

## Population size effects on the behaviour of *Libellula fulva* (Odonata: Libellulidae) males, a five year study

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Received: 11. September 2010 / Accepted: 11. January 2011 / Available online: 24. January 2011

**Abstract.** We tested the hypothesis that population density alters male territorial and mating behaviour of dragonflies. We predicted that males at higher densities fight more and mate less. During five years we studied two *Libellula fulva* populations along two small lowland creeks in East Hungary. Using mark-resight method we marked a total number of 1454 dragonfly males. Our results show that on the two study sites there were different population densities. At higher population densities the number of matings per male decreased, but population size had no effect on the frequency of intraspecific fights. However, the long run study showed remarkable difference from the outcome of partial analyzes which underlines the importance of studies overtaken through several years.

**Keywords:** mark-resight, population size, intraspecific fight, mating success, Odonata.

### Introduction

Higher population densities could affect mating competition for territorial species (Metcalf & Monaghan 2001). This phenomenon is frequently met in the case of dragonflies. The effect of population density on individual mating behaviour and mating success in species where male-male competition for females involves fighting, force small males at high male densities to confine their mate search to areas with low rival density (McLain & Boromisa 1987, Goldsmith & Alcock 1993) or reduces large male mating advantage due to a collapse in resource defence (McLain 1982) or increased disturbance by other males (Conner 1989). Male-male competition should also increase with density (Fincke et al. 1997), because operational sex ratio (OSR) of odonates trends to increase with population density (Fincke 1994). However, daily variation in male mating success is typically much higher than variation over the lifetime of individuals (Koenig & Albano 1987, Fincke 1988, McVey 1988).

The answer of males for increased population density could be very various (Corbet 1999), and to find the adequate response is often difficult. The biggest imperfection of studies of density effects is that these studies have been carried out only on a single population and have recorded density variation during one breeding season. In the present study we analyzed the effect of population density on *Libellula fulva* (Müller, 1764) males mating behaviour in five years of study on two differ-

ent sites with no site overlaps between years. With the exception of the last year (2007) we have partially analyzed the differences in mating and fight frequencies of males beside different population sizes, but these involved each time only a pair of years from different sites, namely for 2002 versus 2006 (Nagy et al., 2009), and for 2003 versus 2005 (Nagy et al. 2006). These studies have given contradictory results regarding for mating and fighting frequency at different male densities.

Most of the studies about population density and territorial behaviour focus on the behaviour of males (Moore 1952, Pajunen 1966, Uéda 1979) despite the fact that male density can influence the behaviour of females as well through OSR changes (Moore 1989). At low densities, there are few interactions among *Ischnura e. elegans* males (Hinekint 1987). The number of matings obtained by territorial males also depends upon the density of males at the habitat (Sherman 1983, Wolf & Waltz 1984). At very low densities, males flying over larger areas to seek females may be more successful than localized or territorial males (Buskirk & Sherman 1984).

Few invertebrates provide better opportunities than dragonflies for quantitative population studies – they are large, diurnal and predatory; their normal densities of population, like those of other carnivores of similar size, are comparatively low (Moore 1953). Therefore dragonflies are popular subjects in population ecology studies, since they often compose small populations of a few thousand individuals, where the recapture ratio could

be very high (Corbet 1999). In addition dragonflies and damselflies are used as model organisms in the development of mark-recapture methods because large data-sets are relatively easy to obtain. One classical method to analyse mark-recapture data was developed to deal with survival rates of age classes in *Ischnura elegans* (Parr 1965). Furthermore dragonflies are easy to catch, to mark, to watch and the populations are often closed, making immigration and emigration negligible (Corbet 1999).

One way to estimate the size of a population is to capture and mark individuals from that population, release them, and then resample to see what fraction of individuals carry marks. The population size is estimated on the base of recapture ratio of marked individuals. In the case of territorial dragonfly species the estimation is based only on the marked males because the recapture rate of the females is low (Pajunen 1962). Many studies deal with the estimation of population size in dragonflies and damselflies (Cordero & Andrés 2002, Bano & Rolando 2003, Kéry & Juillerat 2004, Macagno et al. 2008 etc.). The Cormack-Jolly-Seber method is often used in population size estimations because it is an open population model which makes fewer assumptions (do not assume rates of gain and loss to be zero), and it does not give a biased estimation, as closed population models would do in such cases. However, the estimates of population size that they produce are less precise than those of closed population models (Sutherland 2006).

