 5 species, in the summer in 28, and in the spring in 9 (Figure 6). During global warming, the following changes can be expected. In the arid zone, 0 species have nuptial flight in autumn, 20 species in summer, and 10 species in spring. In the temperate climatic zone, in the autumn, nuptial flight in 7 species, in the summer in 22, in the spring in 8 species. Finally, in the cold climatic zone, nuptial flight in autumn in 4 species, in spring in 3, and in summer in 20 (Figure 7). For most of the ant species that have passed from the cold climatic zone to the temperate one or from the temperate to the arid one, the main dates of the nuptial flight will not change, and will fall on the summer, and some of the spring species will move to this season. Regression analysis showed significant changes in the dates of mating summer for some ant species.

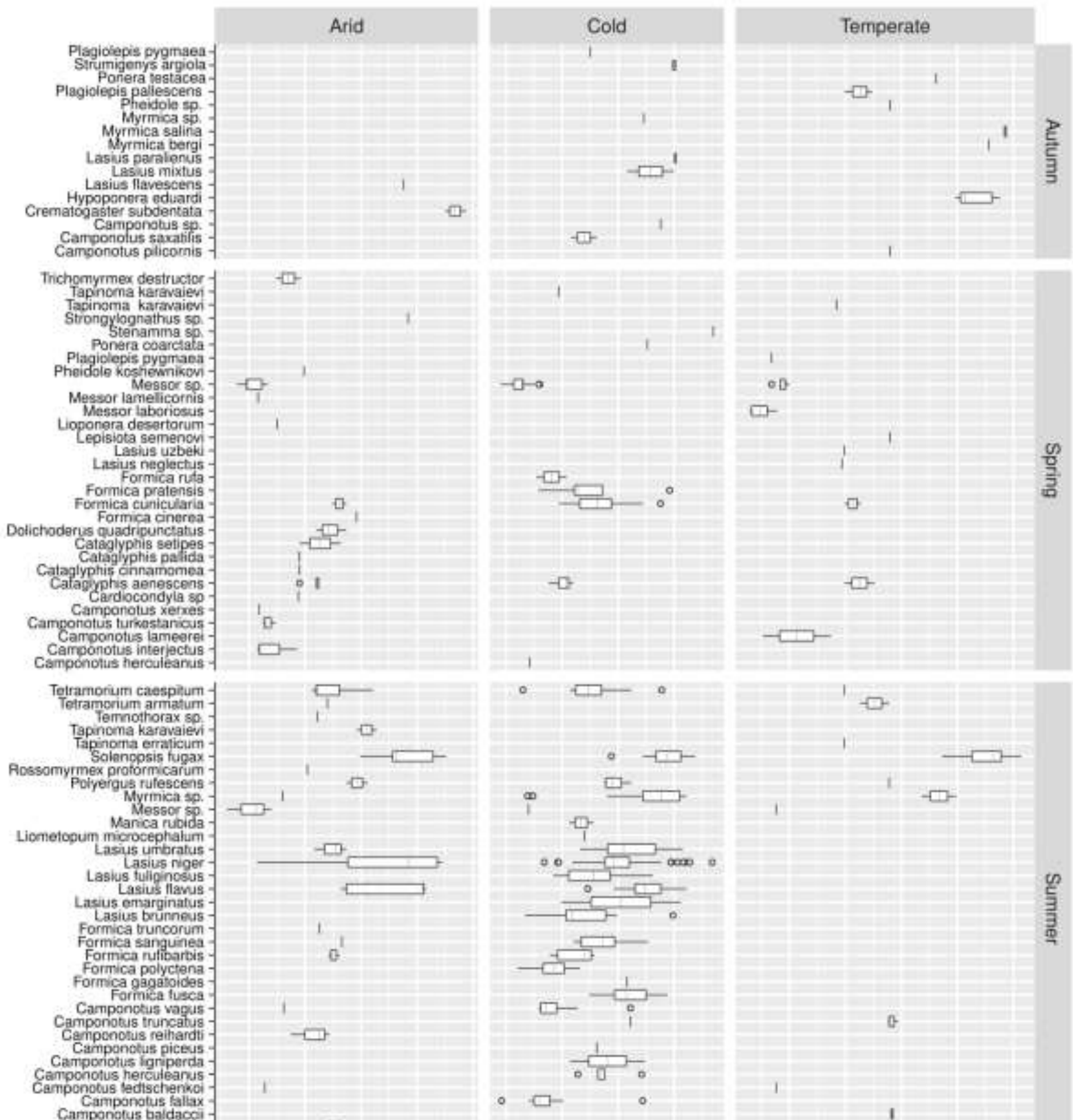

Figure 6. Distribution of ant species depending on the climatic zone and the season

