Survival of dragonfly *Libellula fulva* males according to their mating status: a four year study

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Summary: The dragonfly is one of the favoured experimental groups of behavioural ecology. They can be marked individually and can be easily tracked without considerable disturbing. The use of mark-recapture models for measuring the survival and recapture rate of individuals allows a better understanding of the processes of population dinamics. During four seasons (2000-2003), a closed *Libellula fulva* (Müller, 1764) population was studied along a creek in Eastern Hungary. The movement of marked and solitary males was observed with binoculars and it was recorded along a 350 meter natural section of the Kutas-channel. Our aim was to analyse the recapture and survival rate of two male groups of scarce chaser (*Libellula fulva*) by using mark-recapture models. The model-selection showed that the recapture rate of mated males was higher than of solitary ones. Survival rate of mating males was also higher in every year than the survival of the solitary individuals. This result suggest, that even if it is costly for males to occupy and defend a territory, finding, guarding and mating a female, the succesful males have still a higher survival rate.

Rezumat : Libelulele (Odonata) reprezintă una dintre grupele țintă ale ecologiei comportamentale. Pentru a putea estima corect rata de supraviețuire și mortalitatea indivizilor este necesar ca indivizii să fie marcați. Din rata de recapturare sau de observare a indivizilor marcați se poate deduce schimbarea parametrilor demografici. Odonatele sunt subiecte ideale ale studiilor de acest fel, deoarece, în special, între Anisoptere întâlnim specii bune zburătoare, care pot fi marcate și observate cu ușurință fără a fi deranjate. Studiul s-a desfășurat timp de patru ani între 2000-2003 dealungul canalului Kutas, lângă granița Ungariei cu România. Scopul lucrării este estimarea ratei de supraviețuire și de recapturare a masculilor solitari și în pereche cu ajutorul modelelor de capturare-recapturare în cadrul unei populații de *Libellula fulva*. Rata de supraviețuire și de recapturare a masculilor în pereche a fost mai mare în fiecare an decât cea a masculilor solitari. Concluzia studiului este că deși pentru masculii în pereche ocuparea și protejarea teritoriului, capturarea femelei și copulația este costisitoare, rata lor de supraviețuire și de recapturare este mai mare decât a masculilor solitari.

Key words: survival rate, recapture rate, mating success, *Libellula fulva*

Introduction

The dragonfly (Odonata) is one of the favoured experimental groups of behavioural ecology. Similarly to birds they can be characterised by numerous behavioural patterns, they are excellently adapted to aerial motion, they manoeuvre outstandingly, and as true predators they can catch their prey in the air. In terms of behavioural ecology the easiest way of examining the individuals of a dragonfly population is the mark-recapture method, which became frequently used as models for supraindividual biology during the past few decades (Pajunen 1962). The development of newer models, and the emergence of softwares, suited to them, accelerated this process.

In Zygoptera the survival rate of males is higher than of females in the pre-reproductiv period (Anholt 1991), in the reproductiv period (Bick and Bick 1963, Banks and Thompson 1985, Koenig and Albano 1987) or in both (Úeda 1987, Bennett and Mill 1995). In many species of Coenagrionidae males have greater survival rate (Garrison and Hafernik 1981, Fincke 1982, Anholt *et al.* 2001). In other sudies there are no differencies between the survival rates of sexes (Hamilton and Montgomerie 1989, Córdoba-Aguilar 1994, Beukema 2002) and we found only a few studies where females have greater survival rates (Robinson *et al.* 1983, Cordero 1993). Generally the recapture (resighting) rate of males is higher than of females (Anholt 1997, Anholt *et al.* 2001, Andrés and Cordero 2001), which can be explained with the cryptical behabiour of females. In the case of *Lestes disjunctus* Selys 1862 females have greater recapture rate (Duffy 1994). There are a lot of studies in odonatological literature concerned to study of demographical parameters (Corbet 1952, Van Noordwijk 1978, Robinson 1983, Hamilton and Montgomerie 1989, Beukema 2002). In adult Zygoptera the sexual rate is male biased (Garrison and Hafernik 1981, Hamilton and Montgomerie 1989, Maxwell 1998), which can be explained by the fact that males can be easily captured in the field, females have more cryptical behavior, females and males did not emerge sincronously, the mortality in females is higher in the pre-reproductiv period and the pattern of distribution differed between the two sexes (Garrison and Hafernik 1981, Nylin *et al.* 1995). In a study with *Lestes sponsa* Hansemann, 1823 Stoks (2001) showed that males are present in a great number at the rendezvous- and mating site, due to the strong temporary emigration of females and to heterogenous recapture rate of males. This aspect can be explained by the fact that females are present at the mating site only for mating and oviposition, the feeding place is different from the mating site and for gametogenesis females need more energy and time than males for spermatogenesis (Anholt 1992, Banks and Thompson 1987). In Anisoptera species the higher recapture rate of males is strongly correlated with site fidelity and territorial behaviour.

