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Migrant dragonfly *Pantala flavescens* (Fabricius, 1798) (Odonata, Libellulidae) in western Russia and different migration cycles in the western Palearctic

Стрекоза-мигрант *Pantala flavescens* (Fabricius, 1798) (Odonata, Libellulidae) на западе России и разные циклы миграций в западной Палеарктике

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Key words: *Pantala flavescens,* migrations, annual cycles, migrations zones, western Russia, Europe, Mediterranean.

Ключевые слова: *Pantala flavescens*, миграции, годичные циклы, зоны миграций, запад России, Европа, Средиземноморье.

Abstract. Data are provided on the distribution and phenology of the migrant dragonfly *Pantala flavescens* (Fabricius, 1798) in the western part of Russia. The northernmost point of the range is located in the vicinity of Moscow, the easternmost is in Astrakhan'. Analysis of the phenology of immigrants and residents shows that in the western Palearctic *P. flavescens* has two migration zones that differ in annual cycles. The «Eurasian migration zone» includes most of the continental Europe (excluding the southern part of the Iberian Peninsula), southern Russia and Turkey. Immigrants arrive there in April–May, presumably from the southern regions of South–West Asia. The summer generation appears at the end of June–September. The «Mediterranean migration zone» covers the south of the Iberian Peninsula and the Mediterranean islands (Pelagic, Sicily, Malta and Cyprus). Immigrants of *P. flavescens* arrive here mainly in July–August, presumably from Europe. These are individuals of the European summer generation. Egg laying occurs before the end of the year, and the local generation emerged in October–January. Colonization of the territories of Europe, southern Russia and Turkey by the species has been observed since the end of the last century and is apparently associated with general climatic warming.

Резюме. Приводятся данные о распространении и фенологии стрекозы-мигранта *Pantala flavescens* (Fabricius, 1798) в западной части России. Самая северная точка ареала находится в окрестностях Москвы, самая восточная — в Астрахани. Анализ фенологии иммигрантов и резидентов показывает, что на западе Палеарктики у *P. flavescens* существуют две отличающиеся годичными циклами зоны миграций. В «евроазиатскую миграционную зону» входит большая часть континентальной Европы (без южной части Пиренейского полуострова), юг России и Турция. Сюда иммигранты прилетают в апреле–мае предположительно из южных регионов Юго-Западной Азии. Летнее поколение появляется в конце июня–сентябре. «Средиземноморская миграционная зона» охватывает юг Пиренейского полуострова и средиземноморские острова (Пелагические, Сицилия, Мальта и Кипр). Сюда иммигранты *P. flavescens* прилетают преимущественно в июле–августе, предположительно, из Европы. Это особи летнего европейского поколения. Яйцекладка происходит до конца года, а выплод местного поколения — в октябре–январе. Колонизация видом территории Европы, юга России и Турции наблюдается с конца прошлого века и, по-видимому, связана с общим климатическим потеплением.

Introduction

The dragonfly *Pantala flavescens* (Fabricius, 1798) can be considered one of the most famous migrants in the insect world. A study of migrations using the isotope method showed that among migrant insects, *P. flavescens* is the record holder for flight distance and is able to overcome oceans [Hobson et al., 2012, 2021; Cao et al., 2018; Borisov et al., 2020]. It has also been established that on all continents there are individuals with «isotopic signatures» unusual for a given territory, that is, immigrants, which is isotopic evidence of the migrations of *P. flavescens* throughout its entire range [Ware et al., 2022].

Due to its migratory strategy, *P. flavescens* has the most extensive cosmopolitan range among dragonflies. He spans all continents (except Antarctica) and extends over 100 degrees of latitude on either side of the equator [Kalkman, Monnerat, 2015; Ware et al., 2022; iNaturalist, 2024, https://www.inaturalist.org/taxa/108344-Pantala-flavescens].

However, having extraordinary migration abilities [Anderson, 2009; Hedlung et al., 2021; Ware et al., 2022; Liao et al., 2023; Ranjan et al., 2023], *P. flavescens* began to colonize continental Europe only at the end of the last century [Kalkman, Monnerat, 2015]. The same applies to the southern part of Russia. It is known that in Azerbaijan (Lenkoran') this species was recorded back in 1901 [Akramowski, 1964], but in the south of Russia (Sochi) it was recorded only in 1987 [Kalkman, Monnerat, 2015]. Since the beginning of the new century, findings of *P. flavescens* in Europe have become significantly more frequent [Lester, 2005; Ober, 2008; Finkenzeller, 2010; De Knijf, 2015; Kalkman, Monnerat,

2015; Corso et al., 2017; Buczyński et al., 2019; Piretta, Assandri, 2019; Sánchez et al., 2024]. Currently, this species has significantly moved north and reached the coast of the Baltic Sea [Buczyński et al., 2014, 2019; Jusys et al., 2019] and the latitude of Moscow [Onishko, Kosterin, 2021]. The development of the summer (European) generation of these dragonflies has been established in Switzerland [Henseler et al., 2019], Germany [Günther, 2019b], Poland [Lewandowska et al., 2020; Michalczuk, Buczyński, 2021], Belarus [Observation, 2024 (178642613)], in the Kaliningradskaya Oblast [Shapoval et al., 2022] and in the Moskovskaya Oblast [Onishko, Kosterin, 2021].

