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SPATIAL DISTRIBUTION AND INTERACTIONS BETWEEN *ANAX IMPERATOR* LEACH LARVAE AT DIFFERENT DEVELOPMENTAL STAGES (ANISOPTERA: AESHNIDAE)

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The influence of 4 different factors on spatial distribution was tested experimentally: developmental stage, predator density, duration of site occupation and presence or absence of larvae of different developmental stages. Six parameters were used to characterize spatial distribution. — Three of the factors tested influenced spatial occupation in *A. imperator:* the size of home ranges increased with larval development, the coexistence of larvae of two different larval instars induced an increase of the volume occupied by medium-sized larvae and an instability of the home ranges of final-instar larvae, and the frequency of agonistic interactions increased with larval density.

Analysis of the spatial distribution of aquatic insects is required to understand the dynamics of insects in aquatic environments (HILDREW et al., 1980; JOHNSON & CROWLEY, 1980; SPENCE & SCUDDER, 1980; ALLAN, 1982; HUGGINS & DUBOIS, 1982; MARTIN, 1985). Recent reports have stressed the value of an ethological approach towards interactions (between insects) for understanding modalities of spatial occupation (SIH, 1982; PECKARSKY & PENTON, 1985; SJÖSTROM, 1985).

Interindividual relationships in dragonfly larvae have already been analysed within the framework of either foraging strategies (BAKER, 1980, 1981, 1983) or population dynamics (ROSS, 1971; BENKE et al., 1982; PIERCE et al., 1985; CROWLEY et al., 1987). Thus, according to some authors, the presence of conspecifics on a given site can induce, on the one hand, behavioural (change of site, decrease of duration of food intake, change in prey choice) or physiological modifications (rate of growth, duration of development) (BAKER, 1982; CROWLEY, et al., 1987) in odonatan larvae; and, on the other hand, the emergence of territorial behaviour, territoriality in this case being characterized by agonistic behaviours (ROWE, 1980; HARVEY & CORBET, 1985).

The experiments presented here are a part of a larger project on resource partitioning between species of dragonfly larvae of different developmental stages (BLOIS, 1985a) and concern more particularly the analysis of the spatial component (BLOIS, 1985b). The aim of this paper is to study experimentally the influence of four factors on spatial distribution of *Anax imperator:* developmental stage, larval density, duration of site occupation and presence or absence of larvae of different developmental stages.

MATERIAL AND METHODS

Two groups of *A. imperator* were tested: the first comprised final-instar larvae (FS) and the second, medium-sized larvae (MS) (4 and 5 instars before the last). Each evening, all larvae were fed ad libitum with *Chironomus* larvae. The larvae were marked individually with different coloured nail varnish on the abdomen and/or pronotum. Both groups were tested at three different densities: 5, 10 and 20 larvae in an aquarium. Each density was tested three times (3 aquaria). Then larvae from both size groups were observed together in the same aquarium, where the density was 5 MS and 5 FS. These densities were tested twice (2 aquaria). The day before an observation, the larvae were placed in an aquarium (69x27x20 cm) with a sandy bottom and 8 supports (sprigs of *Elodea*). Daylength was 14L:10D.

At the beginning of each half-hour period during the photophase, from 09.00 h to 18.00 h, on three successive days, the exact position of all the larvae was recorded on a grid (squared millimeters) as well as their orientation and their activity (movement, confrontation, etc.). These observations were made between September 1984 and February 1985.

Six parameters were used to characterize spatial distribution of larvae and its modifications: volume occupied by larvae, overlap of occupied zones (number and volume of overlaps), depth occupied, distance covered, interindividual distance, and interactions between larvae.

Volume occupied by larvae

The volume occupied by a larva was calculated as follows: the aquarium was divided into small cubes (143.4 cm^3 for the FS, and 29.7 cm^3 for MS). The total volume occupied during an observation corresponds to the sum of the volumes of all the cubes where a larva was seen at least once.

