Eur. J. Entomol. **102**: 707–712, 2005
ISSN 1210-5759

Fluctuating asymmetry, body size, reproductive period and life time mating success of males of *Cercion lindeni* (Odonata: Coenagrionidae)

GIANMARIA CARCHINI[1], MARCO Di DOMENICO[1], FLAVIA CHIAROTTI[2], CARLA TANZILLI[1] and TIZIANA PACIONE[1]

[1]Dipartimento di Biologia, Università "Tor Vergata", via della Ricerca scientifica snc, I-00133, Rome, Italy;
e-mail carchini@uniroma2.it

[2]Istituto Superiore di Sanità, Dipartimento di Biologia Cellulare e Neuroscienze, Viale Regina Elena 299, I-00161, Rome, Italy

Key words. Life time mating success, body size, reproductive period, fluctuating asymmetry, Odonata, Coenagrionidae, dragonfly

Abstract. Mating success is linked to reproductive success in males, but parameters influencing it are poorly known. The relationships between lifetime mating success (LMS), fluctuating asymmetry (FA), body size (SIZE), reproductive period (RP) and emergence date (MD) of males of *Cercion lindeni* were investigated. Males were marked and photographed in their pre-reproductive period, and their matings monitored. RP was assumed to be the period between the MD and the last sighting of each individual. Three different FA measures and the size of each individual were determined. The results showed that the individuals not present at the pond during the reproductive period had a higher FA (but not for meristic characters) than those present. For those individuals actually involved in reproductive activity, LMS was only positively correlated with RP, which was negatively related with MD, and this with SIZE.

INTRODUCTION

The linkage between fluctuating asymmetry (FA), i.e. small random deviations from perfect symmetry, and several biological phenomena, including reproductive success, has been highlighted several times in different taxa (Møller, 1997; Møller & Swaddle, 1997; Møller & Thornhill, 1998). However, the predictive value of FA needs to be treated with caution, both because of the vulnerability of FA assessment to measurement error and a possible bias against the publication of studies that fail to find a correlation between FA and fitness (Houle, 1998; Palmer, 1999; Simmons et al., 1999). The studies on FA in Odonata have given contradictory results regarding the correlation with mating success: negative correlation in *Coenagrion puella* (L., 1758) (Harvey & Walsh, 1993), *Ischnura denticollis* (Burmeister, 1839) (Cordoba-Aguilar, 1995) and *Calopteryx maculata* Beauvois, 1805 (Beck & Pruett-Jones, 2002); no correlation in *Coenagrion resolutum* (Sèlys, 1876) (Forbes et al., 1997), *Platycipha caligata* (Sèlys, 1853) (Jennions, 1998), *Xanthocnemis zealandica* (MacLachlan, 1873) (Hardersen, 2000), *Ischnura elegans* (Vander Linden, 1823) (Carchini et al., 2000), *Coenagrion scitulum* (Rambur, 1842) (Carchini et al., 2001) and *Ischnura graellsii* (Rambur, 1842) (Cordero et al., 2002). Recently, Szállassy et al. (2003) reported contradictory results for *Libellula fulva* Müller, 1764, in which there was a negative correlation between mating success and FA of forewing length, but not between mating success and FA of hindwing length.

There are two different approaches to the study of mating success: instantaneous or short term mating success (SMS), in which mated and non-mated individuals, caught over a short period of time, are compared with each other, and long term or life time mating success (LMS), in which the total matings of individuals are recorded over their entire reproductive life span. SMS and LMS are the "cross-sectional" and "longitudinal" data of Arnold & Wade (1984), who warned against extrapolating from results obtained over a short sample period (SMS, in our case) to a longer time span (LMS in our case). In the above cited papers LMS was only assessed in *C. puella*, *P. caligata* and *I. graellsii*; SMS in the remaining species. Furthermore, often only FA or FA plus size were considered in relation to mating success, and not other potentially relevant variables.

