

Diel pattern of activity of *Lestes macrostigma* at a breeding site (Odonata: Lestidae)

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Monitoring methods always recommend gathering data during the maximal activity of adults. Hence monitoring the threatened *Lestes macrostigma* requires knowledge of its activity pattern. Dragonfly “activity” is ambiguous and its intensity can be assessed in different ways, including by the threshold of response to a predator stimulus, i.e. “awareness”. We studied the daily pattern of activity of *L. macrostigma* at the breeding site by monitoring the frequencies of behaviours, especially those of different flights, flight duration and speed, and awareness. We also assessed the abundance together with the probability to detect the species. The pattern of behaviour was characterized by reproduction but also feeding and roosting. Flight activity was more intense in early morning for males, around midday for pairs, and in the evening for males and females. Flight speed was highest around midday. These patterns were related to ambient temperatures and to a trade-off between the needs to mate and to feed. Awareness was almost constant all day long, suggesting new insights on daily activity variations in the Odonata, especially when perching. Slight differences between males and females indicated opposite trends. The pattern of abundance was singularly trimodal. This abundance depends on the true presence at the breeding site and to a probability of detection. The timing of monitoring is therefore not to be related to the activity per se, but to the abundance of adults. We recommend gathering data on *L. macrostigma* during early morning.

Keywords: *Lestes macrostigma*; Odonata; activity; diel pattern; flight; reproductive behaviour; postural adaptation; detection probability; survey; monitoring

Introduction

Lestes macrostigma (Eversmann, 1836) is a threatened stenotopic species (see Lambret, 2010; Lambret, Cohez & Janczak, 2009) inhabiting a disappearing ecosystem in the Mediterranean (Zacharias & Zamparas, 2010). Lambret (2010) underlined that, across its range, two of the major conservation actions for this species are to improve knowledge of its distribution – using surveys – and to assess whether population trends are increasing or decreasing – using monitoring based on the transect method (e.g. Pollard & Yates, 1993) or the occupancy method (McKenzie et al., 2002). Within entomological survey and monitoring (ESM) it is usually required to collect data within the peak(s) of activity of the considered taxon (Odonata: Ketelaar & Plate, 2001; Smallshire & Beynon 2010; Rhopalocera: Manil & Henry 2007) and when ESM focuses on a single species, the

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daily time span is restricted by specific activity pattern (Thompson, Purse & Rouquette, 2003). Identifying a peak of activity implies that one can measure its intensity.

However what exactly constitutes “activity” is not always clearly defined within ESM methods (Bouwman, Groenendijk, Termaat & Plate, 2009; Brooks, 1993; Dolný, 2005; Ketelaar & Plate, 2001; Pont, Faton & Pissavin, 1999; Smallshire & Beynon, 2010; Thompson, Purse & Rouquette, 2003). According to odonatological studies, activity can be understood in different manners. First it is what dragonflies are doing (e.g. perching, fighting, mating, foraging, moving from one habitat to another, dispersing), and the frequency or duration of each activity type can be studied (Higashi, Nomakuchi, Maeda & Yasuda, 1979; Norma-Rashid, 1999; Rehfeldt, 1989; Watanabe, Matsuoka, Susa & Taguchi, 2005). Second, it can reflect flight frequency or duration (Hilfert-Rüppell, 1998; Norma-Rashid, 1999; Watanabe & Matsunami, 1990). Activity is implicitly related to flight behaviour (Corbet, 2004). Recently, Corbet and May (2008) emphasized that perchers (see Corbet, 1962), for instance when feeding, can perch and be active, which implies that only using flights to assess activity may be inappropriate. They suggested that an alteration of response to a predator disturbance defines whether an individual is inactive. A third way to approach activity intensity is therefore to assess the threshold of response – which one can call “awareness” – using, for instance, the distance at which a dragonfly is disturbed. To our knowledge, this has never been used before. Fourth, activity could be assessed using flight speed: a temperate zone Zygopteran flying faster in the middle of the day certainly appears more active than when flying slowly in the morning. Fifth, activity is commonly related to the number of individuals present at the breeding site (Bick, Bick & Hornuff, 1976; Conrad & Pritchard, 1988; De Marco & Resende, 2002; Gorb, 1992, pers. comm; May, 1980; Rehfeldt, 2003; Robinson & Frye, 1986; Testard, 1975; Utzeri, Falchetti & Carchini, 1983). Corbet (2004) highlighted that studying Odonata only at water can provide a misleading idea of their activity pattern. This fifth measure of activity focuses on reproductive behaviour but clearly makes sense because ESM’s are usually carried out at the breeding site, where oviposition, larval growth and emergences occur, and therefore where the autochthony of populations can be explored.

Recent studies emphasize the need to take into account the probability of detecting a species in order to establish realistic trends over the years or comparisons between sites (Bonifait, Defos du Rau & Soulet, 2008; Kéry et al., 2010; van Strien, Termaat, Groenendijk, Mensingb & Kéryc, 2010). Odonate activity depends on ambient temperature, T_a (e.g. De Marco & Resende, 2002; Hilfert-Rüppell, 1998; May, 1980; McKay & Herman, 2008; Pilon, Pilon & Caron, 1995; Sformo & Doak, 2006) and during the day, lestids adapt to T_a and regulate their body temperature T_b by behavioural and postural adaptations (McKay & Herman, 2008; Robert, 1958; Watanabe & Tagushi, 1993). We expect those adaptations to have an impact on the detectability of the species.

The aim of this study was to assess throughout the day, at the breeding site, the following parameters: (i) the nature and frequency of *L. macrostigma* activities and their related flight intensity; (ii) the intensity of activity in terms of flight speed and awareness; (iii) presence; and (iv) exposure to the sun and height of perch, i.e. postural adaptations. We thereby wanted to identify the most favourable time of day for a long-term ESM of *L. macrostigma*.

Materials and methods

Study sites, timing and weather conditions

The study took place in two protected areas of the Camargue, Southern France: the Marais du Vigueirat and the Tour du Valat. The former belongs to the Conservatoire du littoral, i.e. the French coast conservatory, a public establishment. The area is centred on coordinates 43°32′10″N / 04°45′15″E and covers 1200 ha, consisting mainly of marshes. One of these, the Baisse des

Marcells, is a plot surrounded by dams. The surface of its southern part is *c.* 1.5 ha and its bottom is more or less flat, varying between 15 and 28 cm asl (median = 24 cm asl, *n* = 35). The water management consists in the inflow of fresh water from the canal of the Vigueirat from *c.* October to April (valves of ditches between the canal and the plot are open) and evaporation the rest of the year (valves are closed) because of the hot temperature and strong wind of the Camargue (Picon, 1980). This management results in a temporary brackish swamp; during the study period, the water depth varied between 25 and 0 cm (dry soil). Dozens of *Lestes macrostigma* have been seen in the southern part of the Baisse des Marcells every year since 2005. Other encountered Zygoptera are *L. sponsa* Hanseemann, *Sympecma fusca* Vander Linden, *Ischnura elegans* Vander Linden and *I. pumilio* Charpentier. The vegetation is grazed from spring to autumn and includes *Bolboschoenus maritimus* (L.) Palla, *Juncus maritimus* Lam. and *J. subulatus* Forssk, as well as *Schoenoplectus tabernaemontani* (C.C.Gmel) Palla, *Eleocharis palustris* (L.) Roem. & Schult. and *Phragmites australis* (Cav.) Steud.; borders are colonized by *Tamarix gallica* L., *J. acutus* L. and *Arthrocnemum* spp.