Here we surveyed the territorial behaviour of males in two populations of *Libellula fulva* with the data set collected during five years, at two sites with presumably different population densities. Our aims were to estimate the size of the populations and to find out whether population density has a significant impact on aspects of males' mating behaviour such as the frequency of confrontations and the mating success. Our hypothesis was that yearly population density alters daily individual male territorial and mating behaviour. We

predicted that dragonfly males at higher densities fight more and mate less.

#### Material and methods

During five seasons (2002, 2003, 2005, 2006 and 2007) we studied two *Libellula fulva* populations along two small lowland creeks in Eastern Hungary. *Libellula fulva* is a widespread but local species in Europe, which flies between May and early July (Askew 2004). Prior to maturation the male and female look very similar and are highly distinctive with vivid orange colouration, black triangular shaped markings on the upper surface of each abdominal segment and dark bases of the wings (Askew 2004). Once mature the males develop a blue pruinescence on most of the abdomen, although the last three segments become black. *Libellula fulva* is a species of lowland river floodplains and is usually found inhabiting slow flowing rivers, water meadow dyke systems and occasionally mature gravel pits (Winsland 1996) and nearby ponds (Cham 2000). Males can be characterized with hard territorial behaviour, they defend 15-20 meter long territories (Nagy et al. 2004), from where they try to bundle out both conspecific and non-conspecific intruders. Mating is a relatively time consuming and rigorous affair, lasting appreciatively 30-35 minutes (Nagy et al. 2008).

Our studies were carried out with the capture-mark-resighting method. We have spent 99 days on field (Table 1.) between middle of May and early July. During the five year study we marked a total number of 1484 males (Table 1). The marked animals were studied in 2002 and 2003 along a 650 m long section of the Kutas Creek (site no. 1, from now Ártánd) near Ártánd locality (Hajdú Bihar county); and in 2005, 2006, 2007 along a 385 m long section of the Kis-Körös Creek (site no 2, from now Bojt) near Bojt (Hajdú Bihar county) locality. There was also a difference in the width of the water surfaces, the Kutas Creek on Ártánd was narrower (cca. 2 m), while the Kis-Körös Creek on Bojt was wider (cca. 4 m). But, because usually the most part of the lifetime of an adult libellulid male is spent on the shores of the water surface, we considered that the difference in the estimated population size reflected a difference in the density of males on that site. Taking into account the length and the width of studied water bodies the surface on Ártánd was cca. 1300 m<sup>2</sup> and on Bojt was cca. 1540 m<sup>2</sup>. We made no simultaneous observations on the two study sites. Hence the distance between the study sites was cca. 10 km, so there was not any overlap among the studied populations. The aquatic

**Table 1.** Number of marked specimens at the two study sites for five years

Year	Site	No. of surveyed days	No of marked males	Number of males with at least one resight
2002	Ártánd	17	168	118
2003	Ártánd	16	185	139
2005	Bojt	22	314	108
2006	Bojt	23	378	174
2007	Bojt	21	439	197

vegetation was composed by species like *Typha angustifolia*, *Phragmites australis*, *Nuphar lutea*, *Mentha aquatica* etc. and did not differ between the two sites.

We marked the dragonflies with permanent marker (Edding 750, Edding 780) on their right side wings using two colours (blue and red) and at least double characters. The movement of marked animals was followed by two observers using 8×40 binoculars. At each resighting we recorded the number of the respective male or female, its location on the study site, its behaviour (three categories: fighting, perching, mating), and the moment of the observation. We observed the marked specimens daily between 9.00 and 15.00, as the dragonflies showed the highest mating activity in this period.

#### Model selection for the population size estimation

All population size estimation analyses were conducted in RMark (Laake & Rexstad 2008), a newly developed package for program R (R Development Core Team 2010) that uses custom scripts to call program MARK (White & Burnham 1999, Cooch & White 2010).

