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Synchronism, sex ratio at emergence, and voltinism of *Epitheca bimaculata* in Lorraine (North-East France) (Odonata: Corduliidae)

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Abstract

Population size in *Epitheca bimaculata* varied considerably with time in northeastern France. However, emergences were always synchronised with an EM_{50} percentile ranging from four to eight days, irrespective of the population size. The sex ratio of all exuviae collected at one locality varied from ca 0.7 to ca 1.0, depending on the year. Larval development of a large part or of the totality of the population was demonstrated to be completed in one year only. These results compared to published data from other countries are discussed.

Zusammenfassung

Synchronität, Geschlechterverhältnis bei der Emergenz und Voltinismus von *Epitheca bimaculata* in Lorraine (Nordostfrankreich) (Odonata: Corduliidae) – Die Populationsgröße von *Epitheca bimaculata* variierte im Nordosten Frankreichs erheblich von Jahr zu Jahr. Die Emergenz war mit einem EM_{50} von vier bis acht Tagen allerdings immer synchron, unabhängig von der Populationsgröße. Das Geschlechterverhältnis aller an einer Lokalität gesammelten Exuvien variierte zwischen ca. 0,7 und ca. 1,0 in Abhängigkeit vom Jahr. Die Larvalphase eines Großteils oder sogar der gesamten Larvenpopulation wurde in nur einem Jahr abgeschlossen. Diese Ergebnisse werden mit aus anderen Ländern publizierten Daten verglichen.

Introduction

In France, *Epitheca bimaculata* (Charpentier, 1825) was found first in the eastern part of the country (Pidancet 1856; Barra 1963; Verneaux 1972; Jacquemin et al. 1985; Jacquemin & Boudot 1991). For a long time the species has been regarded as very rare, since residence of adults during maturation and foraging is poorly known and observations are mostly occasional. This is certainly not an absolute generality because, although favourable localities remain rare, studies on

the territorial behaviour of this species have been carried out successfully (Coppa 1989; Trockur 2004) and the species has been reported to establish vertically stratified territories in addition to their usual horizontal distribution (I. Sonehara in Corbet 1999: 657, table A.11.9). In fact, the species is especially noticed during emergence, and collecting of exuviae in spring is the best way to provide evidence of establishment and breeding and to find localities where its reproduction takes place (Vincent et al. 1987). As a result, the species is now known to have a trans-Palaearctic distribution (Fig. 1), ranging from western Europe to southernmost Kamchatka and Japan in the East, mostly between latitudes 44° and 63° N, although its Japanese range extends south to 35° N in montane areas. It is therefore possible that its life cycle shows some significant differences from one region to another. In Europe, the core of its range, displaying the approximate shape of a triangle, extends presently from the Northern Balkans to the centre of France and the South of Fennoscandia but is fragmented into regions of high frequency and high local abundance and regions of extreme rarity. This is likely to be the result of poor regional management practices on wetlands and lakes by inhabitants, the drastic elimination of the hydrophytes and helophytes being thought to be the main origin of the species scarcity in many Central European countries (Heidemann & Seidenbusch 2002). More to the east the distribution seems to be mostly scattered throughout eastern Europe and Siberia to the Far East of Russia (Boudot et al. 2015). The southernmost records in western Europe came recently from a sight record from a ship (to be confirmed) in Montenegro near the Albanian border (De Knijf et al. 2013), a chain of findings (both tenerals and exuviae) from the "Vlasina Landscape of Outstanding Features" in southeast-

