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FROM A MEDITERRANEAN INLAND
CATCHMENT IN SOUTHERN SPAIN**

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LIFE-HISTORY PATTERNS AND SPATIAL SEPARATION EXHIBITED BY THE ODONATES FROM A MEDITERRANEAN INLAND CATCHMENT IN SOUTHERN SPAIN

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ODONATES
LIFE HISTORY
SPATIAL AND TEMPORAL
SEPARATION
MEDITERRANEAN INLAND
CATCHMENT

ABSTRACT – Population dynamics of the most abundant odonate species in a mediterranean inland catchment (*Calopteryx virgo*, *Lestes viridis*, *Cercion lindeni*, *Gomphus pulchellus*, *Onychogomphus uncatatus*, *O. forcipatus*, *Boyeria irene* and *Cordulegaster boltoni*) are analysed. At least five different life-history patterns are exhibited by the odonates that inhabit the basin of the River Yeguas. In the river basins of southern Europe seasonal changes are very marked in seasonal streams and middle and lower reaches of the main channel. Spatial separation among species by occupying different habitats through the catchment was evident. Temporal separation due to life-history displacement seems to decrease competition among co-existing populations. In the basin studied, a progressive increase in the seasonal variation of abiotic factors (temperature, current velocity) going downstream along the main channel, correlates with a progressive decrease in faunal richness, and appears to give rise to the dominance of *C. lindeni*, a species with partly bivoltine life history in the Sierra Morena.

ODONATES
CYCLE BIOLOGIQUE
SÉGRÉGATION SPATIALE ET
TEMPORELLE
BASSIN INTÉRIEUR
MÉDITERRANÉEN

RÉSUMÉ – Cette étude traite de la dynamique de populations des espèces d'Odonates les plus abondantes dans un bassin intérieur méditerranéen (*Calopteryx virgo*, *Lestes viridis*, *Cercion lindeni*, *Gomphus pulchellus*, *Onychogomphus uncatatus*, *O. forcipatus*, *Boyeria irene* et *Cordulegaster boltoni*). Les Odonates qui peuplent le bassin de la rivière Yeguas présentent au moins cinq modèles différents de cycles biologiques. Dans les bassins fluviaux du Sud de l'Europe les changements de saison sont remarquables dans les ruisseaux saisonniers et dans les tronçons moyen et bas de l'axe principal. Cette étude montre une ségrégation spatiale parmi les espèces, qui se répartissent entre les différents habitats le long du bassin. Parmi les espèces qui cohabitent la séparation temporelle due aux décalages des cycles vitaux peut contribuer à diminuer la concurrence. L'accroissement progressif de la variation saisonnière des facteurs abiotiques (température, vitesse du courant) vers l'aval, le long de l'axe, est corrélée à une baisse de la richesse faunistique et peut aussi entraîner la dominance progressive d'une espèce, *C. lindeni*, à cycle biologique partiellement bivoltin dans la Sierra Morena.

INTRODUCTION

In the river basins of southern Europe that run through mountains of medium altitude, in general, and in the river system studied here, seasonal changes are very marked (Prat *et al.* 1984, Giudicelli *et al.* 1985) and environmental conditions vary a great deal among the different locations along the basin (Graça *et al.* 1989). These differences are especially evident in summer and early autumn. In many streams of the Mediterranean basin which carry large amounts of water during

the rainy season in winter and spring, the flow is interrupted in summer and autumn. For four or five months of the year, only isolated pools of water remain in the river bed (Giudicelli *et al.* 1985). The spatial distribution of species that allows them to take advantage of different habitats is clearly evident in this type of river.

Most of rheophilous insects (e.g. Plecoptera, Trichoptera, Ephemeroptera) that inhabit rivers with these characteristics have adapted their life-history to the seasonal variations in flow (Petts 1984) such that larvae are confined to winter and

spring, and the emergence (of adults) occurs in spring or beginning of summer. Compared with other aquatic insects, the Odonata exhibit great variety in life-history patterns (Corbet 1962, Norling 1984). Some species that inhabit rivers and streams of southern Europe have a larval stage that lasts for more than a year (Prodon 1976, Suárez *et al.* 1986); some complete their development in a year; and others complete more than a generation per year (Ferrerias-Romero 1991). In all species, except a few in the second (univoltine) category of life-history, larvae occur throughout the year.

On the other hand, whereas in northern and central Europe dragonflies and damselflies occupy, by preference, lentic environments, in the Mediterranean basin these insects represent an important part of the macroinvertebrate communities that inhabit streams and rivers (Carchini and Rota 1982, 1985, Jurzitza 1965, 1993).

The major aims of this study were to find out how the Odonata were distributed in space and time in the varied habitats represented in the River Yeguas, and to evaluate the change taking place in the odonate populations during the year. The River Yeguas runs through a mountainous region in a forested valley that has no industry and negligible agricultural and urban pollution. The models of associations found in the different habitats, especially of those associations that exist during the drier phases of the annual cycle, may be useful in future studies on biological monitoring throughout the year (Armitage *et al.* 1990) or for restoration of rivers in the Mediterranean basin in areas that have characteristics similar to those of the Sierra Morena.