Figure 7. Expected distribution of ant species depending on the climatic zone and season in the future

Nuptial Flight Date Time Trends

In a cold climate, significant changes, towards earlier dates, were recorded in the phenology of nuptial flight for two species: *Lasius flavus* (*P<0.05*) and *Polyergus rufescens* (*P<0.01*) (Figure 8). The corresponding rates of change are 3.9 and 6.25 days per year. In other types of climate, no significant changes in the phenology of the nuptial flight were found. Nevertheless, taking into account the boundaries of future climatic zones in temperate and arid zones, such changes were recorded for several species. Thus, *Solenopsis fugax* in a temperate climate demonstrates a tendency for nuptial flight delay (Figure 9) at a rate of 6 days per year (*P<0.05*). Within the predicted boundaries of the arid climate, the nuptial flight phenology delay was recorded for

Lasius niger (5.8 days per year; *P<0.01*) and *Messor* spp. (4.4 days per year; *P<0.05*; Figure 10). At the same time, in *Polyergus rufescens*, there is a tendency to an earlier nuptial flight at a rate of 8 days per year (*P<0.05*).

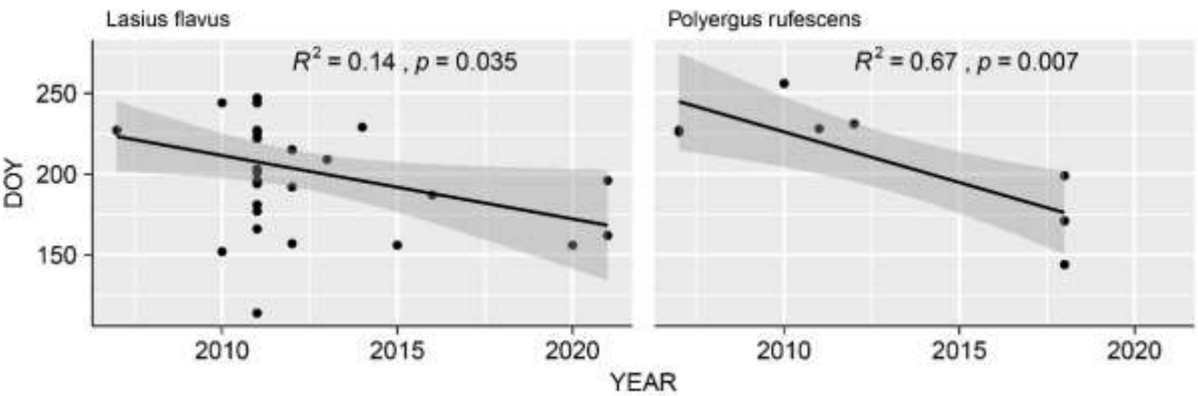

Figure 8. Advancement of flight phenology in *Lasius flavus* and *Polyergus rufescens* in cold climate. DOY is the day of the year. 0.95 confidence interval is shadowed

