ODONATOLOGICA

JOURNAL
OF
THE
SOCIETAS
INTER-
NATIONALIS
ODONATO-
LOGICA
S.I.O.

BIOGEOGRAPHICAL AND ECOLOGICAL DESCRIPTION OF THE ODONATA OF EASTERN VASYUGAN PLAIN, WEST SIBERIA, RUSSIA

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Results of the studies of odonate fauna, carried out in July 2006 in the odonatologically almost unexplored Vasyugan Plain, are presented. The studies concentrated in the northern and northeastern parts of the largest bog in the world, the Vasyugan Bog, and its surroundings. Large primeval complexes of *Sphagnum* bogs and fens and other accompanying habitats, man-made as well, were studied. 25 localities are briefly described and the occurrence of 35 recorded spp. is commented. Due to almost total absence of typically East Palaearctic spp. (only *Shaogomphus postocularis* found), the aspect of the odon. fauna in the studied area is similar to a certain degree to that known from central and eastern Europe, but with some differences in the species composition, abundance of many spp. and their habitat preferences. In *Coenagrion puella*, *C. pulchellum*, *Enallagma risi*, *Nehalennia speciosa*, *Gomphus vulgatissimus*, *Shaogomphus postocularis*, *Somatochlora flavomaculata*, *Leucorrhinia albifrons*, and *L. pectoralis*, the northern limit of their distribution appears further N than it was previously known. This suggests that the actual northern range limit of some of these species in W Siberia does not descend as sharply to the S as it was expected. The first known site of *S. postocularis* W of the Ob' river and on a perfect plain is also worth noticing. Among the most remarkable discoveries was the regular, area-wide occurrence of several previously poorly known in Siberia spp., such as *N. speciosa*, *Aeshna subarctica*, *G. vulgatissimus* and *S. flavomaculata*. Taxonomically interesting is the coexistence, in the studied area but not at the same localities, of two taxa considered as subspecies or separate species, *E. c. cyathigerum* and *E. (c.?) risi*. The fact of clear spatial separation and at most a minimum degree of intergrading (if any) of these 2 taxa suggests their full species status which would agree with morphological and recent molecular data. The regular and not rare presence of 2 androchrome *Calopteryx splendens* ♀ forms and ♂♂ with the wings coloured to the tips, as well as the occurrence of brownish wing 'smoking' of many ♀ *S. flavomaculata* and *S. arctica* are peculiar features of the Vasyugan odon. aspect. The ♂ segregation

in the 'triangle' of peat bog aeshnids, *Aeshna crenata*, *A. juncea* and *A. subarctica*, is described and discussed. Between *A. juncea* and *A. subarctica* it was very advanced, partially spatial and partially weather/temporal, between *A. crenata* and *A. subarctica* almost complete, spatial, and between *A. crenata* and *A. juncea* advanced, weather/temporal. These observations confirm the dominant position of *A. crenata* over the water table, and also suggest the lack of *crenata*-dominance off the water table. The reliability of adult diagnostic features, more and less commonly used to distinguish between *A. subarctica* and *A. juncea*, is discussed.

INTRODUCTION

The knowledge of ecology, biology, genetics and the current state of *Nehalennia speciosa* in Europe is already fairly advanced (BERNARD & WILDERMUTH, 2005a, 2005b; BERNARD & SCHMITT, 2007). On the contrary, still very little is known on *N. speciosa* in Western Siberia where its records were remarkably scarce (BELYSHEV, 1973; ZAIKA, 1974; KOSTERIN, 1987; KOSTERIN et al., 2001; BERNARD & WILDERMUTH, 2005a) though theoretically, considering an incomparably weaker human impact, the conservation status of the species there should be much more favourable than in Europe. To collect samples of *N. speciosa* for DNA studies and to complement the knowledge of the species with West Siberian data, an expedition to the odonatologically almost unexplored Vasyugan Plain was organized. The choice of the area was dictated by the fact that the Vasyugan Plain, extremely abounding in boggy habitats with *Carex limosa*, seemed to be very appropriate for the species.

An analysis of the literature (BELYSHEV, 1973) suggested that dragonflies of boggy landscapes of West Siberian Lowland had been studied only to a small extent so far. Therefore, the second, parallel aim of this expedition was to study, in all possible aspects, the odonate fauna of the area predominated by primeval large complexes of *Sphagnum* bogs and fens. The article presents results of the studies carried out in the largest bog in the world and other accompanying habitats in the Vasyugan Plain.

THE REGION STUDIED

The West Siberian Lowland and the Amazon Lowland are the largest lowlands in the world. A great part of the former, which is within the taiga zone, is substantially boggy, and the total area occupied by bogs has increased at a speed of 0.8 km^2 a year. The largest bog in the world, the Vasyugan Bog (53 000 km^2), occupies a part of the West Siberian Lowland – the very slightly elevated and flat Vasyugan Plain situated between the rivers of Irtysh and Ob'. It extends for 500 km from the WNW (approx 58ºN, 75ºE) to the SSE (approx 55º30'N, 83ºE) as a strip 75-175 km wide. It embraces about 800 000 lakes accumulating in total 400 km^3 of water and is drained by the rivers of the Tara, Om', Vasyugan, Parabel', Chaya and their tributaries. Administratively, this area is divided along its main axis between the Tomsk (N) and Novosibirsk (S) provinces, with the western part belonging to the Omsk province. This mostly peat-moss bog is not continuous: it has a fairly narrow axis of sublatitudinal orientation and side branches which like spurs protrude north and south from the axis. During

our expedition, we explored the two northeasternmost 'spurs' of the bog, called Bakcharskoe and Iksinskoe Bogs, and the Sambusskoe Bog included in a northern spur.

The elevations of the Vasyugan Plain descend from 160 to 100 m a. s. l. from S to N and NE (MESHCHERYAKOV, 1962). The surface of the interfluves is flat, with numerous shallow depressions of thermocarst and suffosion origin. The relief is very shallow and only near the rivers (such as the Shegarka, Iksa, Bakchar) erosion valleys of small water flows are expressed. The soils are formed from subaerial loess-like sediments which cover, with a layer 5-40 m thick, the clays and clayey sediments of lake origin. Hydromorphic soils play a great role in the area, with a variable expression of a relic humus horizon formed in meadow carbonate soils during the climatic optimum of the Holocene (LAPSHINA et al., 2000). The peat bogs covering a large part of the Vasyugan Plain are not connected with ground water and are formed due to the prevalence of precipitation over evaporation in conditions of a negligible water outflux on almost perfectly flat land surfaces (SOROKIN et al., 1999). The growth of the peat layer led to the formation of an inverted relief, where the former ridges of mineral ground, bearing forest islands, appeared surrounded by rising peat-moss bogs. At last they became relief depressions with open *Sphagnum* bogs and fens locally called 'galya'. In these bogs, the water usually flows through the vegetation and peat with quite a considerable speed (up to 20 cm/h). These mires form sources of brooks providing outflux of the bog waters into rivers (LAPSHINA et al., 2000).

According to reconstructions reviewed in LAPSHINA et al. (2000), the bogs of that area appeared first at the end of the Atlantic period and the beginning of the Subboreal time: at places with a 3.6-3.8 m thick peat layer, 5200-5500 years ago; in most areas, with a 2.5-3 m thick peat layer, 3000-3500 years ago. At first they were represented by swamps with *Equisetum*, which occupied the depressions. Very soon they extended beyond depressions, merged and occupied interfluves, leaving buried relic meadow soils. At that time the bogs changed to eutrophic swamp biocenoses with domination of *Carex*, which existed for a long time, leaving 1-1.8 m of peat. The impoverishment of mineral feeding and an increase in precipitation transformed them into mesotrophic *Scheuchzeria-Carex*, *Scheuchzeria-Carex-Sphagnum* and *Carex-Eriophorum-Sphagnum* associations. At the crucial moment of development the bogs enlarged so that water outflux along the slopes of the watersheds began. This led to the mesotrophic bogging of dark-coniferous and mixed forest on the gentle slopes of the Vasyugan Plain, while the watershed bogs passed into the oligotrophic stage of development (which has persisted until now). This occurred at the border-time between the Subboreal and Subatlantic periods, between 2000 and 2200 years ago. At that time overmoisted *Sphagnum* and *Eriophorum-Sphagnum* bogs and pine-*Sphagnum* associations appeared. 1500-1000 years ago the fruticulose-pine peat-moss complexes (locally called 'ryam') spread and became dominating. In Russian literature these *Sphagnum* and pine formations are called ridge-open bog/fen ('gryadovo-topyanye'), ridge-lake-open bog/ fen ('gryadovo-ozerkovo-topyanye') and ridge-open quaking bog ('gryadovo-mochazhinnye') complexes. In these Russian terms the "ridges" correspond to patches (with low pine) only slightly elevated above peat-moss open bog.

Out of the studied bogs, precise structural and climatic data have been available only for the Bakcharskoe Bog: size 10-25 × 150 km, peat depth 2.6-3 m, water pH 3.5-5 (LAPSHINA et al., 2000), mean annual precipitation 420 mm (7 mm in June), mean snow cover 90 mm, average humidity in the warm season 30-40% in the daytime and 100% at night (SOROKIN et al., 1999). In 1986, some irrigation was started with the aim of peat digging, but it was not successful and left only a marginal system of ditches.

There are also fairly numerous secondary aquatic habitats in the Vasyugan Plain. They are represented by various, mostly small man-made water bodies (pools and ponds on mineral substrate), situated in rare villages and along roads and tracks, and by fire-fighting pools, irrigation ditches and canals in peaty areas.

LOCALITIES

The localities together with dates of visits and brief descriptions of habitats are presented below:

(1) Sambusskoe Bog, 1 km S of the road Kyonga – Kedrovyi, 56 km E of Kedrovyi, 57º36'42" N, 80º32'21" E; 20 July; a small lake surrounded by the open *Sphagnum* bog (few dozens meters broad) and further by the vast peat bog overgrown with dense stands of low pines *Pinus sylvestris*; the wide transition mire zone around the open water table very flexible and almost impenetrable (in accessible places the depth of water 15-40 cm), with the vegetation typical of oligotrophic conditions: *Sphagnum* sp., abundant *Carex limosa* and *Scheuchzeria palustris* with the admixture of *Rhynchospora alba*, and very numerous *Drosera anglica*; nymphaeids represented by fairly abundant *Nuphar pumila*.

(2) Next to the bridge across the Emelich River on the road Kyonga – Kedrovyi, 11.5 km W of Kyonga, 57º29'06" N, 80º51'41" E; 20 July.

(3) The road from Vysokii Yar to Parbig, 15 km NE of Parbig, 57º17'48" N, 81º34'46" E; 20 July.

(4) Bakchar town, the Galka River (bridge on the road to Bogatyrevka up to 1.3 km S of it), 57º01'44"-02'25" N, 82º03'20"-04'04" E; 19 July; the small river (12-17 m broad) with the very slow current (faster only locally in corridors between vegetation) bringing brown turbid warm waters, depth up to 2 m, muddy deposits, vegetation locally abundant: predominating *Sparganium emersum* (partly with floating leaves), also *Butomus umbellatus*, *Carex acuta*, *Phalaris arundinacea*, *Glyceria* sp., *Sagittaria sagittifolia*, *Callitriche verna*, many dead tree trunks and branches in the water; surrounded partly by a spruce taiga, with aspens on the edge and willows on the river banks, and partly by open areas (with herbaceous vegetation and bushes) stretching from the town.
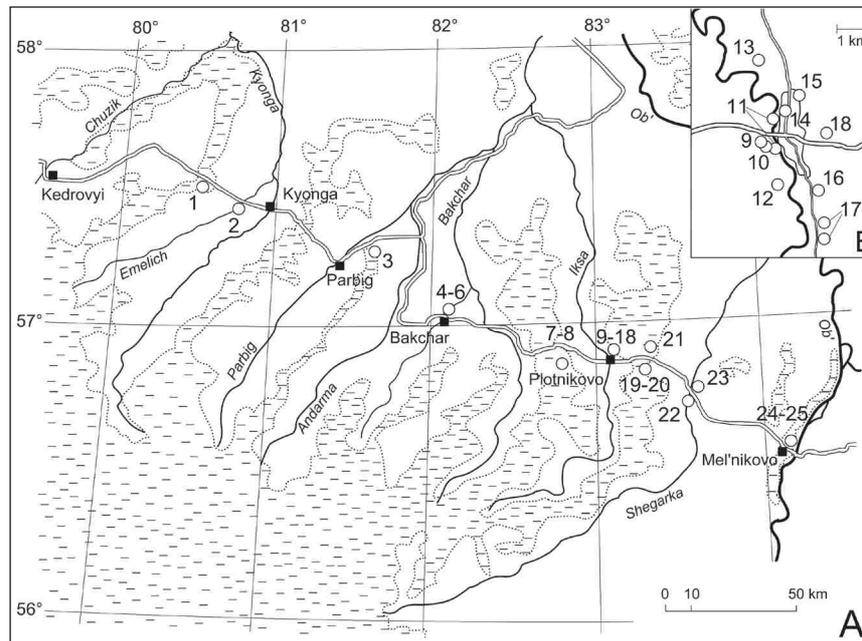

Fig. 1. Situation of studied localities: (A) in the investigated area; – (B) in the environs of Plotnikovo. Numbers correspond to the locality numbers given in the text.

(5) Bakchar, near the bridge on the Galka River, 57º02'22" N, 82º04'04" E; 19 July; a man-made small pool situated in open areas, bounded with high herbaceous vegetation and *Carex rostrata*, very abundant submerged and floating vegetation: *Lemna trisulca*, *Spirodela polyrrhiza*, *Hydrocharis morsus-ranae*.

