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FLUCTUATING ASYMMETRY, SURVIVAL AND MATING SUCCESS IN MALE *LIBELLULA FULVA* MÜLLER (ANISOPTERA: LIBELLULIDAE)

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The studies were conducted at Kutas canal near Ártánd, Hungary. In order to reveal whether there is any relationship between wing fluctuating asymmetry and mating success in mated (observed at least once in wheel position) and solitary ♂♂ (not involved in pairing during the study period), 106 ♂♂ were marked and their wing length between arculus and pterostigma measured. Mated ♂♂ had more symmetrical forewings, but in the case of hindwings there were no differences between solitary and mated individuals. The survival rate did not differ between the 2 groups and it was constant over time. The probability of recapture was higher in mated ♂♂ and varied with time. The number of hours spent with observation did not explain the variation in the recapture rate.

INTRODUCTION

Developmental stability reflects the ability of individuals to avoid genetical and environmental stress (PALMER & STROBECK, 1986). One measure of developmental stability is fluctuating asymmetry (FA) that occurs when small, random deviations from perfect symmetry occur in a bilaterally symmetrical trait. The degree of asymmetry can indicate the quality of an individual: higher-quality individuals are more resistant to stress and develop symmetrical traits (MØLLER & POMIANKOWSKI, 1993). On the other hand some authors suggest that the relationships between developmental stability and various fitness components are weak (CLARKE, 1998; MARKOW & CLARKE, 1997; PALMER & STROBECK, 1997; WHITLOCK & FOWLER, 1997).

In recent years several studies of mating success, survival and fluctuating asymmetry of dragonflies and damselflies have been published (HARVEY & WALSH, 1993; CÓRDOBA-AGUILAR, 1995; CORDERO et al., 1997; FORBES et al., 1997; JENNIONS, 1998; CORDERO RIVERA & ANDRÉS, 1999; CARCHINI et al., 2000, 2001).

Current interest in sexual selection research focuses on the relationship between fluctuating asymmetry and mating success. HARVEY & WALSH (1993) found that males with more symmetrical wings enjoyed higher lifetime mating success in *Coenagrion puella*. CÓRDOBA-AGUILAR (1995) found a similar relationship in short-term mating success in males of *Ischnura denticollis*. In the case of *Ischnura graellsii* the correlation between absolute FA and lifetime mating success was not significant (CORDERO et al., 2002). CARCHINI et al. (2001) did not found any correlation between FA and heterozygosity, body size and short-term mating success. There was also no relationship between wing asymmetry and mating success in *Coenagrion resolutum* (FORBES et al., 1997), *Xanthocnemis zealandica* (HARDERSEN, 2000) and *Ischnura elegans* (SZÁLLASSY et al., 2000).

Investigations covering the whole reproductive period (HARVEY & WALSH, 1993; CORDERO et al., 1997) are directed to the reproductive activity of individually marked specimens and relate the symmetry of bilateral traits to the number of copulations. Several mark-recapture studies show that males marked in copula were more skilled in survival and reproduction (CORDERO et al., 1997; CORDERO & ANDRÉS, 1999). Mark-recapture techniques working with models have become widespread only in recent years (CORDERO et al., 1997; CORDERO & ANDRÉS, 1999; ANDRÉS & CORDERO, 2001; ANHOLT, 1997; ANHOLT et al., 2001). The use of models that take into account both recapture and survival possibilities allows a better understanding of population dynamics of damselflies and dragonflies (ANHOLT, 1997).

Libellula fulva is a sexually dimorphic, territorial libellulid, characterized by a long copulation duration and non-contact guarding during oviposition. This species is particularly suitable for mark-recapture studies, because it shows site-attachment and it is easy to observe and mark. Publications on FA in odonates mainly refer to non-territorial Zygoptera, while in this study our model species was a territorial Anisoptera. Survivorship of *L. fulva* individuals belonging to a nearly closed population was studied using mark-recapture models to analyse survival and recapture rate of mated and solitary specimens. We wanted to reveal whether any correlation exists between wing fluctuating asymmetry and mating success of the selected species.

MATERIAL AND METHODS

Libellula fulva adults were observed at Kutas canal, a small, lowland stream in East-Hungary (23°06'24,5"E, 47°47'26,2"N, 103 m). The larval habitat is restricted to a relatively small section of approximately 2600 m length, from which only 1060 m is natural, the rest was made by replacing the original stream-bed with a straight, artificial ditch in the second part of the 19th century. Both sections support diverse vegetation, the first is dominated by *Typha latifolia* and various species of *Carex* spp., while massive stands of *Sium erectum* and *Mentha aquatica* as well as *Carex* spp. characterizes the latter. Many unique and diverse habitats including the study area have been nearly annihilated in Hungary during the past water regulation processes, which restricted the distribution of *L. fulva* to very confined, small habitat fragments, where large colonies are common. The studied population of *L. fulva* can be regarded as a closed population because no other suitable habitat except for the small fragment of the once natural section of the stream was available for them for resettling.

