ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/226974917

The life cycle of Cordulegaster boltonii (Donovan, 1807) (Odonata: Cordulegastridae) in the Sierra Morena Mountains (Southern Spain)

Article *in* Hydrobiologia · June 1999

DOI: 10.1023/A:1003763819991

CITATIONS
46

READS
1,338

2 authors, including:



Manuel Ferreras-Romero

131 PUBLICATIONS **1,052** CITATIONS

SEE PROFILE

All content following this page was uploaded by Manuel Ferreras-Romero on 06 June 2014.

The user has requested enhancement of the downloaded file.

Hydrobiologia **405:** 39–48, 1999.
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

The life cycle of *Cordulegaster boltonii* (Donovan, 1807) (Odonata: Cordulegastridae) in the Sierra Morena Mountains (southern Spain)

Manuel Ferreras-Romero[1,*] & Philip S. Corbet[2,3]
[1]*Departamento de Biología Animal (Zoología), Facultad de Ciencias, Universidad de Córdoba, Avda. San Alberto Magno s/n, ES-14004 Córdoba, Spain*
[2]*Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, U.K.*
[3]*Present address: Crean Mill, Crean, St Buryan, Cornwall TR19 6HA, U.K.*

Received 14 December 1998; in revised form 4 May 1999; accepted 20 May 1999

Key words: Odonata, life cycle, permanent stream, southern Spain, voltinism

Abstract

The life cycle of the dragonfly *Cordulegaster boltonii* was studied for five consecutive years, mainly by systematic sampling of larvae, in a permanent upland stream in southern Spain, towards the southern part of this species' range. The instar distribution during winter is that of a 'spring species' (Corbet, 1964) in which larvae destined to emerge in the next spring are predominantly in the final instar. During larval development a hatching cohort divides into 'slow' and 'fast' components which respectively complete development in three and two years, the former component predominating. Signs of advanced metamorphosis (in the last larval instar) are confined to late winter and spring. Emergence is protracted, there being a long 'tail' after most of the population has emerged, resulting in a long flying season.

Introduction

Cordulegastrid dragonflies, represented in Europe only by the genus *Cordulegaster* (but see Lohmann, 1992, 1993), typically occur in lotic waters, generally small streams and brooks, where larvae live as shallow burrowers in sediment. In Europe this genus comprises five species, of which *C. boltonii*, a large, polytypic species, is the most widespread. It occurs from southern Spain to southern Scandinavia and is reported from Tunisia, Algeria and Morocco (Askew, 1988).

Information on the life cycle of *C. boltonii* is sparse. In Britain this species is considered to be a partivoltine 'spring species' and to have eggs that do not overwinter (Corbet et al., 1960). Preliminary observations have been published on its voltinism in southern Spain (Ferreras-Romero, 1994). Information on the occurrence, phenology, population density and exuvial measurements in central Germany were given by Brettfeld (1989); and larval microdistribution at the stream margins, diets of larvae and influence of foraging conditions on the distribution in streams draining different environments in Britain were described by Ormerod et al. (1990) and Lloyd & Ormerod (1992). Egg development and early instars were studied by Schütte (1997) in southern France. The work described here was undertaken to characterize larval development of this dragonfly towards the southern part of its geographical range, so that the species' voltinism and seasonal regulation there could be compared with populations at higher latitudes.

Methods

The present study was carried out at the Bejarano Stream (37° 56′ N, 4° 52′ W), a watercourse in the Sierra Morena Mountains, close to Sta. Maria de Trassierra, Córdoba, Andalusia, Spain. The study site was a small, permanent, mountain stream, about

* (author for correspondence)

400 m above m.s.l., with a closed canopy of trees along most of its length. Alder (*Alnus glutinosa* (L.)), elm (*Ulmus minor* Miller), chestnut (*Castanea sativa* Miller) and hazel (*Corylus avellana* L.) grew along the banks. In the watercourse here studied, four other species of Odonata existed as stable populations: *Aeshna cyanea* (Müller), *Boyeria irene* (Fonscolombe), *Calopteryx haemorrhoidalis* (Vander Linden) and *Onychogomphus uncatus* (Charpentier) (Ferreras-Romero & Corbet, 1995; Ferreras-Romero & Puchol-Caballero, 1995; Ferreras-Romero, 1997; Ferreras-Romero et al., 1999); but the population of *C. boltonii* featured the greatest number of individuals in larval samples. At the sampling site the stream's width was 2–5 m and its mean water depth was 35–50 cm. The stream contained no fish. At each visit, water temperature in the stream was recorded between 0900 and 1100 G.M.T. to the nearest 0.5 °C. Additional data relating to abiotic attributes of this watercourse were recorded by Ferreras-Romero (1997).

To confirm the absence of overwintering diapause in the egg, 50 eggs, laid into sand by the stream bank on 15 May 1992, were placed in water in separate tubes and kept in the laboratory at 21 °C.

Monthly from February 1988 to May 1992 (except in November 1989), larvae were collected using handnets with square mesh (one side of a square = 0.25 mm). Because smaller instars of odonate larvae cannot be adequately sampled by handnets of this mesh-size (Lawton, 1970), the frequency of the smaller size-classes would have been underestimated (see Johnson, 1986). In 1992, exuviae (of final-instar larvae) were collected regularly (from 31 March to 20 April, the stream was visited five times at 4–6 day intervals and, from 25 April to 12 October, 35 times at 5 day intervals) and exhaustively (from a standard strip of one bank, about 300 m long) throughout the emergence period; and the presence of adults was also recorded (Ferreras-Romero & Corbet, 1995).

In the laboratory, the head width (HW; i.e. the maximum distance between the lateral margins of the compound eyes) of each larva and the length of the metathoracic (hind) wing sheaths (WS), if present, were measured to the nearest 0.1 mm using a Nikon binocular microscope with an eyepiece micrometer. The number of abdominal segments covered by the metathoracic WS was also recorded.

