23

Habitat selection of larval *Gomphus graslinii* and *Oxygastra curtisii* (Odonata: Gomphidae, Corduliidae)

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Abstract

The microdistribution patterns of larval *Gomphus graslinii* and *Oxygastra curtisii* in three rivers in southern France were studied. While *G. graslinii* was caught mainly in sandy reaches covered with leaf litter, *O. curtisii* was found almost exclusively clinging to alder roots at the river margins. Preferences of habitat structure were determined from habitat selection experiments under outdoor conditions with four types of substrates: (I) gravel, (II) sand, (III) sand covered with leaves, and (IV) alder roots. *G. graslinii* preferred substrate types III and II over I and IV; *O. curtisii* preferred IV and III over I and II.

Introduction

In general, the quality of benthic substrate is considered to be one of the most important factors for habitat selection in aquatic insects living in running waters (Cummins & Lauff 1969). Surveys on this subject dealing with Odonata have been published for Cordulegastridae (e.g. Prodon 1976), Gomphidae (e.g. Keetch & Moran 1966; Huggins & DuBois 1982; Suhling 1994, 1996; Müller 1995), Macromiidae (e.g. Williams 1978; Leipelt et al. 1999) and Calopterygidae (Zahner 1959).

The aim of this study was to investigate microdistribution patterns and habitat preferences in two species of southwestern European running water dragonflies, *Gomphus graslinii* Rambur and *Oxygastra curtisii* (Dale). We took samples of different habitat structures at three running waters in France and carried out microhabitat selection experiments under outdoor conditions by offering four different substrate types.

Habitat selection experiments on four *Gomphus* species (Suhling 1994, 1996; Müller 1995) showed that these species prefer fine substrates like sand over coarse substrates like gravel. In addition *G. pulchellus* Selys and *G. vulgatissimus* (Linnaeus) select substrates covered with a layer of detritus more frequently than the same substrates without such a layer. Whereas data on substrate selection are available for most European *Gomphus* species (see Suhling & Müller 1996), microhabitat selection of larval *G. graslinii* is currently unknown. In comparison, in *Oxygastra curtisii* there

is at least some information about larval residence: Fastenrath (1950) found exuviae covered by mud and Schmidt (1944) hence suggested that larvae of *O. curtisii* are mud-dwellers; d'Aguilar & Dommanget (1998) described them as burrowers in mud or sand. For both species van Helsdingen et al. (1996) pointed out that development of conservation measures, such as the designation of special areas of conservation and the management of such areas, is only possible based on sufficient insight into the habitat requirements and the biology of these species which are protected in France (Dommanget 1994).

Study species, study area, and methods

Study species

Gomphus graslinii is an endemic species of southwestern Europe inhabiting slow running parts of rivers in Spain, Portugal and southwestern France (Suhling & Müller 1996). According to Dommanget (1996a) the larvae occupy mud close to banks often fringed by high and dense riparian shrubs. This species is on the wing from June to September (d'Aguilar & Dommanget 1998).

Like the latter species, *Oxygastra curtisii* occurs mainly in southwestern Europe but its range extends to northern and western parts of Morocco (Jacquemin & Boudot 1999), northwestern Italy, and certain parts of Switzerland, Belgium, Germany, The Netherlands, and England (d'Aguilar & Dommanget 1998). Heymer (1964) considers the species to be confined to streams and to prefer lentic parts of watercourses. He emphasizes the importance of dense riparian shrubs shading the banks for the patrolling adult males. In addition Jacquemin (1994) mentions the presence of alder trees at the location where he observed *O. curtisii* in the Rif, Morocco. Chelmick (1983) emphasizes the occurrence of exposed roots at the water's edge as a typical trait of the habitat. The species has been recorded also from canals and lakes in southern Switzerland (Maibach & Meier 1987) and as an adult from a gravel pit (Klein & Berchtold 1998). The larvae are considered to be mud-dwellers and to develop during 2 to 3 years (Schmidt 1944; Dommanget 1996b). The flying season lasts from late May until the end of August (Dommanget 1996b).

Study area

The field study was carried out at three running waters in southern France. Two of these belonged to the Aveyron River system, southwestern Massif Central, ca 60 km north-northeast of Toulouse in the department Tarn et Garonne (44°10'N, 01°45'E). The third was part of the Gard River system, Cévennes mountains, 12 km west of Alès, department Gard (44°07'N, 3°55'E).

The study area at the Aveyron River system is characterized by an oceanic climate, an annual precipitation averaging ca 700 mm, and the region at the Gardon de Mialet is characterized by a Mediterranean climate and an annual precipitation averaging ca 900 mm (Arléry 1970). The hydrology of rivers of the western Massif Central is described as

pluvio-nival: river discharge is highest in April as a result of thaw, and lowest in summer and winter as a result of evaporation and retention of snow, respectively. Rivers of the Cévennes mountains are also characterized as pluvio-nival: however, river discharge reaches maxima both in late autumn and in early spring (Pagney 1988).

