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Migrations of Dragonflies (Odonata) in the South of the West Siberian Plain

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Abstract—The paper presents a summary of mass dragonfly migrations observed previously in Russia, in particular in West Siberia. From 1969 to 2009, the authors studied the dynamics of dragonfly population, their spatial distribution and movements in the West Siberian forest-steppe. The main studies were conducted in the Lake Chany basin (the Biological Station of the Institute of Animal Systematics and Ecology, Siberian Division, Russian Academy of Sciences). The spatial redistribution of dragonflies is regarded as a balance of homing and wandering behavior. Homing results in a relative stability of local dragonfly populations and assemblages, while wandering leads to dispersal of dragonflies from their emergence sites and colonization of new habitats; the latter is especially important due to the ephemeral nature of many shallow reservoirs where the nymphs develop. The formation of more or less constant migration routes is a peculiar variant of wandering activities. A special type of dragonfly migrations is mass exodus from native habitats, triggered by excessive population growth and leading to elimination of all or most individuals. Such migrations not only optimize the size of dragonfly populations but also facilitate removal of nutrients and organic matter from eutrophic water bodies. An original generalized classification of dragonfly migrations is proposed.

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Mass migrations are among the most interesting phenomena in the biology of dragonflies. Large-scale movements of these insects were described in many publications, most of which contained reports from the densely populated territory of Europe (for review, see Dumont and Hinnekint, 1973). The worldwide literature on dragonfly migrations was summarized by Corbet (1999), who proposed a complicated and sometimes inconsistent classification of the spatial movements of these insects. The nature and cause of dragonfly migrations are still quite obscure and seem to be an ever-topical problem in odonatology. The term “migration” itself can be variously interpreted (Williams, 1929; Kennedy, 1961; Southwood, 1962, 1977; Johnson, 1969; Taylor, 1986, etc.); in this communication it will be used in a broad sense, including the cases of dispersal from the initial habitats into the territories previously unexplored by the population.

Among Russian scientists, Rodzyanko (1892) was the first to describe a migration of dragonflies. Considering the cause of this phenomenon, he supposed that some species of dragonflies had a tendency to gather in flocks and blindly follow the leading individuals. A better known series of publications (Adelung, 1914; Sharleman, 1914; Averin, 1915; Kolosov, 1915; Bartenev, 1919) summarized the data on mass migrations of dragonflies that occurred in 1914 over the entire western half of the Russian Empire, including West Siberia and Kazakhstan. The migrating flocks of *Libellula quadrimaculata*, sometimes with a small admixture of other species, were observed from late April to early June over this enormous territory. Even though each of the authors who reported this phenomenon tried to determine the principal vector of the migrations, in fact the flocks moved in various directions. The migrations were regarded as the result of excess reproduction of one dragonfly species and the supposed “imitative behavior” of dragonflies forcing them to follow one another. Belyshev (1973) described in detail the initial phase of mass flight of the four-spotted chaser which he observed in 1948 in the upper Ob basin near the city of Biisk. According to these observations, the flocks of dragonflies moved from northeast to southwest, from the humid territories of the Ob valley towards the dry steppes of Kazakhstan. Belyshev proposed an original concept to explain dragonfly migrations, including 4 major points: (1) the migration is conditioned by several years of population growth under the conditions favorable for nymphal development; (2) a simultaneous mass emergence of adults follows a relatively long period of bad weather, which delays metamorphosis and synchronizes the final molt; (3) the first flight of many individuals starts simultaneously due to the imitative behavior of dragonflies; (4) the common vector of flight is determined by heliotropism of young adults, which fly in the direction conditioned by the position of the sun before takeoff.

We observed a mass flight of dragonflies near the city of Kurgan in 1969, in North Kazakhstan in 1981, and near the Lake Chany in 1988, 1998, and 2003. These observations, together with the results of long-term monitoring of the abundance and spatial distribution of dragonflies in the south of West Siberia, allow us to consider the problem of dragonfly migrations.

MATERIALS AND METHODS

Our work was carried out from 1969 to 2009 in the territories of Novosibirsk and Kurgan Provinces, Altai Territory, and North Kazakhstan. It included expeditions and stationary field studies at the Chany Biological Station of the Institute of Animal Systematics and Ecology, located near the Lake Chany within the Baraba area of the West Siberian forest-steppe. The species composition of dragonflies, the abundance of their local populations, spatial distribution, and movements were monitored every year.