On the basis of HW and WS length each larva was either assigned to one of the last four instars or designated a 'smaller larva'. Here we follow common practice, designating the final, penultimate and preceding instars as F-0, F-1, F-2 etc. The sex of each larva was determined according to the presence (female) or absence (male) of gonapophyses on the ventral surface of the eighth and ninth abdominal segments.

Table 1. Water temperature (°C) at Stream Bejarano

	1988–89	1989–90	1990–91	1991–92
December	13.0	14.0	13.0	12.0
January	13.5	15.0	12.0	10.0
February	14.0	15.5	14.0	12.0
March	14.0	15.0	14.0	12.0
April	14.0	15.5	15.0	15.0

Presence of a thick coating of allochthonous particles on the body surface, especially on the abdominal venter, allowed 'very clean', 'clean' and 'dirty' larvae to be distinguished and the relative hardness and darkness of the integument of larvae of the last three instars gave an indication of how recently a larva had moulted. Allocation of larvae to categories was not based on quantifiable criteria. Larvae lacking a thick coating of allochthonous particles ('very clean') and with an integument that was light yellow, soft and flexible had apparently just moulted, thus distinguishing them from larvae with a dark, hard integument bearing moderate ('clean') or large ('dirty') amounts of allochthonous particles on the body surface.

Because numbers of larvae collected at each monthly visit were often small (average about 75; range 25–133), because only one habitat was sampled and because interyear variation in water temperature there during summer was slight, we combined data for separate years when constructing size-frequency distributions to trace larval growth (Figure 2). Our confidence in use of this method in the present study was confirmed by the finding that, for the last two instars during autumn, a season when growth occurs, and during winter, a season when temperature varies widely between years (Table 1), the aggregate distribution (Figure 2) was indeed representative of the distribution in each of the individual months that contributed to it, even though the disaggregated frequencies were derived from small numbers (Figure 3).

Onset and progress of metamorphosis (a term we use here to describe intrastadial changes discernible in F-0) were traced by assigning F-0 larvae to one of four arbitrary stages, distinguished (at 10 × magnification) by external features as follows:

(a) No external signs of metamorphosis; WS flat; external edge of fore WS overlain and hidden (in dorsal view) by hind WS; compound eyes without anteromesial (black) extension.
(b) Metamorphosis evident. Compound eyes with anteromesial (black) extension, reaching the basal antennal segment. WS not swollen. Prementum unicoloured, only sometimes bicoloured (distal end dark, void of muscular tissue, see below).
(c) Metamorphosis advanced. Extension of compound eyes (black) progressing (beneath the cuticle) behind the posterior limit of eyes. WS swollen or not. Prementum bicoloured; muscular tissue within prementum of labium (viewed ventrally) not entire, central part of distal third void of muscular tissue (dark); first segment of labial palpi likewise partly void of muscular tissue.
(d) Emergence imminent. WS swollen, costal vein of adult wing visible and folded concertina-like within WS; extension of compound eyes at full extent, appearing black for 2/3 of the length of head; prementum completely void of muscular tissue.

Results

Water temperature

The highest water temperature recorded (°C) was 19 (21 August 1989, 4 September 1990, 3 and 18 August 1992) and the lowest was 10 (22 January 1992) (Table 1). Here we record only water temperatures during winter, this being the season when temperature varied widely between years and correlated with the abundance of F-0 in April and May (Figure 3). Water temperatures for other months are given by Ferreras-Romero et al. (1999: 218).

Determination of instar classes

From June 1989 to May 1992, 2624 larvae were collected (average ca 75 larvae/sample); and 596 larvae were collected from February 1988 to May 1989.

F-0 larvae could always be recognized unequivocally by possession of the following features: HW 7.6–9.6 mm (97.8% of larvae lying between 8.0 and 9.6); WS 9.1–11.4 mm long and reaching to the fourth abdominal segment; HW of female F-0 (mean 8.95 ± 0.24 (S.E.), range 8.3–9.6 mm, N = 240) significantly greater than those of males (mean 8.28 ± 0.20 (S.E.), range 7.6–8.8 mm, N = 230) (t-test = 32.0609, df = 468, $P < 0.05$).

Table 2. Sex ratio (shown as % males) of exuviae and last four larval instars collected each year at Stream Bejarano

	1989		1990		1991		1992	
	N	% m	*N*	% m	*N*	% m	*N*	% m
Exuviae	148	42.5	226	46.0	476	50.6	1091	47.2
F-0	49	55.1	153	49.0	185	49.1	47	40.4
F-1	61	42.6	129	47.2	110	48.1	34	50.0
F-2	85	47.0	101	33.6	128	57.0	53	54.7
F-3	88	56.8	67	46.2	125	53.6	85	56.4

Head widths of F-1 (6.1–7.7 mm, 93.9% lying between 6.4 and 7.4), F-2 (4.8–6.3 mm, 91.1% between 5.1 and 6.0) and F-3 (3.9–5.1 mm, 77.8% between 4.1 and 4.7) larvae overlapped, but WS lengths were discrete, being 4.4–5.7 mm in F-1, 2.2–3.4 mm in F-2 and 1.3–1.7 mm (exceptionally 1.1–2.0 mm) in F-3. In F-1 and F-2 the WS extended to the posterior margin of the second and the first abdominal segment, respectively. In F-3, the WS extended to halfway along the first abdominal segment.

