ISSN 0013-8738, Entomological Review, 2014, Vol. 94, No. 1, pp. 21–28. © Pleiades Publishing, Inc., 2014.
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Mass Reproductive Wanderings of Dragonflies of the Genus *Sympetrum* (Odonata, Libellulidae)

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Received January 15, 2013

Abstract—The results of observing mass flights of some dragonflies of the genus *Sympetrum* forming tandems are presented. These tandems always fly against the wind, some of them landing for oviposition and then joining the flight again. This variant of migration behavior has been unexplained until now. A hypothesis is proposed according to which synchronous mass flights of dragonfly tandems facilitate the most uniform oviposition in all the suitable biotopes. The general direction of the flight depends on the wind. As the wind direction changes, the flight course of the tandems changes accordingly, so that the dragonflies cross the same territory several times, which leads to a denser and more uniform distribution of eggs. It is proposed to refer to this variant of flight as reproductive wanderings. Such a dispersal strategy can maintain the most uniform population density and a more stable abundance of some dragonfly species in the territories with unstable humidity.

DOI: 10.1134/S0013873814010023

Adult dragonflies are the only invertebrates which have successfully explored the niche of aerial predators due to their outstanding flight abilities. The entire variety of spatial movements of dragonflies can be classified into four main types: trivial flights, dispersal, and regular and irregular migrations (Haritonov and Popova, 2010). This communication presents the results of our study of the peculiar mode of dispersal of several species of the genus *Sympetrum* Newman, 1833 flying in tandems. The term “tandem” is commonly used in the literature on dragonfly biology and designates two coupled insects with the male using its claspers to grip the female by the head or pronotum. Dragonfly tandems flying in the same direction can be sometimes observed for several hours in late summer and early autumn. Although such flights were previously mentioned in the literature (Dumont and Hinnekint, 1973; Belyshev and Belyshev, 1976; Corbet, 1999; Haritonov and Popova, 2010, etc.), more or less detailed descriptions of this phenomenon were rare, whereas previous attempts at explaining it were controversial and inconclusive. We also repeatedly observed mass migrations of tandems of *Sympetrum vulgatum* (Linnaeus, 1758) and *S. danae* (Sulzer, 1776) in the Baraba forest-steppe and some other localities in Siberia but the significance and mechanism of these migrations has escaped our understanding for a long time. These two species are characterized by eurytopic occurrence, broad ranges, and a flexible uni- or semivoltine life cycle depending on the development conditions (Popova, 2010). The former species is distributed in the greatest part of the Palaearctic except for the transpolar regions, while the latter has a circumboreal distribution embracing not only the Palaearctic but also a considerable part of North America. In Siberia, these species almost ubiquitously prevail in the dragonfly fauna in late summer and autumn.

The migrations of tandems of *S. vulgatum* and *S. danae* were particularly intensive in the south of West Siberia in 2010. Mass indirectional flights of dragonfly tandems could be observed in late summer and early autumn in the Lake Chany area of the Baraba forest-steppe where our field research was carried out, which allowed us to obtain quantitative assessments of the scale of this phenomenon, to observe the behavior of flying insects under different weather conditions, and to determine the state of their reproductive system and fat reserves. As a result, we were finally able to explain this unusual phenomenon.

No mass flights of tandems of *Sympetrum* dragonflies were observed in 2011 and 2012, possibly due to the droughts in these seasons resulting in low abundance of the species in question.

† Deceased.

MATERIALS AND METHODS

Mass flights of tandems of *Sympetrum* dragonflies were observed by us in 1974, 1981, 1982, 1989, 1993, 1999, and 2010, in the forest-steppe zone of West Siberia within Kurgan and Novosibirsk Provinces and Altai Territory. In 2010, the flight intensity was assessed by counting the tandems traversing a 10-m line marked out across the direction of the flight. The surveys were carried out in open areas where dragonflies could be conveniently observed: in the steppe, over roads, rivers, and stagnant water bodies. The total duration of the surveys was 12.5 h, during which 14 178 dragonfly tandems flying across a 10-m line were recorded. To determine the territorial magnitude of these migrations, the presence of flying dragonflies was additionally recorded (without counting the tandems) from moving cars on the roads, from boats on lakes Fadikha and Malye Chany and the Kargat River, and by pedestrian observers in hard-to-reach parts of the landscape. The total length of automobile routes was 680 km, that of boat routes, 37 km, that of walking routes, 58 km. All the observations were accompanied by recording of the main weather parameters, such as air temperature and humidity, atmospheric pressure, wind velocity and direction, and cloudiness.

