

SEX RATIOS AT EMERGENCE IN POPULATIONS OF SOME CENTRAL EUROPEAN GOMPHIDAE SPECIES (ANISOPTERA)

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At emergence (F-0) a significant bias for ♀♀ was observed within the Moravian (Czech Republic) populations of *Gomphus flavipes* (Charp.), *G. vulgatissimus* (L.) and *Ophiogomphus cecilia* (Fourcroy). ♂♂ represented 45.6% of all specimens (43.5% in the first and 46.4% in the second research year). The results of the χ^2 test supported the ♀-biased sex ratio in populations of all 3 spp. The sex ratio in populations varied significantly in time during the emergence season, caused by the fact that all 3 spp. demonstrated a significant protandric trend. The greatest changes in sex ratio during the emergence season were demonstrated by *G. flavipes* (coefficient value -0.007542); the smallest were recorded in *G. vulgatissimus* (CV -0.008617). Environmental impact did not prove to act be a factor which has an effect on the sex ratio of species with phenotypical determination of sex.

INTRODUCTION

The sex ratio is the ratio of males to females in a population. The primary sex ratio is the ratio in the egg phase, the secondary is at the time of hatching, the tertiary is of immature adults and the quaternary is of breeding adults (PIANKA, 2000). Sex determination in odonates is under genetic control, sex being determined by sex chromosomes (KIAUTA, 1969). Consequently, the theory predicts equal numbers of males and females (HARDY, 2002), but biased sex ratios are relatively common in dragonfly populations (CORDERO RIVERA & STOKS, 2008). The sex ratio at emergence should be more female-biased in territorial than in non-territorial species (CROWLEY & JOHANSSON, 2002). A comprehensive

review of sex ratio at emergence in odonates (CORBET & HOESS, 1998) shows a slightly male biased sex ratio in Zygoptera and a slightly female biased one in Anisoptera.

The question remains whether the difference in sex ratio reflects a real difference in the proportion of males to females or rather an artificially observed and incorrectly assessed phenomenon. The choice of method often plays an important role in the results regarding the sex ratio in dragonfly populations. Several mark recapture studies have concluded that there is a male biased sex ratio, especially since different recapture probabilities occur in the two sexes (see CORDERO RIVERA & STOKS, 2008). Female dragonflies are more 'hidden' than males; however, statistical methods, robust against variant recapture probabilities, have yielded data supporting the male-biased sex ratios in mature Zygoptera populations (ANHOLT et al., 2001; STOKS, 2001a). Several hypotheses explaining the causes for male-biased sex ratio in dragonflies have been proposed, based on observations of just a few species of Zygoptera (ANHOLT et al., 2001; STOKS, 2001a, b). Analyses of the sex ratio in numerous groups of dragonflies, especially from the Anisoptera, are not available or show inconclusive results.

The objective of this work was to assess the sex ratios at emergence, from the larval stage to the adult stage, in populations of Central European species of Gomphidae, based on the high number of collected exuviae, and to analyse trends in the sex ratio during the season and in different types of environment.

METHODS

STUDY SITE. — The study site is situated in the south-east of Moravia in the Czech Republic. From the biogeographical point of view, it is a promontory of the Pannonia province. Four localities were studied on the Morava river between Uherské Hradiště and Hodonín (Loc1: 49°1'51"N, 17°23'35"E; Loc2: 49°0'42"N, 17°23'53"E; Loc3: 48°52'50"N, 17°12'20"E; Loc4: 48°55'11"N, 17°16'30"E; elev. 165-170 m). The individual sites varied significantly due to the anthropogenic impact, from straightened and regulated parts of the river to natural meandering stretches untouched by humans. Three 100 metre stretches were observed (altogether 1200 metres) at each locality. Exuviae were collected up to 150 cm from the bank line. Data collections took place over 2 years; from the third week in May to the end of June 2007 and from the second week in May to the first week in July 2008 (38 research days).

The works of GERKEN & STERNBERG (1999) and HEIDEMANN & SEIDENBUSCH (1993) were used to determine the species and sex. A sex ratio was calculated for each species and tested for expected 'equal ratio' using the χ^2 test. Furthermore, differences in sex ratios over time and as influenced by other factors were evaluated using a generalized linear model (GLM) for binomial response (quasibinomial respectively due to overdispersion). The terms were added sequentially, evaluated by Mallows' Cp statistic (closely related to AIC) and tested by F-test (FARAWAY, 2005). The model was examined for each sex ratio weighted by number of individuals. The analysis was carried out using R software (R DEVELOPMENT CORE TEAM, 2007). The response variable (sex ratio) was weighed by the number of exuviae, as usual.

RESULTS

In 2007/2008, 6897 exuviae of four Gomphidae species were collected: *Gomphus vulgatissimus* (4064 specimens), *G. flavipes* (1181 specimens), *Ophiogomphus cecilia* (1645 specimens) and *Onychogomphus forcipatus* (only 7 specimens; evaluated no further due to the low number).