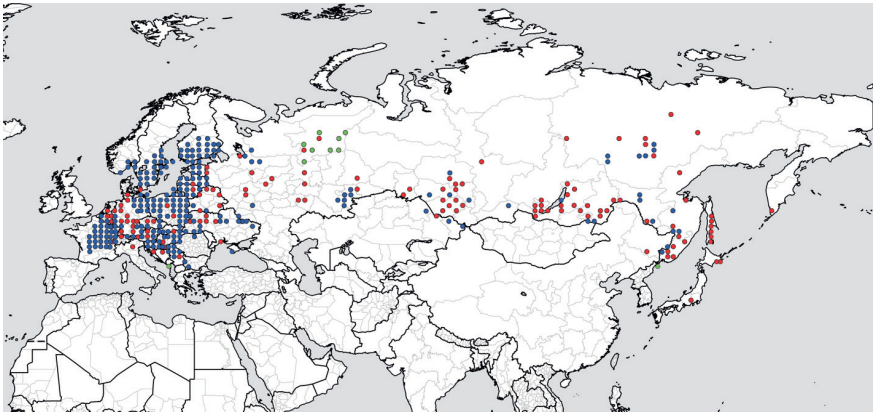

Figure 1. Known world distribution of *Epitheca bimaculata* according to a 50 km UTM grid. ● records dated 1990 onwards; ● records < 1990, ● plausible but uncertain records. Update from Boudot et al. (2015). – **Abbildung 1:** Die bekannte weltweite Verbreitung von *E. bimaculata* auf Basis des 50 km-UTM-Rasters. ● Nachweise ab 1990; ● Nachweise vor 1990; ● plausible, aber ungesicherte Nachweise. Update von Boudot et al. (2015).

ern Serbia (Đukić et al. 2019) and an isolated individual in maturation in the Rila mountains 2,300 m a.s.l. 120 km southeast of the Vlasina localities in southwest Bulgaria (Gainzarain 2017). The northernmost locality came from Verkhoyansk town in the Sakha republic in Eastern Siberia (Kosterin & Sivtseva 2009). Figure 1 gives the current known world distribution of the species.

Large populations of *E. bimaculata* exist in the North-East of France, in the neighbouring regions of Germany (Saarland) as well as in the Northeast of Germany (Mauersberger 2006) and the Northwest of the Balkans (Slovenia), which allowed development and comparison of a number of ecological studies. In odonate species, a number of studies showed that larval development and species voltinism (number of generations per year) are related to ambient temperatures and photoperiod and vary significantly according to latitude, with voltinism often decreasing from multivoltine to partivoltine from south to north in the northern hemisphere, largely as a result of the decrease in overall temperature (Corbet 1999: 219–228; Corbet et al. 2006; Flenner et al. 2010; Śniegula et al. 2012). However, no study seems to refer to the relation of life cycle with longitude, although the continental character of the climate changes drastically as distance from the seacoasts to the centre of the continents increase. Here I will report a study on the dynamics of emergence, on the sex ratio at emergence, and on the voltinism of *E. bimaculata* in Lorraine (northeastern France), and will compare the results with studies made in other regions (Sonehara 1968, 1982; Coppa 1987, 1991; Bedjanič 1997, Trockur & Sternberg 2000; Trockur 2004; Mauersberger 2006; B. Trockur in Wildermuth 2008: 72, 130, 132, 340; Vanappelghem & Quevillart 2013). Unfortunately no study from central Eurasia is available.

Methods and study area

This study was carried out on the Blonnaux pond (48.80583° N, 5.71277° E, 234 m a.s.l.; max depth = 3 m, 940 m long, 300–340 m wide, 20.9 ha), which had a heavy development of hydrophytes and helophytes over half of the surface in early summer. This pond was mostly devoted to waterfowl hunting and no fisherman had ever been seen, either before or after the study. The pond was situated in the municipality of Broussey-Raulecourt, Meuse department, France. The study included a daily collection of exuviae of *E. bimaculata* in 2008, 2013, and 2014. In this forest area, the species was well established in ponds with very variable population sizes varying from ca 1 to 1,000 individuals from one locality to another according to the number of exuviae found during previous regional and local surveys (JPB unpublished). Such variations occur within apparently similar kinds of hydrophyte- and helophyte-rich ponds and cannot be easily related to obvious differences in apparent habitat features and management.

