

## EMERGENCE PATTERNS AND LATITUDINAL ADAPTATIONS IN DEVELOPMENT TIME OF ODONATA IN NORTH SWEDEN AND POLAND

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Using exuviae, data are presented on emergence dates of dragonflies from northern Sweden and northwestern Poland. The 17 spp. sampled in Sweden showed considerable overlap in emergence periods. In Sweden, *Leucorrhinia rubicunda* was the first sp. to emerge (May 31) and *Sympetrum danae* the last (July 19). A comparison of first dates of emergence of spp. in Sweden and Poland showed a difference between 9 and 30 days, with all Polish spp. emerging first. Compared to spring species, summer species and obligate univoltine summer species showed less difference in first date of emergence between Swedish and Polish populations. In a laboratory experiment *Leucorrhinia dubia* was reared from both regions from the egg to final instar larva under northern Swedish and northwestern Polish photoperiods. Swedish larvae developed faster under a northern Swedish photoperiod compared to a northwestern Polish photoperiod. However, no such difference in development was found for northwestern Polish larvae. This suggests that there are genetic differences between both populations in response to photoperiod. The results are discussed in the context of compensation of larval development of northern populations in relation to photoperiod.

### INTRODUCTION

Time of emergence and larval size at emergence are important fitness components in dragonflies (ANHOLT, 1991; DE BLOCK & STOKS, 2005; BANKS & THOMPSON, 1987; SOKOLOVSKA et al., 2000). Time of emergence is important because it must coincide with optimal conditions for dispersal, feeding and reproduction (BUTLER, 1984). In dragonflies, time of emergence varies within and among species. CORBET (1960) recognised three main life cycles among temperate species: “spring species”, “semivoltine summer species” and “univoltine summer species”. Spring species overwinter in the last instar, while summer

species may overwinter in any instar or in the egg stage. The variation within species is probably attributed to environmental conditions such as temperature, food and length of season that might differ between populations.

In general, populations that live at higher latitudes take longer time to complete the life cycle (CORBET, 2003; CORBET et al., 2005). This is believed to be an effect of low temperature and low prey availability (CORBET, 1980). However, in many species this variation is not as pronounced as expected despite differences in latitude, suggesting that some compensating mechanism is operating (CORBET, 2003). The compensating mechanism might be mediated by photoperiod such that odonates adjust their development relative to the photoperiod experienced at the latitude where the population lives. As a consequence, an odonate species living at high latitudes might be able to emerge earlier than it would have in the absence of these photoperiod cues. CORBET (2003) provided data on the flying season of odonates from western Canada and found that some species emerge at the same time in the south as in the north. This pattern of similar emergence time at different latitudes is to be expected if the photoperiodic compensation mechanism occurs. Such photoperiodic compensation occurs in other insects (MASAKI, 1978; NYLIN et al., 1993), but few studies have shown this in dragonflies at the level of populations (ŚNIEGULA & JOHANSSON, 2010). We should expect this kind of compensation because dragonflies do react to time stress mediated through photoperiod by speeding up their development (e.g. JOHANSSON & ROWE, 1999; ŚNIEGULA & JOHANSSON, 2010).

In this study we compare the emergence patterns of northern and southern populations of various species by presenting data from northern Sweden and north-western Poland, two regions that are separated by a distance of about 1100 km, with a difference of ca. 10° in latitude. In addition, in a laboratory experiment on *Leucorrhinia dubia* larvae from northern Sweden and northwest Poland, we compare development of specimens reared at northern Swedish and northwestern Polish photoperiods.

Our data set can also be used to evaluate future shifts in emergence times of odonates from natural habitats. Global warming is predicted to increase annual mean temperature during the 21<sup>st</sup> century (IPCC, 2001). Recent studies show that some odonates have expanded their ranges northward (OTT, 2001; HICKLING et al., 2005). Global warming can also have an effect on insects' time of emergence (HOGG & WILLIAMS, 1996; HARPER & PECKARSKY, 2006; HASSALL et al., 2007). Laboratory experiments show that higher temperature speeds up development in odonates (PICKUP & THOMPSON, 1990; KRISNARAJ & PRITCHARD, 1995) and two studies have shown that time of emergence is influenced by global warming in odonates (HASSALL et al., 2007; DINGEMANSE & KALKMAN, 2008). Here emergence data are provided that can be used in future comparative studies on the effect of global warming.