Of the 6890 exuviae of the three analysed species, 3122 were males and 3722 were females. Damaged exuviae that could not be sexed were excluded (46 specimens). Males represented 45.6% of all specimens (43.5% in 2007 and in 46.4% in 2008). Females were dominant in all three species and also in both years. The results of the χ^2 test supported the female-biased sex ratio in populations of all three species (Tab. I, Fig. 1).

Table I
Sex ratio of the three gomphids calculated for both years and sites in total and the p-value of χ^2 test for an equal proportion of males and females

Species	Male	Female	Male (%)	p
<i>Gomphus flavipes</i>	550	619	47.05	0.0436
<i>Gomphus vulgatissimus</i>	1833	2205	46.05	<0.0001
<i>Ophiogomphus cecilia</i>	739	898	45.05	<0.0001

Despite the main analysis is based on GLM, we can see five of the twelve data sets revealed a significant difference from a 1:1 sex ratio (with majority of females) whereas seven did not when the data was broken down into individual sites (Tab. II).

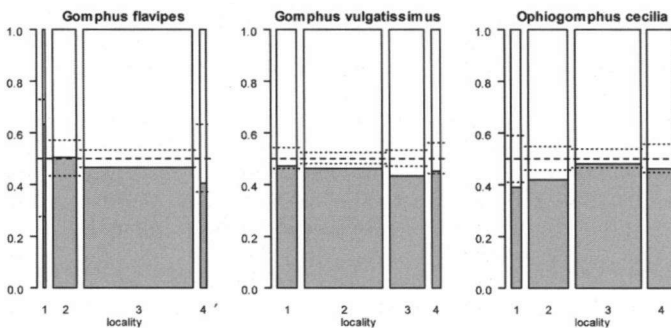


Fig. 1. Proportion of males (gray) and females (white) for the samples from the sites (1-4; severely degraded to natural habitat) with respect to number of specimens (different bar width) in comparison with equal proportion (dashed line) and 95 % confidence intervals for sex ratio = 0.5 (dotted lines).

Table II

Sex ratio of three gomphids in each of the four localities. Values in bold indicate significant difference from a 1:1 sex ratio

Locality	Species	Male	Female	Male (%)	p-value χ^2 test
1	<i>Gomphus flavipes</i>	12	7	63.2	0.251
	<i>Gomphus vulgatissimus</i>	270	303	47.1	0.168
	<i>Ophiogomphus cecilia</i>	46	72	39.0	0.017
2	<i>Gomphus flavipes</i>	100	99	50.3	0.943
	<i>Gomphus vulgatissimus</i>	1020	1198	46.0	<0.001
	<i>Ophiogomphus cecilia</i>	190	266	41.7	<0.001
3	<i>Gomphus flavipes</i>	415	479	46.4	0.032
	<i>Gomphus vulgatissimus</i>	424	559	43.1	<0.001
	<i>Ophiogomphus cecilia</i>	360	392	47.9	0.243
4	<i>Gomphus flavipes</i>	23	34	40.4	0.145
	<i>Gomphus vulgatissimus</i>	119	145	45.1	0.111
	<i>Ophiogomphus cecilia</i>	143	168	46.0	0.156

The differences in sex ratios in individual species and dates of collections were demonstrated by the analysis of deviance. Different localities did not indicate any differences in sex ratios despite significant variation in the character of the environments and the levels of anthropogenic influence (Tab. III).

Using Mallows' Cp statistics for GLM diagnostics of explanatory variable importance we found 'time×species' interaction as the best variable to explain the trends in the sex ratio (Tab. III). All regression coefficient values were negative (see Fig 2) which means that sex ratio is decreasing during emergence season. However, subsequently their proportion in the population declined and at the last stage of emergence time it was females that were in the majority ($F=3.4698$, $p=0.0193$). This protandric trend was observed in all three species (Fig. 2). The greatest changes in sex ratio during the emergence season were demonstrated by *G. flavipes* (coefficient value -0.007542); the smallest were recorded in *G. vulgatissimus* (coefficient value -0.008617).

Table III

Comparison of Mallows' Cp statistics for GLM models using different factors

	Df	Deviance Res.	Df	Resid. Dev.	Cp
NULL			95	154.95	158.03
habitat	1	0.111	94	154.84	161.00
year	1	4.353	94	150.50	156.58
species	2	1.194	93	153.76	163.03
time	1	8.635	94	146.32	152.13
time×species	3	14.782	92	140.17	151.53

