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No trade-off between the size and timing of emergence in the damselfly, *Calopteryx virgo* L.

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Many species of insects have been reported to show seasonally declining size at emergence. This has been explained as an adaptive response to time constraint between size and age at maturity (emergence). We studied seasonal variation in the size of damselfly *Calopteryx virgo* L. in six different creeks in central Finland. The length of hind wings was measured for 942 males and 285 females covering the flying period from mid June to mid August. The length of the hind wings of damselflies did not decrease towards the end of flying period in any river or either sex. In light of this study, seasonal reduction of body size is not a general phenomenon among odonates contrary to common understanding.

Introduction

Many insects with complex life cycles show considerable variation in size at metamorphosis and timing of development. It has been stated that the size of emerging adult insects often decreases over the yearly flight period (*see* review in Atkinson 1994). Reduction in size towards the end of a season has been found in many species of arthropods such as copepods, cladocerans, amphipods and many insect families (*see* review Atkinson 1994). For example, the weight of some aquatic beetles may be reduced by 50% during the summer (Sweeney & Vannote 1978).

There are several explanations for a decrease in body size as the breeding season progresses. The phenomenon has been explained by within-cohort competition (Atkinson & Begon 1988), diet (Palmer 1984) and population density (Peters & Barbosa 1977). Variation in temperature has also been proposed to explain this pattern, when increased metabolic cost at higher water temperatures results in a decreased size at metamorphosis as the water temperature increases (Sweeney & Vannote 1978). However, studies in fairly constant temperatures do not support this hypothesis (Forrest 1987, Sweeney *et al.* 1995).

The purpose of this study was to examine the effects of the emergence date on the size of a damsefly individual. The size of emergent odonates typically declines as the reproductive season progresses (for review, *see* Corbet 1999). During the course of ontogeny, odonates transform from aquatic larvae into terrestrial adults. An ontogenic niche shift theory (e.g. Semlitch *et al.* 1988, Rowe & Ludwig 1991, Zonneveld 1996) proposes that such transformations are adaptive and have evolved to maximize a growth rate (size) to mortality rate ratio. Individuals should, therefore, switch from one niche to the other at an optimal size or state (Rowe & Ludwig 1991).

The damselfly *Calopteryx virgo* L. is a conspicuous zygopteran which occurs in streams and rivers with clean, rather rapidly-flowing water. In the flowing water, the larval growth period lasts from two to three years (Valle 1952). In Finland, emergence is restricted to warmer summer months: June to August (Valle 1952). In streams, *Calopteryx* males defend small isolated patches of freshwater plants into which female oviposit (e.g. Pajunen 1966). Male territory ownership is settled by highly escalated contests of vigorous and energetic flight manoeuvres as in other *Caloperyx* species (e.g. Plaistow & Siva-Jothy 1996). Larger males are more likely to be territory holders (M. J. Rantala *et al.* unpubl. data) and gain access to more females.

In this study, we examined whether the size of an individual decreased with the emergence date in the male and female *C. virgo*. Further, we conducted a meta-analysis of the seasonal decline in six different creeks within our study area in central Finland.

Material and methods

The study was carried out in June–August 1997 in six creeks in the surroundings of Jyväskylä (62°16´N, 25°30´W) in central Finland. Damselflies were captured with a butterfly net. As a measurement of size, we used the length of hind wing which is commonly used as an index of the individual size (*see* Corbet 1999). The lengths of both hind wings were measured with a digital calliper to the nearest 0.01 mm. Individuals with damaged wings were discarded. Recently emerged damselflies were not captured because they were too delicate to handle. After measurements, each individual was marked with a three-digit code on its hind wing with a waterproof pen, to prevent measuring the same individuals again. Measurements were made daily during the flying season. A total of 1227 individuals were caught, marked and released.

Repeatability of the length measurements of a hind wing was assessed by measuring 15 *C. virgo* individuals twice in the laboratory by all five persons, who were responsible for the field measurements. Within-person measurements of the left hind wing were repeatable ($p < 0.05$; correlation coefficients ranging from 0.80 to 0.95). Systematic differences between persons were removed by correcting with the deviance from common mean. Thus, discrepancies arising from personal differences were eliminated from the data. To estimate the overall validity of the seasonal decline in size, we employed meta-analysis following the protocol used by Møller and Alatalo (1999). In the meta-analysis, we used our own data from all six populations in an overall analysis, using each populations as a single replicate.