Search for exuviae was done by walking slowly in the open grassy strip surrounding the pond, which offers favourable supports for emergence and means

the larvae have a strong chance of intercepting suitable plants during their search for an emergence support. The search pathway, the speed of displacement and the collecting effort were all maintained constantly from day to day and from year to year. This pond was isolated and did not show hydrologic connections with the other 25 ponds which are found at a distance of 1.6 to 9 km, mostly in the same large broadleaved forest – namely the 'Forêt de la Reine' of 5,200 ha –, more rarely in open agricultural landscapes. All banks were searched for exuviae, starting on 15 April and continuing to the end of the emergence period, in order to cover the whole time span of published emergence dates in western and southern Europe (Vincent et al. 1987; Bedjanič 1997; Trockur & Sternberg 2000) and to take into account regional year abnormalities. The exuviae of males and females are known to show a similar size (27–32 mm in length and 9–13 mm in width (Heidemann & Seidenbusch 2002)) and no difference in the selection of emergence supports is known, so a bias in detectability of sexes could be excluded. No strong rainy event which could change exuviae detectability over time occurred and exuviae detectability remained fairly complete, thanks to their large size, and substantiated by the low number of new findings obtained during a two way new search in some stretches. All exuviae were immediately collected, brought back home, counted and identified for their sex. The sex ratio has been determined each day and the overall sex ratio was determined as the ratio of the total number of collected males to the total number of collected females when no more exuviae could be found during three consecutive days. The EM_{50} percentile was determined as the number of days necessary for the emergence of half of the local population. The pond was wholly dry from November 2010 to November 2011 due to the construction of an additional pond upwards the existing pond, so emergence failed in 2011 and 2012 and did not start again until 2013.

Results

Total number and emergence period

The emergence periods extended from 7 to 17 May in 2008, 11 to 29 May in 2013, and 24 April to 6 May in 2014. The larvae generally left the water in the morning, around 08:00 h (solar time). The total number of exuviae collected was 992 in 2008, 532 in 2013 and 184 in 2014.

Rhythm and synchronism of emergence

The emergence was always synchronised and the time elapsed necessary for the emergence of half of the local population (EM_{50} percentile) varied from 4 to 8 days, regardless of the total population size (Fig. 2). No significant phenological difference could be observed between the two sexes, both males and females starting to emerge on the same day, ending on the same day and the apparent difference in EM_{50} between the two sexes being at most 1 day (Fig. 2).

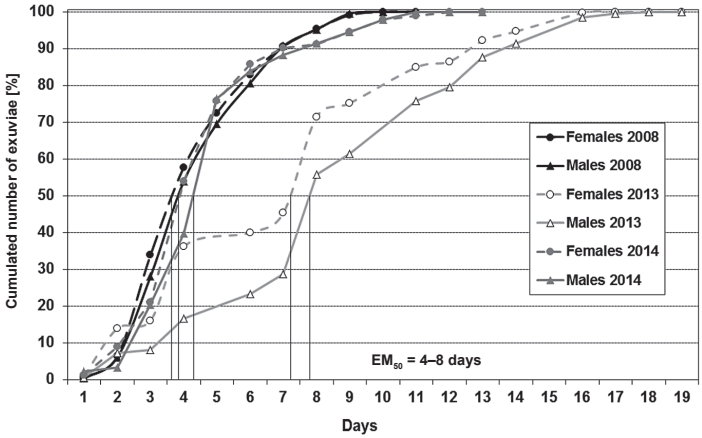

Figure 2. Emergence synchrony in *Epitheca bimaculata* at Broussey-Raulecourt, eastern France, specified for sex and years. The vertical lines mark the EM_{50} for each graph. – **Abbildung 2:** Synchrone Emergenz von *E. bimaculata* bei Broussey-Raulecourt, Ostfrankreich, nach Geschlecht und Jahr getrennt dargestellt. Die vertikalen Striche markieren den EM_{50} für jede Kurve.