The second is an area covering 2560 ha, of which 1845 ha has Regional Natural Reserve status. Located 5 km west of the Marais du Vigueirat (43°30'30"N / 04°40'00"E), both sites are separated by the river Rhône. Over the centuries this river has shaped the area into a set of temporary brackish ponds and marshes of different sizes. *L. macrostigma* is one of the most abundant Odonata and breeds in at least 30 sites in the Tour du Valat. One of them, the Relongues, covers more than 20 ha and its water level depends on rainfall. Other Zygoptera are the same as above but *L. barbarus* (Fabricius) is also present. The vegetation is grazed during winter and consists of *B. maritimus*, *P. australis*, *S. litoralis* (Schrad.) Palla and, on the banks, *J. maritimus*, *T. gallica* and *Arthrocnemum* spp.

Data were gathered between 9 and 30 June 2009 and between 6 June and 21 July 2010, when populations were mature (Lambret, 2010), as it is known that sexual maturity of an individual affects its activity (Mayhew, 1994). Activity may also depend on the age of individuals (May, 1980) but since it was not possible to assess the age of studied animals and since the emergence period lasted in 2010 from 7 to 30 May (Lambret, unpubl.), our dataset reflects a mixture of age classes.

In the Camargue during the study period, solar noon was at *c.* 13:45 h legal time. In summer in France legal time equals solar time plus 2 hours. Hereafter times are given as legal time minus 2 hours. During the study period, the earliest and latest sunrises were at 03:59 h and 04:02 h respectively; the earliest and latest sunsets were at 19:19 h and 19:27 h, respectively. We therefore assumed that the difference of duration between the shortest and the longest day – 8 min – was negligible regarding activity. Time of day was divided into 1-h intervals from 04:00 h to 19:00 h. During each alternate interval, centred on 04:30 h, 06:30 h, 08:30 h, etc., we recorded information on behaviour and numbers of individuals and pairs present (see Assessments, below).

Meteorological conditions affect Odonata activity (Joseph & Lahiri, 1989; Pilon et al., 1995; Robinson & Frye, 1986). Thus, days with rain and/or with cloud coverage over 25% were avoided. Zygoptera can fly into a wind up to 3.5 m s⁻¹ (Hilfert, 1994 in Corbet, 2004, p. 312) but the study site was sheltered by *Tamarix* trees, resulting in a wind speed that was lower at the level of the ground than at the level of the trees, a condition which allows flight activity during windy days (Hilfert-Rüppell, 1998; Pilon et al., 1995). Thus, data were gathered with a wind force up to 3 Beaufort (5.5 m s⁻¹).

Assessments

Three categories of *L. macrostigma* were recognized: males, females and pairs, hereafter noted ♂, ♀ and P, respectively. We studied in all 636 animals or pairs (Table 1).

Table 1. Behaviours of *Lestes macrostigma* throughout the day: frequencies (%) of each behaviour displayed within 5 minutes. Cru & Patr = cruising and patrolling flights, Disp & Dist = wing threat display and disturbance by a conspecific, SpTr & Cop = sperm transfer or copulation. For pairs, only female grooming is shown as they were always the member of the pair which displayed this behaviour, except a single instance when the male did also ($n = 25$).

Category	Behaviour	04:30	06:30	08:30	10:30	12:30	14:30	16:30	18:30 h
♂	Groom	20.69	60.00	26.67	9.68	18.75	20.00	3.33	23.33
	Cru & Patr	72.41	86.67	82.76	45.16	61.29	46.67	60.00	66.67
	Encounter	31.03	36.67	36.67	54.84	25.00	16.67	0.00	20.00
	Disp & Dist	6.90	0.00	3.33	0.00	6.25	0.00	0.00	6.67
	Feed	3.45	36.67	30.00	61.29	62.50	50.00	63.33	83.33
	<i>n</i>	29	30	30	31	32	30	30	30
♀	Groom	13.33	13.33	35.48	29.03	5.88	20.69	23.33	10.00
	Cru & Patr	10.00	23.33	35.48	77.42	23.53	41.38	30.00	66.67
	Encounter	3.33	0.00	3.23	12.90	11.76	3.45	0.00	13.33
	Disp & Dist	0.00	3.33	6.45	6.45	2.94	0.00	0.00	0.00
	Feed	0.00	16.67	48.39	58.06	58.82	62.07	76.67	76.67
	<i>n</i>	30	30	31	31	34	29	30	30
P	Groom ♀	10.34	20.59	4.44	13.33	22.22			
	Cru & Patr	13.79	29.41	42.22	65.52	100			
	Encounter	3.45	5.88	4.44	6.67	44.44			
	Disp & Dist	27.59	17.65	20.00	20.00	11.11			
	Feed	0.00	2.94	2.22	6.67	22.22			
	Reproduction								
	Wait	100	100	93.33	26.67	33.33	0.00		
	SpTr & Cop	0.00	0.00	4.44	53.33	0.00	0.00		
	Oviposit	0.00	0.00	2.22	20.00	66.67	100		
	<i>n</i>	29	34	45	30	9	2		

Animals were found by walking and searching among the vegetation where they usually perch. At first sight, we noted whether or not the animal was exposed to the sun and we assessed the height at which it perched from the water surface or the soil. It was then observed with binoculars for 5 min. If our approach had disturbed the animal, we waited 2 min before starting the 5 min observation. Each behaviour was recorded on a field data form fixed to the forearm, thus allowing the observer also to operate a chronometer. We sorted flight behaviours as cruising and patrolling (*sensu* Watanabe & Matsunami, 1990), feeding, and encountering a single zygopteran or a pair, disregarding for this last type of flight whether or not the focal animal returned to its original perch. If the animal encountered another in the course of cruising, the behaviour was recorded as cruising. The duration of each flight was recorded, and for each instance of cruising, the distance between departure and arrival was estimated. Flight speed was calculated by dividing cruising flight distance by its duration. Disturbance was established when the focal animal, or one or both members of the focal pair, displayed the wing threat or left its perch, apparently due to harassment (e.g. Joseph & Lahiri, 1989; Lutz & Pittman, 1968; McMillan & Arnold, 2003; Robinson & Frye, 1986); in some cases we were not able to see if a disturbed animal displayed the wing threat before flying away. The duration of each instance of grooming was also recorded. For pairs, we noted sperm transfer, copulation and oviposition. At the end of the 5 min, we walked several steps further from the studied animal before we started to search for the next in order to reduce the bias associated with observing the same animal multiple times, i.e. to avoid pseudo-replication (Hurlbert, 1984).

Awareness was studied by finding a perched animal with binoculars as described above. When an animal was localized, we walked toward it until it escaped by flight, and we measured the "disturbing distance", i.e. from its initial position to us, using a rolling metal ruler.

