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NEHALENNIA SPECIOSA (CHARPENTIER, 1840) IN EUROPE: A CASE OF A VANISHING RELICT (ZYGOPTERA: COENAGRIONIDAE)

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Based on all available data, the former and present distribution in Europe is presented and critically analysed. The sp. is extinct or has only survived at single or small clustered and isolated localities in many parts of the western borderlands of its former Eurasian area that extended from Belgium to Japan. It is continuously declining, especially W and S of the line running through the Baltic States, N and E Poland and S Belarus. The attached basic data from Asia reveal incomplete knowledge, but probably indicate a better situation in the eastern part of the range. The main aspects of the ecology and biology are outlined and discussed. Special attention is paid to the elements helpful in understanding the deep regress of the sp., i.e. to its habitat on a macro- and microscale as well as to its life-strategy. The high level of stenotopy and the highly specialized habitat-related behaviour, resulting in successful use of a narrow niche, are emphasized. These aspects make the sp. vulnerable in the face of high anthropogenic pressure in Europe. Limited dispersal abilities augment the danger of local extinction. The main threats are presented and some essential conservation measures are proposed.

INTRODUCTION

Nehalennia speciosa is the only representative of the genus in the Palearctic (DE MARMELS, 1984). The species is known for its small size, high habitat requirements, unusual biological features, and recently also for its sharp declining tendencies. Despite the publication of alarming assessments of the local situation of the species (cf. e.g. BERNARD, 1998; KUHN & BÖRZSÖNY, 1998; MAUERSBERGER, 2000b; SCHMIDT & STERNBERG, 1999; WILDERMUTH, 2004), the knowledge of its state on a continental scale is insufficient.

The main objective of this review is to present the past and present distribution of *N. speciosa* in Europe, this serving both as basis for an analysis of the current situation of the species on the continent and to understand its regressive trends. Data on the distribution in Asia are included to complete the image of the species, its range extending from W Europe to Japan. We search for reasons for the current situation and try to answer the questions why the species is vanishing and why it is so sensitive to environmental changes. This analysis covers details on the habitat of *N. speciosa* and some relevant aspects of its biology. The picture that is obtained of the state of the species in Europe, the assessment of the level of its threat of extinction, and the conclusions following the examination of its ecology and biology constitute a sound fundament for the conservation proposals put forward.

METHODS

All information on distribution, current state, ecology, and biology of *N. speciosa* is based on: (a) literature, (b) comments, investigations and unpublished data provided on inquiry by more than 50 specialists from 21 countries, and (c) our own unpublished data collected in Poland (R. Bernard = RB, H. Wildermuth = HW), Switzerland (HW), Lithuania, Latvia and Estonia (RB). We mostly succeeded to obtain the primary literature or data on the species that could be subsequently analyzed. Only some publications, mainly from Russia, were among a few non-available papers. A selected volume of literature from Asia was also considered.

HISTORICAL AND PRESENT OCCURRENCE IN EUROPE

For each country and region the following information is given: NKL: total number of known localities (includes also those unpublished); – NUL: number of hitherto unpublished localities, only in exceptional cases these are identified here; – NCL: number of current localities (1995-2004); – CAT: category in a corresponding national or, for Germany only, regional Red List/Red Data Book. Only the current IUCN categories or those similar to them are stated. If the national or regional categories differ from those of the IUCN, or the species is not redlisted, a category proposed by us is given in parentheses. – This is followed by the sources of data, encompassing the most condensed but fully representative bibliographic references and personal communications from regional specialists. – The records and the status of *N. speciosa* are briefly commented. In exceptional cases, names of current localities are omitted on explicit request of regional specialists.

THE NETHERLANDS

NKL 2, NCL 0, CAT EX; LE ROI (1917), WASSCHER et al. (1995), WASSCHER & KETELAAR (2001), BERNARD (2001), KALKMAN et al. (2002), VAN DER WEIDE (2002 and pers. comm.), M. Wasscher (pers. comm.), K.-D. Dijkstra (pers. comm.).

There are also some doubtful (Greveschutven) and definitely wrong records (misidentifications) in the literature. The reliable records date from 1899-1912, the doubtful one from 1955. All localities lay in the SW of the country. Some data suggest that in Plasmolen (Mook) = Koningsven, where the habitat was very appropriate for the species till the beginning of the 20th century, a larger population may have existed.

BELGIUM

NKL 6, NCL 0, CAT (Flanders) EX; DE SELYS-LONGCHAMPS & HAGEN (1850), DE SELYS-LONGCHAMPS (1888), BAMPS & CLAES (1893), CAMMAERTS (1967), MICHIELS et al. (1986), DE KNIJF & ANSELIN (1996) and G. de Knijf (pers. comm.).

The localities are situated in the NE, in Flanders, in the provinces of Antwerp and Limburg (Campine district). Almost all records date from the 19th century, the first locality having been discovered already before 1850. *N. speciosa* was fairly abundant at the old localities. In the 20th century, only a published record of a single individual is known (1960) from Turnhout. *N. speciosa* was found in this area already in the 19th century. This is the westernmost (ca. 5° E) locality within the entire species range. Two unpublished records, dated in 1960, localized in the same area, most probably refer to the same site.

LUXEMBOURG

NKL 1, NCL 0, CAT EX; HOFFMANN (1960), PROESS (1996 and pers. comm.), PROESS & GEREND (1998).

Records from the sole locality, 'Bridel = Goepsweiher', date from 1951-1960. Subsequently the species was no longer found there.

SWITZERLAND

NKL 16, NCL 0, CAT CR (EX); RIS (1886, 1890, 1897, 1906), SCHIESS (1973), DEMARMELS & SCHIESS (1977), MEIER (1989), GONSETH & MONNERAT (2002), WILDERMUTH (1980, 2004).

All localities with certain records concentrate in the NE of the Swiss Plateau, 15 of them in the canton of Zürich, all laying between 410 and 495 m a.s.l. The sites probably constituted a part of a larger prealpine entity with *N. speciosa* between lake Zürich and lake Starnberg, from NE Switzerland to SE Baden-Württemberg and S Bavaria. The first records in Switzerland date from 1867 when the species was found near the outskirts of the city of Zürich and by lake Pfäffikon. Both sites harboured fairly large populations that were confirmed approximately up to the turn of the century. Rather strong populations were found in the early seventies of the 20th century at 3 localities in the southern canton Zürich, that of lake Pfäffikon included. By that time the site near Zürich had already been destroyed and those in the northern part of the canton were orphaned, while in the S, on an area of 100 km^2, still 11 localities existed, 8 of them with medium-sized or small populations. They all declined or became extinct after the dry summer 1976. A small population continued to exist another 14 years in a formerly exploited peat bog S of Wetzikon, where the last individual was seen in July 1990. Subsequently, despite repeated efforts, the species could no longer be found. At present it is considered extinct.

FRANCE

NKL ?; DE SÉLYS-LONGCHAMPS (1874, 1876), MARTIN (1889), GRAND (1990), J.-P. Boudot and J.-L. Dommanget (pers. comm.).

N. speciosa is mentioned by de Sélys-Longchamps from Savoy, based on an unknown number of specimens he was given by Bailly, from Chambéry. The statement by Martin that in Savoy it is "rather common in June" seems to be a falsification of de Sélys-Longchamps' account, yet without referring to this author. On the other hand, an unlabelled specimen found in the collection of E. Foudras may be of Savoyan or at least of French provenance. As the species was never recorded in the 20th century, it would have been extinct already before or shortly after 1900. All things considered, the former possible existence in this country remains enigmatic.

ITALY

NKL 4, NCL 0, CAT (EX) (?); BALESTRAZZI & BUCCIARELLI (1971, 1975), RAVIZZA (1973), PECILE (1981, 1991), BALESTRAZZI (1998), MERMET & GALLI (2000), C. d'Antonio and M. Pavesi (pers. comm.).

The localities are situated in the N, at the foothills of the Alps, two in the province of Friuli-Venezia Giulia and two in Lombardy. At 'Lagozetta di Besnate' near Varese the species was very abundant. 'Torbiere d'Iseo' by the lake of Iseo and 'Palude Cima Corso' NW of Udine held also rather strong populations, while at 'Torbiere di Moruzzo' by Udine only few individuals were found. *N. speciosa* was recorded in Italy for the first time in 1970. In 1972, 1980 and 1988 it was found at three additional localities. Since 1989 its occurrence has never been confirmed, yet no systematic survey has been carried out. According to regional experts, the species is thought to be extinct in Italy because of deterioration of its habitats.

AUSTRIA

NKL 10, NUL 1, NCL 5 or 6 (?), CAT CR; PUSCHNIG (1935), PICHLER (1939), LEHMANN (1981, 1983, 1990), EHMANN (1991), HOLZINGER (1991), MUNGENAST (2001), SONNTAG & LANDMANN (2005), KOMPOSCH et al. (2004), G. Lehmann and R. Raab (pers. comm.).

The localities are scattered over the Alpine range of the country and in most cases are situated in valleys, not exceeding 800 m a.s.l. in vertical distribution. Four localities lay in Carinthia, three in Tyrol, two in Styria and one in Upper Austria. Outside this region, by lake Neusiedl, only a single and most probably drifted individual was recorded. Large populations became known from the 'Schwemm' near Walchsee in N Tyrol and the 'Pressegger See' near Hermagor in Carinthia. From the few remaining localities only single individuals or smaller populations were reported, while on others no information is available. The first records of *N. speciosa* date from 1927 and in the course of the past 30 years it was regularly reported from several sites, the most important currently being that of the 'Schwemm' by Walchsee, besides those of the 'Legensteiner Moor' near Selzthal, the 'Ibmer Moor' near Ibm, the 'Kropfsee' by Tarrenz and the 'Egelsee' near Spittal an der Drau. The population of the 'Pressegger See' has not been confirmed since 1943 and must be considered extinct.

GERMANY

In Germany, the regions (Bundesländer) are separately treated due to the extensive knowledge and the long tradition of handling the odonate fauna on a regional level. In the German Red List the species is classified into the category 1 identical with CR (OTT & PIPER, 1998).

Lower Saxony – NKL 4, NCL 2, CAT (EN); DE CHARPENTIER (1840), DE SELYS-LONGCHAMPS & HAGEN (1850), BARTHEL (1985), LEMMEL & NORENZ (1986), CLAUSNITZER (2001 and pers. comm.), GÄRTNER et al. (2004).

The localities lay in the E of the region. The first locality, locus typicus of the species, was discovered in the surroundings of Lüneburg before 1840, the latest one, NSG Helstorfer Moor, in 2003. At current localities, *N. speciosa* occurs in moderate numbers or is fairly abundant.

Northrhine-Westphalia – NKL 1, NCL 0, CAT EX; LE ROI (1917), KIKILLUS & WEITZEL (1981), STEINBORN (1983), C.-J. Conze, R. Jödicke, M. Schorr and R. Rudolph (pers. comm.).

The sole certain locality (Gahlen by Wesel, from 1908-1911) is situated in the northernmost part of the region. Apart from it, one almost certainly erroneous record is known from 1956, and one report was doubtless incorrectly localized by Kikillus & Weitzel, it clearly refers to the locality Koningsven in the Netherlands.

Rhineland-Palatinate – NKL 1, NCL 0, CAT EX; LAUTERBORN (1903), J. Ott and M. Schorr (pers. comm.).

N. speciosa was recorded only in a wetland area near Maudach, Ludwigshafen. It is certainly extinct there since a long time, the site being more or less dried out and isolatedly laying in an urban and agricultural area.

Baden-Württemberg – NKL 10, NUL 1, NCL 4, CAT CR; SENF (1976), BAUER (1977, 1998), EB. SCHMIDT (1982, 1983, and pers. comm.), KÖNIG (1992, 1994), B. SCHMIDT (1994 and pers. comm.), FISCHER (1985), SCHMIDT & STERNBERG (1999), STERNBERG (1999), F.-J. Schiel (pers. comm.).

The localities are situated in the SE, i.e. on the Mettnau Peninsula and in the area NE of lake Constance. An isolated finding of a single larva was reported from a bog in the Black Forest. However, in spite of repeated efforts, the species has never been confirmed at this place. In 1970 and the following years *N. speciosa* was recorded in small numbers on the Mettnau Peninsula near Radolfzell, but no longer found since 1984. In 1977 a large population became known at an extended mire complex near Leutkirch. Later a second strong population was found in another large mire ca 20 km further northwest. At all the other localities only few or single stray individuals could be detected, thus harbouring small or no populations at all. Before the end of the 20th century the species had disappeared from four localities with recorded populations, including those of the 'Holzmühleweiher' near Kisslegg/Immenried and the 'Blindsee' by Bad Buchau, both sites with primary habitats. The current localities – three of them are secondary habitats – lay in Upper Swabia.