(6) Bakchar, in the centre of the town, 57º01'22" N, 82º03'52" E; 19 July; a man-made large eutrophic pond with a clear water, without shore vegetation but with a 5-15 m broad zone of very abundant submerged and floating vegetation: mostly *Ceratophyllum demersum* and *Spirodela polyrrhiza*, additionally *Lemna trisulca* and *Hydrocharis morsus-ranae*.

(7) Bakcharskoe Bog, 14 km W-WSW of Plotnikovo, 4.5 km S of the road to Bakchar, 56º51'17" N, 82º51'01" E; 13 July; areas around the ecologists's hut – a sub-marginal zone of the large complex of *Sphagnum* bogs and fens; 'dwarf forests' of low pines *Pinus sylvestris*, dense shrubbery of *Chamaedaphne calyculata*, *Betula nana*, locally *Ledum palustre*, *Andromeda polifolia*, *Rubus chamaemorus*; old drainage ditches; a vast open poor fen (mainly *Carex lasiocarpa* with an admixture of *Equisetum limosum*) so suffused with water that impenetrable, in the summer the water only locally emerges above mosses, but in the spring it certainly occurs in large quantities on the surface; a fire-fighting pool with dark water and locally sedges on the banks.

(8) Bakcharskoe Bog, 14 km SW of Plotnikovo, 9 km S of the road to Bakchar, 56º48'44" N, 82º51'18" E; 13 July; oligotrophic pools (in the giant complex of peat bogs and fens), surrounded by an open *Sphagnum* bog mostly with Rhynchosporetum albae (*Rhynchospora alba*, *Carex limosa*, *Drosera anglica*, locally *Chamaedaphne calyculata*) and ridges of very low pines *Pinus sylvestris*; observations mainly in a zone of a partly flooded transition mire vegetation ('Schwingmoor') along the shores (*Sphagnum*, abundant *Scheuchzeria palustris*, *C. limosa*, *Menyanthes trifoliata*, also *R. alba*, *Utricularia* sp.; *Nuphar pumila* and rare *Nymphaea tetragona* floating on the water table), marginally in adjacent small depressions in *Sphagnum* mats, with water and sparse *C. limosa* and *S. palustris*.

(9) Plotnikovo village, 0.2-0.3 km W of the bridge on the Iksa River, next the road to Bakchar, 56º51'31" N, 83º03'48" E; 17 July; forest swamps with *Calla palustris*, *Carex* sp., abundant *Lemna minor*, numerous dead spruce and birch trees, a beaver lodge.

(10) Plotnikovo, 0.1 km WSW of the bridge on the Iksa River, near the road to Bakchar, 56º51'30" N, 83º03'52" E; 14, 21 and 22 July; small water bodies most probably post-excavation remains, situated in depressions in the very warm glade bounded by willows and a spruce-birch taiga; astatic and partly temporary pools (one larger and deeper, and a group of small and shallow) overgrown with abundant *Ceratophyllum submersum* and *Lemna trisulca*, with *Spirodela polyrrhiza* and flowering *Hydrocharis morsus-ranae* covering a large part of the water tables; locally *Carex pseudocyperus*, *Alisma plantago-aquatica*, *Typha angustifolia*, and *Calla palustris*.

(11) Plotnikovo, the Iksa River and its close surroundings S and N of the bridge, 56º51'20-41" N, 83º03'58"-04'21" E; mostly 12 and 14 July, marginally 21 and 22 July; the 15-25 wide river with brown turbid water, the current very slow but faster locally between patches of vegetation, bottom deposits muddy and locally sandy-gravely, vegetation locally poorer, mostly on the banks, locally abundant overgrowing also a large part of the riverbed: *Carex acuta*, *Butomus umbellatus*, *Sparganium emersum*, strips of *Nuphar lutea*; close surroundings partly with a dark taiga, but mostly open and sunny with rich herbaceous vegetation and numerous willows.

(12) Plotnikovo, a former oxbow of the Iksa River W of it (0.6 km W of S part of the village), 56º50'49" N, 83º04'20" E; 16 (mostly), 22 (marginally) July; a bow-shaped open area covered with a bog-fen complex predominated by *Sphagnum* and very abundant *Oxycoccus palustris*, with *Carex rostrata*, *C. lasiocarpa*, *C. diandra*, *Drosera rotundifolia*, *Scheuchzeria palustris*, *Equisetum limosum*; in the middle, a strip of *Comarum palustre* with sparse *Menyanthes trifoliata*, *Typha latifolia* and *Thelypteris palustris* and with water locally appearing on the surface; additionally a 'window' of open water among the peat-moss, 50x20 cm in size and quite deep.

(13) Plotnikovo, meadows N of the village, 56º53'10" N, 83º04'14" E; 15 July.

(14) Plotnikovo, field station of the Institute of Soil Science and Agrochemistry, the Siberian Division of the Russian Academy of Sciences, 56º51'41" N, 83º04'28" E; 12 July; meadow patches with tree stands descending to the high bank of the Iksa River.

(15) Plotnikovo, next to the track to Borodinsk (1.3 km N of the road to Tomsk), 56º52'10" N, 83º04'37" E; mainly 16, additionally 15 and 21 July; a man-made eutrophic pond (used by cattle) with a pasture on one side and an aspen grove on the other, the water cloudy and the vegetation rather poor (especially emergent): only rare *Alisma plantago-aquatica*, *Glyceria* sp. and *Carex* sp., locally, a 1 m wide shore belt of *Ceratophyllum submersum* covered with *Spirodela polyrrhiza*.

(16) Plotnikovo, the Yarushka Stream and the track just to the S of the village, 56º50'31" N, 83º05'14" E; 21 July; a 2-4.5 m wide forest stream, mostly shaded, bringing brownish water with a slow current between *Callitriche* mats.

(17) Plotnikovo, next to the track S of the village (2.2-3 km S of the road to Tomsk), 56º49'42"-50'09" N, 83º05'11-17" E; 21 July; two small man-made pools with very abundant *Ceratophyllum submersum*, covered with *Spirodela polyrrhiza* and *Lemna minor*, and bounded by abruptly ending walls of *Carex* sp. and *Glyceria* sp., and locally by *Typha latifolia*, *Eleocharis palustris* and *Alisma plantago-aquatica*.

(18) Plotnikovo, 0.5 km E of the village, next to the road to Tomsk, 56º51'17" N, 83º05'51" E; 12 and 21 July; a small (0.15 ha) roadside pool (surrounded by meadows) with clear shallow water on a loess-like substrate; abundant emergent vegetation: widespread *Eleocharis palustris* interspersed with scattered *Alisma plantago-aquatica*, some patches of *Equisetum limosum*, *Carex acuta*, *Phragmites australis* and *Typha latifolia*; on the water surface some floating leaves of *Potamogeton alpinus*; submerged vegetation: abundant mosses and *Lemna trisulca*.

(19) Iksinskoe Bog, S part, 2.4 km S of the road Plotnikovo-Tomsk, 56º50'05" N, 83º16'35" E; 18 July; two small lakes situated in the marginal zone of the giant peat bog, in the wide strip of open *Sphagnum* bog with *Scheuchzeria palustris, Rhynchospora alba, Drosera (anglica* more abundant than *rotundifolia), Oxycoccus palustris, Eriophorum vaginatum* and side pine ridges ('gryady'); the lakes separated and surrounded by mesotrophic fens with dense *Carex rostrata* and by more oligotrophic bogs; the water table bounded with a transition mire ('Schwingmoor' very suffused with water, partly flooded) with *Sphagnum*, abundant *Carex limosa* and *C. rostrata*, and some admixture of *Menyanthes trifoliata* and *Scheuchzeria palustris*; nymphaeids: *Nuphar pumila* and rarer *Nymphaea tetragona*.

(20) Iksinskoe Bog, S part, 1 km S of the road Plotnikovo-Tomsk, 56º50'55" N, 83º17'33" E; 18 July; a fire-fighting pool with dark but clear water and peaty shores, old drainage ditches and peat bogs overgrown with pine.

(21) Iksinskoe Bog, N part, 4.0-4.4 km N of the road Plotnikovo-Tomsk, 56º54'00-18" N, 83º17'05-19" E; 23 July; three small lakes situated in the vast *Sphagnum* bog, in its open strip; one mesotrophic, rimmed with *Carex rostrata*, one poorer in nutrients with *C. rostrata* and *C. limosa*, and one oligotrophic with much rarer *C. rostrata* and a belt along the shores formed mostly by *C. limosa*, *Menyanthes trifoliata* and *Scheuchzeria palustris*; nymphaeids: *Nuphar pumila* and *Nymphaea tetragona*; in the surroundings, *Sphagnum* mats very suffused with water overgrown with *Rhynchospora alba*, *C. limosa*, *Drosera anglica* and *D. rotundifolia*.

(22) Tazyrachevo (Tyzyrachevo) village, an oxbow of the Shegarka River SW of the road to Tomsk, 56º44'29" N, 83º33'46" E; 17 July; the large oxbow surrounded by a 'cedar' forest (*Pinus sibirica*) on one side, and birch groves and a degraded meadow on the other side; muddy ground and eutrophic but clear water with a thick rim of high *Bolboschoenus maritimus* and some *Cicuta virosa*; in the open water abundant *Lemna trisulca* and *Ceratophyllum submersum* covered with *Spirodela polyrrhiza*; patches of *Nuphar lutea*.

(23) Tazyrachevo (spelling on maps; according to the road sign – Tyzyrachevo), the Shegarka River and its surroundings, from the bridge to 0.25 km NE of it, 56º44'39-45" N, 83º34'08-20" E; 15

and 17 July; the river at the studied section is slightly different than Iksa and Galka: colder and faster, with a more recognizable current, the water slightly turbid but not brown, bottom deposits muddy and sandy-gravely, locally argillaceous, less (only locally) vegetated in shore zones with *Carex* sp., *Butomus umbellatus* and *Sparganium emersum*; the river is partly sheltered by fairly high river slopes overgrown with willows, and surrounded both by forests and open areas.

(24) Obskoe Swamp and adjacent meadows, near the road Mel'nikovo – Staraya Shegarka, 56º32'45"-33'06" N, 84º06'32"-07'02" E; 15 July; the very wide strip of swamps in the floodplain of the Ob' River, hardly penetrable, overgrown with low birches, willow thickets and abundant herbaceous vegetation (mostly *Carex paniculata*, *C. pseudocyperus*, *C. rostrata*, *Caltha palustris, Comarum palustre,* and *Menyanthes trifoliata*), also in reeds and quaking bog patches; in the swamps, a pool of open water with *Typha latifolia*, *Acorus calamus* and *Carex lasiocarpa*; between the swamps and a side western branch of the Ob' River, an overgrazed, rather ruderal meadow, bordered with tall *Salix alba*.

(25) Side W branch of the Ob' River near the road Mel'nikovo – Staraya Shegarka and the Obskoe Swamp, 56º32'59" N, 84º07'06" E; 15 July; the river with turbid water and a fairly fast current.

ANNOTATED LIST OF SPECIES

In the annotated list of species the numbers of localities correspond to the numbers given above. The following abbreviations are used: VA: very abundant, − A: abundant, − FA: fairly abundant, − M: in moderate numbers, − FR: fairly rare, − R: rare, − VR: very rare, − S: single; − Col.: collected, − ten.: presence of teneral individual(s), − ex.: exuviae. The collected specimens are in the collections of: i: R. Bernard, − ii: Faculty of Biology, Adam Mickiewicz University, Poznań, Poland, − iii: O. Kosterin, − iv: Siberian Zoological Museum, Institute of Animal Systematics and Ecology, Novosibirsk, Russia, and − v: Hessisches Landesmuseum, Darmstadt, Germany.

Calopteryx splendens (Harris, 1782)

4: VA, also androchrome females, Col. 27♂ (21 typical, 6 coloured to the tips of the wings), 19♀ (6 typical, 6 androchrome coloured to the tips of the wings, 7 androchrome f. *faivrei*); – 11: FA, also androchrome females, Col. 1♂, 6♀ (3 typical, 2 androchrome coloured to the tips, 1 androchrome f. *faivrei*); – 23: M, only 1 androchrome female, Col. 2♂, 1♀.

Seems to be widespread and mostly abundant, especially in vegetation-rich sections of the rivers. At loc. 4, visual counting and collecting showed a fairly considerable proportion of males with the wings coloured to the tips (6/27 counted, 22%) and a slight advantage of androchrome females (19/34 counted, 56%) over typical ones (15/34, 44%). More than one third of the androchrome females (37%) represented f. *faivrei* with gradually clearing tips of fore wings while almost two thirds (63%) had the wings coloured up to the tips inclusive. Generally, the former constituted ca 21% of all counted females (7/34) and the latter 35% (12/34). The inner end of the coloration varied. In the most extensively coloured females it reached 50-60% of the length between the nodus and the wing base. In the least coloured, it occurred at nodus level or only slightly exceeding it, and such cases were not rare. The proportions evaluated do not fit any simple model of inheritance which would explain all the alternative wing colour morphs observed in both sexes through a single genetic factor. Another population with a

high proportion of androchrome females (including f. *faivrei*) and males with the wings coloured to the tips was discovered by O. Kosterin in the Todzha Hollow in northeastern Tyva Republic, Central Siberia in 2000 (KOSTERIN & ZAIKA, 2003) and 2004 (unpublished). Before these records, androchrome females were considered extremely rare in Siberia (cf. BELYSHEV, 1973), but nevertheless provoked a persisting false notion of the existence of a second species, *Calopteryx johanseni* Belyshev, 1955 (originally described in the subspecies rank) which is in fact identical to f. *faivrei*. The range of spots in the wings of some males as well as the high percentage of androchrome females partly resemble some Turkish populations of the species known as *C. s. intermedia* (DUMONT, 2006).