Abundance at the breeding site was assessed by walking a transect across the southern part of the Baisse des Marcells plot. This transect was 100 m long and divided into two subsequent segments of 50 m. At each sighting of an animal, we recorded if it was alone or paired, in order

to calculate the ratio of individuals in pair to the total number of individuals; we also assessed its distance from us in order to assess the detectability, i.e. the probability of detection, assuming that the further we were able to detect an animal, the higher the detectability.

Air temperature and solar radiation were recorded by a Davis Vantage Pro meteorological station which is set in the Marais du Vigueirat.

Statistical analysis

Behavioural data were treated as binary: animal display a type of behaviour (see above) or not. Corresponding results are given as relative frequencies (sum = 100%). Flight duration results are given as median and sample size (n), considering all animals recorded at a given time of day. Subsequently, we focused on animals which flew, and we give the rate of each kind of flight relative to the sum of flight duration of all animals of the same category. Because abundance at the breeding site was studied over several days and the maximum number of individuals was not the same on each day, data are given as frequencies relative to the daily maximum (sum = 100%).

Significance of contingency tables was tested using χ^2 or G-tests. The normality of datasets was tested with the Kolmogorov–Smirnov test. In the case of a Gaussian distribution, we used one-way ANOVA; otherwise, we used the Kruskal–Wallis non-parametric test. Tukey’s and Dunn’s multiple comparison posthoc tests (MCTs), were performed in order to determine which classes, i.e. categories or times of the day, were responsible for significance in one-way ANOVA and Kruskal–Wallis tests, respectively. Correlations were tested with Spearman rank tests. We expected a quadratic pattern of postural adaptations; we therefore used a generalized linear model to study the effect of time of the day t (in minutes) and its squared value t^2 , the category of animal C , and the interaction tC on exposure to solar radiation E and the height at which animals perched H . The equation of the model is given with the values of the estimates and their standard error between brackets.

Statistical tests were performed with GraphPad Prism software but the GLM tests with Statistica software and G-tests with an Excel spreadsheet available from <http://udel.edu/~mcdonald/statgtestind.html> (accessed 16 January 2011).

Results

Flight duration and behaviour frequencies

Grooming

Changes in grooming frequency throughout the day were significantly different between males and females (Table 1; G-test: $G = 21.60$, $df = 7$, $p < 0.0001$). The peak of grooming frequencies occurred at 06:30 h for males and 08:30 h for females and, at those times, the duration devoted to this behaviour was significantly higher for males than at other times (Kruskal–Wallis test: $H = 37.23$, $df = 7$, $p < 0.0001$; Dunn’s MCT: 06:30 h versus 10:30 h: difference in rank sum = 65.12, $p < 0.01$; 06:30 h versus 16:30 h: difference in rank sum = 72.00, $p < 0.01$), but not significantly higher for females (one-way ANOVA: $F = 1.198$, $df_1 = 7$, $df_2 = 237$, $p = 0.2519$). Peak grooming frequency for males was almost twice the peak for females.

Reproduction

The frequency of pairs varied significantly throughout the day (Kruskal–Wallis test: $H = 48.23$, $df = 7$, $p < 0.0001$). It rapidly increased from 04:30 h to reach the highest frequencies between

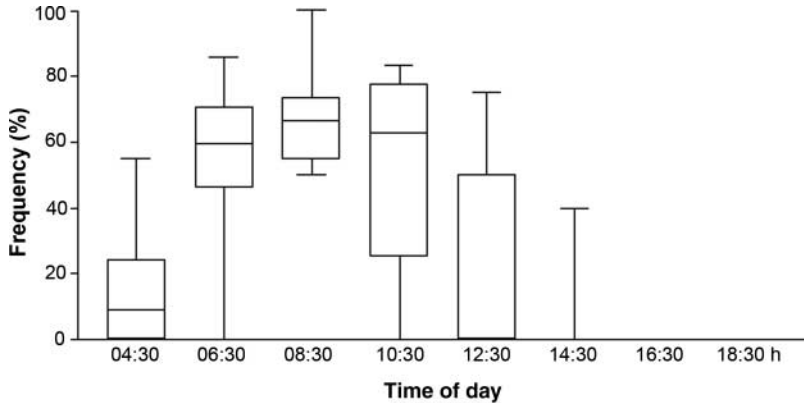


Figure 1. Frequencies of *Lestes macrostigma* pairs throughout the day: ratio of paired individuals to the total number of individuals at a given time of the day. In order to increase the number of replicates both sections of the transect walks were counted separately as well as each date to calculate the medians ($8 \leq n \leq 11$, regarding time of the day).

Table 2. Significant multiple comparison posthoc tests (MCTs): Dunn’s MCT for Kruskal–Wallis tests, Drs = Difference in rank sum; Tukey’s MCT for one-way ANOVA: (a) proportion of paired individuals; (b) total flight duration; (c) feeding duration per 5 minutes; (d) single feeding flight duration, excluding 04:30 h data because of small sample size; (e) abundance at the breeding site; (f) detectability.

		MCT	Drs	<i>p</i>			MCT	<i>q</i>	<i>p</i>		
(a)		06:30 h vs 14:30 h	34.56	< 0.05	(c)		04:30 h vs 16:30 h	7.543	< 0.001		
		06:30 h vs 16:30 h	37.50	< 0.01			06:30 h vs 16:30 h	7.120	< 0.001		
		06:30 h vs 18:30 h	37.50	< 0.01			08:30 h vs 16:30 h	6.129	< 0.001		
		08:30 h vs 14:30 h	40.89	< 0.01			10:30 h vs 16:30 h	6.087	< 0.001		
		08:30 h vs 16:30 h	43.83	< 0.001			12:30 h vs 16:30 h	5.702	< 0.01		
		08:30 h vs 18:30 h	43.83	< 0.001			14:30 h vs 16:30 h	5.251	< 0.01		
		10:30 h vs 16:30 h	33.25	< 0.05			04:30 h vs 18:30 h	9.631	< 0.001		
		10:30 h vs 18:30 h	33.25	< 0.05			06:30 h vs 18:30 h	9.205	< 0.001		
(b)	♂	MCT		Drs	<i>p</i>	(d)	MCT		Drs	<i>p</i>	
			04:30 h vs 14:30 h	60.29	< 0.05			08:30 h vs 18:30 h	8.243	< 0.001	
			06:30 h vs 10:30 h	66.00	< 0.01			10:30 h vs 18:30 h	8.210	< 0.001	
			06:30 h vs 12:30 h	73.54	< 0.001			12:30 h vs 18:30 h	7.861	< 0.001	
			06:30 h vs 14:30 h	108.6	< 0.001			14:30 h vs 18:30 h	7.368	< 0.001	
			06:30 h vs 16:30 h	86.61	< 0.001			MCT		Drs	<i>p</i>
			08:30 h vs 14:30 h	72.52	< 0.001			08:30 h vs 12:30 h	112.5	< 0.05	
			14:30 h vs 18:30 h	-67.51	< 0.01			10:30 h vs 18:30 h	-146.0	< 0.001	
	♀		04:30 h vs 10:30 h	-90.27	< 0.001		12:30 h vs 16:30 h	-74.26	< 0.05		
			04:30 h vs 12:30 h	-62.05	< 0.05		12:30 h vs 18:30 h	-156.6	< 0.001		
			04:30 h vs 14:30 h	-72.12	< 0.01		14:30 h vs 18:30 h	-126.4	< 0.001		
			04:30 h vs 16:30 h	-89.93	< 0.001		16:30 h vs 18:30 h	-82.35	< 0.001		
			04:30 h vs 18:30 h	-130.4	< 0.001	(e)	MCT		Drs	<i>p</i>	
			06:30 h vs 10:30 h	-70.05	< 0.01			04:30 h vs 10:30 h	46.25	< 0.001	
			06:30 h vs 16:30 h	-69.72	< 0.01			04:30 h vs 12:30 h	35.50	< 0.01	
			06:30 h vs 18:30 h	-110.1	< 0.001			04:30 h vs 14:30 h	43.94	< 0.001	
P		08:30 h vs 18:30 h	-76.68	< 0.001	(f)	MCT		Drs	<i>p</i>		
		12:30 h vs 18:30 h	-68.31	< 0.01			04:30 h vs 08:30 h	59.24	< 0.05		
		14:30 h vs 18:30 h	-58.24	< 0.05			04:30 h vs 12:30 h	63.81	< 0.05		
		04:30 h vs 10:30 h	-38.46	< 0.01			04:30 h vs 14:30 h	80.73	< 0.05		
		04:30 h vs 12:30 h	-74.39	< 0.001			04:30 h vs 16:30 h	54.95	< 0.05		
		06:30 h vs 08:30 h	4.721	> 0.05							
		06:30 h vs 10:30 h	-18.75	> 0.05							
		06:30 h vs 12:30 h	-54.68	< 0.01							
	08:30 h vs 10:30 h	-23.47	> 0.05								
	08:30 h vs 12:30 h	-59.40	< 0.01								