Overlap index

PIANKA's (1973) ecological niche overlap index was used to calculate overlap of occupied zones and to compare spatial occupation between larvae.

$$R = \frac{X_{ij} \times X_{ik}}{(X_{ij}) \times (X_{ik})}$$

X_{ij} and X_{ik} are relative frequencies of use by larvae j and k of categories i of the resource being considered. This index varies from 0 to +1, 0 indicating no overlap and +1 complete overlap.

Support selection

Choice of support was evaluated by comparing the number of times each subject was recorded on the ground or on an *Elodea* (Chi-squared test). As available ground surface (GS) was not equivalent to plant surface (PS) theoretical values for random distribution were calculated as follows: X: theoretical number of records on *Elodea;* — Y: theoretical number of records on the ground; — t: total number of observations: X+Y = t; — PS = 1036.68 cm and GS = 1794 cm, GS/ES = 1.73. — Therefore, Y = 1.73 X and Y = 0.63 t and X = 0.37 t.

Table I

Possible types of interation between two *A. imperator* larvae. Case 1: only one larva (B) moves before interaction; — Case 2: both larvae move before interaction. — [A, B: 2 individuals; — F: before an interaction; — T: after an interaction]

Text reference	1	2
a	F: A same position B moves T: A same position B moves	F: A moves B moves T: A same position B moves
b	F: A same position B moves T: A moves B same position	F: A moves B moves T: A moves B same position
c	F: A same position B moves T: A moves B moves	F: A moves B moves T: A moves B moves
c&	idem but A wins	idem but A wins

Interactions

A preliminary study enabled us to define 8 types of interaction (Tab. I) in relation to pre- and post-interaction situations. Given two larvae, A and B, two pre-interaction situations can occur: either both larvae (type 2) or only A (type 1) changed position before the interaction; this mobility was based on the 4 records before an interaction. In addition post-interaction situations were divided into four categories (cf. Tab. I), viz. .

(a) A remained in the same position while B moved;
(b) A moved while B remained in the same position;
(c) both A and B changed positions;
(c&) A and B moved, but one individual "won" the encounter, that is to say either the winner projects its labium against the other larva or the looser turns away and moves away first.

These data, and data for individual distances and distances covered were computed on an Apple

II. As it was not possible to normalize data nor to homogenize variances by any transformation, only non-parametric tests were used.

RESULTS

OCCUPIED VOLUMES

Table II

Interstage comparisons — When all larvae in an aquarium were of the same developmental stage (case 1), FS generally occupied larger volumes than did MS. However, the difference was statistically significant only for the densities D5 and D20 (Mann Whitney, $p < 0.05$).

When larvae of two different developmental stages were in the same aquarium (case 2), although volumes occupied by FS seemed to be larger than those occupied by MS, no significant difference was found (Mann Whitney, $p > 0.05$). Intrastage comparisons between case 1 and case 2 indicated that both FS and MS always occupied larger volumes when different-sized larvae were together than when they were in separate aquaria (Test t, $p < 0.05$).

Interdensity comparisons — Areas occupied by *A. imperator* varied with larval density (Kruskall & Wallis, $p < 0.05$). At density D10 FS occupied smaller

Table II

Mean volume in cm^3 of home range (± S.E.) in relation to developmental stage of *A. imperator* larvae, their density, and time spent in the aquarium. — [D1: first day of observation; — D2: second day of observation; — D3: third day of observation; — T: D1 + D2 + D3. — Values with the same index: no significant difference; — values with different indexes: significant difference]