The aim of this study was to assess the relationships, if any, of LMS with several individual characteristics: size, emergence date, reproductive life span and FA. FA was assessed using both meristic and continuous measurements, and in the latter case by using a recently proposed method (Van Dongen, 2000), which gives estimates of individual FA values corrected for measurement errors. A population of *Cercion lindeni* (Sèlys, 1848) was studied. It is a Mediterranean species with a summer reproductive period (Askew, 1988), whose reproductive behaviour was studied by Utzeri et al. (1983) at the same pond where this study was made. After emergence, adults spend about one week in the pre-reproductive period, when, as in other Coenagrionidae species, they have a paler colour than the sexually mature individuals. The latter remain at a pond for weeks, probably for their remaining life span. The sex ratio at a pond during the reproductive period is highly biased towards males, causing competition for mates as there are few females present each day at a pond.

MATERIAL AND METHODS

Collection of field data

Males were collected at pond no. 5 on the Castel Porziano estate (SITAC pond list, code T1) near Rome, at 67 m above sea level, longitude 12°27´E, latitude 41°35´N. Daily data on temperatures (maximum and minimum), wind velocity and rain were obtained from the estate administration. The individuals were caught in the pre-reproductive period, i.e. when still pale in colour but not teneral, and their right and left hind wings were photographed (Nikon camera with Micronikkor 60 mm lens), while a small glass slide was placed on the wing to press (gently) it against the background. A 15 mm segment of graph paper was used as a scale and was photographed with each wing in order to take into consideration differences in focusing on the right and left wings or wings of different individuals. Afterwards, a permanent non-toxic pencil was used to uniquely number a hind wing of each individual before it was released. Individuals damaged by handling, or unable to fly were eliminated from our samples. No individuals in our samples were infested by water mites. The collection, photographs, marking and releasing were done on the shore of the pond. Marking was done on 4, 12, 13, 23, 26 June and from 7 to 9 July 1997. After the first marking two people checked the activity of the marked individuals at the pond each day continuously from 10 a.m. to 5 p.m., recording the sightings of marked individuals and their mating. This continued until the last week of July when no marked individuals were seen again. The small dimensions (about 25 m × 16 m) of the roughly elliptical pond, and absence of trees or shrubs on shores, made it easy to check (with short focus binoculars) the males, which usually spend all day on the pond and do not mate more than once a day (Utzeri et al., 1983). For each individual, the data collected were the marking date (MD), the reproductive period (RP) assessed from the span between MD and the last day on which that individual was seen and number of matings, i.e. the life time mating success (LMS).

Laboratory measurements

Data were obtained from the photographs of both hindwings of each individual. The distance between the insertion of the radius (R) vein (or R1 vein according to the Tylliard-Fraser definition) on the arculus and the insertion of the same vein on the proximal corner of the pterostigma was measured. Furthermore, a fixed 15 mm segment of the graph paper was measured. All distances on digitised (Nikon scanner) negatives were measured twice with an on screen precision of 1 pixel = 0.018 mm using an image analyzer software (Image Pro-plus 3.1). In accordance with David et al. (1999), all measurements on the same individual were made during the same session to minimize session biases. The wing cells between costa and subcosta veins distal to the pterostigma (pterostigma field), and between the cubital vein and the distal projection of the discoidal cell (margin field) were numbered twice by the "tag and count" software routine. A third count was required in the few cases in which a mismatch occurred. Fig. 1 shows how the measurements were taken. The data collected in the laboratory were, for both right and left hind wings of each individual, two measurements of each wing distance and the number of cells in the two above mentioned wing fields.

