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WANDERING AND TERRITORIALITY IN *LIBELLULA DEPRESSA* L. (ANISOPTERA : LIBELLULIDAE)

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Upon returning to the water after maturation, the male of *L. depressa* behaves as a wanderer (i.e. non territorial), but he turns to behave territorial after mating. The territory is established in the place where his female has oviposited. This conclusion is based on : (1) the decrease of the male flight range, (2) the decrease of the inter-perch distance and (3) the decrease of the distance between perch sites and oviposition site, after copulation. If mating is not repeated in the territory in the following days, territorial attachment weakens and the male begins to wander again, until he mates a new female. Territorial behaviour is then shown at the new place. This alternation between wandering and territoriality can be repeated relative to each of successive copulations. The strong aggressiveness shown by the male in the area where he has guarded a female permits him to displace all the other males from that site. Thus, non-contact guarding probably functions in permitting the male to keep control of the territory, which would be lost if another male mated in it while the owner was tandem-guarding a female.

INTRODUCTION

The males of many libellulid species share the feature of establishing territories in parts of the ponds which contain adequate sites for oviposition, where they wait for females. Although traits of the territorial behaviour are known of about 40 libellulids (review of PARR, 1983a, and more recent papers), there are some questions which have remained unresolved so far. One concerns habitat selection by males and/or females. TSUBAKI & ONO (1986) stated that it is difficult to determine whether the male is attracted by a particular territory for its intrinsic characters or because there are females on it. CAMPANELLA & WOLF (1974) outlined that in odonates it is not known whether the male or female makes the initial choice of site for mating and/or ovipositing, and forwarded three hypotheses : (1) the males are able to recognize suitable sites for oviposition at the water, and females go there being attracted by male activity ; (2) the males are primarily involved in the choice of oviposition sites, and males attend them because they are attracted by females ; and (3) both sexes are equally attracted by oviposition sites. None of these hypotheses have been tested so far, nevertheless, it is generally reported that the mature male, as soon as come to the water, spontaneously places his territory in a water area containing one or more oviposition sites (e.g. JACOBS, 1955 ; ITO, 1960 ; ARAI, 1972 ; CAMPANELLA & WOLF, 1974 ; CAMPANELLA, 1975 ; KRUNER, 1977 ; MILLER, 1983 ; SHERMAN, 1983b ; PARR, 1980, 1983b ; VAN BUSKIRK, 1986 ; HARVEY & HUBBERD, 1987). Thus, CAMPANELLA & WOLF's (1974) hypothesis (1) and (3) seem to be maintained as the most probable one. But there is some evidence, in the literature, of strong attraction of males by females : JACOBS (1955) stated : "After copulation ... the female ... may flit around the pond to another site. In any event, the male follows her ..." (p. 569) ; UEDA (1979) reports that after copulation and successful guarding of the female, a wanderer male of *Sympetrum parvulum* "... seemed to establish his own territory at the site where his female had oviposited" (p. 142), and VAN BUSKIRK (1986) recorded 7 guarding males following their females out of their territories and never returning, these reports suggesting that CAMPANELLA & WOLF's (1974) hypothesis (2) might be true. On the other hand, there are several reports of "wanderer" (i.e. non territorial) or satellite males, in territorial libellulids, which are generally interpreted as alternative strategists in high male density conditions, although their fitness seems to be lower than that of territorial males (SHERMAN, 1983b ; MILLER, 1983 ; HARVEY & HUBBARD, 1987 ; CAMPANELLA & WOLF, 1974 ; CAMPANELLA, 1975). These males behave opportunistically, since they do not defend exclusive territories and move around to meet and mate females in other males' territories (PARR, 1980, 1983b ; HIGASHI, 1969 ; HARVEY & HUBBARD, 1987 ; HILTON, 1983 ; UEDA, 1979 ; KOENIG & ALBANO, 1985 ; PEZALLA, 1977 ; KRUNER, 1977 ; MILLER, 1983 ; SAKAGAMI *et al.*, 1984 ; SIVA-JOTHY, 1984). Wanderer and satellite males are sometimes shown to be the younger mature ones in the population (PARR, 1980 ; PARR & PARR, 1974 ; CAMPANELLA, 1975 ; CAMPANELLA & WOLF, 1974) and may change their behaviour into territorial (UEDA, 1979 ; CAMPANELLA, 1975 ; CAMPANELLA & WOLF, 1974).