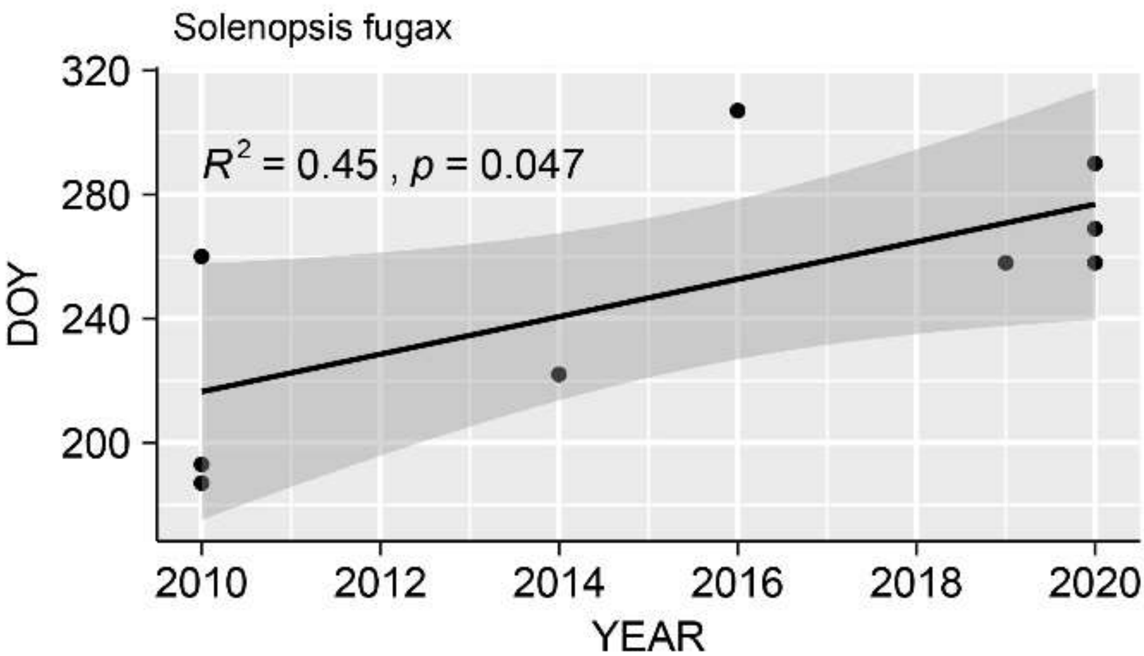

Figure 9. Delayed flight phenology in *Solenopsis fugax* in future boundaries of temperate climate zone. DOY is the day of the year. 0.95 confidence interval is shadowed

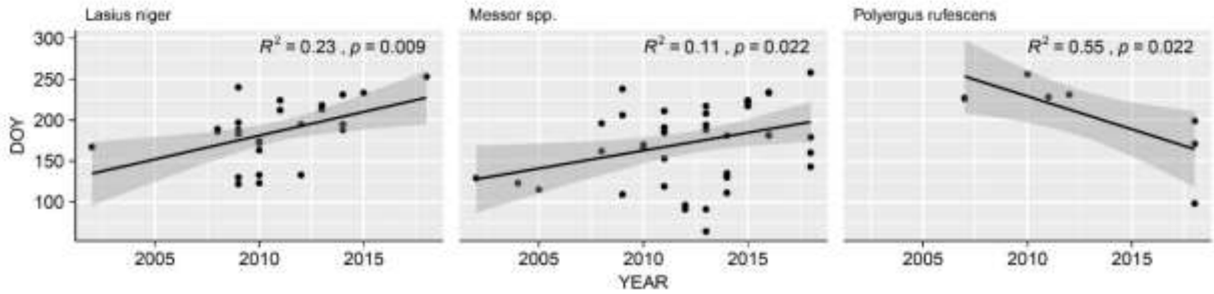

Figure 10. Delayed flight phenology in *Lasius niger* and *Messor* spp. and advancement of flight phenology in *Polyergus rufescens* in future boundaries of arid climate zone. DOY is the day of the year 0.95 confidence interval is shadowed

In Figure 10 shows the extreme and average temperatures recorded for 19 species of ants in the cold climatic zone. The average values up to 20°C include only 1 species (*Formica polyctena*), which has early summer (Table 1; Figure 5). In the majority of species, nuptial flight occurs at a temperature of 20-25°C (12 species), in the remaining 6 - at values from 26°C. The latter category mainly includes species of the steppe zone (*Polyergus rufescens*, *Cataglyphis aenescens*, *Colobopsis truncata*, *Formica rufibarbis*). In addition, the same group includes *Lasius niger*, *Formica fusca*. The range of temperatures in most species falls on 15-30°C, only in *Cataglyphis aenescens* the maximum values can fall at 42°C (Figure 11). Significant differences in preferred temperatures between species were obtained (K-W: P = 3.841E-11; W: F = 5.825, df = 58.82, P = 6.045E-08). Thus, *Myrmica* sp. in the cold climate zone (Myrm_c) prefers lower air temperatures compared to *L. niger* (MW: P = 0.0004565), *L. umbratus* (MW: P = 0.006601), *S. fugax* (MW: P = 0.0004705), *T. caespitum* (MW: P = 0.0003037). *L. niger*, on average, prefers higher air temperatures than *L. fuliginosus* (M-W: P = 0.00616). *L. niger*, *L. umbratus* have no significant difference in temperature preferences, which indicates their relationship with each other (M-W: P = 0.6122). Among species whose nuptial flight occurs mainly in spring, *C. vagus* prefers higher air temperatures than *F. polyctena* (M-W: P = 0.02803). In species with a summer period of nuptial flight, *F. fusca* prefers maximum temperatures, higher than that of *F. cunicularia* (M-W: P = 0.03338).