Bavaria – NKL 62, NUL ca. 10, NCL ca. 35, CAT CR; FISCHER (1950), FREY (1951), LOHMANN (1967), BURMEISTER (1982), K. KUHN (1992), J. KUHN (1992, 1997, 2003 and pers. comm.), KUHN & BÖRZSÖNY (1998).

In no other European country or region there are so many known localities with *N. speciosa* as in Bavaria, and the majority of Germany's populations is found here. They concentrate in the southernmost part of the state, in the prealpine region, within a triangle between lake Constance, Munich and the Chiemsee. Distant from these clustered sites there are two isolated localities in the hilly region of Upper Palatinate and a remote one in the Inner Bavarian Forest near the Czech border. The first records for Bavaria date from 1939 with findings made in the 'Murnauer Moos' S of Munich, but published only in 1951. Up to 1970, 11 sites were known. The relatively high number of recently detected populations results from much increased recording efforts, especially since 1986. As 80-90% of the populations that became known before 1971 are extinct, it is supposed that the number of undetected former localities with the species exceeds that of the current sites several times. Colonized habitats were found from >300 to 1150 m a. s. l., but mainly between 500 and 700 m. Most populations are small or very small. On the other hand, at one of the few localities with large populations in the 'Murnauer Moos', thousands of individuals may be encountered at favourable days in good years, their number probably varying with a factor of more than 100. It is believed that the 'Hohenboigenmoos', a section of the 'Murnauer Moos', harbours the largest population of central Europe. Up to 2003, 27 of the documented populations had disappeared, and the fate of five populations in the Allgäu remained unknown at that time as the last records are dated from the years before 1993. The situation of the species with respect to knowledge and ecological conditions changes continuously. Nevertheless, the Bavarian populations are most important in an international context and the state's responsibility for the survival of *N. speciosa* in Europe is considered correspondingly high.

Schleswig-Holstein and Hamburg – NKL 3, NCL 0, CAT EX; LUNAU (1947), WEISS (1947), SCHMIDT (1975), GLITZ et al. (1989), BROCK et al. (1996, 1997), W. Piper (pers. comm.).

The records, all from the southeastern part of the region, date mainly from 1940-1951. In 1982/83, *N. speciosa* was recorded for the last time in this region, in Hamburg. A recent visit at this locality yielded negative results.

Sachsen-Anhalt – NKL 1, NCL 0, CAT EX; STEGLICH & MÜLLER (2001), MÜLLER & STEGLICH (2004), J. Müller (pers. comm.).

N. speciosa has only recently been recognized as an element of the regional fauna by detection of a specimen in a local collection. The species was found in 1943 in the S of the region, at the 'Heideteiche Waldau', and is presently considered extinct.

Thuringia – There are only two doubtful records from the easternmost part of the region in 1987 and 1992 (JUNGMANN & SYKORA, 1990, 1993) which must have been misidentifications. Therefore, the species is not considered a member of the regional fauna (ZIMMERMANN & KIPPING, 2004).

Mecklenburg-Vorpommern – NKL 6, NCL 3, CAT A.1 (=CR); FÜLDNER (1863), SCHEFFLER (1970), STÖCKEL (1984), ZESSIN & KÖNIGSTEDT (1993), MASIUS (2003), G.

Peters and W. Zessin (pers. comm.).

Four localities, one of them current, are concentrated in the S, constituting, together with neighbouring localities in Brandenburg, a 'Neustrelitz-Rheinsberg-Fürstenberg island' of the range. Two other current localities are situated in the NW and NE of the region. The first known locality dates from 1855-1863, further records from the 1960s and the period between 1975 and 1984. An important site is Grundloser See, 2 km SW of Klein Trebbow, where *N. speciosa* has been known since 1978 although recently found in lower numbers than by G. Peters in 1978-1982.

Brandenburg and Berlin – NKL 18 (+ 1 where the species was temporarily introduced), NUL 0, NCL 5, CAT CR; DE SELYS-LONGCHAMPS & HAGEN (1850), LE ROI (1912), SCHMIDT (1928), KANZLER (1954, 1959), SCHEFFLER (1970), DONATH (1978, 1983), JAHN (1982), HEINRICH & MAUERSBERGER (1991), MAUERSBERGER & MAUERSBERGER (1996), MAUERSBERGER (1998a, 1998b, 2000b, 2004, and pers. comm.), KLAPKAREK & BEUTLER (1999), G. Peters (pers. comm.).

There is a concentration of ten localities in the N and NE of Brandenburg, in a narrow belt running from a northern part of Biosphere Reserve 'Schorfheide-Chorin' up to the Fürstenberg-Rheinsberg area. Other sites are dispersed in the Berlin area and eastern Brandenburg. The first record dates from the years before 1850. Subsequent data were collected mostly in the 1920s and in the early 1930s, and from the mid-1960s until present. In the 1980s, the species was recorded at two localities, in the 1990s at seven sites (at one site temporarily introduced). Large populations of *N. speciosa* were recorded at least at 8 localities, in particular in the 'Kleiner Plagesee' (extinct already in the 1930s), at two sites in the 'Naturpark Uckermärkische Seen', and in the 'Großes Zehme-Moor' by Butzen in NSG 'Lieberoser Endmoräne'. At the last locality even mass occurrence with some thousand individuals was recorded in 1989-91, however, in the 1990s the species became exctinct due to drying out of the habitat. The small 'Berlin' group of localities as well as other sites in the E have been extinct for a long time past. The northern group of localities, comprising two sites in the Rheinsberg area and three in the 'Uckermark', represents the sole region still inhabited by *N. speciosa* in Brandenburg.

Saxony – NKL 8, NUL 1, NCL 0, CAT EX; FEURICH (1896), WAGNER (1957), HERTEL & HÖREGOTT (1961), ARNOLD et al. (1994), T. Brockhaus (pers. comm.).

Seven localities are concentrated in the Upper Lusatia, E Saxony, only the sole unpublished locality, NSG 'Wildenhainer Bruch' (G. Mauersberger pers. comm. to T. Brockhaus), is located in the NW, in the 'Dübener Heide'. One locality dates from the 19th century, six sites from the 1950s and the latest record is from 1960. *N. speciosa* was very abundant at two localities – near Dauban and Tauer. At present, no suitable habitats exist in Saxony.

SWEDEN

NKL 6 (?), NUL 1, NCL 0, CAT EX; DE SELYS-LONGCHAMPS & HAGEN (1850), JOHANSON (1859), WAHLGREN (1915), SAHLÉN (1996), SAHLÉN & NORLING (2000), G. Sahlén and B. Schmidt (pers. comm.).

In basic literature, instead of exact localities most frequently four regions inhabited by *N. speciosa* are given: Skåne, Östergötland, Öland, Gotland. Data are available for five localities: Lund, Gusum, Medevi, Borgholm and Böda-Svartvik in Öland, representing three regions mentioned above, apart from Gotland. However, the true number of localities which is hidden under the names of four mentioned regions remains unknown.

Additionally, a population was discovered in 1984 by B. Schmidt at a lake near Pyntarna, in the environs of Gunnarskog, N of Arvika. This site significantly changes the view on the species range in Sweden. The locality is situated in the W of the country, in the Värmland region, near the Norwegian border, far from all other regions inhabited by the species, all located in the S and SE.

N. speciosa was recorded for the first time in Sweden before 1850. Most records must have been made in the 19th and in the early 20th century. The discovery by B. Schmidt is the latest record in Sweden. Although the species has recently been qualified extinct in Sweden it still may exist here and there. Priority should be given to the confirmation of the locality at Pyntarna.

DENMARK

NKL 2 (?); NCL 2 (?), CAT (EN); HOLMEN (1991 and pers. comm.), PEDERSEN (1999).

One locality, 'Fandens Hul', known since 1990 until present, is situated in the NE corner of Zealand. The population, though variable, was large in some years, reaching even one to two thousand individuals in 1990-1994 and probably some hundred in 2004. The second site, reported without details from the Viborg county, NW Jutland, raises some doubts and needs to be confirmed. Apart from the year of record (1998), nothing is known on *N. speciosa* there.

POLAND

NKL 58, NUL 22, NCL 30, CAT EN; BERNARD (1998, 2004, unpubl. data), BERNARD et al. (2002a), BUCZYŃSKI (2001, 2003, 2004, pers. comm.), BUCZYŃSKI & TOŃCZYK (2004), JÖDICKE (1999), LEWANDOWSKI (2000 and pers. comm.), ŁABĘDZKI (2001), DARAŻ (2005), A. Gawroński, L. Pietrzak and J. Szymański (pers. comm.).

The sites are dispersed or grouped in small local concentrations over most of the territory of Poland apart from mountain areas, 58 % of them localised in the northern part of the country beyond 53°N. A large number of the localities (52 % of NKL) was discovered since 1995 due to increased odonatological exploration and special search for this species, carried out on a large scale mainly by one of us (RB).

Many older localities have not been visited since their discovery and the extinction of *N. speciosa* there seems to be very probable. Only two sites found in Lower Silesia (SW Poland) date from before 1885. Six localities of the species became known in Upper Silesia (S Poland), five of them in the 1950s and the first half of the 1960s. Later it has not been encountered in this region again. In the Wielkopolska region (central Poland), *N. speciosa* was recorded between 1928 and 1977 at five localities, particularly in the broad environs of Poznań. However, despite intense research, it has no longer been found there. A typical example of extinction, caused by habitat changes is Skrzynka lake in the Wielkopolski National Park, where the species occurred in the early 1930s but was already extinct in 1963/64. Data from the last 10 years indicate the current existence of the species only in the northern and easternmost areas of Poland. Considering the possibility of unknown localities in the areas studied insufficiently, ca 40 current localities could be expected in the country.

At least 10-12 current localities harbour large populations, comprising at least several hundred individuals that may be encountered during a visit. Four of them (e.g. Golce, Porost) are outstanding, with particularly large populations, during some visits reaching one to several thousand individuals. Nine current localities, one of them with a very large population, are situated in reserves and national parks.

THE CZECH REPUBLIC

NKL 1, NCL 1, CAT 'close to extinction' (higher than critically endangered); HLÁSEK (1999a, 1999b, pers. comm.), HANEL & ZELENÝ (2000).

N. speciosa is known from a single locality in the Biosphere Reserve 'Třeboňsko' in the S where it was discovered in 1998 and confirmed in 2000. It was fairly abundant, but restricted to a very limited area.

SLOVAKIA

NKL 5, NCL 0, CAT EX; FUDAKOWSKI (1930), TRPIŠ (1957, 1969), DAVID (2001 and pers. comm.).

The localities are scattered, in the SW (2), N, NE and E. The first record dates from 1925, the others from 1956-1960. The record S of Javorina in the Tatry Mountains – one female at a small waterbody on a forest meadow – is noteworthy for its high altitude, ca 1050 m a. s. l. The course of the species extinction is unknown; the habitats of two localities have been destroyed.

HUNGARY

According to FRIVALDSZKY (1879) and later authors who referred to his publication, *N. speciosa* occurred near Budapest. However, based on repeated futile search for voucher specimens in museums, the species was deleted from the list of Hungarian species (DÉVAI et al., 1976; DÉVAI, 1978, pers. comm.) as already suggested by PONGRÁCZ (1936).

ROMANIA

NKL 3, NCL 0, CAT (EX); CÎRDEI (1956), CÎRDEI & BULIMAR (1965).

Three localities out of six given in the first publication were repeated in the second, the others must have been recognized as misidentifications. All localities were recorded in 1953 in northernmost Romania along the Ukrainian border. Very low intensity of odonatological exploration in the recent 20-25 years makes it impossible to reliably define the present status of the species in this country, however, its extinction seems to be certain.

MOLDOVA

NKL 1 (?), NCL 0; BEZVALI (1932), ANDREEV (1998).

The one and only known record, dated from 1911 in the W, is doubtful because the species was given under the name *Nehalennia atrinuchalis*. The specimens described by de Sélys-Longchamps as *atrinuchalis* were identified later as *Cercion hieroglyphicum* (Brauer) and *C. calamorum* (Ris) (DE MARMELS, 1984). If Bezvali used the original description, his *Nehalennia* could have been another species in fact. If he only made a mistake in the species name, his *Nehalennia* could have been true *speciosa*.