In this paper we present the behaviour of *Libellula depressa*, in which both territorial (i.e. localized and dominant in a particular area [KAUFMANN, 1983]) and non-territorial males coexist in the same pond, and show that (1) the wanderer unmated male turns to behave territorially in the place where he has guarded an ovipositing female and (2) the switch between the territorial and wanderer behaviours of the older male depends on his previous mating success in a place in the pond.

METHODS

The research was carried out at a pond of ca. 25 m in diametre in Castel Porziano (Roma) between May 13 and June 27, 1985 and May 5 and June 27, 1986. In 1986, 14 mature males were individually marked as they first appeared at the pond, and their behaviour was recorded from their first sighting onwards. Nine of these males might be unmated, as at their first arrival at the pond in the season the black scratches caused by females' tarsi on male abdomens, and which are often seen in mated males, were lacking.

The sites utilized by females to lay eggs and by males to perch were recorded, in order to compare the male's to the female's abilities of choosing areas where oviposition sites were present.

Localization of males was quantified by estimating their average flight ranges and the reciprocal distances of all the perch sites utilized by them, before and after copulation. Also, the distances between perch sites and oviposition site were estimated becore and after each male's copulations. Estimates were carried out by plotting, in the field, the males' flight paths and the positions of the perch and oviposition sites, on a map to scale of the pond. Measurements were then carried out in the laboratory. In this way, we could record all of the flight paths and the perch and oviposition sites for 2-3 males at the same time, even though a measurement taken in this way is of course a rough one.

Dominance of territorial individuals was investigated by recording all aggressive interactions, and their results, between them and invaders.

RESULTS

TEMPORAL PATTERNS OF MALES AND FEMALES

Males attended the pond between 9 : 40 and 13 : 30 hrs, their presence peaking between 11 and 12 hrs (Fig. 1). Exceptionally a male retreated from the pond at 14 : 40, having mated at 13 : 30. Single males spent between 40-285 min at the pond on a single day. One male spent more than 17 hours on 8 non consecutive days out of 18. The duration of the adult life, as estimated by the interval including the marking day and the intermediate day between the last day a male was recorded and the next day of our presence at the pond, averaged 7.8 ± 1.7 days (R = 1-22 ; N = 14), which represents a conservative estimate since at least some males could have attended other ponds after their last sighting at the study pond.

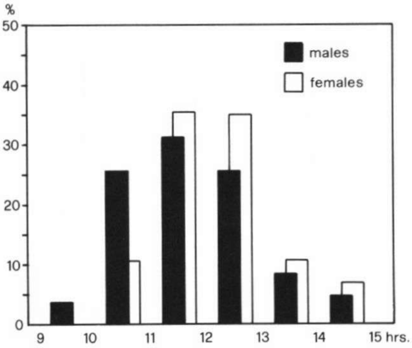


Fig. 1. Hourly temporal patterns of males (N = 105) and females (N = 28).

Females attended the pond between 10 and 15 h, their presence peaking between 11 and 13 h. Thus their hourly distribution roughly overlapped that of the males (Fig. 1). Out of a total 28 recorded females, 13 (46%) mated at the pond and the others oviposited and left the pond without mating.

On cloudy days, both male and female activity was lower.