Males of *L. fulva* were studied by direct observation from 6 until 15 June 2000. A total of 106 fully coloured males was individually marked and immediately released at the site of capture. The unique numbers written by permanent marker (type Edding 100, red and blue) on the right wings remained conspicuous throughout the observation period.

The distance between arculus and proximal corner of the pterostigma was measured with a caliper to the nearest 0.1 mm at the time of marking. A 1340 m long section of the stream (covering the whole natural section and part of the artificial one) was selected for daily surveys made at the peak of the dragonflies' activity, usually between 9.00 and 16.00 h when weather conditions were favourable. Seeking marked individuals was aided by binoculars, and their number, location, reproductive state (mated or solitary) as well as the time of resighting were noted. Considering that the copulation duration of *L. fulva* is long (between 30-50 min, but could be even more, pers. obs.), and that two persons surveyed the study site continuously and observations coincided with daily pairing activity, there is only a weak chance of overlooking pairing individuals and classifying them into a wrong group. At the same time some matings may have remained unnoticed in case individuals occasionally mated after 16.00 h. Observations took on the average 6.2 hours per day.

The value of fluctuating asymmetry (FA) was expressed as the absolute difference between right and left wings. We used the Kolmogorov-Smirnov test to verify the normality of the distribution of FA values and the Mann-Whitney U test to analyse them. Repeatability of wing measurements was calculated according to LESSELS & BOAG (1987). Statistics were performed with SPSS for Windows statistical package (1998).

Mark-resight data were analysed by the program MARK 1.9 (WHITE & BURNHAM, 1999). The suitability of Cormack-Jolly-Seber (CJS) model was tested with the RELEASE GOF (BURNHAM et al., 1987) and with the Bootstrap GOF procedure included in MARK. The model with the best fit to the data was selected from the 25 built-in basic models on the basis of Akaike Information Criterion (AICc) (ANDERSSON et al.,1994) and likelihood-ratio test (LRT) (LEBRETON et al., 1992). The effect of external variables on the recapture rate was tested using LRT test and analysis of deviance test (ANODEV) (SKALSKI et al., 1993).

RESULTS

Of 106 marked and measured males, 35 (33%) were never seen again; thus their measurement values were not included in the statistical analysis of fluctuating asymmetry.

Resighted males were divided into two distinct groups: 'solitary' individuals were never involved in copulations (52 individuals, 49 %), while 'mated' ones were observed at least once in wheel position (19 individuals, 18 %). Only two males were seen in copula two times. Since our study did not cover the whole flight period (observations taking ten consecutive days) and we could not estimate reliable lifetime mating success, the maximum number of copulations per male remained low.

Repeatability of wing measurements was checked on the right wings of 45 previously collected and preserved specimens. The repeatability value (r) was 0,97 (SE=0.0001) for forewings and 0.99 (SE=0,0013) in the case of hindwings. However this is not a

Table I
Differences in mean wing measurements (± SD) on *Libellula fulva* males

Condition	n	Forewing		Hindwing	
		left	right	left	Right
Unmated	52	15.07 (0.48)	15.11 (0.63)	16.69 (0.47)	16.55 (0.52)
Mated	19	14.97 (0.45)	14.98 (0.59)	16.58 (0.56)	16.46 (0.54)

proper way to test the true repeatability because the possibility of measurement error is lower under laboratory conditions than in the field.

Table I gives the measured wing-values of marked males. Both FA values were non-normally distributed (Kolmogorov-Smirnov test, forewings: $Z=1.40$, $p=0.03$, hindwings: $Z=1.35$, $p=0.05$). FA values differed significantly between the two groups in a way that mated individuals had more symmetrical forewings than solitary ones (Fig. 1, Mann-Whitney U test $Z=-1.93$, $p=0.05$). No differences were found in the FA values of the hindwings (Fig. 1, Mann-Whitney U test $Z=-1.48$, $p=0.62$).

The general CJS model, S_{g*t}, P_{g*t}, fit the data (RELEASE GOF: $\chi^2=10.211$, df=13, $p=0.676$) (Tab. II). The bootstrap GOF test of MARK indicated lower level of fit for the CJS model (1000 repeats, $p=0.06$). Further model selection using MARK showed that out of the 25 basic models the S., P_{g+t} proved to be the most appropriate. This model suggests that the survival rate is constant and does not differ between the two groups (S.). The recapture rate differed between mated and solitary males, and varied with time (P_{g+t}), the values being higher for mated males (Fig. 2). Bootstrap GOF test made by MARK supported the fit of the model S., P_{g+t} to the data (1000 repeats, $p=0.138$).

