Lifetime egg production of captive libellulids (Odonata)

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Dear George, with your great enthusiasm for ecology and behavior research you've infected me - thank you very much!

The estimation of lifetime egg production (LEP) is a central question in ecology, since the number of eggs produced determines the potential size of the following generation. In this study, I tried to obtain a rough estimation of the LEPs in libellulids in outdoor cages. The main questions were: (1) does hand feeding influence females' life history traits; (2) how long is the maturation period and the lifespan; (3) does the quality/quantity of eggs vary with female age or size; and (4) how many eggs do females lay in their lifetime? I installed two outdoor cages and kept individually marked specimens of *Orthetrum coerulescens* and *Sympetrum striolatum* under semi-natural circumstances. *Orthetrum coerulescens* had a longer life span in hand-fed specimens compared to not hand-fed. The maturation period, number of clutches, clutch size, egg circumference, and LEP did not differ between hand-fed and not hand-fed specimens. The median maturation period was shorter in *O. coerulescens* (24 days hand-fed; 20 days not hand-fed) than in S. *striolatum* (47 days, all hand-fed). The mortality during the maturation period was high in both studied species (*O. coerulescens* 81.48%, *S. striolatum* 89.16%). *Orthetrum coerulescens* had a shorter median life span than *S. striolatum*. The quality/quantity of eggs did not correlate with females' age and size. *Orthetrum coerulescens* had a mean calculated lifetime egg production of 3081 eggs per specimen and *S. striolatum* 1041 eggs per specimen. The data pertain to outdoor cage experiments (a reduced spectrum of prey, no long flights possible, no predators present). Nevertheless, they may provide a very rough estimation of LEP for two libellulid species.

Keywords: Odonata; dragonfly; Libellulidae; egg size; lifetime egg production; life span; maturation period; outdoor cage

Introduction

The estimation of females' lifetime egg production (LEP) (Arnquist & Nilsson, 2000; Berger, Olofsson, Gotthard, Wiklund, & Friberg, 2012) is essential in the analysis of insect population dynamics since the number of eggs produced determines the initial size of the next generation. LEP is the product of several factors: an individual's reproductive lifespan, its age at first oviposition, the clutch interval, the overall number of ovipositions during its lifetime, the clutch size, and the weather dependency, among other factors (Clutton-Brock, 1988). In odonates, LEP most likely is influenced by body size, food availability, parasitism and weather conditions (Banks & Thompson, 1985; Bennett & Mill, 1995; Corbet, 1999; Fincke, 1986; Waage, 1978; Watanabe & Matsu'ura, 2006). In breeding seasons the LEP might be reduced dramatically by the lack

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of sunny days (Thompson, 1990). LEP cannot be estimated from the males' lifetime mating success (LMS) (LMS for Zygoptera: Banks & Thompson, 1985; Bennett & Mill, 1995; Fincke, 1982, 1986, 1988; Hafernik & Garrison, 1986; LMS for Anisoptera: Koenig & Albano, 1987; McVey, 1988; Michiels & Dhondt, 1991; Kasuya, Edanami, & Ohno, 1997) as not every mating inevitably results in oviposition (multiple mating, sperm removal). Therefore, the product of the number of matings during a lifetime multiplied by the average clutch size might result in a strongly over- or underestimated LEP.

In libellulids, the average clutch size ranges from 100 to more than 2000 eggs (e.g. Convey, 1989; Khelifa, Zebsa, Kahalerras, & Mahdjoub, 2012; Koch, 2015; Lempert, 1987; Schenk, Suhling, & Martens, 2004; Sahlén & Suhling, 2002; Schenk & Söndgerath, 2005). However, clutch size is highly variable within species and has to be used with caution (Sahlén & Suhling, 2002). Unusually large clutches do not necessarily represent the number of eggs normally laid in succession, but may prove a female's inability to oviposit, while follicles continue to mature in their ovaries (Corbet, 1999; Karlsson, Sahlén, & Koch, 2010). Large clutches are more likely in a period of consistently cloudy days while small clutches are more likely under sunny conditions (Gribbin & Thompson, 1990). The abdominal temperature has an important effect on the egg release rates – consequently the clutch size of free-flying libellulids cannot be derived from the duration of oviposition alone (McVey, 1984).