Data analysis

Each wing distance was corrected using the mean of two measurements of the fixed 15 mm segment of graph paper in order to avoid errors due to different focusing on right and left wings and on different individuals. Because of the strong correlation between wing length and body size present in Coenagrionidae species (Fincke, 1982; Cordero, 1994), the mean of the four wing lengths (two for each wing) for each individual was used as the measure of individual size (SIZE). The right minus left (R – L) difference in the number of cells was used as the measure of fluctuating asymmetry for the pterostigma (FAP) and margin fields (FAM), both assumed to be free from measurement error. The (R – L) difference between the distance from arculus to pterostigma was taken as the measure of fluctuating asymmetry for wing length (FAL); individual estimates corrected for measurement error were calculated from the repeated measures of the same wing length on each side according to the Van Dongen (2000) method. All FA measures were tested for normality, and indices of skewness and kurtosis computed for deviations from normal values. The presence of directional asymmetry (DA) and of true FA were tested for all FA measures. The Shapiro-Wilk test was used to verify the normality of the distribution of variables; and paired t-test used to determine the presence of directional asymmetry (DA) for FA measures, plus the mixed model ANOVA to take into account measurement errors in the FAL (Palmer, 1994). The Wilcoxon test was used to assess the presence of true FA in all FA measures, instead of a t-test as suggested by Pomory (1997), in order to take into account the non-normality of the distribution of maximum-minimum differences. The Spearman rank order correlation test (r_s) was used to assess simple relationships among variables. Multiple relationships between re-sighting of individuals (Yes / No) and FAL, FAP, FAM, SIZE and MD were determined using a stepwise logistic multiple regression analysis. In this analysis FA measures were expressed as the absolute difference |R – L|, and were subsequently categorized, as well as SIZE, on the basis of the centile maximising the difference in the distributions of re-sighted vs. never re-sighted individuals. The odds ratios (OR) with 95% confidence intervals (CI) were computed, on the basis of the selected logistic regression model. Because both LMS and RP are count dependent variables, a stepwise Poisson regression analysis was used to assess multiple relationships between LMS (as dependent variable) and FAL, FAP, FAM, SIZE, MD and RP, and between RP (as dependent variable) and FAL, FAP, FAM, SIZE and MD. A stepwise multiple regression analysis was used to assess multiple relationships between the daily mating rate (i.e. LMS/RP, a continuous dependent variable) and FAL, FAP, FAM, SIZE, MD and RP. In all multifactorial analyses FA was expressed as the absolute difference |R – L|, and the forward stepwise procedure applied in order to evaluate which of the many potential predictor variables was independently and significantly associated with the dependent (response) variable, taking into account the multicollinearity problem. The criteria for including or excluding the variables from the logistic, Poisson and linear regression models

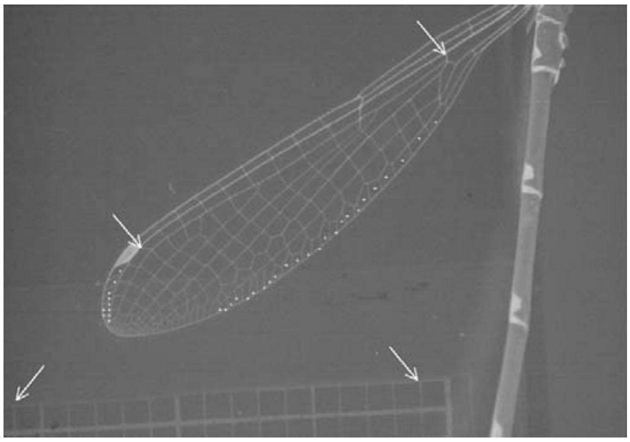

Fig. 1. Digitised image of a hind wing of a male of *Cercion lindeni*. Arrows indicate the two wing points (arculus and proximal corner of the pterostigma), and the 15 mm segment from which length measurements were made. Crosses indicate the wing cells of the two wing fields which were counted.

TABLE 1. Results of normality test, skewness and kurtosis tests, and tests on true fluctuating asymmetry (FA) and the presence of directional asymmetry (DA). FAL – fluctuating asymmetry in wing length; FAP – fluctuating asymmetry for pterostigma field; FAM – fluctuating asymmetry for margin field.