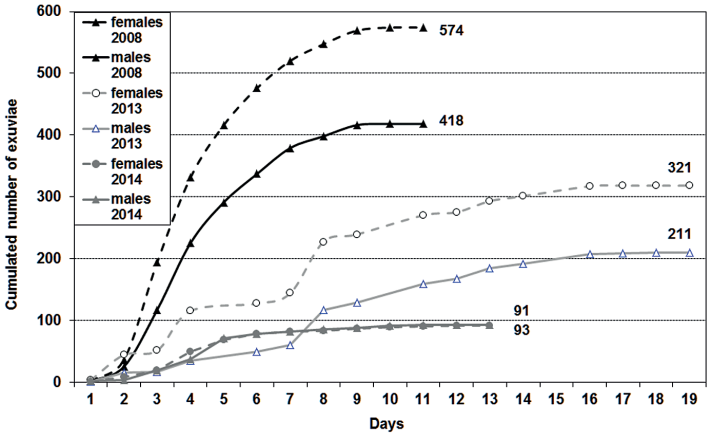

Figure 3. Sex ratio at emergence in *Epitheca bimaculata* at Broussey-Raulecourt, eastern France, specified for sex and years. Sex ratio (♂/♀) = 0.66 [2013], 0.73 [2008] and 1.02 [2014], that represent 60.3%, 57.9%, and 49.5% of females, respectively. – **Abbildung 3:** Geschlechterverhältnis zur Zeit der Emergenz von *E. bimaculata* bei Broussey-Raulecourt, Ostfrankreich, nach Geschlecht und Jahr getrennt dargestellt. Geschlechterverhältnis (♂/♀) = 0,66 (2013), 0,73 (2008) und 1,02 (2014), was einem Weibchenanteil von jeweils 60,3 %, 57,9 % und 49,5 % entspricht.

Sex ratio

The cumulative sex ratio at the end of emergence varied from 0.66 to 1.02 depending on the year, which corresponds to a proportion of ca 50–60% of females (Fig. 3).

Voltinism

The pond was emptied and fell completely dry from November 2010 to November 2011 (Fig. 4) due to the implementation of heavy works in a swamp just beyond the pond tail. No water pocket remained, the sediments became hard and no large population of larvae could survive for 12 months. Consequently, no emergence occurred in 2011 and 2012. Helophytes and hydrophytes grew again during summer 2012 after refilling. Successful collection in 2013 provided 532 exuviae of *E. bimaculata*.

Discussion

In the course of this study, high numbers of exuviae have been collected. This illustrates the paradox of *E. bimaculata*, which remains difficult to be observed as adults and therefore is regarded to be rare or very rare although it presents locally strong populations.

In Western Europe, detailed studies dealing with *E. bimaculata* are available for Slovenia, with emergence extending from the last week of April to the end of June by a latitude of 46.6° N, 245 m a.s.l. (Bedjanič 1997; Kotarac 1997: 108–109), for eastern France (Lorraine province), with the emergence period extending from 6–17 May to 4 June by 48.6° N, 220 m a.s.l. (Vincent et al. 1987), for the French Ardennes, with the emergence period extending from 9 May to 9 June by 49.2–49.9° N, 150–320 m a.s.l. (Coppa 1987, 1991), for Northern France, with the emergence period extending from 4 to 20 May by 50.07° N, 171 m a.s.l., for Saarland (Germany), with emergence extending from 5–15 May to ca 23 May–1 June by 49.38° N, 173 m a.s.l. (Trockur & Sternberg 2000: 221; Trockur 2004), for North Brandenburg (Germany), with emergence extending from 1–22 May to 30 May–8 June, depending of the previous winter, by ca 52.8–53.3° N, 10–100 m a.s.l. (Mauersberger 2006; R. Mauersberger pers. comm.), and at higher elevations for Switzerland with emergence occurring from mid-May to early June on the Swiss Plateau by 46.5–47.6° N, 400–600 m a.s.l., and from early June to early July in the Swiss Jura mountains by 46.96° N, 1,030 m a.s.l. (Monnerat 2005: 268). In quite different climatic areas, emergence is delayed to late May and early June in southern Norway by 58–60° N, 35–370 m a.s.l. (Olsvik 1996; Norwegian Biodiversity Information Centre 2020), and in southern Finland by 60–64° N, 2–180 m a.s.l. (Valle 1938; Finnish Biodiversity Information Facility 2020). In Hokkaido (Japan), the emergence period extends from early June to the end of the same month by ca 43.1° N, ca 5 m a.s.l. (Ubukata 1993).