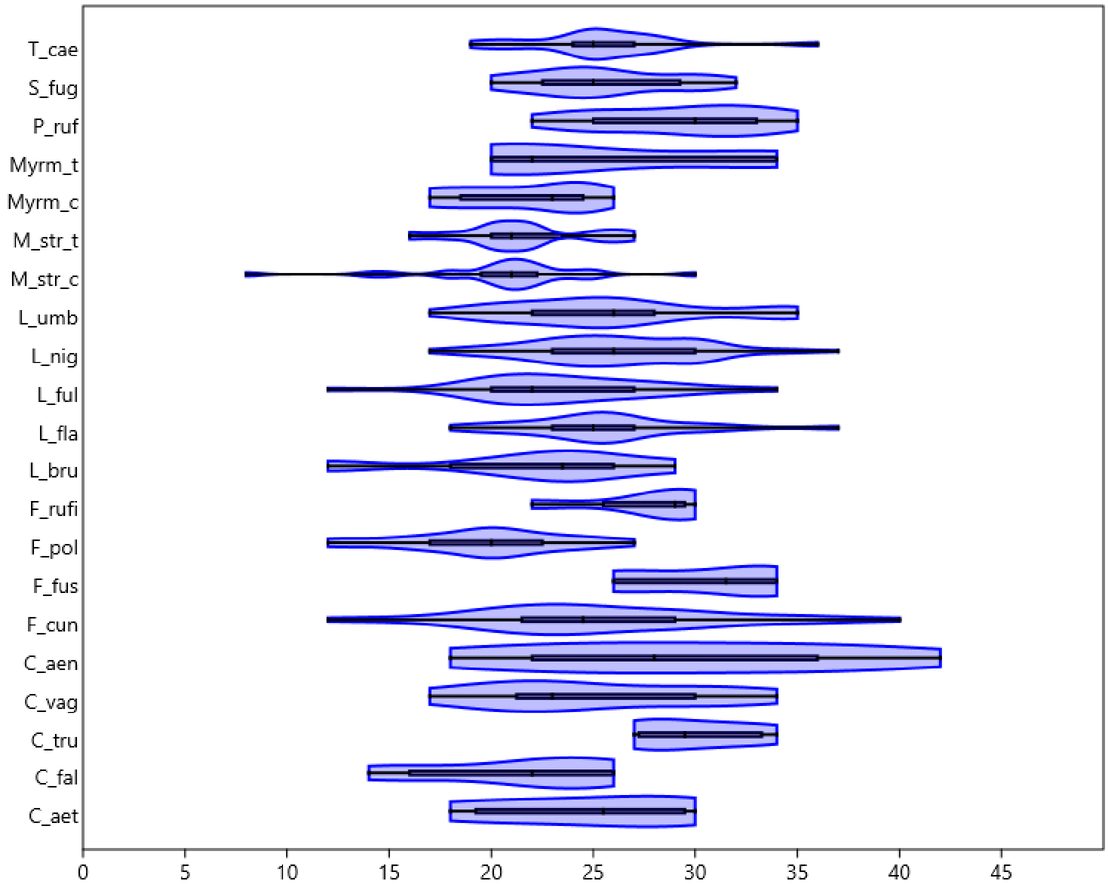

Figure 11. Temperature preferences during nuptial flight in 19 ant species for the cold climate zone (n = 416)

When comparing the time of day when the nuptial flight occurs, we found that different species of ants may prefer different times of the day for nuptial flight (Figure 12). Species of the genus *Camponotus* prefer the second half of the day or even night and twilight (except for *C. vagus*, *C. piceus*), while in most species of the genus *Formica*, nuptial flight occurs in the first half of the day (except for *F. fusca*). The same feature is observed in *T. caespitum*. Species of the genus *Lasius* prefer the second half of the day (period 15-17 hours, except for *L. brunneus*, *L. emarginatus*).