To date, the seasonal migrations of *P. flavescens* in the tropical part of its range, associated with the alternation of dry and wet periods here, are well known [Corbet, 1999; Anderson, 2009; Hobson et al., 2012, 2021; Hedlung et al., 2021]. It is known that dragonflies use the prevailing seasonal winds associated with weather fronts in the Intertropical convergence zone (ITCZ) for migration. At the same time, not only favorable tailwinds for migration exist in the ITCZ, but also ephemeral fresh water bodies appear, due to monsoon rains, which serve as the main habitats for larvae of this species [Corbet, 1999; Holland et al., 2006; May, 2013].

The migrations of *P. flavescens* in temperate latitudes are less well known. Winter development of these dragonflies is impossible there, since the larvae are not able to tolerate low temperatures [Ichikawa et al., 2017]. In spring, they fly there from tropical and subtropical parts of their range to breed. The development of the summer «temperate» generation occurs in approximately two months. In autumn, dragonflies of this generation (descendants of immigrants) presumably migrate to the original «warm» part of the range. Such a migration strategy is known for *P. flavescens* in eastern Asia [Feng et al., 2006; Cao et al, 2018; Borisov, Malikova, 2019], in Middle Asia [Borisov, 2012, 2015; Borisov, Borisov, 2019; Borisov et al., 2020] and in North America [Corbet, 1999; Srygley, 2003; May, Matthews, 2008, 2023; May, 2013], and at the southern limits of its range in Australia [Hawking, Ingram, 1994].

In Russia, *P. flavescens* is known in the western and eastern regions. In the east, this species is distributed from Transbaikalia [Selys-Longchmps, 1887; Kosterin et al., 2004] to the Kuril Islands and Kamchatka [Borisov, Malikova, 2019]. In the European part of its range, it was found no farther east than Astrakhan' [Onishko, Kosterin, 2021].

The purpose of our work is to summarize the available information on the distribution and phenology of *P. flavescens* in the western part of Russia and to figure out the features of the migration cycles of these dragonflies in Europe, in south Russia and the Mediterranean.

Material and methods

When summarizing information about the distribution and phenology of *P. flavescens* in western Russia, along with literary sources, extensive data from the iNaturalist Internet platform was used [2024]. The «research grade» (confirmed by other users) iNaturalist observations are adopted by Global Biodiversity Informational Facility (GBIF) and are traditionally referenced in scientific literature as a whole (with a single DOI index) as iNaturalist contributors, iNaturalist [2024]. All photographic observations in iNaturalist [2024] are georeferenced in the form of decimal degree coordinates, which we report in degrees, minutes and seconds. Hyperlinks to specific observations look like http://inaturalist.org/observations/xxxx, where xxxx is the unique identification number of the observation, which we indicate in parentheses. For convenience and orderliness of the presented materials, the locations of *P. flavescens*, which are located close to each other, are combined and designated as one locality. Locations in southern Russia (locs 4–21) are shown on the map (Fig. 1). The map was prepared using the MapCreator 3 program.

When analyzing the phenology of *P. flavescens* in Europe and the Mediterranean, Observations [2024] data were also used. Hyperlinks to specific observations look like https://observation.org/observation/xxxx, where xxxx is the unique identification number of the observation, which we indicate in parentheses.

Where possible, the physiological state of dragonflies is indicated according to Corbet [1999]: «teneral» — insects with chitinous cover yet completely harden after emergence and poorly developed coloring (this condition typically lasts for at least 24 hours after emergence) and «post-teneral» — insects with chitinous cover that has already hardened, but still with «fresh» sparkly wings and yellow coloring (without red) on the body, reflecting the relatively recent emergence.

When studying seasonal translatitudinal migrations of dragonflies, it is necessary to distinguish between individuals of different generations. These are «immigrants» who flew to a certain region from elsewhere to reproduce and «residents» (descendants of immigrants) whose development took place in this region. To clarify the characteristics of the migration cycles of *P. flavescens* in different regions, we consider the phenology of immigrants and residents in southern Russia, Central and Eastern Europe and the Mediterranean regions.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:DD781252-334E-4979-ADD0-E669A08F035A

Results

List of localities of *Pantala flavescens* in western Russia

Kaliningradskaya Oblast

Loc.1. [Shapoval et al., 2022]: Zelenogradsk District, Courish Spit, Fringilla field station, bird trap, 55°05'17" N, 20°44'04" E, 29.V.2013 (1♂), 6.VI.2019 (1♀) 18.VIII.2019 (1♀, teneral) (Fig. 2), A.P. Shapoval. ***Notes*:** For the findings of *P. flavescens* at the Fringila biological station in 2013, see also Buczyński et al. [2014], Shapoval, Shapoval [2017].