	Shapiro-Wilk test		Skewness[a]		Kurtosis[a]		FA[b]		DA	
	W	*P*	Index	Index/SE	Index	Index/SE	Wilcoxon	*P*	paired t-test	*P*
FAL	0.983	0.511	0.08	0.466	0.04	0.103	0.0 (n = 187)	0.000	0.49 [c]	0.628
FAP	0.963	0.002	–0.03	–0.185	0.37	1.020	0.0 (n = 130)	0.000	0.08	0.934
FAM	0.950	0.000	–0.02	–0.092	–0.44	–1.196	0.0 (n = 138)	0.000	–1.11	0.267

[a] The expected value for skewness is zero for a symmetric distribution, and the expected value for kurtosis is zero for a normal distribution. The ratio of the index to its SE can be read roughly as a standardized score from a normal distribution. Absolute values exceeding 2 are unusual for samples coming from normal populations. [b] In parentheses the number of non-zero differences on which the test is based is reported. [c] Paired t-test is equivalent to the F test of a mixed-model ANOVA, which treats the individual as random blocking factor, the side as fixed factor and the replication as random factor nested under individual and side. Main effect of side: $F_{(1,186)} = 0.24$, $P = 0.628$.

were: entry criterion p < 0.10, removal criterion p > 0.15. Finally, Levene's test was used to test for stabilizing selection on size and mating success, by analysing the differences in variability among three LMS groups (0 matings "0" vs. 1 matings "1" vs. 2 or more matings "2+"). Bonferroni's correction was applied for multiple comparisons. All tests were two-tailed.

RESULTS

For a total of 187 individuals, FAL was normally distributed, FAP and FAM had normal skewness and kurtosis indices and all FA measures had actual FA and no DA (Table 1). There was no correlation between the three FA measures (absolute values): FAL vs. FAP, $r_s = 0.109$, N = 187, $P = 0.139$; FAL vs. FAM, $r_s = 0.142$, N = 181, $P = 0.056$; FAP vs. FAM, $r_s = -0.090$, N = 181, $P = 0.228$. SIZE of 187 individuals ranged from 10.45 to 14.37 mm, and was not normally distributed, showing a slight negative skewness (skewness index = –0.44, index/SE = –2.442; Shapiro-Wilk test: $W = 0.970$, $P = 0.023$). However, the SIZE distribution in each of the marking periods (i.e. June 4, June 12+13, June 23+26 and July 7–9) was normal. SIZE showed a correlation (negative) with MD ($r_s = -0.652$, N = 187, $P < 0.001$) only. Because of the absence of correlation with any FA measure (absolute values), no correction for size was necessary for FA values. RP ranged from 0 to 14 days, and was negatively correlated with MD ($r_s = -0.252$, N = 187, $P < 0.001$) only.

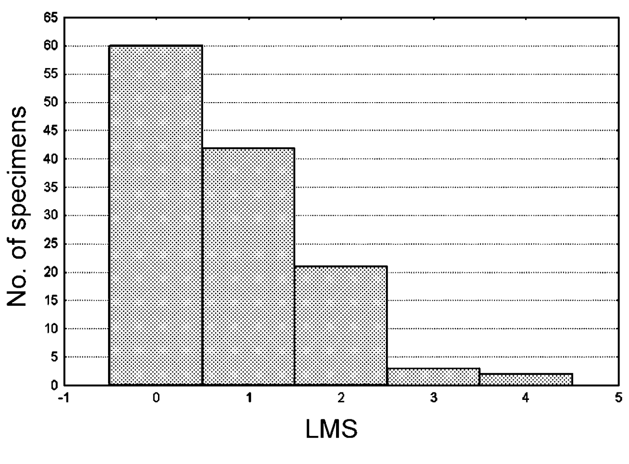

Fig. 2. Frequency distribution of Lifetime Mating Success (LMS) (number of mating) on re-sighted males only.

Fifty-nine individuals were never seen again after marking, so their RP was zero. According to the logistic regression, these 59 individuals did not differ in FAP, FAM, SIZE and MD, but had significantly higher FAL than the 128 re-sighted individuals (OR = 2.02, 95% CI = 1.01–4.05, Z = 1.99, $P = 0.047$; the OR refers to absolute FAL > 0.05 mm vs. absolute FAL ≤ 0.05 mm). RP of the 128 re-sighted individuals was negatively correlated with MD ($r_s = -0.589$, N = 128, $P < 0.001$). LMS of the seen again individuals ranged from 0 to 4, and was strongly skewed (Fig. 2).