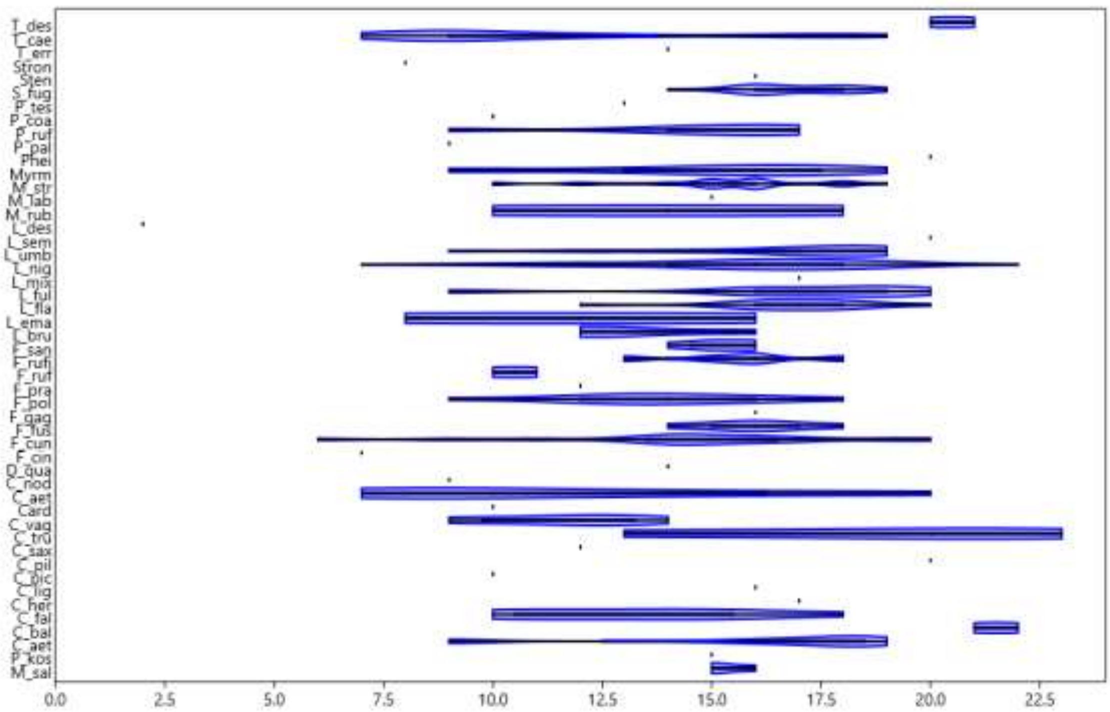

Figure 12. Nuptial flight (local time, hours) in 49 ant species (n = 403)

Mantel Test Results

For none of the studied species in the Mantel test, the alternative hypothesis was not confirmed, i.e. no connection was found between the date of nuptial flight and the distance between populations (or locations).

The Length of the Nuptial Flight

It has been established that nuptial flight can occur in some ant species with one peak (*L. niger*, *L. umbratus*, *F. fusca*, *F. polyctena*, *F. cunicularia*), while other species have several more or less pronounced peaks during the year (*C. fallax*, *C. vagus*, *T. caespitum*, *S. fugax*, *L. fuliginosus*) (Figure 13).