Program Release (Burnham et al. 1987) was also used with RMark to perform the goodness-of-fit test of the general Cormack-Jolly-Seber (CJS) model, where survival and capture probability are treated as separate parameters which vary among different sampling occasions.

Because significant differences in the goodness-of-fit test (Table 3.) we estimated the overdispersion parameter  $\hat{c}$  (Hines 1996) as suggested in Laake & Rexstad (2008) and Choquet et al. (2009). We estimated  $\hat{c}$  by dividing Pearson's  $\chi^2$  by the degrees of freedom (Hines 1996, Laake & Rexstad 2008). This procedure, although not perfect, works generally well as long as the overall ratio does not exceed 3 (Burnham & Anderson 2002 in Choquet et al. 2009). In our case  $\hat{c}$  varied in all cases between 1 and 2, and by setting the calculated  $\hat{c}$  for each case for the model fitting we felt safe against overdispersion.

We selected the most appropriate model with the modification of the Akaike information criterion (QAICc) (Akaike 1973, Burnham & Anderson 2002), which can be viewed as an objective function to adequately describe the data using the model with the fewest parameters, even in the presence of heterogeneity of capture and/or survival probabilities (Burnham et al. 1995).

#### Effect of population size on male reproductive behaviour

The number of assessed matings per individual (mating frequency) was calculated as the daily number of matings

divided by daily estimated population sizes. The number of assessed male-male intraspecific fights per individual (fight frequency) was calculated as the daily number of fights divided by daily estimated population sizes. We used square root transformations on mating and fight frequency to fit the normality assumption for these variables. Kolmogorov-Smirnov tests ( $p < 0.05$ ) were performed to test for normality. To test the homogeneity of variances we used Bartlett-test ( $p < 0.05$ ). Because we had different variances per stratum, and thus the homoscedasticity was not met we used the "varIdent" variance function class in our models (Pinheiro & Bates 2000). Given that the square root transformed mating frequency and fight frequency fit reasonably well to a normal distribution, we implemented models with the error structure defined as normal. Thus a linear mixed-effects model with a normal error distribution was used to analyse the effect of the two different sites (Ártánd and Bojt) on the mating frequency and fight frequency, controlling on year effect. Analyses were performed using R version 2.11.1 (R Development Core Team 2010).

## Results

### Mark-resights

We captured and marked a total number of 353 males in Ártánd and a total of 1092 males in Bojt (Table 1). Of these males, 257 in Ártánd and 479 in Bojt were resighted at least once during the study time. The longest period between capture-marking and the last resight was 17 days at each site.

The survival probability rate was around 80% through the five years (Table 2.). However, in Bojt these estimates were slightly lower than in Ártánd. The mean of the estimates of recapture rates (Table 2.) were again lower in Bojt, moving around 25%, while in Ártánd these were around 46%.

### Population size estimation

Based on the QAICc the best fitted model was always the one with constant survival probability and time-dependent recapture probability (Table 4). Thus for population size estimation we used model 2 ( $\text{Phi}(\sim 1)\text{p}(\sim \text{time})$ ). Yearly gross popu-

**Table 2.** Estimates of survival probability rates (Phi) and mean estimates of recapture rates (p) with 95% confidence intervals for five years and two sites.

Year	Site	Phi	Lower 95% CI	Upper 95% CI	P	Lower 95% CI	Upper 95% CI
2002	Ártánd	0.88	0.86	0.90	0.44	0.33	0.56
2003	Ártánd	0.88	0.86	0.90	0.48	0.37	0.59
2005	Bojt	0.80	0.77	0.82	0.21	0.14	0.31
2006	Bojt	0.80	0.78	0.83	0.24	0.18	0.32
2007	Bojt	0.79	0.76	0.81	0.26	0.20	0.34

**Table 3.** Result of goodness-of-fit tests including the overdispersion parameter ( $\hat{c}$ ). (\* and \*\* denote significance on  $p < 0.05$  for \*, and  $p < 0.001$  for \*\*).

