



Important life history traits of *Chaetopteryx villosa* (Fabricius, 1798) (Trichoptera, Limnephilidae)

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Abstract

Long-term studies of the life cycle of *Chaetopteryx villosa* (Fabricius) have been conducted in Wolbórka Spring, in the vicinity of Łódź (Central Poland). The emergence period of adults lasts from the beginning of October until mid December. During this relatively long period, adults are exposed to diverse weather conditions. Low (sometimes below zero) ambient temperatures influence the survival of adults. Although oviposition usually starts at the end of October, freshly laid eggs were found even in January. These temperatures also determine the activity of predators as well as the development and survival of eggs laid on land. Some egg masses have been transferred to the laboratory and bred at different temperatures.

Key words: biology, trade-off, life history, egg and larval development

Introduction

Chaetopteryx villosa (Fabricius) has been recorded from almost all over Europe, except in the Balkans and Appeninian Peninsula (Tomaszewski 1965, Botosaneanu & Malicky 1978, González 1979). Its larvae are characteristic for spring areas and running waters, but also occur in oxbow lakes and mountain ponds or lakes. The larvae are shredders and feed mainly on detritus. Graf *et al.* (2008), however, also classified them as grazers, gatherers, and even predators.

The life cycle of this caddis species is temperature dependent (Wagner 1990, 2002) and mostly univoltine, but in very cold waters, for example in mountain streams of Norway, it may sometimes be semivoltine (Andersen & Tysse 1984). Because of late emergence of adults, *C. villosa* was classified (Crichton 1960) as an autumnal species and even an autumn-early winter species (Solem 1984). In univoltine populations in Norway, adults are present from the middle of September to the middle of October (Andersen & Tysse 1984) and from the middle of September until the middle of December (Andersen 1983). In Germany, they are present from the beginning of September until the end of December (Wagner 1986). In Poland the occurrence of adults lasts from the end of September to the end of December (Majecki 2006). According to Andersen & Tysse (1984) and Solem (1984), females emerge with mature ovaries and very quickly start to copulate with males. Pairing/copulation is one of the longest among insects and lasts as long as 12 days (Solem 1984). The weight of males and females of *C. villosa* measured by Wagner (2002) was lower in the upper part of Breitenbach Stream (Germany) than in the lower part. The weight of adults (males and females) was significantly higher in the beginning of the emergence period (Wagner 1986).

The aim of the study was to assess:

- adult body sizes from different parts of flight period in the Wolbórka River spring;
- the relationship between weight of adults and time of emergence;
- the time of oviposition;
- egg and larval development times at different temperatures in laboratory and natural conditions.

Study area

The Wolbórka River is a 48-km-long, left tributary of the Pilica River (part of the Vistula drainage basin). The spring area of the Wolbórka River is located in Central Poland (20°28' E, 51°27' N). The springs as well as the upper section of the Wolbórka River are surrounded mainly by alder trees and form a peat bog and alder forest. The environment is rich in detritus, some fallen tree logs, and in autumn is full of leaves of alder and maple trees. Springs are supplied by water deep under the ground; water temperature in summer does not exceed 10°C and in winter never drops below 4°C. The study area could be described as a 25-m-wide and 50-m-long helocrene with sandy/gravel muddy bottom, in some parts covered by water mint (*Mentha aquatica* L.), stones, and fallen trees, which are covered by mosses *Mnium* sp./ *Plagiomnium* sp.

Methods

Adults were collected by hand from the ground, trees trunks, and plants growing inside the spring basin. The studies were conducted from 2000 to 2009, with the exception of 2007, when adults as well as egg masses were observed in the natural environment. Egg masses were described as “new” when the spumaline matrix had a pea shape and a greater cohesion, and “older” when the matrix was flat, had less cohesion, and its eggs were more developed. In the years 2004-2006 some imagines and in 2009 some egg masses were collected for laboratory studies. In the laboratory, the substrate with egg masses was placed on plastic cylinders located inside small containers (15x10 cm) filled with some water. The eggs were always about 2 cm above the water level. Containers with eggs were placed in temperatures described as “high” (group A) and “low” (group B) temperature regimes (Figs 1 and 2), some egg masses were kept outside the laboratory where they were exposed to the normal winter air temperatures (group C), and some (group D) were placed in a refrigerator freezer (about -20°C) (Fig. 3).