We captured 70 tandems to identify the species and determine the age of the migrating insects; 20 females were dissected to determine the phase of the reproductive cycle and the state of the fat reserves.

RESULTS

Emergence of the adults of *Sympetrum vulgatum* and *S. danae* in the south of West Siberia started in the third decade of June, after which its intensity increased gradually, reaching the peak in mid-July. The rate of emergence started to decline at the beginning of August but occasional new adults appeared even in the first decade of September. In August–September these species were dominant in the regional dragonfly fauna. The period of initial feeding of the young adults before the onset of reproduction lasted 2–3 weeks, during which they dispersed over a considerable distance (sometimes several kilometers) from their native reservoirs. These species are only weakly associated with their emergence sites and can lay eggs in various reservoirs and even directly on the ground in some depressed areas which will be flooded with snowmelt waters in spring. Although the first ovipositing couples could be observed since mid-July, the most intensive reproduction took place in August and the first half of September. Mass unidirectional flights of tandems of *Sympetrum* dragonflies may occur between the beginning of the second decade of August and the end of the second decade of September.

Comparison of the results of our observations for many years showed that these flights depended on two factors. The first factor was high abundance of these species in the given season. The second factor was a combination of at least three weather parameters: a high air temperature, at least 20°C, the sun not obscured with clouds, and velocity of wind ranging from 3 to 10–12 m/s. The optimal wind velocity was 5–8 m/s, regardless of its direction. The most important feature of such flights was that dragonflies always moved against the wind: strictly upwind in 80% of the observed cases, and at a small angle to the head wind, in 20% of the cases. The mass flights did not reveal any periodicity since the favorable weather conditions could be only irregularly observed at the end of summer and in autumn (Fig. 1).

In the morning, single males and females of these species sometimes formed large aggregations near birch groves, forest shelter belts, reed bed, and tall herbaceous vegetation along the roads. If the weather was suitable, the dragonflies started feeding at approximately 8 a.m. The first tandems were formed after 9 a.m.; between 10 and 11 a.m. most of the dragonflies formed tandems and started flying against the wind, given the sufficient air temperature and sunny and windy weather. Not all the tandems joined the flight, some of them moving instead to a nearby water body for oviposition. However, the fraction of tandems joining the common flight increased later in the season, as autumn approached. In most of the cases observed, the synchronous flight reached the maximum in the middle of the day, declined after 2 p.m., and ceased completely at 3–4 p.m. Then the tandems broke, the males and females fed, rested, and spent the night separately. On the following morning the tandems were formed again if the weather was favorable.

The "flow density" of the flying tandems varied greatly depending on the locality and the time of observation (Fig. 1); it is hardly possible to calculate the mean value even though it would be very interesting to estimate the extent of such flights. Some survey data obtained in 2010 (August 17, 22, 26, 27, and 30) in the forest-steppe landscape of Zdvinsk District, Novosibirsk Province, are given below as an example.