There are additional factors which have an important impact on clutch size, e.g. female age (Gribbin & Thompson, 1990; Khelifa et al., 2012; Rowe, 1990; Watanabe & Adachi, 1987; Watanabe & Ohsawa, 1984), female size (Corbet, 1999; Gribbin & Thompson, 1990; Khelifa et al., 2012; Watanabe & Adachi, 1987; Watanabe & Ohsawa, 1984), and parasitism (Corbet, 1999; Forbes & Baker, 1991). As females lay their eggs within a period of several days up to weeks and because they sometimes choose several water bodies for oviposition, it is a demanding task to count all egg clutches of one female's life span. In summary, the number of egg clutches per life span is a poor estimation of libellulid LEP.

Libellulids produce their oocytes in panoistic ovaries (Ando, 1962). The size and number of the ovarioles and oocytes per ovariole are known from several species (Corbet, 1999; Johnson, 1973; Karlsson et al., 2010; Koch, Quast, & Sahlén, 2009). However, females are able to produce oocytes either continuously or step wise during their whole reproductive stage (see Karlsson et al., 2010). Therefore, dissecting females and counting ovarioles and oocytes would never give an adequate idea of the whole LEP.

In this study, I tried to get a rough estimation of the size of LEPs in libellulids by operating an enclosure experiment under semi-natural conditions. The main questions of this enclosure study were: (1) does hand feeding influence females' life history traits; (2) how long is the maturation period and the average lifespan; (3) does the quality/quantity of the eggs within a clutch vary with female age or size; and (4) how many eggs do females of these studied species lay in their lifetime? Individually marked specimens of *Orthetrum coerulescens* (Fabricius, 1798) and *Sympetrum striolatum* (Charpentier, 1840) were kept in two outdoor cages under semi-natural conditions, which allowed me to individually follow the complete adult life cycle from emergence to death.

Material and methods

Study species

Orthetrum coerulescens is most common around the Mediterranean but is also widespread in central and northern Europe (Dijkstra, 2006). *Orthetrum coerulescens* prefers running water, such as streams and ditches (Dijkstra, 2006; Wildermuth & Martens, 2014). The flight season

takes place from April to November, with a peak from June to August (Dijkstra, 2006; Sternberg & Buchwald, 2000). The eggs and the larvae develop directly without diapause (Wildermuth & Martens, 2014). In comparison to other libellulids *O. coerulescens* is known to have a rather small ecological niche (Dijkstra, 2006; Sternberg & Buchwald, 2000; Wildermuth & Martens, 2014).

Sympetrum striolatum is common in most areas of Europe, except for most parts of Scandinavia (Dijkstra, 2006). It occurs in a wide range of habitats, preferring warm, stagnant waters (Dijkstra, 2006; Koch, Ziegler, & Griebeler, 2012). There are regional differences concerning flight season: in southern Sweden the dragonfly is seen from July until October (Billqvist, Swash, & Smallshire, 2012), in southern Germany from June until late November (Sternberg & Buchwald, 2000) and in the Mediterranean, the species may be active the whole year-round (Dijkstra, 2006). Eggs develop directly or with a facultative diapause during winter (Corbet, 1999, p. 221). The species is known to have a broad ecological niche, to be very flexible in its behavior and to have a high phenotypic plasticity in its life history traits (Dijkstra, 2006; Koch, 2015; Koch et al., 2012).

I chose the two species used in this study because good knowledge is available of their rearing conditions (Michiels & Dhondt, 1991; Schenk & Söndgerath, 2005; Schmidt, 2008; Koch, 2014, 2015). Moreover, the egg circumference and clutch size of wild-caught specimens of these species are known (Koch, 2015; Schenk & Söndgerath, 2005; Schmidt, 2008). Thus, I had the opportunity to compare the data from the cage conditions with data from field specimens.