Egg development in groups A and B was monitored every 2-3 days and development progress was observed according to a 10-step scale, where: 1 – eggs, 2 – eggs with “eyes,” 3 – larvae inside matrix, 4 – larvae partly leaving the matrix, 5 – larvae walking outside of the matrix and starting to build their cases, 6 – all larvae in cases, 7 – some larvae in II and even in III instar, 8 – some larvae in IV instar, 9 – all larvae in V instar, some of them starting to anchor their cases to the substratum, 10 – emergence (Fig. 1). Eggs which were kept in outdoor conditions (group C) were monitored in days when the temperature rose above zero. The eggs from the refrigerator (group D), after 4 months in temperatures of about -20°C, were kept for 5 days at temperatures just below zero and then they were placed in a refrigerator at a temperature of +6°C. From this moment eggs were checked under a dissecting microscope every 2–3 days.

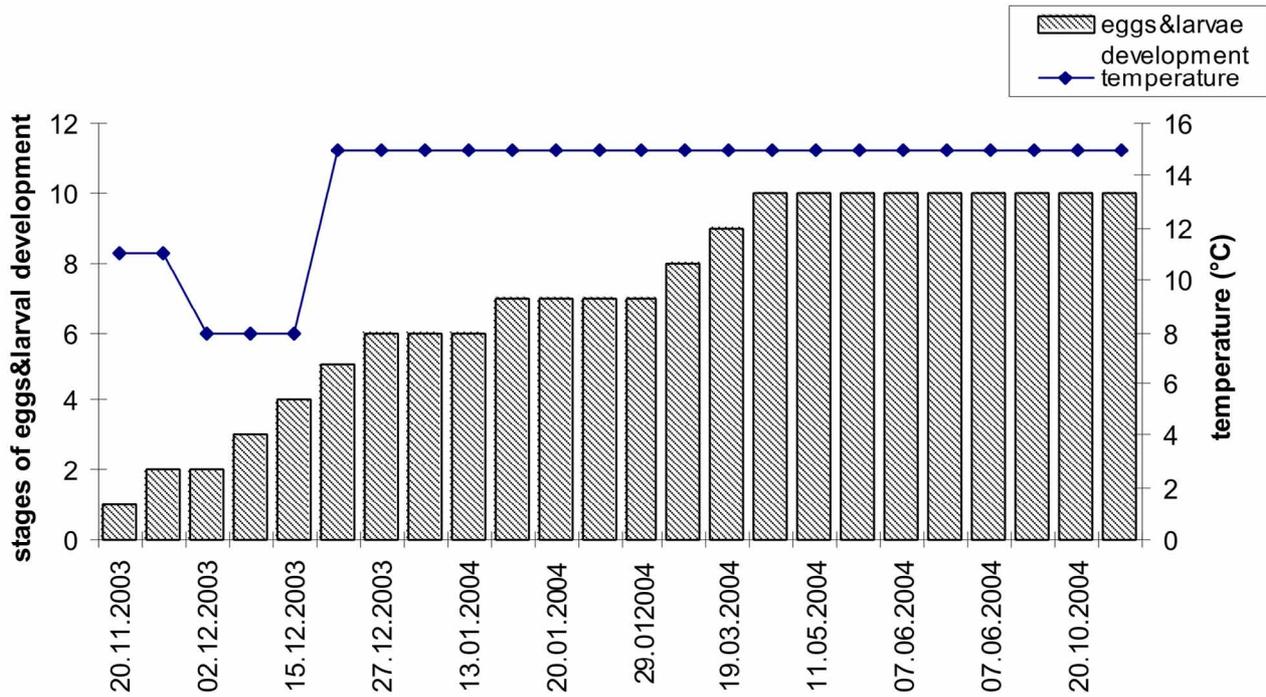


FIGURE 1. Egg and larval development in higher experimental temperatures.