To estimate the survival and mortality rate of individuals, the longevity and population size, it is necessary to mark specimens individually. The specimens then can be easily tracked without disturbing them. The demographic parameters can be estimated using the recapture or resighting rate of marked individuals. At the begining this method was used to estimate the population size, nowadays it is also used to estimate and compare the survival and recapture rate of individuals. The mark-recapture (resighting) method was used in many odonatological studies to estimate the sex ratio, the survival and the recapture rate (Fincke 1982, Koenig and Albano 1985, Van Buskirk 1987, Hamilton and Montgomerie 1989), the dispersal rate and to study the site fidelity of males (Borror 1934, cit. Corbet 1999, Moore 1951, Pezalla 1979, cit. Corbet 1999).

Our aim was to analyse the recapture and survival rate of two male groups of scarce chaser (*Libellula fulva*) by using mark-recapture models.

Material and methods

The study site of our research is a canalised creek next to the Romanian-Hungarian border, called Kutas main channel. The channel came into existence as a result of governing the bed of Csíkos stream, and during the examination period only a 350 metres long reach remained in its natural state. The bed of the main channel before and after this part is a burrowed and straight one, but these parts of the channel are in a nearly natural state. The study of scarce chaser population was restricted to a 650 ms long stage every year which included the natural part. Males, flying along the stream were marked by numbers, written on their right wing by a brush-pen (Edding 100) in every sampling season. Marked individuals were observed daily by a binocular with 8x40 magnification, between 9 a.m. and 4 p.m. when their mating activity was the highest. The spotted, indicated specimens were divided into two groups: the group of copulating ones (observed at least once in wheel position) and the single ones (never observed, while mating). In 2000 108, in 2001 210, in 2002 168 and in 2003 186 individuals were marked. In case of every observation the following data were noted: the number of marked individuals, the status occupied in the area, the mating status, the territorial (the aggressive attitude, the expeling of other specimens, the time when the territory was occupied, and the daily changes in the territorial behavioural pattern) and the mating (the length and place of mating) behavioural patterns.

In case of normally distributed data the relations were analysed by Pearson correlation. When the data were not normally distributed the Spearman rank correlation was used. The analysis of the mark-recapture data was conducted with the help of MARK 4.2 software. The models were chosen by an a priori hypothesis, suggesting a difference between the survival rate of single and mating individuals. The models were then ranked by the Akaike Information Criteria (AIC). The models, fitting in the best way to the recapturing data set were chosen after processing them by the 25 basic models of the MARK software. The fitting of the Cormack-Jolly-Seber (CJS) model was implemented by the U-CARE 2.0 software.

Results

In 2000 65% of marked males (73 individuals) was seen twice or more following the marking. The goodness-of-fit (GOF) test of U-CARE program used for estimate the recapture and survival rate showed that the global CJS model fit to recapture data. During model selection *S(g) P(g+t)* model had the lowest AIC value, meaning that survival rate (*S*) is group dependent (differs in mated and solitary males) and constant over the time, the recapture rate (*P*) is group dependant and varied with time. According to the second model there is a difference between mated and solitary males in survival and recapture, too (Table 1). Mated males have greater survival than solitary ones, but the differences are not significant (Fig. 1).

In the 2001 field season we resighted 73.34% (154 individuals) marked males during.

The global GOF showed a slightly significant trap-dependence [(N(0.1) signed statistic for

Table 1. The general Cormack-Jolly-Seber model fitting best the data from 2000 and the models used in paired comparisons, sorted by the Akaiki Information Criteria (AICc) (abbreviations: *S* – survival rate, *P* – recapture rate, *g* – group, *t* – time)

Model	AICc	AICc Weights	No of parameters	Deviance
S(g) P(g+t)	734.5	0.54	12	306.8
S(g) P(t)	736.5	0.20	11	311.0
S(g) P(g)	737.2	0.14	4	326.6
*S(g*t) P(g+t)*	737.7	0.11	20	291.8
*S(g*t) P(g*t)*	753.5	0.00	28	288.2