Head widths of female F-1 (mean 7.06 ± 0.24 (S.E.), range 6.4–7.7 mm, N = 189) were significantly greater than those of male F-1 (mean 6.60 ± 0.21 (S.E.), range 6.1–7.3 mm, N = 177) (t-test = 19.4768, df = 364, $P < 0.05$). Head widths of female F-2 (mean 5.61 ± 0.23 (S.E.), range 5.1–6.3 mm, N = 215) likewise were significantly greater than those of male F-2 (mean 5.23 ± 0.20 (S.E.), range 4.7–5.8 mm, N = 197) (t-test = 17.2858, df = 410, $P < 0.05$). Head widths of female F-3 (mean 4.50 ± 0.22 (S.E.), range 4.0–5.1 mm, N = 184) were significantly greater than those of male F-3 (mean 4.21 ± 0.22 (S.E.), range 3.9–5.0 mm, N = 220) (t-test = 12.5953, df = 402, $P < 0.05$). So in at least the last four instars male larvae were smaller than female larvae.

Seasonal pattern of emergence and flight period

From 1989 to 1992, 1941 F-0 exuviae were collected (Table 2). During 1992 the pattern was quantified (Ferreras-Romero & Corbet, 1995), 10, 50 and 90% of the annual emergence being accomplished on 5.2, 28.1 and 67.0% of the way through the emergence period. Neither sex appeared to emerge earlier. The emergence of both sexes was protracted (Figure 1), there being a long 'tail' after about 90% of adults of the year had emerged. The sex ratio, which did not depart significantly from 1:1, was 47.2% males (N =

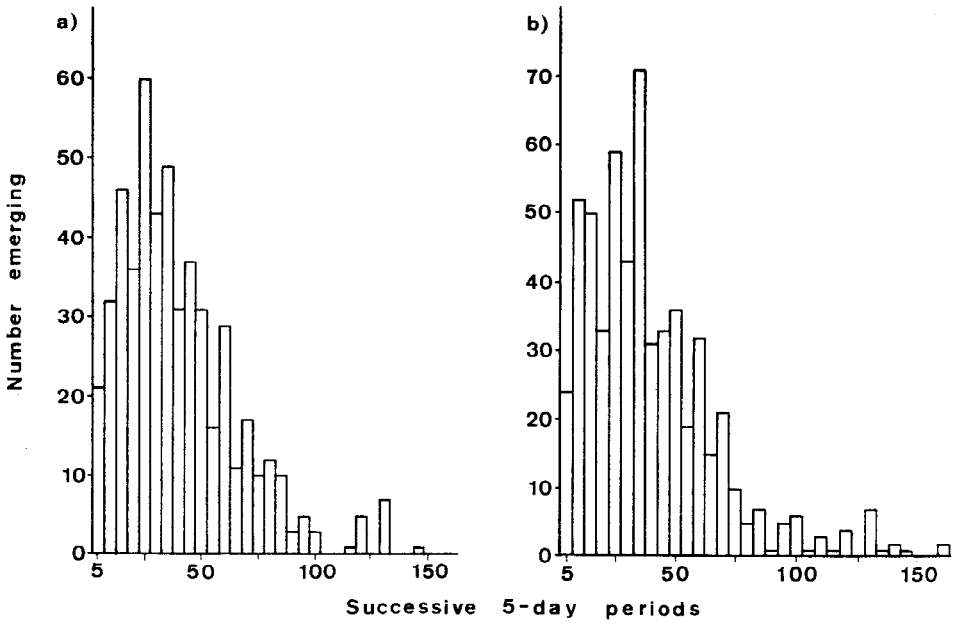


Figure 1. Numbers of males (a) and females (b) of *Cordulegaster boltonii* emerging from Bejarano Stream during successive five-day periods in 1992, shown by exuvial collections. Day 5 is 25 April. The first exuvia was found on 25 April and the last on 27 September.

1091) ($\chi^2_{(1)} = 3.19$, $P > 0.05$). Each year (except 1991) female exuviae were more numerous than male exuviae (Table 2). Sex ratios for F-0 and F-1 appeared to agree with the emergence data, but sex ratios for F-2 and F-3 larvae could not be said to do so.

In 1992, patrolling males were first seen on 5 May and oviposition was first witnessed on 15 May; the last adult (a male) was seen on 8 August.

Egg development

Eggs showed direct development, hatching between 1 and 29 June, 17–43 days after having been laid.

Larval development

The smallest larvae encountered in this study (HW < 0.7 mm) were collected from July to December and no larva with HW < 1.0 mm was found during April through June (Table 3). Each year the smallest larvae to be encountered in May and June had a HW of ca 1.2 mm; despite their small size such larvae must have derived from eggs laid the previous year.

Each year, larvae (derived from eggs hatching in early summer) grew during late summer and autumn (Figure 2). Growth continued during the winter and spring: in June and July most larvae derived from eggs laid the previous year had a HW between 1.7 and 3.0 mm, having reached instars F-7, F-6 or F-5. In September, at the beginning of their second year, some larvae had reached F-3 (HW 4.0–5.0 mm); and three months later, in December, after autumnal growth, some larvae in this cohort had reached F-1, while others were still in F-6 (HW 2.0–2.5 mm). So larval growth within a single hatching cohort can be 'fast' or 'slow'.

Larvae that grow fast can enter F-0 during the next winter and spring and emerge in their second summer, as 'summer species' (*sensu* Corbet, 1964) thus exhibiting a semivoltine life cycle. Consistent with this inference are the percentages of larvae in F-0 during December through March (Table 3) and the decrease in frequency of F-1 from January to March (Figure 2).

Larvae that grew slowly spent their first winter in early instars and their second winter in about F-6 to F-2. They entered F-3, F-2 and F-1 in their second spring and summer (April–July), but did not enter F-0 *en masse* until their third autumn. They then spent their third winter in F-0 and emerged in the spring before their third summer, as 'spring species' exhibiting a partivoltine life cycle. Consistent with this inference are the percentages of F-2 and F-1 from April to June, the rising percentages of F-0 during August through November–December (Table 3) and the paucity of F-0 during June through August.