## MATERIAL AND METHODS

**EMERGENCE PATTERNS.** — To estimate first and last emergence dates of dragonfly species from northern Sweden, we collected exuviae from 21 lakes and ponds during 1999–2001. All lakes are within 10 km of the city of Umeå (63°50' N, 20°15' E). The lakes were visited 2–3 times per week and each was sampled in one year only. Exuviae were sampled along a 16 m stretch of shore from the beginning to the end of the emergence period. The sampled shorelines were representative of a typical odonate habitat and were chosen to be as similar as possible among lakes.

To compare emergence patterns of species' northern and southern populations, we also collected exuviae in northwestern Poland. Suitable odonate habitats in 17 waterbodies within 23 km of the town of Borne Sulinowo (53°34' N, 16°32' E) were sampled in 2005 and 2006. The shoreline stretch sampled varied among the waterbodies. Hence, exuviae were collected quantitatively in Sweden but not in Poland, but we can see no obvious reason why this would bias our results. Collections of exuviae covered the whole emergence period in 2005, but in 2006 we missed the last 2–3 weeks of emergence for late emerging species such as *Sympetrum*. We therefore only compare first date of emergence between the two regions. More species were collected in Poland than in Sweden, but only emergence data for species found in both regions are presented. Comparisons between the two regions are based on the difference of first emergence date for each species irrespective of sex. Admittedly the weather condition between the Swedish and the Polish year of sampling might have differed. However, even if we had sampled the same years in both countries we might have encountered different conditions in each country compared to the average. By sampling more than one year we avoided this problem somewhat.

**LABORATORY EXPERIMENT.** — To examine if dragonflies are able to speed up their development and compensate for the shorter season in the north we set up a laboratory experiment to study larval rate of development in the semi- or partivoltine spring species, *Leucorrhinia dubia* (JOHANSSON, 2000; NORLING, 1984a). The experiment was run in climate rooms at Umeå University. Eggs from 14 females were collected on May 28 and 29, 2007 from a small, fishless, acidic pond near Borne Sulinowo, Poland (locality 3, ŚNIEGULA, 2006). Eggs from 9 females were collected on June 28 from two medium size fishless ponds near Umeå. Females were caught while copulating and induced to lay eggs by dipping the tips of their abdomens into water-filled plastic containers. All egg clutches contained more than 20 eggs. On May 29, samples collected in Poland were sent by regular post to Umeå. To simulate similar handling, the eggs collected in Sweden were kept dark at room temperature for 4 days, which corresponds to the shipping time of the Polish eggs.

On arrival from Poland, the egg clutch from each female was divided into two groups; each was placed in white plastic containers 10×10×6 cm high, filled with tap water. The containers and eggs were placed in two walk-in climate rooms at 22°C, one half of each egg clutch in each climate room. The light regime, from two fluorescent tubes, mimicked natural light on June 1 (excluding Civil Twilight conditions). In one room the light was set to simulate the Polish condition (light went on at 02:32 and off at 19:12) and in the other room to simulate northern Swedish conditions (light went on at 00:41 and off at 20:35). After four days in the dark the Swedish eggs (collected June 28) from each female were treated identically to the Polish samples. To simulate the natural progression of light conditions, the photoperiod regimes were changed once a week, following natural L:D conditions at each geographic locality. To minimize the environmental effects of the rooms, the containers were shifted between rooms once a month.

The eggs from southern and northern clutches started to hatch after about 2 weeks and the hatching was synchronized both within and between clutches. When the larvae entered instar 2–3, each group of samples was separated into two replicates (2×5 larvae) and these were used for rearing. The rest of the larvae were discarded.

During the first several instars, larvae were fed brine shrimp twice a day. After about a month, they were fed a mixture of brine shrimp and *Daphnia pulex* once a day. All larvae received the same food

ratio. The brine shrimp and *D. pulex* came from laboratory cultures.

To imitate natural winter conditions and to ensure that *L. dubia* larvae experienced a diapause initiated by photoperiod (see NORLING, 1984a), on October 14 all larvae were moved into a refrigerated room and held in constant darkness at 4°C. The larvae were kept unfed in dark conditions until November 13, when they were moved back to climate rooms. From this time the photoperiod regimes was set to simulate April 10: Polish L:D; 04:07 – 17:45 and Swedish L:D 03:28 – 17:55. The experiment was terminated on February 27, 2008, which corresponds a photoperiod date of July 15.