The first study site was situated at the Aveyron River in its lowest gorge, 3 km west of St.-Antonin-Noble-Val (ca 110 m alt.). Arising in the southwestern part of the Massif Central, the Aveyron River ran through several gorges in its middle and lower reaches, draining ultimately into the Tarn River. Between St.-Antonin-Noble-Val and Bruniquel in its lowest gorge the river was broad and sluggish. Only a few rapids separated the extensive lentic parts. River margins were either rocky — sometimes shaped by walls of rock — or dominated by alders (*Alnus glutinosa*). At our study site the Aveyron River was ca 40 m in width and structured by several rapids. We sampled near the right riverside in between these rapids and downstream. At the river margin during modal flow depth varied between 0.2 m and 0.8 m at shallow rocky reaches and at deeper parts shaded by alders, respectively. Substrate was dominated by bedrock and gravel, and by sandy reaches covered with leaf litter; the river margin was dominated by alder roots. On 23 July 1999 water temperature measured in the Aveyron River at 17:30 h Central European Summer Time was 24.5°C (air temperature: 22.2°C).

The second study site was situated at the Vère River, 1 km upstream of its mouth in the Aveyron River (ca 110 m alt.) The Vère River was a foothill rivulet about 50 km in length originating 10 km north of Albi, department Tarn, entering the lowest Aveyron Gorge at the village of Bruniquel, 12 km south-west of our first study site. The river, heavily shaded by riparian alders, was 8-10 m wide, and depth varied between 0.35 m and 0.45 m; some pools at the margin were up to 0.8 m deep. The current was low, but high enough to allow deposition of fine sand and debris only at these deeper lentic pools and at the river margins. Otherwise the bottom was mainly covered by coarse gravel. Alder roots at the river margins were coated with bicarbonate resulting in a solid consistency. On 23 July 1999 water temperature in the Vère River was measured twice: at 12:00 h Central European Summer Time the value was 18.8°C (air temperature 20.2°C) and at 18:35 h the value was 19.8°C (air temperature: 25.4°C).

The third site was at the Gardon de Mialet, about 2 km upstream of Mialet. Originating in the southern slope of the Cévennes mountains, the Gardon de Mialet was one of the headwaters of the Gard River which was a tributary to the Rhône. At the study site the river was diversely structured with deep pools and riffles; the banks consisted of a mixture of gravel banks, solid rocks and riparian forest (mainly alder trees). The river was 18 to 22 m wide and its depth varied from a few cm up to 2 m in pools. The current was low in the pools but reached up to 1 ms^{-1} in runs. The substrate consisted mainly of gravel, with some bedrock and fine sediments like sand and detritus in the pools. In July 1999 and in June 2000 the water temperatures reached 24°C and 22.1°C, respectively.

Sampling

Quantitative samples were taken on 22 and 23 July 1999 at the study sites each about 50 m in length at the Aveyron and the Vère Rivers and on 17 June 2000 at the site at

the Gardon de Mialet. Three substrate types were selected at each study site: alder roots at the river margin; coarse gravel; and sandy reaches covered with leaf litter. Seven kick-samples at each type and at each site were taken using a dip-net (mesh size 1 mm) (see Hauer & Resh 1996); each standard sample covered approximately 0.15 m². Samples were sorted by placing the substrate in a white pan and manually searching for all odonate larvae. Two-way ANOVAs (see Sokal & Rohlf 1995) were performed to analyse differences in larval density dealing with substrate types and study sites as independent variables for the two species.

Habitat selection experiments

From 22 to 25 July 1999 habitat selection experiments with different substrate types were carried out in a similar manner to that used by Keetch & Moran (1966). In total we used 48 larvae of *G. graslinii* and 60 larvae of *O. curtisii* of head width varying between 2.2 mm and 3.3 mm and between 1.8 mm and 2.7 mm, respectively. We conducted six replicates with eight larvae in *G. graslinii* and ten larvae in *O. curtisii* using for each replicate a white plastic pan (0.4 m long, 0.25 m wide, and 0.15 m deep) which was divided into four sections of equal size containing four different substrates: gravel, sand, sand covered with leaf litter, and dense alder root material. Water depth in the pans was 0.07 m. Two replicates per species shaded by tents during midday were conducted under field conditions each day starting in the late afternoon and ending after 18 hours the next day by recording the distribution of the larvae. The larvae of *G. graslinii* used in the experiments originated from the Aveyron and the Vère river, and the larvae of *O. curtisii* originated exclusively from the first locality. A two-way ANOVA was performed to analyse differences in larval density dealing with substrate types and species as independent variables; for pairwise comparisons a posteriori analyses on means (Fisher's PLSD; see Sokal & Rohlf 1995) were used.