Moskovskaya Oblast

Loc.2. [iNaturalist, 2024 (67407112)]: Moskovskaya Oblast, Odintsovskii urban district, 55°42'11" N, 36°43'43" E,

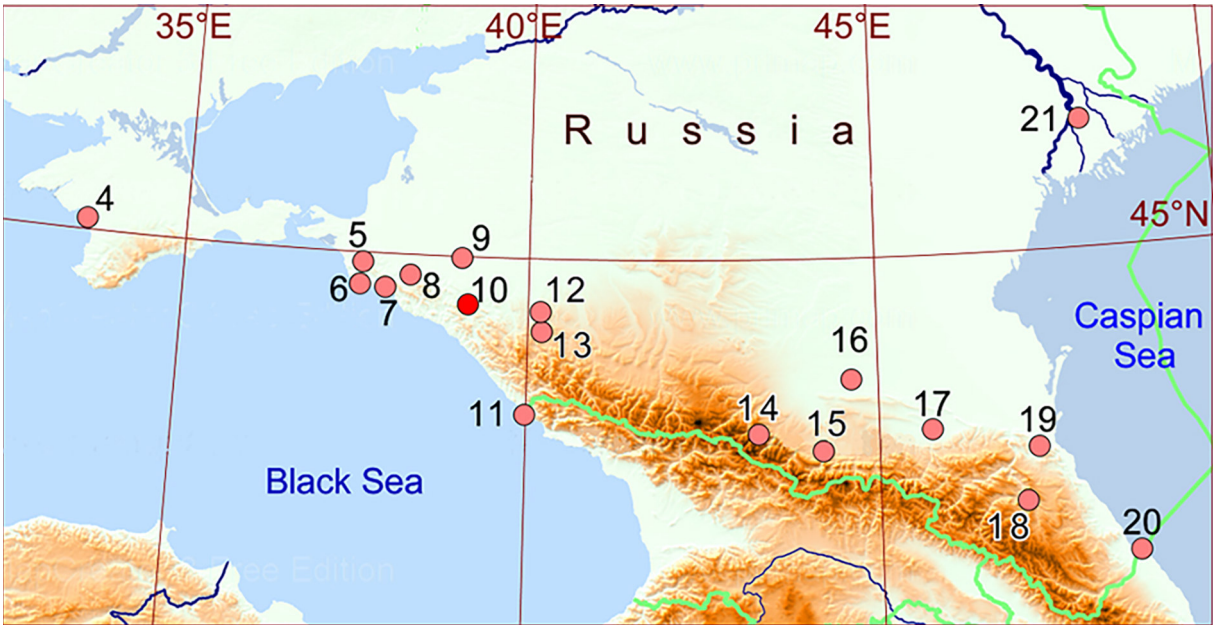


Fig. 1. Distribution map of the *Pantala flavescens* in southern Russia. The locality numbers correspond to those in the list of localities in the text.
Рис. 1. Карта распространения *Pantala flavescens* на юге России. Номера локалитетов соответствуют таковым в тексте.

31.VIII.2020, photo of a male (teneral) of *P. flavescens*, V. Onishko (Fig. 3). ***Notes*:** This finding was published as follows: Onishko, Kosterin [2021]: «On August 31, 2020, a young male was caught by V. Onishko on the bank of the Moscow River near the Zvenigorod biological station of Moscow State University.»

Loc.3. [Skvortsov, 2010: 594]: «Mos: Lytkarino near Moskow!?» data by S.V. Kotachkov (ca. 55°34' N, 37°53' E). *Notes*: The author himself [Skvortsov, 2010], due to the lack of factual material, cited this findind with a question mark. The reliability of the data presented is also questioned by other authors [Buczyński et al., 2014; Kalkman, Monnerat, 2015].

Crimea

Loc.4. [iNaturalist, 2024 (67452679)]: Saki city, Lake Saki, 45°07'01" N, 33°32'06" E, 15.VIII.2020, photo of a female (post-teneral) of *P. flavescens*, I. Voinov. **Loc.4a.** [iNaturalist, 2024 (67452684)]: Saki city, Lake Saki, 45°06'46" N, 33°32'27" E, 15.VIII.2020, photo of a male (post-teneral) of *P. flavescens*, I. Voinov.

Krasnodarskii Krai

Loc.5. [Kosterin, Solovyev, 2017]: South-east of the village of Natukhaevskaya, 44°54'03–24" N, 37°34'47"–35'58" E, 3–5.VIII.2015, several individuals of *P. flavescens* were observed.

Loc.6. [iNaturalist, 2024 (110671615)]: Novorossiysk Municipality, a road through Juniper stand at a S coastal slope 1.5 km W Dyurso village, 44°40'55" N, 37°32'31" E, 20.VII.2017, photo of a female of *P. flavescens*, O. Kosterin. ***Notes*:** This finding was published as follows: [Kosterin, 2017; Kosterin, Borisov, 2018]: 1.5 km west of the village of Durso, 44°40'55" N, 37°32'31" E, 20–21.VII.2017, individuals of *P. flavescens* have been observed, often together with *Anax ephippiger* (Burmeister, 1839). **Loc.6a.** [Kosterin, 2017]: Durso village, 44°40'44" N, 37°33'36" E, 22.VII.2017, individuals of *P. flavescens* patrolled the street in the village.