The study was mostly carried out using the following methods: marking of dragonflies with colored wing labels, including the mark-recapture method of determining the population density; visual surveys along transects; capture of adults in various biotopes (in 15-min sessions); net-sweeping of herbaceous vegetation; collection of the nymphs by means of a hydroiological net or an aquatic volume biocenometer. As an additional method, adults of large dragonfly species were surveyed visually from moving cars or motorcycles. In all, 87 000 adult dragonflies were marked; the total length of survey transects was 3100 km, that of automobile and motorcycle routes, 2650 km; the total duration of 15-min capture sessions was 1406 h.

RESULTS

The observed dragonfly fauna of the Baraba area of the West Siberian forest-steppe consisted of 42 species from 17 genera and 6 families (Popova, 2007). According to the averaged data for all the years of observation, the dragonfly assemblage can be subdivided into 4 abundance groups (the scale of Pesenko, 1982): (1) **common** (15 species): *Coenagrion armatum* (Charpentier, 1840), *C. pulchellum* (Van der Linden, 1823), *C. vernale* Hagen, 1839, *Enallagma cyathigerum* (Charpentier, 1840), *Erythromma najas* (Hansemann, 1823), *Lestes sponsa* (Hansemann, 1823), *Sympecma paedisca* Brauer, 1839, *Aeshna mixta* Latreille, 1805, *Ae. serrata* Hagen, 1856, *Leucorrhinia pectoralis* (Charpentier, 1825), *L. rubicunda* (Linnaeus, 1758), *Libellula quadrimaculata* Linnaeus, 1758, *Sympetrum danae* (Sulzer, 1776), *S. flaveolum* (Linnaeus, 1758), and *S. vulgatum* (Linnaeus, 1758); (2) **moderately abundant** (6 species): *Lestes dryas* Kirby, 1890, *L. virens* (Charpentier, 1825), *Aeshna grandis* (Linnaeus, 1758), *Cordulia aenea* (Linnaeus, 1758), *Somatochlora metallica* (Van der Linden, 1825), and *Sympetrum sanguineum* (Mueller, 1764); (3) **scarce** (15 species): *Coenagrion johanssoni* Wallengren, 1859, *C. hastulatum* (Charpentier, 1825), *C. puella* (Linnaeus, 1758), *Ischnura elegans* (Van der Linden, 1823), *Nehalennia speciosa* (Charpentier, 1840), *Lestes macrostigma* (Eversmann, 1836), *L. barbarus* (Fabricius, 1798), *Aeshna affinis* Van der Linden, 1825, *Ae. juncea* (Linnaeus, 1758), *Ae. viridis* Eversmann, 1836, *Ae. subarctica* Walker, 1908, *Ae. crenata* Hagen, 1856, *Epitheca bimaculata* (Charpentier, 1825), *Somatochlora flavomaculata* (Van der Linden, 1825), and *Leucorrhinia dubia* (Van der Linden, 1825); (4) **occasional** (6 species): *Calopteryx splendens* (Harris, 1782), *Coenagrion ecornutum* (Selys, 1872), *Anax parthenope* Selys, 1839, *Somatochlora arctica* (Zetterstedt, 1840), *Orthetrum cancellatum* (Linnaeus, 1758), and *Sympetrum pedemontanum* (Mueller, 1766).

However, changes in the species abundance and the dominance structure were repeatedly observed. For example, comparison of the data of 15-min capture sessions of 2005 and 2006 (140 sessions every year near the Lake Chany) and the mean values for 1975–2005 shows that the species composition and relative abundance of dragonflies of the genera *Erythromma*, *Enallagma*, and *Coenagrion* have remained similar for 30 years, including 2005 (Fig. 1). The ratio of these taxa changed in 2006, and two new species *Coenagrion johansonni* and *Nehalennia speciosa*, not typical of the forest steppe landscape, were added to the species set. These two species were common in mid-July of 2006, even though they had been encountered only twice (single individuals in all the cases) during the preceding 30 years of monitoring. On the

