International Journal of Odonatology 5 (2): 181-191, 2002

Relationships between egg size and clutch size among European species of Sympetrinae (Odonata: Libellulidae)

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Received 10 September 2001; revised and accepted 27 March 2002.
Key words: dragonfly, egg size, clutch size, local variation, *Sympetrum*, *Crocothemis*.

Abstract

A negative relationship between clutch size and egg size is generally expected. However, no such trade off has been reported in Odonata. In this paper we analyse relationships between egg size and clutch size in the dragonfly subfamily of Sympetrinae using material from Norway, Sweden, Germany and France. Clutch size varied within and among the species, and only maximum clutch size was comparable between species. Both egg length and width varied among species. Moreover, mean egg length differed significantly intraspecifically among individual clutches of all species. We found mean egg length to be negatively correlated to clutch size, confirming the trade off between egg size and clutch size across species. Clutch size was positively correlated to female size, but egg size was not.

Introduction

In their analysis of the evolution of optimal clutch number, Smith & Fretwell (1974) assumed that there is a negative relationship between the number and the size of animal eggs due to spatial limitations. A variety of studies have tested the hypothesis of such a relationship (trade off) between egg and clutch size, and most of them found a negative correlation (see review in Roff 1992). Evidence for such a trade off also exists from several insect orders (e.g. Berrigan 1991). Montague et al. (1981) recorded a strong negative correlation between egg size and clutch size in Hawaiian Drosophilidae. In Odonata, in contrast, despite numerous studies dealing with clutch size (Watanabe & Adachi 1987; Convey 1989; Thompson 1990; Lutz & Rogers 1991; Watanabe & Higashi 1993), we only know one study that shows a trade off. Females of *Coenagrion puella*

(Linnaeus) that laid fewer eggs due to parasitism produced bigger larvae (Rolff 1999), but not bigger eggs. In a similarly sized damselfly, *Pyrrhosoma nymphula* (Sulzer), with no parasites, no relationship between egg volume and clutch size was found (Gribbin & Thompson 1990). Corbet (1999: 37) suggested that possible correlations between egg size, number of ovarioles and eggs, and body size might warrant investigation in Odonata.

In Odonata, an egg clutch is the number of eggs laid by a female during a single egg-laying period, lasting one or several days (Corbet 1999: 38). As odonates have panoistic ovaries and a continuous egg-production during their mature life span, egg-laying periods are interspersed with resting (i. e. eating) periods away from their oviposition sites (cf. Thompson 1990). When eggs are collected from an egg-laying female, the number thus corresponds to either an entire clutch or less than a clutch, depending on time lapsed since last resting period (Corbet 1999). Comparing clutch size from wild-caught females is therefore an inexact procedure, as numbers do not necessarily mirror the actual clutch size. Factors known to correlate with clutch size within odonate species include age (e.g. Watanabe & Adachi 1987; Gribbin & Thompson 1990), size of the female (Gribbin & Thompson 1990; Martens 1996), interclutch interval and temperature (Thompson 1990), parasitism (Forbes & Baker 1991) and probably differences in genotype (cf. Atkinson & Begon 1987a for grasshoppers). Maximum clutch size may be comparable among species, but capturing a large enough number of females to have successive clutch size counts stabilising around a species-specific maximum clutch size is a time-consuming process. Nevertheless this method may work, and although we are aware of the difficulties, we attempt to use it in this paper, even if the number of clutches counted for each species is too small to give us an exact maximum clutch size.

In this study we compared intra- and interspecific variation in egg and clutch size within the Sympetrinae, a subfamily of Libellulidae, containing some of the dragonflies most often encountered in late summer in Europe. Our hypothesis was that there is a trade off between maximum clutch size and egg size among species.

Organisms

The Sympetrinae exhibit a world-wide distribution (Davies & Tobin 1985). In Europe this taxon is represented by the genera *Sympetrum* Newman, *Crocothemis* Brauer, *Diplacodes* Kirby and *Brachythemis* Brauer, totalling 14 species (Wendler et al. 1995). Females oviposit either onto moist ground or onto water (Robert 1958). Breeding sites are often small, temporary waters which reflect the short development time of the larvae (Aguesse 1960a; Corbet 1999: 221). The life history of many species is known (Münchberg 1930; Gardner 1950a; Gardner 1950b; Gardner 1951a; Gardner 1951b; Wenger 1955). Most species complete one generation per year, and in the Mediterranean region some species complete two or three generations (Aguesse 1960b; Schnapauff et al. 2000). Some univoltine species aestivate in the Mediterranean region as prereproductive adults, thus postponing reproduction until the end of the dry season (Samraoui et al. 1998). Many multivoltine and some univoltine species in south, central and north Europe exhibit direct egg development whereas many univoltine species lay overwintering eggs.