Stages of egg & larval development:

- 1 – eggs
- 2 – eggs with larval “eyes” visible under the matrix cover
- 3 – larvae inside matrix
- 4 – larvae partly leaving the matrix
- 5 – larvae walking outside of the matrix and starting to build their cases
- 6 – all larvae in cases
- 7 – some larvae in II and even in III instar
- 8 – some larvae in IV instar
- 9 – all larvae in V instar, some of them starting to anchor their cases to the substratum
- 10 – emergence

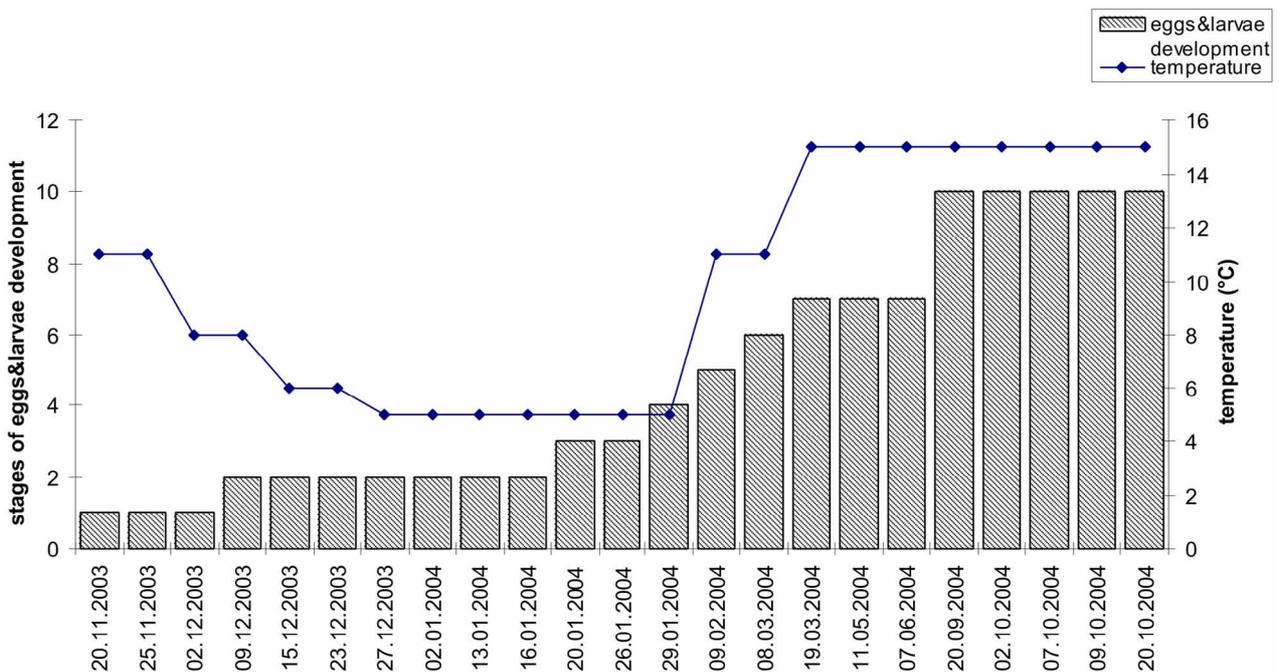


FIGURE 2. Egg and larval development in lower experimental temperatures.

Stages of egg & larval development as explained for Fig. 1.