Poisson regression analysis for all the individuals showed that LMS (which was assumed to be 0 for the individuals not seen again) was affected negatively by FAL, positively by RP and only slightly positively by MD, while FAP, FAM and SIZE did not have any influence on LMS. However, limiting the same analysis to the 128 individuals observed at the pond after marking, LMS was only affected (positively) by RP. For the individuals seen again, a multiple regression analysis showed that the daily mating rate LMS/RP (dependent variable) was only affected (negatively) by RP, but not by FAL, FAP, FAM, SIZE and MD. The Poisson regression analysis for the individuals seen again, but using RP as the dependent variable (and obviously excluding both LMS and LMS/RP from the independent variables), showed that RP was only affected negatively by MD (Table 2). Finally, the comparison of variability in SIZE among the three groups of individuals based on LMS (number of matings "0" vs. "1" and "2+") showed that variability was significantly different (SDs: 0.75 vs. 0.81 vs. 0.50 for "0", "1" and "2+" LMS groups, respectively; Levene's test $F(2,125) = 3.66$, $P = 0.0286$). In particular, only the group of individuals with LMS equal to or greater than two had a significantly smaller variance that the others ($P < 0.05$ for both comparisons).

DISCUSSION AND CONCLUSIONS

The results of the multiple regression analysis of all marked individuals showed that LMS was positively affected by RP and MD and negatively by FAL, as expected if there is an inverse correlation between asym-

TABLE 2. Results of regression analyses of the variables significantly associated with the outcome. LMS – lifetime mating success; MD – marking date; FAL – fluctuating asymmetry of wing length; FAP – fluctuating asymmetry of pterostigma field; FAM – fluctuating asymmetry of margin field; RP – reproductive period.

Model [a]	N	Dependent variable	Independent variable	Partial regression coefficient	*P*
1	181	LMS	RP	0.224	<0.001
			MD	0.027	0.004
			FAL	–8.870	0.038
2	123	LMS	RP	0.100	0.001
3	123	LMS/RP	RP	–0.019	0.010
4	123	RP	MD	–0.030	<0.001

[a] Model 1: Poisson regression. LMS vs. SIZE, MD, FAL, FAP, FAM. All individuals included. Model 2: Poisson regression. LMS vs. SIZE, RP, MD, FAL, FAP, FAM. Individuals not seen again excluded. Model 3: Multiple linear regression. LMS/RP vs. SIZE, RP, MD, FAL, FAP, FAM. Individuals not seen again excluded. Model 4: Poisson regression. RP vs. SIZE, MD, FAL, FAP, FAM. Individuals not seen again excluded.

metry and individual reproductive success. However, when we repeated the analysis using only the individuals seen again, i.e. those individuals actually involved in reproduction, the correlation between FAL and LMS was not significant. Harvey & Walsh (1993) found a negative correlation between LMS and FA in *C. puella*, but they did not report how many of the 497 marked individuals were seen again. In their tests, N varied between 492 and 490, so it is likely that all individuals were considered. In contrast, Jennions (1998), working on *P. caligata*, reported 237 marked individuals but only 147 of which were considered in the assessment of LMS and no correlation with FA was found. The results of Cordero et al. (2002) on *I. graellsii* are not comparable, because they used a different sampling procedure and studied only a few (31) males. The disagreement between the results of Harvey & Walsh (1993) and those of Jennions (1998) may be because the individuals not seen again were not included in the LMS correlation analyses in both studies. In our study, the effect of FA on LMS, when all individuals were considered, appears to be due to the larger FAL values of those individuals not seen again.

The marked individuals that were not seen again at the pond may have died or dispersed but it is not possible to say what happened to them. However, data on male *C. lindeni* movements on the Castel Porziano estate during the reproductive period show that only 2% of the marked individuals were seen again at ponds different from those where they were marked (Carchini et al., 2004). Consequently, we can assume that it is unlikely they dispersed, and the majority of these individuals were probably unable to mature sexually, which accords with the negative correlation between individual FA and individual fitness often recorded in literature. However, there are few such studies on the Odonata and they give contrasting results. Bonn et al. (1996) found a positive correlation between FA and mite parasitism in *C. puella*; Rantala et al. (2000) a negative correlation between FA and encapsulation rate, a defence against infections in insects, in the non-coenagrionidae zygopteran *Calopteryx splendens* (Harris 1782); Hardersen & Wratten (1998) and Hardersen & Frampton (1999) found a positive correlation between carbaryl exposure and FA in wing length or wing cell pattern, depending on experimental conditions in *X. zealandica.* In contrast, Leung & Forbes (1997) did not find a correlation between FA and survival in *Enallagma ebrium* (Hagen 1861).