DISCUSSION

The collection of exuviae has proved to be the optimal method for determining the sex ratio in a population at emergence. When observing imagos, the sex ratio is often misrepresented due to the fact that low numbers of females in breeding habitats are sampling artefacts caused by sex-specific differences in patterns of habitat use (e.g. ANHOLT, 1997; CORDOBA-AGUILAR, 1993; FOSTER & SOLUK, 2006; STOKS, 2001a, 2001b). For instance, in a complex database, DOLNÝ et al. (2008) have drawn from the available data, it is evident that male gomphid imagos were clearly more numerous than females. The real sex ratio in adults at emergence is quite different according to 'the final instar (F-0)' observation. Our results have shown that the real sex ratio is female biased in all three of the observed Gomphidae species. Having also studied exuviae, MÜLLER (1995), stated a slight prevalence of females in *G. flavipes* and *G. vulgatissimus*. A study of *Asiagomphus pryeri*, another representative of the family, demonstrated significantly fewer males than females at emergence. Sex ratios in the three years of this study were 38.8% to 41.5% males (AOKI, 1999). Similar findings were recorded in the representatives of other Anisoptera families. KÉRY & JULLER-AT (2004), based on the mark-recapture method, described a balanced sex ratio for *Orthetrum coerulescens* with a slight female bias (statistically inconclusive, perhaps caused by a small number of marked specimens). The predominance of females over males was also confirmed by BEUTLER (1986), who stated that in Anisoptera almost always emerge more females than males. The situation is usually entirely different in the Zygoptera. Numerous studies concerned with the sex ratio of several species of Zygoptera have yielded data demonstrating a significant prevalence of males (ANHOLT, 1997; ANHOLT et al., 2001; STOKS, 2001a, 2001b). Whereas some studies on Zygoptera have suggested that the sex

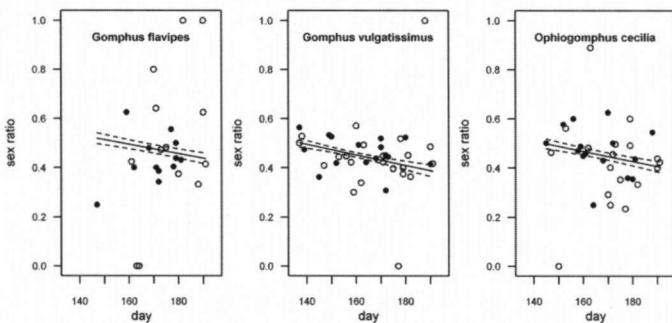


Fig. 2. Changes in proportional representation of males in populations during the season (dark colour is used for the higher statistical-weight values; — empty circles: ratio based on less than 30 individuals).

ratio does not significantly differ from 1:1 (e.g. BENNETT & MILL, 1995), other workers have found that the sex ratio may differ from 1:1 in one researched species but not in the other analysed species (PURSE & THOMPSON, 2003).

There are different opinions regarding the reasons, purposes and advantages of unbalanced sex ratios in dragonflies. There are several evolutionary ecological hypotheses explaining biased sex ratio in dragonflies at emergence and these focus on the larval stage as well as on adults. LAWTON (1972) pointed out that higher mortality in males during the larval stage may be a reason for the unbalanced sex ratio. According to this theory, the subsequent higher numbers of females should act as an advantage during selection. Nevertheless, he does not mention what may be the cause for the higher mortality in males. However, a recalculation of Lawton's data, separating larvae from exuviae, revealed that no difference from 1:1 at emergence was found. There was no significant difference in the proportions of larvae or exuviae (BENNETT & MILL, 1993). BAKER et al. (1992) stated that male and female larvae can differ in activity level, though little is known about this. Alternative reasoning for the biased sex ratio at emergence highlights the importance of the adult stage, and especially immature adults. It is thought that, from the evolutionary point of view, one of the sexes should incur higher losses during the maturation period or asymmetric selection pressure on one of the sexes (which is the case in the Zygoptera).

The higher mortality rate in male imagos may be caused by different life histories of each sex (CROWLEY, 2000; CROWLEY & JOHANSSON, 2002). It is to a certain extent determined by the length of the maturation period. The length of maturation period is significantly longer in females of primarily non-territorial species. This relates to a higher level of foraging and dispersal rates in immature females (STOKS, 2001b). CORBET (1999) also pointed out that the highest natal dispersal is connected with immature stages. Due to the fact that higher dispersal rates as well as foraging rates generally correlate with higher risks of predation (WERNER & ANHOLT, 1993), it may be assumed that immature individuals, in this particular case females, will have higher mortality rates. Different life histories may result in different preferences of females for alternative habitats. This bias has been attributed, in particular, to the females of non-territorial species using alternative habitats to avoid male harassment (FOSTER & SOLUK, 2006; UTZERI et al., 1988).

It was remarkable to observe that the sex ratio in the gomphid populations changed with time, therefore it changes significantly during the emergence season. Males emerged earlier than females. However, the situation gradually changed to the point of females being prevalent (Fig. 2). This protandric trend in Gomphidae was also observed by SUHLING & MÜLLER (1996) and it was observed during one season by AOKI (1999). Very few studies have attempted to explain the causes and consequences of this phenomenon. INDEN-LOHMAR (1997) speculated that there is a connection between protanders and the reproductive

success of *Aeshna cyanea*, where individuals hatched earlier had a greater reproductive success. According to this hypothesis, there is a higher selection pressure for faster development on males than on females and it may correspond with the mating system of a given species (CORBET, 1999).

No significant differences were found in the sex ratios from different localities, even though there were significant differences among the environments in individual localities. Environmental impact (such as predation, resources, habitat quality) could be one of the important factors influencing the sex ratio (CORBET, 1999; CORDERO RIVERA & STOKS, 2008; STOKS, 2001b). However, the impact of the environment on the sex ratio in the studied species has, according to our results, proved to be insignificant.

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