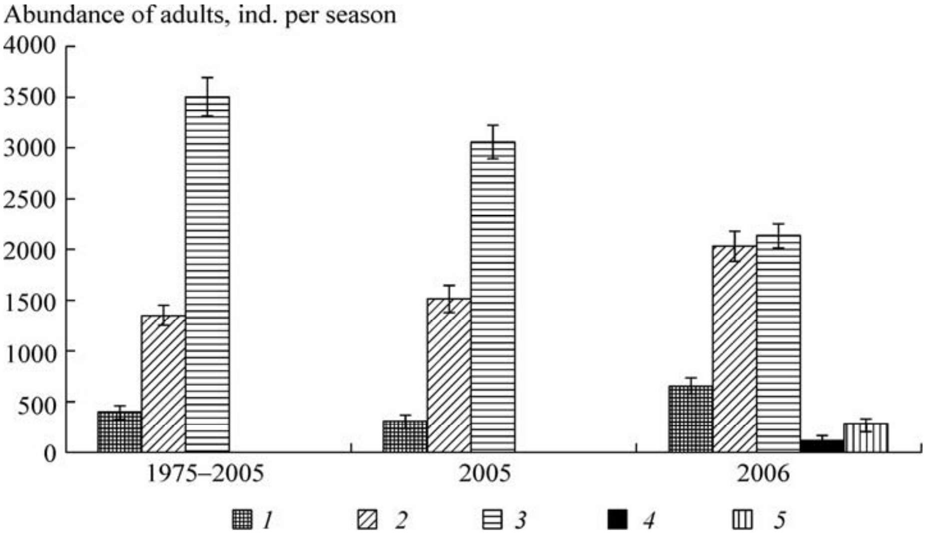

Fig. 1. The mean abundance of genera and some species of damselflies of the family Coenagrionidae near the Lake Chany: *Erythromma* (*1*), *Enallagma* (*2*), *Coenagrion* (*3*), *Coenagrion johansonni* (*4*), and *Nehalennia speciosa* (*5*).

contrary, some mass and common species became scarce (Popova and Kharitonov, 2008). Such abrupt changes in the composition and structure of the local dragonfly assemblage cannot be solely explained by population dynamics of individual species. They appear to be largely determined by spatial redistribution of the entire dragonfly assemblage.

Our observations of the variable composition of the local dragonfly assemblage and the appearance of uncharacteristic species agree with data for other territories. For example, 10–15 species of dragonflies originating from the mainland are observed every year on the North Sea islands and coast, although the local water bodies are unsuitable for nymphal development (Schmidt, 1974, 1980; Finch and Niedringhaus, 1996). Long-term observations of small ponds in continental Europe revealed large quantities of dragonflies passing them with or without transit stops (Corbet, 1999). The sudden appearance of numerous dragonflies of several species, usually not characterized by migrations, was recorded on American reservoirs as well (Soltesz et al., 1995).

During the period of observations, the density of local populations of different dragonfly species near the Chany field station fluctuated to a varying extent. Among the 21 species classified as common and moderately abundant, the density of 14 species remained relatively stable, the minimum and maximum values differing by no more than 3–4 times. At the same time, the abundance of 8 species (*Libellula quadrimaculata*, *Leucorrhinia pectoralis*, *Sympetrum sanguineum*, *Aeshna grandis*, *Coenagrion pulchellum*, *Enallagma cyathigerum*, *Lestes barbarus*, and *L. dryas*) varied by many times from year to year.

Especially great fluctuations were observed in *L. quadrimaculata*: the minimum and maximum densities of the local population of this species differed by 250 times (0.04 and 10 ind./m^2, respectively). At low densities of representatives of the family Libellulidae, they were more uniformly distributed over different biotopes, whereas at high densities the dragonflies tended to aggregate in the periphery of birch forests and reed thickets, which sometimes resulted in abnormal local crowding. For example, an aggregation of *L. quadrimaculata* with admixture of *Leucorrhinia pectoralis* and *L. rubicunda* which formed in early June, 1988 along the boundary of a birch forest occupied 400 000 m^2 and included about 4 million dragonflies (at the mean density of 10 ind./m^2). Given the average individual live weight of 0.31 g, the total biomass of the aggregation was about 1240 kg. This aggregation existed for four days, after which it started to diminish rapidly. The dragonflies left the aggregation mostly in the southern and southwestern direction, singly or in groups of different size, without forming "organized" flocks. By the middle of June the population density dropped to 0.7 ind./m^2, or less than one-tenth of the original value. Aggregations and migrations of dragonflies were observed in many localities of the West Siberian forest-steppe during that season.