Noteworthy is the complete absence of *Calopteryx virgo* (L.) which is still unknown for the large area of West Siberia between the Tobol-Ishim interfluve (a map point in BELYSHEV, 1973) and Tomsk (BARTENEF, 1910). The Altaian localities given by BELYSHEV (1973) concern in fact *Calopteryx japonica* Selys, 1869, considered by this author as conspecific to *C. virgo* (MALIKOVA, 1995). However, *C. virgo* was recorded in Siberia even further east, from Bunbuy, Krasnoyarskii Krai (3/6-VI-1915, Valdaev leg.), noteworthy that sympatrically with *C. japonica* (MALIKOVA, 1995).

Lestes dryas Kirby, 1890
10: R, Col. 1♂, 1♀; – 17: R, Col. 3♂; – 18: A, tandems, Col. 1♂, 1♀.

Not widespread, recorded only in secondary habitats on mineral grounds.

Lestes sponsa (Hansemann, 1823)
1: A, ten., Col. 2♂, 1 ex.; – 5: VR, Col. 1♂; – 8: A, ten., Col. 1♂, 2♀; – 10: R, ten., Col. 1♀; – 11; – 15: Col. 2♂; – 17: A, tandem, Col. 2♂, 1♀; – 19: A, ten., Col. 1♂, 1♀; – 21: A, ten., Col. 3♂, 6 ex.; – 22: FA, tandem, Col. 2♂; – 23: R, tandem, Col. 1♂; – 24: R, Col. 2♂.

Widespread, common and abundant, inhabiting both primary and secondary habitats.

Lestes virens (Charpentier, 1825), ssp. *vestalis* (Rambur, 1842)
8: Col. 1♂ ten.; – 18: VA, ten., Col. 1♂, 1♀.

Scarce, however, may be locally very abundant. The rarity is probably a result of situation of the studied area at the northern border of the species' distribution (cf. BELYSHEV, 1973). The thoracic pattern is typical of the ssp. *vestalis*, however, the individuals observed in the field seemed to be smaller in comparison to those from central Europe. BELYSHEV (1973) considering the West Siberian *virens* wrote about its transitional size between East European *vestalis* and a small Asian subspecies, *marikovskii*.

Sympecma paedisca (Brauer, 1877)
11: Col. 1♀ old; – 15: FR, only ten., Col. 1♀; – 22: FA, only ten., Col. 3♀.

The teneral individuals of the new (summer) generation were observed only

four days after collecting the last representative of the old (spring) generation in the same village. These records suggest a 'time-touching' of these generations in the scale of a small area. This phenological phenomenon is rather typical in Siberia (e.g. KOSTERIN et al., 2001 and unpublished data), but in Europe there is rather a short break (several-week-long, mostly in July) between generations. Although very rare records show a possibility of occasional overlapping of generations also in Europe, but nobody has confirmed it in the scale of a small area so far (cf. JÖDICKE, 1997). The overlapping of generations in Siberia may result from a shorter and late warm season of the year. To adapt the life cycle to these conditions, the larval development is certainly faster and shorter. Though eggs may be laid in Europe already in April, an emergence starts in the last pentade of July (JÖDICKE, 1997). In Plotnikovo, there is no possibility to oviposit before early or mid-May, but on 16 July the emergence of the population was already quite intensive. The shorter egg/larval development combined with the delayed period of spring activity of imagines, and hence their later death, make 'the meeting of generations' possible.

Coenagrion hastulatum (Charpentier, 1825)

4: VR; – 5: R, Col. 2♂, 1♀; – 6: S; – 7 (pool): Col. 1♂; – 8: M, copulation, Col. 2♂, 3♀; – 10: R, tandem, Col. 1♀; – 11: M, tandems, oviposition, Col. 1♂; – 15: A, tandems, Col. 3♂, 1♀ androchrome; – 18: A, tandems, Col. 1♂; – 19: VR, Col. 2♂, 1♀; – 20 (pool): VR; – 22: FA, Col. 3♂; – 23: VR.

Widespread and the commonest coenagrionid in the studied area. Fairly eurytopic. It does not avoid even current waters, however, the occurrence of imagines is limited only to lentic shore zones of very slow and brown rivers. The question arises whether these imagines are native or originate from standing waters in the surroundings. The observed reproductive behaviour at the Iksa River weigh in favour of the former option.

Coenagrion johanssoni (Wallengren, 1894)

1: FA, Col. 3♂, 3♀; – 8: FA, tandems, Col. 3♂, 2♀; – 10: FA, ten., ovipositions, Col. 1♂, 1♀; – 11: 1 ♂, allochthonous; – 17: S, Col. 1♂; – 18: VA, ovipositions, Col. 2♂, 2♀; – 19: FA, ten., Col. 2♂, 1♀; – 21: M, Col. 6♂, 2♀.

Widespread and locally fairly abundant, related to standing waters, inhabiting both primary and secondary habitats but with a preference to the former. An important proximate cue for the species is an emergent fairly low vegetation (up to 50-60 cm high) providing important ultimate factors, at least the activity space and wind shield. This requirement, stressed in the literature (BERNARD & SAMOLĄG, 2002), underlay the clear opposition observed in the studied area, between inhabited and uninhabited localities. The former (lakes in *Sphagnum* bogs, a roadside pool) were rich in such vegetation while in the latter (man-made large ponds and small fire-fighting pools) it occurred at most in very small numbers. Two exceptions only confirm the rule. Small pools in Plotnikovo (No.

10) were poor in the emergent vegetation but they were situated in land depressions surrounded by dense bushes and trees which created a warm and sufficiently calm microclimate. The significance of dense shrubbery for this highly wind sensitive species was communicated by BELYSHEV (1966). On the other hand, an oxbow (No. 22) abounded in the emergent vegetation along the shore but not of the preferred structure as being too tall and dense. What is more, water was probably too eutrophic for *C. johanssoni* as the species prefers waters poorer in nutrients.

At loc. 18, a tandem of *C. johanssoni* was caught by male *L. dubia*. When the male had been eaten, the female managed to escape. This was an excellent example of the significance of more cryptic colours of females as the attack of *dubia* was directed at the much more bright male.

Coenagrion lunulatum (Charpentier, 1840)
   6: only 1 male, Col. 1♂.
The rarity of the species was related most probably to the very end of its flight season.

Coenagrion puella (Linnaeus, 1758)
   5: S, Col. 1♂; – 6: FA, tandem, Col. 4♂, 1♀; – 10: FA, tandems, Col. 4♂, 2♀; – 15: FA, tandems, Col. 1♂, 1♀; – 17: S, Col. 1♂; – 22: R, Col. 1♂; – 23: VR, Col. 1♀.
The known distribution of the species in Siberia reached 55-56º N (BELYSHEV, 1973; KOSTERIN et al., 2001). Therefore, the records in the studied area, where the species is local but fairly widespread, expand the species' known distribution limit significantly (at least 1º) north, up to 57º02'. Considering the moderate abundance of *C. puella* in this area as well as its European range reaching above 60º (DIJKSTRA, 2006a), an occurrence of the species even at higher latitudes in W Siberia is very probable. In the Vasyugan Plain, *C. puella* is a fairly regular inhabitant of secondary habitats, i.e. village and roadside ponds and pools, and very rarely occurs in primary habitats, exactly only in an oxbow of the Shegarka River. An abundant submerged vegetation and a higher trophy are their common features. A total absence of the species in water bodies in *Sphagnum* bogs and fens is noteworthy in comparison with the situation in central and eastern Europe where the species inhabits similar biotopes regularly. The narrowed habitat spectrum in the borderlands of the distribution is certainly an effect of a greater sensitiveness of the species in such a situation combined with more severe microclimatic conditions in some habitats there. This phenomenon is known also for many other dragonfly species, e.g. *Erythromma lindenii* (BERNARD, 2000) and *Aeshna crenata* (BERNARD, 2002).

Coenagrion pulchellum (Vander Linden, 1825)
   6: M, tandems, Col. 4♂, 1♀.
In Siberia, the species was known in the SW part up to ca 56º20' N, however,

was very abundant in the part of the Novosibirsk Province east of the Ob' River (BELYSHEV, 1973; KOSTERIN et al., 2001). The new locality situated more than 0.5º north (57º01') suggests the generally more northern run of the distribution limit of this species. The recorded rarity may result from the situation of the locality in the borderlands of the species range.

Enallagma cyathigerum (Charpentier, 1840) (*Enallagma c. cyathigerum* Charpentier, 1840)
   1: only 1♂, Col. 1♂; – 8: Col. 1♂; – 15: S, Col. 1♂; – 19: R, Col. 2♂; – 20 (pool): VR; – 21: FR, Col.: 6♂; – 22: VR.

Enallagma risi Schmidt, 1961 (syn. *Enallagma cyathigerum risi* Schmidt, 1961)
   4: M, autochthonous?, possibly originating from the pond (6), Col. 2♂; – 5: S, Col. 1♂; – 6: VA, Col. 16♂ 6♀.

Individuals of *Enallagma* collected during our expedition represented two distinct types. Specimens obtained at the pools in *Sphagnum* bogs, where they were never numerous, structurally represented the typical *E. c. cyathigerum*, with the pale tubercle protruding distally to the black terminal hook of the cerci. Some of them exhibited an abdominal melanisation (to a variable extent), with dark stripes of different expression appearing at the tergite sides. It was hypothesized that such melanised forms are environmental modifications (DUMONT et al., 2005). According to this view, the melanisation may be a response to severe microclimatic conditions, perhaps due to the larval development prolonged to two and more years, or this may be related to very low trophy of the habitat. A male from the pond in Plotnikovo belonged to the same subspecies. In contrast, a series of 19 males collected at the pond, the small pool and the Galka River in the town of Bakchar structurally represented *E. risi*, treated by some authors as the subspecies *E. cyathigerum risi* (e.g. SAMRAOUI et al., 2002; KOSTERIN, 2004) with the pale tubercle not protruding distally to the robust black hook but directed inwards and down beneath the hook (cf. KOSTERIN, 2004). In Bakchar, especially at the pond, individuals of *Enallagma* were astonishingly numerous and were not melanised. According to observations by O. Kosterin in many regions of S Siberia, a strong preference for large lentic or slow-flowing waters with an open surface, a great abundance of individuals and an absence of melanisation are characteristic of *risi*. Hence, during our expedition we faced a correlation between the morphological characteristics distinguishing the two taxa and the habitat type, and also the presence/absence of the variable abdominal melanisation (the last element, however, may be only a consequence of different habitat conditions). This correlation supports recent morphological and molecular data suggesting that these taxa are bona species (STOKS et al., 2005; TURGEON et al., 2005). However, the presumed reproductive isolation may be incomplete, since among 30 collected males of *Enallagma* two individuals looked intermediate between the two taxa as they had only a very narrow part of the pale tuber-

cle protruded distally and much larger its part situated proximally of the hook as in *risi*: one from the Sambusskoe bog and one from the southern part of the Iksinskoe bog. In Novosibirsk, just 200 km southwards, only *E. risi* occurs (BE-LYSHEV (1973) thought them *E. cyathigerum*) while in northern West Siberia only *E. c. cyathigerum* is known (KOSTERIN, 2004). The area of our study may represent a zone of contact of both taxa, most probably separated spatially but also possibly intergrading to a some extent. It is noteworthy that the flourishing population of *E. risi* is related to the man-made pond. This fact may result from a penetration of the more southern taxon northwards, into the range of *E. cyathigerum*, conditioned by human activity.

Erythromma najas (Hansemann, 1823)

6: VA, tandems, copulation, Col. 2♂, 1♀; – 8: VR; – 10: 1♂; – 11: 1♂; – 15: A, tandems, Col. 1♂, 1♀; – 22: A.

Moderately widespread, however, only locally in greater numbers. Spectrum of habitats seems to be narrower and preferences within it more recognizable than in central and eastern Europe. The species favoured eutrophic larger standing water bodies, both secondary and primary, with rich submerged vegetation (+ nymphaeids, pleustophytes) while at other localities, such as small man-made pools, natural poor in nutrients pools in peaty-miry complexes, slow rivers with nymphaeids, only single individuals were recorded or the species was absent at all.

Ischnura elegans (Vander Linden, 1820)

11: S, Col. 1♂.

The laconic data in BELYSHEV, 1973 suggest only a small amount of information on this species from Siberia. However, it was recorded in large numbers at medium-sized rivers at Novosibirsk and in Omsk, where also at some oxbows (KOSTERIN, 1996 and unpublished data; KOSTERIN et al., 2001). Extremely rare in the area of studies. Reasons for such a rarity are unclear. However, it is possible that specific brown Vasyugan rivers are hardly acceptable for the species.

Nehalennia speciosa (Charpentier, 1840)

1: R, only ♀♀, Col. 2♀; – 8: FR, Col. 6♂, 5♀; – 19: FR, copulation, Col. 5♂, 7♀; – 21: FR, Col. 2♂, 3♀.

Considering areas between 70° and 90° E, the new localities are situated ca 1.8°-2.6° north of the previous northernmost record near Novosibirsk (cf. BELYSHEV, 1973; KOSTERIN et al., 2001) and reach 57°36'N. This suggests that the actual northern range limit of the species in W Siberia does not descend so sharply to the south as it was previously considered (BELYSHEV, 1973; BERNARD & WILDERMUTH, 2005a), and remains possibly even more close to the level of 60° known from the record in the basin of the Konda River in the westernmost Siberia.