Some species facultatively lay diapause or non-diapause eggs (Corbet 1999: 221). The egg-laying behaviour of several *Sympetrum* species was described by Münchberg (1930) and Robert (1958).

Materials and methods

Eggs of nine species of *Sympetrum* and *Crocothemis* were collected in central Norway, central Sweden, north Germany and south France, in August-October 1999 and August-September 2000 (Table 1) by dipping the abdomen of wild-caught females of unknown age in small vials of water (Tillyard 1917; Krull 1929; Gardner 1952). Females were caught either during egg laying in sunny weather or in open terrain close to water on cast-over days. They were allowed to deposit eggs until they stopped by themselves. The eggs were left in these vials for 48 h to let their light brownish colour (signifying that they are fertilised) develop. The total number of eggs laid was counted and the length and width of 20 of them (using fertilised eggs only), selected randomly from each female, were measured at 0.01 mm accuracy using an ocular micrometer in a standard stereo microscope. Some specimens laid only a few eggs, in which cases the number measured was as low as five eggs per female (Table 2). *S. nigrescens* from Norway, which appears to be a subspecies or colour form of *S. striolatum*, is treated as a separate taxon in this study solely on account of differences in egg size. Names and authors of all species studied are given in Table 1, others in the text.

Corbet (1999: 38) stated that if uninterrupted, a female probably lays most or all of the mature eggs in her ovaries during each visit to the oviposition site. In this paper we assume that by allowing the females to lay eggs until they stopped by themselves we got a measure of the maximum number of eggs for that particular female. The theoretical maximum number of eggs in one clutch for a certain species is, however, as mentioned above, difficult to measure due to ongoing egg-production during the entire life of the adult female, and to the amount of mature eggs already deposited prior to capture.

Table 1. Origin and number of egg clutches of different females analysed.

Species	Year	Origin	Clutches measured
Crocothemis erythraea (Brullé)	1999	S France	3
Sympetrum danae (Sulzer)	1999, 2000	N Germany	7
S. depressiusculum (Selys)	2000	N Germany	6
S. flaveolum (Linnaeus)	1999	N Germany	8
S. fonscolombii (Selys)	1999	S France	3
S. nigrescens Lucas	1999, 2000	C Norway	6
S. sanguineum (Müller)	1999, 2000	N Germany	18
S. striolatum (Charpentier)	1999, 2000	N Germany	8
S. vulgatum (Linnaeus)	1999, 2000	N Germany, S Sweden	16

Table 2. Minimum and maximum clutch size and egg size of the species investigated.

Species	Eggs measured	Clutch size		Egg width [mm]		Egg length [mm]	
		min	max	min	max	min	max
Crocothemis erythraea	60	34	1,835	0.30	0.36	0.38	0.52
Sympetrum danae	138	488	991	0.34	0.42	0.52	0.64
S. depressiusculum	130	145	632	0.30	0.45	0.48	0.62
S. flaveolum	122	5	241	0.38	0.48	0.53	0.63
S. fonscolombii	20	426	951	0.33	0.44	0.48	0.57
S. nigrescens	120	267	951	0.29	0.43	0.42	0.66
S. sanguineum	324	11	403	0.50	0.62	0.57	0.72
S. striolatum	120	315	1,004	0.35	0.52	0.50	0.65
S. vulgatum	282	7	1,438	0.32	0.50	0.48	0.65

Thompson (1990) stated for *Coenagrion puella* that clutch size is highly variable at intervals of one or two days, but stabilises near a maximum after five days without egg-laying. By obtaining a number of clutches we expected to get at least one of each species that had close to the maximum number of eggs in her ovaries, allowing for the variables of female age, season and time of day (cf. Thompson 1990; Higashi & Watanabe 1993), thus enabling us to do a first-generation analysis of the relationship between size and number in these species. However, we are aware that our material is limited and that the actual maximum clutch size may be considerably larger.

We analysed (1) between- and (2) within-species variation in egg size using ANOVAs. For (1) we used the species as independent variables and the mean egg size of 20 eggs per individual of each species as dependent variables. *S. fonscolombii* was omitted from this analysis due to the fact that eggs of only one clutch could be measured. Thus, the units for the analysis were the egg clutches, i.e. the females, per species. For (2) the individuals of each species were the independent variables and the mean egg size of 20 eggs per individual were the dependent variables. The units for this analysis were the individual eggs. For pairwise comparisons of means we used *a posteriori* analyses (Tukey-Kramer post hoc test; Sokal & Rohlf 1995).