Case	Days		Densities	
Stage		D5 (n = 15)	D10 (n = 30)	D20 (n = 60)
	Case 1			
Medium	D1	451.44 ± 173.25	313.83 ± 177.12	317.32 ± 176.08
	D2	401.94 ± 199.82	426.69 ± 162.01	346.50 ± 199.10
	D3	881.10 ± 252.54	518.76 ± 238.21	350.67 ± 203.88
	T	578.16 ± 385.98ae	419.76 ± 210.63e	338.16 ± 194.84a
Final	D1	678.62 ± 417.87	606.93 ± 307.46	828.63 ± 517.66
	D2	879.34 ± 819.79	468.34 ± 303.39	1032.80 ± 649.29
	D3	783.76 ± 549.60	430.11 ± 294.06	1049.80 ± 570.03
	T	780.57 ± 610.23b	501.79 ± 307.91e	970.38 ± 586.92b
Case 2				
		5± 5 (n = 20)		
Final		1023.25 ± 510.58c		
Medium		780.09 ± 271.23d		

volumes than at densities D5 and D20 (Mann Whitney, $p < 0.05$). MS occupied smaller areas at density D20 than at D10 (Mann Whitney, $p < 0.02$).

Interday comparisons — Volumes occupied by MS varied with time at densities D5 and D10 (Kruskall & Wallis, $p < 0.01$). At D5, volumes were significantly larger on the 3rd day (Mann Whitney, $p < 0.02$). At D10 volumes increased with time (Spearmann rank correlation, $rs = 0.39$, S, $p < 0.05$). On the contrary, volumes occupied by FS, but at density D10 only, decreased with time (Mann Whitney, $p < 0.02$).

OVERLAP OF OCCUPIED VOLUMES

Tables III-IV

Interindividual overlaps

Interstage comparisons — When larvae of different developmental stages

Table III

Variations of mean overlap indices (± S.E.) and of number of overlaps of occupied volumes in relation to developmental stage of *A. imperator* larvae, their density and the time spent in the aquarium. — [Values with the same index: no significant difference; — values with different indexes: significant difference]

Stage	Days	D5	D10	D20
Medium	D1	0.11 ± 0.17 n = 11	0.20 ± 0.30 n = 28	0.09 ± 0.12 n = 113
	D2	0.17 ± 0.21 n = 8	0.09 ± 0.11 n = 44	0.14 ± 0.21 n = 132
	D3	0.05 ± 0.07 n = 20	0.10 ± 0.14 n = 49	0.11 ± 0,14 n = 114
	T	0.10 ± 0.16e n = 39a	0.12 ± 0.18e n = 121b	0.11 ± 0.16e n = 359c
Final	D1	0.34 ± 0.30 n = 18	0.32 ± 0.33 n = 66	0.29 ± 0.28 n = 301
	D2	0.23 ± 0.26 n = 18	0.52 ± 0.31 n = 55	0.23 ± 0.26 n = 304
	D3	0.22 ± 0.23 n = 18	0.45 ± 0.37 n = 79	0.22 ± 0.23 n = 276
	T	0.27 ± 0.26f n = 54a	0.42 ± 0.35g n = 200b	0.25 ± 0.26f n = 881d

cf. Table II for details

were in different aquaria, developmental stage did not influence significantly the number of overlaps at densities D5 and D10 (Mann Whitney, $p > 0.05$); but at density D20, the number of overlaps was higher between FS than between MS (Mann Whitney, $p < 0.02$) (Tab. III).

When larvae of two different developmental stages were in the same aquarium, there were no more overlaps between larvae of the same developmental stage than between larvae of different developmental stages (Chi-squared test, $p > 0.05$) (Tab. IV).

The number of interindividual overlaps between larvae of the same developmental stage did not differ significantly whether they were with larvae of another developmental stage (case 1) or not (case 2) at density D5 (Chi-squared test, $p > 0.05$). However there was a significant difference between case 1 and case 2 at density D10 (Chi-squared test, $p < 0.001$): the amount of overlap was higher when larvae of only one developmental stage were present in an aquarium, at both developmental stages.