Table 3. Monthly range and mean of larval head width in the last four instars; the size range of smaller larvae is also indicated. The number and percentage of larvae in the last four instars collected each month (three years combined) are shown in parentheses

Months in 1989–1992	Larval instars				
	F-0 (*N*=412)	F-1 (*N*=315)	F-2 (*N*=329)	F-3 (*N*=329)	Smaller larvae
June	8.2–9.4(8) $x = 8.51$ (1.9%)	6.2–7.5(40) $x = 6.83$ (12.7%)	5.0–6.0(44) $x = 5.41$ (13.3%)	3.8–5.1(36) $x = 4.33$ (10.9%)	1.3–4.0(189)
July	8.1–9.2(5) $x = 8.77$ (1.2%)	6.3–7.4(19) $x = 6.86$ (6.0%)	5.1–5.6(12) $x = 5.34$ (3.6%)	3.8–4.7(21) $x = 4.24$ (6.3%)	0.5–3.8(123)
August	7.8–8.8(7) $x = 8.39$ (1.7%)	6.5–7.3(22) $x = 7.00$ (6.9%)	5.0–6.0(20) $x = 5.41$ (6.0%)	4.0–5.0(16) $x = 4.46$ (4.8%)	0.4–3.8(131)
September	8.1–9.3(14) $x = 8.60$ (3.4%)	6.2–7.3(27) $x = 6.86$ (8.5%)	5.1–5.8(13) $x = 5.47$ (3.9%)	3.8–4.6(23) $x = 4.36$ (7.0%)	0.5–3.7(103)
October	7.7–9.6(33) $x = 8.71$ (8.0%)	6.2–7.3(26) $x = 6.86$ (8.2%)	4.7–6.1(30) $x = 5.30$ (9.1%)	3.8–4.6(34) $x = 4.25$ (10.3%)	0.5–3.8(72)
November	8.2–9.4(38) $x = 8.76$ (9.2%)	6.3–7.3(22) $x = 6.89$ (6.9%)	5.1–5.8(13) $x = 5.44$ (3.9%)	4.1–4.8(9) $x = 4.55$ (2.7%)	0.5–4.0(50)
December	7.8–9.3(52) $x = 8.64$ (12.6%)	6.1–7.1(15) $x = 6.75$ (4.7%)	4.7–6.1(23) $x = 5.49$ (7.0%)	4.0–5.0(21) $x = 4.46$ (6.3%)	0.5–4.0(55)
January	7.8–9.4(57) $x = 8.61$ (13.8%)	6.2–7.4(36) $x = 6.79$ (11.4%)	5.0–5.7(16) $x = 5.50$ (4.8%)	3.8–4.7(22) $x = 4.41$ (6.6%)	0.8–3.8(52)
February	7.7–9.2(59) $x = 8.62$ (14.3%)	6.3–7.7(23) $x = 6.92$ (7.3%)	5.1–6.0(31) $x = 5.45$ (9.4%)	4.0–4.7(31) $x = 4.41$ (9.4%)	0.7–4.0(86)
March	7.7–9.2(71) $x = 8.56$ (17.2%)	6.4–7.3(18) $x = 6.77$ (5.7%)	4.8–6.2(35) $x = 5.48$ (10.6%)	3.8–4.8(41) $x = 4.37$ (12.4%)	0.8–4.0(110)
April	7.6–9.4(38) $x = 8.73$ (9.2%)	6.4–7.6(22) $x = 6.91$ (6.9%)	5.0–6.1(44) $x = 5.51$ (13.3%)	3.8–4.8(27) $x = 4.32$ (8.2%)	1.4–3.8(103)
May	8.0–9.6(30) $x = 8.71$ (7.2%)	6.4–7.6(45) $x = 6.93$ (14.2%)	4.8–6.3(48) $x = 5.46$ (14.5%)	3.8–5.0(48) $x = 4.36$ (14.5%)	1.2–3.8(165)