To find a trade off between egg size and clutch size we correlated (Pearson correlation) maximum and mean number of eggs per clutch with mean egg size per species. As the size of the female may affect the relationship, we also correlated female abdomen width against mean egg length and mean egg width derived from all clutches measured. For female abdomen width, we measured the width of segment 7 using line drawings in Robert (1958), which are of high precision. The width of the posterior part of the abdomen limits the number of mature eggs. To determine if the correlation coefficients were significant from zero, we used Fischer's r to z transformation (Sokal & Rohlf 1995).

Results

Variation in clutch size

The maximum clutch size varied widely among species (Table 2). The largest clutch was laid by *Crocothemis erythraea* (> 1,800 eggs). In contrast, the maximum clutch size in *Sympetrum flaveolum* was < 250 eggs. In *C. erythraea*, *S. flaveolum*, *S. sanguineum* and *S. vulgatum*, the minimum egg number was ≤ 5% of the maximum.

Inter- and intraspecific variation in egg size

The egg length as well as the egg width varied significantly among the species (Fig. 1; ANOVA, $F_{7,61} = 378.73$, $p < 0.001$; $F_{7,61} = 1685.8$, $p < 0.001$). Pairwise comparisons revealed significant differences among all species in both measures (*a posteriori* analysis, Tukey Kramer post hoc test, p at least < 0.02) except for egg length in the pairs *S. danae* / *S. vulgatum* and *S. depressiusculum* / *S. nigrescens* and for egg width in *S. danae* / *S. nigrescens* (Tukey Kramer post hoc test, $p > 0.05$). There was a wide intraspecific variation in egg size in all nine species. Egg length as well as egg width differed significantly within each of the species (ANOVA; p at least < 0.01).

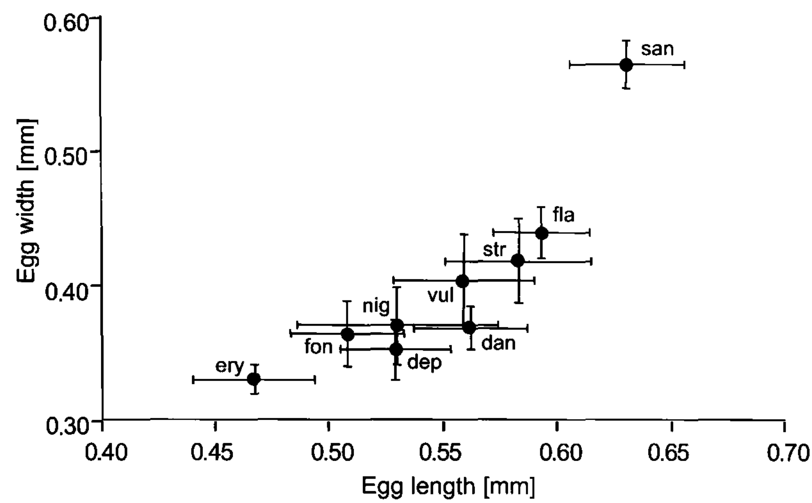

Figure 1. Relationship of egg length (± s.d.) to egg width (± s.d.) in eggs of Sympetrinae — ery: *Crocothemis erythraea*; dan: *Sympetrum danae*; dep: *S. depressiusculum*; fla: *S. flaveolum*; fon: *S. fonscolombii*; nig: *S. nigrescens*; san: *S. sanguineum*; str: *S. striolatum*; vul: *S. vulgatum*.

Relationship between clutch size, egg size and female size

Mean egg length decreased significantly with maximum clutch size comparing all species (Table 3; Fig. 2). Egg width did not decrease significantly with maximum clutch

Table 3. Correlations among clutch size, egg size and female size across nine European Sympetrinae species. Size measurements of females derived from Robert (1958); see methods.