Experimental procedure

For the two outdoor cages (4 m × 4 m × 2 m), I built a scaffolding covered with fine white gauze (for more details see Koch, 2014). At the end of April 2009, 190 larvae of *O. coerulescens* were caught in the Canal de Vergiere, a small canal situated in the stony steppe of the Crau in Southern France (43°34′ N, 4°50′ E) (e.g. Rehfeldt, Schridde, & Suhling, 1991; Suhling, 1995). At the end of May 2008, 160 larvae of *S. striolatum* were caught in a small lake near Worms in Germany (49°43′ N, 8°25′ E). The penultimate instar larvae of both species were transferred into several plastic basins (0.4 × 0.4 × 0.2 m; up to 10 larvae per basin) placed in these outdoor cages. The basins were filled with pond water and some sticks/stems were added as resting and emergence substrate. The water was changed weekly and larvae were fed twice a week with chironomid larvae *ad libitum* plus a mixture of small macroinvertebrates from a small pond nearby.

Each of the cages contained four large plants for the adults to rest on. Every day I checked the cages for emerged and dead animals. For each specimen, I recorded emergence day, sex, size (head width, abdomen length without cerci, forewing length) and the day of death. All animals were marked individually with consecutive numbers on their forewings using a black permanent marker (see Koch, 2014). Additionally, numerous flies (fruit flies *Drosophila hydei* (Sturtevant, 1921) as well as house flies *Musca domestica* Linnaeus, 1758, and flesh flies *Calliphora* sp.) were kept in the cages and served as prey for the adults (for more details see Koch, 2014). All specimens of *S. striolatum* were hand fed (as described by Koch, 2014). Of *O. coerulescens* those specimens marked with an even number were hand fed daily with up to six fruit flies or one housefly. Both treatments (hand-fed and not hand-fed) and both sexes were evenly distributed in the two enclosures. The measured value of the mean daily air temperature was taken from a nearby weather station (Mainz-Marienborn, 49° 57′ N, 8° 14′ E; situated 3 km south of the study area).

Beside the small larval basins, no additional open water was provided in the cages. Due to the lack of additional open water within the enclosure, it was impossible for females to lay eggs in

an uncontrolled manner. Ten days after emergence I tried to obtain egg clutches on a daily bases. The maturation period is the phase of adult life (including the teneral stage) that precedes the onset of reproductive behavior (Corbet, 1999). For this study, the first successful oviposition was defined as the first reproductive behavior and end of the maturation period.

Oviposition was initiated by dipping a female's abdomen into a jar filled with water (c.f. Boehms, 1971). Khelifa et al. (2012) dissected females just after artificial oviposition and counted the remaining mature oocytes. The maximum number of oocytes counted was less than 0.5% of the total clutch, which indicates that the procedure gave good estimates of the total clutch size (Khelifa et al., 2012). I counted the clutch size and separated randomly 20 eggs from each clutch. I measured length and width of these 20 eggs using a dissecting microscope. As the eggs are elliptical I applied a common formula for an ellipse to calculate egg circumference, C: $C = 3.142 \times (1.5 \times (a + b) - \sqrt{a \times b})$; where a = egg length, b = egg width (see Schenk et al., 2004; Schenk & Söndgerath, 2005).

Statistical analysis

In *O. coerulescens* only half of the specimens were hand fed. With a χ^2 test of homogeneity, I tested whether the hand-fed and not hand-fed specimens differed in their body size (head width, forewing length, and abdomen length). The hand-fed and not hand-fed specimens did not differ in their body size (Table 1). In order to test whether the hand feeding influenced females life history traits, for *O. coerulescens* I ran χ^2 tests of homogeneity. The independent variable was hand-fed or not hand-fed, and dependent variables were duration of the maturation period, the life span, number of eggs per life span, mean clutch size, and mean egg circumference. Only life span was significantly affected by hand feeding (Table 1). Analyses with life span as an independent variable refer to hand-fed specimens only.

With help of ANOVAs I tested whether the maturation period, the mean life span, the number of egg clutches per life span, the clutch size, the egg circumference or the LEP differed significantly between the two studied species. For both species, I tested with linear regression analyses whether the female and the females' size parameters (head width, forewing length, and abdomen length) correlated with the egg circumference, the clutch size or the life span. All statistical analyses were performed with SPSS 22.0 (IBM, New York).

Table 1.   Comparison of females of *Orthetrum coerulescens* fed by hand with those not fed by hand. The results of the χ^2 test of homogeneity showed that only the life span differed significantly between not hand-fed and hand-fed specimens.