The aggregations observed in the second half of summer are formed by representatives of the genera

Aeshna and *Sympetrum*, especially *Ae. mixta* and *S. vulgatum*. The aggregations of *Ae. mixta* appear in late August—September of every year on the borders of some birch groves. The concentration of dragonflies may be indistinct in some seasons and quite considerable in others. The largest aggregation of *Ae. mixta* was observed in 2002 in a birch forest near the Kargat estuary, the density of dragonflies in late August–early September reaching 1.4 ind./m^2. Dragonflies of the genera *Aeshna* and *Sympetrum* usually do not move in any particular direction, but there may be exceptions to this rule. For example, an intensive flight of *S. vulgatum*, directed from northwest to southeast, was observed in early August of 1993. The dragonflies flew in pre-copulatory tandems at heights exceeding 5 m; although the individual tandems were positioned no less than 10 m apart, the flight in general appeared to be an organized migration flow. Similarly directed but less distinct migrations of the tandems of *S. vulgatum* were also observed in 1974, 1981, 1982, 1989, and 1999.

It is known that the newly emerged dragonflies tend to fly away from their native water bodies and then return to them for reproduction. Annual route surveys in different biotopes showed that the dispersing adult dragonflies covered distances of many kilometers. We regularly observed dragonflies of at least 14 species at up to 18 km from the nearest water body, which is the maximum possible distance in the forest steppe zone where reservoirs are abundant. According to our observations made in Northeast Kazakhstan where reservoirs are sparser, the dispersal distance may exceed 50 km. These data suggest that many individuals, contrary to the common belief, never return to their native reservoir for reproduction. Mass marking of *Leucorrhinia rubicunda* on a small standalone reservoir showed that only 30% of males emerging in a local population during a season were observed in the reproductive stations of the same reservoir and participated in reproduction, whereas 70% migrated into other territories (Kharitonov, 1991, 1994). Similar results for species of the same genus were obtained in Finland. The males of *L. rubicunda* that emerge early, at the beginning of the period of metamorphosis, became resident on the same reservoir, while those emerging in a later period left the territory (Pajunen, 1962a). As the population density of *L. dubia* increased, the emerging young males also left the reservoir, while the mature ones stayed (Pajunen, 1962b). A similar situation was described for *Sympetrum danae* populations in Belgium, where up to 80% of the mature males observed on a reservoir proved to have migrated from elsewhere (Michiels and Dhondt, 1991).

The main area of our study, the Baraba forest-steppe, is characterized by large fluctuations of humidity, because of which many reservoirs may periodically become shallow, mineralized, or even dry up completely. Comparison of the survey data at different distances from reservoirs in the Baraba forest-steppe and the Salair forest-steppe characterized by a more stable humidity regime revealed no significant differences in the abundance of dragonflies at distances shorter than 0.5 km from the nearest reservoir; however, the number of dragonflies recorded at greater distances from the reservoirs in Baraba was 2–3 times as great as in the Salair area. This difference indicates a higher migration activity of dragonflies in the ecologically unstable Baraba forest-steppe.

At the same time, different variants of spatial distribution and movements of dragonflies may be observed even within the same local population. The reservoirs in the forest-steppe landscapes of West Siberia are usually overgrown with reed and have a relatively small area of open water. The nymphs of many dragonfly species inhabit both the reed thickets and the open part of reservoirs, i.e., they develop under considerably different conditions. According to our data obtained for the Fadikha Lake near the Chany biological station, this may lead to intrapopulation differentiation, not only in the age structure and spatial distribution but also in behavior. Before the emergence of adults, all the nymphal instars occur in the reed thickets, whereas only the middle and older instars are present in the open water area. The emergence of damselflies in this lake starts on average at the end of the first decade of May, when the daytime water temperature is stabilized at no less than 12–13°C. During the spring and summer season, the water temperature in the open area is on average 4–5°C higher than in the reed border (Popova, 2006). Adults of the “spring” species *Coenagrion armatum* and *C. vernale* first emerge, i.e., undergo the final molt, in the open water area. The young adults remain in this area around the clock and do not fly to the shore, which is not a typical behavior for damselflies. It is obvious that even tall reed thickets present no obstacle for these insects; they probably do not need to leave the open area, which provides abundant food (small dipterans) and night shelters along the inner boundary of the reed thickets. Several