Figure 4. Views of the Blonnaux pond, breeding site of *Epitheca bimaculata* in eastern France, from the same place and direction. (**a**) Filled on 30-vii-2007 (focal length 70 mm); (**b**) emptied and dried on 23-iv-2011; focal length 24 mm. – **Abbildung 4:** Der Blonnaux-See, ein Reproduktionsgewässer von *E. bimaculata* in Ostfrankreich, vom selben Standort aus und mit derselben Blickrichtung fotografiert. (**a**) Gefüllt am 30.07.2007 (Brennweite 70 mm); (**b**) abgelassen und ausgetrocknet am 23.04.2011 (Brennweite 24 mm).

The emergence periods recorded in this study in northeastern France (24 April – 29 May), which have been obtained during years with a well-marked preceding winter, match therefore with most other dates known from western Europe which all show a small adjustment to the local altitude and latitude, being the earliest in the south and the latest in the north and in the mountains.

At the Blonnaux pond, in each year emergence was clearly synchronised, so that the emergence of half of the local population has been achieved within four to eight days only. These findings agree with values reported from northern France (Vanappelghem & Quevillart 2013), North Brandenburg (Mauersberger 2006) and Saarland (Trockur & Sternberg 2000: 221; Trockur 2004) with an EM_{50} = 4–6 (9) days. This reveals a species in which all the larvae emerging in the same year spend their last winter in diapause in the F-0 stadium ("spring species" sensu Corbet 1954.)

No significant phenological difference between the two sexes could be evidenced. Both sexes begin to emerge on the same day, and half of the population has emerged on the same day in both males and females, which is in accordance with data published by Coppa (1991). The sex ratio at emergence points, however, towards a frequent numeric prevalence of the females over the males, with occasional near-equilibrium. Coppa (1991) found sex ratios ranging from 0.86–0.89 (53.8–52.9% females) using 922–1,020 exuviae. Values produced by Bedjanič (1997) in Slovenia (0.90–0.92 using 502–679 exuviae) are rather more equilibrated (52–52.7% of females). Those obtained by B. Trockur in Saarland using 113–352 exuviae show some variability (0.69–1, which is 59.1–49.9% of females) (in Wildermuth 2008). Values of sex ratio at Broussey-Raulecourt (ca 50–60% of females) agree with the later values. In Japan, Sonehara (1982 [cited in Corbet & Hoess 1998 and Wildermuth 2008]) pointed to a sex ratio of 0.75 (57.1% of females) using 329 exuviae, which match the values found in Western Europe.

Indeed, the frequently higher numbers of females at emergence observed in this species seem to be a rather common phenomenon in Corduliidae and more generally in Anisoptera (Corbet & Hoess 1998; Cordero-Rivera & Stoks 2008). The reasons leading to a sex ratio diverging from 1, however, are far from being understood. Within Odonata the sex is not controlled by environmental conditions but is determined by the XX-X0 chromosomic system, in which only one sexual chromosome occurs (Kiauta 1969). Females are homogametic (XX), possessing two X chromosomes, and produce only gametes with an X chromosome. Males are heterogametic (X0), possessing only one sexual chromosome, and produce two kinds of gametes in the same amount during meiosis; one with the X chromosome, the other without. The sex of the egg is therefore controlled by whether it possesses the male gamete or not. In these conditions the primary sex ratio of the overall clutch has little chance to differ from 1 (Lawton 1972; Corbet & Hoess 1998; Corbet 1999: 252; Cordero-Rivera & Stoks 2008). The disequilibrium appears therefore after egg-laying, during clutch survival and development (Corbet & Hoess 1998). Several possibilities may be considered. The hypothesis of a different distribution of males and females along the banks can be excluded in the