Female parameter	With hand feeding			No hand feeding			χ^2	df	p
	n	Mean	SD	n	Mean	SD	χ^2	df	p
Head width [mm]	44	4.89	0.42	36	4.95	0.53	20.92	18	0.27
Forewing length [mm]	44	28.07	1.33	36	28.57	1.57	37.92	40	0.56
Abdomen length [mm]	44	24.35	1.45	36	24.04	1.39	37.56	41	0.62
Maturation period [d]	13	23.92	4.17	2	20.50	2.12	0.64	1	0.42
	n	Median	Q1; Q3	n	Median	Q1; Q3	χ^2	df	p
Life span [d]	44	12	5; 29	36	5	4; 8	17.62	4	0.001
Number of egg clutches	13	7	3.0; 14	2	7.5	2; 17	15	11	0.182
Clutch size	41	216	82; 432	98	229	116; 454	7.85	8	0.448
Egg circumference [mm]	1892	2.75	2.62; 2.88	666	2.72	2.62; 2.82	46.47	19	0.363
LEP	13	1584	661; 2765	2	4250,5	2656; 5845	15	14	0.378

Abbreviations: SD, standard deviation; LEP, lifetime egg production; Q1 and Q3, lower and upper quartiles; df, degrees of freedom.

Results

The emergence rate of *O. coerulecsens* was 65.85% and that of *S. striolatum* was 88.75% (Table 2). The emergence period covered 115 days in *O. coerulescens* and 63 days in *S. striolatum* (Figure 1). The sex ratio was slightly female-biased in both species (Table 2). In *O. coerulescens* the life span differed significantly between hand-fed and not hand-fed specimens (Table 1). In contrast, the duration of the maturation period, the number of egg clutches, the clutch size, the egg circumference and the LEP did not differ significantly between the hand-fed and not hand-fed specimens (Table 1).

The median maturation period in *O. coerulescens* was 24 days in the hand-fed and 20 days in the not hand-fed specimens, and in S. *striolatum* 47 days (Tables 1, 3). The duration of the maturation period differed significantly between the two studied species (F = 61.68, df = 1, p < 0.0001). The mortality during the maturation period was high in both species; in *O. coerulescens* 81.48% of the females died during their maturation period, in *S. striolatum* 89.16%. The females' life span differed significantly between the two species (F = 46.75, df = 1, p < 0.0001). *Orthetrum coerulescens* had a shorter median life span than *S. striolatum* (Tables 1, 3). The maximum individual life span for males of *O. coerulescens* lasted 62 days and for females 59 days. *Sympetrum striolatum* males lived no longer than 93, females no longer than 86 days. The flight period of both populations in the outdoor cages took 116 days in *O. coerulescens* and 120 days in *S. striolatum*.

I found no correlation between the females' age and the egg circumference in either species (*O. coerulescens*: F = 4.31, R^2 = 0.002, p = 0.04; *S. striolatum*: F = 46.23, R^2 = 0.051, p < 0.001) or the clutch size (*O. coerulescens*: F = 0.36, R^2 = 0.003, p = 0.55; *S. striolatum*: F = 0.62, R^2 = 0.014, p < 0.44) (Figure 2). In addition, the females' size did not correlate with the egg circumference or the clutch size (low R^2 values, Table 4).

The mean number of egg clutches during the life span was higher in *O. coerulescens* than in *S. striolatum* (Tables 1, 3); however, because of the high variance within this parameter, the number of egg clutches did not differ significantly between the two species (F = 1.92, df = 1, p = 0.179). The mean clutch in *O. coerulescens* (n = 139) was significantly larger than in *S. striolatum* (F = 3.71, df = 1; p = 0.046; n = 46) (Tables 1, 3). The two study species differed significantly in their egg circumference (F = 1276.65, df = 1, p < 0.0001); the mean egg circumference of *O. coerulescens* (n = 2558) was significantly smaller than of *S. striolatum* (n = 860) (Tables 1, 3). The mean LEP did not differ between the two studied species (F = 3.05, df = 1, p = 0.094).

In the group of *O. coerulescens* 15 females reached the end of the maturation period and laid altogether 46,242 eggs in their life span, or a calculated mean LEP of 3082.80 eggs per specimen. In *S. striolatum* the nine mature females laid in total 9366 eggs during their life span, a calculated mean LEP of 1040.66 eggs per specimen.