Loc.7. [iNaturalist, 2024 (103417489)]: Kabardinka village, 44°39'31" N, 37°55'22" E, 24.VII.2020, in the photo there are 9 *P. flavescens* soaring at the same time, I. Voinov (Fig. 4). **Loc.7a.** [iNaturalist, 2024 (37925853)]: Gelendzhik gorsovet (near the village of Kabardinka), 44°40'16" N, 37°55'06" E, 25.VI.2019, photo of a female (post-teneral) of *P. flavescens*, V. Onishko (Fig. 5). **Loc.7b.** [Kosterin, Solovyev, 2017]: Mountain slope near the village of Kabardinka, 44°39'07–40'32" N, 37°56'51–58'30" E, 28.VII.2015, 1♂, 1♀. Here, on July 27–28, 2015, many individuals constantly flew at low altitude.

Loc.8. [iNaturalist, 2024 (55123171)]: Abinskii district, south of the village of Akhtyrskii, 44°48'01" N, 38°16'47" E, 22.VII.2019, photo of a male (post-teneral) of *P. flavescens*, macrohunter_ls.

Loc.9. Southern outskirts of Krasnodar, 44°59'07" N, 39°01'21" E, 7.IX.1988, *P. flavescens* individuals have been observed hovering, S.N. Borisov [unpubl.]. 4 specimens (teneral) of *Anax ephippiger* were also collected here. [Kosterin, Borisov, 2018].

Loc.10. [Onishko, 2019]: Krasnodarskii Krai, Goryacheklyuchevskii district, Fanagoriyskoye village, 44°31'16" N, 39°07'08" E, 25.VIII.2016, 2♂♂.

Loc.11. [iNaturalist, 2024 (67613482)]: Sochi, Adler, 43°24'02" N, 39°58'13" E, 22.VII.2020, photo of a female (post-teneral) of *P. flavescens*, I. Voinov. **Loc.11a.** [iNaturalist, 2024 (67613511)]: Sochi, Adler, 43°23'53" N, 39°58'35" E, 22.VII.2020, photo of a female (post-teneral) of *P. flavescens*, I. Voinov. **Loc.11b.** [Voinov, 2022]: Adler, Sochi Park, ponds in the Imeretinskaya Lowland, 43°24'01" N; 39°58'22" E, 22.VII.2020, observed of *P. flavescens*. **Loc.11c.** [Skvortsov, 2010]: Krasnodarskii Krai, Sochi District, Khosta, data by S.V. Kotachkov (ca. 43°31' N, 39°53' E). **Loc.11d.** [Kalkman, Monnerat, 2015]: Neighborhoods of Sochi, 19–24.VIII.1987, 6 specimens of *P. flavescens* collected, R. Mauersberger.

Adygea

Loc.12. [Shapovalov et al., 2022]: Maykopskii district, Podgorny village, 44°27'27" N, 40°10'16" E, 188 m a.s.l., 9.VIII.2020, 1♂.

Loc.13. [Shapovalov et al., 2022]: Maykopskii district, vicinity of Dakhovskii village, Mountain Legend tourist center, 44°15'19" N, 40°11'52" E, 447 m a.s.l., 6.VIII.2019, 1♂, 1♀.

Kabardino-Balkaria

Loc.14. [Skvortsov, 2010]: Bezengi, data by S.V. Kotachkov. (ca. 43°13' N, 43°17' E).

North Osetia

Loc.15. [iNaturalist, 2024 (131730982)]: Alagirskii district, near Alagir, 43°02'23" N, 44°11'30" E, 21.VIII.2022, photo of a male (post-teneral) of *P. flavescens*, G. Khokhov.

Loc.16. iNaturalist, 2024 (67643478)]: Mozdok, 43°45'34" N, 44°36'36" E, 16.VII.2020, photo of a female (post-teneral) of *P. flavescens*, I. Voinov. **Loc.16a.** [iNaturalist, 2024 (67643623)]: Mozdok, 43°45'52" N, 44°36'54" E, 17.VII.2020, photo of a female (post-teneral) of *P. flavescens*, I. Voinov.

Chechnya

Loc.17. [iNaturalist, 2024 (171353450)]: Grozny district, Gikalo, 43°13'02" N, 45°44'25" E, 6.VII.2023, photo of a female (post-teneral) of *P. flavescens*, aminat19.

Dagestan

Loc.18. [iNaturalist, 2024 (146024416)]: Gergebilskii district, near the village of Khvartikuni, 42°26'58" N, 47°01'59" E, 12.IX.2022, photo of a female (post-teneral) of *P. flavescens*, V. Onishko.

Loc.19. [iNaturalist, 2024 (86089999)]: Sarykum Barkhan, 42°59'55" N, 47°13'43" E, 27.VIII.2019, photo of a female (teneral) of *P. flavescens*, E. Pylev (Fig. 6).

Loc.20. [iNaturalist, 2024 (146467479)]: Samursky National Park, 41°51'48" N, 48°33'38" E, 16.IX.2022, photo of a *P. flavescens*, V. Onishko. **Loc.20a.** [iNaturalist, 2024 (146467515)]: Samursky National Park, 41°51'48" N, 48°33'38" E, 16.IX.2022, photo of a *P. flavescens*, V. Onishko. **Loc.20b.** [Ilyina et al., 2022]: Samursky National Park, 41°51'07"– 41°52'01" N, 48°32'56"– 48°34'01" E, 27.VI.2021 One young individual of *P. flavescens* was encountered near the reserve's cordon.