STUDY AREA

The River Yeguas system can be physiographically divided into three distinct habitat types. *a) Streams with permanent flow.* In the upper part of the catchment, a naturally vegetated area, are stable streams that always have a current. Their banks are lined by deciduous trees – *Alnus glutinosus* (L.), *Ulmus minor* Miller – and, except in winter, sunlight rarely reaches the stream bed. Water temperature never exceeds 20 °C. The origin of the river's main channel is found in two streams of this description: the Cereceda and Pradillo. *b) Seasonal streams.* The middle and lower portions of the catchment are also well vegetated, but this is in part due to human influence by conifer plantings. In this area the tributaries are seasonal, intermittent streams that lack surface water in summer and early autumn. Their banks are populated only by shrubby greenery – *Nerium oleanders* L., *Securinega tinctoria* (L.) – that allows sunlight to reach the riverbed readily.

c) Main channel. The main channel of the river flows southward from its origin and after 85 km empties into the River Guadalquivir between Montoro and Marmolejos. Although in the upper reaches the flow is not completely interrupted, closer to the river's mouth seasonality increases progressively such that below 500 m a.s.l., after July, there remain only pools of water in the river bed. The volume of these pools gradually decreases during the summer until the rainy season begins again in mid-autumn (November). The width of the upper river and lower river is 6-10 m and 25-30 m respectively. Marginal trees are sparsely distributed and thus the bottom of the river receives direct and abundant sunlight.

This system drains an area of approximately 828 km² and has an annual average volume of 160 hm³. The average gradient of the main channel is between 1.8% in the upper tract and 0.3% near the river's mouth.

METHODS

Sampling sites

From May 1983 to April 1984, chemical and biological samples were collected monthly in the last week of each month at 8 sampling sites along the catchment (Fig. 1). Two sampling sites were established in the headwater streams. Site 1 was on the stream Cereceda (700 m a.s.l.) and Site 2 was on the stream Pradillo (660 m a.s.l.). Two other sampling sites were established in seasonal tributaries. Site 4 was on the stream Los Términos (570 m a.s.l.) and Site 7 was on the stream Fresnedoso (220 m a.s.l.). Four sampling points were established on the main channel of the River Yeguas. The uppermost, Site 3, was situated 2 km below the confluence of two headwater streams (600 m a.s.l.). Sites 5, 6 and 8 were established downstream at 550, 300 and 200 m a.s.l. respectively. The last site, located near the mouth of the River Yeguas at the Guadalquivir is affected by a dam upstream.

Chemical and Physical Features

Current velocity and water temperature were recorded monthly at each site. Alkalinity, pH, dissolved oxygen (Winkler method), and Cl⁻ concentration were also measured monthly at all sites. Moreover, at two extremes phases of the annual cycle, July and January, Ca⁺⁺, Mg⁺⁺, Na⁺, K⁺, SO₄⁼ and P₂O₅ concentrations were measured.

Odonata Collection

Insect samples were collected with two 0.5 mm-mesh needed handnets, one with a triangular mouth (30 cm each side of the frame) and the other with a square

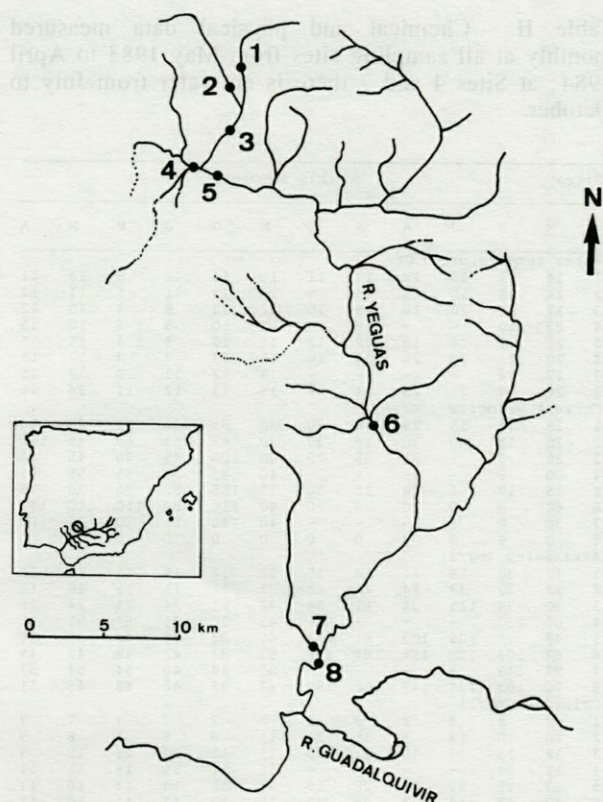


Fig. 1. – Location of the study area on the Iberian Peninsula. The numbers are the sites of the catchment where physical, chemical and biological samples were collected monthly from May 1983 to April 1984. 1, stream Cereceda; 2, stream Pradillo; 4, stream Los Términos; 7, stream Fresnedoso; 3, 5, 6 and 8, main channel of River Yeguas.

mouth (15 cm each side of the frame). The nets were used simultaneously for 45–60 minutes, collecting larvae in everyone of the habitats existing in each sampling sites. Similar sampling techniques have been used successfully for odonate population studies by Macan (1964), Lawton (1970), Johannsson (1978) and Crowley and Johnson (1982). This method does not necessarily provide high numbers of larvae in each sample, but a sufficient number of samples can allow different environments to be compared (Castella 1987); moreover, it appears to be the best method for collecting larvae of all the species that inhabit sampling sites such as those in this study (Carchini and Rota 1985). A circular aerial insect net, 30 cm in diameter and 80 cm in length of handle, was used to collect adults. Larvae and exuviae were preserved in the field in 70% ethanol for later identification in the laboratory.