The older data on *N. speciosa* in W Siberia were scarce, hence it was regarded as a rare and local species (BELYSHEV, 1973). In the recent 30 years nothing changed in this opinion as only several records were added to the list (ZAIKA, 1974; KOSTERIN, 1989; KOSTERIN et al., 2001; BERNARD & WILDER-MUTH, 2005a; Yu.A. Yurchenko and A.Yu. Haritonov, unpublished data). Contrary to this view, *N. speciosa* has turned out to be a widespread and regular inhabitant of large complexes of *Sphagnum* bogs and fens in the studied area. However, it is worth noticing that, although seemingly omnipresent in pools in these bogs (recorded at every water body studied), *N. speciosa* was not so abundant there. Local populations were small or even very small with density of individuals low to very low and individuals (or their small groups) very scattered. This picture significantly contrasts with the situation observed at many European localities, most frequently being isolated and with a small area of appropriate habitats, where local populations are large with a high density of individuals (BERNARD & WILDERMUTH, 2005a). The presence of only old reddish bronze females and a state of *Carex limosa*, locally already turning yellow, suggest that we probably observed the final phase of the flight period. The low numbers of the species may be also partly related to more severe microclimatic conditions. Nevertheless, the pattern of the species occurrence in the Vasyugan Plain seems to be based on very numerous and dense but small local populations, probably forming extensive metapopulation structures. Fairly similar situation, with a higher density of small local populations was also observed in the Baltic States (BERNARD & WILDERMUTH, 2005a). However, taking into account the total size of the giant boggy area abounding in appropriate sites, the total population size of the species in the Vasyugan Plain is certainly enormous.

The habitat of *N. speciosa* in the Vasyugan Plain is the same as in Europe (BER-NARD & WILDERMUTH, 2005a), i.e. shore zones of pools with flooded and floating-sinking mats of vegetation with *Carex limosa* and *Sphagnum* sp. as the most important components and admixtures of *Scheuchzeria palustris*, *Carex rostrata*, and *Menyanthes trifoliata*. A quite interesting element at Vasyugan localities is the lack of the wind-shield (higher trees) adjacent to the *Nehalennia*-habitat; the nearest low pines (1-4 m high) were 20 m distant certainly not influencing the strength of the wind to a large degree. The significant wind-protection is frequently present at European localities and seems to be preferred by the species there (BERNARD & WILDERMUTH, 2005a). It is quite possible that the strength and frequency of winds in June-July in the continental Siberia is smaller than in Europe much more influenced by maritime climates.

Aeshna crenata Hagen, 1856

1: M, Col. 1♀, 4 ex.; – 2: Col. 1♂; – 4: M, territorial ♂♂; – 5: 1 territorial ♂; – 6: R, 1 territorial ♂ and a ♀ searching for an oviposition site; – 7 (fire-fighting pool): 1 territorial ♂; – 8: FA, Col. 1♂; – 11: FR, territorial ♂♂; – 12: S, probable oviposition; – 15: R, Col. 1♂; – 17: 2 territorial ♂♂; – 18:

2 territorial ♂♂, oviposition, Col. 1♀, 4 ex.; – 19: VA, oviposition, Col. 2♂; – 20 (pool): S; – 21: M, oviposition, Col. 1♂, 1 ex.; – 22: FR, ovipositions, Col. 1♂; – 24: 1 territorial ♂.

The widespread and very common, really omnipresent habitat generalist in the studied area.

Aeshna grandis (Linnaeus, 1758)
3: S, foraging; – 4: R, territorial, possible oviposition; – 5; – 6; – 9: A in a crepuscular flight; – 10: 2 territorial ♂, ovipositions; – 11: S; – 12; – 15; – 19: S; – 22: VA, ovipositions; – 23: FA, oviposition; – 24: R, oviposition.

Widespread and common, however, practically absent on pools in large complexes of *Sphagnum* bogs and fens. The most abundant in an eutrophic oxbow of the Shegarka River. An intensive low crepuscular flight of numerous *grandis* was observed in the beaver forest swamps near Plotnikovo up to 22:55-57 (the sunset for this place 22:07), i.e. almost to the end of the civil twilight (23:05).

Aeshna juncea (Linnaeus, 1758)
9: A in a crepuscular flight, Col. 1♂, 2♀; – 11: S, foraging; – 12: Col. 1 ex.; – 14: S, foraging, Col. 1♀; – 19: S, Col. 1♀; – 21: A, Col. 2♂, 1♀.

Rarer than it was supposed to be (only at 2 localities certainly autochthonous), however, most probably widespread and inhabiting more localities. Two reasons for this gap may be considered:
− presence of aggressive males of *A. crenata* driving *juncea*-males from a water body (a segregation between aeshnids, see below); if exuviae were not found, occurrence of *juncea* at the water body might have been overlooked,
− possibly the species avoids these *Sphagnum*-habitats which are too poor in nutrients (as pools in Sambusskoe and Bakcharskoe Bogs) and prefers more mesotrophic conditions as in the northern part of Iksinskoe Bog.

A crepuscular flight of several individuals in the beaver forest swamps near Plotnikovo was observed. They predominated in the first phase of the crepuscular activity of aeshnids at this site, around and after sunset (for this place 22:07), but later (probably already after 22:30) they were not observed among still numerous *A. grandis*. A mass flight of foraging individuals of this species was also observed in the early evening on 20 July somewhere above the road from the Sambusskoe Bog to Parbig. An early crepuscular flight seems to be characteristic of this species.

Aeshna subarctica Walker, 1908, ssp. *elisabethae* Djakonov, 1922
1: FA, Col. 1♂, 6 ex.; – 4: Col. 1♂ next to the river, allochthonous; – 8: Col. 1♂, 1♀; – 19: M, Col. 3♂, 3 ex.; – 21: FA, Col. 2♂, 1 ex.

BELYSHEV (1973) informed that *A. subarctica* is widespread in Siberia but everywhere rare and encountered in single individuals. On the contrary, the species appeared to be a regular and common inhabitant of large complexes of *Sphagnum* bogs and fens in the Vasyugan Plain, certainly omnipresent where pools sur-

rounded by *Sphagnum* mats and overmoist depressions in *Sphagnum* occur. In our opinion, this state may occur in the whole West Siberian Plain. Considering the thoracic pattern, most individuals represented f. *elisabethae* and only two were intermediate between it and f. *interlineata*: one male (to a small extent only) and one female (to a larger degree).

Aeshna viridis Eversmann, 1836

9: 1 ♀ in a crepuscular flight; – 22: M, oviposition, Col. 1♀; – 23: foraging (?), 2♂, 1♀, Col. 1♂.

Rare, however, this state was not a result of biogeography of the species but rather a domination of inappropriate habitats in the studied area. The behaviour of *A. viridis* above the Shegarka river was striking. One individual, most frequently a male, appeared several times above the water as soon as the sun hid behind a cloud, but very rarely in sunshine. It flew along an irregular route but mostly downstream and remained over the water table only for a short time (the female really briefly), coming back to the bank willows. In Siberia, *A. viridis* is mostly a crepuscular species, and its appearance in the early afternoon was obviously correlated with the ceased sunshine. Such *A. viridis* may be interpreted as foraging(?) individuals originating from another locality nearby, e.g. an oxbow – loc. 22.

An autochthonous occurrence of the species in a habitat without *Stratiotes aloides*, a large oxbow of the Shegarka river was interesting. The lack of *crenata*-pressure during our visit allowed *A. viridis* to be active above the water. Its male appeared only once but at least two females were repeatedly seen flying over the *Nuphar*-groups and between them and the *Bolboschoenus*-belt. Their specific flight over the *Nuphar* suggested a search for oviposition sites. And in fact, one of them (later collected) oviposited a longer moment into a leaf stalk of *N. lutea* which served as a surrogate for the favourite but absent *Stratiotes aloides*. In Europe, ovipositions in other plants than *S. aloides* are very rare (MÜNCHBERG, 1956; STERNBERG, 2000a; ASKEW, 2004) while in Siberia the situation is not completely clear. There are not rare records of clear association with *S. aloides* in W Siberia, e.g. at Novosibirsk, Chernyi Mys village in Ubinskoe district of Novosibirsk province, Artyn village in Muromtsevo district of Omsk province (KOSTERIN et al., 2001; SUKHACHEVA et al., 2003; A.Yu. Haritonov, pers. comm.), but there is also a statement (BELYSHEV, 1973) suggesting a lack of the association.

Gomphus vulgatissimus (Linnaeus, 1758)

4: A, possible oviposition and male-male tandem, Col: 4♂; – 11: A, Col. 2♂, 4♀; – 23: R, Col. 1♀.

Widespread and mostly abundant in appropriate habitats. So far, *G. vulgatissimus* was known in Siberia only from a group of localities in the small area situated between 30-70 km SE and 50-70 km ENE of Novosibirsk (KOSTERIN et al., 2001) where it was discovered in the 1990s. Additionally, a very doubtful old

record is known from the surroundings of Omsk, considered by BELYSHEV (1973) as erroneous; the species was not found there between the 1970s and 2007 by KOSTERIN (1996 and unpublished data). Therefore, among the most remarkable discoveries of our expedition was the occurrence of the species at each river studied by us in the Vasyugan Plain, 170 km N to 225 km NNW of the nearest known locality. This suggests that *G. vulgatissimus* is widely distributed in this area, and most probably reaches much further north than the northernmost latitude 57º02' recorded by us. The discoveries of *G. vulgatissimus* in SW Siberia only in the 1990s and 2000s may suggest the colonization of these areas from the west, which might proceed along the southern taiga zone rather than along the forest-steppe zone where most odonatological activity has been confined to. This could be interpreted as a range extension northeastwards related to climate change. Such an interpretation would correspond to a model used by RICHTER et al. (2005) which predicts that indications of global climate change should imply a geographical extension of *G. vulgatissimus*. However, it is necessary to be cautious in such an interpretation as the genesis of so late discoveries in Siberia is unclear. Considering the low intensity of earlier studies in the forest zone of W Siberia and even a complete lack of them in large areas (the Vasyugan Plain inclusive), overlooking the species was simply possible.

Worth noticing was the record of an anomalous male-male tandem of the species. This uncoordinated tandem was startled from a bank, crossed the river and landed quite high onto a willow bush where it was collected.

Shaogomphus postocularis epophthalmus (Selys, 1872)
   11: S, Col. 1♀.

Only one individual collected on 14 July on willows 100 m from the Iksa River. This locality, situated 185 km NNW from the nearest known population of *S. postocularis* at the Otgonka railway station (HARITONOV, 1981; KOSTERIN et al., 2001; KOSTERIN, 2005), became the first known site of this species west of the Ob' River, and the westernmost and northernmost record of this species. What is more, it was the first record of *S. postocularis* on a perfect plain, for earlier it was considered to occur in the northern and western foothills of the Altai-Sayan Mountain System (KOSTERIN, 2005).

Cordulia aenea (Linnaeus, 1758)
   15: S, Col. 1♂; – 19: Col. 4 old ex.; – 23: S, Col. 1♂; – 24: S, Col. 1♀.

Uncommon due to the very end of the flight season. All individuals were checked for the possibility of species/subspecies *Cordulia amurensis* (Selys, 1887) / *C. aenea amurensis* but according to the measurements given in BELYSHEV (1973) and DUMONT et al. (2005) they clearly represented the typical *aenea* with the male fore wing length 34.1 and 34.4 mm and female 34.6 mm, and with the male hind wing length 33.5 and 33.9 and female 34.0 mm. DUMONT et al. (2005) pro-

posed also the male hamuli as another discriminating feature, marking, however, the necessity of testing the validity of this feature across the range of the species. KOSTERIN & DUBATOLOV (2005) informed that the legends to the figures 5 and 6, depicting this characteristic in DUMONT et al. (2005), are confused with each other: in fact, the lack of concavity at the dorsal surface of the male hamulus is typical of *amurensis*. In this light, one male collected in the Vasyugan Plain, has this feature typical of *amurensis* but the hamulus of the second male is difficult to interpretation, rather intermediate between *aenea* and *amurensis*. This picture, completely contradictory to that showed by the wing length (being a reliable discriminating feature), signalises unusefulness of male hamuli in the determination between *aenea* and *amurensis*.

Somatochlora arctica (Zetterstedt, 1840)

4: Col. 1 dead ♀ in water; – 7 (ecologists' hut): several foraging individuals; – 10: FA, foraging, Col. 1♀; – 11: FA, foraging ♂♂ and ♀♀; – 12: S, foraging, Col. 1♀; – 13: R, foraging; – 14: A, foraging, Col. 2♂, 5♀; – 16: Col. 1 foraging ♀; – 18: foraging in surroundings, Col. 1♀; – 20 (bogs): single foraging ♀; – 22: S, foraging, Col. 1♀; – 23: Col. 1 foraging ♀.

Surprisingly widespread, almost ubiquitous, and generally abundant, however, these terms concern only foraging activity of this species, it seems that of females and immature individuals only. Foraging individuals were recorded over roads, roadsides, yards in a village, meadows, also over dry parts in large complexes of *Sphagnum* bogs, rarely at/near water bodies and rivers but always with non-breeding habitats. This picture shows that individuals of *arctica* disperse in huge areas around their original habitats. In contrast to the situation presented above we did not found/recorded any breeding locality of this species, any its reproductive activity (territorial males, oviposition), any exuviae! This resembles the situation described by DIJKSTRA & KOESE (2001) from Belarussian Polesse, where huge numbers of immature *arctica* were observed and there was no observation of *arctica* reproduction or breeding habitats. It seems that the breeding, stem habitats of this species in the Vasyugan Plain may be situated in more central, hardly accessible, largely flooded or more sinking parts of large *Sphagnum* complexes, possibly also in large areas of impenetrable mesotrophic fens overgrown with Caricetum lasiocarpae. After three first days of the expedition (12-14 July), foraging *S. arctica*, though still widespread, became much more rare. This striking decrease is interpreted by us as focusing of already mature individuals in and near these unknown habitats for reproduction.

Individuals with the wings 'smoked' brown or amber-brownish to a various extent (most frequently small or moderate) were encountered fairly frequently. This agrees with the data of BELYSHEV (1973) from the Middle Ob' Lowland, adjacent to the Vasyugan Plain in the north, where such a 'smoking' of wings was especially strongly developed in comparison to other regions of Siberia. Possibly, this significant tendency of 'smoking' is typical just of boggy parts of W Siberia.