Astrakhanskaya Oblast

Loc.21. [Onishko, Kosterin, 2021]: Astrakhanskaya Oblast (ca. 46° N, 48° E), August 2020, observations of *P. flavescens*, I. Voinov.

Discussion

The northern limits of distribution and development

Currently, the northernmost location and place of development of *P. flavescens*, both in Europe and on the planet as a whole, is noted in the Moscovskaya Oblast (loc. 2, 55°42'11" N). On August 31, 2020, a young male was caught by V. Onishko on the banks of the Moscow River near the Zvenigorod biological station of Moscow University [Onishko, Kosterin, 2021]. Somewhat further south, this species was recorded on the coast of the Baltic Sea — in Lithuania (Ventės ragas, 55°20'29" N) [Jusys et al., 2019] and Kaliningradskaya Oblast (loc. 1, 55°05'17" N) and in Poland (Lębork, 54°33'20" N) [Buczyński et al., 2019].

In eastern Asia, back in the second half of the 19th century, *P. flavescens* was found at the junction of the Argun' and Shilka Rivers to form the Amur River (Pokrovka, ca. 53°20' N) [Selys-Longchmps, 1887] and in Kamchatka (Petropavlovsk, ca. 53° N) [Hagen, 1856]. At the same time, in Middle Asia this species is known not further north than 45° N [Borisov, 2012]. In the New World, numerous findingss of *P. flavescens* are known in the northern USA and southern Canada [iNaturalist, 2024, https://www.inaturalist.org/taxa/108344-Pantala-flavescens]. In the Canadian state of Manitoba, this species was recorded in the vicinity of Husavik (ca. 51°30' N) [Walker, Corbet, 1975].

The northernmost points of the range where the development of *P. flavescens* has been established were also located in Europe. This is the above mentioned location in the Moskovskaya Oblast (loc. 2, 55°42'11" N), as well as on the Courish Spit (loc. 1, 55°05'17" N). Here on August 18, a young female fell into an ornithological trap [Shapoval et al., 2022]. In eastern Asia, in the vicinity of Blagoveshchensk, the development of *P. flavescens* was noted at 50°17' N [Borisov, Malikova, 2019]. In the New World, the northernmost place of development of *P. flavescens* is still known in the south of Canada (45°25' N) [Trottier, 1967].

Immigrants and residents: phenology and differences in numbers in southern Russia

To date, in the western part of Russia, immigrants of *P. flavescens* have been recorded only on the Courish Spit in the Kaliningradskaya Oblast. Two individuals were caught there in a bird trap on May 29, 2013 and June 6, 2019 (loc. 1).

Below we consider the phenology of *P. flavescens* in southern Russia, where so far all observations concern individuals of the local generation. It can be assumed that in the spring in the southern Russian regions, immigrants of *P. flavescens* appear as early as April. This is evidenced by the fact that young individuals of the local generation were recorded there at the end of June – June 25 (loc. 7a (Fig. 5)) and June 27 (loc. 20b). In this case, egg lying should have occurred at least at the end of April. It is known that the pre-imaginal development of *P. flavescens* in different conditions can occur foe 30-65 days [Suhling et al., 2004; May, 2013]. In temperate latitudes this period is longer, for example, in Middle Asia, approximately 2 months [Borisov, 2012; Borisov et al., 2020].