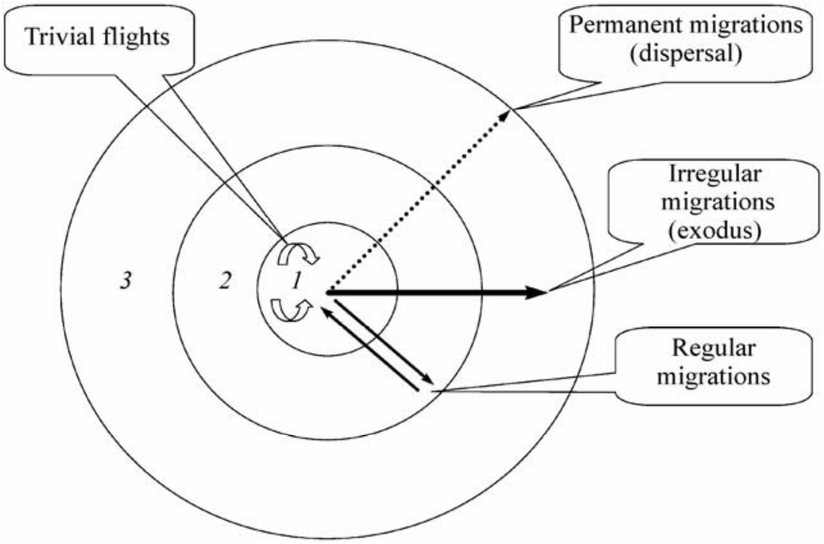

Fig. 2. The types of movements in dragonflies: the initial habitats (the reservoir where the adults have developed, and the adjacent territory) (*1*), the remote habitats (*2*), and the territory still unexplored by the species (*3*).

days later these damselflies reach maturity and start to reproduce in the same area. Until the end of the second decade of May these species can be recorded only in the water areas but are absent in the periaquatic terrestrial biotopes. At the end of the second decade of May, adults of *Coenagrion armatum* and *C. vernale* start to emerge in the reed border and fly to the shores. The second wave of emergence coincides with the appearance of young adults in terrestrial biotopes. These damselflies spend the feeding phase in terrestrial biotopes and then return for reproduction to the reed thickets where they had emerged. Thus, the populations of *C. armatum* and *C. vernale* include two ecological groups, associated with open water and reed thickets, respectively. Each group is characterized by specific traits of biotopic distribution, emergence, and adult behavior, demonstrating the flexible and polyvariant nature of migratory behavior.

DISCUSSION

Our long-term observations of the abundance, spatial distribution, and movements of dragonflies in the southern part of West Siberia allow us to state the following facts: (1) the composition and structure of the regional fauna is subject to considerable changes from year to year; some species not typical of the territory in question may appear in considerable numbers during some seasons; (2) many species of dragonflies after emergence disperse far from their native reservoirs, especially in regions with unstable humidity regime; (3) some species are characterized by wide fluctuations of abundance, which may change by tens and even hundreds of times; (4) the intensity of dragonfly migrations increases with their abundance; (5) some species of dragonflies tend to form dense local aggregations; (6) most of the mass migrations of dragonflies observed in the southern part of the West Siberian plain were directed southwards. Below we shall discuss the problem of dragonfly migrations and try to classify the movements of these insects considering the above facts.

First of all, it should be noted that most dragonfly species develop in shallow freshwater reservoirs, including temporary ones. This peculiarity of the environment determines the need for migrations in search for new reservoirs, the more so as these insects are highly mobile owing to their morphophysiological organization and mode of life. Dragonflies of different species move constantly in irregular ways, and their movements are quite difficult to classify. Proceeding from the existing terminology and typification (Kennedy, 1961; Southwood, 1962, 1977; Johnson, 1969; Taylor, 1986; Corbet, 1999), we propose a more general variant of classification including four principal types of movements of dragonflies (Fig. 2).

Trivial flights are short-term movements related to such direct and evident tasks as hunting, thermoregulation, escape from predators, evading bad weather, seeking mates, searching for places of oviposition, and defense of individual areas. This category also includes the first flight after emergence, which some authors distinguish as a separate type, the so-called maiden flight (Corbet, 1999). Many authors consider the maiden flight to be of crucial importance for the dragonfly, serving as a starting point of migration. Although this may be true in some rare cases, most frequently the maiden flight is indeed trivial, merely a short flight from the emergence site that is followed by up to several hours of rest. The insect often leaves the emergence site in a series of short flights with irregular intervals. In fact, the term “maiden flight” should refer not to a single act but to the entire set of takeoffs and landings during the first phase of maturation, before the beginning of hunting.