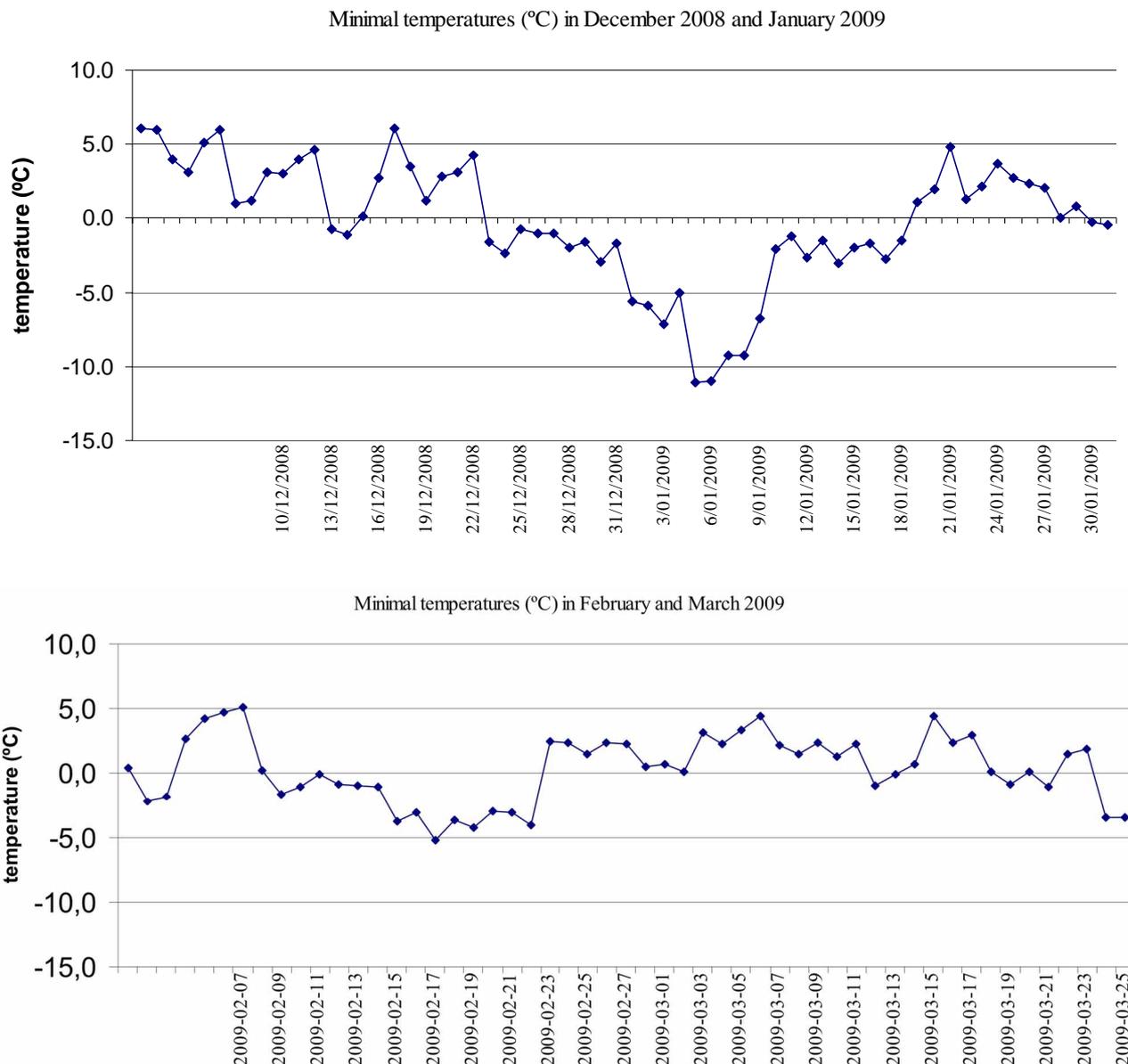


FIGURE 3. Minimum air temperature (°C) from December 2008 to March 2009.

When the young larvae dropped to the water, they were fed alder and maple trees leaves conditioned in water, and water was exchanged every 2 days. When all larvae had left the matrix, they were moved to bigger, aerated dishes where water and food was changed regularly.

Imagines collected in the field were sexed and weighed with an accuracy of 0,0001 g. A flight period from 1 to 20 October was named “B – beginning,” from 25 October until 15 November “M – middle” and between 23 November to 31 December was named “E – end.” The differences in weight (g) of specimens in each emergence period were analyzed (ANOVA I and the Tukey post-hoc test) separately for females and males.

Every day, the minimum air temperature was recorded near Wolbórka Spring with an accuracy of 0.1°C.

Results

Eggs

Eggs of *C. villosa* were laid above water, often on fallen tree logs covered by mosses. The favorite places for egg laying was under the tree logs that have fallen into the spring basin and were covered with mosses and where egg masses formed detached clutches of up to 6 masses. In some cases, egg masses were fixed to alder tree roots protruding from the edge of the spring. A few egg masses were laid on the leaves of plants growing inside the spring basin and 1 was deposited on an alder leaf on the ground about 1.5 m from the spring edge. Egg masses were never observed under water. Egg masses described as “new” were found even in the 2nd half of December and some eggs were discovered in the beginning of March (Table 1). On 22 January, 6 eggs masses containing larval remnants (larval shadows) were found (Table 1).