Table IV

Variations of mean overlap indices (± S.E.) of occupied volumes between *A. imperator* larvae of the same or of different developmental stages. — [n: number of overlaps; — i: number of larvae]

Medium stage - Final stage	0.22 ± 0.23	n = 18	i = 5
Final stage - Final stage	0.20 ± 0.20	n = 9	i = 5
Final stage - Medium stage	0.21 ± 0.25	n = 39	i = 10

Interdensity comparisons — The number of overlaps increased with density, whatever the developmental stage. However, this increase differed slightly between these two groups (Chi squared test, $p < 0.01$): the increase in the number of overlaps between density D10 and density D20 was more important for FS than for MS (Mann Whitney, $p < 0.02$) (Tab. III).

Interday comparisons — No significant variations in the number of overlaps with time were found for FS whatever their density, or for MS at densities D10 and D20 (Tab. III).

OVERLAP INDICES

Interstage comparisons — When all larvae in an aquarium were of the same developmental stage, on the average, overlap indices were higher for FS than for MS, whatever the density considered (t test, $p < 0.05$) (Tab. III).

When larvae of different developmental stages were in the same aquarium, no significant difference was found between overlap indices calculated between larvae of different developmental stages and those for larvae of the same stage (Mann Whitney, $p > 0.05$) (Tab. IV).

Overlap indices for FS were not higher when they were alone in an aquarium at density D5 than when they were with MS (Mann Whitney, $p > 0.05$). However these indices were higher when they were alone at density D10 (Mann Whitney, $p < 0.001$). Interindividual overlapping between MS was always higher when they were with FS than when they were alone at densities D5 and D10 (Mann Whitney, $p < 0.01$).

Interdensity comparisons — Overlap indices for MS did not vary with density (Kolmogorov Smirnov, $p > 0.05$), but these were higher for FS at density D10 than at the other two larval densities (Kolmogorov Smirnov, $p < 0.001$) (Tab. III).

Interday comparisons — Overlap indices did not vary with time for MS whatever their density (Kruskall & Wallis, $p > 0.05$), nor for FS at densities D5 and D20 (Kruskall & Wallis, $p > 0.05$) (Tab. IV).

DEPTH OCCUPIED

Interstage comparisons — After pooling data for larvae on the ground and on a support and taking into account relative surfaces of vegetation and ground, it appeared that FS, in the presence of MS are not usually found on the ground (Chi-squared test, $p < 0.05$). When MS were alone in an aquarium, they were generally observed on plants (Fisher, $p = 0.019$) but when they were with FS, they showed no such preference (Chi-squared test, $p > 0.05$).

Interdensity comparisons — Density did not significantly influence depth distribution (Kendall coefficient of concordance, $p < 0.05$) of either category of larvae.

Interday comparisons — Depth distribution did not vary in relation to time in either category of larvae (Kendall coefficient of concordance, $p < 0.05$).

DISTANCE COVERED

Table V

Interstage comparisons — When there was only one size category in an aquarium, mean distances covered by larvae varied with developmental stage. At densities D5 and D10, these mean distances were greater for MS (Mann Whitney, $p < 0.05$). However, at density D20, the difference between mean distances covered by MS and FS was less (Mann Whitney, tendency) and then these mean distances were higher for FS.

When two developmental stages were in the same aquarium, distances covered did not vary with developmental stage (Mann Whitney, $p > 0.05$).

Although distances covered by FS were always greater when they were with MS, a significant difference was found only between distances covered when both categories were together and when FS were alone at density D10 (Mann Whitney,

Table V

Variations of mean distances (± S.E.) in mm covered by *A. imperator* larvae in relation to their developmental stage and density. — [Values with the same index: no significant difference; — values with different indexes: significant difference]