Data Analysis

Species diversity for each sampling point was assessed using the Shannon-Weaver function (larvae only have been used). The abundance values (larvae only) were distributed among five classes, each of which is given a value of between 1 and 5, according

to Verneaux's method (1973). Furthermore, by using this method, species having an ubiquitous distribution but a very low level of occurrence are easily shown. 85% of odonates collected were larvae.

The terms 'spring' and 'summer' species, applied to life-history patterns, are used throughout the text in the sense defined by Corbet (1954, 1962).

RESULTS

Physical-Chemical Characteristics

For most of this fluvial system the physical-chemical characteristics varied significantly from winter to summer. Whereas the headwater streams showed high stability, the summer-to-winter differences in the main channel were very pronounced, especially for the seasonal tributaries that lacked surface water from July to early November. For several parameters the range of variation is greater for sampling sites on the River Yeguas than for those on headwater streams. Notwithstanding this, the variation was especially high for the first site on the upper river (Site 3), where the highest Na^+ , $\text{SO}_4^{=}$, Cl^- and P_2O_5 concentrations were measured during the summer (Table I). This is the only area on the river which is affected by urban pollution, coming from Fuencaliente, a small riverside village.

The River Yeguas is slightly alkaline at all sampling sites (Table II), although the alkalinity increases downstream. Mean annual values for sampling sites were 16, 21, 51, 66, 63, 89, 75 and 90 mg/l HCO_3^- . The dissolved oxygen levels were high, most of them exceeding 7.0 mg/l, except for July's samples in the upper river where Sites 3 and 5 showed 2 and 3 mg/l respectively. In general, there is a progressive increase in instability along the main channel of the catchment which is due to the very clearly seasonal nature of this type of river basin (Fig. 2). Whereas in the

Table I. – Concentration of ions at the sampling sites in July (s) and January (w); at Sites 4 and 7 (seasonal streams) there is no water in July.

Samples	Water concentration ions (mg/l)							
	Ca	Mg	Na	K	HCO_3	SO_4	Cl	P_2O_5
S-1 (s)	20.0	12.2	2.3	0.0	18	0.8	8	0.12
S-1 (w)	12.0	2.4	3.3	0.0	15	3.0	7	0.00
S-2 (s)	20.0	14.6	5.6	1.0	33	28.8	13	0.35
S-2 (w)	16.0	4.9	3.5	0.9	15	22.9	9	0.00
S-3 (s)	40.1	9.7	25.4	9.7	125	44.3	30	0.56
S-3 (w)	12.0	4.9	5.7	1.1	24	19.9	10	0.00
S-4 (w)	20.0	4.9	10.7	1.1	51	19.9	15	0.00
S-5 (s)	36.1	7.3	16.0	2.8	109	3.0	21	0.20
S-5 (w)	20.0	7.3	7.3	1.0	36	34.9	13	0.10
S-6 (s)	44.1	9.7	16.0	3.3	115	17.0	18	0.00
S-6 (w)	16.0	7.3	8.7	0.9	42	31.9	12	0.17
S-7 (w)	20.0	4.9	10.7	0.0	48	5.7	12	0.12
S-8 (s)	40.1	7.3	22.0	2.1	134	1.3	18	0.00
S-8 (w)	16.0	7.3	9.4	0.9	42	7.8	12	0.15

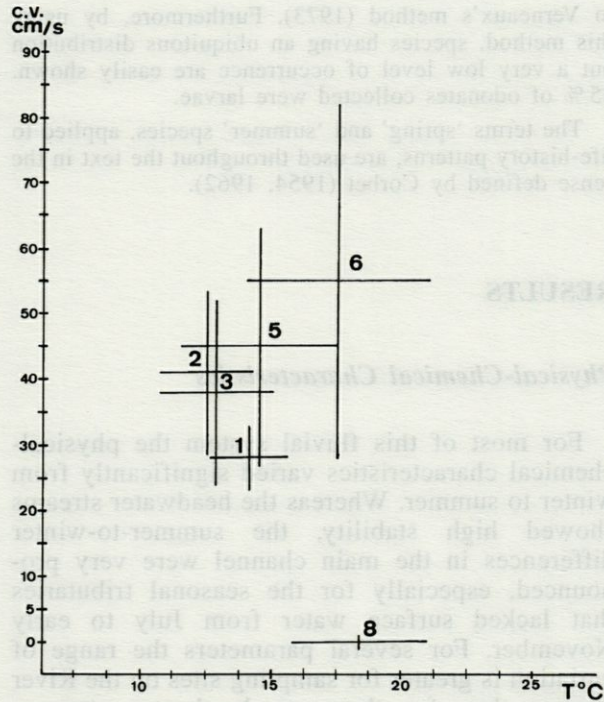


Fig. 2. - Distribution of sampling sites (except seasonal streams, sites 4 and 7) according to annual mean values of temperature and current velocity. Standard deviation is indicated. Current velocity in Site 8 (affected by a dam upstream) was imperceptible on days when this locality was visited. A progressive increase in instability along the main channel (sites 3, 5 and 6) is evident.

upper parts of the river the flow is not interrupted in summer and the maximum water temperature was less than 20 °C, the pools which remain in the middle and lower reaches of the river may experience water temperatures of 30 °C in summer.