Somatochlora flavomaculata (Vander Linden, 1825)

3: S, foraging; – 4: VR outside the river, in the village, Col. 1♀; – 7 (fen): R, copulation, (hut): 1 foraging ♀, Col. 2♀; – 10: 1 foraging ♀; – 11: R, foraging; – 12: FA, foraging, Col. 1♂, 2♀; – 13: foraging, Col. 3♀; – 14: M, foraging, Col. 2♀; – 18: FA, foraging in surroundings, Col. 1♂; – 19: S, foraging?, Col. 1♀; – 22: M, foraging above the glade; – 24: R, Col. 1♂.

Widespread and generally rather abundant. Mostly a foraging activity was recorded. However, we encountered the species also in habitats and behavioural situations suggesting an autochthonous occurrence, especially in the mesotrophic fen in Bakcharskoe Bog, but also in the localities 12, 18, 19, 24. The relative commonness of the species in the studied area remains in contrast to the previously known data. BELYSHEV (1973) gave this species in Siberia only from a rather small area around the Upper Ob' (up to 54º N), suggesting its isolated situation in the species range, and from a doubtful record near Tomsk (ca 56º30'). He stressed the occurrence of *S. flavomaculata* exclusively on lakes situated within or at pine forest. In the light of rich new data, collected by us between 56º32 and 57º17', the species compact distribution reaches significantly more northwards, indirectly confirming also the old Tomsk record. The habitat spectrum is also certainly wider as the species occurs in boggy areas probably inhabiting waters in bogs and fens and other small water bodies.

Worth noticing were numerous dark-winged, to a various extent, females. In their wings, next to an intensive amber colour, extending frequently along the anterior margins and comprising also bases, a brownish 'smoking' occurred. It was clearly recognizable in a part of wings or even covered non-amber areas almost completely. The variable feature of coloured wings were also stressed by BELYSHEV (1973) for west Siberian individuals. However, such brownish 'smoking' is extremely rare in the area of Novosibirsk (O. Kosterin, unpubl. data) and unknown in Europe (H. Wildermuth, pers. comm.).

Somatochlora metallica (Vander Linden, 1825)

2: Col. 1♀; – 4: A, Col. 3♂, 1♀; – 7 (drainage ditches): FR, Col. 1♂; – 11: VA, Col. 1♂, 1♀, 4 ex.; – 12: R, foraging, Col. 1♂; – 13: foraging, Col. 1♂, 4♀; – 14: Col. 2♂; – 15: VR; – 16 (stream): FA; – 20 (drainage ditches): single ♂; – 22: R, foraging (?) above the glade; – 23: FA, oviposition, Col. 1♂; – 25: S.

Widespread and common, abundant. An autochthonous occurrence of the species restricted only to current waters where occurred everywhere, from smallest (narrow canals in marginal zones of complexes of peat bogs and fens; the stream Yarushka) to medium-sized (Galka, Iksa, Shegarka, the side branch of the Ob' river), from very slow, almost without current (the narrow canals, Iksa, Galka) up to relatively fast (the side branch of the Ob' river). The individuals seem to correspond to the (dubious?) subspecies *abocanica* Belyshev as their pterostigma is black (magnified blackish-brown), however, hindwing bases are in most individuals not completely clear as there are remains of amber in their anal triangle. In some individuals, a very delicate yellowish-brownish 'smoking' occurs locally

on the wings, mostly in their distal parts. However, this feature seems to be of another nature than in other *Somatochlora*-species as it is more related to the age of individuals.

Leucorrhinia albifrons (Burmeister,1839)

19: S, Col. 1♂.

Only one territorial male in an appropriate habitat. This record considerably expanded the knowledge of the distribution of *L. albifrons* since it was situated more than 200 km N of the nearest known localities of the species at Novosibirsk (BELYSHEV, 1973; KOSTERIN et al., 2001; O. Kosterin, unpublished data).

Leucorrhinia dubia (Vander Linden, 1825)

1: M, tandem, copulation, Col. 1♀, 1 ex.; – 7 (fire-fighting pool): R; – 8: FA, Col. 1♀; – 10: S, autochthonous (?), Col. 1♀; – 18: FR, autochthonous (?), Col. 1♂, 2♀; – 19: A, tandems, copulation, Col. 1♀, 6 ex.; – 20: A (fire-fighting pool); – 21: FA, copulation, oviposition, Col. 1♀, 4 ex.

Widespread, regular and abundant inhabitant of pools in large *Sphagnum* complexes of peat bogs and fens. The individuals of the species present at two pools in Plotnikovo, with rich vegetation but completely without *Sphagnum*, may be treated as stray immigrants from *Sphagnum*-habitats. However, a marginal native occurrence of *L. dubia* in non-*Sphagnum* habitats is possible as in Europe as an effect of 'radiation' of neighbouring large stem populations from *Sphagnum* habitats (cf. e.g. STERNBERG, 2000b). This may be confirmed by Siberian habitats given in BELYSHEV (1973) where the relation to *Sphagnum* is not mentioned. At one of these pools in Plotnikovo, the male of *L. dubia* caught a tandem of *C. johanssoni* and ate the male while the female escaped.

Leucorrhinia pectoralis (Charpentier, 1825)

10: R, oviposition, Col. 1♂, 1♀.

Very scarce but autochthonous. BELYSHEV (1973) marked the northernmost locality of the species somewhere southeast of Novosibirsk but O. Kosterin found the species in Novosibirsk Akademgorodok (KOSTERIN et al., 2001, Kosterin unpubl. data). Therefore, the new locality is situated 215 km north of the previously known nearest site of the species.

Leucorrhinia rubicunda (Linnaeus, 1758)

5: S, Col. 1♂; – 10: A, copulation, Col. 1♂, 4♀; – 11: Col. 1♀ (allochthonous); – 17: R, Col. 1♀; – 18: A, oviposition, Col. 1♀; – 22: S.

The picture of a lower abundance of *L. rubicunda* than it had been expected might have been a result of the final phase of its flight season and a predominance of biotopes inappropriate for the species as it seemed to be related mostly to pools situated not in *Sphagnum* bogs. Considering a moderate abundance of *L. rubicunda* on 22 July at loc. 10, the end of its flight season in W Siberia, given for 20 July by BELYSHEV (1973) should be moved rather to the end of the month.

Libellula quadrimaculata Linnaeus, 1758

5; – 8: R, Col. 1♂; – 10: A; – 11: M, oviposition; – 12: FR, Col. 1 ex.; – 15: VA; – 18: FA; – 19: M; – 21: FR, oviposition; – 22: FR; – 24: R.

Generally widespread and common, but absent or very rare in waters poorest in nutrients (pools in Sambusskoe Bog, Bakcharskoe Bog). Man-made eutrophic pools and ponds, not related to complexes of *Sphagnum* bogs, seemed to be optimal for the species. Worth noticing was also the occurrence in lentic zones of a slow river.

Sympetrum danae (Sulzer, 1776)

5: R, ten., Col. 1♂, 1♀; – 10: R, ten.; – 15: VR, ten., Col. 1♀; – 17: S; – 18: VR, ten., Col. 2♀; – 19: VR, ten., Col. 2♀; – 20 (fire-fighting pool): R; – 21: R, ten., Col. 1♂, 3 ex.; – 22: FR, ten., Col. 1♂; – 24: R, ten., Col. 2♂, 1♀.

Widespread, fairly common, occurred in most of standing water habitats where it mostly was emerging. A teneral individual stuck on a leaf of *Drosera anglica* (loc. 19) was found.

Sympetrum flaveolum (Linnaeus, 1758)

1: Col. 1♀; – 3; – 4: A next to the river, Col. 1♂; – 5; – 7 (fen): R; – 8: R; – 10: FA, Col. 2♂; – 11: R, Col. 1♂; – 12: A, tandems, Col. 2♂, 1♀; – 17: R, tandem; – 18: Col. 1♂, 1♀; – 19: FR, tandems, copulation, oviposition, Col. 2♀; – 20: scattered; – 22: A in the surroundings, Col. 1♂; – 23: A at meadows, FR at the river, tandems; – 24: FR, tandems, oviposition, Col. 1♂, 1♀.

Widespread and common, recorded everywhere; it seemed to be rarer and not abundant only in large *Sphagnum* complexes of peat bogs and fens. Many individuals of this species were parasitised by Hydrachnida, and bore their larvae (frequently large and red) from 1 up to 117 per one individual.

Sympetrum sanguineum (O.F. Müller, 1764)

10: VR, Col. 1♂; – 23: S, Col. 1♂; – 24: VR, Col. 1♂.

Rare as the studied area is situated at the northern limit of the species distribution (BELYSHEV, 1973).

Sympetrum vulgatum (Linnaeus, 1758)

6: S; – 20 (bogs): S, Col. 1♀; – 23: S, Col. 1 teneral ♂.

Rare, probably mainly due to the late flight period, in Siberia from 15 July at the earliest (BELYSHEV, 1973).

SEGREGATION BETWEEN AESHNIDS

The partially spatial and partially temporal/weather segregation in the 'triangle' of peat bog aeshnids, *A. crenata*, *A. juncea* and *A. subarctica*, was observed in large Vasyugan *Sphagnum* complexes, in a complete form in the Iksinskoe Bog where all three species were recorded. *A. subarctica* was strictly related to *Sphagnum* carpets surrounding pools, especially to very wet and sinking or shallowly

flooded parts of them overgrown with low *Rhynchospora alba*, *Carex limosa* and *Drosera* species. The area of activity of males might occasionally reach a border between shore vegetation and the open water table, however individuals preferred to remain several and more metres from it. Activity of territorial males was restricted to better weather conditions (sunny and warm, at least subdued sunshine), and was characterized by low flights, mostly 40-70(90) cm above the ground and 30-50(80) cm above low *Rhynchospora*, with frequent stops with hovering.

Territorial males of *A. crenata* were flying over the open water table up to several metres from the shore vegetation. Their behaviour resembled that described in detail in Lithuania (BERNARD, 2002). During territorial flights-'loops' they approached a shore line, sometimes 'hooking' it but deeper than 1 m penetration of *Sphagnum* mats was rare and restricted to short moments, so marginal. Therefore, the spatial segregation between *A. crenata* and *A. subarctica* was strict: when the heterospecific males met near the border of open water and mire, any *subarctica*-intruder was chased away from water. It was interesting that if the meeting took place above the 'land' (several observations), some metres deep over *Sphagnum* mats, *A. subarctica* was the winner in spite of being smaller, chasing *crenata* away. Territorial activity of *crenata* was, similarly to *subarctica*, rather restricted to better weather conditions when it was sunny (at least subdued sunshine) and warm. Males were absent when it was overcast. This restriction does not contrast with the activity at Lithuanian localities continued also when territories became shaded by forests (BERNARD, 2002) as during observations in Lithuania was very calm, warm and the sun was still shining around the shaded places while at the Siberian locality was less warm and rather windy in these cloudy periods.

A. juncea was a lacking piece in this puzzle until last day of our studies. The species seemed to be absent in large *Sphagnum* complexes but this day showed that this might have been an effect of weather conditions which were too good at previously studied localities. When we had arrived at small lakes in the northern part of the Iksinskoe Bog, it was still overcast and aeshnids were represented only by *A. juncea*. Fairly abundant males regularly patrolled along the border line of vegetation mats just before them over the water or, at most, exactly over the border line of vegetation and open water. They sometimes visited places 1-2 metres (occasionally several metres) distant from the open water. During the patrolling flights over the water individuals stopped and hovered in flight with the head directed at the border vegetation, most probably searching for females. A copulating pair in sedge at the very water was also observed. After some time the sun, at first subdued, then clear, appeared, and males of *A. crenata* and *A. subarctica* immediately appeared. At first the impression arose that *A. juncea* had completely disappeared suggesting a total weather separation of that species and *A. crenata*. However, later we noticed and collected several males of *A. juncea* which flew typically low along the very shore even in the sun, but never were male *A. crenata* nearby. When appearing, they chased *juncea* away. What is more, half a minute

after collecting of a territorial *crenata* a territorial *juncea* appeared in that place taking the opportunity. This resembled the cases with *crenata* versus *cyanea* and *subarctica* described from Lithuania (BERNARD, 2002)

A spatial segregation between *A. grandis* and *A. crenata* (dominant) was documented on the Galka River where *grandis*-individuals occupied only places without *crenata*. When both species encountered, *grandis* avoided *crenata* due to its flight at a greater height.

A segregation between *A. crenata* and *A. viridis* was not directly observed during the expedition, however, the picture recorded at the oxbow of the Shegarka River probably reflected this state. A temporal absence of aggressive males of *crenata* or their general rarity (only females occurred) made a presence of *A. viridis* possible. It is quite possible that males and females of the latter meet and copulate normally far from breeding habitats being under *crenata*-pressure. The willows next to the Shegarka River, where we observed both sexes, might have been such a place.

DISCUSSION

One important result of our expedition is the picture of the summer aspect of the odonate fauna in these mostly primeval and remote boggy areas. In total, 35 odonate species were recorded, that is quite a few for an area of that size situated at such latitudes in Siberia and having a rather narrow spectrum of habitats predominated by large complexes of *Sphagnum* bogs and fens, and slow rivers bringing brown waters.