Results

The mean length of a hind wing in males was 30.6 ± 1.03 mm, $n = 942$, and it varied from 26.2 to 34.6 mm (Fig. 1). The corresponding lengths for females were 33.5 ± 1.16 mm, $n = 285$, with range of 28.5 to 36.4 mm (Fig. 2). The lengths of hind wings of damselflies did not decrease to-

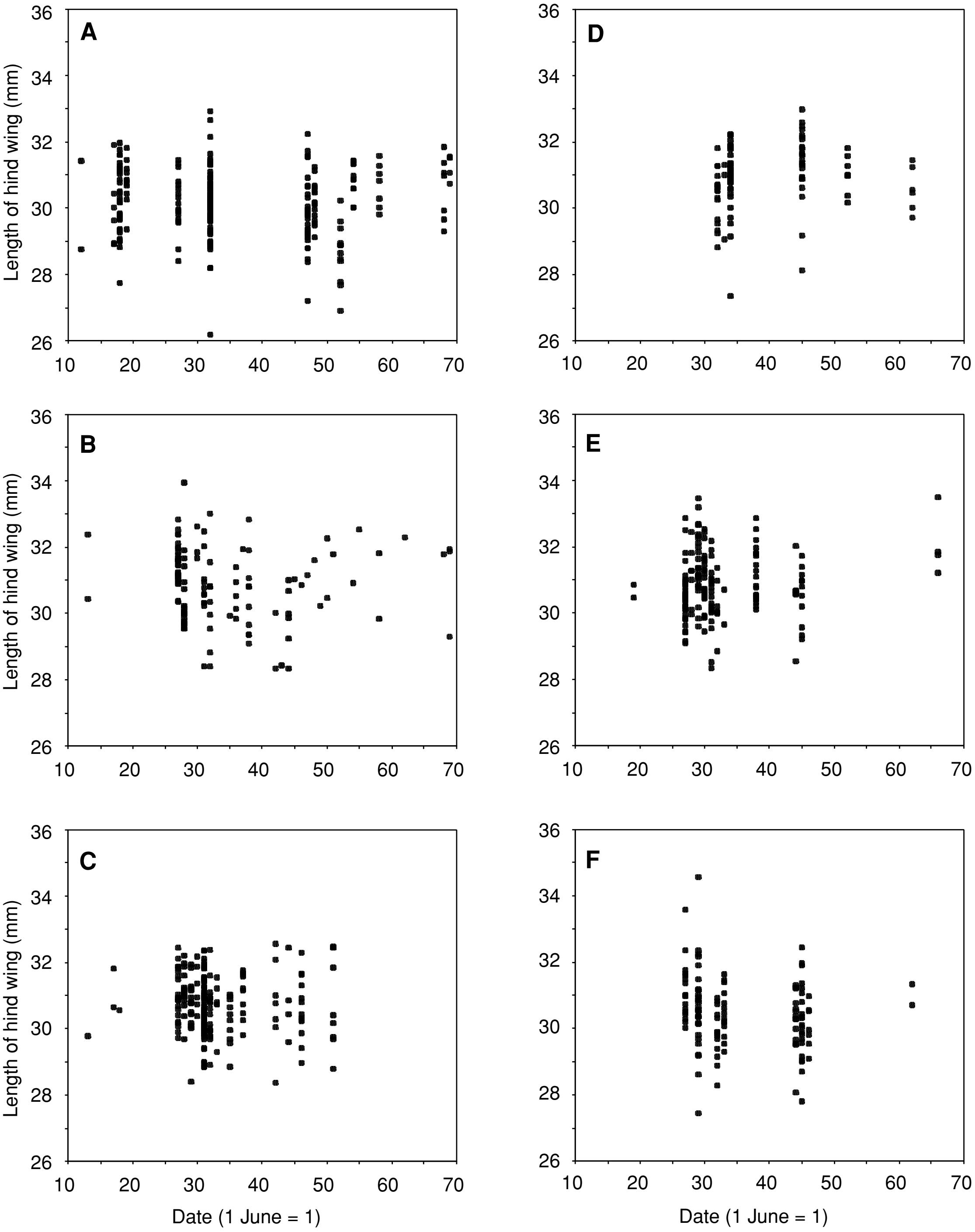

Fig. 1. The length of male *C. virgo* hind wings plotted against time through the emergence period. The day of capture was calculated by giving each date a numerical value (Day 1 = 1 June). Rivers: (**A**) Neulajoki, (**B**) Mustajoki, (**C**) Syväoja, (**D**) Uhkujoki, (**E**) Vasarajoki, and (**F**) Kalmujoki.