Odonates species richness, abundance and diversity analysis

The greatest species richness (larvae, exuviae and adults have been used) occurred in the upper part of the main channel where 14 species were collected at Sites 3 and 5 (Fig. 3). Many fewer species were found in the permanent headwater streams : eight and six species were found at Sites 1 and 2 respectively. In seasonal streams at Sites 4 and 7, 8 and 5 species respectively were found. Near the river's mouth only seven species were found. Abundance values are shown in the Table III A.

Although the richness was slightly different at Sites 1 and 2, which are on headwater streams, when diversity for those sites was calculated the Shannon-Weaver index value was similar for the two streams (Fig. 3). At Site 1 the most abundant

Table II. - Chemical and physical data measured monthly at all sampling sites from May 1983 to April 1984; at Sites 4 and 7 there is no water from July to October.

Sites	Monthly samples											
	M	J	J	A	S	O	N	D	J	F	M	A
Water temperature (°C)												
1	14	17	17	17	17	11	15	14	13	8	13	11
2	14	18	19	15	14	9	12	13	11	5	11	11
3	17	18	20	16	15	10	12	12	8	4	10	12
4	23	19	-	-	-	-	10	10	9	6	10	15
5	22	19	24	18	20	12	11	10	9	4	10	15
6	20	21	30	25	24	16	15	13	7	7	17	15
7	17	24	-	-	-	-	14	12	11	10	12	15
8	20	27	25	23	24	18	15	13	12	11	16	16
Current velocity (cm/s)												
1	25	15	15	25	18	30	30	35	35	30	33	50
2	25	15	20	30	18	30	30	60	65	60	45	100
3	25	6	1	20	38	25	40	100	45	40	45	80
4	30	0	-	-	-	-	40	83	55	55	55	65
5	15	17	1	18	15	30	55	125	50	70	70	75
6	60	0	0	0	0	0	60	110	80	110	110	140
7	30	0	-	-	-	-	40	140	55	70	70	100
8	0	0	0	0	0	0	0	0	0	0	0	0
Alkalinity (mg/l)												
1	12	30	18	21	12	15	12	12	15	15	15	21
2	27	32	33	24	21	18	21	12	15	15	18	12
3	30	94	125	94	61	54	42	21	24	24	24	18
4	82	137	-	-	-	-	45	30	51	67	51	61
5	48	79	109	103	91	73	61	33	36	42	39	36
6	67	103	115	158	167	176	67	33	42	48	45	45
7	97	149	-	-	-	-	85	48	48	64	54	57
8	70	103	134	149	152	189	67	33	42	48	45	51
Chloride (mg/l)												
1	7	8	8	8	9	8	8	7	7	7	7	7
2	10	10	13	9	11	10	11	8	9	9	8	9
3	12	18	30	19	21	15	17	12	10	11	10	9
4	12	24	-	-	-	-	16	11	15	16	11	11
5	13	19	21	28	28	19	17	12	13	14	10	11
6	12	17	18	22	26	27	15	10	12	11	10	11
7	12	18	-	-	-	-	15	11	12	11	10	12
8	12	16	18	21	34	36	15	10	12	11	10	11
Dissolved oxygen (mg/l)												
1	7	7	7	8	8	9	8	8	9	8	8	8
2	8	7	7	7	8	9	8	8	9	10	9	8
3	7	5	2	4	6	8	9	9	10	9	9	8
4	7	5	-	-	-	-	9	10	11	10	8	8
5	6	6	3	6	7	9	9	10	11	11	9	8
6	7	6	9	8	9	9	9	9	10	9	8	8
7	8	9	-	-	-	-	9	9	10	9	8	7
8	7	6	8	7	8	10	8	9	11	9	8	7

species were *Onychogomphus uncatus* (Charpentier) (35% of larvae collected) and *Boyeria irene* (Fonscolombe) (26%); the value of the dominance index (McNaughton and Wolf 1970) was 61%. At Site 2, 46% of larvae collected were *B. irene* and 28% were *Cordulegaster boltoni* (Donovan); dominance index 74%.

The richness also differed in the two seasonal streams studied, but in this case the values obtained for diversity differed even more (Fig. 3). At Site 4 on a stream in the middle part of the catchment, *Coenagrion coerulescens* (Fonscolombe) was the most abundant species, making up 50% of the larvae taken. At Site 7 on a stream in the lower part of the catchment, however, 84% of the larvae captured were *Lestes viridis* (Van der Linden). The massive appearance of this species in spring and its clear dominance gave this stream the lowest diversity along the catchment.