Table 3. Flight activity of *Lestes macrostigma* throughout the day: total flight duration per 5 minutes [median (*n*)] and percentage of the duration of each kind relative to the total flight duration of all animals of the same category and same time of the day. Note that these percentages can be given even if the median equals zero. Abbreviations are the same as those in Table 1.

Category	Flights	04:30 h	06:30 h	08:30 h	10:30 h	12:30 h	14:30 h	16:30 h	18:30 h
♂	Duration	6.6 (25)	22.88 (24)	8.69 (26)	2.72 (29)	2.53 (30)	0.69 (30)	1.55 (30)	5.12 (27)
	Cru & Patr	87.37%	85.76%	81.18%	39.56%	39.92%	38.42%	38.03%	44.37%
	Encounter	10.87%	12.68%	15.73%	51.82%	40.92%	21.87%	0.00%	4.41%
	Feed	1.76%	1.56%	3.09%	8.62%	19.16%	39.70%	61.97%	51.23%
♀	Duration	0 (30)	0 (30)	0.84 (30)	1.91 (30)	1.02 (34)	1.4 (29)	1.86 (30)	6.38 (27)
	Cru & Patr	35.71%	67.80%	55.16%	56.07%	33.33%	47.54%	23.49%	55.56%
	Encounter	64.29%	0.00%	0.84%	23.12%	21.16%	4.46%	0.00%	3.05%
	Feed	0.00%	32.20%	44.00%	20.81%	45.51%	48.00%	76.51%	41.39%
P	Duration	0 (28)	0 (34)	0 (44)	1.13 (28)	6.00 (8)			
	Cru & Patr	100%	82.65%	95.13%	93.72%	84.94%			
	Encounter	0.00%	16.07%	2.46%	3.95%	13.50%			
	Feed	0.00%	1.28%	2.42%	2.33%	1.55%			

06:30 h and 10:30 h, and then decreased until 14:30 h (Figure 1, Table 2a). No pairs were ever seen after 14:30 h. Pairs had three successive reproductive behaviours over the course of the day (Table 1). After the male had seized the female, the pair did not show any further motion for several hours, but occasional grooming and changes of perch, an interval we called the “waiting phase”. Pairs then copulated between 08:30 h and 10:30 h. Oviposition started not long after copulation (1.5 to *c.*10 min, *n* = 3 observations) while the male and female were still paired. Females rarely deposited eggs alone (14.29%, *n* = 14). Non-contact guarding was never observed.

Flights

Disregarding time of the day, the total flight duration per 5 min was higher for males than for females and pairs (Table 3; one-way ANOVA: $F = 18.32$, $df_1 = 2$, $df_2 = 412$, $p < 0.0001$; Tukey multiple comparison post hoc test: ♂ versus ♀: $q = 7.753$, $p < 0.001$; ♂ versus P: $q = 6.055$, $p < 0.001$; ♀ versus P: $q = 0.2597$, $p > 0.05$). It varied significantly throughout the day for all categories (Table 1; Kruskal–Wallis test: ♂: $H = 52.24$, $df = 7$, $p < 0.0001$; ♀: $H = 74.42$, $df = 7$, $p < 0.0001$; P: $H = 32.11$, $df = 4$, $p < 0.0001$; Table 2b). For males, flight duration rapidly increased from 04:30 h to reach its maximum at 06:30 h and then decreased toward 14:30 h; it then increased again toward the evening. Females flew for longer periods at 10:30 h, 16:30 h and 18:30 h. Pairs flew for longer periods at 12:30 h.

Cruising flights were much more abundant than patrolling flights (respectively 93.71% and 6.29%, *n* = 795). Most patrolling flights were executed by males (76.00%, *n* = 50) but their rate relative to all flights of both types – cruising and patrolling – did not differ between sexes ($\chi^2 = 1.129$, $df = 1$, $p = 0.288$). Pairs rarely patrolled (0.69%, *n* = 145). Taking both cruising and patrolling flights together, the pattern of their frequency varied significantly between categories (Table 1; G-test: $G = 357.68$, $df = 14$, $p < 0.0001$). Males cruised and patrolled more frequently and for longer periods from 04:30 h to 08:30 h than during the rest of the day (Tables 1, 3). Females cruised more frequently at 10:30 h and 18:30 h and longer at 18:30 h. Pairs cruised more frequently and for longer periods at 12:30 h.

The pattern of encounter flight frequencies differed significantly among categories (Table 1; G-test: $G = 118.54$, $df = 14$, $p < 0.0001$). The highest frequencies of encounter flights were observed in males, especially in the first half of the day with a peak at 10:30 h, in pairs at 12:30 h and, to a smaller degree, by females at 10:30 h (Table 1). Encounter flights represented a higher proportion of total flight duration at 10:30 h for males (Table 3). They were targeted at conspecifics,

seldom at *Lestes sponsa* (respectively 90.57% and 9.43%, $n = 106$) and never at *Sympetma fusca* or at *Ischnura* spp. Focusing on conspecific encountering flights, individuals were more frequently targeted than pairs (respectively 79.17% and 20.83%, $n = 96$).