In laboratory conditions in higher experimental temperatures, larvae reached the final larval instar in April and some larvae started to pupate (Fig. 1). In lower experimental temperatures larvae developed slower and started to pupate and emerge in September (Fig. 2). Egg masses kept in outdoor temperatures (group C) (Table 2) only partly finished their development. According to a rough estimation, about 1/3rd of eggs decomposed in the matrix, whereas the others finished their development. All Group D eggs died and decomposed at +6°C temperature.

Weight

In total, 478 adults (297 males and 181 females) collected in 2005 and 2006 were weighed.

Analysis of variance (ANOVA) shows significant differences in size of specimens in 3 periods; for males ($F_{1,295}=30.472$, $p<0,0001$) and females ($F_{1,179}=11.890$, $p<0.0001$). Multiple comparisons (the Tukey test) revealed that females and males from the beginning (B) and medium (M) emergence periods of the flight season were significant bigger than those from the end (E) (Table 3).

Discussion

Confirming the observation by Wagner (1986), we found that body size of females and males of *C. villosa* emerging at the end of the flight season were smaller than those emerging in the beginning and middle of the flight season. Similar changes in body size were described by Wong-Muñoz *et al.* (2010) for some Odonata species. Females with smaller body size have lower fecundity/fitness because heavier females have more eggs and/or eggs are provided with higher amounts of nutritive substances (Honek 1993).

According to Solem (1984) for *C. villosa*, mean lethal temperature for adults was about -8.5°C. Therefore, females of *C. villosa* emerging at the beginning of the flight period may have an advantage because of good weather conditions at the beginning of autumn in central and northern Europe. Even though conditions may quickly change to heavy rainfalls, snowfalls and temperatures below -10°C, adults may find shelter under cover of dry leaves (personal observation) or even move to warmer places (Andersen & Tysse 1984). Late maturation could confront adults with harsh winter conditions and they could be often exposed to lethal conditions which increases their mortality. Because egg masses of *C. villosa* are terrestrial, higher October air temperatures may also accelerate the development of eggs and larvae inside egg masses. In this case, young larvae may leave their matrix and drop into the water before winter frosts, in contrast to late-laid egg masses, where low winter temperatures stop the development of eggs and larvae until the spring months. For this reason, different larval instars of *C. villosa* were present in spring months (Andersen & Tysse 1984) and

even all 5 instars occurred during April and May on some sites in Breitenbach Stream (Wagner 1986). Such desynchronisation of development complicated the life cycle and limited the use of a huge source of food in form of autumnal fallen leaves (Otto 1981) (autumnal leaves were absent in spring). Although egg masses were laid often under the cover of mosses growing on fallen and partly decomposed tree logs, some of our field observations, as well as field and laboratory experiments indicated that low temperatures may partly destroy eggs and/or developing larvae, and under our experimental conditions (group D) very low temperatures, lasting nearly 4 months, destroyed all eggs. While it cannot be concluded that imagines and eggs are not adapted to harsh winter conditions, it can be stated that fitness of late-maturing imagines may be lowered not only by harsh conditions acting directly on them, but also by higher mortality of developing eggs and embryos. On the other hand, the presence of bigger and heavier females and males at the beginning of autumn together with favorable weather conditions (higher temperatures) increase the fitness by a higher number of laid eggs (heavier females), reduction of adults mortality in better weather conditions, and reduction of eggs and larval mortality by acceleration of development in higher autumnal temperatures. There seems to be a “trade off” between favorable weather conditions for adults and developing eggs and young larvae in the beginning of the emergence period and the pressure put on adults by predators. At the end of autumn and beginning of winter, adult mortality risk by invertebrate and vertebrate predators is lower than at the beginning of the imaginal flying period. In contrast, in the beginning of autumn, during warm, sunny days, slowly moving, paired adults are at higher risk of predation by spiders, frogs, and birds still active at this time. Although frog predation on *C. villosa* adults was not examined during the period of this research, many active *Rana temporaria* L. frogs were observed in the Wolbórka Spring basin on warm autumnal days. According to Collier *et al.* (1998) frogs are very efficient invertebrate predators and sometimes remains of Trichoptera were present in frog feces (Majecki unpublished data).