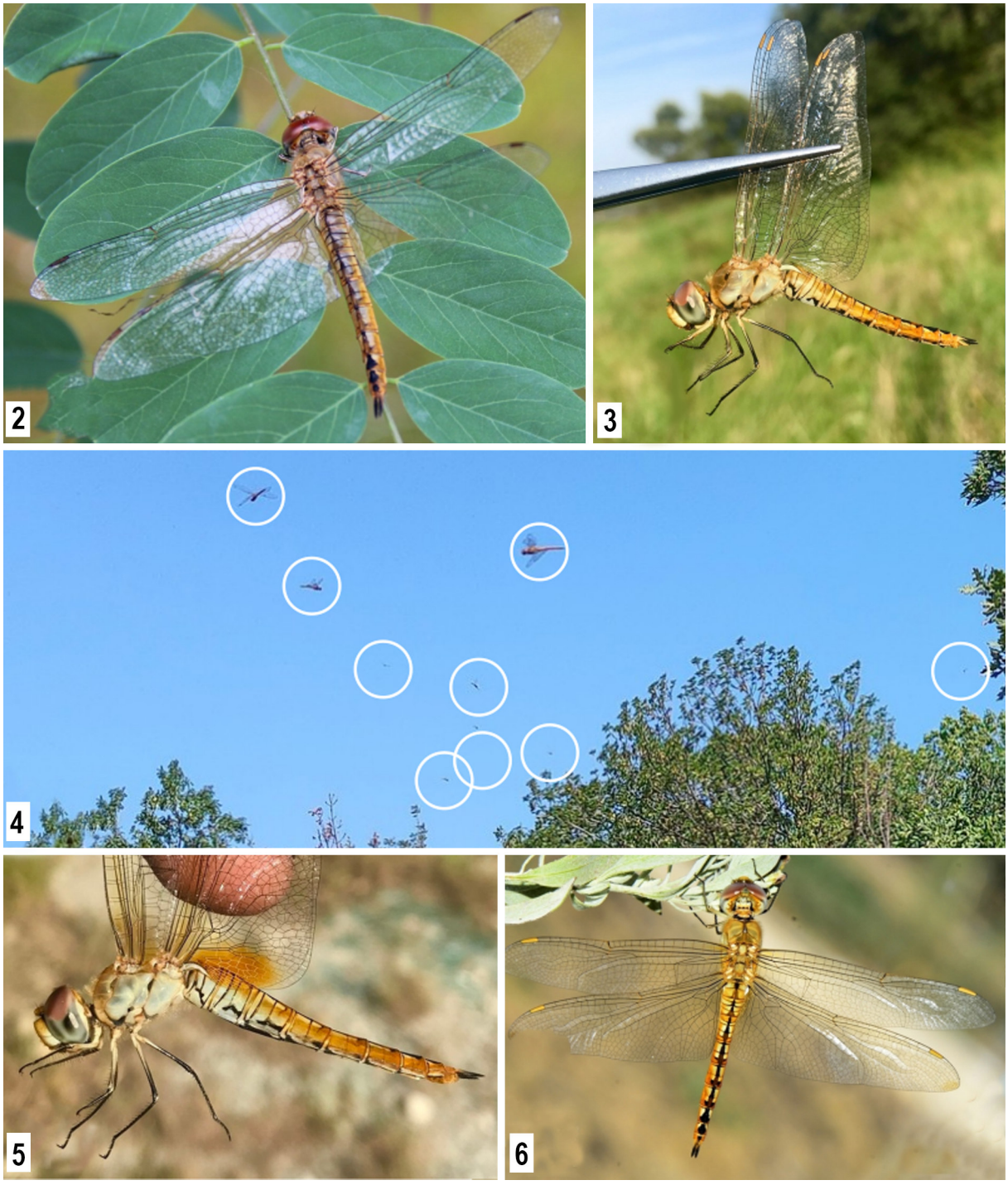
Individuals of the summer generation (residents) of *P. flavescens* in the south of Russia were recorded mainly in July and August, the extreme dates being June 25 (loc. 7a, Fig. 5) and September 16 (locs 20, 20a).

Thus, in the southern regions of Russia, the period of immigration (and oviposition) of *P. flavescens* presumably begins at the end of April, and individuals of the local generation (residents) were recorded there from the end of June to mid-September.

In general, residents in the south of Russia are quite common. Congregations of these dragonflies («soaring» or «swarm feeding») have been repeatedly noted (locs 5, 6, 7 (Fig. 4), 7b, 9) [Kosterin, 2017; Kosterin, Solovyev, 2017; Kosterin, Borisov, 2018]. This behavior is typical for this species at the post-teneral stage, that is, for recently emerged dragonflies [Corbet, 1999; Borisov, 2012, 2015]. At the same time, the lack of information about immigrants suggests their relatively low numbers.

A similar picture was observed in Middle Asia, where the number of spring immigrants *P. flavescens* is low from year to year and therefore the mass appearance of adults of the summer generation here looks very contrasting. At the same time, dragonflies gather in giant flocks so that many hundreds of individuals can be in the view field of an observer [Borisov, 2012, 2015]. Flocks of thousands of individuals of the local generation of *P. flavescens* were also recorded in rice fields in Northeastern Iran [Ikemeyer et al., 2015] and in southern Turkey [Boudot et al., 2021; Observations, 2024 (178702606)].

Thus, in the northern part of the range, the number of the summer generation of *P. flavescens* is many times higher than that of immigrants (their ancestors). This



Figs 2–6. Selected photos of *Pantala flavescens* from various localities. 2 — loc.1; 3 — loc.2; 4 — loc. 7; 5 — loc.7a; 6 — loc.19. Photograph 2 by A. Shapoval, 3, 5 by V. Onishko, 4 by I. Voinov and 6 by E. Pylev.

Рис. 2–6. Избранные фото *Pantala flavescens* из различных локалитетов. 2 — loc.1; 3 — loc.2; 4 — loc. 7; 5 — loc.7a; 6 — loc.19. Фото 2 — А. Шаповал, 3, 5 — В. Онишко, 4 — И. Войнов, 6 — Е. Пылев.

confirms that the state of populations of migrant insects, which are characterized by seasonal translatitudinal migrations, largely depends on the success of their summer reproduction in high-latitude regions [Chapman et al., 2012, 2015].

Phenology in Europe

Here we consider observations of *P. flavescens* in Central and Eastern Europe, which are likely to be attributed to either immigrants or residents.