Feeding flights of pairs were infrequent, initiated by the male, and sometimes successful. The pattern of feeding flight frequencies was the same for males and females (Table 1; G-test: $G = 19.82$, $df = 7$, $p = 0.0060$). This behaviour was more frequent toward the evening and, pooling male and female durations, the time devoted per 5 min to catch prey was higher at 16:30 h and 18:30 h (one-way ANOVA: $F = 12.35$, $df_1 = 7$, $df_2 = 471$, $p < 0.0001$; Table 2c). Furthermore, the duration of feeding flights was higher in the evening than the rest of the day (Kruskal–Wallis test, excluding 04:30 h data because of small sample size: $H = 67.81$, $df = 6$, $p < 0.0001$; Table 2d).

Disturbance

Pairs were more frequently disturbed by conspecifics or triggered to display the wing threat – by at least one member of the pair – than were unpaired individuals (respectively 76.56% and 23.44%, $n = 64$). However, these disturbances never resulted in the break-up of pairs. The pattern of disturbance was different among categories (G-test: $G = 56.91$, $df = 14$, $p < 0.0001$): disturbance of pairs decreased from 04:30 h to 14:30 h, that of females increased from 04:30 h to 08:30 h and decreased from 10:30 until evening, and that of males was irregular.

Postures

Males, females and pairs changed their exposure to direct sunlight – and therefore to solar radiation – during the day (Figure 2a). Focusing on males and females only, the best model resulted in $\text{Logit}(E) = at^2 + bt + ctC + d + e\varphi$, with estimates $a = 40.710$ (6.871), $b = -48.405$ (8.124),

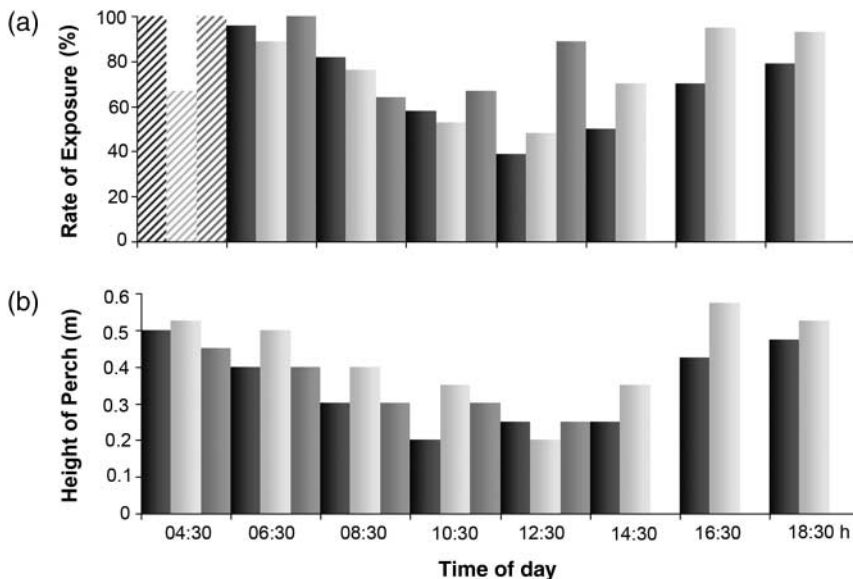


Figure 2. Postural adaptations of *Lestes macrostigma* throughout the day (black: ♂, light grey: ♀, dark grey: pairs). (a) Proportion of animals exposed to solar radiation; (b) height at which animals perched at first sight (median). Sample sizes are given in Table 4. Exposure data are scarce for 04:30 h because the sun was low in the sky and *Tamarix* trees shaded much of the breeding site. From 14:30 h, pairs were too rare or absent.

$c = 3.378$ (1.069), $d = 14.378$ (2.331) and $e = -1.803$ (0.627), where d is the ordinate origin and e its correction for females, the model being based on males. The significant interaction tC suggests that males and females behaved differently: in the morning males perched more in the sun than did females, a situation that was reversed after 12:30 h. However the pattern was similar: exposure frequency was higher in early morning, decreased toward solar noon, then increased toward the evening. When pairs were included in the model, no reliable estimates of a , b , c , d and e were obtained, probably because the size of the dataset was not large enough. Univariate analysis suggests that pairs tended to behave differently from males and females (G-test: $G = 21.97$, $df = 6$, $p = 0.012$): their exposure frequency also decreased from 06:30 h to 08:30 h but then increased toward solar noon, i.e. from copulation toward oviposition.

Regarding the height of perch H (Figure 2b), the best model resulted in $\text{Log}(H) = at^2 + bt + c_C + d$, with estimates $a = 5.672$ (0.534), $b = -6.449$ (0.599), $c = 5.255$ (0.147) and $d_{\sigma} = -0.044$ (0.027), $d_{\varphi} = 0.129$ (0.025), $d_P = 0$, where c is the ordinate origin and d its correction regarding the category; $d_P = 0$ because the model was based on pairs and no correction to the ordinate origin was therefore needed. Males and pairs behaved similarly (d_{σ} 95% CI included zero). In contrast, d was higher for females, indicating that they perched at greater heights. There was no influence of tC , indicating that males, females and pairs followed the same pattern: the height at which animals perched was higher at 04:30 h, decreased toward solar noon, and increased toward 18:30 h.

Ambient temperature and solar radiation varied significantly during the day (Kruskal–Wallis test: T_a : $H = 232.7$, $df = 7$, $p < 0.0001$; Sol Rad: $H = 378.9$, $df = 7$, $p < 0.0001$. Spearman rank correlation: $r = 0.6269$, $p < 0.0001$, $n = 447$) both increased from 04:30 h to 10:30–12:30 h and then decreased toward 18:30 h (Table 4).

Flight speed and awareness

Flight speed was highest when temperatures were highest, i.e. 12:30 h (Table 4 and Figure 3). Flight speed was positively correlated with ambient temperature in males, females and pairs (Spearman rank correlations: σ : $r = 0.5531$, $p = 0.0001$, $n = 148$; φ : $r = 0.3846$, $p = 0.0002$, $n = 87$; P : $r = 0.3705$, $p = 0.0036$, $n = 60$).

The disturbing distance of males and females showed significant variations throughout the day, while it remained constant for pairs; furthermore, for males, awareness was highest at 04:30 h and decreased toward the evening. By contrast, awareness for females increased toward 16:30 h (Figure 4; Spearman rank correlations: σ : $r = -0.2950$, $p < 0.0001$, $n = 242$; φ : $r = 0.3813$, $p < 0.0001$, $n = 220$; P : $r = 0.068$, $p = 0.4418$, $n = 131$).

Table 4. Variation of environmental conditions throughout the day for *Lestes macrostigma* individuals for which height of perch and exposure to direct sunlight were recorded. Results are given as a median.