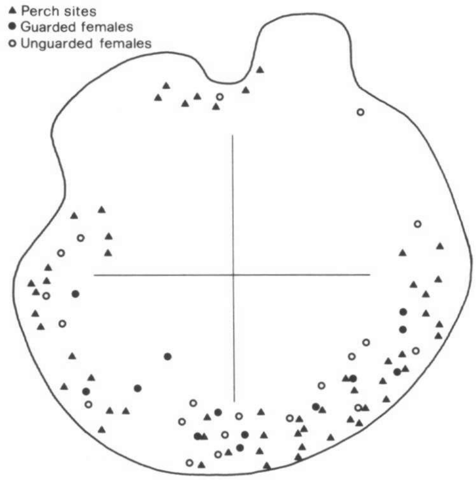


Fig. 2. Spatial patterns of unmated males' perch sites and females' oviposition sites.

SPATIAL PATTERNS OF MALES AND FEMALES

In order to compare the males' to the females' abilities of chosing those areas in the pond which contained suitable oviposition sites, we recorded all the perches of the unmated males and the sites in which either mated (guarded) or unmated (lone) females oviposited (Fig. 2). The differences observed, in the northern versus southern halves of the pond, then in the eastern versus western, then in the N-W, N-E, S-W and S-E quarters, show no significance at the chi-squared test.

BEHAVIOUR OF THE UNMATED MALE

From their first coming to the pond up to their first mating, which occurred later in the same day in some males, but two and three days later in males Y25d and P6d respectively, the males that were assumed as unmated continued alternating between long perching and short flying periods, frequently changing their perch sites. Apparently they flew over the entire pond or a larger part of it, and their perches were very scattered along the shoreline. While either perched or in flight, sometimes males approached other males passing nearby, and "dual flights" occurred (JACOBS, 1955), which could bring the males several metres inland, with the chasing male frequently changing to be chased and vice-versa. Upon returning to the pond, males perched on their previous or another perch, but due to their repeated shifts, there did not appear to be any dominance of either individual in any particular place in the pond. Thus, all the unmated males always behaved as wanderers (HIGASHI, 1969).

MATING BEHAVIOUR

Females coming to the pond flew low above the water and generally behaved as if they were going to oviposit, either doing short dives to the water surface, without dipping their abdomens (these probably being the virgin ones), or actually dipping it (probably the previously mated ones). Upon entering a range of 1.5-2 m from a perched or flying male, they were seized and immediately mated by the latter (N = 13). The intra-male sperm translocation lasted very briefly (UTZERI, 1985) and was always recorded in the tandem male. Copulation averaged 8.1 ± 0.7 seconds ($R = 6\text{-}14$; $N = 13$) and was completely aereal. Six females, with which males firstly mated, oviposited within 5.3 metres from the place where they had been captured, but 3 ended to lay between 7 and 12.6 m far from the place where seizure occurred (chi-squared = 0.44 ; $p > 0.5$). Upon release of the female, always the male followed her until she began to oviposit. All of the mated males were able to overcome take-over of their females by non-contact guarding, but the ovipositions insistently disturbed by other males on average lasted considerably shorter than those of the undisturbed ones ($x = 32.4 \pm 5.1$ sec ; $R = 10\text{-}55$; $N = 9$; $x = 96.5 \pm 10.3$; $R = 72\text{-}122$; $N = 4$, respectively) (Mann-Whitney, $U = 0$; $p < 0.001$). Assuming that (1) the oviposition rate did not decrease with the time elapsing (but see McVEY, 1984 ; MILLER & MILLER, 1985), (2) the duration of the undisturbed oviposition corresponded to complete egg-laying, and (3) females that interrupted oviposition due to male harassment returned to complete oviposition later, but only 46% of total females were mated (cf. above), the amount of potentially fertilizable eggs of the harassed female, that the male probably lost due to sperm displacement, corresponds to 29 seconds of oviposition, which is almost one third of the average full batch of eggs.