Generally, the complex of peat-moss bog species is flourishing in the studied area which is reflected in the widespread and common occurrence of some tyrphobiontic and tyrphophilic species, such as *A. subarctica*, *S. arctica*, *L. dubia*, *N. speciosa*. However, the species representation of this group was not very rich. Some absences should be stressed, especially of the typical northern (Arctic- and boreo-mountain) species, *Somatochlora alpestris* (Selys) and *Aeshna caerulea* (Ström), which theoretically might be expected in the studied area (cf. BELYSHEV, 1973). However, an analysis of distribution maps shows that the former species has not been recorded below 60° N in lowlands of Europe and below 58° N in lowlands of West Siberia so far, and records in lower latitudes were practically restricted to altitudes higher than 600 m a. s. l. (BELYSHEV, 1973; MIELEWCZYK, 2004; WILDERMUTH, 2006). Considering these tendencies as well as the recent climatic situation, the absence of *S. alpestris* in the Vasyugan Plain seems to be real. The range of *A. caerulea* in West Siberia was, however, marked on the map as being much broader and reaching even northern areas of the steppe zone (BELYSHEV, 1973). In the light of these data, the current absence of the species in the Vasyugan Plain is interpreted by us as the possible distribution shrinkage as a result of climate warming.

Tyrphobiontic *A. subarctica* and tyrphophilic *N. speciosa* turned out to be much more abundant in the studied area than it was previously imagined (BE-LYSHEV, 1973; KOSTERIN et al., 2004). This earlier underrecorded state was certainly a result of the scartity of studies in complexes of *Sphagnum* habitats in Siberia. However, in the case of *A. subarctica* some misidentifications ('in favour of' *A. juncea*) might have also played a role as different diagnostic characters to distinguish these two species, given in literature, have different degrees of usefulness, some of them are even unreliable. This has been studied and checked during the Vasyugan expedition and earlier investigations by R. Bernard at many localities in Poland and the Baltic States. In fact, the two species are markedly different. Firstly, in their secondary genitalia (cf. e.g. SCHMIDT, 1929; BELEVICH, 2005). The fore processes of the hamuli in *A. subarctica* are wider throughout their length and widely rounded versus those in *A. juncea* which are clearly narrower, often slightly turned along their axes and with a slightly inflated, 'shoe-like' apex. Hamular folds situated below, are smaller and significantly less visible in *subarctica*. Also a very good feature is the shape of cerci of females (cf. e.g. ASKEW, 2004; BELEVICH, 2005), which in *subarctica* are leafy, horizontally flat and widely rounded, while in *juncea* they are narrower and turned along their long axes to a more vertical position in their distal parts. This difference is not so distinct in males, however, also their cerci are flatter and slightly wider in *subarctica* as opposed to the somewhat turned along their axes and narrowed appendages in *juncea*. The presence of a specific patch below the mesothorax spiracle is one of the best distinguishing features. In both sexes of *A. subarctica*, there is a clear-cut light patch there which, very importantly, has a characteristic narrow projection ('leg') beneath it directed downwards along a suture. In *A. juncea*, there is no such patch or there is only a very small one, always without the projection – 'leg'. This feature, very useful in the field, was tested by R. Bernard in hundreds of specimens, always with a positive result. It is underestimated in literature, although sometimes shown, as e.g. on a figure in NIELSEN et al. (1987). All these diagnostic characters between the two species are reliable throughout their range, including North America (cf. e.g. illustrations in HUDSON & ARM-STRONG, 2005). Other distinguishing features, such as coloration, pattern of other thoracic spots, and presence of light spots behind eyes, should be treated as helpful but not as decisive. Some of them, being variable or not repetitive in all individuals, may lead to misidentifications. For example, the width of the black stripe between the frons and clypeus, is given by BELYSHEV (1973) and DIJK-STRA (2006b, 2006c) as the most important feature, being of constant thickness or even widened at the eyes in *subarctica*, and narrowed at the sides in *juncea*. In fact, the pattern in this area of the head is more complicated and the feature is different in some individuals, especially those of *subarctica* (our own data and BELEVICH, 2005). One its individual collected during the expedition would be, according to this feature, incorrectly determined as *juncea*, another one would

bring very serious doubts, as well as one *juncea* male in which the black line is narrowed at the one side of the head … but not narrowed at the other side. The presence /absence of light spots behind eyes seems not to be completely reliable as well. Although in the practice of R. Bernard, the pattern: absent in s*ubarctica*, present in *juncea*, was repetitive but there are signals that these spots are sometimes absent in *juncea* as well (BELEVICH, 2005). Hence, the feature needs to be studied on a very wide range of material. Finally, we would like to stress that according to our observations given above and the experience of R. Bernard in Europe, the difference in behaviour of territorial males may also be helpful in determination in many cases, as well as the well-known difference in habitat. *A. subarctica* is a stenotopic species related to *Sphagnum* bogs, while *A. juncea* demonstrates a greater ecological plasticity (cf. e.g. DIJKSTRA, 2006b, 2006c).

Almost total absence of typically East Palaearctic species practically confirmed earlier conclusions that they mostly reach westwards at most up to the Ob' River and the Altai-Sayan mountain system; if some of them occur more to the West, they occupy relict far isolates, e.g. in the Urals and their foothills (KOSTERIN, 2005). Only *Shaogomphus postocularis* seems to locally penetrate the West Siberian Lowland as one collected individual suggests. Therefore, the species composition of the odonate fauna in the studied area is similar to a certain degree to that known from central and eastern Europe. However, there are some differences in habitat preferences of some species, as e.g. a narrower habitat spectrum in the Vasyugan Plain of *C. puella* and *L. pectoralis*, and wider of *A. crenata* and *C. johanssoni*. An explanation for these differences is mostly zoogeographical, as these species are more stenotopic in the borderlands than in the cores of their distributions. There are also significant differences in the abundance of many species. More widespread and more abundant in the Vasyugan Plain are e.g. *C. hastulatum*, *C. johanssoni*, *A. crenata*, *S. flavomaculata*, *S. arctica*, and less widespread and abundant are e.g. *L. virens*, *C. pulchellum*, *L. albifrons*, *L. pectoralis* and *S. sanguineum*. These differences are zoogeographically (situation at the northern limit of the species range) and/or ecologically (abundance of appropriate habitats) determined.

The studies in the Vasyugan Plain brought many important zoogeographical data. For nine species, i.e. *C. puella*, *C. pulchellum*, *E. risi*, *N. speciosa*, *G. vulgatissimus*, *S. postocularis*, *S. flavomaculata*, *L. albifrons*, *L. pectoralis*, these data let situate the northern limit of their distribution further north (in one case – northwest) than it was previously known (cf. BELYSHEV, 1973; KOSTERIN et al., 2001, KOSTERIN, 2005). This suggests that the actual northern range limits of some of these species in W Siberia do not descend so sharply to the south as it was expected, and is possibly even closer to the northernmost latitudes reached in Europe. Generally, the difference between the previous knowledge and the picture of the odonate fauna recorded by us confirmed that landscapes predominated by large *Sphagnum* complexes of peat bogs and fens have not been odonatologically

penetrated so far in this peaty region of SW Siberia and have been hardly studied in the whole W Siberian Lowland. We have to say here that also our studies have not brought an exhaustive picture as we had not reached a real interior of these complexes (and of the Vasyugan Plain) and we can only speculate about its fauna.

Taxonomically interesting was the coexistence in the studied area, but not at the same localities of *Enallagma cyathigerum* and *E. risi*, the latter at the northernmost known locality. The fact of clear spatial separation and at most minimum degree of intergrading (if any) of these two taxa suggests their full species status that agrees with morphological and recent molecular data (STOKS et al., 2005; TURGEON et al., 2005).

The morphological dragonfly feature typical of West Siberia, and possibly only to its boggy parts, is brownish 'smoking' of the wings recorded by us in many females of some *Somatochlora* species in the Vasyugan Plain. It was the most explicit and most frequent in *S. flavomaculata*, less frequent and more varying in *S. arctica*, and at most weakly marked in rare *S. metallica*. And while the amber colour extending along the costal margin of wings and comprising also the wing bases is widely known as being rather typical of younger individuals, the brownish 'smoking' is unknown for these species in Europe (H. Wildermuth, pers. comm.) and reported mostly or only for West Siberia by BELYSHEV (1973). It seems to us that this feature is related to boggy landscapes (peaty waters?) of this region, however, the basis and nature of this relation remains unclear.

The regular and not rare presence of two forms of androchrome females of *C. splendens* and its males with the wings coloured to the tips is another distinguishing element in the morphology of Vasyugan odonates. Though these forms are known from other areas of Eurasia but in Siberia were previously recorded mostly from the Tyva republic (KOSTERIN & ZAIKA, 2003 and O. Kosterin unpublished data).

The small studied rivers of the Vasyugan Plain, slowly bringing brown turbid and warm waters and abounding in muddy bottom deposits and locally in vegetation, have a rather specific odonate fauna, a mixture of rheophilous species and dragonflies more typical of lentic habitats. However, the former group was rather poorly represented, exactly by abundant *C. splendens*, *G. vulgatissimus* and *S. metallica*.

A dominating position of *A. crenata*, in relation to *A. juncea*, *A. grandis* and *A. viridis*, was given from Siberia by BELYSHEV (1973), and some spatial segregation between *crenata* and *juncea* was signalised by KOLOSOV (1915). However, both these communicates were only general without descriptions and details, so not allowing to see the picture of segregation clearly. The paper on *A. crenata* in Lithuania (BERNARD, 2002) brought more detailed data concerning some aspects of the segregation between aeshnids (*crenata*, *cyanea*, *juncea/subarctica*) at *crenata*-localities, however, *juncea* and *subarctica* were treated mostly together

in it and a question about nature of segregation between *crenata* and *juncea* remained. The rich new observations from the Vasyugan Plain allowed to answer this question and see the picture of segregation between imagines of aeshnids more precisely.

At the studied Siberian localities the male segregation between *A. juncea* and *A. subarctica* was very advanced, partially spatial and partially weather/temporal, between *A. crenata* and *A. subarctica* – almost complete, spatial, and between *A. crenata* and *A. juncea* – advanced, weather/temporal.

All these observations confirmed the dominant position of *A. crenata* over the water table as described already by BELYSHEV (1973) and BERNARD (2002). However, suggested also the lack of *crenata*-dominance out of the water table.

ACKNOWLEDGEMENTS

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FACTORS AFFECTING INTERACTION RATES
IN *PLATHEMIS LYDIA* (DRURY)
(ANISOPTERA: LIBELLULIDAE)

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Interspecific interaction rates and space use were observed for *P. lydia* at 3 ponds in north-central Texas from June to August 2007. Aggressive interactions of marked individuals were tallied for each interacting sp. by which individual was the aggressor or target and which sp. won or lost. The space used was also mapped. These data were also collected for one individual each of the libellulids *Pachydiplax longipennis* and *Tramea lacerata* and compared to *P. lydia*. Interaction rates were different depending on the category of interacting odon. (perching or flying), supporting the hypothesis that the thermoregulatory categories of perching and flying aid in habitat partitioning among spp.

INTRODUCTION

Aggressive behavior in Odonata is due to territorial competition (aggressive defense of a unit of space) and encounter competition (interactions between mobile organisms that cause injury or loss of energy or time) (SCHOENER, 1983). These two types of competition can apply both intra- and inter-specifically. Competition usually does not affect the overall species assemblage at a pond (MOORE, 1964, 1991), but the aggressive interactions can affect local spatial distribution of species. For example, HUTCHINSON (1977) observed two species of *Epitheca* (Corduliidae), similar in flight pattern and appearance, flying together at territories along a river. One species excluded the other from the river shore. In the absence of the more aggressive species, the second species could fly along the shore. Additionally, TYNKKYNEN, et al. (2006) discussed two *Calopteryx* (Ca-

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lopterygidae) species where experimental removal of one species allowed members of the other species to expand their territories.

Changes in space use can be caused by interspecific interactions. REHFELDT & HADRYS (1988) found spatial partitioning promoted by aggressive interactions between two *Sympetrum* (Libellulidae) species. The presence of heterospecifics changed perching heights and interaction times for both species. This spatial separation has the potential to reduce conflict between interacting species, such as the aforementioned *Epitheca* and *Calopteryx*. For example, MICHIELS & DHONDT (1987) noted that habitat separation occurred between three *Sympetrum* species, but they did not determine if separation was due to current or past interspecific interactions.

There are differences in space use related to other aspects of life history, such as the dragonfly being a perching or flying species. CORBET (2004) defines fliers as the odonates that "typically remain on the wing when active" and perchers as those that "spend most of their time on a perch from which they make short flights." Some species do not fit neatly into a single category (PARR, 1983) and may change behavior depending on temperature (MAY, 1977). Although the dichotomy is based on thermoregulation, it could also prevent conflict because the dragonflies use different spaces at the pond.

This study examines the connection between space use (the perching/flying dichotomy and patterns of territory use) and interspecific interaction rates in *Plathemis lydia*, with tentative data on two sympatric libellulids, *Pachydiplax longipennis* and *Tramea lacerata*.

METHODS

STUDY SITES − The three study ponds were located in northeastern Wise county in the Cross Timbers and Prairies ecoregion of north-central Texas (DIGGS, et al., 2000; Fig. 1). Of these ponds, two were located on the Lyndon B. Johnson National Grasslands (grasslands units 67 and 71). The remaining pond, named the pit, was located on private property near Greenwood, Wise county, Texas. All three sites had few to no trees immediately surrounding the ponds. These were simple in shape (basically round with no long inlets of water). The two grasslands ponds were similar in being somewhat round stock tanks with clay-lined bottoms. The pit was an abandoned drilling mud pond lined with clay and bentonite; it was rectangular with a peninsula in the middle. Unit 71 was visited by cattle and was stocked with fish; the other two ponds (Unit 67 and the pit) lacked fish and were not visited by cattle.

A grid of 2×2m squares was marked around each pond, similar to McMILLAN (2000), which used 1×1m observation grids. The Unit 67 pond was enclosed completely by the grid (1024 m^2), whereas smaller portions of the pit (about half of the pit; grid area 1120 m^2) and Unit 71 had a grid (360 m^2). The grid areas on Unit 67 and Unit 71 were small enough to be completely visible from outside the grid. McMILLAN (2000) similarly used small ponds so the observation areas would be completely visible from the bank. The pit's surface was also visible from all angles until cattails grew up at one end of the grid. Each pond was visited for data collection and marking one or two times per week.