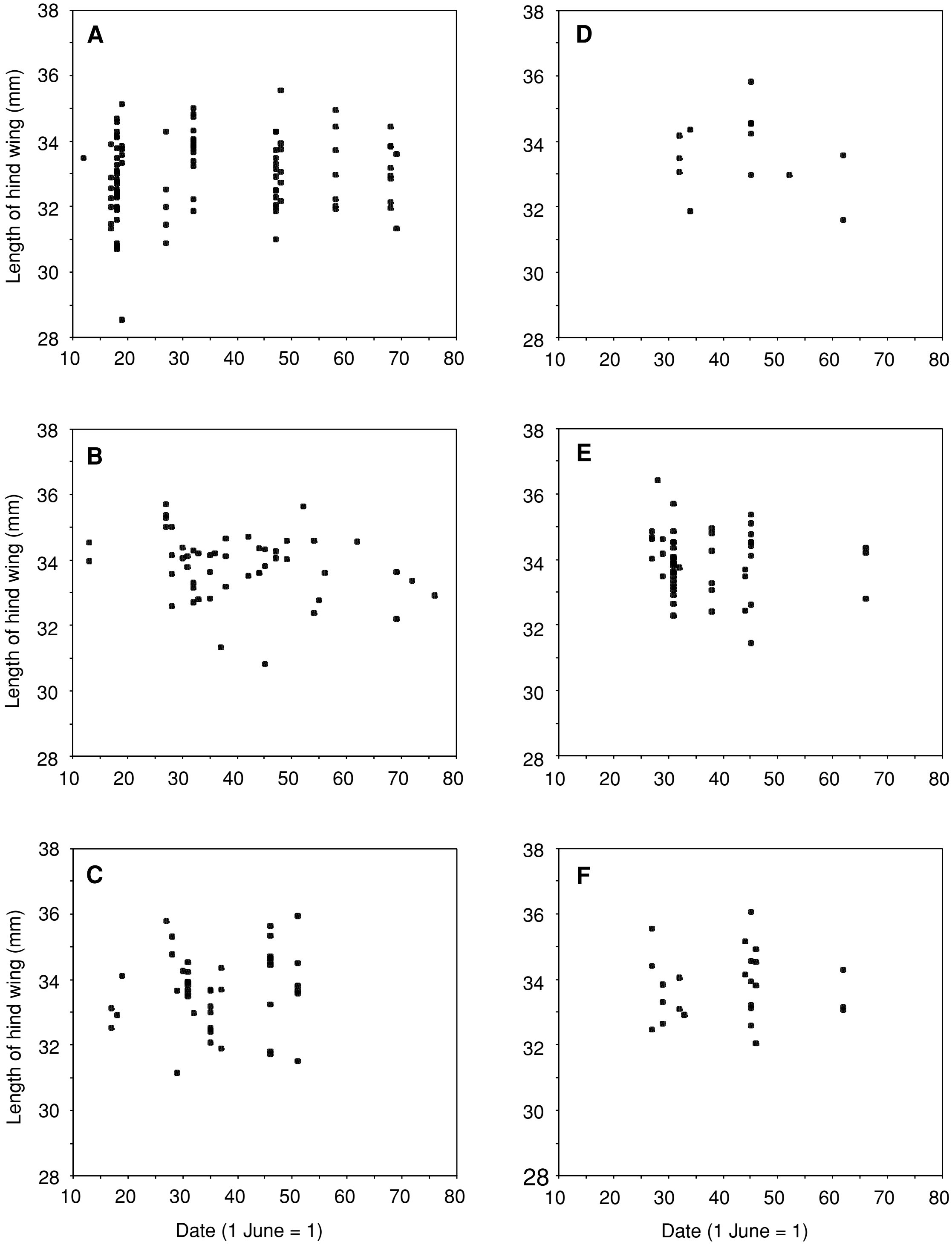

Fig. 2. The length of female *C. virgo* hind wings plotted against time through the emergence period. The day of capture was calculated by giving each date a numerical value (Day 1= 1 June). Rivers: (**A**) Neulajoki, (**B**) Mustajoki, (**C**) Syväoja, (**D**) Uhkujoki, (**E**) Vasarajoki, and (**F**) Kalmujoki.