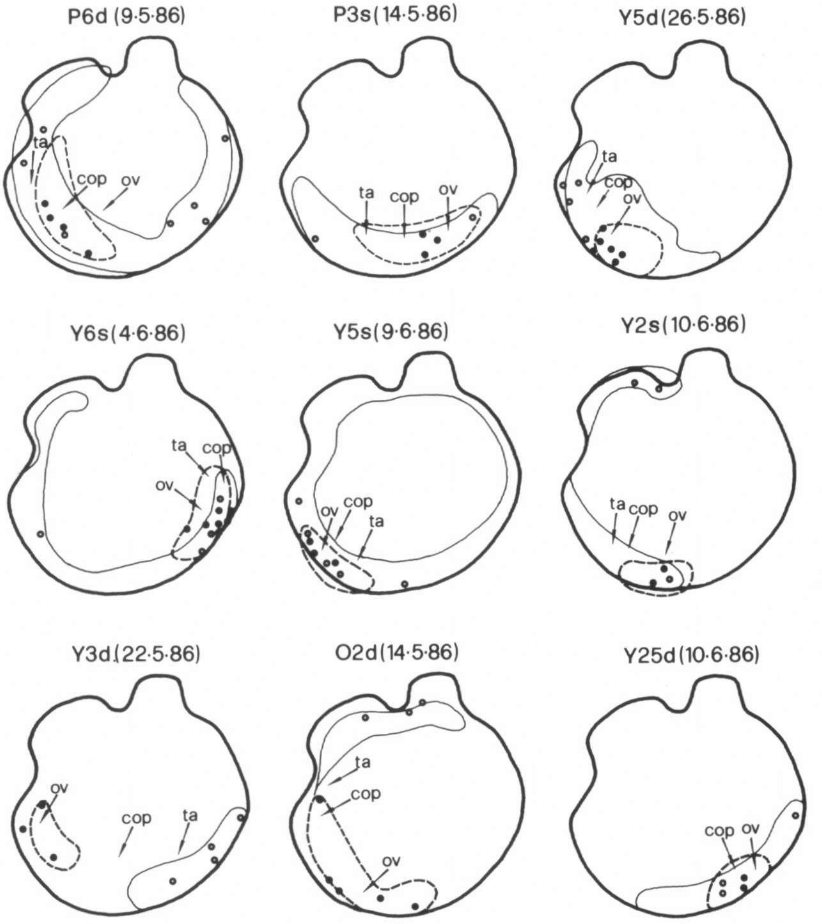
MALE POST-MATING BEHAVIOUR : THE ONSET OF TERRITORIAL BEHAVIOUR

The range of pre- and post-copula flights of all the 9, presumably unmated, males averaged 12.3 ± 1 m ($N = 48$) and 6.4 ± 0.5 m ($N = 44$) respectively, this difference being significant (Mann-Whitney, $z = 4.8$; $p < 0.00003$). A decrease of flight range after copulation was observed in 8 of the 9 males (McNemar test, chi-squared = 4 ; $p < 0.025$) and is significant in 5 (Fig. 3, Tab. I). This means that after copulation, the males tended to restrict their movement.

The average inter-perch distances for all of the same males before and after copulation were 8.5 ± 0.8 m ($N = 68$) and 3.4 ± 0.4 m ($N = 48$) respectively. This difference is significant (Mann-Whitney, $z = 5.69$; $p < 0.00003$). Eight of the 9 males showed more scattered perch sites before than after copulation (McNemar test, chi-squared = 4 ; $p < 0.025$), the difference being significant in 4 (Fig. 3, Tab. II). This means that after copulation the males perched in a restricted area, that is, they became localized.

The distance of the perch sites from the oviposition site before and after copulation averaged 8.7 ± 0.9 m ($N = 35$) and 2.7 ± 0.3 m ($N = 29$) respectively. This difference is also significant (Mann-Whitney, $z = 5.09$; $p < 0.00003$). All of the males showed a decrease of the perching distance from the oviposition site after copulation (McNemar test, chi-squared = 7.1 ; $p < 0.005$), the difference being significant in 5 (Fig. 3, Tab. III). This means that the localization of the males took place near the oviposition sites.

Each of the nine males showed a significant decrease of at least one of the above values (Tabs I, II, III).