Year	Site	$\chi^2$	df	p	$\hat{c}$	
2002	Ártánd	64.95	48	0.05	1.35	
2003	Ártánd	86.09	57	0.01	1.51	**
2005	Bojt	69.9	61	0.20	1.15	
2006	Bojt	98.90	63	0.00	1.57	**
2007	Bojt	77.79	58	0.04	1.34	*

**Table 4.** Candidate models for population size estimation on the basis of QAICc. (K is the number of estimated parameters. The  $\hat{c}$  overdispersion parameter is given for each year.)

Year	Site	model	K	QAICc	QAICc weight	$\hat{c}$
2002	Ártánd	2 $\text{Phi}(\sim 1)p(\sim \text{time})$	17	1112.25	1.00	1.35
		1 $\text{Phi}(\sim \text{time})p(\sim \text{time})$	32	1131.68	0.00	1.35
		3 $\text{Phi}(\sim \text{time})p(\sim 1)$	17	1148.46	0.00	1.35
		4 $\text{Phi}(\sim 1)p(\sim 1)$	2	1182.90	0.00	1.35
2003	Ártánd	2 $\text{Phi}(\sim 1)p(\sim \text{time})$	16	1137.69	0.89	1.51
		4 $\text{Phi}(\sim 1)p(\sim 1)$	2	1141.92	0.11	1.51
		3 $\text{Phi}(\sim \text{time})p(\sim 1)$	16	1149.49	0.00	1.51
2005	Bojt	1 $\text{Phi}(\sim \text{time})p(\sim \text{time})$	30	1151.83	0.00	1.51
		2 $\text{Phi}(\sim 1)p(\sim \text{time})$	22	1320.03	1.00	1.14
		1 $\text{Phi}(\sim \text{time})p(\sim \text{time})$	42	1339.07	0.00	1.14
		4 $\text{Phi}(\sim 1)p(\sim 1)$	2	1370.57	0.00	1.14
2006	Bojt	3 $\text{Phi}(\sim \text{time})p(\sim 1)$	22	1375.77	0.00	1.14
		2 $\text{Phi}(\sim 1)p(\sim \text{time})$	23	1242.13	1.00	1.57
		1 $\text{Phi}(\sim \text{time})p(\sim \text{time})$	44	1258.62	0.00	1.57
2007	Bojt	3 $\text{Phi}(\sim \text{time})p(\sim 1)$	23	1283.41	0.00	1.57
		4 $\text{Phi}(\sim 1)p(\sim 1)$	2	1305.34	0.00	1.57
		2 $\text{Phi}(\sim 1)p(\sim \text{time})$	21	1831.98	1.00	1.34
2007	Bojt	1 $\text{Phi}(\sim \text{time})p(\sim \text{time})$	40	1848.92	0.00	1.34
		3 $\text{Phi}(\sim \text{time})p(\sim 1)$	21	1870.58	0.00	1.34
		4 $\text{Phi}(\sim 1)p(\sim 1)$	2	1885.48	0.00	1.34
		2 $\text{Phi}(\sim 1)p(\sim \text{time})$	21	1870.58	0.00	1.34

lation size ( $N^*$ -hat) estimates were lower in Ártánd than in Bojt (Table. 5). Yearly estimated population size was at a magnitude of a few hundreds in Ártánd, and in Bojt it varied around one thousand. Daily estimated population sizes ( $N$ -hat) showed significant difference between study sites if controlled by years (LMM:  $t = 7.06$ ,  $df = 3$ ,  $p = 0.005$ ). Population sizes in Ártánd were significantly smaller than in Bojt (Welch two sample t-test:  $t = -7.9198$ ,  $df = 68.126$ ,  $p < 0.001$ ).

Taking into account that the length and width of the studied sections of the water bodies was different and, as it was already mentioned, because usually the most part of the lifetime of an adult libellulid male is spent on the shores of the water surface, we considered that the difference in the estimated population size reflected a difference in the density of males at that site.

