

Stable hydrogen isotopes indicate latitudinal migrations of the dragonfly *Anax parthenope* (Selys, 1839) in southern Russia

Изотопный состав водорода свидетельствует о трансширотных миграциях стрекозы *Anax parthenope* (Selys, 1839) на юге России

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KEY WORDS: dragonflies, *Anax parthenope*, seasonal migrations, deuterium, southern Russia.

КЛЮЧЕВЫЕ СЛОВА: стрекозы, *Anax parthenope*, сезонные миграции, дейтерий, юг России.

ABSTRACT. The migrations of the dragonfly *Anax parthenope* (Selys, 1839) (Odonata: Aeshnidae) were studied for the first time using the isotopic composition of hydrogen ($\delta^2\text{H}$) in metabolically inert wing tissues as markers of the natal region. The analysis included 12 samples of immigrants *A. parthenope* from southern Russia and 14 samples of resident *A. parthenope* from Tajikistan (original data), as well as previously published data (11 samples of 3 species of resident dragonflies from southern Russia and 16 samples of 9 species of resident dragonflies from Iran). The mean $\delta^2\text{H}$ values of the wings of *A. parthenope* immigrants in southern Russia ($-61.1 \pm 12.2\text{‰}$) were significantly higher than those of resident dragonfly species ($-121.7 \pm 9.5\text{‰}$) and similar to those of dragonfly species from Iran ($-72.3 \pm 18.4\text{‰}$). Based on the geostatistical model of global $\delta^2\text{H}$ values in precipitation, the most probable area of origin of *A. parthenope*

immigrants arriving in Russia includes northeast Africa and southwest Asia. The putative area of *A. parthenope* migrations covers the territory between approximately $26\text{--}28^\circ$ and $57\text{--}59^\circ$ N, and the migration range can reach 2000–4000 km. Unlike other species of migrant dragonflies in the Palearctic, *A. parthenope* can winter throughout its entire range, including its northern part, where both immigrant and resident individuals of this species are present during the warm period of the year.

РЕЗЮМЕ. Впервые исследованы миграции стрекозы *Anax parthenope* (Selys, 1839) с использованием в качестве маркеров natalной области изотопного состава водорода ($\delta^2\text{H}$) в метаболически инертных тканях крыльев. Анализ включал 12 образцов иммигрантов *A. parthenope* из южной России и 14 образцов резидентных *A. parthenope* из Тад-

жикистана (оригинальные данные), а также ранее опубликованные данные (11 образцов трех видов резидентных стрекоз из южной России и 16 образцов девяти резидентных видов стрекоз из Ирана). Средние значения $\delta^2\text{H}$ крыльев иммигрантов *A. parthenope* на юге России ($-61,1 \pm 12,2 \text{ ‰}$) были значительно выше, чем у резидентных видов стрекоз ($-121,73 \pm 9,5 \text{ ‰}$) и схожи со значениями резидентных видов стрекоз из Ирана ($-72,3 \pm 18,4 \text{ ‰}$). На основе геостатистической модели глобальных значений $\delta^2\text{H}$ в осадках наиболее вероятная область происхождения иммигрантов *A. parthenope*, прилетающих в Россию, охватывает Северо-Восточную Африку и Юго-Западную Азию. Предполагаемая область миграций *A. parthenope* охватывает территорию, примерно, между $26\text{--}28^\circ$ и $57\text{--}59^\circ$ с.ш., а дальность миграций может достигать 2000–4000 км. В отличие от других видов стрекоз-мигрантов в Палеарктике, зимовка *A. parthenope* возможна на всем протяжении ареала, включая его северную часть, где в теплый период года одновременно присутствуют и иммигранты, и резидентные особи этого вида.

Introduction

Many species of dragonflies (Odonata) perform large-scale seasonal flights, comparable in range to bird migrations [Hobson *et al.*, 2012a, b, 2021; Hallworth *et al.*, 2018]. The migrations of dragonflies and other insects are fairly well studied, largely due to the active use of endogenous isotopic markers of the place of origin, such as the isotopic composition of hydrogen ($\delta^2\text{H}$) [Hobson, 2019].