P6d (9·5·86) P3s(14·5·86) Y5d(26·5·86)

Y6s(4·6·86) Y5s(9·6·86) Y2s(10·6·86)

Y3d(22·5·86) O2d(14·5·86) Y25d(10·6·86)

Fig. 3. Flight ranges and perch sites before (thin line, open circles) and after (dashed line, black spots) 1st copulation.

Following guarding, the males kept localized near, and defended, the oviposition sites, that is, they behaved territorially, their territories extending for 6-8 m along the shoreline. 55 (91,6%) out of 60 aggressive interactions between territorial and invader males were won by the former, while 4 (6,7%) led to an only temporary displacement of the residents (chi-squared test, $p < 0.001$). Nevertheless, the residents regained their territories soon after. This shows complete dominance of the males in their territories. Only once (1,7%) was a male permanently displaced from his territory. The winner had mated and guarded a female there while the previous owner was absent for a short time. The ability of a freshly mated male to displace a territorial owner was also observed by PARR (1983b) in *Orthetrum coerulescens.*

Table I

Average flight range variation after 1st copulation (m)

Male	Before	After	Significance
P6d	$\bar{x}$ = 13 ± 2.5 R = 3.3-20.2 N = 6	$\bar{x}$ = 7.9 ± 1.7 R = 4.5-12.8 N = 5	U = 7; $p > 0.05$
P3s	$\bar{x}$ = 20 ± 0.9 R = 18.5-21.6 N = 3	$\bar{x}$ = 12 ± 0.8 R = 10.8-13.5 N = 3	U = 0; $p = 0.05$
O2d	$\bar{x}$ = 10.9 ± 1.8 R = 6.2-15.4 N = 5	$\bar{x}$ = 11 ± 0.9 R = 8.9-13.1 N = 4	U = 10; $p > 0.5$
Y3d	$\bar{x}$ = 8.9 ± 1.6 R = 4.7-12.8 N = 5	$\bar{x}$ = 5.5 ± 0.6 R = 4.1-7.1 N = 5	U = 5; $p > 0.05$
Y5d	$\bar{x}$ = 11 ± 1.5 R = 6.6-16.8 N = 6	$\bar{x}$ = 5.5 ± 0.6 R = 4.1-6.8 N = 4	U = 1; $p < 0.05$
Y6s	$\bar{x}$ = 13.8 ± 5.1 R = 2.3-35.1 N = 6	$\bar{x}$ = 7.1 ± 3.2 R = 4.1-11.6 N = 5	U = 11; $p > 0.05$
Y5s	$\bar{x}$ = 16 ± 5 R = 7.8-39.8 N = 6	$\bar{x}$ = 5.3 ± 1 R = 3.5-9.1 N = 5	U = 2; $p < 0.05$
Y25d	$\bar{x}$ = 10.2 ± 0.3 R = 9.3-11.4 N = 5	$\bar{x}$ = 4.1 ± 0.7 R = 1.8-7.1 N = 8	U = 0; $p < 0.05$
Y2s	$\bar{x}$ = 9.2 ± 1.5 R = 3.5-14.8 N = 6	$\bar{x}$ = 3.7 ± 0.7 R = 2.3-5.9 N = 5	U = 2; $p < 0.05$
All together	$\bar{x}$ = 12.3 ± 1 R = 2.3-39.8 N = 48	$\bar{x}$ = 6.4 ± 0.5 R = 1.8-13.5 N = 44	z = 4.80; $p < 0.00003$

Table II

Average inter-perch distance variation after 1st copulation (m)
In brackets the number of perch sites