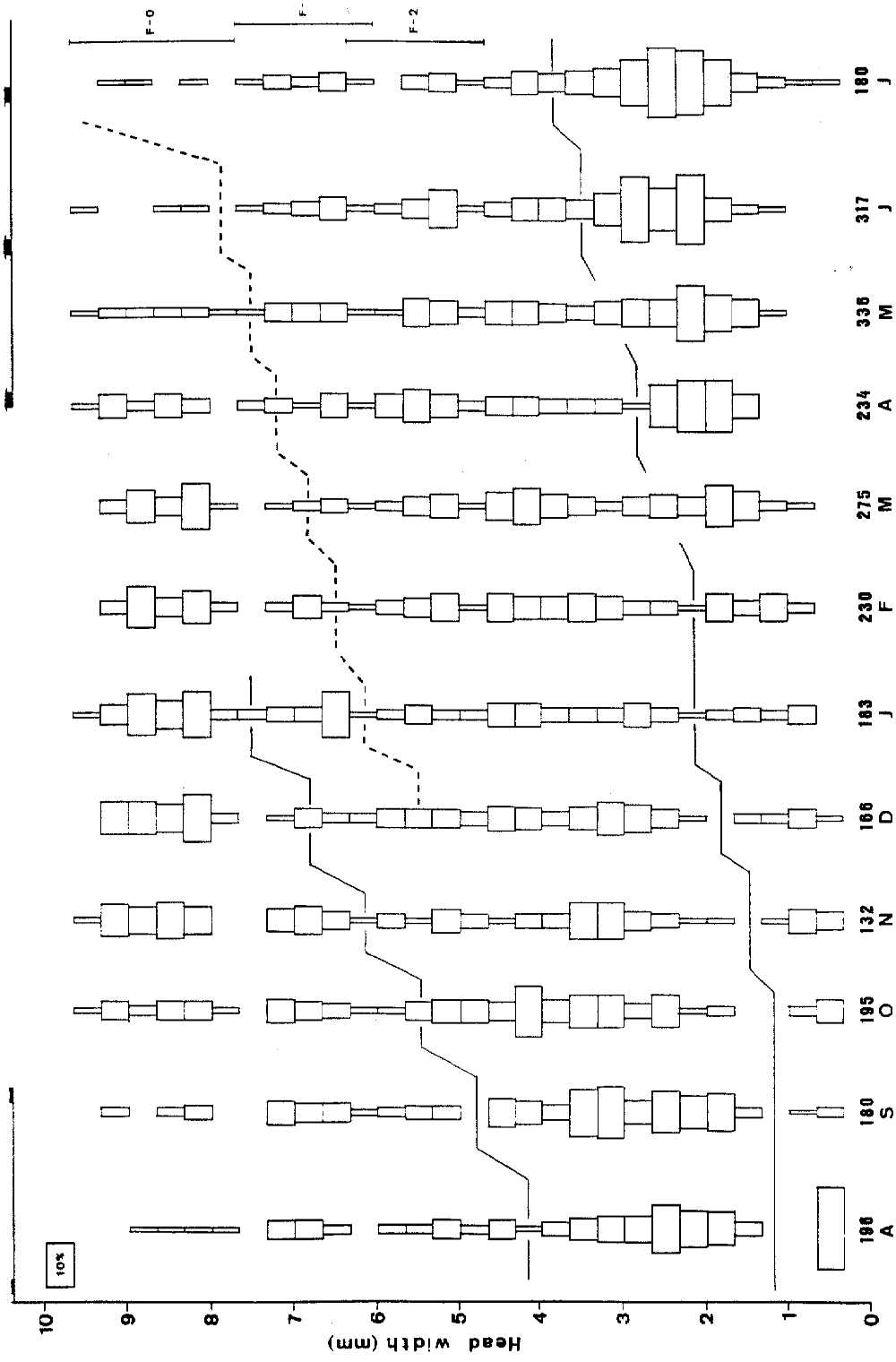


Figure 2. Larval development of *Cordulegaster boltonii* in Bejarano Stream shown by combined results from three consecutive years (June 1989–May 1992). Size ranges of the last three instars are indicated. Continuous lines ascending from left to right indicate inferred boundaries between successive hatching cohorts. The broken line indicates the inferred boundary between the two components that result from cohort-splitting in the two-year-old hatching cohort, thus distinguishing larvae that grow fast (above line) and slowly (below line). The emergence period during April through September is shown. Numbers above month designations denote sizes of the combined samples.

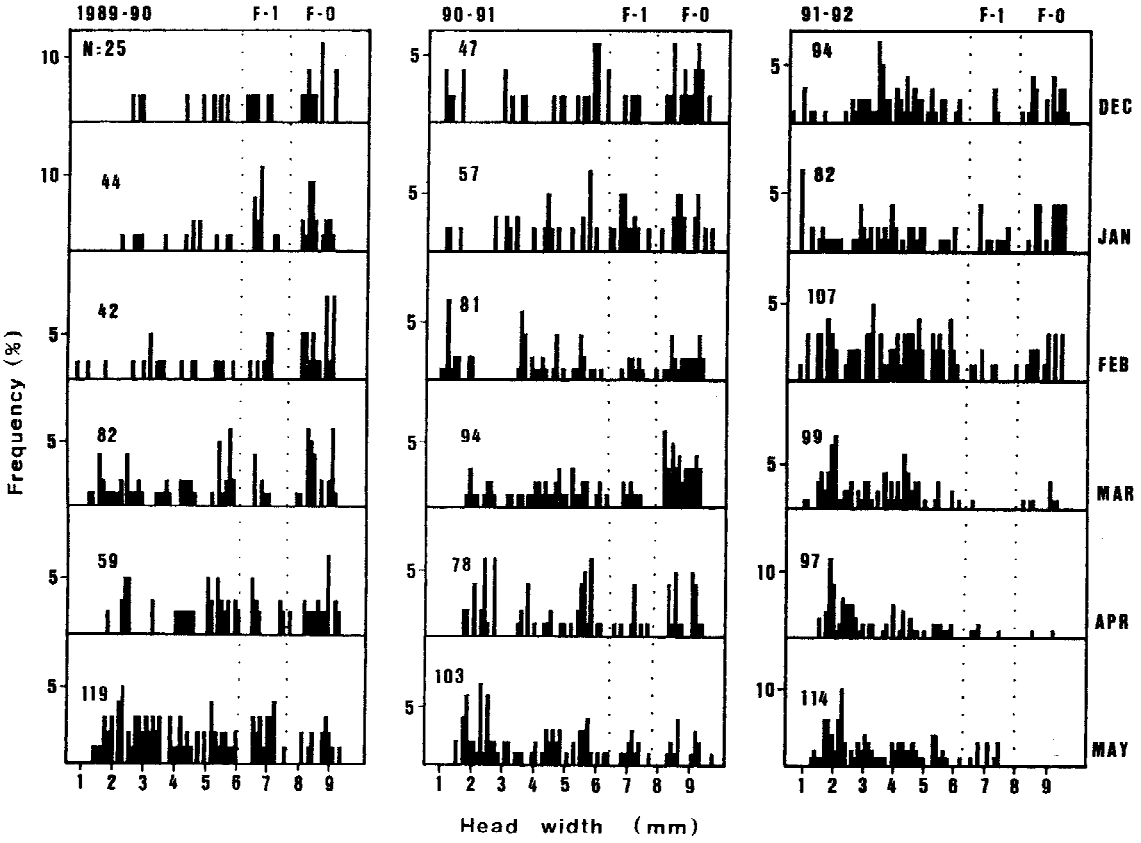


Figure 3. Frequency distributions for larval head width of *Cordulegaster boltonii* at Bejarano Stream in the two last instars collected on different sampling dates in three successive years. From top downward: December (late autumn), January–March (winter) and April and May (early spring). During late winter and early spring (e.g. 1990 and 1991) some larvae with a semivoltine life cycle reach the final instar; during spring of 1992, after a winter colder than those preceding it, the number of such larvae was apparently reduced.