To get an estimate of development for the two populations under the different photoperiod regimes, larval head widths were measured 4 times: September 5, 2007, October 14, 2007, December 13, 2007 and February 27, 2008. The four dates correspond to the following photoperiod dates: September 5, October 14, May 9 and July 24. For the first, second and fourth measurement, first the largest individual for each female genotype was taken, preserved in 70 % ethanol and then measured. Due to the limited number of live larvae left in replicates before the third measurement (December 13, 2007), the largest live individuals for each female genotype were measured instead. Larval size was estimated as head width (distance between outer margin of eyes) using a microscope with an ocular scale. Larvae from each female within photoperiod and country did not differ very much within and among containers. Using a mean value of head width instead of taking the measurement of the largest individual did not change the main results. There was some mortality during the experiment, resulting in 5 and 6 larvae from each Swedish female remaining and 7 and 11 for the Polish ones.

Development of *L. dubia* larvae was analyzed with a repeated measures ANOVA. Head width was used as the dependent and photoperiod as the independent variable and time (date of size estimate) as repeated measures. Because the growth of the Polish and Swedish larvae did not begin at the same time a separate repeated measures analysis was undertaken for each country. Comparisons between countries were done by visual inspection of error bars. The date of each measurement was entered as a categorical variable. The experiment lasted for 196 and 169 days for Polish and Swedish larvae respectively, but since we shortened the winter period by several months the corresponding photoperiod days are 420 and 393 days respectively. We will use these days in our graphs although the real length of development was shorter. The logic behind this is that larvae do grow and develop very little during the winter period.

## RESULTS

### EMERGENCE PATTERNS

Exuviae of 17 species were collected in Sweden. Eight species were collected in 10 or more lakes and we collected more than 100 exuviae of nine species. The overlap between first and last emergence was quite high among species (Fig. 1). We suggest that the overlap in emergence times is due to the short season at this latitude. For most species the emergence data should be reliable, but for those species with very few exuviae (*Coenagrion armatum*, *Aeshna subarctica*, *Sympetrum danae*), data should be interpreted with caution.

Fourteen of the 17 species found in the Umeå region were also collected in Poland (Tab. I). The five species to emerge first in Poland were *Coenagrion hastulatum*, *Cordulia aenea*, *Leucorrhinia rubicunda*, *L. dubia*, and *Libellula quadrimaculata*. These species were also among the first to emerge at Umeå. Similarly, four of the last five species to emerge were the same at Umeå and in Poland: *Sympetrum danae*, *Lestes sponsa*, *Aeshna grandis*, and *A. subarctica*.

The mean difference among species in first date at emergence between the two regions was 17.5 ( $\pm 2.1$  S.E.) days and the range is 8-27 days. Species that emerged late in both regions were those which differed the least in difference in emergence time between the regions. For example, the mean difference between species emerging in May in Poland and their corresponding Umeå populations is 24.4 days, while the difference for species emerging in June and July in Poland and their corresponding Umeå population is 10.6 days. This difference was statistically significant (t-test:  $t = 8.74$ ,  $df = 12$ ,  $p < 0.001$ ).

LABORATORY EXPERIMENT

Polish larvae of *Leucorrhinia dubia* had reached a head width of 5.1 mm at the end of the experiment; this width corresponds to that of the final instar (Fig. 2). Larvae tended to develop faster in the northern Swedish photoperiod but light regime did not significantly affect larval size. At the end of the experiment there was no difference in the size of larvae growing in the two light regimes (Tab. II); an F-test showed this ( $F_{1,16} = 0.002$ ,  $P = 0.97$ ). Swedish larvae in the northern