Male	Before	After	Significance
P6d	$\bar{x}$ = 11.8 ± 2.6 R = 2.3-31.7 N = 21 (7)	$\bar{x}$ = 4.1 ± 0.7 R = 2.1-7.4 N = 6 (4)	$z = 2.54$; $p < 0.01$
P3s	15.1 R = N = 1 (2)	$\bar{x}$ = 2.5 ± 0.2 R = 2.2-2.8 N = 3 (3)	- -
O2d	$\bar{x}$ = 3.8 ± 1 R = 1.6-5.6 N = 3 (3)	$\bar{x}$ = 6.4 ± 1.1 R = 1.3-13.2 N = 10 (5)	$U = 7$; $p > 0.05$
Y3d	$\bar{x}$ = 6.3 ± 1.1 R = 1.3-11.7 N = 10 (5)	$\bar{x}$ = 4.1 ± 0.5 R = 3.1-5.2 N = 3 (3)	$U = 8$; $p > 0.05$
Y5d	$\bar{x}$ = 4 ± 0.8 R = 2.1-6.7 N = 6 (4)	$\bar{x}$ = 1.9 ± 0.2 R = 1-3.1 N = 15 (6)	$U = 12$; $p < 0.01$
Y6s	$\bar{x}$ = 8.7 ± 1.6 R = 1.6-19.3 N = 15 (6)	$\bar{x}$ = 2.2 ± 0.3 R = 1.3-2.9 N = 6 (4)	$U = 11$; $p < 0.01$
Y5s	$\bar{x}$ = 6.4 ± 1 R = 2.1-12.1 N = 10 (5)	$\bar{x}$ = 2.6 ± 0.7 R = 1.3-3.8 N = 3 (3)	$U = 3$; $p < 0.05$
Y25d	9.8 R = N = 1 (2)	1.5 R = N = 1 (2)	- -
Y2s	11.2 R = N = 1 (2)	2.1 R = N = 1 (2)	- -
All together	$\bar{x}$ = 8.5 ± 0.8 R = 1.3-31.7 N = 68 (36)	$\bar{x}$ = 3.4 ± 0.4 R = 1-13.2 N = 48 (32)	$z = 5.69$; $p < 0.00003$

Table III

Average distance variation of perch sites
from oviposition site after 1st copulation (m)

Male	Before	After	Significance
P6d	$\bar{x}$ = 8.9 ± 1 R = 5.8-13.6 N = 7	$\bar{x}$ = 5.2 ± 0.6 R = 3.8-6.9 N = 4	U = 2; $p < 0.05$
P3s	$\bar{x}$ = 8 ± 5.5 R = 2.5-13.5 N = 2	$\bar{x}$ = 2.8 ± 0.8 R = 1.3-4.1 N = 3	- -
O2d	$\bar{x}$ = 18.1 ± 0.8 R = 16.8-19.5 N = 3	$\bar{x}$ = 2.6 ± 0.6 R = 1.3-4.1 N = 4	U = 0; $p < 0.05$
Y3d	$\bar{x}$ = 15.3 ± 1.5 R = 10.6-19.4 N = 5	$\bar{x}$ = 2.6 ± 0.4 R = 2.1-3.5 N = 3	U = 0; $p < 0.05$
Y5d	$\bar{x}$ = 7 ± 1.2 R = 4.8-10 N = 4	$\bar{x}$ = 1.6 ± 0.2 R = 1.3-2.1 N = 4	U = 0; $p < 0.05$
Y6s	$\bar{x}$ = 3.8 ± 0.6 R = 2.4-5.9 N = 5	$\bar{x}$ = 2 ± 0.2 R = 1.5-2.7 N = 4	U = 1; $p < 0.05$
Y5s	$\bar{x}$ = 4.2 ± 1.1 R = 1.7-8.1 N = 5	$\bar{x}$ = 1.6 ± 0.3 R = 1.1-2.1 N = 3	U = 2; $p > 0.05$
Y25d	$\bar{x}$ = 7.3 ± 4.6 R = 2.7-12 N = 2	$\bar{x}$ = 3.4 ± 0.2 R = 3.2-3.6 N = 2	- -
Y2s	$\bar{x}$ = 6 ± 4.1 R = 1.9-10.1 N = 2	$\bar{x}$ = 2.1 ± 0.7 R = 1.5-2.9 N = 2	- -
All together	$\bar{x}$ = 8.7 ± 0.9 R = 1.7-19.5 N = 35	$\bar{x}$ = 2.7 ± 0.3 R = 1.1-6.9 N = 29	z = 5.09; $p < 0.00003$