Table 2. Overview of initial number of larvae, emergence, mortality, and sex ratio (m = males; f = females) of *Orthetrum coerulescens* and *Sympetrum striolatum*.

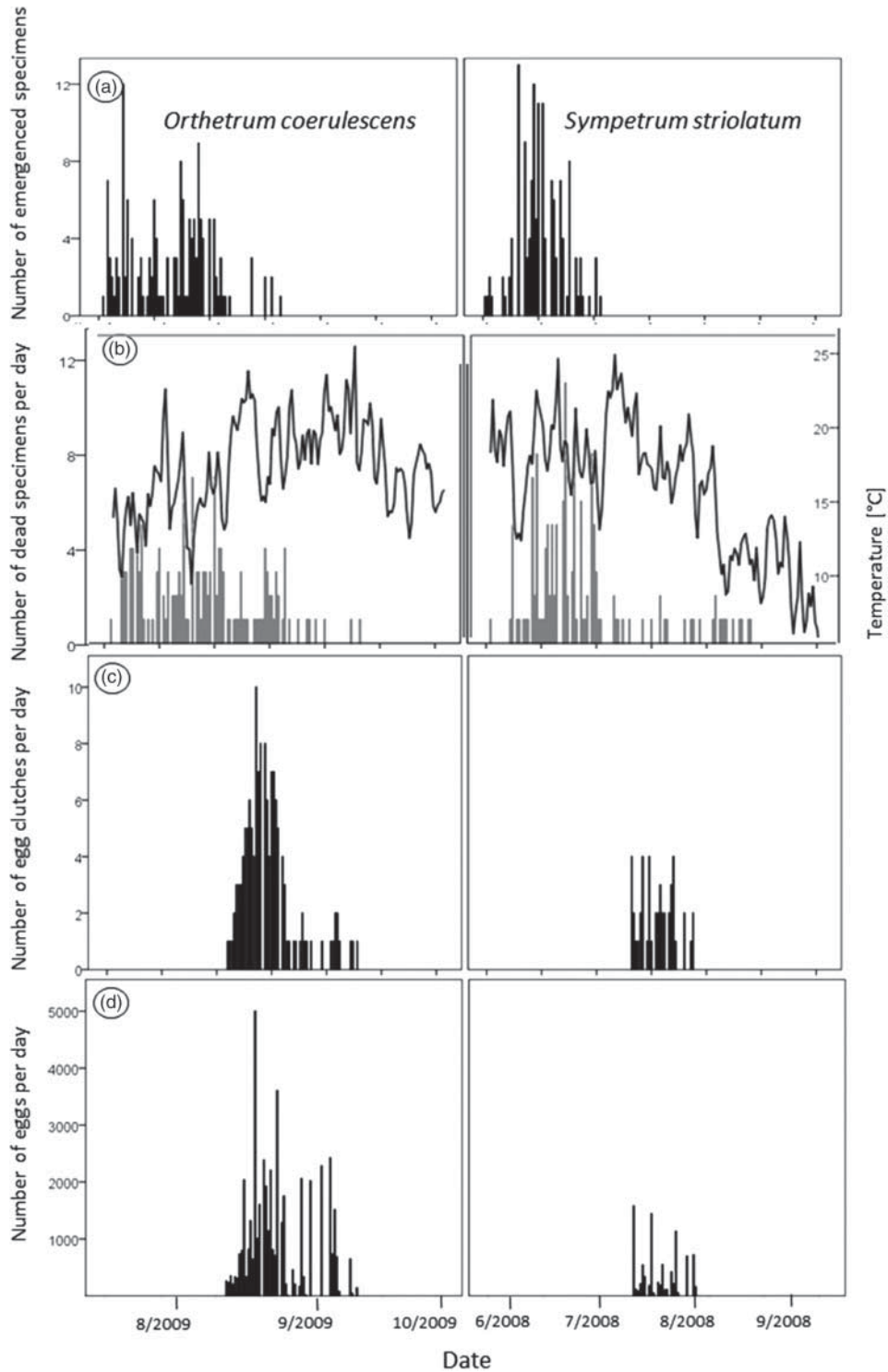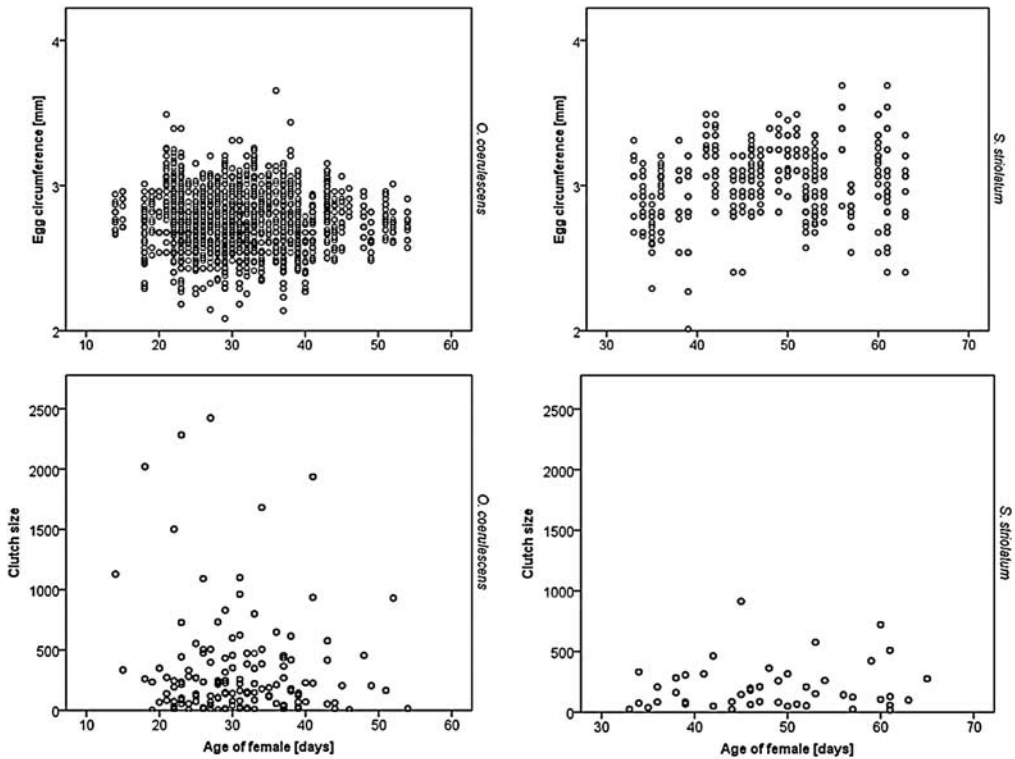|	*Orthetrum coerulescens*		*Sympetrum striolatum*	
	Number	Value	Number	Value
Larvae (both sexes)	190		160	
Emergence rate (both sexes)	154	65.85%	142	88.75%
Lethal emergence accidents (both sexes)	4	2.59%	5	3.52%
Sex ratio (m:f)	154	1:1.11	142	1:1.18
Survival rate during maturation period (f)	15	18.52%	9	11.84%