In the tropical monsoon climate (Intertropical convergence zone), seasonal migrations of dragonflies are associated with the changes of dry and wet periods. In the temperate zone, migrations are determined by the alternation of warm and cold periods of the year and have a predominantly latitudinal direction. Ph. Corbet [1999], emphasizing the adaptive significance of these migrations, designates them as “drought avoidance” and “cold avoidance”. In the Palearctic, seasonal latitudinal migrations are currently known for four species of dragonflies [Borisov, 2015]. Using the isotope method, they were established in *Pantala flavescens* (Fabricius, 1798) [Cao *et al.*, 2018; Borisov *et al.*, 2020a; Hobson *et al.*, 2021] and *Sympetrum fonscolombii* (Selys, 1840) [Borisov *et al.*, 2020b, 2024]. For two other migrating species, *Anax ephippiger* (Burmeister, 1839) and *A. parthenope* (Selys, 1839), migration studies using isotopic markers have not been conducted.

Our work is devoted to the study of *A. parthenope* migrations in southern Russia. The range of this species covers Africa north of the Sahara, most of Europe, and the western part of Asia, including Hindustan. Since the end of the last century, there has been a noticeable increase in the number and expansion of the range of this species in the northern direction [Kalkman, Proess, 2015], including in the European part of Russia [Onishko, Kosterin, 2021].

In Europe, the tendency of *A. parthenope* to migrate and the existence of local populations north of its main range are well known. But unlike other species of migrating dragonflies in the Palearctic, *A. parthenope* larvae are capable of overwintering at the northern limits of their range [Lempert, 1984; Corbet, 1999; Werzinger, Werzinger, 2001; Mauersberger *et al.*, 2002; Parr *et al.*, 2004].

In the western regions of Russia, *A. parthenope* is one of the most common and often widespread dragonfly species. In Crimea, the Caucasus, and southern European Russia, single mature individuals appear as early as April. It is assumed that they could have flown here from the Eastern Mediterranean [Onishko, Kosterin, 2021]. There are no other data on the migrations of these dragonflies in the Russian part of the range. It is known that the breeding of *A. parthenope* in the south of Russia begins in mid-May and continues almost all summer. The peaks of emergence occur in May and August. The activity of imagoes lasts until the end of September – beginning of October [Onishko, Kosterin, 2021].

The aim of our work was to clarify the features of *A. parthenope* migrations in the south of Russia. Isotopic composition of hydrogen ($\delta^2\text{H}$ values) in metabolically inert wing tissues was used as a natural endogenous marker of the natal region. To prove the migrations, we compared the $\delta^2\text{H}$ values of presumed *A. parthenope* immigrants with those of resident dragonflies in the south of Russia and in the southern parts of the *A. parthenope* area, and determined the probable origin of *A. parthenope* immigrants based on a geostatistical model of the global $\delta^2\text{H}$ values of precipitation.

Material and methods

Sample collection

Wings of *A. parthenope* ($n = 12$) collected from three locations in southern Russia were used for isotope analysis; all individuals were “old”, with conspicuously worn-out wings. Photos of some specimens are available in iNaturalist [2025, <https://www.inaturalist.org/taxa/94048-Anax-parthenope>].

1. Goryachiy Klyuch ($44^\circ 38' \text{ N}$, $39^\circ 07' \text{ E}$), April 13–23, 2021 ($n = 6$), collector V.V. Onishko. Photos: [iNaturalist, 2025, <https://www.inaturalist.org/observations/75177444>], [iNaturalist, 2025, <https://www.inaturalist.org/observations/75178831>].
2. Teberda ($43^\circ 20' \text{ N}$, $41^\circ 40' \text{ E}$), July 8, 2019 ($n = 1$), collector O.E. Kosterin. Photo: [iNaturalist, 2025, <https://www.inaturalist.org/observations/109854679>].
3. Astrakhan' ($46^\circ 26' \text{ N}$, $48^\circ 04' \text{ E}$), May 1, 2021 ($n = 5$), collector I.O. Voinov. Photos: [iNaturalist, 2025, <https://www.inaturalist.org/observations/76245578>], [iNaturalist, 2025, <https://www.inaturalist.org/observations/76248150>], [iNaturalist, 2025, <https://www.inaturalist.org/observations/78237919>].