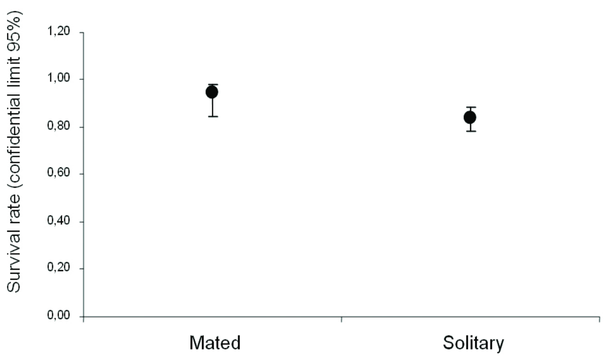

Fig. 1. The estimation of survival rate of two male groups according to *S(g) P(g*t)* model

trap-dependence = –1.96, p = 0.048]. This difference dissapeared when performing the TEST2.CT separately for the two male groups [mated males: Log-Odds-Ratio statistics for trap-dependence= –1.24, df = 7, p (two-sided) = 0.21; solitary males: LOR statistics for trap-dependence = –1.29, df = 7, p (two-sided) = 0.19]. During the model selection there was only a small difference between AIC value of first three models. Comparing models we can observe that the difference between AIC weights is small too: between the first and second model is 0.03, between the second and the third model is 0.01 (Table 2).

Table 2. The general Cormack-Jolly-Seber model fitting best the data from 2001 and the models used in paired comparisons, sorted by the Akaiki Information Criteria (AICc) (abbreviations: *S* – survival rate, *P* – recapture rate, *g* – group, *t* – time)

Model	AICc	AICc Weights	No of parameters	Deviance
*S(g*t) P(t)*	857.5	0.30	21	320.7
S(g+t) P(g+t)	857.7	0.27	17	329.8
*S(g*t) P(g+t)*	857.8	0.26	23	316.5
*S(g*t) P(g*t)*	859.2	0.13	28	306.4
S(g+t) P(t)	861.5	0.04	17	333.7

According to each model there is a difference between survival of mated and solitary males. In the first and third model it is group and time interaction in the survival, in the second model the survival is group dependent and it is changing with the time. The recapture rate is time dependent in the first model, in the second and third model it is group dependent and it is changing with the time.

In 2002 we resighted twice or more 75.73% (128 individuals) of marked males (169). The GOF test made on pooled data showed significant difference only in trap-dependence [(N(0.1) signed statistic for trap-dependence = –4.8, p < 0.001]. From the test components only the TEST2.CT showed a trap-dependence in both groups [mated males: LOR statistics for trap-dependence = –3.79, df = 13, p (two-sided) < 0.001; solitary males: LOR statistics for trap-dependence = –2.68, df = 13, p (two-sided) = 0.007].

The best model, which had the smaller AIC and the bigger AICc Weight was *S(g) P(g*t)*. According to this model there is a constant difference between the survival of solitary and mated males, in the recapture rate there is group and time interaction. In the Table 3. we present the models with the best fit to our data.

Table 3. The general Cormack-Jolly-Seber model fitting best the data from 2002 and the models used in paired comparisons, sorted by the Akaiki Information Criteria (AICc) (abbreviations: *S* – survival rate, *P* – recapture rate, *g* – group, *t* – time).

Model	AICc	AICc Weights	No of parameters	Deviance
*S(g) P(g*t)*	1428.8	0.93	32	823.7
*S(.) P(g*t)*	1435.2	0.04	31	832.4
*S(g+t) P(g*t)*	1437.4	0.01	43	807.1
*S(g*t) P(g*t)*	1438.3	0.01	48	796.2
S(g+t) P(g+t)	1438.9	0.01	27	844.9

Mated males had greater survival than unmated ones. The recapture rate was higher in the case of mated males, except the 5., 12., 14. and 16 days, when we saw more solitary males (Fig. 2).

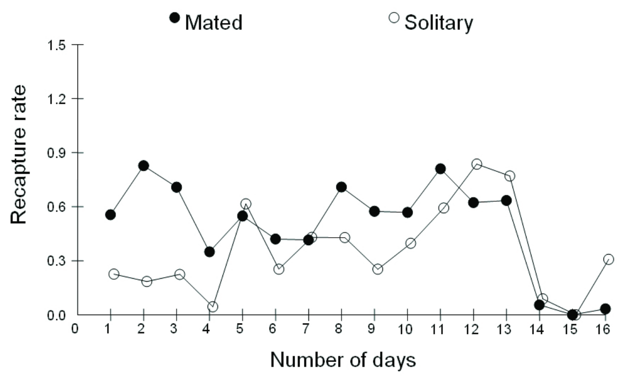

Fig. 2. Recapture rate of mated and solitary males according to *S(g) P(g*t)* model

In 2003 81.73% of marked males were resighted more than two times. The global GOF test on the general CJS model (*S(g*t)P(g*t)*) made by the U-CARE program did not show any significant fitting problems, except the signed component of the trap-dependence test made on pooled data [(N(0.1) = -5.1, p < 0.001]. Three test components (TEST3.SR, TEST3.Sm, TEST2.CL) were not showing any significant fitting problems.