Six males returned to their territories on the day following the mating day and no male attended the same territory for over two consecutive days. Male Y6s mated twice on the same day; male Y5s mated the second time the day after, and P6d did so 4 days later. The latter mated the third time 13 days after his second mating. The males which were recorded at the pond, but did not mate, on the one-two days following the mating day, showed significant average increases of both their flight ranges, from 5.6 ± 0.5 (N = 37) to 8.0 ± 0.4 (N = 35) and inter-perch distances, from 3.4 ± 0.4 (N = 20) to 4.5 ± 0.4 (N = 22) (Mann-Whitney, $z = 3.75$; $p < 0.0001$ and $z = 1.82$; $p < 0.05$ respectively). Thus, it seemed as if these males which did not mate in the following days tended to adopt the searching strategy again. However, those males that mated again restricted their flight ranges and inter-perch distances after each new mating, and the distances of their perch sites from the new oviposition sites also decreased (Tab. IV).

DISCUSSION

FEATURES OF THE MALE BEHAVIOUR

The male of *L. depressa* does not seem to localize in a particular area in the pond on the first instance he comes to the water. Even though he behaves aggressively against other males, he does not show any aggression-based dominance in any place. Instead, he behaves as a wanderer, on account of perch sites scattered along the shore line and of rather long flights between perching. Although the distribution of perch sites did not differ significantly from the distribution of the oviposition sites, this might be due to more numerous perch and oviposition sites in the same parts of the pond. It is possible however that males are actually attracted by those places which contain adequate sites for oviposition, as far as indicated by females' choices, this agreeing with CAMPANELLA & WOLF's (1974) hypothesis (3). Nevertheless, at this time they do not show any preference for any particular place, as evidence of their lack of localization. Apparently, the mature unmated male adopts a searching strategy for the female over the entire pond, or at least that zone of the pond where adequate sites for oviposition are present.

Since females oviposit, and males perch, all over the pond (Fig. 2), pair forming and copulation can probably take place in any part of the pond. Then the released female flies in search of a site to oviposit, closely followed by the male, who successfully non-contact guards her until she stops ovipositing. Upon the departure of the female, the male keeps localized at the oviposition place, where he flies over a restricted area and utilizes one or more perches much closer to each other than those utilized before mating. Apparently the male is attracted by that particular site in which his female has oviposited. Localization together with dominance in that area indicates that he now behaves territorially (KAUFMANN, 1983).

The numbers of males whose females oviposited near the capture place and several metres away did not significantly differ, thus suggesting that the former might

Table IV

Variation of average flight range, inter-perch distance and distance between perch and oviposition sites after successive copulations

Male		1st COP		days	2nd COP		days	3rd COP	
		Before	After		Before	After		Before	After
P6d	flight range	13.0	7.9	4	11.2	6.1	13	15.2	5.4
	inter-perch distance	11.8	4.1		16.2	4.4		4.0	2.3
	perch/oviposition sites distance	8.9	5.2		11.1	2.7		6.9	1.6
Y6s	flight range	13.8	7.1	0	7.1	5.6			
	inter-perch distance	8.7	2.2		2.2	3.4			
	perch/oviposition sites distance	3.8	2.0		4.3	1.8			
Y5s	flight range	16.0	5.3	1	9.1	6.0			
	inter-perch distance	6.4	2.6		7.9	4.3			
	perch/oviposition sites distance	4.2	1.6		7.6	2.6			

be perched at, or flying over, suitable oviposition sites as a matter of pure chance. Thus it seems, from the male behaviour, that he does not need the ability of recognizing a suitable site for oviposition. In fact, the behaviour of the males which defended oviposition places far from the respective capture places (Fig. 3), indicates that they did find one basing on their females' choice rather than on their own. This supports CAMPANELLA & WOLF's (1974) hypothesis (2).