For comparative purposes, wings of *A. parthenope* residents from Central Asia were also used for isotope analysis: Samples were collected in Southwestern Tajikistan, Tigrovaya Balka Nature Reserve ($37^\circ 18' \text{ N}$, $68^\circ 27' \text{ E}$), April–May 1978, 1979, and 2019 ($n = 14$), collectors S.N. Borisov and A.S. Borisov.

The $\delta^2\text{H}$ values of *A. parthenope* immigrants were compared with those of resident dragonflies in southern Russia and

Iran using previously published data [Borisov *et al.*, 2024]. Residents from Russia were represented by 11 samples of three migratory species (*Anax ephippiger* (n = 6), *Pantala flavescens* (n = 1) and *Sympetrum fonscolombii* (n = 4)). These were representatives of the summer generation, the descendants of immigrants. They were collected in different years between July 16 and September 7 (collection materials of the Institute of Zoology and Ecology of Animals SB RAS, Novosibirsk). Residents from Iran were represented by 16 samples of 9 local (non-migratory) dragonfly species collected in May 2017 by O.E. Kosterin.

The names of dragonfly species, places, and dates of collection and $\delta^2\text{H}$ values of the samples are given in the Supplementary Table S1.

Stable isotope analysis

The $\delta^2\text{H}$ values of the wings were determined using the comparative equilibration method [Wassenaar, Hobson, 2003; Hobson *et al.*, 2012b]. Samples of dragonfly wings were cleaned of surface lipids using 2:1 chloroform: methanol mixture, dried for several days at 50 °C, and stored for further two weeks in the laboratory along with an array of reference materials covering a wide range of $\delta^2\text{H}$ values. Isotopic analysis was conducted using TC/EA Flash 1112 and isotope ratio mass spectrometer Thermo Delta V Plus as described in Borisov *et al.* [2024]. Isotopic composition of hydrogen is expressed in per mil of deviation from international standards (VSMOW), δ (‰): $\delta X \text{ sample} = (R \text{ sample}/R \text{ standard} - 1) * 1000$, where R is the heavy isotope to light isotope molar ratio. Analytical error (SD) of the determination of $\delta^2\text{H}$ values in standard materials did not exceed 2‰.

In addition to USGS reference materials KHS (kudu horn, non-exchangeable $\delta^2\text{H}_{\text{VSMOW}} = -35.3 \pm 1.1\text{‰}$) and CBS (caribou hoof, non-exchangeable $\delta^2\text{H}_{\text{VSMOW}} = -157.0 \pm 0.9\text{‰}$), custom-made laboratory standards were used: homogenised dragonfly wings of *Crocothemis erythraea* (Brullé, 1832) from Tajikistan (DS1, $\delta^2\text{H}_{\text{VSMOW}}: -111.6\text{‰}$), of *Sympetrum sanguineum* (Müller, 1764) from Kazakhstan (DS2, $\delta^2\text{H}_{\text{VSMOW}}: -110.1\text{‰}$), of *Sympetrum flaveolum* (Linnaeus, 1758) from Kazakhstan (DS3, $\delta^2\text{H}_{\text{VSMOW}}: -110.2\text{‰}$), mountain hare fur (*Lepus timidus* Linnaeus, 1758) from the Arctic Circle (Chukotka) (DS4, $\delta^2\text{H}_{\text{VSMOW}}: -138.2\text{‰}$), and human hair (DS5, $\delta^2\text{H}_{\text{VSMOW}}: -70.8\text{‰}$). The non-exchangeable $\delta^2\text{H}_{\text{VSMOW}}$ values for the laboratory standards were obtained from IsoAnalytical Ltd (Crewe, Great Britain).