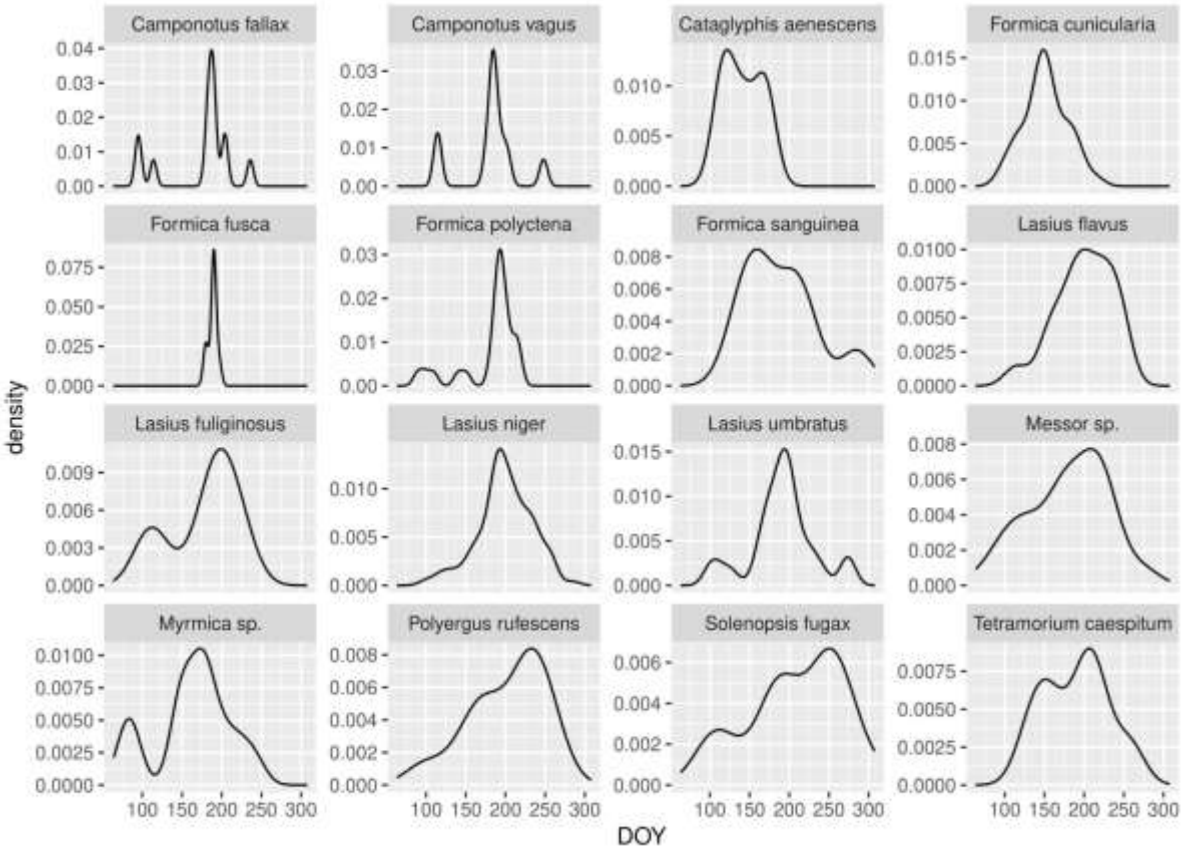

Figure 13. The length of the nuptial flight during the year

DISCUSSION

The data we obtained allowed us to establish that on the territory of Eastern Europe (Ukraine, Moldova, the European part of Russia) and Asia (the Asian region of Russia, Uzbekistan, Kazakhstan and other countries), nuptial flight in most ant species occurs on average for at least 2 weeks earlier than the known data for Central and Northern Europe (Seifert 2018). This may be due to the fact that the more east the region is in Eurasia, the more the effect of the continental climate is manifested. If in North America January temperatures are in the range of -28 -30°C, with a minimum of -50°C, then for Eurasia, in the taiga zone (Yakutsk), the same values are -40 -50°C, with a minimum of -70°C (Oymyakon). Air masses, moving from west to east, lose some of the moisture; in addition, Arctic air masses dominate in northern Asia. All these factors determine the large differences in temperature compared to Europe, even during the day. If the maritime climate prevails in Western Europe, then the temperate continental climate is characteristic of the European part of Russia and Ukraine, and the sharply continental climate is characteristic for Eastern Siberia. In this regard, in the inner regions of Eurasia, significant areas belong to deserts and semi-deserts. Global warming, which has increased significantly over the past decade, has further exacerbated temperature fluctuations, and also determined a trend towards a steady increase in temperature. The latter is unevenly manifested in different regions. It is known that in the Arctic zone, the rate of temperature increase occurs twice as fast as in other regions (Post et al. 2019).