The highest frequencies of F-0 occur from December to March (Table 3) and reflect the combination of three-year-old larvae exhibiting slow growth and two-year-old larvae exhibiting fast growth. No clear temporal separation was detectable between emergence of the two groups (Figure 1).

The frequency of F-0 declined progressively from late winter into spring (Table 3), which coincided with the emergence period (90% during April through June). This effect might be accentuated if during metamorphosis F-0 larvae are inactive and are therefore unlikely to be captured. Only a few F-0 were encountered in summer, and their presence indicates that entry to F-0 was recommencing, because those F-0 larvae collected from July to autumn did not show any signs of metamorphosis (Table 5).

Many ‘clean’ F-1 larvae (some apparently having just moulted) were collected from March or April to June (1991) or August (1990) (Table 4). The moult from F-2 to F-1 was probably concentrated in spring and early summer, the highest percentages of F-1 larvae being found in May and June (Table 3). From summer (July) to winter there was moulting to F-0, but it was especially intense (as shown by the high frequency of ‘very clean’ F-0 larvae) during October and November (among partivoltine larvae); but ‘very clean’ F-0 larvae (probably belonging to the semivoltine component) were also found, in small numbers, in April and May. Increased numbers of ‘dirty’ F-0 larvae were found from December to April, the months preceding the onset of emergence. Probably such larvae had spent their last winter in a short-day diapause (Norling, 1976, 1984) and were partivoltine, requiring three years to develop.

Interannual variations in rate of development were detected, especially during spring. Although in February the proportion of F-0 was similar every year, the abundance of F-0 larvae in April and May differed

Table 4. Monthly number of 'very clean' (soft) (a), 'clean' (b) and 'dirty' (c) larvae, tabulated to show temporal pattern of moulting to the penultimate (above) and final instars. Larvae in category (a) are assumed to have entered an instar recently.

	1990–91			1991–92		
	(a)	(b)	(c)	(a)	(b)	(c)
Penultimate-instar larvae (F-1)						
June	4	4	6	4	9	7
July	5	6	1	0	1	4
August	3	8	1	1	2	5
September	1	2	2	0	4	4
October	0	2	7	0	1	4
November	2	5	7	0	2	6
December	2	1	2	0	1	3
January	1	5	8	0	0	10
February	2	3	4	1	1	5
March	6	2	2	1	0	0
April	2	2	3	2	3	0
May	2	2	7	7	4	0
Final-instar larvae (F-0)						
June	2	1	1	0	2	1
July	1	1	0	0	3	0
August	0	3	0	0	1	0
September	0	2	0	0	5	1
October	5	6	3	4	6	3
November	2	9	6	3	15	3
December	1	9	8	0	14	9
January	1	9	8	0	11	9
February	0	6	18	0	6	11
March	0	20	19	0	4	4
April	1	4	11	0	1	1
May	1	8	6	0	0	0

Table 5. Seasonal distribution of last-instar larvae according to stages a–d of metamorphosis (see text) and proportion of such larvae showing metamorphosis. Seasons distinguished are winter (January through March), spring (April through June), summer (July through September) and autumn (October through December). Winter 1988, February and March only; autumn 1989, October and December only; spring 1992, April and May only

	Season					Larvae undergoing
	N	a	b	c	d	metamorphosis as % of all F-0 larvae
Metamorphosis stage						
Winter 1988	11	1	9	1	0	91
Spring 1988	20	1	3	14	2	95
Summer 1988	10	10	0	0	0	0
Autumn 1988	9	8	1	0	0	11
Winter 1989	10	3	7	0	0	70
Spring 1989	13	3	3	3	4	77
Summer 1989	9	8	1	0	0	11
Autumn 1989	17	8	9	0	0	53
Winter 1990	61	20	34	7	0	67
Spring 1990	36	4	14	13	5	89
Summer 1990	7	7	0	0	0	0
Autumn 1990	49	21	28	0	0	57
Winter 1991	81	16	51	14	0	80
Spring 1991	37	2	10	24	1	94
Summer 1991	10	10	0	0	0	0
Autumn 1991	57	26	31	0	0	54
Winter 1992	45	9	32	4	0	80
Spring 1992	2	0	1	1	0	100

markedly between successive years (Figure 3). Apparently the semivoltine (later) component of the annual emergence can vary greatly in size between years (1990 and 1991 vs 1992).

Metamorphosis

Frequencies of successive stages of metamorphosis in F-0 in summer, autumn, winter and spring are given in Table 5. The frequency distributions of stages did not differ markedly between years. F-0 larvae collected during summer usually (in ca. 97% of the total sample) showed no signs of metamorphosis; but every year some larvae showing incipient metamorphosis (stage b) were present in autumn (ca. 52% in 1989, 1990 and 1991).

Larvae showing signs of advanced metamorphosis (stage c) were found in samples during the second half of winter, being first collected in February in 1988, 1990, 1991 and 1992, but not until April in 1989, a year when the number of F-0 collected was low (Table 5). Stage d (emergence imminent) was detected in spring only, during the emergence period.