Conclusions

1. Prolonged autumnal emergence as well as a prolonged mating and egg laying period may influence imagines and developing eggs through different weather conditions.
2. Larvae hatched from “early” eggs may leave egg masses before the onset of low air temperatures, in contrast to “late” eggs which can freeze and delay development until March.
3. In particular, later emerging imagines and their later developing eggs and larvae may be exposed to very harsh winter conditions and temperatures below zero.
4. Some field and laboratory observations indicated that such conditions may increase the mortality of adults and larvae developing outside of water in egg masses.
5. The presence of bigger and heavier females and males in the beginning of autumn together with usually better weather conditions (higher temperatures) increase fitness by a higher number of laid eggs, heavier females, reduced adult mortality, and reduced egg and larval mortality because of accelerated development.
6. In contrast, at the beginning of autumn, especially during, warm sunny days, slowly moving, paired adults are at higher risk of predation by spiders, frogs, and birds, still active at this time.
7. In cold weather conditions of winter, later emerging adults are smaller and females consequently have lower fecundity and higher mortality. In winter, developing larvae may be destroyed by subzero temperatures.

TABLE 1. Number of males, females, and imagines of *Chaetopteryx villosa* in copula as well as egg masses observed in Wolbórka Spring during the years 2000–2009, with the exception of 2007.

year/date	males	females	in copula	new egg masses	older egg masses
2000					
10 October	20	8	34	1	0
27 October	10	8	35	0	0
08 November	12	5	26	0	0
23 November	17	4	7	1	1
07 December	1	0	0	5	2
2001					
14 October	10	11	1	0	0
2002					
25 October	13	3	14	2	0
08 November	58	1	4	0	0
2003					
13 October	5	10	3	2	0
21 November	28	18	20	9	3
04 December	6	7	0	0	0
2004					
19 October	25	6	16	0	0
28 October	7	3	5	5	2
16 November	6	1	6	6	2
09 December	1	2	1	0	4
2005					
07 January	0	0	0	7*	0
17 March	0	0	0	0	5**
05 October	27	8	13	0	0
19 October	16	7	17	0	0
09 November	19	6	25	8	3
23 November	40	1	5	11	5
14 December	6	4	1	3	4
2006					
27 September	7	3	1	0	0
3 December	0	0	0	2	4
2008					
30 October	9	4	16	3	0
21 November	5	3	9	2	1
18 December	1	0	0	8	3
2009					
22 January	0	0	0	0	6*
06 March	0	0	0	0	3

* some egg masses with eggs, some with developing larvae

** empty egg masses with larval remains, suggesting decomposition of developing larvae inside egg masses

TABLE 2. Development of 6 eggs masses of *Chaetopteryx villosa* collected on 18 December 2008 and kept at outdoor conditions (group C) in temperatures indicated on Fig. 3 and in a freezer with temperature about -20°C (group D).

Group C	Group D
Outdoor conditions	Freezer (-20°C)
11 December—3 “new” egg masses	11 December—3 “new” egg masses
21 December—matrix less cohesive	
23 January—some eggs with larval eyes	
27 February—in matrix were some moving larvae and a lot of eggs	27 February—eggs placed for 5 days in subzero temperatures and later at a temperature of $+6^{\circ}\text{C}$
15 March—no larvae inside of matrix, a lot of dead eggs	15 March—all eggs are evidently dead
1 April—matrix and eggs decomposing	1 April—matrix and eggs decomposing

TABLE 3. Differences in weight (g) of adults of *Chaetopteryx villosa* in different emergence periods. B – beginning: flight period from 1 to 20 October, M – middle: from 25 October until 15 November, E – end: from 23 November to 31 December.

	Males			Females		
	B	M	E	B	M	E
Number of specimens	145	64	88	91	49	41
Mean weight (g)	0,0161	0,0161	0,0118	0,0356	0,0356	0,0258
Standard Deviation	0,004	0,006	0,003	0,012	0,012	0,008

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