wards the end of the flying period in any of the rivers or either sex (Table 1). We employed a meta-analysis to estimate the overall strength of a seasonal decline in size and a weighted mean correlation coefficient for males $r = -0.010$ (95% CI = –0.074 to 0.055, $n = 6$), $p = 0.38$, and females $r = -0.003$ (95% CI = –0.12 to 0.12, $n = 6$), $p = 0.48$, respectively. The mean length of a hind wing varied between populations in males (ANOVA, $F_{5,936} = 17.67$, $p < 0.001$) and females ($F_{6,279} = 7.80$, $p < 0.001$).

Discussion

We studied here the seasonal changes in the size of emergence in the damselfly *C. virgo*. We found that the size of emerged individuals did not decline towards the end of the emergence period. Thus, according to our results, it seems that seasonal reduction in size is not a general phenomenon in all dragonfly species. In contrast to our results, Plaistow and Siva-Jothy (1999) found that body size of closely related damselfly, *Calopteryx splendens xanhostoma*, declined throughout the season in southern France. For measuring the size, they used wing length and amount of fat reserves (Plaistow & Siva-Jothy 1999).

According to the time constraints hypothesis, timing of metamorphosis of insects must balance the benefits of the extended larval growth to maximize size and fecundity with the cost of delaying reproduction or increased risks of predation (Semlitch *et al.* 1988, Rowe & Ludwig 1991, Zonneveld 1996). In the studies with *Lestes congener*, Johansson and Rowe (1999) experimentally altered individual perception of the proximity to a time constraint. They found that time-constrained larvae accelerated the development rate, and thereby, matured significantly earlier and at a smaller size. On the other hand, dragonflies born late in the season may have accelerated development rates for a variety of reasons other than the response to an impending time constraint. For example, food supply, predation risk and maternally provided nutrition may all differ between early- and late-born individuals. Differences between the studies might result from species differences in possible costs and benefits in the decisions to emerge. Those differences may arise from differences in life history traits or ecological causes and consequences of ontogenetic niche shifts.

The larval period of *C. virgo* in northern latitudes is about three years long (semivoltine) compared to one-year-long (univoltine) larval life of *C. splendens xanhostoma* in southern France (e.g. Valle 1952, Corbet 1999). It is possible that, with semivoltine larval life, there is a choice between emerging late as a small one and spending another winter under the ice. On the other hand, there may also be other environmental variables which may affect the underlying seasonal decline in an opposite direction causing a non-significant pattern.

Ontogenetic niche shifts are believed to have evolved as an adaptation aimed at maximizing growth rates while minimizing mortality risks (Werner & Gillliam 1984, Werner 1986). We found in *C. virgo* that the mortality rate of adults was highest during the beginning of the flying season and decreased towards its end (T. Toivanen, M. J. Rantala, & J. Suhonen unpubl.). Thus, it is possible that this high mortality rate reduces benefits of early emergence and may affect the

Table 1. Estimated seasonal decline in six populations of *Calopteryx virgo* in central Finland. To estimate seasonal decline for male and females Pearson's correlation coefficient (*r*) between length of hind wing and date of capture was calculated. *N* is the sample size in each population.

River	*r*	*P*	*N*
Male			
Neulajoki	–0.01	0.90	240
Mustajoki	–0.06	0.50	115
Syväoja	–0.06	0.42	208
Uhkujoki	0.14	0.18	90
Vasarajoki	0.12	0.11	170
Kalmujoki	–0.17	0.06	119
Female			
Neulajoki	0.13	0.19	101
Mustajoki	–0.26	0.07	50
Syväoja	0.13	0.39	46
Uhkujoki	–0.18	0.55	13
Vasarajoki	–0.10	0.47	51
Kalmujoki	0.03	0.91	24

optimal developmental rate, which might explain why we did not find seasonal reduction in size at emergence in *C. virgo*.

Forsyth and Montgomery (1987) stated that the size at emergence is fixed in the damselfly *C. maculata* (Beauvois). This is the opposite to what we found in *C. virgo*. Instead, we found a wide variation in the size of individuals.

In conclusion, our data show a considerable variation in the size at metamorphosis, but the variation was not dependent on the timing of emergence. In the light of these results and contrary to previous suggestions (*see* Corbet 1999), a seasonal reduction in body size is not a general phenomenon among odonates.

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