The category of trivial flights should also include regular daily movements between reproduction and feeding biotopes, and also flights to the night and weather shelters and back, even though such flights may cover several kilometers (Belyshev and Stepanchuk, 1964). Corbet (1999) regarded such movements as a special type of “commuting flights” which is hardly appropriate.

Permanent (dispersal) migrations are diffuse movements in search of resources and dispersal of some individuals from the sites of their emergence, resulting in colonization of new habitats. Dispersal is a realization of the universal strategy of territory exploration, establishment and expansion of the distribution range.

Although permanent migrations are a universal phenomenon, their intensity is different in different species; it may depend on the degree of stability of habitats, reaching the maximum in temporary reservoirs and territories with unstable humidity regime. Only part of individuals in the population takes part in dispersal. Although the fraction of such individuals may be small, the efficiency of colonization of new habitats is sometimes very high; this may be illustrated by rapid colonization of new artificial reservoirs (Parr, 1973; Popova, 1996, 1999; Borisov, 2007, etc.). The dispersing adults fly in all directions from the sites of emergence, singly or in small groups. These migrations are inconspicuous and can be revealed only by their results: local changes in the abundance or a sudden appearance of species new to the particular territory or reservoir. The intensity of permanent migrations increases with population density; in extreme cases the permanent migrations may be gradually transformed into a different type of movements, mass migrations.

Regular migrations are movements between remote biotopes or geographically separated territories along more or less strictly determined routes. This type of movements corresponds to the term “migration” in its strict sense. Regular migrations allow the species to use the territory in the most efficient way based on the adaptive experience of the population fixed in behavior.

Migrations of this type are quite rarely observed in dragonflies. Their regularity may be relative; although such migrations are species-specific, they usually occur only in particular regions or localities within the species range. The regular migration may involve the entire local population, for example, when the dragonflies leave an area affected by drought in a contrasting climate, or only part of individuals. The latter case was best studied in the American species *Anax junius* which performs large-scale annual migrations along the Atlantic US coast and the south of Canada. The local populations of the species are represented by two seasonal cohorts with different life cycles, one of which migrates and the other remains resident (May and Matthews, 2008).

Two variants of regular migrations can be distinguished:

(1) Seasonal meridional migrations: the adults migrate from the region of emergence to new areas of reproduction, and the return migration is performed by their offspring. Such migrations cover hundreds and thousands of kilometers. This variant appears to be quite rare, being known in a few species: *Pantala flavescens*, *Hemianax ephippiger*, *Sympetrum fonscolombei*, *Anax junius*, and some others. In the south of West Siberia, migrations of this type manifest themselves only by occasional appearance of temporary local populations of *A. parthenope*, probably consisting of migrants from the south. Due to the large spatial scale, these phenomena are still insufficiently studied despite the rapid accumulation of the relevant data (Belyshev and Kharitonov, 1981; Corbet, 1999; Srygley, 2003; Borisov, 2007, 2008, 2009; May and Matthews, 2008; Anderson, 2009, etc.).

(2) Seasonal interstational migrations: movements from the sites of emergence to the feeding biotopes, or “refugia” in the terminology of Corbet (1999) and back. They are usually connected with seasonal drying up of reservoirs or some other periodical changes of conditions at the emergence sites. These migrations vary in the distances covered: from hundreds of meters to many tens and even hundreds of kilometers. They often take the form of seasonal relocation from the hot

valleys to the mountains. Sometimes they are accompanied by reproductive diapause, because of which the duration of stay in the "outruns" may vary from several days to several months even in the same species. The migrating individuals may form very loose flocks and often fly in tandems. Such migrations are typical of some species of the genera *Sympetrum* and *Sympecma*, and may be also observed in *Hemianax ephippiger*, *Selysiothemis nigra*, and some other dragonflies. In the forest-steppe of West Siberia, dragonflies often migrate from reservoirs to isolated forest patches and then back to the reproduction sites. The seasonal interstational migrations were described by many authors (Kumar, 1972; Hiura, 1976; Miyakawa, 1994; Samraoui and Corbet, 2000; Borisov, 2005, 2006, 2007; Borisov and Kharitonov, 2007; Kharitonov et al., 2007, etc.).