#### Effect of population density on male behaviour

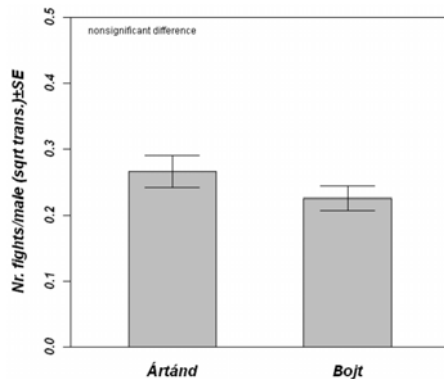
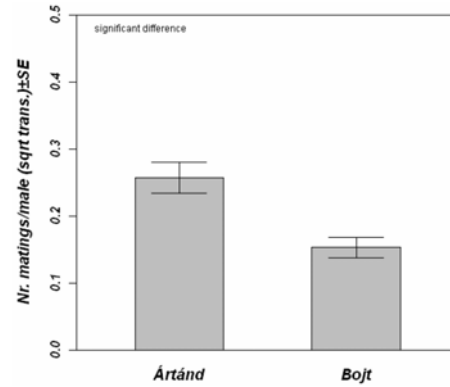
In the case of fight frequency we did not find any significant effect of study sites (LMM:  $F_{1,3} = 0.43$ ,  $p = 0.55$ ) (Fig. 1.), while in the case of mating frequency we found a significant effect (LMM:  $F_{1,3} = 12.20$ ,  $p = 0.03$ ) (Fig. 2) if controlled by year. We also found that per male mating frequency was significantly higher at the smaller population density, at Ártánd, than at the larger, Bojt (Two sample t-test:  $t = 3.89$ ,  $df = 97$ ,  $p < 0.001$ ) (Fig. 2).

#### Discussion

On the whole we found a significant difference among the studied *Libellula fulva* populations. Namely, in Ártánd there was a lower population density than in Bojt. Beside lower population den-

**Table 5.** The yearly (gross) population size estimates by the CJS-model with constant survival, and time dependent recapture with standard error and the 95% CI.

Year	Site	N	SE	lower 95% CI	upper 95% CI
2002	Ártánd	219.97	8.98	202.37	237.57
2003	Ártánd	233.40	9.35	215.08	251.72
2005	Bojt	801.91	69.60	665.49	938.32
2006	Bojt	979.96	101.10	781.81	1178.11
2007	Bojt	1058.24	77.96	905.44	1211.03

**Figure 1.** The daily number of fights per one male for the two study sites in the five years.**Figure 2.** The daily number of matings per one male for the two study sites in the five years.

sity the males had a higher mating rate, but the density had not any effect on frequency of territorial fights.

However, if analysed separately – only pairs of years – there is a departure in the long run compared to the partial results. When we compared the mating success and the frequency of intraspecific fights in males of *Libellula fulva*, for 2002 versus 2006, and for 2003 versus 2005, in both cases we compared the behaviour of males beside two significantly different male densities. Regarding for the years 2002 and 2006 the results did not show differences between the two populations (Nagy et al., 2009), while regarding for 2003 versus 2005 we have found a higher mating and fighting frequency per day in the population with higher male density, namely in 2005 (Bojt) the males fought and mated more than in 2003 (Ártánd) (Nagy et al. 2006). We have to note that in Nagy et al. (2006) the comparison of male's behaviour was made only for 8 days in each of the years, and the mating/fighting frequency was calculated for each day by dividing the number of matings/fightings per day and the number of all resightings per day. The comparison for the years 2002 and 2006 was

based on the number of yearly matings/fightings divided with the number of fieldwork days per year and with the total number of marked individuals per year. Thus we consider that the present paper which contains the CJS population size estimation for the five years of study and the frequency of fights and matings per day divided with the daily estimated population densities represents a more ample and an enhanced analyses than the previous two (Nagy et al. 2006, Nagy et al. 2009).