Likelihood-based assignment of geographic origins

The geographic origin of the dragonflies was estimated using IsoMAP [Bowen *et al.*, 2014]. A mean annual isoscape of $\delta^2\text{H}$ values in precipitation ($\delta^2\text{H}_p$) as a function of elevation, latitude and squared latitude over the years 1960–2010 was modeled across the *A. parthenope*'s range within 18.7° W to 92.3° E and 35.9° S to 58.5° N (680 stations, $r^2 = 0.575$). The $\delta^2\text{H}$ values of wings were converted into the precipitation hydrogen equivalents by applying the equation $\delta^2\text{H}_{\text{wing}} = 0.91 * \delta^2\text{H}_p - 42.54\text{‰}$ [Hobson *et al.*, 2012b]. We generated a geographic probability assignment for the $\delta^2\text{H}_p$ value of each dragonfly sample by including it and a standard deviation of 14.7‰, estimated from the residuals of the regression linking $\delta^2\text{H}_{\text{wings}}$ and $\delta^2\text{H}_p$ values [Hobson *et al.*, 2012b], to 'individual assignment' tool in IsoMAP. We arbitrarily chose a 2:1 odds ratio to include only pixels (coded 1) with at least a 67% probability of origin versus all others (coded 0) and summed up the binary value maps of individual assignments by stacking the surfaces.

Analysis of variance (ANOVA) and an unequal n Tukey's HSD test we used to compare the $\delta^2\text{H}_{\text{wings}}$ values of hypoth-

esized *A. parthenope* immigrants in south Russia and (1) resident Russian dragonflies, (2) resident Iranian dragonflies, and (3) middle Asian resident *A. parthenope*. Means $\pm$ 1 SD are reported.

Results

The groups of dragonflies differed significantly in the $\delta^2\text{H}$ value of wings ($F_{3,49} = 48.7, p < 0.0001$). The $\delta^2\text{H}$ values of *A. parthenope* immigrants in southern Russia ranged from -43.6 to -81.6‰ (mean $-61.1 \pm 12.2\text{‰}$, n = 12). These values were significantly ($p < 0.001$) higher than those of resident dragonflies in southern Russia (range from -107.4 to -135.2‰ , mean $-121.7 \pm 9.5\text{‰}$, n = 11) and resident *A. parthenope* from Tajikistan (range from -81.2 to -125.8‰ , mean $-104.5 \pm 12.5\text{‰}$, n = 14) and close ($p = 0.168$) to those of resident dragonflies from Iran (range from -34.1 to -96.1‰ , mean $-72.3 \pm 18.4\text{‰}$, n = 16) (Fig. 1).

Based on a geostatistical model of global $\delta^2\text{H}$ values in precipitation and considering the distribution and phenology of *A. parthenope*, the probable area of origin of the immigrants includes North-East Africa and South-West Asia (Fig. 2).

Discussion

Isotopic evidence of *Anax parthenope* migrations in southern Russia and the probable area of origin of immigrants

In this paper, we confirmed for the first time the migrations of *A. parthenope*. This is evidenced by a strong difference in the $\delta^2\text{H}$ values of immigrants and local (resident) dragonflies in the south of Russia. Moreover, the $\delta^2\text{H}$ values of immigrant *A. parthenope* in Russian do not differ from those of resident dragonflies from Iran, whose development took place 1,500 kilometers to the south (Fig. 1).

On the map, the probable area of origin of *A. parthenope* immigrants (dark green) covers a large southern part of the species' range, excluding East Africa and the central and southern regions of the Arabian Peninsula (Fig. 2).

It is known that in the temperate zone, seasonal migrations of dragonflies have a predominantly latitudinal direction [Corbet, 1999; May, 2013; Borisov *et al.*, 2024], and the arrival of *A. parthenope* immigrants from regions that are significantly distant from the south of Russia in longitude is unlikely. Therefore, the regions of Hindustan, as well as the Maghreb in Northwest Africa, can be excluded from the supposed natal area.