Environmental parameter		04:30 h	06:30 h	08:30 h	10:30 h	12:30 h	14:30 h	16:30 h	18:30 h
T_a (°C)	Height	16.3	19.5	22	24.9	26.6	23.7	23.95	21.4
	Exposure	16.8	19.4	22	25	26.7	23.7	23.8	21.7
Solar radiation (W/m ²)	Height	36	304	653	888	925	709	398	31
	Exposure	72	318	664	890	939	743	419	47.5
UV dose (μW/lumen)	Height	0	0.1	0.4	0.71	0.74	0.39	0.1	0
	Exposure	0	0.1	0.41	0.73	0.75	0.42	0.11	0
n	Height	86	94	104	91	75	61	60	60
	Exposure	13	73	97	83	61	45	41	34

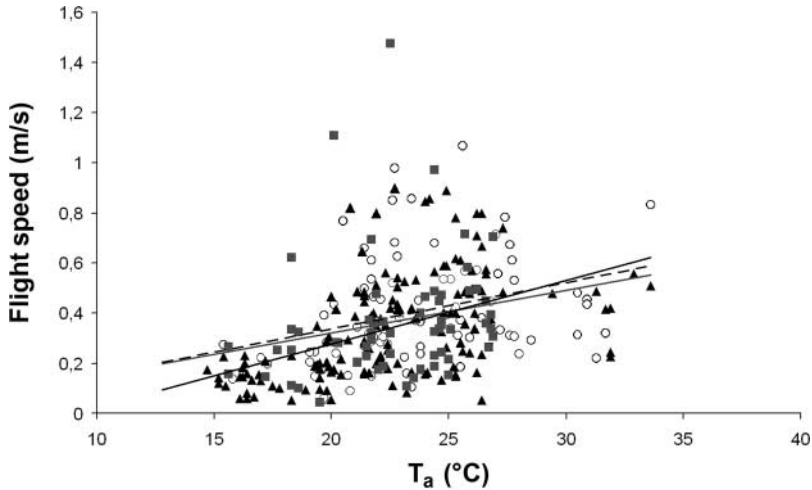


Figure 3. Flight speed of *Lestes macrostigma*: linear regressions of flight speed against ambient temperature (σ : triangle and solid black line; φ : circles and dotted line; pairs: squares and solid grey line).

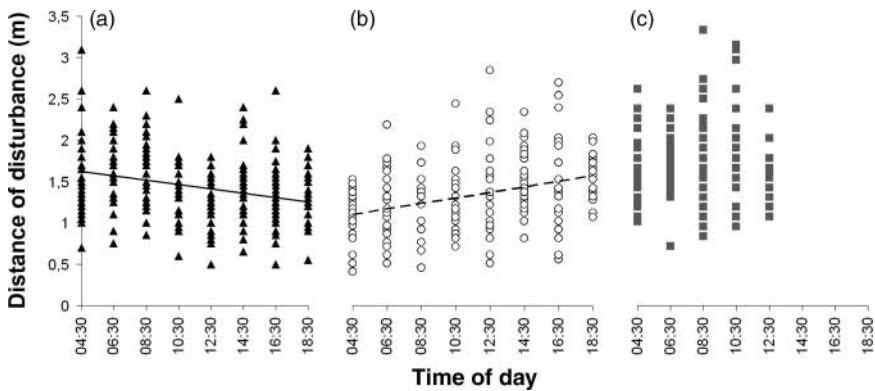


Figure 4. Activity per se, i.e. “awareness” (responsiveness to disturbance) of *Lestes macrostigma* throughout the day: linear regressions of “disturbing distance” against time of day. (a) Males; (b) females; (c) pairs.

Abundance at the breeding site and detectability

The number of adults present at the breeding site varied significantly throughout the day (Kruskal–Wallis test: $H = 36.53$, $df = 7$, $p < 0.0001$) and was highest on average at 04:30 h (Table 2e). Furthermore, the daily maximum always occurred at 04:30 h, though sometimes the same value was also recorded at 12:30 h and 18:30 h (Figure 5).

The distance to which the observer was able to spot animals varied significantly throughout the day (Kruskal–Wallis test: $H = 32.75$, $df = 7$, $p < 0.0001$): detectability was higher at 04:30 h (Table 2f). Very few animals were spotted while in flight (1.82%, $n = 275$), even at 04:30 h, 06:30 h and 18:30 h, when flight activity was more intense.

Discussion

Not surprisingly, most behaviour of *Lestes macrostigma* at the breeding site was related to reproduction. The temporal pattern of reproduction was unimodal, which is common among Odonata (e.g. Doerksen, 1980; Utzeri & Ercoli, 2004). Reproduction involved the following phases: seizure

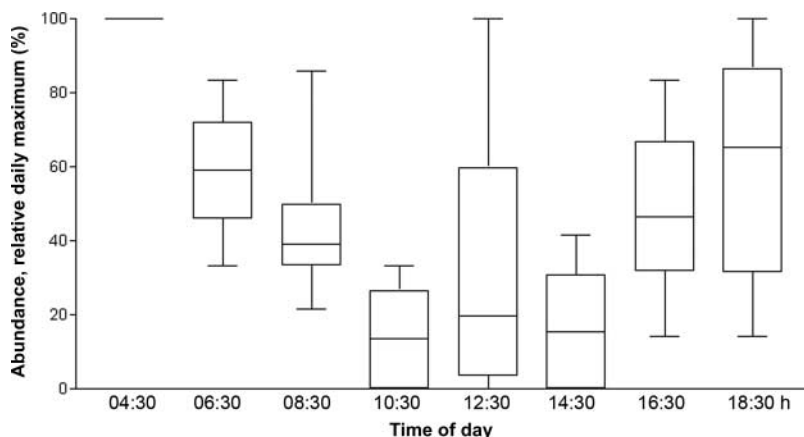


Figure 5. Presence of *Lestes macrostigma* at breeding site throughout the day: abundance relative to the daily maximum recorded on five days (15, 22, 25, 29 and 30 June 2010). Each combination of transect section and date was treated as an independent observation except for 29 and 30 June 2010, which were pooled because of the small number of adults. Resulting sampling size: $n = 8$. Daily maximum: $6 \leq \max \leq 14$, total over the eight samples = 84.

of females by males in the morning, a long waiting phase, copulation and immediate oviposition. *L. macrostigma* males are twice as abundant as females (Lambret, 2010), and Thornhill and Alcock (1983) emphasized the need for males to mate as soon as possible when females are rare. The observed waiting phase is therefore a form of male mate guarding (Ishizawa, 2006). The pattern described above has been already reported in *Enallagma cyathigerum* Charpentier (Doerksen, 1980; Miller & Miller, 1981), *Mortonagrion hirosei* Asahina (Watanabe & Mimura, 2004) and *Sympetrum depressiusculum* (Selys) (Miller et al., 1984); in contrast, a long precopulatory guarding bout is absent in some other Lestids such as *Archilestes grandis* (Rambur), *L. disjunctus australis* Walker and *L. sponsa* (Bick & Bick 1961, 1970; Stoks, De Bruyn & Matthysen, 1997). Reproductive and oviposition behaviour of *L. macrostigma* has been studied by monitoring pairs as long as possible (Lambret & Patry, unpubl.). Although we were unable to measure the total duration of oviposition, we can say that oviposition lasts many minutes (median = 68, min = 26, max = 85, $n = 7$). A split of the pair was most often observed mode of termination of oviposition (94.12%, $n = 17$). The male released the female, apparently after the latter failed, for several minutes, to curve her abdomen in the manner used to insert eggs into the plant (see Matushkina & Lambret, 2011). Although one female was observed ovipositing before she was seized by a male, mated, and oviposited again, we believe that females do not mate more than once during the day. Hence the unimodal reproduction pattern could be explained by this distinctive reproductive cycle which influences both males' and females' timing.