Case Stage	Days	D5 ($n = 15$)	D10 ($n = 30$)	D20 ($n = 59$)
Case 1				
Medium	D1	111.64 ± 66.75	34.68 ± 26.92	46.97 ± 42.29
	D2	63.72 ± 54.85	65.14 ± 38.49	44.90 ± 42.12
	D3	57.29 ± 42.48	84.68 ± 56.13	44.06 ± 38.15
	T	77.58 ± 39.37a	61.50 ± 24.97c	45.17 ± 28.40e
Final	D1	38.40 ± 41.76	43.68 ± 40.90	56.56 ± 53.30
	D2	52.47 ± 53.32	20.52 ± 17.97	53.40 ± 68.24
	D3	49.98 ± 52.80	16.95 ± 21.08	57.53 ± 41.55
	T	46.95 ± 33.82bde	27.05 ± 19.06d	62.49 ± 43.56e
Case 2				
Medium		51.93 ± 28.97	($n = 10$)	
Final		82.36 ± 48.67	($n = 10$)	

cf. Table II for other details

$p < 0.05$).

Interdensity comparisons — Mean distances covered by MS decreased as density increased (Kruskall & Wallis, $p < 0.01$). A significant difference was found between mean distances covered by FS at density D20 and at density D10 (Mann Whitney, $p < 0.001$).

Interday comparisons — These results are heterogeneous. A day effect was found for MS at densities D5 and D10, and for FS at density D10 (Friedman, $p < 0.01$). On day 1, MS moved more at density D5 (Wilcoxon, $p < 0.01$), but less at density D10 (Wilcoxon, $p < 0.002$). Distances covered by FS increased with time at density D10 (Wilcoxon, $p < 0.03$).

INTERINDIVIDUAL DISTANCES
Tables VI-VII

Interstage comparisons — When different developmental stages were in different aquaria, MS adopted greater interindividual distances than FS. This difference was significant at densities D5 and D20 (Mann Whitney, $p < 0.05$) (Tab. VI).

When both developmental stages were in the same aquarium, interindividual distances between larvae of the same developmental stage did not vary with developmental stage (Mann Whitney, $p > 0.05$). In addition, interindividual distances between larvae of different developmental stages did not differ signifi-

Table VI

Variations of interindividual distances (in mm) (± SE) between *A. imperator* larvae in relation to density, developmental stage and time spent in the aquarium. — [Values with the same index: no significant difference; — values with different indexes: significant difference]

Stage	Days	D5	D10	D20
Medium	D1	325.61 ± 44.34	322.14 ± 34.63	336.02 ± 20.95
	D2	331.27 ± 34.76	304.30 ± 24.27	324.33 ± 17.79
	D3	310.91 ± 83.47	328.67 ± 35.97	321.44 ± 18.34
	T	311.84 ± 66.03abc	318.37 ± 33.50b	327.26 ± 19.99c
Final	D1	275.60 ± 151.66	412.72 ± 17.56	310.63 ± 44.52
	D2	308.60 ± 86.63	318.37 ± 64.37	311.75 ± 73.00
	D3	215.60 ± 68.43	176.23 ± 107.62	307.21 ± 49.98
	T	263.91 ± 115.25d	302.44 ± 121.59b	309.87 ± 56.88f

cf. Table II for other details

Table VII

Variations of interindividual distances (± SE) between *A. imperator* larvae of the same and of different developmental stages when coexisting in the same aquarium

Final stage - Final stage	352.48 ± 186.22	n = 60
Medium stage - Medium stage	372.08 ± 191.83	n = 60
Medium stage - Final stage	382.61 ± 183.65	

cantly from distances between larvae of the same developmental stage (Mann Whitney, $p > 0.05$) (Tab. VII).

Interdensity comparisons — Interindividual distances varied with density (Kruskall & Wallis, $p < 0.03$). Interindividual distances between FS increased with density. The same tendency was shown by MS but the difference was significant only between densities D10 and D20 (Mann Whitney, $p < 0.003$) (Tab. VI).

Interday comparisons — Although interindividual distances varied from day to day (Kruskall & Wallis, $p<0.05$), no consistent tendency was found. Thus interindividual distances between larvae of both size categories were shorter on day 3 at density D5; but at density D10, they were shorter on day 2 for MS, while they decreased with time for FS (Mann Whitney, $p < 0.007$). At density D20 interindividual distances between MS decreased with time (Mann Whitney, $p<$ 0.02) whereas no significant variation was found for FS (Mann Whitney, p $p >0.05$) (Tab. VI).