STUDY SPECIES − *Plathemis lydia* is considered a perching species based on field observations in this study; it tended to perch in a core area. However, it is an intermediate percher since individu-

als spent anywhere from 0% (one observation) to over 75% of the time perching. *Pachydiplax longipennis* was also studied but only one observation under comparable weather conditions to the *P. lydia* observations occurred. Additional species were captured and marked, but observations were made on only one *Tramea lacerata*. Categories of perching and flying were defined for each interacting species based on the field observations and descriptions of behavior in ABBOTT (2005).

MARKING − Each captured individual was painted on the abdomen with 1-3 stripes of colored acrylic paint. Numbers were written on the wing using a black permanent Sharpie © marker. Re-sighted individuals were identified by the unique color combination and number.

OBSERVATIONS − Observations of interactions were made on re-sighted individuals from June to August 2007; observation periods varied with how long the odonate was visible. Weather data were recorded at the end of each observation period. Observations were made with the observer sitting

Fig. 1. Location of study area in Texas and Cross Timbers ecoregion. Sources of data layers: county layer: GLO (no date given); − ecoregion layer: ACKERSON (2007)'s digitized version of GOULD, F.W., 1975. *Texas plants: a checklist and ecological summary*. Texas agric. exp. stn, Publ. 585.

outside the grid or at least 2-4m from the odonate's flight area. Amount of time spent perching in the grid, flying in the grid, perching outside the grid, flying outside the grid, and time not visible were recorded. The starting and ending times for the observation were also recorded.

For each interacting species (including intraspecifics), status in interactions was recorded as aggressor or target and win or lose for both the observed and interacting individuals. Aggressor/target was based on the observed individual; if the observed individual attacked another odonate, that individual was considered the aggressor.

The observed individual was defined as winning the interaction if

When the aggressor,
- It caused the other individual to change flight path
- It caused a perching odonate to leave its perch and not return immediately
- When interacting with an intraspecific female, it caught the female

When the target,
- It was not forced to leave its perch by the interacting odonate
- It was not forced to change flight path by the interacting odonate

The observed individual lost if

When the aggressor,
- It failed to cause the other individual to change flight path
- It failed to cause a perching odonate to leave its perch and not return immediately

When the target,
- It was forced to leave its perch by the interacting odonate
- It was forced to change flight path by the interacting odonate
- When interacting with an intraspecific female, it failed to catch the female

Space use was mapped for each observed individual on a map of the pond and grid. The map showed major features of the pond, such as trees, cattails, areas of sedge, and the shape of the pond
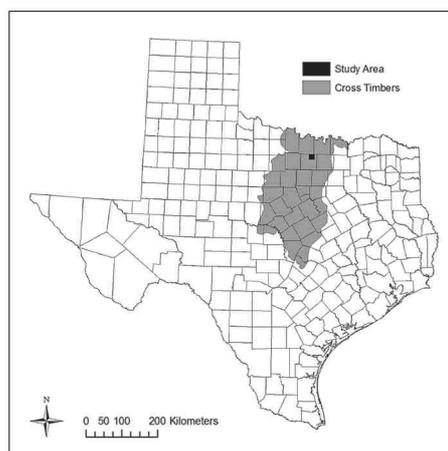
to allow flight paths and perches to be drawn on the map. Examples of maps (with data for *P. lydia, P. longipennis,* and *T. lacerata*) are found in Figure 4.

DATA ANALYSIS − Interaction rates were calculated from the number of interactions divided by time visible (in minutes). Interaction rates (interactions per minute) can be calculated from the data for each interacting species, category, or other characteristics of interacting species. Alternately, the interaction rates for each observed individual can be summed for an overall interaction rate for the observation period. Area used was calculated by multiplying the number of grid squares time the area in each grid ($4m^2$)

Analysis was performed on observations made under standard conditions (>11:00am, cloud cover < 70%, maximum wind speed ≤7KT, and time visible <60 min) to reduce variations in interaction rates from weather conditions, time of day, and observer effort. Graphs were created in Sigmaplot 9.01 (SysStat Software, Inc., 2004).

RESULTS

INTERACTION RATES

All data are for *Plathemis lydia* except where noted. Interactions with flying species decrease with more time spent perching (Fig. 2A), while interactions with perching species stay approximately the same (Fig. 2B). When interaction rates with flying species were examined by status in interaction and proportion of time spent perching, each status category decreased with increased time perching (Fig. 3). The interaction rates with the observed individual as a target were higher than the individual as aggressor. *P. lydia* is targeted by flying species at reduced interaction rates when it spends more time perching (r^2=0.36, p=0.011, n=17). Interaction rate as aggressor decreases with more time perching (less likely to encounter fliers while perching), but the trend is not statistically significant (r^2=0.16, p=0.14, n=15). Perching species as aggressor (linear regression: negative correlation, r^2=0.0024, p=0.86, n=16) and target (linear regression: positive correlation, r^2=0.034, p=0.66, n=8) showed no such correlation.

When averaged over all perching times, the interspecific interaction rate for *P. lydia* was higher with flying species than with perching species (ANOVA: p=0.0049, flying n=19, perching n=17). When this is analyzed by status in interaction, there are slightly more interactions with flying as a target (ANOVA: p=0.040, aggressor n=15, target n=17). Interaction rate with perching species is approximately the same for each interaction status (ANOVA: p=0.90, aggressor n=16, target n=8).

SPACE USE

Tramea lacerata flew around the pond and through the middle, with no focal territory or perches (Fig. 4A). *Plathemis lydia* had a core territory (a main patrol or perching area) as shown in Figure 4B, instead of the whole-pond use shown by the one *T. lacerata* mapped. Finally, use of the pond by *Pachydiplax longipen-*

nis was centered over multiple perches consisting of debris and sedges in Unit 67, which had a low water level at the time (Fig. 4C).

Additionally, each species spent different amounts of time perching (ANOVA, p=0.091). *P. longipennis* spent more time perching (82.61%, n=1) than *P. lydia*
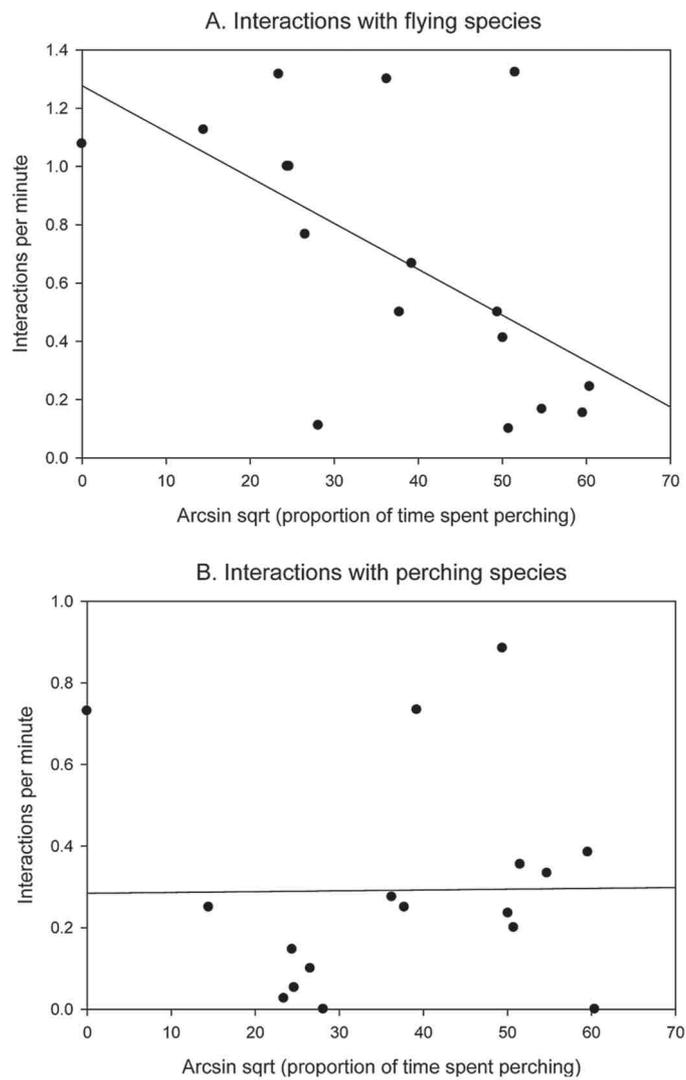

Fig. 2. Interspecific interactions per minute of *Plathemis lydia* by category as a function of proportion of time spent perching (arcsine square-root transformed). (A) flying r^2=0.36, p=0.010, n=17; − (B) perching r^2=0.011, p=0.69, n=17.
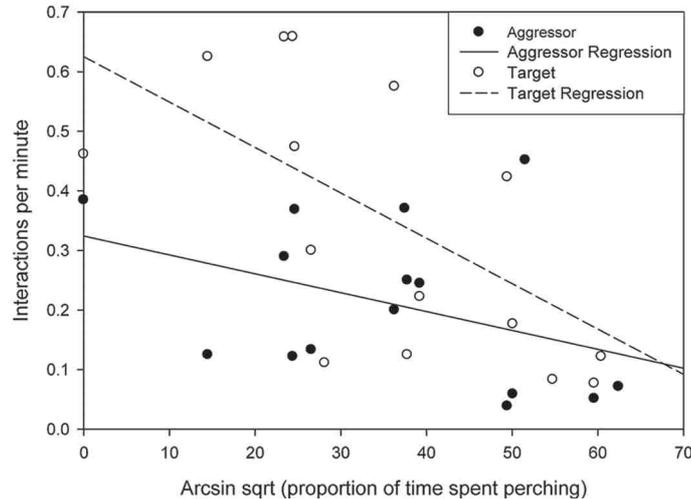
Fig. 3. Interaction rate of *Plathemis lydia* with flying species (interspecific) as a function of proportion of time spent perching (arcsine square-root transformed), with status in interaction: aggressor (r^2=0.16, p=0.14, n=15) and target (r^2=0.36, p=0.011, n=17).

(39.16±24.72%, n=17), while *T. lacerata* (0%, n=1) did not perch during the observation.

Interspecific interaction rates for each species are shown in Table 1. *P. longipennis* tended to interact more with other perchers, while *T. lacerata* mainly interacted with flying species. *P. lydia*, although classified as a percher, had a statistically significant higher interspecific interaction rate with flying species (ANOVA: p=0.0049, flying n=19, perching n=17) consistent with its intermediate amount of time spent perching.

The higher rate of flying interactions for *P. lydia*, a perching species, is due to attacks by *Libellula luctuosa*. The latter species contributed an average of over 30% of the flying species interactions with *P. lydia*, over 70% of flying species interactions with *T. lacerata*, and was the only flying species to interact with *P. longipennis* (*L. luctuosa* was the aggressor). When *L. luctuosa* is excluded from analysis, *T. lacerata* still has a higher interaction rate with flying species (0.61 interactions per minute) than with perching species (0.13 interactions per minute). For *P. lydia*, however, the difference between perching and flying interactions becomes insignificant (ANOVA: p=0.37, flying n=19, perching n=17) when *L. luctuosa* is excluded.

DISCUSSION

The prediction of this study was that interspecific encounter competition should cause perching species and flying species to affect each other less because they are using different spaces and are thus less likely to have time- and energy-consuming aggressive encounters. The interaction rate data supported this prediction with variation in interaction with flying species being dependent on the percent time spent perching (i.e., the amount of overlap in space use) for *Plathemis lydia*. The interaction rates and space use diagrams for *Pachydiplax longipennis* and *Tramea lacerata* tentatively support this conclusion as well.

The interspecific interaction rate divided by category (Fig. 2) shows that interactions with flying species decrease with more time spent perching, while interactions with other perching species stay the same. For interactions with heterospecific perchers, no trends are statistically significant, but it appears that *P. lydia*
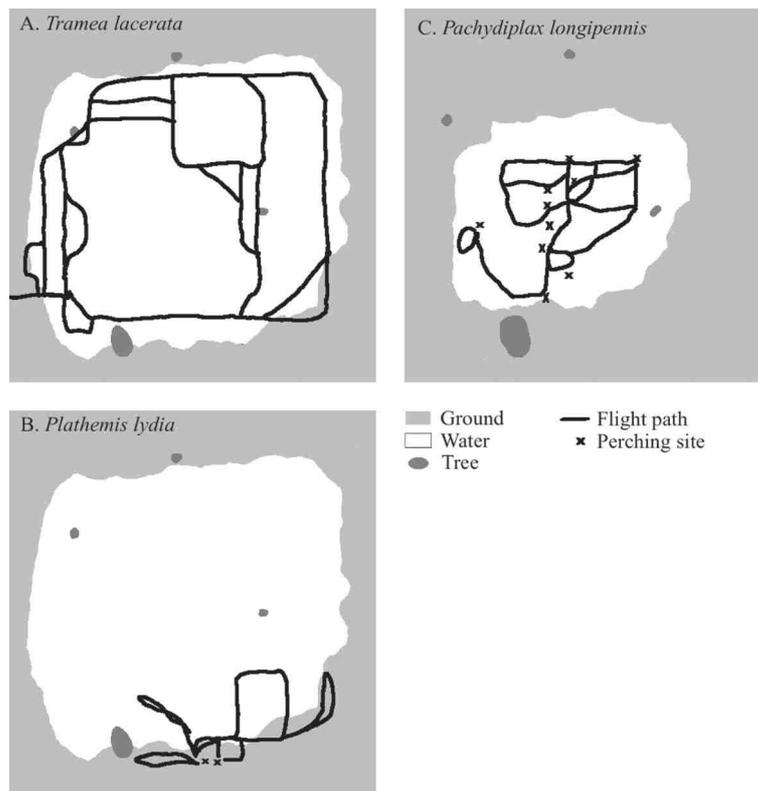

Fig. 4. Map of typical territories for: (A) *Tramea lacerata* (11 June 2007, Unit 67, visible for 25 minutes); − (B) *Plathemis lydia* (2 July 2007, Unit 67, visible for approximately 30 minutes); − (C) *Pachydiplax longipennis* (17 August 2007, Unit 67, visible for approximately 25 minutes).