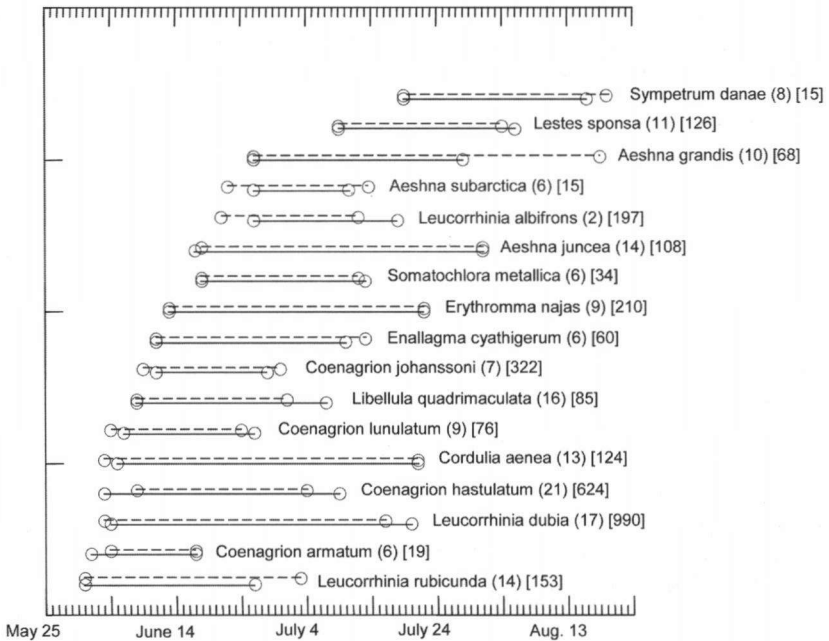


Fig. 1. First and last emergence dates for 17 species of Odonata in northern Sweden (Umeå). Solid lines are males and hatched lines are females. Numbers within parenthesis indicate the number of lakes at which each species was collected; numbers within square brackets are the number of exuviae collected. Data from 1999-2001.

Swedish photoperiod also reached the final instar at the termination of the experiment, while Swedish larvae in the Polish photoperiod had developed into a size corresponding to the penultimate instar (Fig. 2). Hence, in contrast to Polish larvae the northern Swedish ones did react differently to photoperiod in their development. Larvae reared in the northern Swedish light regime were much larger at the end of the experiment compared to those reared in the Polish photoperiod, suggesting that their development increased considerably in the northern Swedish light level (Fig. 2, Tab. II). The size of the northern Swedish larvae at the end of the experiment differed significantly between larvae reared in the two different light regimes ( $F_{1,8} = 30.9$ ,  $P = 0.001$ ).

## DISCUSSION

Although there was a difference in date of emergence between the two regions our data cannot falsify the hypothesis that northern species compensate for latitude by emerging earlier. The reason is that we do not know what the emergence time would have been without the potential compensation mechanism. The laboratory results from our rearing of *L. dubia* larvae do, however, show that such a compensating mechanism does occur, because the larvae from northern Sweden developed faster under the northern Swedish photoperiod than those of Polish origin under the same light conditions. In addition, laboratory data are also available for three *Lestes* species and do support the hypothesis that larvae acceler-

Table I

First day of emergence of dragonflies from the Borne Sulinowo region in Poland, and the difference in mean date of first emergence between populations in northwestern Poland and northern Sweden. Symbols within parenthesis denote which sex emerged first

Species	Date	Difference in emergence between Polish and northern Swedish populations (days)
<i>Cordulia aenea</i>	May 8, 2005 (♂ & ♀)	26
<i>Coenagrion hastulatum</i>	May 10, 2006 (♂ & ♀)	24
<i>Leucorrhinia rubicunda</i>	May 11, 2006 (♂)	20
<i>L. dubia</i>	May 12, 2006 (♀ & ♂)	20
<i>Libellula quadrimaculata</i>	May 15, 2006 (♂ & ♀)	24
<i>Erythromma najas</i>	May 17, 2006 (♂ & ♀)	27
<i>L. albifrons</i>	May 22, 2006 (♂ & ♀)	30
<i>Enallagma cyathigerum</i>	June 2, 2006 (♂ & ♀)	9
<i>Somatochlora metallica</i>	June 5, 2006 (♂)	13
<i>Aeshna subarctica</i>	June 12, 2006 (♂)	8
<i>A. grandis</i>	June 16, 2005 (♂ & ♀)	10
<i>A. juncea</i>	June 26, 2005 (♀)	9
<i>Lestes sponsa</i>	June 27, 2006 (♂ & ♀)	12
<i>Sympetrum danae</i>	July 6, 2005 (♀)	13