FINLAND

NKL 10 (partly not true localities, see below), NCL 1, CAT EN; KARVONEN (1923), SUOMALAINEN (1935), FREY (1937), OKSALA (1939), VALLE (1952), VALTONEN (1980), HÄMÄLÄINEN (1981, pers. comm.), RASSI et al. (2001), KARJALAINEN (2002, pers. comm.), KARJALAINEN et al. (2003), ARNABOLDI (2003).

All data were collected in southern and southwestern Finland including the Åland Islands, on the mainland close to the coast or directly on it, and on small islands. *N. speciosa* was discovered first in 1922, further records concentrated during 1934-1954, subsequent additions were made only in 1981 and 2002-2004. It must be emphasized that only two localities with true populations, both in the Hanko-Tammisaari area, have been recorded so far: that with a formerly thriving population in Täktom (Täktomtrask lake) where the habitat dried up in the 1960s and the current one near Tammisaari, the population of which, though not large, appears viable in S. Karjalainen's and M. Hämäläinen's opinion. At other sites only one or two individuals were found, probably as a result of 'radiation' from the neighbouring populations, in some cases certainly strayed, carried by wind from the coast to small islands. In M. Hämäläinen's opinion, the presence of unknown populations is still possible 'here and there on the coast'.

ESTONIA

NKL 19, NUL 4 (+ 1 site with a record of a migrating individual only), NCL 4, CAT (VU); BRUTTAN (1878), KAURI (1949), REMM (1963), R. Bernard (unpubl. data).

The localities are scattered in a wide area apart from the NE, with a small concentration in the SE. *N. speciosa* was recorded for the first time prior to 1878. Fifteen localities date from the period before 1963 and four from 2002 (only in the SE). However, the scarcity of current data is due to low intensity of faunistic studies rather than to rarity of the species, in the opinion of one of us (RB), not rare at least in the SE of the country. A large current population in an optimal habitat at the small Vinnora lake near Kerigumäe lake is noteworthy.

LATVIA

NKL 23, NUL 5, NCL 7, CAT 2 (VU); SPURIS (1952, 1956, 1960, 1963, 1964, 1998), BERNARD (2003 and unpubl. data), M. Kalniņš (pers. comm.).

The localities occur almost throughout the country save its westernmost part, and are concentrated (80%) in its eastern half, especially in the SE. *N. speciosa* was recorded for the first time in 1950. Most data were collected during the main period of odonatological activity of Z. Spuris (1950-1964). Later seven new localities, mostly from 2002, became known. However, this number does not reflect the current situation, since only very few surveys have been carried out during the past 20 years. In the opinion of one of us (RB), the species is at present fairly rare in Latvia, but locally in the E it probably occurs at more localities. Mostly single, rare or fairly rare individuals were observed, only at four localities the species was more abundant.

LITHUANIA

NKL 21, NUL 15, NCL 17, CAT (VU); STANIONYTĖ (1963, 1993a, 1993b, pers. comm.), BERNARD (2002, unpubl. data), BERNARD & SAMOLĄG (2002).

Apart from three old localities in the NE and SW, the bulk of the sites lay in the E and S, the most forested (dominated by pine forest) parts of the country, particularly in the E (from the surroundings of Pabradė, through the Labanoras Regional Park, Aukštaitija National Park and Gražutė Regional Park up to the environs of Visaginas). Generally, *N. speciosa* is fairly rare, but in the E it is locally a rather regular inhabitant of small forest lakes bounded with specific vegetation.

N. speciosa was recorded for the first time in 1936. Most data originate from studies of one of us (RB) in 2001-2003. The scarcity of earlier records is due to the low level of odonatological exploration. The species occurs frequently in low or very low numbers, only at six localities it was more abundant but a truly large population was found nowhere. Small populations possibly represent only the remnants of larger ones or they are the result of dispersal from undiscovered source populations. In E Lithuania there are numerous waterbodies, located not far from each other, with suitable but not always optimal habitat conditions. It is suggested that the number of small populations in suboptimal habitats exceeds that of large populations in optimal habitats by far.

BELARUS

NKL 6, NCL 3, CAT (DD); BARTENEV (1907), WNUKOWSKY (1937), KIPENVARLITS (1939), PISANENKO (1985), MAUERSBERGER (2000a), DIJKSTRA & KOESE (2001), MOROZ et al. (2002).

Apart from six known localities, the species was reported generally for the Minsk, Vitebsk and Homel districts; at least in the Minsk district, an unknown locality must be considered. The knowledge of Belarussian Odonata is very incomplete and it is assumed that only a small percentage of the Belarussian *N. speciosa* localities has been detected. The entire Belarussian population is most probably still large and in a good shape. Two localities lay in lake districts of northeastern Belarus, another four in the S, in the marshy Polesse (Palessia) region. Both are certainly centres of *N. speciosa* occurrence in the country. Three localities were found in 1905 and 1933, three more between 1996 and 2001. A large current population at Simanichy (Simonichi) Bog in Polesse deserves special attention, possibly the species is not less abundant in the 'Sporauski' ('Sporovskii') reserve.

RUSSIA (West of Ural)

NKL 8, NCL 1, CAT (DD); ULIANIN (1869), ZOGRAF (1907), LE ROI (1911), MELANDER (1927), KOLESOV (1930), DUMONT (1996), BOLSHAKOV (2003).

Three sites are located in the Kaliningrad district, formerly part of Ostpreußen. One site is known from the midwestern part of the country (Smolensk region) and three localities are in the Moscow region. The latest and the sole currently known locality was discovered in the Tula district in 2003. Seven localities are old, the latest dating from the 1920s. At Glubokoe lake, W of Moscow, *N. speciosa* was reported in 1907, but its occurrence could not be confirmed during 1992-1995.

It is possible that the number of published localities is slightly higher since a few of the Russian publications were not available to us. However, this does not change the fact that the *N. speciosa* records are very scarce. They certainly do not reflect its true status in European Russia, whether old or current. Odonata of this huge area were studied almost exclusively before World War II and the level of exploration has always been low. *N. speciosa* may be fairly abundant, at least locally.

UKRAINE

NKL 19 or 20, NUL 1 (see below), NCL 0, CAT (CR?); GORB et al. (2000), WIERZEJSKI (1883), MEDVEDEV (1963), SHESHURAK & PADALKO (1996), R. Pavliuk and L. Frantsevich (pers. comm.).

At the unpublished locality near Luck, a female was found by R. Pavliuk on 24 June 1969. The NKL remains unclear because L. Frantsevich has not confirmed the record of *N. speciosa* in Vyshhorod, therefore this locality should probably be considered as a mistake. The localities are scattered in wide parts of the Ukraine, mainly in the W and N. The records in the S (only 2, in the steppe zone) and NE (1) are very rare. The locality near Yevpatoriia in the Crimea (ca 45°12'N) – the southernmost in Europe – was discovered in 1914. After 1950, the species was found only in the northern part of the country. Larger populations were reported from old localities only, for most sites there are no data on population strength or solely single individuals were recorded. More than half of the data were collected in the 19th and during the first twenty years of the 20th century, six localities date from 1951-1980, and the last site (a single specimen) was recorded in 1993. A serious decline of the species is apparent. However, considering the situation in the neighbouring areas of Poland and Belarus, some (probably very few) populations must have survived in the North, i.e. in the Ukrainian Polesse.

OCCURRENCE IN ASIA

RUSSIA (from Ural to the Far East)

KLAPÁLEK (1901), VALLE (1932), BELYSHEV (1973, 1974), KHARITONOV (1976, pers. comm.), KHARITONOVA (1990), KOSTERIN (1989, pers. comm.), KOSTERIN et al. (2001, 2004), MALIKOVA (1993, 2002, pers. comm.), ZORINA et al. (2000).

The occurrence seems to be restricted to two areas: (a) to the SW, from the southern Ural and the Tura and Konda rivers up to the upper run of the Barnaulka river, the northern Altai and the Tuba river, and (b) to the southeastern corner of Russia, mainly in the basins of the Amur and Ussuri and Khanka lake, small islands in the Japanese Sea, Putiatin and Furugelm inclusive, i.e. to the Amurskaia oblast, Khabarovskii Krai and Primorskii Krai. Between these two parts there is a broad area (more than 2300 km) with no certain data. Only a very doubtful report exists from Transbaikalia, giving no details. Thus, it remains unknown whether there is a true discontinuous distribution in this area. The upper limit of occurrence of *N. speciosa* does not exceed 500 m a. s. l. both in the Altai and in Primore.

The first record of *N. speciosa* in Asian Russia dates from 1880 and the first published report from 1901. Records are mostly concentrated in three periods, viz.: from the end of the 19th century to the 1920s, from the 1950s to the early 70s, and from the late 1980s until present. Four records became known for the SW during the last 25 years only, while they are fairly numerous for the SE. *N. speciosa* was previously reported as a rare species, however, the old and current data from the Russian Far East indicate that it may be fairly abundant locally. It was encountered at individual localities in very low numbers, apart from local areas in the Far East and lakes in the pine forests of the upper Ob river region.

KAZAKHSTAN

BRAGINA & KHARITONOVA (1989), CHAPLINA (2004, pers. comm.), O. Kosterin (pers. comm.).

N. speciosa is given from the Naurzum Nature Reserve (Naurzumskii Zapovednik) in the N. Additionally, a single female, deposited in a museum collection, is reported from the Chu (= Shuw, = Shū) river. In view of its location in the S of the country, ca 1000 km from any other known localities and in a zone of poor steppes and deserts that are unsuitable for the species, this record is puzzling and needs confirmation.

CHINA

BARTENEV (1912, 1914, 1956).

Considering the records of *N. speciosa* in the Russian Far East along the Chinese border, in the areas along the Amur and Ussuri and in the Khanka lake basin, an occurrence in Manchuria, NE China, seems very probable, but we did not find any clear evidence for it in the literature. In his 1956 publication BARTENEV clearly states: 'In China [*speciosa*] does not occur.' His Far Eastern records refer to the Russian territory only.

KOREA

LEE (2001), KOSTERIN et al. (2004).

According to Lee, *N. speciosa* was reported from the Korean Peninsula only once, in 1943, from the northern mountain area in the present People's Republic of Korea. However, the Russian authors give information on a few records in Korea. In the light of the records in the Russian Far East near the Korean border, its current occurrence in N Korea seems very probable.

JAPAN

HAMADA & INOUE (1985), SUGIMURA et al. (1999), INOUE (2004, pers. comm.), H. Naraoka (pers. comm.).

N. speciosa occurs in central and northern Honshu and in Hokkaido. The upper range reaches most probably ca 1500 m a. s. l. More than 30 localities were brought on record so far. *N. speciosa* is not redlisted, although locally it seems to decline. Regress is recognizable both in the number of localities and in abundance at individual sites; some populations are extinct.

HABITAT

In Europe the sites known to be or to have been inhabited by *N. speciosa* comprise both primary and secondary habitats (Figs 1-3), with a significant preference for the former. While in the core of the distributional range the species is almost entirely restricted to the primary habitats, in borderlands, obviously due to the extensive destruction of the primary habitats, the proportion of the colonized secondary habitats is much higher. For example, apart from one locality only primary habitats are known from Lithuania (BERNARD, 2002, RB; BERNARD & SAMOLĄG, 2002; STANIONYTĖ, 1963), and only four secondary habitat sites were found in Poland, in contrast to at least 40 primary ones (BERNARD, 1998, RB; BUCZYŃSKI, 2001; BUCZYŃSKI & STANIEC, 1998; SAWKIEWICZ & ŻAK, 1966). Two of them lay in the S, at the edge of the core of the species range. On the other hand, in Switzerland and Lower Saxony the species was reported exclusively from secondary habitats (LEMMEL & NORENZ, 1986; GÄRTNER et al., 2004; WILDERMUTH, 2004). In Bavaria and Baden-Württemberg it occurs in both habitat types (KUHN & BÖRZSÖNY, 1998; SCHMIDT & STERNBERG, 1999).

The habitats of *N. speciosa* may be grouped into four general types: (a) Lakes and (b) bogs as primary habitats, (c) fens and marshes both as primary and secondary habitats, and (d) man-made pools and ponds as secondary habitats. Lakes inhabited by the species are mostly small, in Poland and the Baltic States usually 50-100 m long and 40-100 m broad, and at least partly bordered by a narrow zone of specific low transition-mire vegetation (Figs 1-2; see below). Considering *Sphagnum* bogs and fens, these are either flooded with shallow water or, more frequently, comprise some small pools and shallow water filled depressions.