Irregular (sporadic) mass migrations consist in expulsion of a great number of individuals from the habitats, or "dumping" of excess population without the purpose of colonizing new territories. As a result, most of the migrating individuals are eliminated.

Such migrations occur only in numerous and widespread species, mostly in those inhabiting eutrophic lentic reservoirs, and do not cover the entire distribution range. They are irregular but may be correlated with cyclic climatic changes, such as humidity fluctuations. In particular, in some temperate regions of Eurasia, including West Siberia, such migrations tend to occur with 10-year intervals. They are especially pronounced in *Libellula quadrimaculata*. The sporadic migrations involve many individuals, in some cases the great majority of the population. Once the migration has started in one local population, other populations may join it, sometimes forming enormous flocks. For example, the migrating flock of *Libellula quadrimaculata* observed by us in Kokchetav Province in 1981 included about 100 million insects or 30 tons of living biomass (the description of this migration and the method of estimating its parameters will be published separately).

There have been few attempts to estimate the number of insects in migrating flocks; such estimates are very coarse but still impressive. For example, Fontaine observed mass migration of dragonflies near the city of Ath (Belgium) and estimated their abundance at several hundred million (cited after Cornelius, 1866). Cornelius himself (1866) described the dragonfly migration on May 19, 1862 near Mettmann (Germany) and make calculations according to which the flock consisted of 2 400 000 000 ind. Even though this number may be exaggerated, the estimated size of 100 million individuals or more appears to be quite realistic.

Mass migration may be preceded by enhancement of permanent migrations and aggregation of individuals in isolated groves, reed patches, and other contrasting areas that attract dragonflies. The direction of flight appears to be random, although migrating insects often fly along linear landmarks, such as river beds (including dry ones), elongate elevations or depressions, roads, or railroads. Mass migration appears to be triggered by the visual stimulus, i.e., constant perception of numerous neighbors signaling the excess population density. This stimulus may act at the nymphal phase as well.

Further development of migration events may follow different scenarios. However, regardless of the particular variant, all the participants of the mass (in fact suicidal) migration enhance the exchange of nutrients between the neighboring ecosystems. It should be noted that the estimated biomass of migrating flocks is very great and that amphibiotic insects (with aquatic preimaginal phases and terrestrial adults) represent the main biological factor of the return transfer of nutrients from depressions (reservoirs) to watershed plain areas from which the nutrients are removed by natural drainage.

Since the proposed classification of dragonfly migrations (Fig. 2) reflects a complicated and largely continual phenomenon, the distinguished types are not absolute but may be transformed from one into another. For example, the inconspicuous "trickles" of permanent migrations (dispersal) may form a powerful flow of irregular mass migration in case of coincidence of some density-dependent population events, weather conditions, behavioral status, and other phenomena. On the other hand, some individuals participating in a regular or irregular migration may fall out of it and settle in a new locality, especially if this locality is really new (for example, an artificial reservoir still unexplored by the potential local competitors). In fact, this constitutes an act of dispersal, which is normally accomplished by permanent migrations.

The spatial movements of individuals in a local population may be determined by a balance between two opposite types of behavior: homing and wandering. It may be assumed that these types of behavior manifest themselves within the genetically determined reaction norm of the population and are modified by both internal and external factors. This phenomenon was demonstrated for a number of animal taxa (Begon et al., 1989) but was not specially studied in dragonflies.

The migrations of dragonflies are complex and multielement phenomena. A particular form of migration does not usually constitute a species' attribute but instead can be observed only in some places, in certain periods, and only in some individuals of a population. In view of this, it is hardly feasible to distinguish obligatory and facultative migrations in dragonflies (Corbet, 1999). In this case the "obligatory" migrations represent merely some part of the continuum of migratory behavior. The adaptive significance of migrations is quite obvious in many cases. Some of them occur in response to deterioration of living conditions or in "anticipation" of such events. The adaptive value of sporadic mass migrations may consist in optimization of the population density. However, the great scale and recurrence of such migrations suggests that this phenomenon may also have some ecosystemic significance and be regulated at a higher level than that of a population. Otherwise it would be difficult to explain the southern vector of most dragonfly migrations observed in the south of West Siberia, i.e., transfer of a considerable biomass of amphibiotic insects from excessively humid landscapes to more arid ones, less favorable for dragonflies.

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