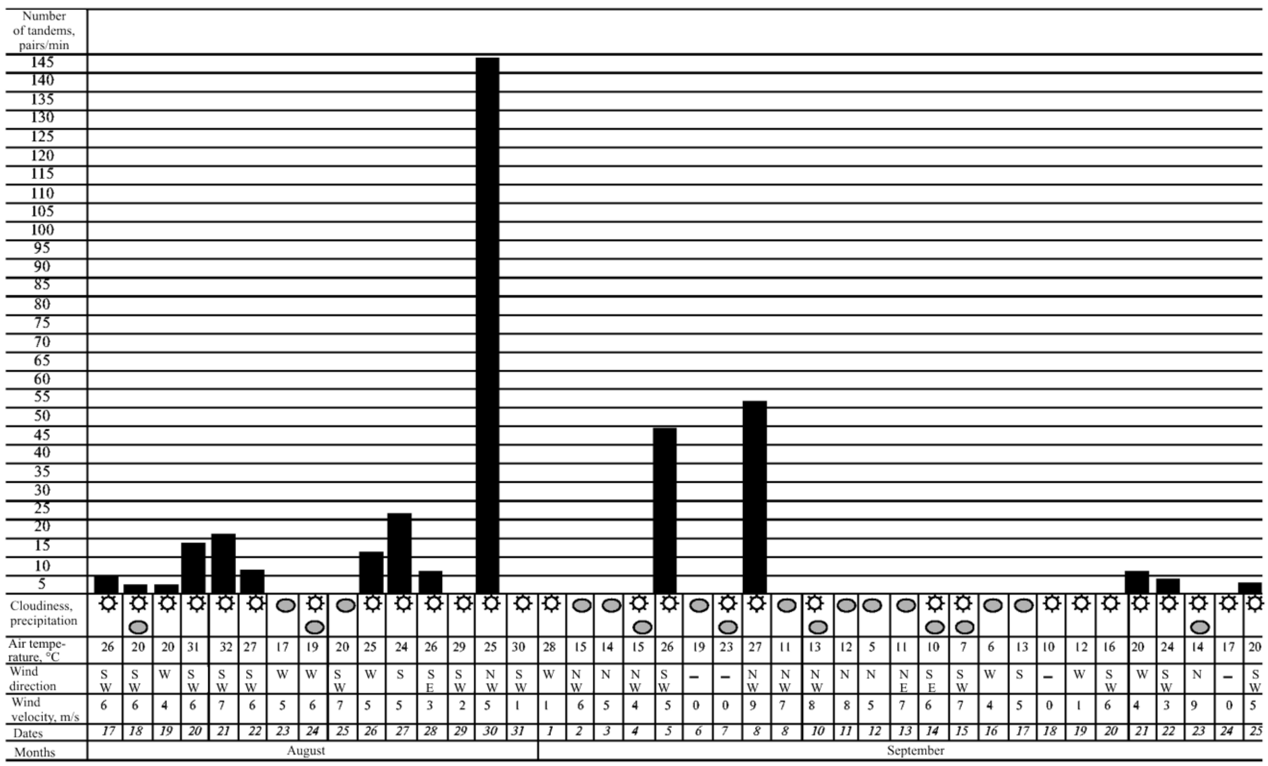

Fig. 1. The flight of tandems of *Sympetrum* dragonflies in August–September 2010 in the Lake Chany area, the Baraba forest-steppe. The histogram bars correspond to the number of tandems traversing a 10-m line in 1 minute.

In the season of 2010, a unidirectional flight of *Sympetrum* tandems was recorded for the first time in the middle of the day on August 17, in clear weather with an air temperature of 26°C and a southwest wind of 5–7 m/s. The dragonfly tandems moved against the wind with the intensity of 40 ± 8.8 pairs (range 25–52) traversing a line 10 m long during 10 min of observation, i.e., 4 pairs/min (Fig. 2). They flew along a low ridge covered with steppified vegetation about 500 m wide, situated between Lake Fadikha and reed beds in the Kargat floodplain.

The flights of *Sympetrum* tandems were observed both in this locality and within a radius of tens of kilometers from it during all the subsequent days with the weather meeting the above conditions, almost until the end of September. Some observations made within 600 km from the principal study area confirmed that the flights of *S. vulgatum* and *S. danae* tandems occurred in the West Siberian forest-steppe at least in the entire Ob–Irtysh interfluve territory.

On August 22, the flight of *Sympetrum* was observed along a 20-km segment of the Zdvinsk–Barabinsk asphalt road, in clear weather with a southwest wind of 5–8 m/s and an air temperature of about 30°C. Both *S. vulgatum* and *S. danae* were observed, the former species being an order of magnitude more abundant. The dragonflies flew upwind and across the highway running from northwest to southeast, which provided good conditions for observation. A quite uniform flow of dragonflies traversing the highway was recorded along the entire 20-km segment between approximately 11.30 a.m. and 2.30 p.m. A series of 10-min surveys showed that on average, 60 ± 8.7 tandems (range 48–70) traversed a 10-m segment of the road in 10 min, which corresponded to 6 pairs/min (Fig. 2). Thus, the flow of dragonflies across the entire 20-km highway segment could be estimated at 12 thousand per 1 min or 720 thousand per 1 h; the flight lasted for 3 h, during which over 2 million tandems, or over 4 million individuals, flew across this highway segment. Although the exact spatial extent of this migration could not be estimated, the observed segment was clearly only a small part of the territory covered by the flight. In any case, we can be certain that many millions of dragonflies took part in it.