The earliest findings of dragonflies were made on May 29, 2013 and June 6, 2019 at the Fringila biological station on the Curonian Spit (loc. 1) [Shapoval et al., 2022] and on May 25, 2019 in Lithuania in Ventės ragas [Jusys et al., 2019]. In these cases, immigrants were identified through the use of ornithological traps, where dragonflies often end up during migrations [Borisov, 2009, 2015]. In Germany, in the southeast of Brandenburg, a male patrolling a pond (reproductive behavior) was recorded on July 6, 2019. The attached photo clearly shows that this is an old individual with a characteristically reddish body [Günter, 2019a: 129, Fig. 1]. In Poland, males with reproductive behavior were observed on June 8 and August 13, 2016 [Buczyński et al., 2019]. The photographs show that these are «old» individuals [https://wazki.pl/wazki_pantala_flavescens.html].

Residents of *P. flavescens* in Europe are observed more often. In Belarus, a young individual was registered on July 15, 2019 [Observations, 2024 (178642613)]. In Switzerland, a young male *P. flavescens* was discovered on August 23, 2019, and exuviae were found in the same location on September 4 [Henseler et al., 2019]. In Germany, on August 17, 2019, exuvia and «fresh» adults were discovered [Günter, 2019b]. In Poland, newly emerged adults were noted on August 12, 2020 [Lewandowska et al., 2020], and exuviae were discovered on August 21, 2020 [Michalczuk, Buczyński, 2021]. In northwestern Italy, a young female was photographed on August 14, 2019. It is believed that it may be a descendant of immigrant to Europe [Piretta, Assandri, 2019].

Thus, in Europe, immigrants of *P. flavescens* were recorded only sporadically on May 25 and 29, June 6 and 8, July 6, and August 13. Individuals of the summer generation (residents) were observed more often — from July 15 to September 4.

Phenology in Mediterranean regions

A completely different phenological picture, compared to Central and Eastern Europe and southern Russia, is observed in *P. flavescens* in a number of Mediterranean regions. In the south of the Iberian Peninsula, the Pelagic Islands and the island of Sicily, Malta and Cyprus, this species has become quite common in recent years [Corso et al., 2017; Sparrow et al., 2020; Gauci, 2022; Sánchez et al., 2024].

In Spain, *P. flavescens* was first recorded in 2021, and already in 2023, these dragonflies were recorded repeatedly on the southern coast [Sánchez et al., 2024]. Flocks of *P. flavescens* numbering up to 30 individuals were observed here from August 27 to 30. Some individuals were also noticed on subsequent days. In the same year, on September 21, a rather «old» male with a reddish body, which is characteristic of sexually mature individuals, was noticed in Cadiz [Observations, 2024 (290994647]. Exuviae (125 pieces) and teneral specimens (10 pieces) were found in Cadiz from October 19 to November 19 [Sánchez et al., 2024].

Approximately the same periods of residence and development of *P. flavescens* have been revealed on the Mediterranean islands. In Malta in 2020, adults were recorded from July 29 to November 27, egg laying from August 19 to November 27, emergence from October 9 to November 18 [Gauci, 2022]. A post-teneral *P. flavescens* was also photographed here on December 8, 2023 [iNaturalist, 2024 (193406580)].

In Sicily, *P. flavescens* has been observed regularly from July to December, but no breeding data is available [Corso et al., 2017; Piretta, Assandri, 2019]. In the Pelagic Islands, this species has so far been recorded only in October-December [Corso et al., 2017].

Very detailed data on the phenology of *P. flavescens* are available for the island of Cyprus [Sparrow et al., 2020]. During the period 2013-2017, this species was a rare migrant here, but since 2018 and especially in 2019, these dragonflies have been quite common there. In 2019, the residence period of *P. flavescens* was set from mid-July to January, oviposition — from August 2 to December 2, emergence — from October to the end of the year. The main flight season was observed from early August to mid-November, after which the dragonfly number rapidly declined. In 2015, one teneral individual was recorded on January 11 [Sparrow et al., 2020].

In 2023, *P. flavescens* was observed in Cyprus as early as June 27 [Observations, 2024 (279090346)], egg laying was recorded on July 2 [Observations, 2024 (278983337)]. Territorial behavior (reproductive activity) was observed until December 17 [Observations, 2024 (294757802)].

In the Eastern Mediterranean (Israel, 31° N), photos of *P. flavescens* tandems were taken on November 14, 2020 [iNaturalist, 2024 (68752127)] and November 23, 2019 [iNaturalist, 2024 (68718678)], which indicates late autumn oviposition of these dragonflies.

Thus, *P. flavescens* immigrants arrive in the above considered regions of the Mediterranean at the end of June – August, egg lying occurs in July-December, and the emergence of the local generation occurs in October and December and even in January. In this case, we can speak about the 'winter; development of these dragonflies.