present study as all banks were searched for exuviae and showed a similar sex ratio. A possible discrepancy in phenology was also eliminated as no exuviae could be found before or after the dates reported here. As a result, physiological and behavioural hypotheses remain the most reliable possibilities. Homogametic sexes (here the females) are believed to exhibit a higher survival rate under adverse conditions (Lawton 1972) and a higher larval survival has been observed under controlled experimental conditions (Dunkle 1985). Additionally, predation could be more effective on males than on females in relation to differences in microhabitat selection and to a more dynamic and exposed behaviour (Baker et al. 1992). Alternatively, if embryonic mortality is male-biased, that would result in female-biased sex ratio at birth of the prolarvae. Also, Farkas et al. (2013) suggested that in semi- and partivoltine species variations in sex ratio could be related to variation in water temperature occurring in the year preceding the emergence, although this may not cause a long-term consistent bias but rather should create year-to-year variations. However, all this remains poorly understood.

Information about the length of the larval development in this species is somewhat variable. Wildermuth (2008: 72) listed values from (one) two to five years using data from Europe and Japan, the value of two years being the most frequent. Trockur (2004) determined in Saarland that a large part of a population emerges in two years, a further large part needs three years, and a very small part (0–2.7%) needs four years. In the present study successful collection in 2013 provided 532 exuviae of *E. bimaculata* after one year refilling following a one year period during which the pond was fully dry. In such a dry condition, pre-existing larvae are known to survive in the mud and the vegetation for not more than 14 days (Kotarac 1997: 108). This showed that a fast recolonization and breeding took place during 2012 as a result of the dispersion of the populations of the surrounding ponds of the 'Forêt de la Reine' (inter-pond exchanges) and demonstrated an efficient optimisation of the regionally available habitats (low site fidelity and high colonization power) as well as a full larval development over one year of at least a large part of the 2012 larval generation.

This study provides evidence that in this species at least a large part of an annual larval population may complete its full development in one year only. In France, Krieg-Jacquier (2010) observed similarly a fast recolonization of two dried ponds by the same species and a larval development lasting one year of ca one hundred larvae in the Ain department (Franche-Comté region, eastern France) and also concluded that in this area at least a part of an annual larval population emerges after only one year. This indicates that faster larval development time, now known in eastern France, may be occur rather frequently in the westernmost part of the species range whereas development may slow down to take two to four years or more to the East. Further detailed studies are needed in central and western France, in central and northern Europe and in Siberia to confirm this hypothesis, which may be linked to West to East climate shift. An alternative hypothesis would be that filling a pond after one year drying results in a higher trophic level of the restored pond due to a fast biodegradation of the

organic components of the sediment, a phenomenon well known in drained soils after desiccation and subsequent moistening. This, in turn would accelerate larval development and shorten the larval period. Further experimental studies are necessary to test such a hypothesis. However, there is no present evidence that the trophic level of softwater habitats would control the velocity of the larval development and the voltinism in Odonata.

Conclusion

Epitheca bimaculata is a typical "spring species" with synchronised emergence and an EM_{50} percentile of 4–9 days. Larval development seems faster in the western part of the species range than generally known in the core of its range and appears to be largely completed in one year. Although a frequent prevalence of females over males is observed, the onset and the dynamic of the emergence are identical in both sexes and no phenological difference has been evidenced. The origin of the unbalanced sex ratio, female biased, is unclear but should be linked either to differences in embryonic or to larval survival.

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References

Baker R.L., M.R.L. Forbes & H.C. Proctor (1992) Sexual differences in development and behaviour of larval Ischnura verticalis (Odonata: Coenagrionidae). *Canadian Journal of Zoology* 70: 1161–1165

Barra J. (1963) Introduction à l'étude écologique des odonates autour de Strasbourg. *Bulletin de la Société Zoologique de France* 88: 108–124

Bedjanič M. (1997) [Process of metamorphosis, sex structure and the population size of Epitheca bimaculata (Charpentier, 1825) in the clay pit of the Pragersko Brick Factory, NE Slovenia (Odonata: Corduliidae)]. Seminar thesis, University Ljubljana [Slovenian]

Boudot J.-P., R. Bernard & M. Martin (2015) Epitheca bimaculata (Charpentier, 1825). In: Boudot J.-P. & V.J. Kalkman (Eds) Atlas of The European dragonflies and damselflies: 234–235. KNNV Publishing, Zeist