Watanabe and Matsunami (1990) differentiated cruising from revolving flights in that for the latter, the perch on which the animal lands is the same one that it left. They observed in *L. sponsa* an increase in the duration and frequency of flights of both types from 04:00 h to noon followed by a decrease in the afternoon, a pattern which corresponded to that of the number of pairs and therefore to reproductive behaviour. They did not find any significant pattern difference between sexes, while the peak of cruising and patrolling flight frequency of *L. macrostigma* females (peak at 10:30 h) was later than in males (peak at 06:30 h). Cruising and patrolling flights were performed by males more frequently in the morning and for a longer time at 06:30 h, when most pairs formed. Although male patrolling flights have been interpreted to occur for "no reason" (see Furtado, 1974) or thought to be driven by a "need to attack" intruders (Utzeri et al., 1983), Watanabe and Matsunami (1990) assumed that they were related to mate-searching. McMillan and Arnold (2003) noticed that solitary male *L. congener* Hagen exhibit little site tenacity, and they

experienced difficulties keeping them in sight during oviposition. Conrad and Pritchard (1988) observed that males of *Argia vivida* Hagen which had not yet encountered mates continued their flights to new areas. Bick et al. (1976), based on their observation of numerous cruising flights among unpaired males, hypothesized that if these were frequent enough they would be sufficient to encounter a female with neither “active” search nor maintenance of territory. Finally Watanabe and Mimura (2004) noticed that the peak frequency of shift flights of *M. hirosei* males corresponded to the time of coupling, suggesting that females had a diurnal physiological rhythm for the acceptance of males. Hence, we assume that both cruising and patrolling flights are part of the male’s strategy to find a mate. The same may be true for females: their peak of cruising and patrolling flight was at 10:30 h, just before the time of copulation, corresponding to the male’s peak of encountering flight.

The frequency of interactions is related to reproductive activity (Doerksen, 1980; May, 1980; Rehfeldt, 1989; Watanabe & Matsunami, 1990). As the abundance of pairs increases, lone females become less available toward midday and the need for solitary males to find a mate should therefore increase toward 12:30 h. This is reflected in the increase of encountering flights performed by males and the number of wing displays and disturbances undergone by pairs.

Robinson and Frye (1986) witnessed repeated shifts of perch by *Telebasis salva* (Hagen) pairs as well as lone males disturbing them while copulating. Also, ovipositing *A. grandis*, *L. d. australis* and *L. sponsa* often shift from stem to stem (Bick & Bick, 1961, 1970; Stoks et al., 1997). Utzeri and Ercoli (2004) suggested that cruises of pairs could be a response to male harassment in addition to the wing threat display, although solitary males usually fail to split lestad pairs during oviposition (McMillan & Arnold, 2003; Stoks et al., 1997; Utzeri et al., 1983). In accordance with the increasing intensity of male harassment, cruising flights were performed by pairs at an increasing rate up to a maximum at 12:30 h, which corresponds to the main oviposition period. During this period, pairs search for suitable oviposition substrates and thereby often change perch, a behaviour also reported for *E. cyathigerum* (Doerksen, 1980).

Aside from reproduction, a second noteworthy behaviour at the breeding site was feeding. The frequency of feeding flights increased toward the evening and the time allocated to this behaviour was highest at 16:30 h and 18:30 h. *L. macrostigma* has a sit-and-wait foraging tactic throughout the day (see Watanabe et al., 2005) and this increased frequency could be associated with a higher abundance of prey, especially mosquitoes, in the evening (De Marco & Resende, 2002). Mosquitoes are very harassing in Camargue at dusk, although also at dawn, when *L. macrostigma* do not feed. Furthermore, feeding flight frequency started to increase well before dusk and this increase accompanied the decrease in reproductive activity. These two activities do not overlap in time (Higashi et al., 1979; Mayhew, 1994; Watanabe & Mimura, 2004). We assume that this non-overlapping pattern in *L. macrostigma* suggests a trade-off between energetic expenditure and intake – mating and feeding respectively. The latter may be more profitable in the evening, enhancing the probability to survive overnight and mate the day after (see Mayhew, 1998). This hypothesis is supported by the longer duration of feeding flights at 18:30 h, suggesting that *L. macrostigma* invests more in pursuing its prey just before nightfall.

Measured by total flight duration, maximal activity was shown by solitary males in the morning and solitary females in the evening, while that of pairs peaked at solar noon, during oviposition. This finding suggests that when solitary, males and females invest in finding mates and in finding food, respectively; when paired, they invest in copulating and ovipositing. The physiology of mature lestad females is greatly influenced by egg production (Watanabe & Adachi, 1987) and the importance of feeding for females could be related to this egg production. The earlier peaks of grooming frequency and duration for males, compared to females, may also be related to differences in flight activity, because grooming seems to be important before first flights.

Our awareness results give new insight on the variation of Odonata activity throughout the day: in spite of an expected peak in intensity we found that *L. macrostigma* was active all day

long. Slight differences, however, occurred: the intensity of males activity decreased during the day and that of females increased. These results support the hypothesis formulated above and illustrate the usefulness of the new method of assessment of activity proposed by Corbet and May (2008). The probability of detecting intruders depends on the angle at which they are viewed and the background behind them (Switzer & Eason, 2000) but, because these factors should not vary regarding time of day, we assume that this had little impact on our awareness assessment. Hence, we expect *L. macrostigma* to be inactive only when roosting, i.e. at night. Indeed daylight is known to have an impact on dragonfly activity with reduced intensity during cloudy weather (Norma-Rashid, 1999; Pilon et al., 1995), its nocturnal duration (Joseph & Lahiri, 1989), and its pattern during darkness caused by a solar eclipse (Mitra, 1996 in Corbet, 2004), during which it is possible to catch them by hand (J.L. Dommanget, pers. comm.). Our awareness results suggest that perchers, while perching, are not inactive because they still promptly react to any disturbance. This responsiveness is associated with their sit-and-wait foraging tactic (Watanabe et al., 2005) based on an ability to react opportunistically to their prey. Even when assuming a roosting posture, damselflies may be active and still able to detect danger since they choose their perching stem so that their eyes exceed its width (Askew, 1982). It would be interesting to apply Corbet and May's (2008) method to a flyer (see Corbet, 1962) which has an apparent roosting phase during the day – *Anax parthenope* Selys for instance, when avoiding the hottest T_a .