The last 6 years of observations accounted for the highest air temperatures, and in Russia the air temperature already in 2020 was on average 3.22°C above the norm. For the period 1976-2019, the rate of increase in air temperature in Russia was 0.47°C every 10 years, which is 2.5 times faster than the increase in global temperature (greenpeace.ru website data). In Ukraine, in the period 2011-2019 the average annual temperature was above the norm by 1.8°C, and in 2019 it was already 2.7°C above, which is a sign of faster changes compared to other regions. In the countries of Central Asia, even greater aridization of the climate should be expected. The result of these global climate changes is the same - an earlier onset of a period of high temperatures. Consequently, the timing of the nuptial flight season in ants will also shift either to spring time or vice versa, to autumn. The spring shift may also be associated with an earlier development of the brood, when winged queens and males will appear earlier.

We have obtained results for some species (*Lasius flavus*, *Polyergus rufescens*) confirming the shift of the nuptial flight season to an earlier time: 3-6 days per year. For other species, on the contrary, there is a tendency to shift to later dates (*Solenopsis fugax*, *Lasius niger*, *Messor* sp.), 4-6 days per year. These shifts may be correlated with favorable climatic conditions, as well as with the timing of the breeding of winged females and males (alates). For other ant species, no such trends have been established, which may be due to insufficient of data.

Consequently, in the cold climate zone one should expect the most rapid changes in the phenology of plants and animals living here. Rapid climatic changes also affected the dates of nuptial flight in ants, which, on average, fly earlier in the studied territory for a period of two weeks or more. In addition to the cold climate, these shifts also occurred in the ant species living in the arid climate zone, since the temperature values here increased even more, and the optimum zone in most species narrowed, moving to an earlier date. Apparently, this is due to the fact that an early increase in temperature determines the achievement of values that are optimal for the nuptial flight. In arid areas, a kind of adaptation of ants to dry conditions is the reduction of their wings (Tinaut & Heinze 1992). In species of ants with the spring development of the brood of alates (*Formica*), an increase in temperature every year will determine its more rapid development, and an earlier achievement of the adult state by males and females. Air temperature is one of the main factors determining the probability of nuptial flight in ants, as was shown by the example of *Manica rubida* (Depa 2006). *Leptothorax acervorum* is characterized by preferences at 20-22°C (Franks et al. 1991); in a number of species studied by us, the temperature optimum is wider. For leaf-cutting ants, the temperature optimum is between 26-32°C, that is, wider (Staab & Kleineidam 2014).

The size of the winged queens can also be important - the larger queens of *L. flavus, L. niger* prefer higher air temperatures compared to *Myrmica*, since they are easier to fly (Boomsma & Leusink 1981). This has been confirmed by us for some other species, for example, *C. vagus*, *F. polyctena*; *L. fuliginosus*, *L. niger*. Some species, such as *Cataglyphis aenescens*, prefer high air temperatures; this is also known for other species, for example, *Camponotus detritus* (Curtis 1985).

We have confirmed the data on similar or coinciding terms of nuptial flight in host species and their parasites, for example, *L. niger* and *L. umbratus*, *L. platythorax* and *L. umbratus* (Dekoninck et al. 2004; Dunn et al. 2007). Moreover, phylogenetically close species also have similar terms of nuptial flight, which is also confirmed by us. The species from arid regions (Uzbekistan, Kazakhstan) examined by us, on the whole, have the same dates as from the literature data (Marikovsky 1979; Tarbinsky 1976). The exception was *Camponotus interjectus*, the timing of which shifted by 1 month in comparison with the data of Dlussky (Dlussky 1988; Dlussky et al. 1990).

We have also shown that in the case of coincidence of favorable weather conditions for several species of ants (from different genera), nuptial flight can occur at different times of the day. The nuptial flight is usually associated with warm weather and pre-precipitation, as has been shown for *Solenopsis invicta* (Tschinkel 1998), as well as for *Messor barbarus* (Gómez & Abril 2007). For the latter species, the average distance at which the nuptial flight took place at the same time was 637 km, with a maximum of 1075 km, that is, nuptial flight can occur at fairly significant distances. Our data confirmed this statement - in a number of cases, the nuptial flight of *L. niger*, *L. umbratus* took place simultaneously in Moscow and St. Petersburg.