Correlation of	Correlation coefficient	p-value
Maximum clutch size vs female abdomen width	0.694	0.036
Egg length vs maximum clutch size	–0.701	0.033
Egg length vs mean clutch size	–0.129	0.751
Egg length vs female abdomen width	–0.318	0.421
Egg width vs maximum clutch size	–0.593	0.095
Egg width vs mean clutch size	–0.338	0.388
Egg width vs female abdomen width	–0.161	0.691

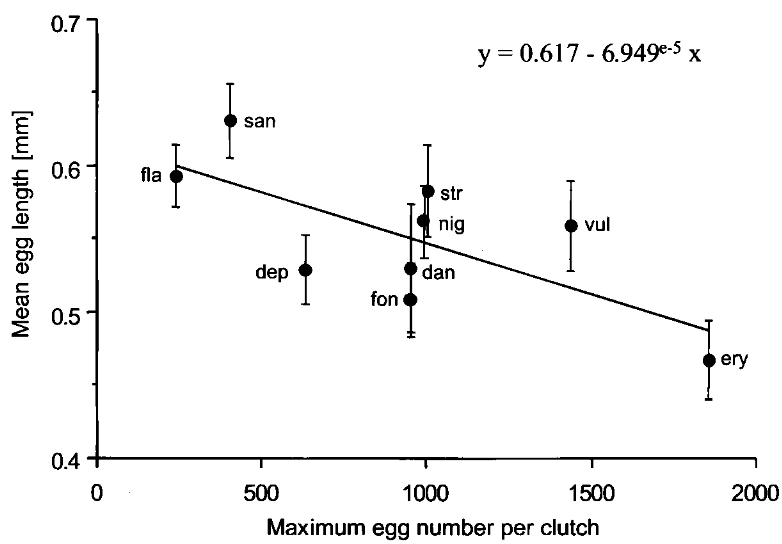

Figure 2. Regression plot of egg length (± s.d.) against maximum clutch size by species. For abbreviations see Figure 1.

size (Table 3). Neither the length nor the width of the egg correlated significantly with mean clutch size or female abdomen width (Table 3). Maximum clutch size, on the other hand, was positively correlated with female abdomen width (Table 3). Due to high intra-specific variation, there was no significant correlation between egg length and maximum clutch size in *S. sanguineum* (Pearson correlation 0.090, p = 0.725) and *S. vulgatum* (correlation –0.004, p = 0.988) (Fig. 3).

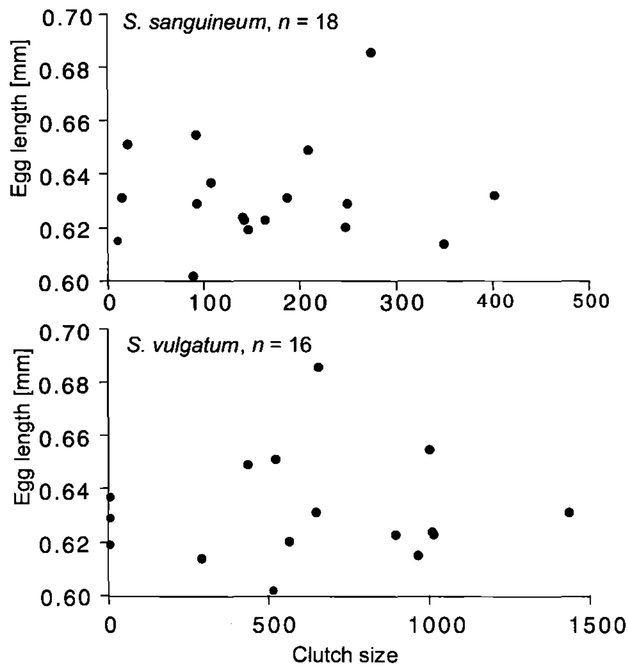

Figure 3. Intraspecific relationships between egg length and clutch size in *Sympetrum sanguineum* and *S. vulgatum*.

Discussion

In our study we recorded a negative correlation between clutch size and egg size among species in nine species of European Sympetrinae. In their analysis on the evolution of optimal clutch number, Smith & Fretwell (1974) assumed that such a negative relationship generally exists. Most studies that tested this hypothesis also found a negative correlation among species (see review in Roff 1992).

We found a wide range in the maximum clutch size across species. The highest value was in *Crocothemis erythraea* (1,837 eggs), the lowest in *Sympetrum flaveolum* (241 eggs). However, a literature survey revealed that the maximum clutch size may be higher, at least in some species (e.g. *S. fonscolombii* and *S. striolatum*; Table 4). Thus, our maximum clutch size numbers may be underestimated. Including the higher literature values into a correlation, we found that this maximum clutch size is still significantly correlated with egg length (correlation –0.665, $p < 0.05$), although slightly less strongly. The reason may be that we do not know the egg size of these larger egg clutches. Our measurements show that there is a significant intraspecific variation in egg size in all species (see below). If eggs from the larger clutches are smaller than those measured by us, the correlation will obviously get stronger.

Table 4. Maximum clutch size of European Sympetrinae derived from different studies. *n* = number of clutches, - = no data available.