Coppa G. (1987) Nouvelles observations sur la présence d'Epitheca bimaculata (Charpentier, 1825) dans le département des Ardennes (Odonata Anisoptera: Corduliidae). *Martinia* 6: 15–24

Coppa G. (1989) Note sur le vol d'Epitheca bimaculata (Charpentier, 1825) (Odonata, Anisoptera: Corduliidae). *Martinia* 5: 69–73

Coppa G. (1991) Notes sur l'émergence d'Epitheca bimaculata (Charpentier) (Odonata: Corduliidae). *Martinia* 7: 7–16

Corbet P.S. (1954) Seasonal regulation in British dragonflies. *Nature* 174: 655, erratum 777

Corbet P.S. (1999) Dragonflies. Behaviour and ecology of Odonata. Harley Books, Colchester

Corbet P.S. & R. Hoess (1998) Sex ratio of Odonata at emergence. *International Journal of Odonatology* 1: 99–118

Corbet P.S., F. Suhling & D. Soendgerath (2006) Voltinism of Odonata: a review. *International Journal of Odonatology* 9: 1–44

Cordero-Rivera A. & R. Stocks (2008) Mark-recapture studies and demography. In: Córdoba-Aguilar A. (ed.) Dragonflies: model organisms for ecological and evolutionary studies: 7–20. Oxford University Press, Oxford

De Knijf G., C. Vanappelghem & H. Demolder (2013) Odonata from Montenegro, with notes on taxonomy regional diversity and conservation. *Odonatologica* 42: 1–29

Đukić A., R. Mirić, J. Skejo, S. Rajkov & I. Tot (2019) Survey on the damselfly and dragonfly fauna (Insecta: Odonata) of the Landscape of Outstanding Features "Vlasina". *Kragujevac Journal of Science* 41: 133–146

Dunkle S.W. (1985) Larval growth in Nasiaeshna pentacantha (Rambur) (Anisoptera: Aeshnidae). *Odonatologica* 14: 29–35

Farkas A., T. Jakab, O. Müller, A. Móra, I. Lajter & G. Dévai (2013) Sex ratio in Gomphidae (Odonata) at emergence: is there a relationship with water temperature? *International Journal of Odonatology* 16: 279–287

Finnish Biodiversity Information Facility (2020) https://laji.fi/en, last access: 30-xi-2020

Flenner I., O. Richter & F. Suhling (2010) Rising temperature and development in dragonfly populations at different latitudes. *Freshwater Biology* 55: 397–410

Gainzarain J.A. (2017) Epitheca bimaculata – a new species for the fauna of Bulgaria. *Notulae Odonatologicae* 8: 369–373

Heidemann H. & R. Seidenbusch (2002) Larves et exuvies des libellules de France et d'Allemagne. Société Française d'Odonatologie, Bois d'Arcy

Jacquemin G. & J.-P. Boudot (1991) Les Odonates (libellules) de la Réserve de la Biosphère des Vosges du Nord: état actuel de nos connaissances. *Annales Scientifiques de la Réserve de Biosphère des Vosges du Nord* 1: 35–48

Jacquemin G., J.-P. Boudot, P. Goutet & F. Schwaab (1985) Présence d'Epitheca bimaculata (Charp.) en Lorraine (Odonata, Corduliidae). *Bulletin de la Société d'Histoire Naturelle de la Moselle* 45: 229–242

Kiauta B. (1969) Sex chromosomes and sex determining mechanisms in Odonata, with a review of the cytological conditions in the family Gomphidae, and references to the karyotypic evolution in the order. *Genetica* 40: 127–157

Kosterin O.E. & L.V. Sivtseva (2009) Odonata of Yakutia (Russia) with description of Calopteryx splendens njuja ssp. nov. (Zygoptera: Calopterygidae). *Odonatologica* 38: 113–132

Kotarac M. (1997) Atlas of the dragonflies (Odonata) of Slovenia, with the Red Data List. Atlas faunae et florae Sloveniae 1. Center za kartografijo favne in flore, Miklavž na Dravskem Polju