The two sites on the upper reach of the main channel showed the greatest richness, 14 species, whereas at Sites 6 and 8 (on the middle and lower reaches) 12 and 7 species respectively were found. When the diversity for the two sites on the upper

Table III. - A, Species found in this study; *Calopteryx* spp. include *C. haemorrhoidalis* and *C. xanthostoma*; *Platycnemis* spp. include *P. acutipennis* and *P. latipes*. Abundance values have been transformed into semi-quantitative data according to Vernaux's method (1973), thus reducing the influence on the calculations of the most abundant species and eliminating species with ubiquitous distribution or with a very low level of occurrence. i/N is the upper limit of class three (see explanation in text). B, Larval body-length in millimetres, two age-groups are separated.

A									
Species	Sites								i/N
	1	2	3	4	5	6	7	8	
<i>C. virgo</i> (L.)	5	1	2	-	-	-	-	-	7
<i>Calopteryx</i> spp. Leach	4	-	3	-	4	1	-	-	7
<i>L. viridis</i> (V.d.Linden)	-	-	1	-	1	5	-	-	13
<i>Platycnemis</i> spp. Burm.	-	-	1	-	4	4	-	2	6
<i>P. nymphula</i> (Sulzer)	-	-	-	-	-	-	-	-	(2)
<i>I. graellsii</i> (Rambur)	-	-	-	-	-	-	-	-	(3)
<i>C. lindeni</i> (Sélys)	-	-	1	5	4	1	4	-	53
<i>C. coerulescens</i> (Fonsc.)	-	-	-	5	2	-	-	-	7
<i>G. pulchellus</i> Sélys	-	-	-	2	4	-	4	-	7
<i>O. uncatus</i> (Charp.)	5	4	3	-	1	-	-	-	34
<i>O. forcipatus</i> (L.)	-	1	4	1	5	4	1	-	6
<i>B. irene</i> (Fonsc.)	4	5	1	-	1	-	-	-	35
<i>A. imperator</i> Leach	-	-	-	-	-	-	-	-	(1)
<i>C. boltoni</i> (Donovan)	4	4	1	-	-	-	-	-	31
<i>M. splendens</i> (Pictet)	-	-	-	-	-	-	-	-	(2)
<i>P. depressum</i> (L.)	-	-	3	-	-	-	-	-	6
<i>O. coerulescens</i> (F.)	-	-	4	-	3	1	-	-	4
<i>O. chrysostigma</i> (Burm.)	-	-	-	-	-	-	-	-	(1)
<i>C. erythraea</i> (Brullé)	-	-	-	-	-	-	-	-	(3)
<i>S. striolatum</i> (Charp.)	-	-	-	-	-	-	-	-	(2)
<i>T. annulata</i> (Pal.Beauv.)	-	-	-	-	-	3	-	4	5

B			
	<i>Onychogomphus forcipatus</i>	<i>Gomphus pulchellus</i>	
May 1983	10.0	18.3-22.2	17.5
June	10.0-16.8	21.3-24.4	21.3
July	10.6-15.4		21.3
August	10.7		22.0-22.6
September	14.0-14.6		21.6-27.9
October	9.0	18.7	
December			12.7
January 1984	11.8		25.2
February	13.4		28.3
March	10.9-11.0		14.4
April	12.5	19.7-24.2	

reach was calculated we found that, although the same number of species had been collected, the diversity was clearly lower at Site 5. The dominance index at site 3 was 43%, the lowest along the catchment. The decrease in diversity values continued progressively toward the mouth of the river. This fact is due to two circumstances: the decrease in species found at each site as one proceeds downriver; and the progressive effect of the dominance of one species, *Cercion lindeni* (Sélys). Of the larvae collected at Sites 5, 6 and 8, 59%, 63% and 79% respectively were *C. lindeni*.

Temporal variation in community structure

Among the 23 species found during this study, 79.4% of the individuals collected belong to only six species (*L. viridis*, *C. lindeni*, *O. uncatus*, *O. forcipatus*, *B. irene* and *C. boltoni*). Two other species, *C. virgo* and *G. pulchellus*, are less abundant but of significance to the structure of associations.

Larvae of *O. uncatus*, *B. irene* and *C. boltoni* were found on headwater streams throughout the year. The range in size of these larvae, featuring a bimodal instar-distribution of overwintering larvae, demonstrates that these species are semi-voltine. Adults of these three species were collected only in June and July. In general, *O. uncatus* and *B. irene* can be regarded as typical summer species. 76.5% of final-instar larvae of *B. irene* were collected from late January to late May; 52.9% were collected between March and