The secondary habitats are represented by moist litter meadows, reported

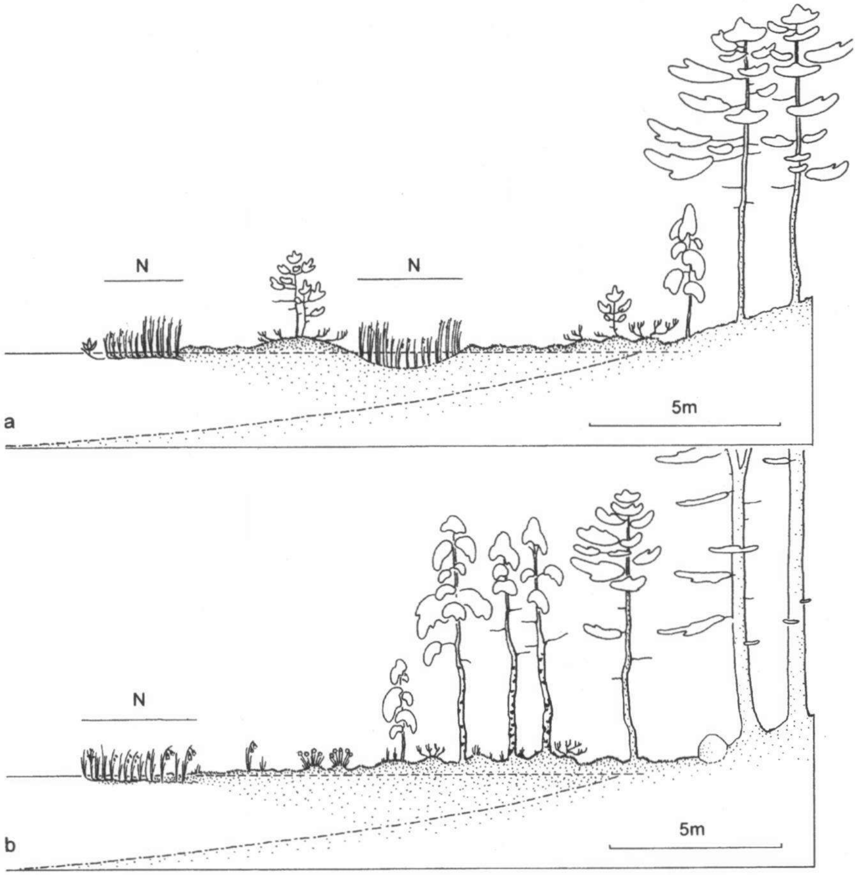

Fig. 1. Primary habitats of *N. speciosa* bordering small lakes in Poland; cross-section on macroscale: (a) typical habitat with floating helophyte/bryophyte vegetation at lake edge and similar vegetation in shallow depression ('Schlenke'), surrounded by coniferous (pine) forest. Głodne Jeziorka, Drawieński National Park; – (b) habitat with floating vegetation at lake edge within deciduous forest (birch swamp and beech wood) near Porost. – [N = zones inhabited by the species]

from Bavaria (KUHN & BÖRZSÖNY, 1998), some fens as those in the Nežárka floodplain in the Czech Republic (HLÁSEK, 1999a), two former fish ponds in Luxembourg (HOFFMANN, 1960; PROESS, 1996) and Baden-Württemberg (BURBACH & SCHIEL, 2004) but mostly post-excavation pools. The abandoned peat diggings, partly overgrown, are the main type of secondary habitats in Poland (BUCZYŃSKI, 2001; BUCZYŃSKI & STANIEC, 1998; B. Daraż pers. comm.), Brandenburg (DONATH, 1983), Lower Saxony (LEMMEL & NORENZ, 1986; GÄRTNER et al., 2004), Schleswig-Holstein (GLITZ et al., 1989), Bavaria (KUHN & BÖRZSÖNY, 1998) and Switzerland (WILDERMUTH, 2004). Still used clay pits in Polish Upper Silesia, inhabited by the species only in their oldest parts and densely overgrown with sedges (SAWKIEWICZ & ŻAK, 1966), are the sole exception.

Both, small isolated objects, as mostly found in Poland and the Baltic States (BERNARD, 1998, 2002, unpubl. data), and more rarely fragments of large wetland complexes, as e.g. in the 'Murnauer Moos' (KUHN, 1997), in the Sporauski (= Sporovskii) Nature Reserve in Belarus (MOROZ et al., 2002), and in the Girutiškis Nature Reserve in Lithuania (BERNARD & SAMOLĄG, 2002), harbour *N. speciosa*.

There is a striking coincidence between the distribution of *N. speciosa* and the areas that were covered by Pleistocenic glaciers, although some localities are situated outside this area. In NE Germany, N Poland and the Baltic States habitats in postglacial cauldron-like depressions or shallow channels (Figs 1, 2) are frequently colonized. Such habitats, accurately denominated 'Kesselmoore' in German, comprise a *Sphagnum* bog with a central small lake or some pools. In Switzerland and in SE Germany the distribution of the species is also mainly confined to areas formed by the Pleistocenic glaciation. Localities situated in large flat areas are in minority, with 'Simonichi' ('Simanichy') bog in a marshy basin of the Prypiats river in S Belarus (DIJKSTRA & KOESE, 2001) as a typical example.

In the core of the species range almost all localities lay in woodland. The same is true of many localities in the SW borderlands. In Poland and the Baltic States they are situated most frequently in large forest complexes and almost never at their edges (RB). On mineral soils these are in most cases coniferous forests or they are at least dominated by coniferous components, such as pine (*Pinus sylvestris*) and spruce (*Picea abies*) (Fig. 1). As an exception, the small isolated locality near Porost (Poland) is surrounded by an old deciduous forest, dominated by beech (*Fagus sylvatica*) (Fig. 1). In NW Poland where the indigenous spruce is almost lacking, *N. speciosa* sites are surrounded by pine stands. In Lithuania where the two tree species are indigenous, *N. speciosa* occurs mainly in pine forests. Most wetland habitats in spruce forests reveal inappropriate for the species (RB). Regardless of the kind of forest overgrowing mineral soils, in many cases the localities of *N. speciosa* are directly bordered by narrow tree stands on wet peat grounds, mainly pine and more rarely birch (*Betula pubescens*) (Fig. 1).

Adults and larvae generally use the same habitat, i.e. (a) a rather narrow zone of floating or flooded vegetation mats bordering the open water of lakes and pools, and (b) shallow waterbodies within bogs and fens, in *Sphagnum* bogs most frequently small depressions ('Schlenken') (Figs 1-3) (e.g. ARNABOLDI, 2003; BERNARD, 1998, 2004; BERNARD & SAMOLĄG, 2002; BUCZYŃSKI, 2001; DEMARMELS & SCHIESS, 1977; HLÁSEK, 1999a; HOLMEN, 1991; KUHN & BÖRZSÖNY, 1998; MAUERSBERGER, 2000a, pers. comm.; OKSALA, 1939; SCHEFFLER, 1970; SCHMIDT & STERNBERG, 1999; B. Schmidt pers. comm.; SPURIS, 1964; WILDERMUTH, 2004; G. Peters pers. comm.), exceptionally also laggs, i.e. waterbodies of the outer bog zone (cf. SCHEFFLER, 1970; SONNTAG & LANDMANN, 2005). The flooded areas can also occur in the vicinity of large waterbodies. The proportion of the (a)-habitats and the (b)-

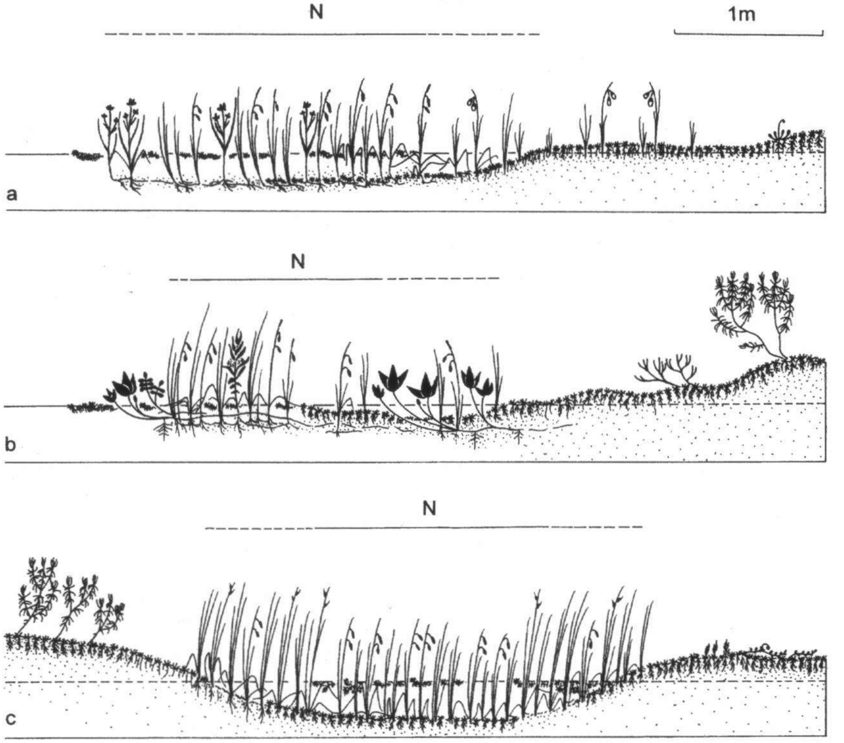

Fig. 2. Primary habitats of *N. speciosa* in Poland; cross sections on microscale: (a) lake edge with floating vegetation predominantly consisting of *Carex limosa*, *Scheuchzeria palustris* and *Sphagnum*, near Porost; – (b) lake edge with floating vegetation mainly comprising *Carex limosa* and *Sphagnum*, interspersed with *Menyanthes trifoliata*, *Potentilla palustris*, and *Lysimachia thyrsiflora*, near Węgorzyno; – (c) depression ('Schlenke') in transition mire with *Carex lasiocarpa* (edge), *C. limosa* (centre), and floating *Sphagnum*, Głodne Jeziorka. – [N = zones inhabited by the species; – continuous lines = main zones of the species activity; – dotted lines = marginal zones of the species activity]

habitats in individual regions varies. In Poland and the Baltic States the colonized habitats adjoining lakes predominate while in SW Germany those separated from large waterbodies are prevailing.

Adult individuals leave the breeding sites only on a limited scale (BERNARD, 1998; SCHMIDT & STERNBERG, 1999). In Lower Saxony and SE Poland they were found among *Molinia* vegetation adjacent to former peat diggings (LEMMEL & NORENZ, 1986; GÄRTNER et al., 2004; RB). In N Poland and the Baltic States only very few imagines were seen on *Sphagnum* mats some metres distant from the water and at only three of about 40 investigated localities imagines occurred regularly – but very locally – in such places (BERNARD, 1998, RB). This suggests that soaked *Sphagnum* mats, as noticed in Golce (Poland) or on Pašeškinės Pelkė (Lithuania), may locally yield appropriate conditions for the larvae. So far, their development in *Sphagnum* vegetation has been confirmed only in the 'Simonichi' (= 'Simanichy') bog in Belarus, where the entire *N. speciosa* population was found away from open water (DIJKSTRA & KOESE, 2001).

N. speciosa is often attached to limited areas within a locality, in extreme cases to 10-12 m^2 at the Samanykštis lake in Lithuania (RB). Sometimes it inhabits solely a fragment of a potentially suitable area as in the Kramářka fen in the Czech Republic (HLÁSEK, 1999a, pers. comm.) or at the brackish-water locality in Finland (ARNABOLDI, 2003).

N. speciosa is typically related to specific vegetation (Figs 2-3) as analysed by SCHMIDT & STERNBERG (1999), BERNARD (1998) and DEMARMELS & SCHIESS (1977) and confirmed at more than 40 localities in Poland and in the Baltic States (RB). The crucial factor is the texture of the vegetation.

The emergent vegetation inhabited by imagines comprises the helophyte stratum above the water surface and above the directly adjacent *Sphagnum* mats. Despite a wide spectrum of plant species noticed in *N. speciosa* habitats and some geographical and ecological variability in the species composition, *Carex limosa* and *C. lasiocarpa* are by far the most important components at least in Europe (Figs 2-3). One of these species but more frequently both were recorded at the sites across the whole European range of *N. speciosa* (BERNARD, 1998, 2002, 2003, 2004, RB; BERNARD & SAMOLĄG, 2002; BUCZYŃSKI, 2001; DEMARMELS & SCHIESS, 1977; DIJKSTRA & KOESE, 2001; HOLMEN, 1991; KUHN & BÖRZSÖNY, 1998; MAUERSBERGER, 2000a, pers. comm.; OKSALA, 1939; SCHEFFLER, 1970; SCHMIDT & STERNBERG, 1999; SPURIS, 1964; WILDERMUTH, 2004; G. Peters and B. Schmidt, pers. comm.). Certainly in Poland, Lithuania, Belarus, Sweden and Denmark one or both of these species predominate in the *N. speciosa* habitats, while in other countries and regions they at least constitute an important component of the plant spectrum. *C. limosa* and *C. lasiocarpa* frequently occur together although in various proportions at different sites. At two localities in Poland (Golce and Głodne Jeziorka), where Caricetum limosae and Caricetum lasiocarpae occur side by side, a preference of *N. speciosa* for *C. limosa* stands or for those combined with *C. lasiocarpa* was noticed (RB & HW).