On August 26, the flight of *Sympetrum* was observed from 11.30 a.m. to 1.40 p.m. in the steppe area between the Zaichikha River and Chulym Village, in

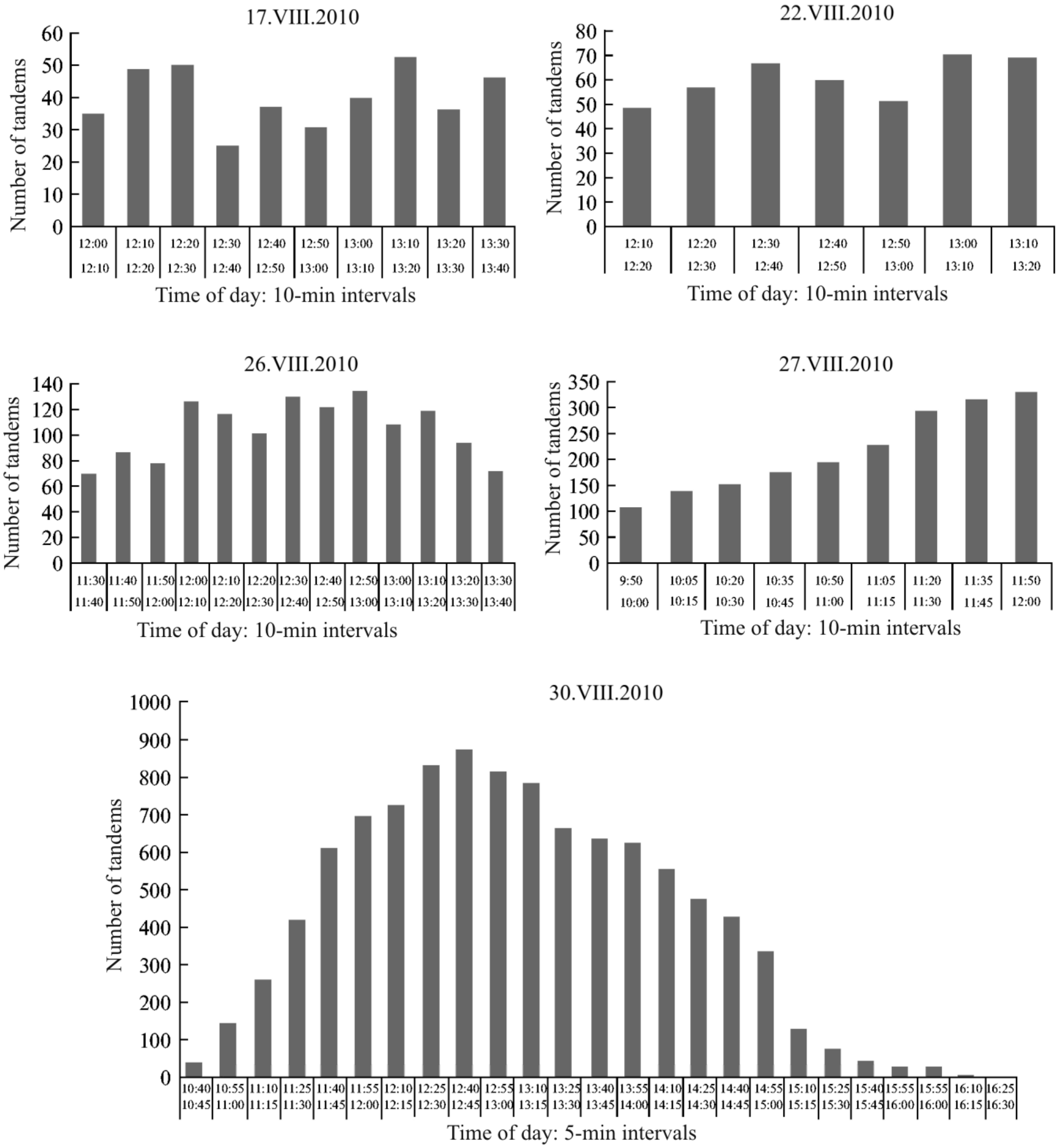

Fig. 2. The intensity of the flight of tandems of *Sympetrum* dragonflies.

clear weather with a west wind of 4–6 m/s and an air temperature of 24–26°C. A uniform flight against the wind was recorded over the entire observation area of about 25 km^2; its intensity was 103 ± 22.3 tandems (range 69–133) across a 10-m line in 10 min, which corresponded to 10.3 pairs/min (Fig. 2).