Species	*n*	Max egg no.	Reference
Crocothemis erythraea	21	1,837	Katzur (1998)
	3	1,835	this study
	31	1,570	Convey (1989)
Sympetrum danae	7	991	this study
	1	> 910	Waringer (1983)
	37	905	Michiels & Dhondt (1988)
S. depressiusculum	6	632	this study
	17	440	Katzur (1998)
S. flaveolum	8	241	this study
S. fonscolombii	1	≈ 2,200	Lempert (1987)
	51	956	Katzur (1998)
	3	951	this study
S. meridionale	2	247	Aguesse (1959)
S. nigrescens	6	951	this study
S. sanguineum	18	403	this study
	6	301	Convey (1989)
	-	≈ 240	Miller (1995)
S. striolatum	3	1,525	Katzur (1998)
	6	1,004	this study
S. vulgatum	16	1,438	this study

The factors affecting clutch size within a species, listed in the introduction, include age, size of the female, egg volume, interclutch interval, temperature, and differences in genotype and parasitism (see Atkinson & Begon 1987a; Corbet 1999: 38). In spiders, female body size plays a central role in both offspring number and size (Simpson 1995). Similar results are known within odonate species (Gribbin & Thompson 1990; Martens 1996). Comparing across dragonfly species, particularly those with exophytic oviposition, it is known that larger species tend to lay more eggs than small ones (Convey 1989; Lutz & Rogers 1991). We found that maximum clutch size increased with female size across species – which one should expect.

Several factors are known to affect egg size in Odonata (Corbet 1999: 44; cf. also Simpson 1995; Iverson et al. 1993). Sahlén (1994) reported the eggs of *S. sanguineum* from central Sweden to be up to 0.73 mm in length, larger than the largest egg found in north Germany (cf. Table 2). *S. sanguineum* eggs are obligate overwinterers if laid in autumn (Gardner 1950a), and speculatively the more severe winters in Sweden act as a selection tool for larger egg size, because a larger (and thicker) egg shell may provide protection against harsh conditions (Sahlén 1994). There may also be an age-related size reduction in the eggs of Sympetrinae. Watanabe & Adachi (1987) found that egg size of the damselflies *Lestes temporalis* Selys and *L. sponsa* (Hansemann) decreased in size with female age, eggs from old females being 75% and 88% the size of eggs from young females respectively. However, they found no such size reduction in eggs of *L. japonicus* Selys, and the reduction is thus species-specific. As we did not consider female age in our study, we have to keep the possible influence of this factor in mind when interpreting the present data. Corkum et al. (1997) found that in the mayfly *Hexagenia limbata* emergence dates of adults had a significant effect on egg size, but not maternal size. In our study we also did not find a correlation between female size and egg size (Table 3). Miller (1995) stated that egg size generally varies less than body size. In our material, egg size appears to be species specific, with few exceptions, despite significant intraspecific variation in all species. This agrees with Atkinson & Begon (1987b), who, studying grasshoppers, argued that egg size is determined primarily by selection pressures on the size of hatchlings, but that poor feeding, both for juveniles and adults, resulted in smaller eggs in one species.

Roff (1992) stated that tests on relationships between clutch and egg size comparing species and comparing populations within the same species are suspect because selective regimes may be very different, and hence patterns of allocation to reproduction could vary widely. Nevertheless, in his review he found more cases in which a trade off exists than not. A negative correlation also exists in European Sympetrinae: the maximum clutch size explains about half the variation of mean egg length per species (Fig. 3). All the other factors that may affect egg size (see above) seem to play minor roles. We already stated that the female body size does not correlate with the egg length of the Sympetrinae.

Michiels & Dhondt (1988) reported the average clutch size of *S. danae* to be 274. Likewise, other studies have reported the mean clutch size of libellulids (e.g. McVey 1984; Convey 1989). But, as clutch size is a highly variable number, the lowest value always being one — or five as in our study — the mean would end up somewhere between one and the maximum due to female condition (see e.g. examples of *S. sanguineum* and *S. vulgatum*, Fig. 3). Consequently, we found a significant correlation between maximum clutch size and egg length but not between mean clutch size and egg length. Thus, a maximum clutch size should be comparable among species, whereas an average clutch size should not – unless the samples are very large and normally distributed.

Acknowledgements

We thank Philip S. Corbet and Anders Berglund for helpful comments on an earlier draft of this paper. Klaus Guido Leipelt, Dirk Mikolajewski and Hans Olsvik provided additional egg clutches. The study was partly funded by a grant from Deutscher Akademischer Austauschdienst (DAAD) to GS.

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