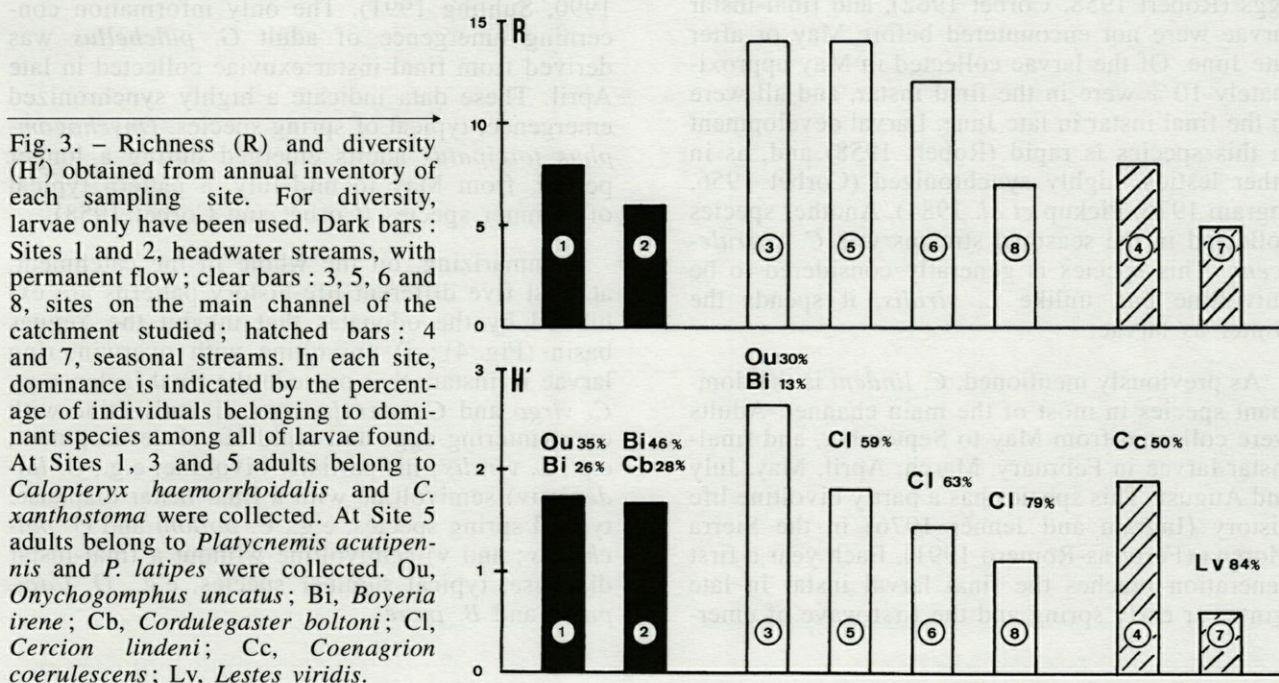


Fig. 3. - Richness (R) and diversity (H') obtained from annual inventory of each sampling site. For diversity, larvae only have been used. Dark bars: Sites 1 and 2, headwater streams, with permanent flow; clear bars: 3, 5, 6 and 8, sites on the main channel of the catchment studied; hatched bars: 4 and 7, seasonal streams. In each site, dominance is indicated by the percentage of individuals belonging to dominant species among all of larvae found. At Sites 1, 3 and 5 adults belong to *Calopteryx haemorrhoidalis* and *C. xanthostoma* were collected. At Site 5 adults belong to *Platycnemis acutipennis* and *P. latipes* were collected. Ou, *Onychogomphus uncatus*; Bi, *Boyeria irene*; Cb, *Cordulegaster boltoni*; Cl, *Cercion lindeni*; Cc, *Coenagrion coerulescens*; Lv, *Lestes viridis*.

May. From late January to late May 73.9% of the final-instar larvae of *O. uncatus* were collected and 60.8% between March and May. However, 4 of the 10 *O. uncatus* larvae collected in October were in the final instar; the fact that a certain number of larvae enter the final instar during autumn suggests that this species does not have a very clearly defined life-history pattern, as in some other Odonata (Paulson and Jenner 1971, Norling 1984). On the contrary, *C. boltoni* is a typical spring species: between January and May only 53.3% of final-instar larvae of this species were collected. From late March to late May only 13.3% of the final-instar larvae were collected.

Another species found principally in headwater streams was *C. virgo*. Adults of this species were collected in May, June and July, and final-instar larvae were collected only in February and March. The larvae of this species collected in December were from penultimate and antepenultimate instars. Although our data for this species are not numerous and more extensive studies are required, it is possible that the life history in the south of the Iberian Peninsula differs from that in Britain (Corbet 1957a) and Switzerland (Robert 1958). In our study area it may be that the life history is completed in a year and the final instar is not a diapause stage. This insect appears to function as a summer species.

Dominant in astatic environments (Castella 1987), *L. viridis* is the most characteristic species of the seasonal streams of the Sierra Morena (Ferrerias-Romero 1984, 1988a, Ferrerias-Romero and Gallardo-Mayenco 1985). Adults were collected in June and October and larvae between April and June. This species has overwintering eggs (Robert 1958, Corbet 1962), and final-instar larvae were not encountered before May or after late June. Of the larvae collected in May approximately 10% were in the final instar, and all were in the final instar in late June. Larval development in this species is rapid (Robert 1958) and, as in other lepidoptera, highly synchronized (Corbet 1956, Ingram 1976, Pickup *et al.* 1984). Another species collected in the seasonal streams was *C. coerulescens*. This species is generally considered to be univoltine but, unlike *L. viridis*, it spends the winter as larvae.