Likelihood ratio tests between the nested models showed that

- survival rates did not differ between mated and solitary males (S., P_{g+t} *vs* S_g P_{g+t} model; $\chi^2=0.005$, df=1, $p=0.944$)
- survival was constant over time (S., P_{g+t} *vs* S_t, P_{g+t}; $\chi^2=7.383$, df=5, $p=0.194$)
- the recapture rate differed between mated and solitary males (S., P_{g+t} *vs* S., P_t; $\chi^2=5.536$, df=1, $p=0.019$). The recapture rate of mated males was higher than that of solitary ones
- the recapture rate was not constant over time (S., P_{g+t} *vs* S., P_g $\chi^2=26.13$, df=8, $p=0.001$)
- the observation effort (no. of hours spent daily with observation) did not explain the variation in the recapture rate (S., P_{g+t} *vs* S., $P_{g+effort}$ $\chi^2=25.884$, df=7, $p<0.001$). The ANODEV test supported that observation effort, considered as group covariate, could not explain the variation in the recapture rate over time ($F_{1,7}=0.067$, $p=0.804$).

DISCUSSION

The marked individuals were resighted with high frequency in the study area. 67 % of marked males were seen at least twice, mostly because there was no other similar habitat in the neighbouring areas to which they could disperse. Compared with other similar studies on Anisoptera species, our resighting rate was very high [(23.1 % for *Orthetrum coerulescens* PARR (1983) and 22.89% for *Libellula pulchella* in

McMILLAN (2000)].

The analysis of the relationship between a trait asymmetry and mating success has resulted in contradictory findings in different studies. In many taxa symmetry correlates with male mating success in a way that males with low level of asymmetry achieve more matings [LIGGETT et al., 1993 (*Scatophaga stercoraria*); ALLEN & SIMMONS, 1996 (*Sepsis cynipsea*); MARKOV & RICKER, 1992 (*Drosophila* spp.)], but the study of TOMKINS & SIMMONS (1998) on earwigs has shown no correlation between mating success and FA.

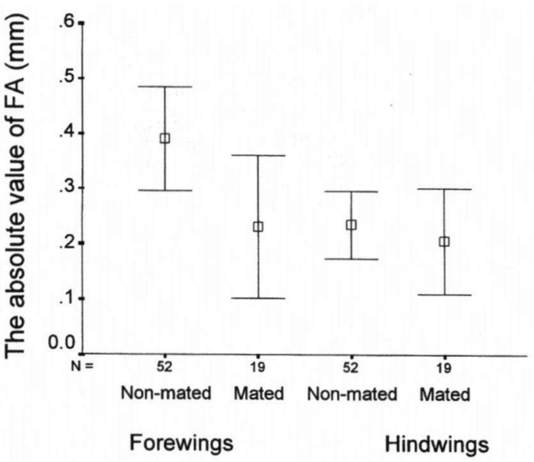

Fig. 1. Wing asymmetry values of mated and solitary *L. fulva* males. The differences were significant only in the case of forewings.

In odonates wing asymmetry was negatively correlated with mating success in *Coenagrion puella* (HARVEY & WALSH, 1993) and *Ischnura denticollis* (CÓRDOBA-AGUILAR, 1995). In *C. resolutum* there was no relationship between wing asymmetry and mating success (FORBES et al., 1997), similarly between natural levels of asymmetry in tibial whiteness, mating rate, courting rate and fighting behaviour in *Platycypha caligata* (JENNIONS, 1998).

FA may sometimes influence flight performance in the field (PALMER, 1994). MØLLER (1992) reported that males of *Hirundo rustica* with symmetrical wings and outermost elongated tail feathers were preferred by females, while BALMFORD et al. (1993) stated that more symmetrical males were aerodynamically superior. McLACHLAN (1997) reported that increased asymmetry reduced flight duration, wing-beat frequency and increased wing-beat amplitude in midges. Mating success was also reduced in asymmetrical male midges.

In our case the mated males had more symmetrical forewings than the solitary ones, but no difference was found in the asymmetry of hindwings. The different wings are playing different roles in flight: forewings have a principal role in manoeuvrability and hindwings serve mainly for acceleration. Therefore it is possible that forewing asymmetry can influence flight abilities. Males with a good manoeuvrability can fight more efficiently with rivals and acquire mates more easily (CONVEY, 1989), although our results do not unanimously support this conclusion. Individuals in wheel position with heavily damaged wings were also observed in several cases, thus FA may not be a good measure of male quality and therefore has no significant effect on mating success. LEUNG & FORBES (1997) came to the conclusion that FA was not related to an

Table II

Models with best fit, the Cormack-Jolly-Seber and the nested models used in likelihood ratio tests. Abbreviations: AICc – Akaike Information Criterion, Par – parameters, S – survival rate, P – recapture rate, g – group, t –time, effort – no. of hours spent daily with observation