Dragonfly activity is known to depend on T_a and the ability to regulate T_b (e.g. De Marco & Resende, 2002; Hilfert-Rüppell, 1998; May, 1980; McKay & Herman, 2008; Pilon et al., 1995; Sformo & Doak, 2006). Lestids are perchers that regulate T_b by behavioural and postural adaptations, especially via radiation gain and loss – exposure to the sun and in the shade respectively (McKay & Herman, 2008; Robert, 1958; Watanabe & Tagushi, 1993). Furthermore, *L. macrostigma* flew faster at higher T_a , and flight efficiency should increase with temperature (Gibo, 1981). We thereby assume that, more generally, metabolic efficiency should follow the same trend. May (1980) emphasized that temperature influences the costs of mating and, further, that the daily pattern reflects the costs and benefits of activity at a given time of the day. Our exposure results also support the hypothesis of different activity patterns for the sexes. Indeed males perched in sunlight more often than females in the morning and inversely in the afternoon. Also the wing beat of a male in a pair is higher than that of the seized female (Watanabe et al., 2005), and the highest T_b is experienced during copulation and oviposition by males and females, respectively (Ishizawa, 2006). Copulation and oviposition of *L. macrostigma* occurred around solar noon, when pairs again increased their exposure to solar radiation up to 89%, a high frequency which cannot be due to a random perch shift effect. We think that those intense bouts of reproductive behaviour, which are very energy consuming for the male and the female – strong abdominal movements of the male while in copula (P. Lambret, pers. obs.), numerous shifts while in tandem, continuous movements of the female while ovipositing (Matushkina & Lambret, 2011) – are most frequent during the hottest part of the day for energetic reasons. Unless a temperature threshold exists over which flight or reproductive activity declines (Hilfert-Rüppell, 1998; Rehfeldt, 2003), the peak of reproductive behaviour (i.e. highest number of pairs) is often recorded during the hottest part of the day (Conrad & Pritchard, 1988; Ishizawa, 2006; McMillan & Arnold, 2003; Utzeri et al., 1983). Females often bathe as soon as their mate has released them after oviposition (Lambret & Patry, unpubl.), suggesting a need to cool down (Corbet, 2004, p. 284).

The timing of tandem oviposition may also and/or alternatively be influenced by a decrease in the abundance or activity of *L. macrostigma* predators (Corbet, 2004, p. 303) such as the dragonflies *Orthetrum cancellatum* Linné and *Crocothemis erythraea* (Brullé) or the crab spider *Runcinia grammica* C.L. Koch, but data are lacking on this point.

The pattern of abundance of adults at the breeding site was trimodal with peaks at 04:30 h, 12:30 h and 18:30 h. Usually abundance patterns are unimodal or bimodal among Odonata (see

Corbet, 2004, p. 305). Such a trimodal pattern resembles that of *L. d. australis* which can be irregularly bimodal (Bick & Bick, 1961). By contrast, the pattern we found here is truly trimodal: our results are in agreement with those of Lambret (2010). In this latter study, transect counts were restricted to a width of 2.5 m and were made from 03:30 h to 19:30 h and the number of adults at these time were smaller than at 04:30 h and 18:30 h. One can observe as early as 03:00 h some adults, usually covered by dew and absolutely unable to fly despite sensory awareness – they fall down within the vegetation when the observer approaches. They evidently used the breeding site also as a roosting site (Bick & Bick, 1961), as has already been reported for *L. macrostigma* (Schweighofer, Hochebner & Rotheneder, 2010). In Corsica, *L. macrostigma* adults fly to higher branches of *Tamarix* trees at the end of the day, for feeding and for roosting afterward (H. Dupiczak, pers. comm.). This suggests that, although some adults roost at the breeding site, others arrive at the breeding site for reproduction and leave it afterward. On the other hand the trimodal pattern may not be general across sites (see May, 1980) and more precisely across microhabitats: our adult counting was made across the reproductive site, i.e. transect walks perpendicular to the bank, but transect walks parallel to the bank of deeper ponds, where vegetation consists of *Phragmites australis*, *Tamarix gallica* and *Arthrocnemum* spp., i.e. around the reproductive site per se, could give different trends.

The rendezvous phenomenon is common among Odonata (e.g. Chlorophycidae: Rehfeldt, 1989; Lestidae: Stoks et al., 1997; Utzeri & Ercoli, 2004; Coenagrionidae: Bick et al., 1976; Gomphidae: Rehfeldt, 2003; Libellulidae: Norma-Rashid, 1999). In such a pattern, males arrive before females (e.g. Rehfeldt, 2003; Testard, 1975; Utzeri et al., 1983). However, Lambret (2010) reported that the sex ratio of a *L. macrostigma* mature population at the same study site used here in Marais du Vigueirat did not change throughout the day, so males did not precede females. This is contradictory to our hypothesis (see above).

When the wind is strong, *L. macrostigma* shelters in denser *Juncus* spp. clumps (P. Lambret, pers. obs.) or in taller *P. australis* reeds (M. Marinov, pers. comm.). But our data were gathered when wind was not strong enough to induce such behaviour. Movements between habitats are due as well to other exogenous factors, such as T_a and cloud index, but also to an endogenous rhythm (Bick & Bick, 1961; Norma-Rashid, 1999). Between two peaks of a bimodal pattern, individuals can go to other sites to avoid high temperatures (De Marco & Resende, 2002; Rehfeldt, 1989; Watanabe et al., 2005). Lestid pairs often copulate in a different area from where they oviposit (Bick & Bick, 1970; Gower & Kormondy, 1963; McMillan & Arnold, 2003). Contact mate-guarding is effective but costly (Utzeri & Ercoli, 2004) and predation risks may be higher for pairs than for individuals because they represent a bigger target. The lower abundance observed at 08:30 h, 10:30 h and 14:30 h could be due to microhabitat shifts. However, among all pairs monitored from seizure to oviposition (Lambret & Patry, unpubl.), none has been observed to leave the breeding site. The reasons for these periods of lower abundance therefore remain unclear.

Some exogenous parameters may impact the probability of detecting *L. macrostigma*. Sunlight is more intense toward solar noon, especially during June in the Camargue, and this could be a disadvantage for the observer's vision compared to the softer light of the morning and the evening. In the morning, the body and wings of *L. macrostigma* are covered by dew and their wings, highlighted by the sun's rays coming from a low angle, are especially easy to spot. In early morning individuals often beat their wings, producing a sound, not to warn predators (Joseph & Lahiri, 1989) but to remove dew drops (Helitas & Lambret, 2010; Robert, 1958). Some individuals are consequently detected by their sounds. When animals perch lower in the vegetation, they may be more hidden to the observer and less easily detected. These circumstances may explain, at least in part, the higher detectability we observed in the morning. On the other hand, the low percentage of individuals detected in flight suggests that it is unlikely that flight activity had an effect on detectability.

Epilogue

In spite of variation in detection probability related to postural behaviour, and although the habitat shifts of *L. macrostigma* throughout the day remain unclear, we assume that our abundance results reflect the realistic presence at the breeding site. Flight activity does not reduce the probability of detecting *L. macrostigma*, as most of animals were spotted while perching; similarly, neither do metabolic efficiency and awareness. Therefore, the timing of ESM should not be related to activity but simply to presence at water. Finally, peak numbers of individuals were always counted at 04:30 h. Because the size of *L. macrostigma* populations can vary from one year to another (Aguesse, 1961; Cohez et al., 2010; Plattner, 1967), starting investigations at 04:30 h would increase the chance of detecting the presence of this species during a low abundance year, at least at the latitude of this study. The trimodal pattern of presence at the breeding site, along with yearly variations in abundance, could explain the apparent absence of *L. macrostigma* in some years, even when it is rediscovered latter on the same sites (e.g. Befeld, 2010; Faton, Deliry & Dorgère, 2000). Further studies at other sites might determine whether this pattern is found across the species' whole range. In any case, long-term monitoring should be applied strictly at the same time of day from one year to another.

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