The southern part of Central Asia is also highlighted in dark green, indicating a possible origin of the immigrants from this region. However, the resident *A. parthenope* that developed in Tajikistan differ significantly in $\delta^2\text{H}$ values from the immigrants of this species in southern Russia (Fig. 1), with average $\delta^2\text{H}$ values of -104.5‰ and -61.1‰ , respectively. Therefore, a Central Asian origin of the immigrants of this species in southern Russia can also be ruled out.

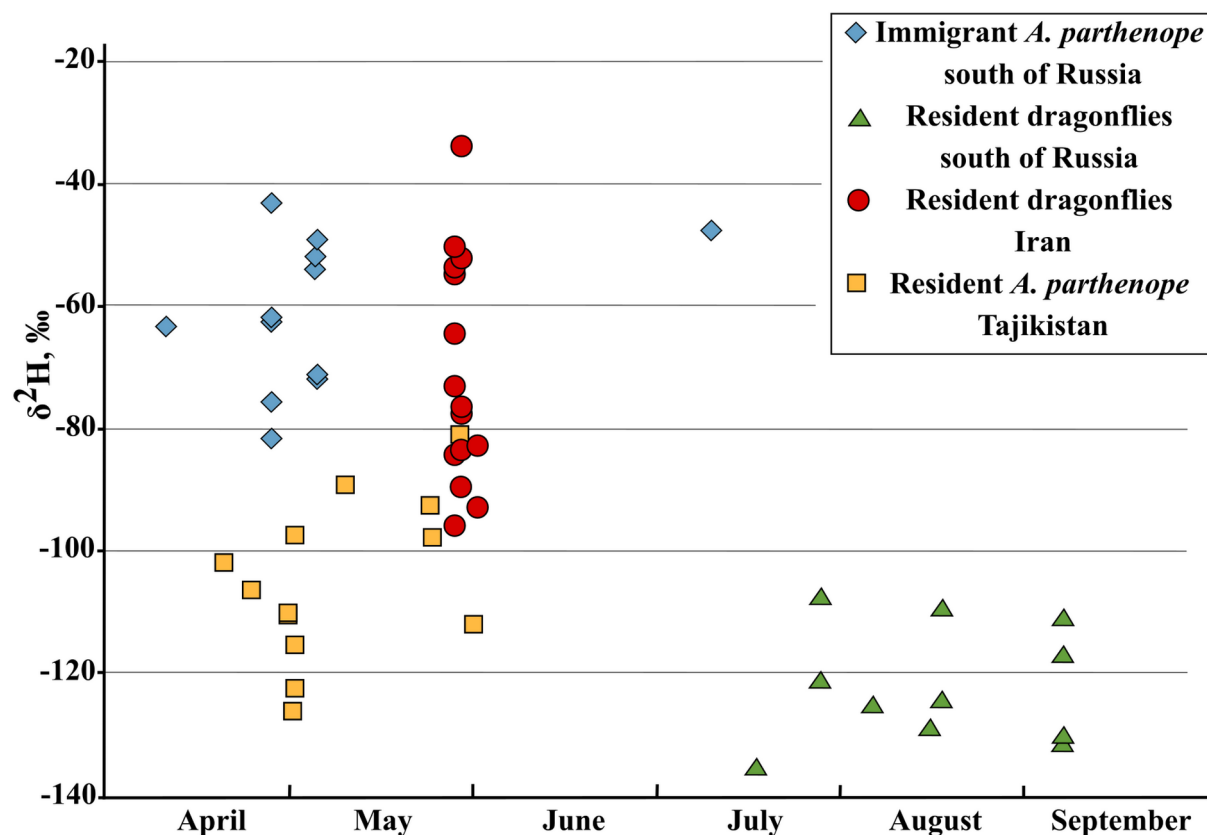


Fig. 1. The $\delta^2\text{H}$ values of wings of immigrant *Anax parthenope* in southern Russia (blue diamonds, $n=12$), residents dragonfly species in southern Russia (green triangles, $n=11$), residents dragonfly species from Iran (red circles, $n=16$) and residents *Anax parthenope* from Tajikistan (yellow squares, $n=14$).