Carex rostrata is prevailing in the habitats only locally, e.g. at five localities in E Poland, three of them representing secondary habitats (BUCZYŃSKI, 2001; BUCZYŃSKI & STANIEC, 1998; JÖDICKE, 1999; B. Daraż, pers. comm.) but not in the NW of the country (RB), although also at some places in Latvia, Estonia, the Czech Republic, Hamburg, Bavaria, Baden-Württemberg (RB; GLITZ et al., 1989; HLÁSEK, 1999a; KUHN & BÖRZSÖNY, 1998; SPURIS, 1964; SCHMIDT & STERNBERG, 1999). In 'Fandens Hul' (Denmark) only scattered individuals were found in belts of *C. rostrata* while the bulk of them were located in *C. limosa* stands (M. Holmen, pers. comm.). *C. elata* may also have a leading position in *N. speciosa* habitats (Fig. 3), but only locally and mostly in the SW corner of the species' European range, i.e. in Switzerland, Baden-Württemberg and Bavaria (DEMARMELS & SCHIESS, 1977; KUHN & BÖRZSÖNY,

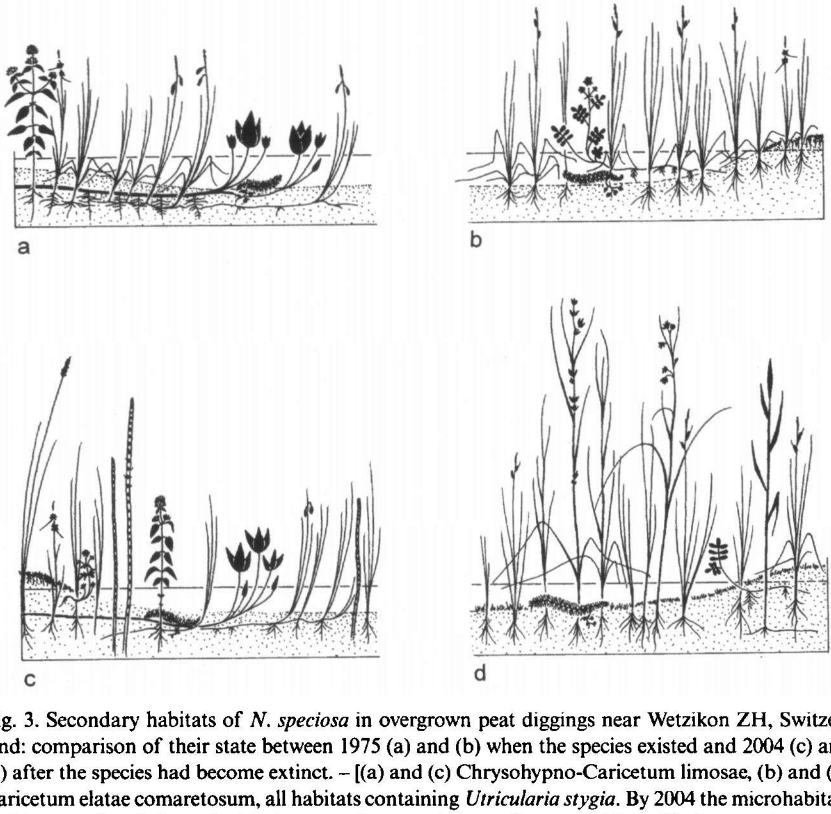

Fig. 3. Secondary habitats of *N. speciosa* in overgrown peat diggings near Wetzikon ZH, Switzerland: comparison of their state between 1975 (a) and (b) when the species existed and 2004 (c) and (d) after the species had become extinct. – [(a) and (c) Chrysohypno-Caricetum limosae, (b) and (d) Caricetum elatae comaretosum, all habitats containing *Utricularia stygia*. By 2004 the microhabitats had become invaded e.g. by *Equisetum palustre* and *Potentilla erecta* (c) or *Cladium mariscus* and *Phragmites australis* (d)]

1998; SCHMIDT & STERNBERG, 1999), and at some localities in Brandenburg (KLAPKAREK & BEUTLER, 1999; R. Mauersberger, pers. comm.). Generally, it seems that *C. rostrata* and *C. elata* occur more frequently in the secondary *N. speciosa* habitats than *C. limosa* and *C. lasiocarpa* which are more representative for the vegetation of its primary habitats. Other *Carex* spp., such as *C. diandra* and *C. chordorrhiza*, are only very locally important (DEMARMELS & SCHIESS, 1977; SCHMIDT & STERNBERG, 1999; RB). From Hotokenuma marsh in Japan *C. thunbergii* and *C. dispalata* are reported, the leading species in the *N. speciosa* habitat (NARAOKA, 1996).

Other vascular plants only exceptionally and mainly in the border parts of the *N. speciosa* range constitute the main component of emergent vegetation: *Rhynchospora alba* in Switzerland (DEMARMELS & SCHIESS, 1977), *Equisetum fluviatile* in SW Germany (KUHN & BÖRZSÖNY, 1998; SCHMIDT & STERNBERG, 1999), *Juncus effusus* at one locality in Brandenburg (R. Mauersberger, pers. comm.), and *Molinia caerulea* (not in water) in Lower Saxony (LEMMEL & NORENZ, 1986; GÄRTNER et al., 2004). At two sites in Poland, *Scheuchzeria palustris* and *Agrostis canina* play an important but not a leading role (RB & HW). Other species such as *Menyanthes trifoliata*, *Lysimachia thyrsiflora*, *Peucedanum palustre* and *Comarum palustre*, are regular additives in the habitats. Where present, the vegetation appears less dense.

The emergent vegetation is mostly 30-80 cm high. Where *C. limosa* dominates, the vegetation reaches 30-50 cm, where *C. lasiocarpa* prevails it stands 60-80 cm high. Taller plants, such as *Peucedanum palustre* or exceptionally *Phragmites australis* (cf ARNABOLDI, 2003) may be interspersed.

The texture is mainly formed by the narrow-leaved *Carex* vegetation. Typically clustered vegetation, such as that of *Molinia caerulea* (GÄRTNER et al., 2004), is merely exceptionally inhabited. Only 'lawn-like' vegetation (Figs 2-3), according to SCHMIDT (1994) and SCHMIDT & STERNBERG (1999) with 40-200 vertical stems or blades per 0.04 m^2, is colonized though looser parts of it may also be marginally used (RB). Some distance between plant elements appropriate for the flying imagines is necessary. A mosaic of loose and dense formations, with a predominance of fairly dense ones, seems to constitute the best conditions for the species (RB & HW). In dense formations there are many small gaps, corridors and looser sections used by *N. speciosa*. It avoids only very loose and very dense formations (RB).

The submerged vegetation (Figs 2-3) is mainly composed by: (a) flooded parts of helophytes, both live and dead, (b) edge parts of *Sphagnum* mats, (c) floating *Sphagnum*, (d) other floating mosses, as e.g. *Scorpidium scorpioides*, *Warnstorfia fluitans*, *Limprichtia revolvens*, *Calliergon* spp., and (e) *Utricularia* spp. (*stygia, intermedia, minor*) (BERNARD, 1998, RB; DEMARMELS & SCHIESS, 1977; KUHN, 1992; SCHMIDT & STERNBERG, 1999). With the exception of (a) all other components are optional. However, the microhabitat usually contains a bryophyte species and frequently an *Utricularia* sp. While *S. scorpioides* is one of the most frequent components in SW Germany and Switzerland (DEMARMELS & SCHIESS, 1977; SCHMIDT & STERNBERG, 1999), it is rare in habitats in the core of the *N. speciosa* range (RB; R. Mauersberger, pers. comm.) where mostly floating *Sphagnum* occurs. Out of three *Utricularia* spp. that are important in the SW corner of the range (SCHMIDT & STERNBERG, 1999), this is only true for *U. minor* in the core of the range (RB). Regardless of the composition of submerged vegetation, its covering and density are frequently high. According to SCHMIDT & STERNBERG (1999), *Utricularia* spp. often cover more than 20% and floating mosses mostly far less than 60%, however, in Poland and the Baltic States the covering by mosses is locally higher (RB).

Plant communities were identified mainly in the SW part of the European range, in Switzerland, Baden-Württemberg and Bavaria, from where the following phytocoenoses are reported: Caricetum elatae, Caricetum elatae comaretosum with *Scorpidium scorpioides* (= Scorpidio-Caricetum f. dissolutae), Caricetum limosae, Caricetum lasiocarpae, Caricetum rostratae, Caricetum diandrae, Caricetum chordorrhizae, Rhynchosporetum albae, and submerged Scorpidio-Utricularietum minoris, Sphagno-Utricularietum stygiae (DEMARMELS & SCHIESS, 1977; KUHN & BÖRZSÖNY, 1998; SCHMIDT & STERNBERG, 1999). The first four communities and both submerged ones play a leading role in this area. Here, the spectrum of phytocoenoses is broader than in the remaining part of the European range of *N. speciosa*, where Caricetum limosae and Caricetum lasiocarpae prevail and Caricetum rostratae and Caricetum elatae are definitely of secondary importance (e.g. BERNARD, 1998, 2004, RB; BERNARD & SAMOLĄG, 2002; BUCZYŃSKI, 2001; DIJKSTRA & KOESE, 2001; HLÁSEK, 1999a; HOLMEN, 1991, pers. comm.; JÖDICKE, 1999; KLAPKAREK & BEUTLER, 1999; MAUERSBERGER, 2000a, pers. comm.; OKSALA, 1939; SCHEFFLER, 1970; B. Schmidt and G. Peters, pers. comm.).

While the water quality is generally mentioned in many publications, detailed data on the physico-chemical conditions are available only from a few localities, mainly from Baden-Württemberg (SCHMIDT & STERNBERG, 1999) and for 15 localities in Poland (e.g. BERNARD, 1998; BUCZYŃSKI, 2001). The water of the larval habitat is characterized by:

(a) depth between a few and 30 (40) cm; for the sole exception – wet *Sphagnum* without open water – see above;

(b) colour frequently slightly brownish-yellowish caused by huminic acids;

(c) fast warming up and high temperatures which may reach 30°C in sunny summer days. Even in cool and windy summer days at some localities in N Poland, the water temperature exceeded that of the air by 1.5-7°C, the difference being most perceptible between September and early November, i.e. in a period of intensive larval growth. In winter, temperatures in depressions ('Schlenken') covered with snow remain at about 0°C and the water freezes only in harsh conditions;

(d) fairly low pH, ranging from 3.3 to 7.2, in Poland mostly 4.0-5.5, below 4 only at one locality in Lower Saxony and at two sites in Poland; for one Brandenburg locality the given term 'alkaline habitat without *Sphagnum*' suggests an even slightly higher pH than 7;

(e) low conductivity (10-150 µS/cm), at Polish localities mostly between 20 and 90, and frequently below 50 µS/cm. 167-378 µS/cm at one locality in E Poland (Uroczysko Jęzior) is exceptional;

(f) low hardness, < 0.1-5.7 but mostly not exceeding 0.5°dH;

(g) low trophy, most frequently described as oligotrophic or mesotrophic, however at many sites water may be designated dystrophic

(BERNARD, 1998; BUCZYŃSKI, 2001; BUCZYŃSKI & STANIEC, 1998; DEMARMELS & SCHIESS, 1977; GÄRTNER et al., 2004; KUHN & BÖRZSÖNY, 1998; SCHEFFLER, 1970; SCHMIDT & STERNBERG, 1999; SPURIS, 1964; RB & HW; R. Mauersberger, pers. comm.). The occurrence of *N. speciosa* in brackish waters (< 0.5-0.7% salinity) is exceptional, it was reported from a single locality in Finland (ARNABOLDI, 2003).

Summing up, the typical habitat contains stagnant, shallow, warm, and fairly acid water. It is poor in carbonate and other electrolytes and may be locally influenced by mineral groundwater.