Phenology at the Mediterranean coast of Turkey

At the Mediterranean coast of Turkey (less than 100 km from the island of Cyprus), the annual cycle of *P. flavescens* is more similar to that in southern Russia and Central and Eastern Europe. The development of this

species in Turkey was first reported by J. Arlt [1999]. On June 23, 1998, in the delta of the Göksu River (Antalya), young, recently emergence individuals were discovered, and 100 km to the west — an exuvia and a teneral individual Arlt [1999]. It can be assumed that oviposition in this case occurred in the second half of April. It is interesting to note that 11 years later (August 20, 2019) in the same place (the Göksu delta) *P. flavescens* was found in gigantic numbers. Millions of dragonflies hovered in the air [Boudot et al., 2021; Observations, 2024 (178702606)]. The spring immigration of *P. flavescens* to the Mediterranean coast of Turkey is also evidenced by the registration of these dragonflies there on May 10, 2024 [Observations, 2024 (309059076)] and May 12, 2024 [Observations, 2024 (309197545)]. In 2023, near Antalya, *P. flavescens* was observed on October 24 [iNaturalist, 2024 (189572336)] and December 28 [iNaturalist, 2024 (195094177)]. The origin of these dragonflies remained unclear. These could be either individuals of the "local" generation or immigrants from the north.

The discovery of teneral female on August 29, 2001 on the Greek island of Rhodes, located in close proximity to the Turkish coast [Leister, 2005] can also be attributed to the summer generation.

Different migrations cycles of *Pantala flavescens* in Europe and Mediterranean regions

Our analysis of the phenology of immigrants and residents showed that in the southwestern Palearctic, *P. flavescens* has two migration zones, which differ in annual cycles. The northern zone («Eurasian migration zone») includes most of the continental Europe (without the southern part of the Iberian Peninsula), southern Russia and Turkey. Dragonflies immigrate there from somewhere in the south already in April – May. The summer generation appears at the end of June – September. It has been suggested that immigrants who arrive in Central and Eastern Europe in the spring may originate from Asia rather than Africa [Sparrow et al., 2020]. There is also an opinion that to penetrate Europe, dragonflies can use a migration corridor from the tropical Africa through the Nile Valley [Buczyński et al., 2019].

The southern zone («Mediterranean migration zone») covers the south of the Iberian Peninsula and the Mediterranean islands (Pelagic, Sicily, Malta and Cyprus). Immigrants of *P. flavescens* arrive there mainly in July–August, egg laying occurs before the end of the year, and the local generation emergence in October–January. For immigrants of *P. flavescens* which arrive in the Mediterranean zone in summer, the African origin was also assumed. It is believed that they could have flown to southern Spain in August from West and Central Africa [Sánchez et al., 2024]. Immigrants which fly to Cyprus in the summer may be from North-East Africa (Nile Valley) [Sparrow et al., 2020].

Probable migration pattern of *Pantala flavescens* in the «Eurasian» and «Mediterranean» zones

The differences in the annual cycles of *P. flavescens* in the «Eurasian» and «Mediterranean» migration zones are quite distinct. The question of the geographic origin of immigrants in both cases remains open. However, based on phenological differences, a possible migrations pattern for these dragonflies can be outlined.

First of all, attention is drawn to the fact that in the northern, «Eurasian zone», immigration and development of *P. flavescens* occurs much earlier (May – September) than in the «Mediterranean zone» (July – December). This is only possible if in the spring dragonflies were flying from the south, bypassing the Mediterranean Sea, for example, from the southern regions of South-West Asia or from East Africa. If immigrants flew to Europe from Africa via Sahara, they would have to cross the Mediterranean Sea. In this case, they could be observed in April-May on the Mediterranean islands. In fact this does not happen so far.

We do not exclude the possibility that *P. flavescens* immigrants arrive in the «Mediterranean migration zone» from the Palearctic part of Africa in July – August. For example, they may well fly to Cyprus from the Nile Valley [Sparrow et al., 2020], and to the south of Spain from North-West Africa [Sánchez et al., 2024].

At the same time, another migration scenario is quite likely, as followss: in July-September, *P. flavescens* arrives in the «Mediterranean migration zone» from the «Eurasian migration zone», that is, from the north. This is evidenced by the fact that an increase in number of *P. flavescens* in the Mediterranean has been observed after 2019, when many facts of the successful development of these dragonflies were established in Europe, including southern Russia, and Turkey.

To infer the geographical origin of European and Mediterranean immigrants, the use of stable isotope analysis is highly desirable. The «isotopic signatures» of dragonflies that develop in the temperate latitudes and in the tropics are contrastingly different [Borisov et al., 2020], so the «northern» or «southern» origin of Mediterranean immigrants would become obvious.

One of the reasons why *P. flavescens* previously could not penetrate into Europe and, especially, into its western part, is assumed to be the presence of a powerful migration barrier — the Sahara Desert. This desert cuts off Maghreb from the interior of the continent and is dominated by dry winds, which are especially unfavorable for dragonfly migrations [Corbet, 1999; Buczyński et al., 2014, 2019; De Knijf, 2015]. This barrier apparently still prevents migrations of *P. flavescens* from tropical Africa to Europe, and the main migrations of these dragonflies to the north come from Southwest Asia, where *P. flavescens* is now quite common [Boudot et al., 2021; iNaturalist, 2024, https://www.inaturalist.org/taxa/108344-Pantala-flavescens]. The main reason for the modern expansion of the species to the north is apparently the current general climatic warming.

It should be expected that in future, *P. flavescens* will increasingly colonize the European continent, since the climate there is noticeably milder than in other continents of the northern hemisphere. It is possible that the winter development of these dragonflies (wintering) in the Mediterranean regions will become a natural phenomenon.

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