Figure 1.   Summary of the temporal changes in the outdoor cages over the study periods of *Orthetrum coerulescens* (left column) and *Sympetrum striolatum* (right column): (a) number of emerged specimens; (b) number of dead animals and mean air temperature; (c) number of egg clutches; and (d) number of eggs laid per day.

Table 3. Morphological and life history characteristics of female *Sympetrum striolatum* (abbreviations as in Table 1).

Female parameter	Number	Mean	SD
Head width [mm]	76	5.75	0.04
Forewing length [mm]	76	27.89	0.12
Abdomen length [mm]	76	25.10	0.12
Maturation period [d]	9	46.89	10.41
		Median	Q1; Q3
Life span [d]	76	8	5; 16.75
Number of egg clutches	9	4	1.5; 7.5
Clutch size	46	145	68; 283
Egg circumference [mm]	860	3.05	2.86; 3.20
LEP	9	599	347; 1865

Figure 2. The egg circumference and clutch size of *Orthetrum coerulescens* (left column) and *Sympetrum striolatum* (right column) did not differ with the females' age.

Discussion

It was possible to establish small populations of *O. coerulescens* and *S. striolatum* in outdoor cages (see Koch, 2014). The sex ratio was slightly female-biased in both species. A balanced sex ratio at the beginning of juvenile development (Charnov, 1993) does exist in theory. Therefore, the observed imbalance in the sex ratio at emergence could reflect gender-specific mortality during the aquatic stages (Corbet & Hoess, 1998).