BIOLOGY

PHENOLOGY

N. speciosa is generally univoltine and overwinters in the larval stage. However, 10-20% of a population may be semivoltine (SCHMIDT & STERNBERG, 1999). The flight period in Europe ranges from the second decade of May till the first decade of September but mainly from early June to early August (BERNARD, 1998; KUHN & BÖRZSÖNY, 1998; SCHMIDT & STERNBERG (*l.c.*). Dates earlier than 25 May and records from the end of August and of early September are rare (RB; KUHN & BÖRZSÖNY, *l.c.*; TRPIS, 1969; G. Peters, pers. comm.; cf. also NARAOKA, 1996 for Japan). The latest known record, between 16 and 20 September, originates from the S of the Ussuri region in the Far East (BARTENEV, 1912). The border dates of the flight period are similar in a large part of the European range, the difference is only a few days. However, in the northernmost borderlands (Finland), the flight season starts at least three weeks later than in central Europe but ends no more than one to two weeks earlier (BERNARD, 1998, RB; KARJALAINEN, 2002, pers. comm.; KUHN & BÖRZSÖNY, 1998).

EMERGENCE

Emergence lasts up to the end of July with an EM_{50}-Index of 10-36 days. It reaches daily its maximum in the early afternoon (SCHMIDT, 1994; SCHMIDT & STERNBERG, 1999; RB). SCHMIDT & STERNBERG (*l.c.*) give 10-20 cm above the water as the predominating height of emergence. In Poland and the Baltic States, almost all exuviae were found truly low, between 2 and 10 cm above water, only exceptionally higher (RB). Stems of sedges in rather densely overgrown places are the main emergence substrate (SCHMIDT & STERNBERG,1999; RB).

SITE FIDELITY AND DISPERSAL

The whole life history of *N. speciosa*, comprising development, foraging, resting, roosting and reproduction takes place in a spatially restricted habitat. Tight site attachment is mentioned by several authors. SCHMIDT & STERNBERG (1999) report that 92% of the individuals stayed within the larval site including the range up to 10 m away from it and almost no individual was found more than 100 m aside the zone of oviposition. Marked individuals shifted maximally 25 m within 10 days (REINHARDT, 1994).

Imagines are exceptionally found far from any suitable habitat such as: (a) those encountered up to 5 km mentioned by SCHMIDT & STERNBERG (1999), (b) those observed on small Finnish islands (see above: Finland), (c) one individual on the camp site next to lake Külajärv (inappropriate for the species) in SE Estonia (RB), (d) one individual found in a spider's web on a balcony in the center of Kyiv (L. Frantsevich, pers. comm.). Records of individuals in unusual places, also distant from breeding sites, may be the result of disturbance by observers and/or wind drift.

ACTIVITY PATTERN AND INFLUENCE OF WEATHER

The activity of *N. speciosa* begins early in the morning. Two hours after sunrise many individuals may already be active and males even begin to search for females (NARAOKA, 1996; RB & HW). Such early activity was observed not only at temperatures 19-20°C in Japan (NARAOKA, *l.c.*) but also at relatively low temperature of 15.5°C with slight mist after a foggy and fairly warm night in N Poland (RB & HW). First tandems were found shortly afterwards, e.g. 2.5 h after sunrise both in Poland and Baden-Württemberg (RB & HW; SCHMIDT & STERNBERG, 1999). Copulations begin 2.5-3.25 h after sunrise (NARAOKA, 1996; SCHIESS, 1973; SCHMIDT & STERNBERG, 1999; RB & HW). Since copulations – especially those begun in the morning – last most frequently long, copulation wheels accumulate in the subsequent hours reaching the numerical peak of numbers in the late morning (NARAOKA, 1996; SCHIESS, 1973;

SCHMIDT, 1994; SCHMIDT & STERNBERG, 1999; RB & HW). At two sites in N Poland the last formations of tandem links took place 2 and 2.25 h after solar noon and the last two tandems were observed 2 h 20 min after noon (at 15:20 CEST) while half an hour later no tandem was detected. Oviposition occurs between late morning and afternoon (NARAOKA, 1996; SCHIESS, 1973; SCHMIDT & STERNBERG, 1999), in the SW part of the European range from 11 to 17 CEST, i.e. up to ca 3.5 h after solar noon.

In favourable weather imagines stay in the upper parts of the vegetation until and during the night. In the late afternoon they are less active, although feeding may occur, and in the evening they remain practically inactive (NARAOKA, 1996; SCHMIDT & STERNBERG, 1999; RB & HW). In the late afternoons and in the evenings, especially in calm and sunny conditions, they bask on top parts of plants, catching the last sunrays (SCHMIDT & STERNBERG, 1999; RB & HW). SCHMIDT & STERNBERG (*l.c.*) report that the imagines crawl down into the lower parts of the vegetation after sunset. Possibly this is not the rule. It was observed in N Poland that numerous imagines stayed for the night exactly at the same height as during sunset, i.e. in the uppermost fourth of the vegetation, only 1 to 7 cm below tips of the plants (RB & HW).

The activity of imagines is modified by the weather, i.e. by a combined effect of temperature, humidity, insolation and wind. However, the modification differs from that what is typical of other European Zygoptera (SCHMIDT, 1994; SCHMIDT & STERNBERG, 1999; RB & HW). The species is active, also reproductively, already at temperatures between 15 and 18 °C. The individuals avoid strong insolation, especially the scorching sunlight during the central hours of very warm days, according to LEMMEL & NORENZ (1986) with temperatures above 25°C, while the morning and late afternoon-sunshine, although not obligatory, seems favourable (SCHMIDT, 1994; RB & HW; cf. also OKSALA, 1939; BALESTRAZZI & BUCCIARELLI, 1971). Cloudiness seems to be no obstacle for the species. At the appropriate temperatures imagines remain active even in drizzle or light rain (RB & HW; KUHN & BÖRZSÖNY, 1998). During heavy rain they can even stay in top parts of vegetation, being inactive with strongly lowered abdomens. Wind is a very limiting factor for *N. speciosa* (SCHMIDT, 1994; SCHMIDT & STERNBERG, 1999; RB & HW). The individuals stay low in vegetation or search for a wind-protected place already at moderate wind forces. At the same locality striking differences in the activity are noticeable between open places and those protected against the wind (RB & HW).

Most favourable weather conditions for imagines are calm or slight wind only, moderate temperatures, partial clouding or thin light clouds with subdued sunshine, i.e. no strong insolation, and preceding warm nights. In full sunshine on hot days or on sunny days with cool wind *N. speciosa* stays mostly hidden low in vegetation. Many individuals may be noticed at first sight at the same site in windless and fairly warm conditions with partly cloudy sky (RB & HW).

BEHAVIOUR

Generally, *N. speciosa* is a rather sluggish zygopteran, its activities are bound almost exclusively to the same habitat that is jointly used by tenerals, subadults and adults of both sexes. The operational sex ratio is slightly male biased (SCHIESS, 1973) and changes in the course of the day with an increase of females (REINHARDT, 1994; SCHMIDT, 1994). Perching and flying short distances, 'hopping' from one perch to another, are most typical behavioural elements. The angle between the body axis and the more or less vertical perch, the frequency of flights and aggressive behaviour as well as the intensity of reproductive behaviour indicate the level of activity. We found that at temperatures of 10-10.5°C and at complete darkness, the specimens did not react neither to a torchlight nor to an almost touching approach of the observer's hand despite good lighting. During the day, at temperatures below 13°C, but also at slightly higher ones with cool wind, individuals did not fly at all (RB & HW). When in danger, they often sidle round a thin plant stem to hide the body but still allowing unimpeded vision owing to the appropriately wide eye spacing (BERNARD, 1998) like in other zygopterans (ASKEW, 1982). This behaviour is sometimes also shown at higher temperatures and regularly by teneral specimens regardless of temperature.

At low temperatures or during heavy rainfalls the individuals adopt roosting posture with the body almost parallel to the support or at an angle up to 30°. Prevailing angles between 30 and 60° in an individual population indicate a rather low general level of activity which may comprise few displays, rare short flights and beginning reproductive behaviour. A range of 45-90° with mean values between 60 and 80° is typical of active individuals. The dominance of angles of 70-90° in population was observed in late afternoon after a fine day despite low flying activity, the individuals probably catching the late sunrays in this posture (RB & HW).

Flights are generally short and low, only exceptionally ascending beyond vegetation, even during periods of maximal activity. At initial and final phases of activity the flight distances rarely exceed 10-15 cm while at the peak they range usually between 10 cm and 1 m, however the flights of males in search for females and those of some copulating pairs may be longer (RB & HW). The flights rarely last longer than 10 s apart from male searching flights that may continue up to 2 min (SCHMIDT & STERNBERG, 1999). Very short flights upwards and downwards may serve vertical displacement among vegetation (RB & HW). This may also be achieved by crawling up and down in the initial and final phases of activity (SCHMIDT & STERNBERG, 1999).

Aggressive behaviour very rarely ends up in physical body contact that probably involves grasping and biting. Most frequently it is limited to threat displays of a perching or flying male in response to an approach of another male or a tandem, both conspecific and heterospecific (e.g. *Coenagrion* sp.). Threat display comprises lifting abdominal segments 8-10 with their conspicuous light blue spot, in perching males also enhanced by their wings partially spread and sometimes fluttering. In the most vigorous form threat display finds its expression in face-to-face hovering, sometimes including ‘dances’, i.e. sudden rises and descents of low amplitude (SCHIESS, 1973; RB & HW).

Refusal display of females comprises ventral curving of the abdomen, in perching individuals also wing spreading, in flight sometimes ‘dances’ similar to those between males but with higher amplitude up to 20 cm (NARAOKA, 1996; SCHIESS, 1973; RB & HW). In young females that are coloured like males threat display may replace refusal display (NARAOKA, *l.c.*).

The reproductive behaviour of *N. speciosa* as described by SCHIESS (1973), SCHMIDT (1994), NARAOKA (1996), SCHMIDT & STERNBERG (1999) and studied by ourselves resembles that of other coenagrionids and comprises the following elements: (a) waiting for females at oviposition sites or active mate search by males in dense vegetation, (b) grasping of female and tandem formation, (c) male invitation to copulation followed by intramale sperm translocation, this lasting a few seconds, and "genital touching" by female, all these elements performed in tandem position on perch, (d) copulation with three stages, including rapid ‘kicking’ by the male, occurring in series with a fairly regular rhythm, the function of it remaining unknown; copulations may continue from ca. 0.5 to 4.5 h, the duration diminishing in the course of the day, (e) oviposition, mostly following copulation less than 1-3 min after its termination, mostly unguarded and lasting up to nearly 2 h; eggs are deposited in decaying stems and leaves of *Carex* floating on the surface.

PREY AND PREDATORS OF IMAGINES

N. speciosa preys on small insects, mostly on Diptera as supposed, but also on Microlepidoptera (*Elachista* sp.) (NARAOKA, 1996; RB & HW). Feeding activity, though concentrated in the afternoon, lasts the whole day. Main predators are most probably spiders (Araneidae, Tetragnathidae) and frogs (*Rana lessonae*) which occur numerously in many places inhabited by *N. speciosa* (SCHMIDT & STERNBERG, 1999; RB & HW). However, while imagines were rather frequently found in spiders’ webs, no successful attack by a frog has been witnessed by us. Young individuals are sometimes fed by lestids and coenagrionids (SCHMIDT & STERNBERG, 1999; RB). Tenerals are sometimes infested by larvae of water mites (*Arrenurus* sp.) (SCHMIDT & STERNBERG, *l.c.*). These may significantly lower the flight abilities of the imagines (REINHARDT, 1996).

DISCUSSION

COLONIZATION OF EURASIA

N. speciosa is the only Eurasian representative of the small and essentially American genus, rather closely related to *N. gracilis* Morse (DE MARMELS, 1984). It may have evolved from the ancestral *gracilis*-like species which immigrated from North America into E Siberia in the Oligocene (BELYSHEV & KHARITONOV, 1977; DE MARMELS, *l.c.*). Subsequently it colonized large areas of Eurasia. According to BELYSHEV & KHARITONOV (1977), during the glaciation, the species range was divided into some isolated parts which became centres of postglacial colonization, the former still recognizable as a discontinuous distribution pattern in Asia. However, in the opinion of O. Kosterin (pers. comm.), this disjunction is much younger and resulted after the climatic optimum of the Holocene (cf. DUBATOLOV & KOSTERIN, 2000 for Lepidoptera). This supposition may be supported by the lack of recognizable symptoms of allopatric speciation. BELYSHEV & KHARITONOV (1977) indicate the morphological homogeneity of the species across its whole distributional range and therefore synonymize the formerly described subspecies *N. s. sibirica* Belyshev, 1964 with the nominal form.