Рис. 1. Значения $\delta^2\text{H}$ крыльев иммигрантов *Anax parthenope* на юге России (синие ромбы, $n=12$), резидентных видов стрекоз на юге России (зеленые треугольники, $n=11$), резидентных видов стрекоз из Ирана (красные круги, $n=16$) и резидентных *Anax parthenope* из Таджикистана (желтые квадраты, $n=14$).

In this regard, it should be noted that the $\delta^2\text{H}$ values of resident dragonflies in the arid climate of the plains and foothills of Central Asia vary significantly depending on the time of year in which they develop. The development of *A. parthenope* specimens used in this study occurred in the winter-spring period, which accounts for the maximum amount of precipitation during the year. As a result, *A. parthenope* residents have relatively high average $\delta^2\text{H}$ values (-104.5‰). Residents of two other species, which developed here in the summer, with virtually no precipitation, had lower average $\delta^2\text{H}$ values: -123.5‰ for *Pantala flavescens* [Borisov *et al.*, 2020a] and -134.3‰ for *Sympetrum fonscolombii* [Borisov *et al.*, 2020b]. In summer, the reservoirs where dragonflies develop receive their supply from mountain rivers, which primarily rely on runoff from glaciers and snow cover due to the high altitude of their catchment areas [Borisov *et al.*, 2020b]. According to the altitudinal pattern, $\delta^2\text{H}$ values of precipitation are lowest in the mountains and differ sharply from those on the adjacent plains [Terzer *et al.*, 2013; Bowen *et al.*, 2014]. Apparently, this is the main reason for the difference in the $\delta^2\text{H}$

values of dragonflies that develop in Central Asia in the winter and summer periods.

Thus, the geostatistical analysis based on the composition of hydrogen isotopes confirmed Onishko & Kosterin's [2021] assumption about the Eastern Mediterranean origin of *A. parthenope* immigrants in southern Russia. Moreover, the most probable natal area can be expanded to include territories in northeastern Africa, specifically the northern regions of Libya and Egypt, as well as in southwestern Asia, extending to Hindustan and the coastline of the Arabian Sea.

Phenology of immigrants and residents

Available data on the phenology of *A. parthenope* suggest that during the warm period of the year, its populations can simultaneously contain both immigrants arrived from other regions and residents whose preimaginal development occurred here. The phenology changes significantly at different latitudes. With the advance to the north, the arrival of immigrants and the emergence of adults from the local population shift towards the summer and fall seasons.

Thus, in the south of Turkey (36° N) at the very end of March and the beginning of April, reproductive actions (tandems) of *A. parthenope* immigrants and newly emergent adults of the local generation were simultaneously observed [Dijkstra, Kalkman, 2001].

In the southern regions of Russia (41°–46° N), the first immigrants of *A. parthenope* were recorded from April 13 [this paper]. The emergence of the local generation from overwintered larvae begins here in the first ten days of May. According to iNaturalist, newly fledged individuals (teneral) of *A. parthenope* were observed in Crimea on May 9 [iNaturalist, 2025, <https://www.inaturalist.org/observations/214634122>], and in Dagestan — on May 6 [iNaturalist, 2025, <https://www.inaturalist.org/observations/214348993>] and May 8 [iNaturalist, 2025, <https://www.inaturalist.org/observations/214377011>].

At the northern limits of the range in Russia (56°–59° N) the first immigrants of *A. parthenope* appear only in the very end of May. The earliest recorded observation of immigrants in the Novgorod region is May 31 [iNaturalist, 2025, <https://www.inaturalist.org/observations/219573614>], while the earliest date of emergence of individuals of the local generation is June 15 [iNaturalist, 2025, <https://www.inaturalist.org/observations/222947040>]. It remains unclear what happens to the newly emerged resident individuals at the northern limits of the range, i.e. whether they reproduce here or