Table 4.   Linear regression analyses with female size parameters (head width [mm], forewing length [mm] and abdomen length [mm]) as independent variables and egg circumference, clutch size, and life span as dependent variables for *Orthetrum coerulescens* and *Sympetrum striolatum*.

Species	Independent variable	Dependent variable	F	R^2	*p*
O. coerulescens	Head width	Egg circumference	33.76	0.013	< 0.0001
	Forewing length	Egg circumference	6.36	0.002	0.012
	Abdomen length	Egg circumference	0.66	0.001	0.412
	Head width	Clutch size	151.42	0.056	< 0.0001
	Forewing length	Clutch size	99.33	0.037	< 0.0001
	Abdomen length	Clutch size	165.84	0.061	< 0.0001
	Head width	Life span	0.55	0.004	0.464
	Forewing length	Life span	0.42	0.003	0.515
	Abdomen length	Life span	0.04	0.001	0.848
S. striolatum	Head width	Egg circumference	9.75	0.011	0.002
	Forewing length	Egg circumference	28.52	0.032	< 0.0001
	Abdomen length	Egg circumference	1.14	0.001	0.286
	Head width	Clutch size	2.31	0.003	0.129
	Forewing length	Clutch size	56.08	0.058	< 0.0001
	Abdomen length	Clutch size	1.88	0.002	0.172
	Head width	Life span	1.11	0.008	0.294
	Forewing length	Life span	0.43	0.003	0.516
	Abdomen length	Life span	0.27	0.002	0.600

In *O. coerulescens* hand feeding had a great impact on the survival rate, especially during the maturation period (see Koch, 2014). In contrast, the duration of the maturation period, the number of egg clutches per life span, the clutch size, the egg circumference, and the LEP were not significantly influenced by the hand feeding. Moreover, the clutch size and the egg circumference of the hand-fed and the not hand-fed specimens were comparable to those from wild caught specimens (Schmidt, 2008; own unpublished data). All *S. striolatum* were hand fed. Only the clutch size of the caged females was much lower than of wild caught females; the egg circumference was equal/similar (Schenk & Söndgerath, 2005).

In both species, the amount of food delivered by hand feeding did not influence the oocyte production strongly. Instead, the amount of food fed by hand seemed to be too low. Mortality during maturation period was rather high in both species. In both studied species, just a small number of females survived the maturation period and laid eggs. Probably most of the females died of hunger and the egg production might have been limited by food supply. The semi-natural conditions of the experiment differed from natural conditions: the specimens in the enclosures got a reduced spectrum of prey, they had no possibilities to perform long flights and no predators were present. Nevertheless, the data of this study might give a very rough estimation about the LEP of two libellulid species.

The literature provides comparatively little information about the individual female maturation period of libellulids. Most values of the duration of the maturation period result from calculations of the difference between the first emergence and the first mature female per species in one population (e.g. Sternberg & Buchwald, 2000; Wildermuth & Martens, 2014). Instead, in outdoor cages, it was possible to measure the individual mean maturation period from emergence until the first reproductive behavior. In *O. coerulescens* the mean maturation period took 23 days whether hand-fed or not. This exceeds the number of 10 days documented in Sternberg and Buchwald (2000), and is in accordance to the average of almost three weeks mentioned by Wildermuth and Martens (2014). For *S. striolatum* in the cage the mean female maturation period lasted 46.8 days. This period of time matches the results taken from the literature of *S. striolatum* (21–56 days, Sternberg, 2000; 21–140 days, Wildermuth & Martens, 2014). *Sympetrum striolatum* is a species with a high phenotypic plasticity (Koch et al., 2012). Considering the entire range of distribution

of this species the duration of the maturation varies a lot (Dijkstra, 2006; Koch et al., 2012; Ott & Koch, 2014). In the arid south of its range, *S. striolatum* has a long maturation period, called prereproductive diapause (Samraoui, Bouzid, Boulahbal, & Corbet, 1998; Samraoui & Corbet, 2000; Sternberg, 2000). This prereproductive diapause is assumed to be an adaptation to arid climate conditions in summer time when bodies of water are drying out. The rather long mean maturation period of *S. striolatum* in this study might be a hint that a prereproductive diapause can exist also in the temperate zone.