Considering only the individuals actually involved in the reproductive activity, the Poisson regression analysis showed that LMS was correlated (positively) only with RP. The positive effect of length of reproductive period (or of the longevity) on LMS in Odonata has already been highlighted (Fincke et al., 1997; Corbet, 1999), and recently found in *I. graellsii* by Cordero et al. (2002). However, it is also interesting to know what intrinsic individual characteristics determine RP and, in turn, LMS. The results of the multiple regression show that RP was only correlated (negatively) with MD. Thus individuals that emerged first had a longer RP, as already noted in *C. puella* by Banks & Thompson (1985) and Harvey & Walsh (1993). That the end of the flying season had an effect on the late emerging individuals of our sample can be excluded because *C. lindeni* is on the wing until September or even October in Mediterranean areas (Ferreras-Romero, 1991). Furthermore, there were no differences in temperature, occurrence of storms or high winds during the observation period which could have modified dragonfly activity or survival. However, multiple regression analysis showed that LMS/RP, i.e. the daily mating rate, is linked negatively with RP. This means that the reproductive advantage of a long RP diminishes when RP increases, and may compensate for the effect of a longer RP. This has already been noted in *C. puella*, in relation to individual size: small males have a higher daily mating rate but large males survive longer (Banks & Thompson, 1985). Furthermore, these authors noted that early emerging individuals are bigger than those that emerge later. In our case, the compensation was not complete (otherwise, there could be no correlation between LMS and RP), but probably resulted in the lack of correlation between LMS and MD and/or SIZE, even if RP is correlated with MD and this to SIZE. In other words, the first adults in the season are bigger and have longer RP, but only the latter influences the LMS.

The lack of an effect of SIZE on LMS is intriguing. In general, body size is supposed to be positively related to mating success, and a recent analysis on odonate species supports this (Sokolovska et al., 2000). However, Cordero et al. (2002) refute this conclusion with, in particular, reference to non-territorial Odonata, and Thompson & Fincke (2002) strongly criticized the methods of analysis used by Sokolovska et al. (2000). According to Utzeri et al. (1983) *C. lindeni* shows an intermediate type of behaviour, with both territorial and non-territorial males present at a pond at the same time. Furthermore, some individuals were observed alternating between the two behaviours on the same day. So, the lack of a relationship between LMS and SIZE neither contradicts nor confirms the supposed positive link between these variables in territorial species. On the other hand, the lower variance of the more successful individuals may be due to a stabilizing selection for SIZE, as already shown in non territorial Coenagrionidae (Fincke, 1982).

Finally, the three FA measures were not correlated with each other, as is often found in FA studies, and only FAL (i.e. the difference in wing length) and not FAP and FAM (i.e. differences in number of wing cells) had a significant effect. This is surprising. In theory, FA measures of meristic characters appear to be a better choice than continuous characters, if they can be made without error, as in our case. However the simple difference in number of cells proved to be misleading. In some individuals, the number of cells was the same for both wings, but the form of the cells was not or some cells were incompletely divided, so that FAP and FAM underestimated the asymmetry in the wing morphology. The effectiveness of FAL may be because wing length asymmetry probably affects the flight ability of the individuals. However, the average ratio of the FAL (after correction for measurement errors) on wing length was roughly 0.3%, about ten times lower than usually found in FA studies, e. g. in *C. maculata* by Beck & Pruett-Jones (2002) (but without correction for measurement errors). As Coenagrionidae individuals with damaged wings engage in reproductive activity, it is unlikely that such small differences between wings could affect individual fitness. So, FAL might indicate the quality of the individuals.