Discussion

Our findings are consistent with those of Schütte (1997) in showing that eggs hatched promptly, without

overwintering and that nearly one year after oviposition some larvae were still in very early instars. Head widths of female F-0 larvae were significantly greater than those of males. Similar differences between female and male final-instar exuviae (females larger than males) were reported by Brettfeld (1989). On the other hand, each year (except 1991) female exuviae were more numerous than male exuviae (Table 2), as appears to be usual in Anisoptera (Corbet, 1962; Lawton, 1972; Corbet & Hoess, 1998). Our data are insufficient to test for differential mortality of the sexes in late larval instars.

Our results support the conclusion that at the study site *C. boltonii* showed protracted, relatively flexible, larval development such that larvae hatching from eggs laid in the same spring (or early summer) segregated into 'slow' and 'fast' components, unequal in size, which completed development in three (most larvae) and two years and which passed their last winter in F-0 and F-1, respectively. Most of the population, which was partivoltine, underwent diapause in F-0 and therefore conformed to the designation 'spring species' (Corbet, 1964). Each year, some larvae grew rapidly, lacked diapause in F-0 and were semivoltine. Apparently the semivoltine component included each year in the emergence cohort, though always in a minority, can vary greatly in size. In the study population, after a cool winter (e.g. 1992), larvae moulting to F-1 could be poorly represented so that in the following spring–summer the emergence cohort would be composed almost exclusively of the partivoltine component. Water temperature during the previous winter (1990 and 1991 vs 1992), together with other abiotic and biotic factors (Johnson et al., 1995) not studied in this work, may contribute to these differences.

Our finding that at the study site *C. boltonii* completed larval development in 2 or (mainly) 3 years may be compared with estimates of larval duration of this species elsewhere in Europe, namely: 2 or 3 years in southern France (Schütte, 1997), 3 or 4 years in the Midi and 5 years or more in the Alps and Jura (Robert, 1958), 4 or 5 years in the uplands of Yugoslavia (Kiauta, 1964), 4 or 5 years in northeastern Germany (Donath, 1987) and sometimes more than 5 years in United Kingdom (Corbet et al., 1960). These findings are consistent with a prolongation of development at higher latitude and altitude.

Our results demonstrate the existence of cohort-splitting, a phenomenon first detected in a population of *Anax imperator* Leach in southern England, where about 90% of the emerging population were semivoltine and 10% were univoltine (Corbet, 1957). Subsequently cohort splitting has been revealed in temperate-centred Odonata in two other riverine species, both gomphids (Ferreras-Romero et al., 1999), and several species occupying lentic habitats in North America (Johnson, 1986; Krishnaraj & Pritchard, 1995), northern Europe (Macan, 1964; Corbet & Harvey, 1989), Sweden (Norling, 1976, 1984; Johansson & Norling, 1994) and northern Japan (Ubukata, 1980).

Though they can only be speculative, some probable implications of cohort splitting for inclusive fitness deserve mention. Because, after cohort splitting, the reproductive population in any one year is derived from the progeny of parents reproducing in more than one previous year, there will presumably be gene flow between progeny selected for lifetime reproductive success in different years (Hutchinson, 1993). In most, perhaps all, habitats, especially those in temperate latitudes, conditions favouring lifetime reproductive success of adults (e.g. the frequency distribution of sunny days, see Thompson, 1990) vary markedly between years (e.g. Fincke, 1988; Thompson , 1990; Anholt, 1991). Likewise, because larvae from fast and slow growth cohorts sometimes emerge at different times during the emergence period (Corbet, 1957), they are likely to be exposed to different environmental conditions, biotic as well as physical (see Thompson, 1997). Accordingly a plausible consequence of cohort splitting will be that the population emerging each year will have a genetic composition selected for during more than one previous year and during more than one part of a flying season. So, whatever the main selective pressures that maintain cohort splitting may be, one of its probable benefits is to dilute the risk imposed by interyear variation in weather during the reproductive period. Such considerations make it unlikely *a priori* that cohort splitting itself will lead to sympatric divergence (see Hutchinson, 1993).

Exuvial counts for *C. boltonii* in 1992 (Figure 1) showed a relatively synchronised emergence, conforming to expectation for 'spring species' (*sensu* Corbet,1964), and did not reveal clearly the existence of two components in the temporal pattern (Ferreras-Romero & Corbet, 1995). Emergence was protracted, there being a long 'tail' after about 90% of adults of the year had emerged. We do not know if the rate of metamorphosis was similar in semivoltine and partivoltine larvae, but our results do not conflict with the prediction that two-year-old larvae (without a final-instar diapause) could initiate and complete metamorphosis concurrently with some three-year-old

larvae which had remained in diapause until early spring.

Acknowledgments

We thank two anonymous referees for valuable comments on the manuscript.

References

Anholt, B. R., 1991. Measuring selection on a population of damselflies with a manipulated phenotype. Evolution 45: 1091–1106.

Askew, R. R., 1988. The dragonflies of Europe. Harley Books, Colchester.

Brettfeld, R., 1989. Die Zweigestreifte Quelljungfer (*Cordulegaster boltoni* Donovan) aus der Gruppe der Fliessgewässerlibellen (Insecta, Odonata). Veröff. Naturhist. Mus. Schleusingen 4: 2–12.

Corbet, P. S., 1957. The life-history of the Emperor Dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). J. Anim. Ecol. 26: 1–69.

Corbet, P. S., 1962. A biology of dragonflies. Witherby, London.

Corbet, P. S., 1964. Temporal patterns of emergence in aquatic insects. Can. Ent. 92: 264–279.

Corbet, P. S. & I. F. Harvey, 1989. Seasonal regulation in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae) 1. Seasonal development in nature. Odonatologica 18: 133–145.

Corbet, P. S. & R. Hoess, 1998. Sex ratio of Odonata at emergence. Int. J. Odonatol. 1: 99–118.