Table I

Interspecific interaction rates (interactions per minute) by category for *Pachydiplax longipennis*, *Plathemis lydia* (average ± 1 S.D.; flying interaction is significantly different, ANOVA: p=0.0049, flying n=19, perching n=17), and *Tramea lacerata*

Species	Interaction rate with perching species	Interaction rate with flying species
P. longipennis (n=1)	0.48	0.043
P. lydia (n=19)	0.30±0.25 (n=17)	0.68±0.46 (n=19)
T. lacerata (n=1)	0.13	2.09

interacts with other perchers at similar rates regardless of status in interaction or percent of time perching. These data indicate that changes in time spent perching (which is a change in space use) can change the interaction rates by category of interacting odonates.

When solely looking at category, interaction rate with flying species is on average higher than with perching species (excluding intraspecifics). *P. lydia* is more often a target than an aggressor in interactions with fliers and is targeted less when perching more (Fig. 3). No differences are apparent for its interactions with perching species. This could be due to the potential tendancy of flying species to attack any airborne odonate. *P. lydia* appears to mainly concentrate on chasing conspecifics while in flight.

Because data was collected mainly for *P. lydia*, a comparison of territory space use between different categories is tentative. The lone *T. lacerata* datum did show a different pattern of territory use, flying extensively around the pond instead of having a core territory like *P. lydia*. Additionally, it showed a different pattern of interaction rates, mainly interacting with other flying species. *P. longipennis*, a perching species that spent more time perching than *P. lydia*, mainly interacted with perching species and used several different perches, of which many were available due to low water in the pond. These data for *P. longipennis* and *T. lacerata* are useful despite the small sample size because they follow the trend observed in *P. lydia*. They suggest that the perching and flying species will tend to interact with other species in the same category. However, another factor that could be affecting the interaction rates is the degree of overlap between each species' preferred perching sites and flight heights within each category. For example, *P. longipennis* and *P. lydia*, both perchers, had different flight patterns and sometimes perched at different locations in the pond, which probably reduced their interaction rate in spite of both being perchers.

Categories of perching and flying are regarded as thermal adaptations (COR-BET, 2004) but they could aid in segregating species and preventing unnecessary conflicts. The data in the current study supports this supposition, but more

data are needed. Other studies have looked at how interspecific interactions affect perching heights (REHFELDT & HADRYS, 1988), habitat (MICHIELS & DHONDT, 1987), and space use (HUTCHINSON, 1977; TYNKKYNEN, et al., 2006), but this is the first study to examine how the perching/flying dichotomy might partition the environment.

The species composition of the ponds would have to be altered or ponds with more species similar in appearance would be needed to see if this effect acts on *P. lydia*. Some of the differences noted could be due to the presence of highly aggressive species such as *L. luctuosa*. Comparisons of different species' interactions could shed light on exactly why certain species tend to attack others. Is it only a coincidence of shared space for non-similar species or does it depend more on the aggressiveness of the interacting species, such as with the highly aggressive *L. luctuosa*? This hypothesis needs further examination in areas with different species in each category to determine the effect of species composition on category interaction rates. If it is the perching/flying dichotomy, then species composition should only make a slight difference depending on aggressiveness of the species present.

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LIFE HISTORY OF AN ENDANGERED DRAGONFLY, *NANNOPHYA PYGMAEA* RAMBUR, IN KOREA (ANISOPTERA: LIBELLULIDAE)

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Aspects of the *N. pygmaea* life history, an endangered sp. in Korea, were studied at an abandoned paddy field in Mungyeong, Gyeongsangbuk-do, Korea. The larvae were sampled quantitatively at monthly intervals (every 2 weeks during the emergence period) from June 2006 to July 2007 and the adults were counted via a line-transect method. Based on the analyses of larval body length distribution, degree days (DD), and emergence time, the sp. is considered univoltine with an emergence period from mid-May to early August. The estimated sum of the thermal amount, effective to larval development during the study period, was 2468 DD. The relationship between the larval head width and wingsheath width, which is coincident with the temperature fluctuation pattern, shows that the population harbors at least 4 size groups (cohorts) in a generation.

INTRODUCTION

Nannophya pygmaea Rambur, a member of the dragonfly family Libellulidae is the smallest in the world in terms of body length (ca 13-14 mm) (ISHIDA et al., 1988; BAE, 1998). Although it is widely distributed throughout tropical and subtropical East Asia, the Korean population, which is regarded as an isolated population on the northernmost distributional border in continental Asia (36°33' N), is fragmentally distributed over southern portion of the Korean Peninsula. Thus far, only a few habitats have been reported in South Korea (KIM, 1997; BAE et al., 1999; LEE, 2001). It was, therefore, designated as an endangered species by the Ministry of Environment of Korea in 1988 (BAE et al., 1999) and

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is considered a flagship species in the wetland protection and conservation. In Japan, *N. pygmaea* is common and widespread, occurring up to 40°50' N in the Aomori prefecture (HAMADA & INOUE, 1985; SUGIMURA et al., 1999).

The understanding of voltinism is crucial to an appreciation of how the life cycles of organisms have adapted to certain environments inherent to different regions. Although the general Odonata life history aspects are relatively well known, those of *N. pygmaea* are poorly understood. The general biological characteristics of *N. pygmaea*, including habitat, distribution, and behavioral ecology, have been previously studied in both Japan and Korea (TSUBAKI, 1985; KIM, 1997; BAE et al., 1999).

With regard to the effects of environmental parameters on life history patterns, temperature may play a major role in a variety of aspects of Odonata biology, including oviposition, egg hatching, ecdysis, and developmental time (HASSALL et al., 2007). In this study, aspects of the life history of *N. pygmaea* are investigated with regard to accumulated degree days, voltinism, and larval cohorts on the basis of quantitative sampling and field observations.

MATERIAL AND METHODS

STUDY AREA AND TEMPERATURE MONITORING − Field studies were conducted in a wetland located in Mungyong-si, Gyeongsangbuk-do, Korea, between June 2006 and July 2007. This study site (36°33′15.9″ N, 128°00′20.2″ E, alt. 243 m a.s.l.), composed of 15 small stair-like wetlands, was a paddy field that had been abandoned for approximately three to five years. The water depth at the sampling points was approximately 5 to 10 cm. The substrate consists principally of silt and sand, with abundant organic detritus. The wetland vegetation includes *Juncus effusus* and *Persicaria thunbergii*.

The water temperature at the sampling area was monitored at 2-hour intervals with a water temperature data logger from the Onset Computer Corporation (Model: Optic StowAway® Temp, USA). The temperature recorder was installed on the surface of the bottom (ca 5 cm deep), and care was taken to avoid any direct sunlight at the monitoring point. The water temperature was converted to degree days (DD) via the rectangle method, demonstrated by the following equation (LEE et al., 1999):

Rectangle DD = $(T_{max} + T_{min})/2 - T_b$,

where the T_{max} is daily maximum temperature, T_{min} is the daily minimum temperature, and T_b is the base temperature for larval development. The T_b value of 14.3°C, which was derived from a laboratory experiment on egg development (KIM et al., 2006), was utilized for *N. pygmaea* in this study.

SAMPLING − The larvae were sampled every two weeks during the emergence period but only at monthly intervals during the non-emergence period. Since this is an endangered species and despite the sampling permission was acquired from the Ministry of Environment of Korea, only a limited number of individuals could be sampled. Two quantitative samples were obtained using a hand net sampler (40×20 cm, mesh 0.25 mm). Two sampling points were selected at the side and middle of the wetland; all the organic material, including larvae, was sampled within a 40×100 cm area at each of the sampling points (4000×2 = 8000 cm² in total area). It was maintained in a 500 ml bottle and the larvae were sorted in the laboratory. Larval body length was assessed to determine the emergence time. The adults were counted using the line-transect (25×4 m) method. Larval body length and wing-sheath width were measured using a stereomicroscope (Zeiss Stemi 2000-C). All measurements were conducted with computer images captured under an image analyzer using the AxioVision Rel. 4.5 program. Larval body length classes were categorized in increments of 0.5 mm.

RESULTS

WEATHER CONDITION

Annual precipitation in the study area in 2006 was 1352 mm (unpublished data from a local meteorological station); more than 66% (903 mm) of the precipitation occurred during the rainy season (July--August) (Fig. 1). The water level of ca. 5-10 cm was maintained during the study year.

The mean water temperature detected during the study period was 16.01 ± 5.94ºC (mean ± SD). The highest water temperature was recorded as 41.28ºC (August 8 and 15, 2006) and the lowest was -3.31ºC (December 29, in 2006).
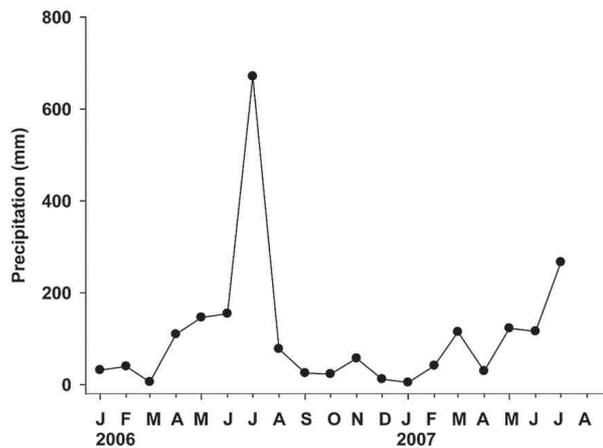

Fig. 1. Precipitation in the study area.

The temperature fluctuation pattern was influenced by the amount of rainy days (Fig. 2). The daily water temperature recorded between November 6 and April 8 did not exceed the base temperature (14.3ºC) for the larval development of *N. pygmaea*; thus, no effective temperature was accumulated during that period. As a result, the estimated sum of the thermal amount, which was effective in terms of larval development over the study period, was 2468 degree days (Fig. 3). The water temperature was 3.81±2.93ºC higher than the air temperature.

POPULATION DENSITY AND LIFE HISTORY

A total of 186 larvae was collected during the study period from June 2006 to July 2007. The collected number per sampling area (8000 cm^2) was largest on October 20, 2006 (n=31) and the smallest on July 7, 2006 (n=3) (Fig. 4). Figure 4 shows the frequency distribution of larval body length, ranging between 2.76-10.69 mm, during the study period.

As a result of the observation of adults using the line-transect method, more males (145) were observed than females (55) per sampling area (100 m^2) on June 17, 2006. This sex ratio pattern was similar to that recorded in 2007 (Fig. 5). The females appeared earlier than the males during the emergence period. Emergence begun
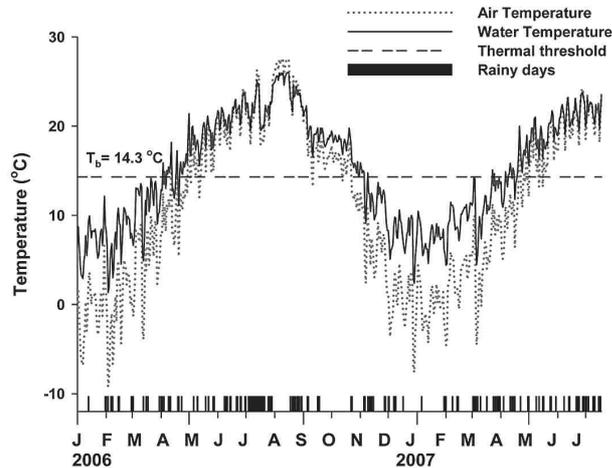
Fig. 2. Temperature in the study area. − [T_b = base temperature for larval development].

during mid-May and continued until early August. Its peak occurred during the period between late May and mid-June.

Figure 6 shows the relationship between larval head width and wingsheath width, the ranges of which are 1.05-3.15 mm and 0.00-2.75 mm, respectively. If the number of sampled larvae was sufficiently large enough (e.g., October 20, 2006), at least four larval size clusters or cohorts were recognized from this relationship.

DISCUSSION

The type-locality of *N. pygmaea* is not precisely known, although it was later identified as Borneo (STEINMANN, 1997). The distributional origin of the species is thus considered a tropical region. Local populations recorded from several locations in the southern part of the Korean Peninsula, belong to isolated populations on the northernmost continental distributional border in temperate region. The recent increase observed in the number of local populations on the Korean Peninsula can probably be attributed to the increase in wetland habitats, e. g., abandoned rice fields, as well as to global warming (BAE et al., 1999).

Generally, the tropical libellulids are multivoltine and have a larger number
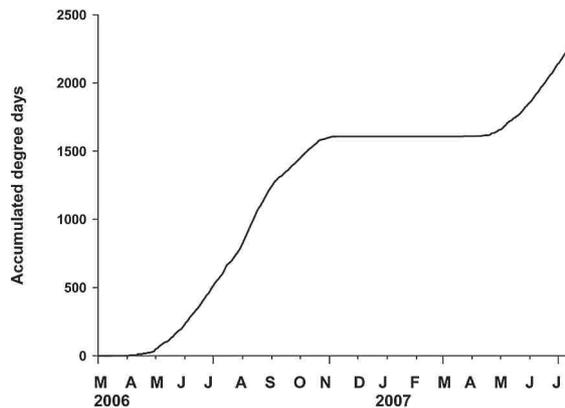

Fig. 3. *Nannophya pygmaea*: accumulated degree days (DD) during larval development.