In conclusion, FA in *C. lindeni* did not significantly affect the LMS of the reproductively active males, but, as predicted, it seems to be negatively linked with the ability of the males to became reproductively active. For the reproducing males, LMS was positively related to RP. However, a reduction in the daily mating rate (LMS/RP) was observed in the longer lived males, diminishing but not annulling, the advantage of a longer RP. As noted in other Coenagrionidae, the first individuals to emerge were larger and had a longer RP, but neither SIZE nor MD appeared to affect per se LMS.

ACKNOWLEDGEMENTS. We wish to thank the Italian Presidency of the Republic for allowing us to conduct this study on the presidential estate of Castel Porziano, and the personnel of the estate for valuable help with the field work. We wish also to thank S. Van Dongen for the details on how to calculate FA estimates corrected for measurement error. This study was funded by a grant from the University of Tor Vergata to G. Carchini, program "Biologia della fauna delle acque dolci e dei suoli".

REFERENCES

ARNOLD S.J. & WADE M.J. 1984: On the measurement of natural and sexual selection: application. *Evolution* **38**: 720–734.

ASKEW R.R. 1988: *The Dragonflies of Europe*. Harley Books, Colchester, 291 pp.

BANKS M.J. & THOMPSON D.J. 1985: Lifetime mating success in the damselfly Coenagrion puella. *Anim. Behav.* **33**: 1175–1183.

BECK M.L. & PRUETT-JONES S. 2002: Fluctuating asymmetry, sexual selection, and survivorship in male dark-winged damselflies. *Ethology* **108**: 779–791.

BONN A., GASSE M., ROLFF J. & MARTENS A. 1996: Increased fluctuating asymmetry in the damselfly Coenagrion puella is correlated with ectoparasitic water mites: Implications for fluctuating asymmetry theory. *Oecologia* **108**: 596–598.

CARCHINI G., CHIAROTTI F., DI DOMENICO M. & PAGANOTTI G. 2000: Fluctuating asymmetry, size and mating success in males of Ischnura elegans (Van der Linden) (Odonata: Coenagrionidae). *Anim. Behav.* **59**: 177–182.

CARCHINI G., CHIAROTTI F., DI DOMENICO M., MATTOCCIA M. & PAGANOTTI G. 2001: Fluctuating asymmetry, mating success, body size and heterozygosity in Coenagrion scitulum (Rambur) (Odonata: Coenagrionidae). *Anim. Behav.* **61**: 661–669.

CARCHINI G., PACIONE T., TANZILLI C., DI DOMENICO M. & SOLIMINI A. 2004: Temporal variation of Odonata species assemblage. *Odonatologica* **33**: 157–168.

CORBET P.S. 1999: *Dragonflies.* Cornell University Press, Ithaca, New York, 829 pp.

CORDERO A. 1994: Reproductive allocation in different-sized adults Ischnura graelsii (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* **23**: 271–276.

CORDERO A., PERÉZ F.J. & ANDRÉS J.A. 2002: The effect of handling damage, mobility, body size and fluctuating asymmetry on lifetime mating success of Ischnura graellsii (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* **31**: 117–128.

CORDOBA-AGUILAR A. 1995: Fluctuating asymmetry in paired and unpaired damselfly males Ischnura denticollis (Burmeister) (Odonata: Coenagrionidae). *J. Ethol.* **13**: 129–132.

DAVID P., HINGLE A., FOWLER K. & POMIANKOWSKI A. 1999: Measurement bias and fluctuating asymmetry estimates. *Anim. Behav.* **57**: 251–253.

FERRERAS-ROMERO M. 1991: Preliminary data on the life history of Cercion lindeni (Sélys) in Southern Spain (Zygoptera: Coenagrionidae). *Odonatologica* **20**: 53–63.

FINCKE O.M. 1982: Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* **10**: 293–302.

FINCKE O.M., WAAGE J.K. & KOENIG W.D. 1997: Natural and sexual selection components of Odonata mating patterns. In Choe J.C. & Crespi B.J. (eds): *The Evolution of Mating System in Insects and Arachnids.* Cambridge University Press, Cambridge, pp. 59–74.