Model	AICc	No. Par	Deviance
$S_{.}, P_{g+t}$	631.6	11	326.0
S_{g}, P_{g+t}	633.8	12	326.0
$S_{.}, P_{t}$	634.9	10	331.5
S_{t}, P_{g+t}	635.5	16	318.6
$S_{.}, P_{g}$	640.6	3	352.1
$S_{.}, P_{g+effort}$	642.4	4	351.9
S_{g*t}, P_{g*t}	672.5	34	310.1

index of quality, the wet mass of newly emerged or mature adult damselflies. CORDERO et al. (2002) reported that in the case of *Ischnura graellsii* FA was not an important correlate of lifetime mating success.

In most studies differences of recapture and survival rates of males and females have been investigated. According to FINCKE (1986) no differences in survival between sexes should be expected to occur in most populations of Odonata. However, empirical results seem to contradict this assumption. WAAGE (1972) reported that males of territorial damselfly *Calopteryx maculata* had lower survival rates than females. In an *I. elegans* population the probability of daily survival of males was higher than that of females (ANHOLT et al., 2001). The probability of daily survival did not differ between sexes in *C. puella* (ANHOLT et al., 2001) and *Ceriagrion tenellum* (ANDRES & CORDERO, 2001). STOKS (2001b) found that during maturation females of *Lestes sponsa* had slightly lower daily survival probabilities than males, which generated male-biased mature sex ratio. In mature populations he found equal survival for males and females in one field population, while in the other, mature survival probabilities were higher in males than in females.

The model selection with MARK showed that the survival rate of the two male groups was the same and constant over time. The daily survival rates of both solitary and mated males were high as revealed by the model with the best fit. The high survival rates could be a result of the favourable weather conditions (dry, warm and sunny) during the study period (THOMPSON, 1990). Similar high daily survival rates were found in the case of *Hetaerina cruentata* (CÓRDOBA-AGUILAR, 1994), *I. elegans* and *C. puella* (ANHOLT et al., 2001).

Higher recapture rates for males have been reported widely in damselflies (PARR & PARR, 1972; GARRISON, 1978; ANHOLT, 1997; ANDRÉS & CORDERO, 2001; STOKS, 2001a), only DUFFY (1994) reported higher recapture rate for females. In the background of low female recapture rates lies the more cryptic behaviour of females, as well as the fact that they spend less time at the water's edge and more time with feeding on adjacent areas (ANHOLT, 1992). In damselflies, females come to the water for oviposition, between visits they stay away from the pond to mature a new clutch (BANKS & THOMPSON, 1987). In one study of *I. elegans* the recapture rates for males and females were similar (ANHOLT et al., 2001).

The higher recapture rate of mated individuals over solitary ones can be associated with the territorial behaviour of mated males. Territory holders are more conspicuous

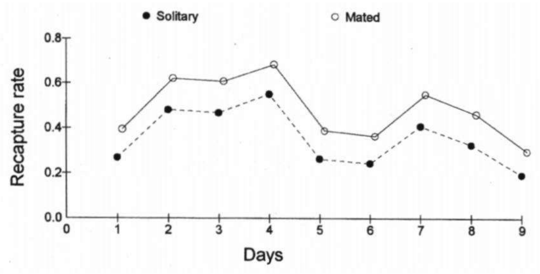

Fig. 2. Recapture rate of mated and unmated *L. fulva* males according to the S., P_{g*t} model, where the survival rate (S) was constant and the recapture rate (P) was different in the two male groups (g) and varied with time (t).

at oviposition sites where they defend a small area with patrol flights and perching on sites with good visibility options. Males engaged in mating, in wheel position or guarding female during her oviposition are also easier to observe than solitary ones. The behaviour of solitary males in this study and that of females observed in other studies seem to be similar in a way that both of them behave inconspicuously and spend a lot of time far from the oviposition site. On the other hand we cannot exclude the effect of a temporal emigration of solitary males on their lower recapture rate. As the recapture rates of both male groups were running in a parallel way (Fig. 2) and the observation effort did not affect it, it is possible that both are influenced by a common external variable (like weather).

Past reproductive success is thought to be an important factor in habitat selection and breeding fidelity. Among more correlational studies covering different taxa there are just a few experimental manipulations of reproductive success (e.g. SWITZER, 1997; BOLLINGER & GAVIN, 1989) that controlled other interacting factors, but their findings seem to be reliable. A relevant example is the study of SWITZER (1997) on *Perithemis tenera*, where males prevented from mating were much more likely to change sites in the following day than control ones that were allowed to mate. This could provide an other explanation why unpaired males in our study were seen less frequently, although their survival was similar to the mated males.

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