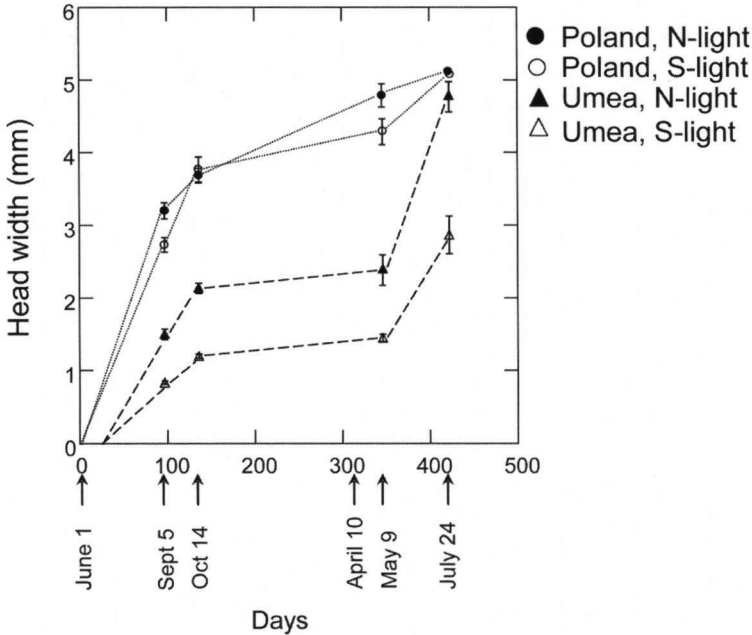


Fig. 2. Growth of *Leucorrhinia dubia* larvae from northwestern Poland (circles, Poland) and northern Sweden (triangles, Umeå) reared at two different photoperiods: northern Swedish (N-light) and northwestern Polish (S-light). Polish larvae were started from the egg stage on June 1 and Swedish larvae on June 28. The larvae were put into diapause on October 14 and out of diapause on April 10. They were measured on September 5, October 14, May 9, and July 24.

ate their development under longer photoperiods, such as those at higher latitudes (JOHANSSON & ROWE 1999; JOHANSSON et al., 2001; DE BLOCK & STOKS, 2004; ŚNIEGULA & JOHANSSON, 2010). However, data on more species are certainly needed.

The Swedish and Polish populations of *L. dubia* larvae differed in their response to photoperiod, suggesting that there is a genetic difference between the two in this response. Such differences in photoperiod response have been found in *Lestes sponsa* (ŚNIEGULA & JOHANSSON, 2010) and species of other insect groups (e.g. MASAKI, 1978; NYLIN et al., 1993; BRADSHAW & HOLZAPFEL, 2006), and are believed to be adaptive as populations at northern latitudes are time-constrained because of a short growth season. Several studies indicate that odonate larvae from different populations differ in their response to photoperiod (NORLING 1984a, b) but ours is one of the few that compares populations by simulating natural photoperiods of different latitudes (ŚNIEGULA & JOHANSSON, 2010). We hypothesise that many more examples will be found in odonates;

Table II

Results from repeated measures ANOVAs on the size of *Leucorrhinia dubia* from northwestern Poland and northern Sweden during development at different photoperiods. Light corresponds to photoperiod treatment and time to development day

POLAND				
Source	df	MS	F	P
Between subject				
Light	1,15	0.24	4.16	0.06
Within subject				
Time	3,45	5.29	107.7	<0.001
Time * Light	3,45	0.11	2.25	0.10
SWEDEN				
Between subject				
Light	1,4	1.65	58.4	0.002
Within subject				
Time	3,12	3.21	199.3	<0.001
Time * Light	3,12	0.05	3.06	0.07

indeed, there are several potential comparative studies that would be informative with respect to photoperiod. For example, comparative genetic studies of different latitude populations would extend our knowledge of the genetic basis of photoperiodic response within and between populations and species (BRADSHAW & HOLZAPFEL, 2007).

We should expect the least difference in emergence date between summer species because these species spend the winter in the last three or four instars and therefore have a greater potential to adjust development compared to species in the other two categories.

We found some support for this pattern. In our study, the aeshnids and *Enallagma cyathigerum*, which have been categorised as summer species (CORBET, 1960: 143), showed the least difference with respect to the first day of emergence between the two regions. Spring species spend the winter in the last instar and can, for that reason, not speed up their development as much as summer species. Examples of typical spring species in our study are the *Leucorrhinia* species, *Cordulia aenea* and *Libellula quadrimaculata*, all exhibiting the largest difference in first date of emergence between populations. Surprisingly, the obligate univoltine species, *L. sponsa* and *Sympetrum danae*, show a small difference between the regions with respect to first day of emergence. These species overwinter in the egg stage and, therefore, can adjust development time considerably during the spring and early summer. The fact that summer species and obligate univoltine species show the least difference between the regions lends some support to the hypothesis that the rate of larval development is positively correlated with photoperiod (CORBET, 2003; ŚNIEGULA & JOHANSSON, 2010).

We hope that our data from northern Sweden can be used to compare emergence patterns in future studies that evaluate the effect of global warming. Emerging at the right time is important for aquatic insects because terrestrial environmental conditions such as prey availability, mating opportunity and ambient flying temperature must be optimal for a sustainable population.



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