migrate south. It was suggested that in such cases alternative developmental pathways may depend on a critical photoperiod signal [May, Matthews, 202]. Remarkably, in the south of Russia two peaks of *A. parthenope* emergence were observed — in May and August [Onishko, Kosterin, 2021]. It is very likely that in the spring local dragonflies emerge from overwintered larvae, while in August the summer generation of dragonflies emerges, which are descendants of spring immigrants. However, both the duration of preimaginal development and the extended immigration period should be taken into account. In Europe, the summer generation of *A. parthenope* develops in 3–4 months [Schnapauff *et al.*, 2000; Werzinger, Werzinger, 2001]. The situation is approximately the same in the south of Russia. The development of summer generation occurs here from April–May to August. On the other hand, the duration of the immigration period of *A. parthenope* in the south of Russia remains unclear. The finding of an individual with the $\delta^2\text{H}$ values characteristic of immigrants (Fig. 1) on July 8 suggests that the influx of immigrants from the southern part of the range continues till mid-summer. In this case, the larvae apparently do not have time to develop in the current year and go into wintering, with imagoes emerging the following spring. Such a scenario for the development of *A. parthenope* is known in Germany [Werzinger, Werzinger, 2001].

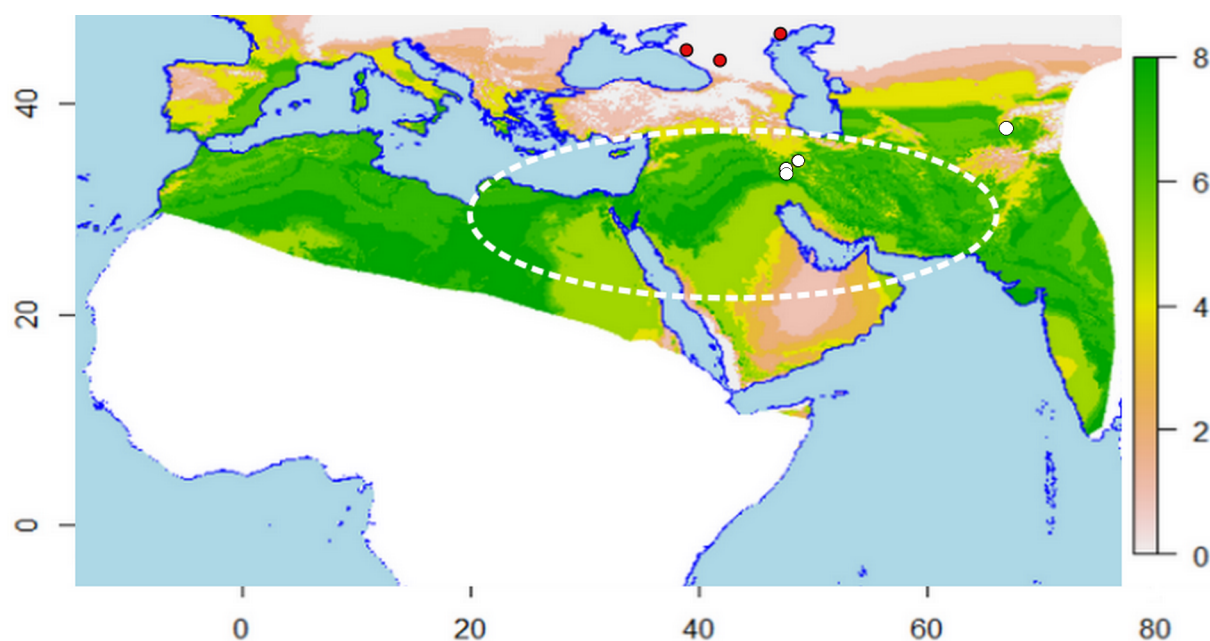


Fig. 2. Map of probable natal area of *Anax parthenope* immigrants ($n=12$) captured in 3 locations in southern Russia (red dots). The scale shows the number of individuals assigned to a given pixel according to the chosen 2:1 odds criterion. The probability map is displayed within the species range. The white dotted ellipse indicates the most probable natal area given the species distribution and phenology. White dots indicate collection sites of resident dragonfly species in Iran and resident *Anax parthenope* from Tajikistan.