As previously mentioned, *C. lindeni* is the dominant species in most of the main channel. Adults were collected from May to September, and final-instar larvae in February, March, April, May, July and August. This species has a partly bivoltine life history (Ingram and Jenner 1976) in the Sierra Morena (Ferrerias-Romero 1991). Each year a first generation reaches the final larval instar in late winter or early spring and the first wave of emer-

gence occurs in spring. The first final-instar larvae were collected in late February at Site 8; at Sites 5 and 6, however, final-instar larvae were not collected before late March. By May many adults were collected. The second generation resulting from cohort splitting consists of individuals that had hatched in spring from eggs laid by the earliest emerging adults. These individuals had grown rapidly, and within a single summer had completed development and emerged in late July, August or September. Other members of the same cohort experienced slow growth such that they were destined to overwinter and then emerge as the first wave the following year.

Two other species that were relatively abundant in the main channel are *O. forcipatus* and *G. pulchellus*, the first of which is found more frequently upstream and the latter downstream. Both species are semivoltine, as demonstrated by the bimodal size-distribution of larvae (Table. III). However, the life-history patterns seen in these insects are not the same in both species. The great majority of *O. forcipatus* larvae collected in autumn and winter were in the antepenultimate instar or were even smaller. Only one larva, collected in October at Site 5, was in the penultimate instar. From July to March no final-instar larvae were collected. Final-instar and penultimate-instar larvae were often collected in April and May. Thus this species is a typical summer species. Final-instar larvae of *G. pulchellus*, on the other hand, were collected in September, December and February. The senior cohort attained the final instar at the beginning of autumn and overwintered in that instar. *Gomphus pulchellus* is a typical spring species. Similar results have been obtained in Lower Saxony (Germany) (Müller and Suhling 1990, Suhling 1991). The only information concerning emergence of adult *G. pulchellus* was derived from final-instar exuviae collected in late April. These data indicate a highly synchronized emergence, typical of spring species. *Onychogomphus forcipatus* adults emerged during a longer period, from May to mid-July, a pattern typical of summer species (Corbet and Corbet 1958).

Summarizing, on the whole in the catchment, at least five different life-history patterns are exhibited by the odonates that inhabit the Yeguas basin (Fig. 4): i) univoltine with overwintering larvae in instars that precede the final instar, e.g., *C. virgo* and *C. coerulescens*; ii) univoltine with overwintering eggs and rapid larval development, e.g., *L. viridis*; iii) partially bivoltine, e.g., *C. lindeni*; iv) semivoltine with a final-instar diapause, typical spring species, e.g., *C. boltoni* and *G. pulchellus*; and v) semivoltine without a final-instar diapause, typical summer species, e.g., *O. forcipatus* and *B. irene*.

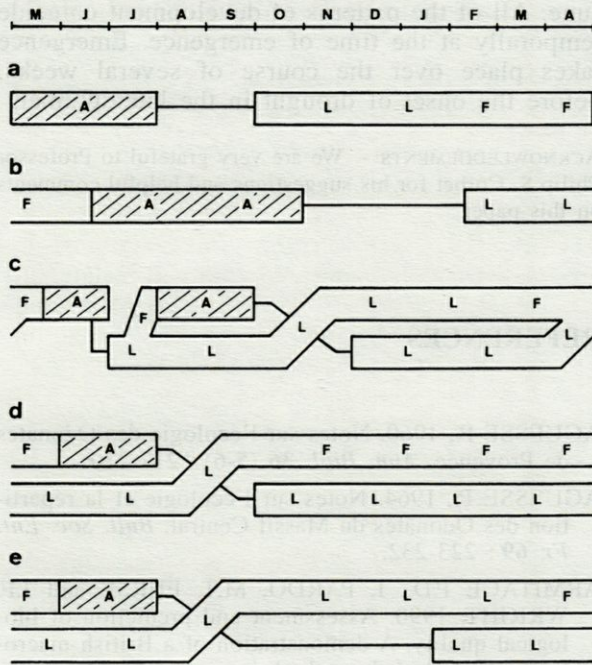


Fig. 4. - Life-history patterns exhibited by the odonates that inhabit the Yeguas basin: a and b, univoltine; c, partially bivoltine; d and e, semivoltine. A in hatched area, adult stage; in clear area, F final-instar larvae, L larvae of smaller instar; line, eggs.

DISCUSSION

The few studies that have been carried out on the structure and functioning of the odonate community of an entire river basin (Perry 1981) show that the species are distributed according to models that are easily explained as a function of the physiognomy of the river's successive reaches. This is determined by factors such as slope, current-velocity and stability or seasonality of flow (Jarry and Vidal 1969, Aguesse 1960, Voshell and Simmons 1978), parameters that largely dictate the type of river bottom and determining the annual variation in water temperature and the concentration of dissolved oxygen in the water.

In this study highest abundance values correspond to the headwater streams (Sites 1 and 2) and the second half of the upper reach of the main channel (Site 5). Several semivoltine Anisoptera (*O. uncatus*, *B. irene* and *C. boltoni*) find their optimal ecological situation in the headwater streams, and a relatively important population of *C. lindeni* was encountered at Site 5, where *O. forcipatus* also has its ecological optimum.