Surprisingly, according to the TEST2.CT component there was a strong 'trap-happiness' at the solitary males [N(0.1) LOR statistics for trap-dependence= –3.95, p (two-sided)<0.001] and had a near-significant value in the case of mated males [N(0.1) LOR statistics for trap-dependence = –1.87, p (two-sided)=0.06].

After model selection, the model with best fit to our data was *S(g)P(t)*, where the survival of two male groups was different (group-effect), the recapture rate varied with time. Due to AIC weight this model fit twice more better to data that the following models (Table 4).

Table 4. The general Cormack-Jolly-Seber model fitting best the data from 2003 and the models used in paired comparisons, sorted by the Akaiki Information Criteria (AICc) (abbreviations: *S* – survival rate, *P* – recapture rate, *g* – group, *t* – time)

Model	AICc	AICc Weights	No of parameters	Deviance
S(g) P(t)	1715.4	0.48	17	1026.9
S(g) P(g+t)	1717.0	0.22	18	1026.4
S(g+t) P(t)	1717.2	0.20	28	1005.0
S(g+t) P(g+t)	1718.5	0.10	29	1004.1
*S(g*t) P(g*t)*	1739.3	0.00	50	977.2

According to *S(g) P(t)* model, the survival rate of mated males was higher than of solitary ones (Fig. 3).

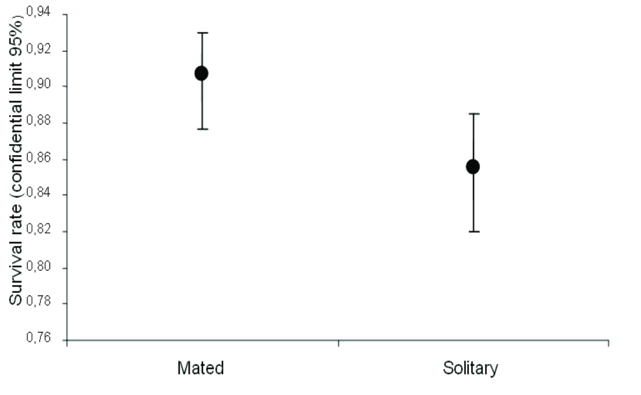

Fig. 3. The estimates of survival rate of mated and solitary males according to *S(g)P(t)* model.

Discussion

After marking we resighted at least twice more a 65% of marked males, showing that the marking itself had no marked negative effect on individuals. Similarly to our results a higher recapture rate was showed in the case of *Haeterina cruentata* (Rambur, 1842) (64.8%) (Córdoba-Aguilar 1994) and *Ischnura gemina* Kennedy, 1917 (90%) males (Garrison and Hafernik 1981). In 2000 1/5 (17.59%), in 2001 1/3 (33.86%), in 2002 and 2003 half procent (47.61% and 45.4%) of marked males were seen in copula.

The higher recapture rate of mated individuals over solitary ones can be associated with their territorial behaviour. Territory holders are more conspicuous at oviposition sites where they defend a small area with patrol flights and perching on sites with good visibility options.

The survival rate of mated males was higher in every study year than of solitary ones. A positive correlation between mating success and survival was found in several species: *I. pumilio* Charpentier, 1840 (Cordero and Andrés 1999), *I. gemina* Kennedy, 1917 (Garrison and Hafernik 1981), *Enallagma hageni* (Walsh, 1863) (Fincke 1982), *Coenagrion puella* (Linnaeus, 1758) (Banks and Thompson 1985).

We suggest that individuals of better condition can occupy and defend a territory easily and due to the fact that mating occurs inside the territory, they also can find more easily a pair. The solitary males are less successful, they have smaller survival rate than mated individuals, they probably have greater mortality rate and they emigrate from the study site. Those individuals who have less access to food-sources have less chance to have a territory and to copulate, therefore they have a higher emigration-rate as their succesful conspecifics (Lomnicki 1978, Lawrence 1987).

Based on data from this four year study period we can conclude that even if occupying and holding a territory, attracting, protecting and pairing a female are all costly, the survival of mated males is still higher than of solitary ones.

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