FORBES M., LEUNG B. & SCHALK G. 1997: Fluctuating asymmetry in Coenagrion resolutum (Hagen) in relation to age and male pairing success (Zygoptera: Coenagrionidae). *Odonatologica* **26**: 9–16.

HARDERSEN S. 2000: The role of behavioural ecology of damseflies in the use of fluctuating asymmetry as a bioindicator of water pollution. *Ecol. Entomol.* **25**: 45–53.

HARDERSEN S. & FRAMPTON C.M. 1999: Effects of short term pollution on the level of fluctuating asymmetry – a case study using damselfly. *Entomol. Exp. Appl.* **92**: 1–7.

HARDERSEN S. & WRATTEN S.D. 1998: The effect of carbaryl exposure of the penultimate larval instar of Xantocnemis zealandica on emergence and fluctuating asymmetry. *Ecotoxicology* **7**: 297–304.

HARVEY I.F. & WALSH K.J. 1993: Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly Coenagrion puella (Odonata: Coenagrionidae). *Ecol. Entomol.* **18**: 198–202.

HOULE D. 1998: High enthusiasm and low R-squared. *Evolution* **52**: 1872–1876.

JENNIONS M.D. 1998: Tibial coloration, fluctuating asymmetry and female choice behaviour in the damselfly Platycypha caligata. *Anim. Behav.* **55**: 1517–1528.

LEUNG B. & FORBES M.R. 1997: Fluctuating asymmetry in relation to indices of quality and fitness in the damselfly, Enallagma ebrium (Hagen). *Oecologia* **110**: 472–477.

MØLLER A.P. 1997: Developmental stability and fitness: A review. *Am. Nat.* **149**: 916–932.

MØLLER A.P. & SWADDLE I.P. 1997: *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford, 291 pp.

MØLLER A.P. & THORNHILL R. 1998: Bilateral symmetry and sexual selection: A meta-analysis. *Am. Nat.* **151**: 174–192.

PALMER A.R. 1994: Fluctuating asymmetry analysis: a primer. In Markov T.A. (ed.): *Developmental Instability: Its Origins and Evolutionary Implications*. Kluwer Academic Publishers, Amsterdam, pp. 335–364.

PALMER A.R. 1999: Detecting publication bias in meta-analyses: A case study of fluctuating asymmetry and sexual selection. *Am. Nat.* **154**: 220–233.

POMORY C.M. 1997: Fluctuating asymmetry: Biological relevance or statistical noise? *Anim. Behav.* **54**: 225–227.

RANTALA M.J., KOSKIMAEKI J., TYNKKYNEN K. & SUHONEN J. 2000: Immunocompetence, developmental stability and wingspot size in the damselfly Calopteryx splendens. *Proc. R. Soc. Lond. (B)* **267**: 2453–2457.

SIMMONS L.W., TOMKINS J.L., KOTIAHO J.S. & HUNT J. 1999: Fluctuating paradigm. *Proc. R. Soc. Lond. (B)* **266**: 593–595.

SOKOLOVSKA N., ROWE L. & JOHANSSON F. 2000: Fitness and body size in mature Odonates. *Ecol. Entomol.* **25**: 239–248.

SZÁLLASSY N., BÁRDOSI E., SZABÓ Z. D., SZÉPT T. & DÉVAI G. 2003: Fluctuating asymmetry, survival and mating success in male Libellula fulva Müller (Anisoptera: Libellulidae). *Odonatologica* **32**: 143–151.

THOMPSON D.T. & FINCKE O.M. 2002: Body size and fitness in Odonata, stabilizing selection and a meta-analysis too far? *Ecol. Entomol.* **27**: 378–384.

UTZERI C., FALCHETTI E. & CARCHINI G. 1983: The reproductive behaviour in Coenagrion lindeni (Selys) in Central Italy (Zygoptera: Coenagrionidae). *Odonatologica* **12**: 259–278.

VAN DONGEN S. 2000: Unbiased estimation of individual asymmetry. *J. Evol. Biol.* **13**: 107–112.

Received October 10, 2004; revised January 21, 2005; accepted May 9, 2005