On August 27, observations of the flight of *Sympetrum* over Lake Fadikha were carried out from 9.50 a.m. to noon, in clear weather with a south wind of 3–5 m/s and an air temperature of 23–25°C. The dragonflies were surveyed from an anchored boat for 10 min, after which the boat moved for 5 min along the nearshore reed beds and dropped anchor again for the next survey. The tandems flew to the south, strictly against the wind, with the intensity of 211 ± 81.4 tandems (lim 105–330) across a 10-m line in 10 min, which corresponded to 21.1 pairs/min (Fig. 2).

The most extensive mass flight in the history of our observations was recorded on August 30. It occurred in clear weather within an air temperature of 23–25°C and north-northwest wind with the mean velocity of 5 m/s. The observations were carried out along a 1-km segment of the Lake Fadikha shore. The most intensive flight was observed between 11.40 a.m. and 2 p.m. (Fig. 2). The dragonflies flew in great quantities almost strictly to the north, at a small angle to the head wind direction. Up to 200 tandems were present simultaneously in the observer's field of view. Due to the difficulty of counting such great quantities of insects, we had to reduce the time of each survey to 5 min. According to the data of 10 surveys carried out during the flight peak, as many as 722 ± 94.8 tandems (lim 610–870) traversed a 10-m line in 5 min, which corresponded to 144.4 pairs/min. Thus, about 14 440 tandems flew across the 1-km segment of the lake shore in 1 min, which corresponded to over 866 thousand tandems per 1 h, or about 2 million tandems for the period of the most active migration which lasted 2 h 20 min.

The intensity of concerted flights of *Sympetrum* tandems was gradually reduced in September but these flights were observed until the end of that month. Although the reproduction of *S. vulgatum* and *S. danae* continued until the middle of October, the tandem flights became less frequent; regardless of the wind direction and the behavior of other tandems, the newly formed couples usually flew to the closest water bodies for oviposition.

In all the observed cases of unidirectional flight of dragonfly tandems, the swarm of migrating dragonflies always included a small fraction of solitary individuals of both sexes, which flew together with the tandems. Very rarely, the dragonflies formed "triplets," i.e., chains of three individuals, with the leading male using its claspers to grip the head of another male which, in its turn, gripped the female in the usual manner. The tandems and "triplets" displayed high maneuverability and were as difficult to capture in flight as the solitary dragonflies. Most tandems flew 1–3 m above the ground but some of them moved very close to the surface or, on the contrary, ascended to 10 m and more. When flying over water bodies potentially suitable for reproduction, some tandems alighted briefly for oviposition, after which they always moved on in the same direction. The fraction of such tandems was very small. For example, in the peripheral zone of Lake Fadikha, providing good conditions for reproduction of these dragonflies, only 12 tandems out of the 10 thousand that traversed the 10-m observation sector (0.12%) landed for oviposition on August 30.

Dissection of 20 females of *S. vulgatum* from the captured tandems showed that their abdomens were densely packed with eggs. On average, one female contained 1130 ± 235 mature eggs and about 100–200 smaller, immature eggs in the oviducts; in other words, the reproductive system of the flying females was perfectly ready for oviposition.

DISCUSSION

Data on the migrations of solitary dragonflies of the genus *Sympetrum*, but not of their tandems, were reported by many authors (for review, see Corbet, 1999). These dragonflies sometimes migrate from the places of emergence to the so-called "refugia" where they feed but do not reproduce, and return to the reproduction areas after aestivation. Such flights can be classified as regular seasonal interhabitat migrations (Haritonov and Popova, 2011). In particular, *S. frequens* in Japan is well known for its seasonal migrations from the plains to the mountains in July and in the opposite direction in September–October (Hiura, 1976a, 1976b; Miyakawa, 1976, 1994; Ban, 1980; Tanaka, 1983, 1985a, 1985b). These seasonal migrations of *S. frequens* depend not only on the terrain but also on the latitude: they are absent in Hokkaido but are regularly observed in Honshu to the south of 40°N (Miyakawa, 1994). No regular seasonal interhabitat migrations of *Sympetrum* dragonflies are known in the temperate belt of continental Asia to the north of 43°N; however, such migrations were described in more southern areas of Central Asia for *S. arenicolor* Jodicke, 1994, *S. striolatum pallidum* (Selys, 1887), and *S. meridionale* (Selys, 1841). They follow the same pattern as those observed in Japan: migration to the mountains in summer, reproductive aestivation, and return to the plains for reproduction in autumn (Borisov, 2008, 2009). The dragonflies *S. fonscolombii* (Selys, 1840) are characterized by southward latitudinal migrations: in autumn they migrate from their northern places of emergence to new reproductive biotopes in the more southern parts of their geographic range (Borisov, 2012).