A place which has been experienced to be attractive for a female is worth to be defended, since it is likely to attract other females. Accordingly, the male *L. depressa* turns from the searching (i.e. wandering) to the waiting strategy (i.e. territoriality), in places where female arrival is predictable. The libellulid males attend their territories for a period of several days (review of PARR, 1983a), and the same might occur in *L. depressa*, since some males were recorded in the same territories at least on two consecutive days. But, failing to mate again, the localization of the territorial male weakens and he turns to the searching strategy again, as evidence of his wider flight range and more scattered perch sites (Tab. IV). Some males did not show an appreciable increase of their inter-perch distance, but this apparently depended on male density at the pond, since other males prevented them from perching in their territories. Nevertheless, some males happened to mate again out of their former territories, following which they localized at, and successfully defended, the new oviposition sites. A repeated switching from wandering to territoriality, and vice-versa, is witnessed by the two/three-mated males in Table IV. Thus, in *L. depressa*, wanderer males may be both unmated males and older ones which have experienced a low mating success in their territories. This was also reported by PARR (1980) for *Orthetrum julia*, in which "... Those insects with relatively low reproductive fitness may join the inexperienced 'wanderers' and tend to appear anywhere in the breeding area". Also, KOENIG & ALBANO (1987) observed territorial males of *Plathemis lydia* to abandon their territories after some days of very low reproductive success, and WATANABE *et al.* (1987) reported that the territorial males of *Platycnemis echigoana* more frequently move from their defended sun-flecks in case they meet fewer females there.

In conclusion, basing on both male and female spatial distributions at the pond, the assumption that the male might be instinctively attracted – as the female probably is – by those arreas which contain suitable sites for oviposition, cannot be rejected for *L. depressa*. Nevertheless, it seems that learning, rather than instinct, is probably involved in the choice of the area to defend, since the oviposition behaviour in a particular site seems to indicate to the male that it is a good site in which to wait for other females and hence to defend.

THE ADVANTAGE OF NON-CONTACT GUARDING

During oviposition, the male of *L. depressa* guards its female while flying above her, according to the mode called the "non-contact guarding". In comparison to the tandem guarding, this mode has probably the advantages of (1) permitting a male to mate again while guarding previous mates (ALCOCK, 1979) and (2) permitting a male to guard his female without losing control of the territory (SHERMAN, 1983a; WAAGE, 1984). ALCOCK (1987), on the other hand, outlines that in *Paltothemis lineatipes* the above advantages are not evident because: (1) a too limited number of females arrive while one is in a territory, and (2) the time required for mating, including female seizure to oviposition, is very short, and it is not obvious that a male would lose dominance on his territory by this time; he concludes that non-contact guarding is possibly of some advantage for the female, which can keep free to move away if molested. The same considerations apply to *L. depressa*, since (1) never a male remated while guarding a female and only one mated twice in the same day (Tab. IV). Also, the harassed, non-contact guarded, females oviposited for a time of only one third that of the unmolested females, this probably implying a loss of potentially fertilizable eggs for the non-contact guarding male; (2) the males spent a maximum of about 150 seconds from seizure to complete oviposition (which is equivalent to an unmolested female), this time being comparable to that required by *P. lineatipes* (ALCOCK, 1987). However, the strong site attachment shown by the male *L. depressa* during and after female guarding, together with its ability to displace all the other males from that site, can contribute to explain the problem. PARR (1983b) and we (this paper) have shown that a male can lose its dominance in the territory if another male mates there. This is probably due to a marked increase of male aggressiveness just after mating, which is also known of other libellulids (PAJUNEN, 1962; 1964; 1966; TSUBAKI & ONO, 1985). Thus, it would be probably extremely dangerous for the male to keep the female in tandem, since another male might mate in the undefended territory during that time and immediately after displace the former owner. Of course, this has the same probability of occurring as a second female's arrival while the territorial male is guarding one, but the cost of losing the territory, which generally implies losing opportunities of further matings, likely represents a by far stronger selective pressure than the advantage of securing another mate while guarding one.

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