Corbet, P. S., C. Longfield & N. W. Moore, 1960. Dragonflies. Collins, London.

Donath, H., 1987. Untersuchungen in einer Larvenkolonie von *Cordulegaster boltoni* (Donovan) in der Niederlausitz. Libellula 6: 105–116.

Ferreras-Romero, M., 1994. Life history of the species that make up the odonate association characteristic of a permanent stream in the western Mediterranean basin: preliminary results. Adv. Odonatol. 6: 45–48.

Ferreras-Romero, M., 1997. The life history of *Boyeria irene* (Fonscolombe, 1838) (Odonata: Aeshnidae) in the Sierra Morena Mountains (southern Spain). Hydrobiologia 345: 109–116.

Ferreras-Romero, M. & P. S. Corbet, 1995. Seasonal patterns of emergence in Odonata of a permanent stream in southwestern Europe. Aquat. Insects 17: 123–127.

Ferreras-Romero, M., & V. Puchol-Caballero, 1995. Desarrollo del ciclo vital de *Aeshna cyanea* (Müller, 1764) (Odonata: Aeshnidae) en Sierra Morena (sur de España). Boln. Asoc. esp. Ent. 19: 115–123.

Ferreras-Romero, M., M. D. Atienzar & P. S. Corbet, 1999. The life cycle of *Onychogomphus uncatus* (Charpentier, 1840) (Odonata: Gomphidae) in the Sierra Morena Mountains (southern Spain): an example of protracted larval development in the Mediterranean basin. Arch. Hydrobiol. 144: 215–228.

Fincke, O. M., 1988. Sources of variation in lifetime reproductive success in a nonterritorial damselfly (Odonata: Coenagrionidae). In Clutton-Brock, T. H. (ed.), Reproductive Success. Univ. Chicago Press, Chicago: 24–43.

Hutchinson, G. E., 1993. A treatise on limnology. Vol. 4, The zoobenthos. John Wiley & Sons, Inc., New York.

Johansson, F. & U. Norling, 1994. A five-year study of the larval life history of *Coenagrion hastulatum* (Charpentier) and *C. armatum* (Charpentier) in northern Sweden (Zygoptera: Coenagrionidae). Odonatologica 23: 355–364.

Johnson, D. M., 1986. The life history of *Tetragoneuria cynosura* (Say) in Bays Mountain Lake, Tennessee, United States (Anisoptera: Corduliidae). Odonatologica 15: 81–90.

Johnson, D. M., T. H. Martin, M. Mahato, L. B. Crowder & P. H. Crowley, 1995. Predation, density dependence and life histories of dragonflies: a field experiment in a freshwater community. J. n. am. Benthol. Soc. 14: 547–562.

Kiauta, B., 1964. [Beobachtungen betreffs der Biologie, der Ökologie und der Ethologie der Quelljungfern im Bergland von Skofja Loka (Odonata – Cordulegasteridae).] In Slovene; German summary. Loski Razgledi 11: 183–192.

Krishnaraj, R. & G. Pritchard, 1995. The influence of larval size, temperature, and components of the functional response to prey density, on growth rates of the dragonflies *Lestes disjunctus* and *Coenagrion resolutum* (Insecta: Odonata). Can. J. Zool. 73: 1672–1680.

Lawton, J. H., 1970. A population study on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). Hydrobiologia 36: 33–52.

Lawton, J. H., 1972. Sex ratios in Odonata larvae, with particular reference to the Zygoptera. Odonatologica 1: 209–219.

Lloyd, E. C. & S. J. Ormerod, 1992. Further studies on the larvae of the Golden-ringed Dragonfly, *Cordulegaster boltoni* (Donovan) (Odonata: Cordulegasteridae), in upland streams. Ent. Gaz. 43: 275–281.

Lohmann, H., 1992. Revision der Cordulegastridae. 1. Entwurf einer neuen Klassifizierung der Familie (Odonata: Anisoptera). Opusc. Zool. Fluminensia 96: 1–18.

Lohmann, H., 1993. Revision der Cordulegastridae. 2. Beschreibung neuer Arten in den Gattungen *Cordulegaster*, *Anotogaster*, *Neallogaster* und *Sonjagaster* (Anisoptera). Odonatologica 22: 273–294.

Macan, T. T., 1964. The Odonata of a moorland fishpond. Int. Rev. ges. Hydrobiol. 49: 325–360.

Norling, U., 1976. Seasonal regulation in *Leucorrhinia dubia* (Vander Linden) (Anisoptera: Libellulidae). Odonatologica 5: 245–263.

Norling, U., 1984. Life history patterns in the northern expansion of dragonflies. Adv. Odonatol. 2: 127–156.

Ormerod, S. J., N. S. Weatherley & W. J. Merrett, 1990. The influence of conifer plantations on the distribution of the Golden Ringed Dragonfly *Cordulegaster boltoni* (Odonata) in upland Wales. Biol. Conservation 53: 241–251.

Robert, P.-A., 1958. Les libellules (odonates). Delachaux et Niestlé, Neuchâtel.

Schütte, C., 1997. Egg development and early instars in *Cordulegaster boltonii immaculifrons* Selys: a field study (Anisoptera: Cordulegastridae). Odonatologica 26: 83–87.

Thompson, D. J., 1990. The effects of survival and weather on lifetime egg production in a model damselfly. Ecol. Ent. 15: 455–462.

Thompson, D. J., 1997. Lifetime reproductive success, weather and fitness in dragonflies. Odonatologica 26: 89–94.

Ubukata, H., 1980. Life history and behaviour of a corduliid dragonfly, *Cordulia aenea amurensis* Selys. III. Aquatic period, with special reference to larval growth. Kontyû 48: 414–427.

View publication stats