The nuptial flight can occur twice a year, for example, in autumn and spring, under the same temperature conditions (Woyciechowski 1987). In addition, we have established that in one or several closely related ant species (*L. niger*, *L. umbratus*) nuptial flight can occur simultaneously, over long distances. Finally, the time of day can play a significant role - for example, in many representatives of the genus *Formica*, nuptial flight occurs in the morning (with the exception of *F. rufa*, *F. pratensis*) (Ayre 1957; Ito & Imamura 1974; Kannowski 1959; Ueda & Komatsu 2014). In the tropics, the nuptial flight in many ant species are shifted to the dawn and pre-dawn hours (Torres et al. 2001); in nocturnal ant species, queens and males have a greater number of ommatidia compared to diurnal species, as was shown in leaf cutter ants (Moser et al. 2004). Nuptial flight in temperate latitudes can occur almost continuously, for at least a month (*Myrmica rubra*, *M. scabrinodis* - Woyciechowski 1987; *Formica rufa*, *F. polyctena*, *F. lugubris*, *F. pratensis* - Klimetzek & Faas 1994), with more or fewer winged alates, or for shorter periods (*Myrmica lobicornis*, *Leptothorax nigriceps*) (Woyciechowski 1987).

The use of the Internet and media resources as a source of information about the nuptial flight has already been carried out earlier (Hart et al. 2018). The authors were able to collect a database for a 3-year period, including more than 16 thousand observations in the UK (of which more than 13 thousand were included in the sample), 88.5% of which were *L. niger*. The authors found that the determining factors for the beginning of the nuptial flight are the air temperature, as well as the wind speed (positive and negative dependences), in comparison with the values of atmospheric pressure. These patterns were also established for fire ants, *Solenopsis invicta* (Milio et al. 1998). In addition, for the beginning of the nuptial flight, higher humidity and lower insolation are of great importance compared to days without nuptial flight (Nene et al. 2016).

In conclusion, Hart et al. (2018) point out that for *L. niger* the spatio-temporal synchronization of flights is lower than previously thought, and the local temperature and wind speed are critical, since ants may have at least a limited ability to predict weather, due to which they can adjust their behavior (Hart et al. 2018). In the conditions of Eurasia, when zones of cyclones and anticyclones can occupy significant areas, this rule, most likely, does not work, since we have recorded a simultaneous nuptial flight in large territories. An interesting observation is that, in urban conditions, the formation of alates imago occurs earlier than in the surrounding rural regions (Hart et al. 2018).

We have established the presence of nuptial flight in the invasive species *Lasius neglectus* on the territory of its primary range (Uzbekistan, Stukalyuk et al. 2020; 2021). This confirms the experimental data obtained by Espadaler & Rey (2001), which established the possibility of independent founding of new colonies of this species, although previously only intra-nest mating in *L. neglectus* was known.

Intra-nesting mating is associated with the transition to polygyny; on the other hand, large queens with developed wing musculature participate in a full-fledged nuptial flight. During the transition in polygyny, the musculature of the wings is weakened, as a result of which the transition to intra-nest mating occurs (Seifert 2010). This pattern is illustrated by the example of *S. invicta*, in which queens from polygynous colonies did not move more than a few hundred meters from the maternal colony (Goodisman et al. 2000). The bulk of the species studied by us found nests independently (most species of the genus *Formica*, all *Camponotus*, *Messor*, some species of the genus *Lasius*), however, the formation of large swarms during the nuptial flight was recorded only in some of them (*Lasius niger*, *L. flavus*). It is known from the literature that swarms form *L. niger*, *Stenamma debile*, *Myrmica rubra*, *M. ruginodis*, *Temnothorax nylanderi*, but not *L. umbratus* (Noordijk et al. 2008). At the same time, after the nuptial flight, we noted significant numbers of *L. umbratus* queens that flew around.

CONCLUSIONS

In this work, the authors managed to establish the features of the spatial distribution of ant species that have a massive nuptial flight that occur simultaneously at large distances. In addition, we have established a significant shift to earlier dates (from two weeks or more) in the dates of the nuptial flight in the period 2006-2021. Compared to the data from Central and Northern Europe, the shift exists initially (also for a period of two weeks), which is associated with a more pronounced continental climate. For a number of species, data are presented for the first time on the dates of the nuptial flight, as well as on preferences in time of day and in temperature values.

ACKNOWLEDGEMENTS

The article is dedicated to the memory of Professor Yu. G. Verves (Kyiv, Institute for Evolutionary Ecology, National Academy of Sciences of Ukraine). The research leading to this publication has received funding from “The support of the priority research areas development of Ukraine, KPKVK 6541230.”

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