The hypothetic migratory routes along which *N. speciosa* might have immigrated from its periglacial refuges into central Europe were reconstructed by STERNBERG (1998). The main route may have run from SW Siberia through the S of European Russia, the Ukraine, Belarus, Poland and N Germany up to the westernmost bridgeheads in Benelux and W Germany. These areas may have constituted a stepping stone to reach southward the N of Romania and northward central and N Russia, the Baltic States and Fennoscandia. Two side branches of this main route may have originated in S Poland and run through the Moravian Gate: the northern across the Danube river to the Prealpine Region, the southern, through the Vienna basin to the southern foothills of the Alps in N Italy. In our opinion, the colonization of Europe on a more extended front due to the wind drift and not only following the low valley routes should also be considered in the case of this little mobile species. Furthermore, the expansion from E to W during the Holocene was probably discontinuous because of periodic temperature fluctuations.

DISTRIBUTION IN EURASIA

The range of *N. speciosa*, as defined on the basis of the data from the last 165 years, extended between 5° and 145° E, from Belgium up to easternmost Japan. The latitudinal range limits are satisfactorily known for Europe only. The species occurred between N Italy, N Romania and the Crimean Peninsula in the S and S

Sweden and S Finland in the N, between 45.2° and 61.6° N (Fig. 4). In Asia, the species range is far less known. The northern range limit probably declines from ca 60° N in the W up to 51-52° N in the E due to the increasing harshness of climate. The Asian range of *N. speciosa* is most probably divided into two parts: (a) a western part covering the Southern Ural Mountains and SW Siberia up to the Altai Mountains, including N Kazakhstan locally, and (b) an eastern part, comprising mainly the Russian Far East and northern and central Japan, also northern Korea and probably the northeasternmost China. In Japan, the southern range limit reaches 36°20' N. Due to the specific habitat requirements of *N. speciosa* its range has probably always been patchily populated and only locally concentrated. However, at least in Europe and in Japan, two centuries ago the density of sites was certainly higher than nowadays. Inferred from the European distribution of the species currently known, we assume that originally a core range existed in mideastern Europe comprising easternmost Germany, Poland, the Baltic States, Belarus, northern Ukraine and the central latitudes of Russia (cf. Fig. 4). This core was bordered by a broad bowshaped area that was less densely inhabited but still interspersed by more densely populated spots, with the Prealpine region as a typical example. Climatic conditions, e.g. in Fennoscandia, and the shortage of appropriate habitats, as e.g. in southern Ukraine, Romania or France may have limited a further expansion of the species. The total absence of *N. speciosa* in Britain, especially in Scotland, may be explained by its late postglacial arrival at the North Sea, i.e. at a time when the landbridge between the British Isles and continental Europe no longer existed, as suggested by STERNBERG (1998) for *Aeshna subarctica.*

The vertical distribution of *N. speciosa* in Europe is most probably also climatically determined. The species occurs mainly in lowlands, locally in uplands, and only rarely in lower mountains. It generally concentrates below 500 m a. s. l., however, in some Alpine regions at slightly higher altitudes, i.e. at 500-700 m in Bavaria and at 500-800 m in Austria. Except for one enigmatic record from the Slovak Tatry Mountains (1050 m a. s. l.), the uppermost localities are situated at ca. 750 m in Baden-Württemberg, 793 m in Austria, 839 m in Italy, and 1150 m in Bavaria. The regular occurrence in upland wetlands is also known from Japan (Honshu) where *N. speciosa* reaches even ca 1500 m. Both, in the Alpine countries and in Honshu, its occurrence at higher altitudes is mainly related to the presence of unimpaired habitats. In central Japan an influence of the regional climate, displacing the species from the lowlands, may also be considered.

In Europe there is a striking relationship between the ranges of *N. speciosa* and periglacial landscapes. The species only locally crosses the southern range limits of the former glaciation, e.g. in S Ukraine and Romania, and does not strongly exceed these limits.

CHANGE IN DISTRIBUTION FROM 1850 TO 2000

Considering the past 150 years, significant changes in distribution and population strength must have occurred in the European range of *N. speciosa*. Their course and scale are hard to judge because of low odonatological exploration of many areas between 1850 and 1950. However, it is beyond any doubt that the changes were especially drastic in the border parts of the range (Fig. 4) and more intense in the second half of the 20th century. This has become obvious in complete withdraw of the species from many regions and in decreased numbers of colonized localities or weakened populations strengths in others.

The changes became manifest first – i.e. in the end of the 19th century and in the first decades of the 20th century – in the West: in Belgium, the Netherlands, western Germany (Northrhine-Westphalia, Palatinate) and in easternmost France. The very rare and old records at the southernmost border of the range, in S Ukraine, ended also in the early 20th century, suggesting that the species disappeared there long ago. Although the decline in Europe progressed gradually, a wave of intensification of this process is recognizable from the 1950s to the 1970s, indicated

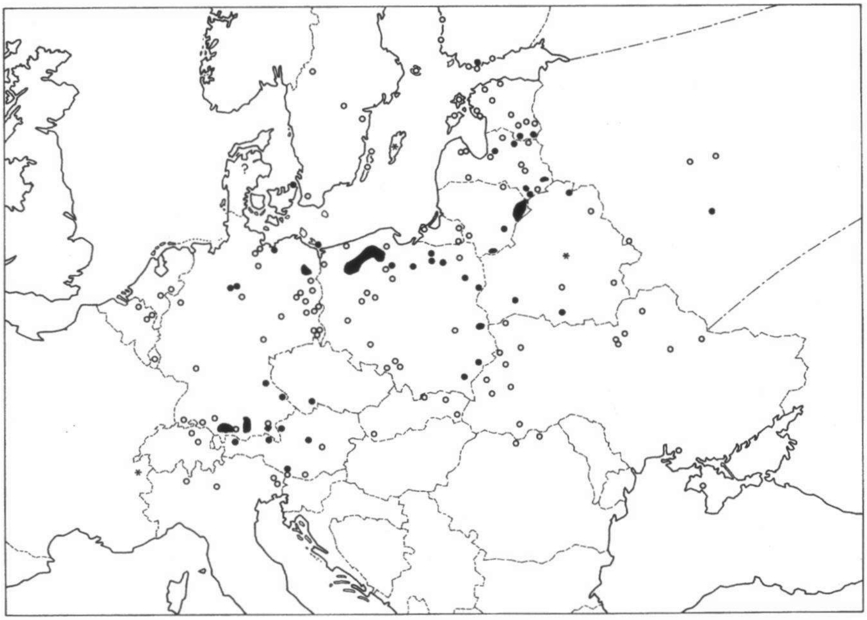

Fig. 4. Distribution of *N. speciosa* in Europe. – [Open circles = old records, collected before 1995; – black circles and spots = recent data, collected between 1995 and 2004; – asterisks = not localized data (a region only); – ? = not localized and doubtful data. One symbol may cover an area with several or many localities. Localities with old and recent data available are shown by black symbols. For European Russia a hypothetic range of the species is drawn]

e.g. by the difference in the number of literature data for some countries and regions between this period and subsequent years. In Sachsen-Anhalt *N. speciosa* was recorded only in 1943, in Schleswig-Holstein from 1940 to 1951, in Romania in 1953, in Saxony, Slovakia and Luxembourg mostly or solely in the 1950s and only up to 1960. The Swiss populations, all clustered in the NE, broke down definitely in the 1970s. In northern Italy the species probably became extinct in recent years. In Baden-Württemberg, Bavaria and Austria *N. speciosa* is still existing, though in declining number of localities and shrinking population sizes. In S Fennoscandia, the species may still occur here and there. In Sweden the latest record dates from 1984, and in Finland the species, found after 1954 merely at two localities, is currently known from one site only. The core of the range in Europe has not been exempted from the decline either. Between 1950 and 1980 *N. speciosa* became locally extinct in southern and central Poland and regressed deeply in the Ukraine where the latest record dates from 1993. The number of localities significantly decreased also in Brandenburg and Mecklenburg-Vorpommern. In other countries of E Europe, the paucity of data does not enable to judge the decline, though it is probably significantly less advanced. It must be stressed that the recent discoveries of new localities of *N. speciosa* in Finland, Denmark, the Czech Republic, Baden-Württemberg, Bavaria and especially in Poland and the Baltic States are only the result of intensified exploration and do not indicate an improvement of its status.

In summary, *N. speciosa* currently occurs mainly in eastern Europe, up to Estonia, central Latvia, E Lithuania, N and E Poland, S Belarus, and possibly up to 52-54°N in Russia. In all the other regions it has mostly survived in single or very rare local populations (cf. Fig. 4). Single up to six sites are known from Lower Saxony, Baden-Württemberg, Austria, the Czech Republic, Brandenburg, Mecklenburg-Vorpommern, Denmark and Finland. The species probably still exists very rarely in N Ukraine and S Sweden. The Bavarian Prealpine Region constitutes the sole exception among the borderlands, still harbouring about three dozens of local populations, but many of them are weak and also rapidly declining.

The strength of local populations of *N. speciosa* is hard to evaluate due to both relative paucity of precise data and fluctuations of the population sizes. In many cases only single or few individuals were recorded and the species had disappeared at corresponding places in the subsequent years. It must be stressed, however, that even large populations were not exempted from extinction due to habitat changes, as shown by examples from Switzerland ('Robenhauser Riet', 'Lutiker Riet'), Austria ('Presegger See'), Brandenburg ('Kleiner Plagesee' and 'Großes Zehme') or central Poland (Skrzynka lake).

At present only 25-30 large populations are known in Europe, mostly in N and E Poland and in S Bavaria. Further large populations may be discovered further East, in Belarus and Russia. In the Baltic States the low number of known large populations is compensated by a higher number and density of localities harbouring smaller populations. Only very few large populations seem to be in a relatively favourable situation: (a) being accompanied by satellite populations in the surroundings, as e.g. that of 'Hohenboigenmoos' within the 'Murnauer Moos' in Bavaria and most probably also Vinnora lake in Estonia, or (b) comprising some adjacent subpopulations, as e.g. near Zgon in Poland. Other large populations such as those near Walchsee in Austria or near Golce and Porost in Poland, are largely isolated.

On the whole, the current state of *N. speciosa* in Europe is defined as a regress, deep everywhere W and S of the line running through the Baltic States, N and E Poland and S Belarus with S Bavaria perhaps constituting an exception. Therefore, the species was rated among the critical species in Europe (SAHLÉN et al., 2004).

The situation in Asia is hardly comparable to that in Europe, mainly due to the relative paucity of data. It may be assumed that the state of the species in many areas is better than in Europe as the number of suitable habitats is still rather high. Only in Japan some symptoms of decline have been noticed.

HABITAT SELECTION AND LIFE HISTORY – AN EVOLUTIONARY SUCCESS AND A REASON FOR DECLINE

N. speciosa exhibits very high stenotopy. Its habitat preference, considered to be an evolutionary success, is an important part of life history that includes much avoidance strategy. On the other hand, due to little ecological plasticity, the species is expected to react sensitively to slight habitat changes.

The specific habitat (a) allows *N. speciosa* to complete its development in one year in a permanent aquatic environment with simultaneous avoidance of high predator pressure on larvae, (b) provides appropriate microclimatic conditions for the tiny imagines, these being protected against fatal weather influences, (c) supplies prerequisites for minimal inter- and intraspecific competition among imagines and for reduced predator pressure on them.

One of the crucial factors of the species microhabitat is the low depth of water, this frequently being brownish, allowing it to warm up fast and accelerate embryonic and larval development. Furthermore, shallow water largely refrain fish predators from penetrating the larval habitat. On the other hand, shallow waters easily desiccate. Desiccation may be caused by long term precipitation deficits that result in lowered groundwater table. The same will happen as a consequence of superficial drainage or groundwater extraction for economic reasons. Drying up of the habitats is one of the most frequently reported reasons for local extinction of *N. speciosa*, as e.g. in Täktom, Finland (HÄMÄLÄINEN, 1981, pers. comm.), 'Kleiner Plagesee' and 'Großes Zehme' in Brandenburg (KANZLER, 1954; R. Mauersberger, pers. comm.) or Skrzynka lake in Poland (MIELEWCZYK, 1966).

According to literature data and our own experience, it may be assumed that unimpaired primary habitats of the species rather rarely dry up. In many cases these are floating mats at lake borders that follow the changing water table with no or only little influence on the hydrological micro-situation, the depth of water in the *Nehalennia* habitat therefore remaining more or less constant. Similar conditions may prevail in *Sphagnum* mats suffused with water or in flooded depressions within large mire complexes. Additionally, eggs and larvae of *N. speciosa* may survive short periods of partial desiccation in wet *Sphagnum* pads. The exceptional Belarussian case described by DIJKSTRA & KOESE (2001) could be possibly assigned to this category.