Our hypothesis assumed that both frequencies of intraspecific fights and matings are density dependent, but with different directions. Namely while with increasing male density the frequency of intraspecific fights grows, the frequency of matings will decrease because of the higher investment in pre-mating behaviour. Regarding the hypothesis only one of the two predictions was supported, namely which supposed that at higher densities dragonfly males mate less. As in Ártánd we found higher mating frequency than in Bojt, this means that some factor indeed interferes with mating frequency, but not the fights frequency alone. This could be also the time spent by males

in tandem or in mating wheel because of maximizing the probability of the success of the mating (Uéda 1979). Adding abiotic components (such as daily temperature or precipitation, which can alter the individual behaviour) or biotic components (fat reserves or body size, differences in copulation duration) to this study may extend our understanding on this species behaviour.

Accordingly to the population size estimation the dragonfly population in Ártánd was smaller than in Bojt. We choose open population models for estimation because of the biased estimations in the case of the use of closed models for open populations. However, we did not find any marked specimens in the neighbourhoods of the study area on the whole study time in each year, but it may be possible, that specimens wander along the water surfaces. There is no interference between the two studied populations, because of the distance (10 km in a straight line) of the two sites. We can report a smaller male density on Ártánd and a larger one on Bojt even though the length of the studied sections of the water bodies and their widths was different because these differences actually polarized and underlined this departure in densities.

Our studies did not support the prediction that male – male competition increased with increased population density. Regarding the fight frequency in the higher population density site, males should use scrambling competition instead site fidelity, which may be caused by the crowding of males on a territory of a given size where resources (oviposition site, sunny resting place) are limited. However, in the long term study the fight frequency was not greater in the larger population than in the smaller one, contrary to two partial studies (Nagy et al. 2006, 2009). The increase of intraspecific fights was described in case of the males *Paltothemis lineatipes* (Alcock 1989), *Ischnura elegans* (Hinneking & Dumont 1989), *Libellula pulchella* (Pezalla 1979). At the same time beside high population densities, males of some species (*Paltothemis lineatipes*, *Libellula pulchella*) defend smaller territories (Alcock 1989, Pezalla 1979), a phenomenon which was not proven in *Libellula fulva* males, since the territories defended were 15-20 m long at both study sites.

A possible explanation for our results is that beside high population densities holding a territory becomes so energetically unprofitable that males may gain more by changing their mating tactics from territoriality to non-territoriality

(Cordero 1999, Kokko & Rankin 2006). Furthermore, under these conditions mated males would be expected to guard their mates more intensively, whereas solitary males would try to achieve tandem forcibly (Cordero 1999). In this work we studied neither the duration of male mate guarding nor the frequency of forced copulations.

We found that population density had a significant effect on the mating frequency. Regarding the smaller mating frequency in the higher population density site, its occurrence is possible, because males presumably use scrambling competition instead site fidelity, and this could lead to a decreased mating number because of lowered energetic resources (fat reserves). This difference in mating frequency is not in concordance with a partial study (regarding years 2002, 2006), when no significant difference in mating frequency was found (Nagy et al. 2009). Therefore we point out again the importance of long term study comparisons, which in our case showed different results compared to the short term ones.

Alonso-Pimentel & Papaj (1996) reported that population density had no effect on copulation duration in the walnut fly. Males should guard mated females for the same duration regardless of the density level when OSR is held constant because the probability that males will find another mate after copulation or that their sperm will be displaced should be the same.

Accordingly to Suhonen et al. (2008, in Córdoba-Aguilar 2008) the biggest deficiency of studies of density effects is that these studies have been carried out only on a single population and have recorded density variation during one breeding season only. They suggest that future empirical studies should take into account the possibility of between-year and between-population variations in both male and female density, to see how this variation affects male mating success, the ratio of males implementing non-territorial and territorial mating tactics, and the transition frequency between these tactics. Our five-year study perfectly shows that the relationship between the given variables suggested by the analysis of a long term field-work can be much different from the one suggested by a short-term field-work. The final conclusion we can draw is that in the species *Libellula fulva* population density influences male mating frequency, but not *via* male-male competition.

**Acknowledgements.** We thank Adrienn Tóth and Zoltán Varga for help in the fieldwork, Béla Tóthmérész for comments on the manuscript. The work of Zoltán László was supported by MNCISIS-UEFISCSU, project number PN II-RU 413/2010. We would like to thank all the authors who kindly sent pdfs or reprints of the papers cited in this analysis.

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