Рис. 2. Карта вероятной natalной области иммигрантов *Anax parthenope* ($n=12$), отловленных в 3 локациях на юге России (красные точки). На шкале указано число особей, присвоенных каждому пикселю в соответствии с выбранным критерием шансов 2:1. Карта вероятности отображается в пределах ареала вида. Белым пунктирным эллипсом обозначена наиболее вероятная natalная область с учетом распространения и фенологии вида. Белыми точками обозначены места сбора резидентных видов стрекоз в Иране и резидентных *A. parthenope* в Таджикистане.

Migration strategy of *Anax parthenope*

The migration strategy of *A. parthenope* remains largely unclear, although it is likely very similar to that of the well-studied North American migrant species *Anax junius* (Drury, 1770) [May, 2013; Hallworth *et al.*, 2018; May, Matthews, 2023]. Both species belong to the tropical genus *Anax* Leach, 1815. It is believed that *A. junius* has adapted to colonize the temperate zone due to the presence of facultative diapause at the larval stage, which allows it to overwinter in cold regions [May *et al.*, 2017]. A similar adaptation is probably characteristic of *A. parthenope* in the Old World.

Our study shows that in the spring, sexually mature individuals of *A. parthenope* fly to Russia from the southern parts of their range. It is highly likely that individuals of the summer generation (descendants of immigrants) migrate south in autumn. Autumn southward migrations of *A. parthenope* were observed in August–September in southwestern Portugal [Corbet, 1999], in August–October at the Col de Bretolet bird ringing station in the Alps [Thoma, Althaus, 2015], and at the end of August on the Balearic Islands in Spain [Márquez-Rodríguez, 2019]. A sudden autumn “disappearance” (apparently, departure) of *A. parthenope* in Bavaria is also known [Werzinger, Werzinger, 2001]. Large-scale regular autumn migrations of *A. parthenope* were observed in Central Asia. From late August to October, dragonflies migrate in large numbers and fall into ornithological traps at the Chokpak Pass (southern Kazakhstan) [Borisov, 2009, 2012, 2015; Borisov *et al.*, 2022]. Indirect evidence of the autumn migrations of *A. parthenope* is also provided by a report of a mass arrival and reproduction of these dragonflies in the autumn and winter of 2009/2010 in the eastern part of the Arabian Peninsula. The authors [Campbell, Reimer, 2011] suggested these dragonflies could have arrived only from the northern parts of their range.

Thus, it can be stated that seasonal latitudinal migrations between different climatic zones are typical of *A. parthenope*. The migration strategy includes the dispersal of different generations – to the north in spring, to the south in autumn. The supposed “migration circuit” covers regions located approximately between 26°–28° N in the south (North-East Africa and South-West Asia) and 57°–59° N in the north (Leningrad and Novgorod regions of Russia). The length of the flights can therefore reach 2000–4000 km.

Obligate migration strategy allows dragonflies to efficiently colonize new habitats and territories, and, under favorable conditions, rapidly expand their range northwards, which is now observed against the backdrop of a steady trend of global warming. This strategy is similar to that of other insect migrants, aiming to make the best use of available environmental resources both in space and in time, and serving as a safeguard against the degradation or loss of larval habitats.

Competing interests. The authors declare no competing interests.

Supplementary data. The following materials are available online.

Supplementary Table 1. Species of dragonflies, cohorts (immigrant, resident), dates and places of collection and isotopic composition of hydrogen ($\delta^2\text{H}$ values, ‰) of wings.

Acknowledgements. We express our gratitude to O.E. Kosterin and I.O. Voinov for providing the material for isotope analysis. The study was supported by the Federal Fundamental Scientific Research Program for 2026–2030 (A.S. Borisov, S.N. Borisov, T.A. Novgorodova, FWGS-2026-0008) and (I.K. Iakovlev, FWGS-2026-0009). S.M. Tsurikov and A.V. Tiunov were supported by the state assignment of IEE RAS No. 1022061500271-3-1.6.20.

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