The danger of drying up is much raised in secondary habitats, especially in peat diggings with advanced natural succession where the roots of the plants form a firm felt. During long-lasting dry periods the water table may lower even 50 cm or more and for the surface there is little or no possibility to lower because the felt is rather fixed. The microhabitat of *N. speciosa* subsequently dries up. This may be the reason for the local extinction of the species, in combination with the increasing overgrowth of the shallow waterbodies, especially in regions with nutrient influx from the environment of the habitats, thus accelerating plant growth. This scenario of extinction is assumed for some Swiss localities as a result of an extremely dry period in early summer 1976 (cf. WILDERMUTH, 2004).

Abundant submerged vegetation serves as hiding place for larvae, strengthening the antipredator effect of shallow water. Furthermore, it serves as substrate for the vertical shift of the larvae along the temperature gradient and it protects them temporarily against drought. On the other hand, the direct linkage to submerged vegetation constitutes a limiting factor. In Poland, many dystrophic lakes are inappropriate for the species because emergent *Sphagnum* mats are rather firm and end abruptly at the water side, thus lacking gradually submerging and floating stems. Hence, the accompanying *Carex* vegetation mostly does not stand in the water either. Submerged *Sphagnum* mats without emerging stalk vegetation are likewise unsuited for *N. speciosa.* As a result, inappropriate lakes are much more frequent than appropriate ones. This restricts the colonization of numerous water bodies and explains the isolated situation of many populations.

The emergent vegetation with its texture and microclimate provides the imaginal habitat. A common feature of the vegetation that is colonized by *N. speciosa* is its texture. The vegetation consists of rather dense, to a large extent more or less evenly dispersed stands of thin stems and blades of helophytes. This miniature jungle constitutes an ideal habitat for the tiny species enabling it to pass the adult life period in a very restricted space. Foraging requires only short distance flights. The same holds true to the reproduction activities because both sexes live close together usually in rather high density and the oviposition sites adjoin directly the copulation places. Reduction of flight activities in favour of sitting allows to save energy, thus diminishing food requirement. Very low flight activity combined with blending into vegetation and corresponding perching postures makes *N. speciosa* hardly perceptible for conspecifics, heterospecifics and predators, thus diminishing agonistic behaviour and threat.

The thin and in most phases predominantly green body is barely visible among the stems and leaves of *Carex*. This camouflage is especially effective in tenerals and resting and roosting adults with bodies more or less parallel to perches. Sidling round a stem, hiding the body and the ability to simultaneously control with the spaced eyes is a behavioural component of the antipredator device. The females of brownish colour in their mature phase blend into the oviposition substrate. Disturbance of young females is reduced by their temporal androchromatism and imitation of male threat display which could be interpreted a female tactic to avoid sexual approaches by males.

Only generally rare helophytes such as *Carex limosa* and *C. lasiocarpa* provide both, effective hiding-places and enough clear space of action. *C. rostrata* and *C. elata* are used to a lesser extent and not in lush form, i.e. rather narrow--leaved. Other species with a similar habitus, such as *Molinia caerulea* and *Agrostis canina*, may also be exceptionally used. Stands of broad-leaved plants are clearly avoided.

N. speciosa is obviously adapted to a habitat with blade texture that provides enough space for imaginal activity and suitable microclimatic conditions as accentuated by SCHMIDT (1994) and confirmed in our studies. This texture with rather dense but thin and more or less parallel elements facilitates vertical and horizontal movements of the imagines. For flying less dense parts or half open places are used, i.e. the upper story, as well as numerous narrow corridors, also shaped by the bulky leaves of *Menyanthes*, constituting communication routes especially in the under story with dense vegetation. Due to the density of vegetation the habitat is almost exclusively inhabitable for *N. speciosa*. Anisopterans hardly ever intrude the *Nehalennia* habitat and encounters with other coenagrionids and lestids are mainly restricted to the top parts of the vegetation. *N. speciosa* individuals staying there in the time of activity of other coenagrionids and lestids are sufficiently active to avoid the disturbance and predation or even to repel the aggressive intruders. Concentrating the activity on the upper story or, in lower sections, to the rather dense parts of the vegetation may also protect the imagines from frog attacks but not from death in spider webs.

The microclimate, largely determined by the texture of the habitat, is most essential for imaginal life. The vegetation protects the individuals from wind and excessive insolation. It creates relatively high humidity and well-balanced temperature conditions. Hence, too loose vegetation, even that formed by the preferred plants, is inappropriate for the species due to the bad microclimate.

The adaptation to the specific microclimate of its habitat allows *N. speciosa* to be active at relatively low ambient temperatures, cloudiness and even slight rain, i.e. at conditions that are unfavourable for syntopic species, e.g. in the early morning. Therefore, also partial temporal separation between imagines of *N. speciosa* and heterospecifics occurs. On the other hand, the sensitiveness of the imagines towards heavy insolation at high temperatures and wind conditions probably restricts the colonization of open habitats.

Water quality has most probably only little direct effect on *N. speciosa*, as shown by successful rearing of larvae under hydrochemical conditions different from natural ones (BERNARD, 1998, RB). However, hydrochemical conditions largely determine the vegetation and its texture, i.e. the microhabitat of both, larvae and imagines. The essential plant species, *Carex limosa* and *C. lasiocarpa*, both typical of oligotrophic to mesotrophic conditions, are displaced as soon as the hydrological or the nutritional conditions change. The same holds true to the small *Utricularia* spp. An inflow of nutrients into the *Nehalennnia* habitats from deforested or agriculturally used surroundings or by atmospheric fallout may cause an increase in trophy and an undesirable change in acidity. In consequence, species composition and structure of vegetation will alter. This is clearly recognizable at small lakes in N Poland surrounded by completely or partly deforested areas and within intensively used agricultural regions. *C. limosa* and *C. lasiocarpa*, if present at all at these localities, occur mostly on emergent mats or are too sparse to form appropriate habitats for *N. speciosa*. The role of forests as buffer zones is therefore evident and especially important at small isolated localities that are not embedded in broad mires as typical for Poland and the Baltic States. Furthermore, forests contribute to the stabilization of the hydrological conditions and serve as windshields. The general conservation significance of forests encircling dragonfly habitats was also confirmed for species with partivoltine life-cycles in Sweden (SAHLÉN, 1999).

The size of the colonized water body is of minor importance. Small depressions or pools within *Sphagnum* bogs may be lesser exposed to strong winds than habitats at lake edges, with the disadvantage that they can harbour only small populations and may dry up easier. Between individual populations of neighbouring localities, possibly forming metapopulations, genetic exchange is possible. This will be prevented in largely isolated populations, this situation becoming more frequent.

Considering the whole, *N. speciosa* occupies a narrow habitat niche with little possibility for evasion, thus bearing high risks for local extinction. Even small – natural or anthropogenic – changes of the hydrological conditions or the composition of the vegetation may be fatal for a population.

Tight binding to a spatially restricted habitat also during the adult stage, combined with delicate body build and little flight inclination characterise *N. speciosa* as a species with low dispersal ability. However, encounters of individuals far from appropriate habitats as well as some colonizations of new localities in Bavaria and Poland (SCHMIDT & STERNBERG, 1999; BURBACH & SCHIEL, 2004; P. Buczyński, pers. comm.) indicate that dispersal of the species occurs. Drift by wind, as aerial plankton, is supposed to play the main role. Active dispersal is probably limited to localities in close neighbourhood.

Summing up, the life strategy allows *N. speciosa* to perfectly use a highly specific niche with minimal interspecific competition, intraspecific aggression and predator pressure, thus saving energy but with the danger of reaching a deadlock. Even slight habitat changes may imply risks of extinction, at least locally and especially under human impact possibly enhanced by extreme weather situations or climate changes. As shown in Lepidoptera (SCHMITT & HEWITT, 2004), impoverished genetic diversity, predominantly towards the western end of the range, is perhaps another factor that renders future survival difficult.

CONSERVATION

Summing up, the main factors and processes currently threatening to *N. speciosa* constitute (cf. also BERNARD et al., 2002b; KUHN, 2003; WILDERMUTH, 2004):

(a) drying out of habitats
  - natural, caused by extreme weather events (hot dry summer) and long-lasting climatic changes
  - as a result of human activity both in the wetlands and their surroundings, especially of drainage

(b) changes in the species composition and structure of vegetation caused by an increase in pH and the most important – in trophy, these changes in water chemistry are effects of an increased load of nutrients from:
  - superficial flow from the deforested or agriculturally used drainage basin
  - aerial influx
  - angling, especially the usage of large amounts of lure

(c) overgrowth of habitats, especially of secondary ones

(d) increased scatter of localities as a result of changes mentioned above, in many areas almost eliminating natural dispersal.

Based on the findings that concern regress in distribution, habitat-binding and sensitiveness towards changes of the habitat the following conservation measures are suggested:

POLICY. – This comprises global and national assessment of the level of threat and policy-based actions: classifying of the species into Red Lists and legal norms, inclusion of the species into the FFH-Directive and the Bern Convention. Not considering countries and regions where *N. speciosa* is extinct, the species has been included in 13 national and regional Red Lists, mostly in categories CR and EN, rarely in VU. The species was also suggested a candidate to the new IUCN Red List, being classified to the category NT (BERNARD & WILDERMUTH, 2004). In some countries, e.g. in Germany or Poland, *N. speciosa* is legally protected. However, these instruments of passive conservation, though recommended as useful e.g. for the evaluation of wetlands, frequently do not lead to effective realization of conservation measures. Therefore, international efforts for active conservation, i.e. practical realization of action plans are required.

RESEARCH. – Subjects are determination of range, number and size of local populations, monitoring and assessment of demographic trends. Biogeographical studies may allow to confirm the occurrence or to find sites of the species in NE China and N Kazakhstan. In Europe intensive search for the species is urgently needed in Belarus and European Russia as current data are very fragmentary compared to the supposed number of populations. The local state of *N. speciosa* in some insufficiently explored countries and regions (e.g. S Finland, N Ukraine), especially in those where the species is possibly extinct (Sweden, Italy) waits for clarification. Long-term monitoring of the number and size of individual populations at intervals of one to three years is required in all countries where *N. speciosa* currently occurs. This is especially needed for the largest populations in Europe. Besides faunistic studies there is need for further investigations of larval biology, behaviour of adults, dispersal and regional stenotopy. Furthermore, the possible impact of global warming on the species has to be assessed. Studies on genetic diversity, in order to analyse the phylogeographical pattern, similar to those in Lepidoptera (SCHMITT & HEWITT, 2004) may help to understand the current situation and assessing the future chances of the species in Europe.

HABITAT AND SITE-BASED ACTIONS. – Priority must be given to full conservation of all primary habitats of the species, e.g. by their integration in national parks, nature reserves or Natura 2000 areas, protected from any human interference that may impair the microhabitat as e.g. angling or bathing and – what is important – drainage of wetland and groundwater extraction in the surroundings. For example, only ten current localities enjoy in Poland this kind of protection; at least five others with large populations are not covered by it.

The immediate surroudings of the habitats must be included in the protected areas by designation of wide buffer zones, untouched forest at best. In agricultural landscapes buffer zones free of pesticides and fertilizers should be especially broad. Buffer zones in the range of up to 100 m around all localities with *N. speciosa,* proposed by one of us (RB), were legally implemented in Poland in 2004 by the Ministery of Environment, so far in theory only, with the aim to prevent deforestation and any other impact on the species habitat. So far, conservancy measures of this type have been used in Poland mainly for birds. Its application for an invertebrate species – currently unique – may be a model for future measures in other regions.

Secondary habitats, most of them being former peat diggings, require similar measures as the primary habitats. In contrast to the latter they generally overgrow rather fast and become inappropriate for *N. speciosa*. In this case local extinction could be avoided by preparing a new habitat in close vicinity of the old one, as currently realized at one locality in Lower Saxony (H.-J. Clausnitzer, pers. comm.).

Finally, new habitats for the species may also be created by bog regeneration, based on restoration of former hydrological conditions in drained mires.

SPECIES-BASED ACTIONS: LOCAL REINTRODUCTION. – A trial of introduction of *N. speciosa* was made in Brandenburg (MAUERSBERGER, 1998a; pers. comm.). Ten imagines were introduced into a small garden pond and one young individual was observed there in the following year. The result, although weak, indicates the possibility of successful introduction or reintroduction at appropriate sites. However, this measure is strongly limited and has to be realized under optimal conditions only, i.e. when appropriate habitats and rich source material from nearby localities harbouring large populations are available. In Poland this method is in elaboration and will be tested in due course.

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