Krieg-Jacquier R. (2010) Epitheca bimaculata (Charpentier, 1825) dans le département de l'Ain (Odonata, Anisoptera, Corduliidae). Actes des Rencontres odonatologiques 2010, Saint-Laurent (Ardennes), 26, 27 et 28 juin. *Martinia* 26: 83–97

Lawton J.H. (1972) Sex ratios in Odonata larvae, with particular reference to the Zygoptera. *Odonatologica* 1: 209–219

Mauersberger R. (2006) Verbreitung und Phänologie des Zweiflecks, Epitheca bimaculata Charpentier, 1825 (Odonata, Corduliidae), im Norden Brandenburgs. *Entomologische Nachrichten und Berichte* 50: 45–53

Monnerat C. (2005) Epitheca bimaculata (Charpentier, 1825) – Zweifleck – Cordulie à deux taches. In: Wildermuth H., Y. Gonseth & A. Maibach (Eds) (2005) Odonata. Les Libellules de Suisse: 266–269. Fauna Helvetica 12. CSCF/SEG, Neuchâtel

Norwegian Biodiversity Information Centre (2020) Artsdatabanken. https://artskart1.artsdatabanken.no, last access: 30-xi-2020

Olsvik H. (1996) Flyvetid og fenologiske ekstremumstider for øyenstikkere i Norge. *Nordic Odonatological Society Newsletter* 2: 26

Pidancet L. (1856) Catalogue des Libellulidées des environs de Besançon. 2° Mémoires Communiqués. *Mémoires de la Société d'Émulation du Département du Doubs* (2ème Série) 7 [1855]: 2–6

Śniegula S., V. Nilsson-Örtman, F. Johansson (2012) Growth pattern responses to photoperiod across latitudes in a northern damselfly. *PLOS ONE* 7 (9): e46024

Sonehara I. (1968) [The larval period of Epitheca bimaculata sibirica in Japan]. *Tombo* 10: 2–24. [Japanese]

Sonehara I. (1982) [Life history of Epitheca bimaculata sibirica at mount Yatsugatake]. Shinshu Shizenkagaku Series 2. Shinano Kyoikukai Corporation, Nagano [Japanese]

Trockur B. (2004) Untersuchungen zur Habitatwahl von Epitheca bimaculata Charpentier, 1825. Dissertation, Hochschule Vechta

Trockur B. & K. Sternberg (2000) Epitheca bimaculata (Charpentier, 1825) – Zweifleck. In: Sternberg K. & R. Buchwald (Eds) Die Libellen Baden-Württembergs. Band 2: 218–231. Eugen Ulmer, Stuttgart

Ubukata H. (1993) Kushiro Shitsugen nature guide. Dragonflies of Kushiro Shitsugen. Japanese Society for Preservation of Birds Kushiro Onnenai, Tsurui Vil., Akan-Gun, Hokkaido

Valle K.J. (1938) Zur Ökologie der finnischen Odonaten. *Annales Universitasis Turkuensis* (Serie A) 6 (14): 1–76

Vanappelghem C. & R. Robin Quevillart (2013) Émergence d'Epitheca bimaculata sur les étangs de la Forge à Glageon (Nord) (Odonata: Corduliidae). *Martinia* 29: 125–138

Verneaux J. (1972) Faune dulçaquicole de Franche-Comté. Le bassin du Doubs (Massif du Jura). Ve partie: Les Odonates. *Annales Scientifiques de l'Université de Besançon*, Zoologie, Physiologie et Biologie Animale (3e Série) 8: 15–20

Vincent G., J.-P. Boudot, G. Jacquemin P. Goutet & F. Schwaab (1987) Epitheca bimaculata (Charpentier, 1825) dans l'est de la France: rare, ou discrète et méconnue? (Odonata, Anisoptera: Corduliidae). *Martinia* 6: 3–13

Wildermuth H. (2008) Die Falkenlibellen Europas. Corduliidae. Die Neue Brehm-Bücherei 653. Westarp-Wissenschaften, Hohenwarsleben