There is little data in the literature on migration of *Sympetrum* dragonflies in tandems, whereas the proposed explanations of this phenomenon appear inconclusive. A flight of tandems on September 29, 1909 in East Prussia was reported by Bartenev (1915). Another description of the flight of tandems in Aragon, northern Spain was published by Codina (1910): on September 19, 1910, a great number of tandems, probably formed by *S. s. striolatum* (Charpentier, 1840), flew against the southwest wind from 8 a.m. to noon. However, the cited author made no attempt to estimate the abundance of dragonflies; as for the possible reasons of migration, he suggested that the insects could be trying to evade early cold spells or pursuit by flocks of swallows and starlings.

On October 8, 1921 a mass migration of tandems of *S. meridionale* was observed in the Hérault Department of France, near the Mediterranean coast (Lichtenstein and Grasse, 1922). The tandems were moving in a compact flow against the southeast wind of 5 m/s for at least two hours. The migrating swarm was estimated to be tens of kilometers long. The authors of the report tried to explain this migration by the hydrological conditions of the region or some combination of climatic factors but failed and finally characterized the phenomenon as enigmatic. It is interesting that the migrating *S. meridionale* were accompanied by small quantities of *Aeshna mixta* Latreille, 1805. It should be noted in this connection that Dyatlova and Kalkman (2008) recently described an aggregation of the same two species on the Black Sea coast near the Danube delta, on August 18, 2006. The aggregation counting tens of thousands of dragonflies was discovered in coastal reed beds in the afternoon (after 4 p.m.) and regarded as the result of mass migration. Since the weather on that day was hot and clear with a steady north wind, the cited authors suggested that the dragonflies were brought to the coast by the wind and accumulated in front of a water barrier. However, in our opinion, this aggregation may well have been the result of a typical migration of tandems which flew from the Danube delta against the wind and alighted in the afternoon, so that the researchers found the dragonflies already separated. This scenario appears quite consistent with the topography of this coastal area.

One more description of the tandem migration was published by Fraser (1945), who regarded this phenomenon as unique and inexplicable. The migration took place in Italy on November 1, 1945. The dragonflies (probably *S. s. striolatum*) flew against the south-southeast wind for several hours since 9 a.m., passing the observer with the frequency of about 60 pairs per minute. This description contains two interesting additional observations: (1) about 11 a.m. the wind changed by approximately two points of compass, and the dragonflies changed their course so as to keep flying against the wind; (2) during the time of observation, one pair of dragonflies formed the mating wheel and landed for a short time on the side of a gravel road, apparently for oviposition.

A detailed description of the migration flow of tandems of *S. vulgatum* with some admixture of *S. danae* flying over the city of Irkutsk on September 13, 1968 was published by Belyshev and Belyshev (1976). The dragonflies flew in the north-northwest direction against a light wind from 11 a.m. to 2 p.m. In all the parameters, this flight strongly resembled what we observed in the Baraba forest-steppe. The cited authors considered 7 climatic and biological factors which in their opinion could have triggered this large-scale unidirectional flight of dragonfly tandems. However, all the points on this list are in rather poor agreement whereas some of them appear far-fetched, for example, an assumption that the dragonflies mated "the night before the flight, i.e., on September 12" (Belyshev and Belyshev, 1976, p. 138). The authors then assumed that "late in the evening, the couples of dragonflies alighted for the night's rest, all of them being oriented with their heads towards the setting sun." However, our long-term observations and the abundant published data attest to the opposite: as a rule, dragonflies of the genus *Sympetrum* do not mate in the afternoon and do not spend the night in tandems, even though they may indeed orient themselves with their heads towards the setting sun (the direction depends not only on the sun's position but also on a number of other factors). Finally, in the following morning the dragonflies "took to the air and all flew to the northwest, i.e., in the same direction where they had been oriented" (p. 138). Even if we assumed that heliotropism in dragonflies is so strong that they always fly towards the sun, it would still be hard to believe that they would get their bearings from the position of the setting sun on the previous day, rather than from the actual position of the sun in the morning when the migration started (probably at 10–11 a.m.). Moreover, if the setting sun really determined the reference point for the following day's flight, all the mass flights would be directed to the northwest, whereas in reality dragonflies can move in any direction (Corbet, 1999; Haritonov and Popova, 2011). Thus, although the cited authors reported interesting factual data, they could not explain the phenomenon of mass flight of dragonfly tandems.