INTERACTIONS
Tables VIII-IX

Quantitative analysis of interactions

Interstage comparisons — When larvae of different developmental stages were in separate aquaria, more confrontations were observed between MS than between FS; indeed these larvae presented very few interactions (Tab. VIII).

When larvae of both developmental stages were in the same aquarium, very few interactions ($N = 3$) were observed; and these always occurred between MS.

Interdensity comparisons — Interactions increased quantitatively with density of MS (linear correlation $r = 0.80$, S, $p < 0.01$) (Tab. VIII).

Interday comparisons — There were not significantly more interactions on one given day (Chi-squared test, $p > 0.05$).

Table VIII

Number if interactions between *A. imperator* larvae in relation to density and developmental stage

Stage	D5	D10	D20
Medium	15	23	50
Final	3	0	1

Types of interactions

Interdensity comparisons — No particular type of interaction prevailed at densities D5 or D10 (Chi-squared, $p > 0.05$), but at density D20 there were more type 1a and 2c& interactions (Chi-squared test, $p < 0.01$) (Tab. IX).

Interday comparisons — At densities D5 and D10 no particular type of

Table IX

Amount of each type of interaction between MS in relation to *A. imperator* larval density and time spent in the aquarium

Text	D5				D10				D20			
reference	D1	D2	D3	T	D1	D2	D3	T	D1	D2	D3	T
1a	0	0	1	1	0	0	1	1	7	4	3	14
1b	0	0	1	1	0	2	0	2	1	2	0	3
1c	2	0	1	3	1	0	1	2	1	1	0	2
1c&	0	0	1	1	1	1	0	2	1	0	2	3
2a	0	0	1	1	0	2	2	4	0	2	1	3
2b	0	0	0	0	0	0	1	1	0	0	0	0
2c	1	2	3	2	2	3	5	7	2	5	3	10
2c&	0	1	2	3	1	3	0	4	6	4	5	15
T	*3*	*3*	*9*	*15*	*5*	*10*	*8*	*23*	*18*	*18*	*14*	*50*

cf. Table II and text for other details

interaction prevailed on a given day (Chi-squared test, $p > 0.05$). However, at density D20, type 1a and 2c& interactions prevailed on observation day 1 and 2 (Chi-squared test, $p < 0.05$).

DISCUSSION

These experiments indicate that three of the four factors tested here appear to modify spatial distribution of *A. imperator*. Larvae of different developmental stages occupy available space differently. Final-instar larvae (FS) occupy much larger volumes than medium-sized larvae (MS) and overlapping between their individual volumes is more important. On the other hand, distances covered by MS and their interindividual distances are greater than those for FS. Agonistic interactions were observed only between MS. Therefore it seems that FS "tolerate" conspecifics better than MS do. In addition, interstage comparisons of spatial distribution modalities indicated a tendency to spatial partitioning between larvae of different developmental stages. For example, MS were generally observed near the surface in the vegetation whereas FS were observed mainly on the ground. Similar results were reported by JOLY (1984) for *Ranatra linearis:* first-instar larvae occupy areas just below the water surface, while adults occupy deeper zones, nearer the ground.

Analysis of spatial distribution of larvae when those of two different developmental stages were together showed that the presence of individuals of another developmental stage modified certain characteristics of spatial occupation by these larvae. When larvae of both developmental stages were together in an aquarium, home ranges and distances covered increased, but overlapping between volumes occupied by FS decreased. This increase in home-range volumes in FS can be interpreted as the result, not of a simple widening of exploitation areas, but as a search for different sites. On the contrary, MS tended to widen their home ranges by increasing the volumes exploited, and by varying their choice of support (plant and ground). Although this widening of occupied volumes induced an increase in overlapping volumes, the number of agonistic interactions did not increase. It seems therefore that coexistence between larvae of two different developmental stages leads to an increase in volumes occupied by MS and to an instability of the home ranges for FS.