The uppermost part of the main channel (Site 3) was the only area in the catchment that experiences some level of eutrophication of the water in summer, highest concentration of ions

Na^+ , K^+ , SO_4 , Cl^- , P_2O_5 (Table. I) and low levels of dissolved oxygen (Table. II). The influx of nutrients at this point on the river is explained by the fact that the only source of urban pollution in the catchment is found some 2.5 km upstream. According to Aguesse (1964), a certain level of eutrophication in the water leads an increase in the variety of odonate species in a given area. The high richness in this site (Fig. 3) must also be explained because some larvae belong to rheophilous species (*O. uncatus*, *B. irene*, *C. boltoni*) must arrive by drift at this area, in winter and spring, from points upstream.

A progressive decrease in richness and diversity were observed going downstream along the main channel. This decrease seems to correspond to a progressive increment in the seasonal variation of abiotic factors (temperature, velocity of current) which, in turn, appears to give rise to the dominance of one species, in this case *C. lindeni*. This insect is partially bivoltine and completes two generations each year (Ferrerías-Romero 1991). *Cercion lindeni* is, probably, the species best adapted to the particular environmental conditions of the rivers of the Sierra Morena (Ferrerías-Romero 1982, 1984, 1988b, Ferrerías-Romero and Gallardo-Mayenco, 1985), conditions characterized by marked seasonality and interrupted flow during several months each year.

Besides *C. lindeni*, in the main channel, two semivoltine species (*G. pulchellus* and *O. forcipatus*) are also abundant. These last species, besides appearing to be partially separated spatially, also exhibit different life histories which in turn are different from the model shown by the more abundant *C. lindeni*. Similarly, in the headwater streams, *B. irene*, *C. boltoni* and *C. virgo* have different life histories. This is probably a useful strategy for counteracting interspecific competition (Butler 1984), because differences in temporal patterns, developmental rates of larvae and, in general, the temporal separation of life cycle events may be important in enabling the species to exist sympatrically (Ingram and Jenner 1976).

The co-existence of several species of Odonata with high abundance levels and different modes of larval development is apparently frequent in ponds (Benke and Benke 1975, Ingram and Jenner 1976) and lakes (Crowley and Johnson 1982). For certain communities the spatial separation of populations occupying different microhabitats appears to be more important to their co-existence than temporal separation (Johannsson 1978). However, among species with similar ecological characteristics, such as odonates, the temporal separation due to life-cycle displacement works importantly to decrease or eliminate competition among populations (Benke 1970), thus favouring their co-existence (Johannsson 1978). Moreover, a niche differentiation in foraging behaviour (a sit

and wait or an active mode) may be one of several ways to reduce food competition between co-existing species (Johansson 1991).

According to Crowley and Johnson (1982), larval habitat and seasonality are important factors in the odonate communities. The results obtained in the Yeguas basin clearly support Crowley and Johnson's conclusions for lentic environments, but here for a river system. The distribution of populations across the catchment seems to reduce the interaction among dominant populations, whereas the seasonal distribution reduces the overall intensity of these interactions. In each of the different types of habitat in the catchment where this study was carried out there exist two or more species with different patterns of life history.

The life-history pattern of *O. uncatus* is unclear because in southern Europe some species that inhabit streams that are highly stable in terms of water temperature, flow and food availability, probably not enter winter diapause in the no-final instars. Although the winter diapause in the larval stage is a well known feature of insects at higher latitudes (Corbet, 1962; Norling, 1984), in southern Europe certain species may only become quiescent in winter. If this is indeed so, the growth of the cohort may be continuous until the larvae reach the final instar. Depending on the season in which a larva reaches the final instar, either it will proceed quickly to maturity (in spring and early summer), or its development will temporally stop (in late summer, autumn and winter). Such a facultative diapause was first recognised in *Anax imperator* Leach (Corbet 1957b); it permits larvae that have spent their last winter in the latest larval instars (the last two in the case of *A. imperator* in England) to emerge in the same year.

How semivoltine species (*G. pulchellus*, *O. forcipatus*) can complete their life cycles in watercourses that are reduced to a series of isolated ponds from July to October, with elevated water temperature (> 30 °C) and, consequently, very low dissolved oxygen level, is a subject requiring further investigation. Our working hypothesis is that the larvae remain, perhaps in quiescence, in the hyporheic zone. The ecological significance of the hyporheic habitat in rivers has been discussed for several aquatic insects (Williams 1984, Stanford and Ward 1988, Puig *et al.* 1990) including dragonflies (Reygrobellet and Castella 1987, Strommer and Smock 1989). The hyporheic zone offers protective advantages for benthic invertebrates during the dry season (Bishop 1973, Williams 1977).

The diversity in life-history patterns contrasts with the uniformity in the time of year in which almost all of the species studied here are on the wing. All of the species collected as adults were found from May to July; 74% being collected in

June. All of the patterns of development coincide temporally at the time of emergence. Emergence takes place over the course of several weeks, before the onset of drought in the late summer.

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