Migrating tandems of *S. frequens* were sometimes observed in Japan, besides the usual seasonal inter-habitat migrations of this species. For example, a flow of migrants flying to the south or southwest against the wind was observed on October 7, 1976 in the environs of Osaka (Miyatake, 1977). As many as 130 pairs flying in the same direction were recorded in 5 min; the cited author considered this "strange" flight to be a return migration to the places of oviposition. A mass flight of *S. frequens* tandems moving to the north from 8 to 9.15 a.m. was observed on September 24, 1984 in the town of Kawagoe; the number of tandems was characterized as "great" but the intensity of their flow was not estimated quantitatively (Miyakawa, 1994, p. 128). It is interesting that one more migration flow of this species was observed later on the same day, after 3 p.m.; however, it consisted of solitary individuals and was directed to the southeast. According to the data of the survey of the flying individuals, the intensity of the second migration flow could be estimated at 1.5 individuals traversing a 1-m line in 1 min. The cited author provided detailed data on the dynamics of the air temperature and illumination during the survey but did not specify such important weather factors as the velocity and direction of the wind. Having no actual data, we may only assume that in the morning the tandems flew against a north wind, whereas in the second half of the day their reproductive behavior was replaced by the usual seasonal migration of solitary individuals from the mountains to the plain, based on topographic landmarks and not depending on the wind direction. The different direction of the migration flights of tandems and solitary dragonflies was only ascertained in the cited paper but no explanation was proposed.

A migration of tandems of *S. vulgatum* was observed on August 12, 1982 in the region of Lake Neusiedler See in Burgenland, Austria. The tandems moved to the southeast from 11 to 11.45 a.m. These observations were not accompanied by any data on the wind, and the very fact of migration in tandems was regarded as strange (Harz, 1982).

To summarize the results of our observations and the published data, we may conclude that large-scale unidirectional flights of tandems of *Sympetrum* dragonflies constitute a peculiar and highly adaptive variant of dispersal facilitating the most uniform distribution of eggs over the landscape. Since dragonflies of this genus lay eggs not only in existing water bodies but also in any depression which is likely to be flooded with snowmelt waters in spring, the strategy of flying over the territory and laying eggs in all the potential reproductive biotopes appears to be advantageous. According to the observations, only a few individuals of the thousands of tandems passing by lay eggs even in the most suitable biotopes. However, since some of the dragonflies do lay their eggs "along the way," we may assume that the purpose of this migration is not to reach a certain area of oviposition but to spread eggs over the entire territory, in the "carpet bombing" manner. Eggs are laid in small batches as they get ready for oviposition; since the timing of this event varies between the tandems, oviposition by the large mass of migrating tandems should be quite uniform. The flying tandems do not form dense swarms which are typical of other types of migrations, but move in the same general direction in a wide front extending over whole landscapes. The direction of the entire migration flow is determined by the wind. Our observations and some published data (Fraser, 1945; Owen, 1957; Krylova, 1969; Mikkola, 1980; Borisov, 2009, 2010) indicate that at a moderate surface wind velocity, the migrating dragonflies always move against the wind. In case of long-distance latitudinal migrations, they wait for the head wind matching the needed direction of flight; whereas in case of tandem migrations observed by us, they would fly against the wind regardless of its direction. As the wind direction changes, so does the flight course of the tandems. As a result, the dragonflies fly over the same territory several times in different directions, which ensures a denser and more uniform distribution of eggs. Strictly speaking, the mass flights of tandems following the above scenario can hardly be called migrations; perhaps a better term would be "reproductive wanderings." In any case, such a dispersal strategy can maintain the most uniform population density and a more stable abundance of some dragonfly species in the territories lacking a stable network of water bodies.

ACKNOWLEDGMENTS

This work was financially supported by the Russian Foundation for Basic Research (grant no. 12-04-00824a).

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