Differential spatial occupation by larvae of different developmental stages has been reported for other aquatic insects. SIH (1982) and STREAM & SHUBECK (1982) showed that in *Notonecta hoffmani* and *N. lunata* spatial occupation differed between young larvae and adults and that young larvae moved less when adults were present. However, it does not seem that the mechanisms causing this partitioning are the same in notonectids and Odonata. Partitioning between notonectids is, one supposes, a consequence of cannibalism of young by adults, whereas no cannibalism was observed in *A. imperator* larvae during these experiments; so the interpretation of the modifications of spatial distribution of these larvae is more difficult.

Behavioural modifications due to the presence of conspecifics of different developmental stages have been reported in *Tetragoneuria cynosura* (Anisoptera) by CROWLEY et al. (1987), who revealed an increase in distances covered by older larvae when they were with younger individuals, as reported above for *A. imperator.*

Although it appears that the presence of larvae of different developmental stages modifies spatial distribution modalities in some Odonata, the question as to whether there is a real interstage recognition remains open. The comparison, for example, of the number and volume of home-range overlaps between larvae of the same or of different developmental stages, revealed no significant difference in relation to stage. The same conclusions were reached when interindividual distances were considered. It does not seem that *A. imperator* reacts differently towards conspecifics of the same developmental stage or of different stages.

Nevertheless, agonistic interactions were observed only between MS, whether they were with larvae of other size categories or not. This specificity of interaction could be the sign of an interstage recognition. ROWE (1980), studying *Xanthocnemis zealandica* (Zygoptera) of two different instars, indicated no behavioural differences when comparing interactions between larvae of the same instar or of different instars. Therefore there does not seem to be only interstage recognition in Odonata larvae. Further experiments are required before any more definite conclusions can be drawn.

Agonistic interactions between dragonfly larvae are the result, according to some authors (ROWE, 1980; HARVEY & CORBET, 1985), of territorial behaviour, though no real proof of territoriality has been given. MACAN (1977) only suggested the presence of such a phenomenon. The only reports which show, not the presence of territories, but the presence of a defended foraging area, insist on the fact that exclusion of conspecifics from a site should be interpreted in terms of a general dominance system and tendency for larvae to remain near areas of food "concentration" (BAKER, 1981). This type of territoriality was also reported for *Dinocras cephalotes* (Plecoptera) (Sjostrom, 1985).

The above evidence indicates clearly that, similarly to *Cordulegaster boltoni* (PRODON, 1976), no territoriality is present in *A. imperator.* The observed agonistic interactions could simply be the demonstration of an attempt to establish a dominance system: the frequency of these interactions depends solely on the encounter rate between larvae. In our case the interactions increased quantitatively with density.

Larval density indeed appears to influence spatial distribution modalities in *A. imperator.* The main consequence of an increase in the number of larvae is an increase in the amount of overlap between home ranges, and, paradoxically, an increase in interindividual distances. Besides, distances covered by MS decreased, while the number of agonistic interactions increased. The increase of interactions between dragonfly larvae was also reported by PIERCE et al. (1985) in *Enallagma aspersum* and *E. traviatum*. The influence of predator density on their own behaviour has been rarely investigated in Odonata larvae. Studies taking this parameter into account usually focus on the influence of density on survival or on development rate (BENKE, 1978; BENKE et al., 1982; CROWLEY et al., 1987).

Thus, it appears that a certain number of factors — developmental stage, density and presence of different developmental stages — can modify spatial occupation modalities in *A. imperator* larvae. However, the importance of intra- and inter-stage relationships on spatial distribution still needs to be specified in relation to all factors implied in structuring spatial occupation in Odonata larvae such as, for example, distribution and availability of prey or interspecific relationships.

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