For O. coerulescens held in cages the maximum individual lifespan of adult males was up to 62 and of adult females up to 59 days. For *S. striolatum* held in cages the maximum individual lifespan for adult males was 93 and for adult females 86 days. These lifespan values cannot directly be compared with free flying specimens. In nature, most dragonflies are caught by predators before they die due to old age. Within the cages no predators were present and the dragonflies received a limited amount of food. However, the large individual life span of some specimens observed over a relatively long period of time in cages might indicate that the living conditions in the outdoor cage were adequate for both studied species. Adequate living conditions are an important basis to estimate a rough value of the LEP.

The mean clutch size of both studied species in cages was smaller than the mean clutch size of free-living specimens (*O. coerulescens:* 332.68 $\pm$ 436.21 eggs in this study and 704.17 $\pm$ 382.28 eggs for free-living specimens (Schmidt, 2008); *S. striolatum:* 204.76 $\pm$ 191.97 in this study and 719.8 $\pm$ 642.0 for free-living specimens (Schenk & Söndgerath, 2005)). Thompson (1990) discussed clutch size as a function of interclutch interval. Females might face a trade-off between laying a small clutch each day (which might incur a higher mortality risk at the oviposition site) or laying fewer but larger clutches (which is advantageous in allowing them to spend more time hunting to renew their energy reserves, but imposes the risk of dying before the next clutch can be laid). In this study, I tried to get egg clutches every day. Assuming instead a mean interclutch interval of two or three days, as documented in several odonate species (Fincke, 1988; Koenig & Albano, 1987; Michiels & Dhondt, 1991; McVey, 1988), the clutch size of specimens held under semi-natural conditions was comparable to the clutch size of wild specimens. Therefore, I suppose that the oocyte production rate in the ovaries under semi-natural and natural conditions were comparable.

So far, small egg clutches have been mainly interpreted as interrupted ovipositions, implying that they did not contain the maximum number of eggs (e.g. Sahlén & Suhling, 2002). However, also under the controlled experimental conditions for the cage populations, clutch size was highly variable in both species. The high standard deviation might be seen as an additional confirmation that *O. coerulescens* and *S. striolatum* are species which produce their oocytes stepwise (Karlsson et al., 2010; Ware, Karlsson, Sahlén, & Koch, 2012).

In contrast to several other studies (Corbet, 1999; Gribbin & Thompson, 1990; Khelifa et al., 2012; Rowe, 1990; Watanabe & Adachi, 1987; Watanabe & Ohsawa, 1984), in both species females' age and size had no significant influence on the clutch size and egg circumference. Egg quality and egg quantity did not change with females' size and age. The adult life span of libellulids and the space for eggs in the females' ovarioles is limited. To maximize the fitness under these restricted circumstances, a trade-off exists for the females: they can either lay a higher number of eggs or process a smaller amount of eggs with a larger egg circumference. The mean clutch size and the calculated LEP were higher in *O. coerulescens*, whereas in *S. striolatum*, the egg circumference was slightly higher.

In Odonata, fecundity is commonly known to be very high while egg mortality is estimated to be very low (Corbet, 1999), so that the total LEP can be translated more or less into the number of larvae. Larval mortality, however, can differ considerably between different habitats, stages and seasons and is thus generally difficult to evaluate. Emergence accidents are relatively uncommon (below 4% in this study; Corbet, 1999), but the predation risk during emergence, as well as

the mortality during maturation, seems to be comparatively high and critical. This study on the LEP referred only to those females that reached emergence and excludes predation during egg, larval and adult stages. Therefore, the calculated females' LEPs of 3082.80 eggs per specimen in *O. coerulescens* and of 1040.66 eggs per specimen in *S. striolatum* are overestimated. This study can offer only a rough estimation of the potential LEP in libellulids. The LEP represents the potential initial size of the next generation. However, this LEP cannot be translated into the lifetime reproductive success (LRS). The LRS in dragonflies is hard to estimate or measure. Several parameters influence the LRS. For determining the LRS, random environmental factors are often of more importance than the mating efficiency (Koenig, 2008; Thompson, Hassall, Lowe, & Watts, 2011).

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