Results

Microdistribution

The larval density of *Gomphus graslinii* varied significantly with the sample site and the substrate (two-way ANOVA: site x substrate $F_{4, 54} = 4.717$, $p = 0.0024$). The larvae were found in two out of the three substrates investigated at the Vère River and in all three substrates at the Aveyron River (Fig. 1). At the Gardon de Mialet the species was found only once in a sample taken from roots. Therefore the Gardon de Mialet was excluded from further analyses. At the two other sites density was highest in sandy reaches covered with leaf litter. The distribution pattern did not differ significantly between the Aveyron and the Vère (two-way ANOVA, $F_{2, 36} = 2.366$, $p = 0.1083$).

Larvae of *Oxygastra curtisii* were caught almost exclusively amongst alder roots (Fig. 1). A two-way ANOVA revealed a significant difference in density between the three types of substrate ($F_{2, 54} = 10.83$, $p < 0.001$) but not between the sample sites (site $F_{2, 54} = 1.57$, $p = 0.217$; substrate x site $F_{4, 54} = 1.55$, $p = 0.201$).
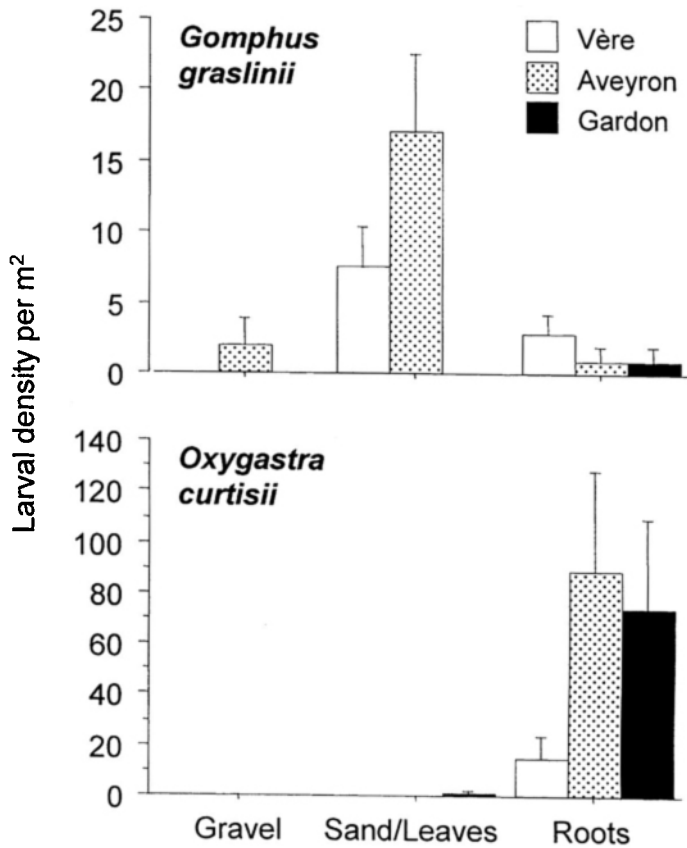
Figure 1. Microdistribution of *Gomphus graslinii* and *Oxygastra curtisii* in different types of substrates of three rivers in southern France. Bars indicate mean densities per m² (+ s.e.).

The distribution of all odonate species among the three substrate types and the study sites is given in Table 1.

Habitat preferences

In the experiments habitat selection varied significantly with substrate type and species (two-way ANOVA, $F_{3, 40} = 12.263$, $p < 0.001$) (Fig. 2). The density of *G. graslinii* was highest in "sand covered with leaves" and "sand". In contrast, the density of *O. curtisii* was highest in "roots" and "sand covered with leaves". For comparison of substrate types in pairs see Fig. 2.

Table 1. Distribution of the larvae of all odonate species collected during the field study at the three running waters in southern France.

Taxon	No. of larvae per 7 samples								
	Vère			Aveyron			Gardon de Mialet		
	Gravel	Leaves	Roots	Gravel	Leaves	Roots	Gravel	Leaves	Roots
Calopteryx splendens (Harris)	-	-	1	-	-	5	-	1	14
Platycnemis spp. *	-	2	1	-	-	33	-	-	25
Cercion lindenii (Selys)	-	-	-	-	-	71	-	-	-
Boyeria irene (Fonscolombe)	-	1	11	-	-	24	-	-	3
Gomphus graslinii Rambur	-	8	3	2	18	1	-	-	1
Gomphus pulchellus Selys	-	-	-	-	2	2	-	1	-
Gomphus simillimus Selys	-	1	-	-	-	-	-	1	-
Gomphus vulgatissimus (Linnaeus)	1	13	-	-	2	-	-	9	-
Onychogomphus forcipatus **	1	1	-	8	-	-	6	36	27
Onychogomphus uncatus (Charpentier)	4	4	1	-	-	-	2	2	14
Cordulegaster boltonii (Donovan)	5	1	1	-	-	-	-	-	-
Oxygastra curtisii (Dale)	-	-	16	-	-	93	-	1	78
Macromia splendens (Pictet)	-	-	-	-	-	-	-	1	-
Total	11	31	34	10	22	229	8	52	162

* Including *P. acutipennis* Selys, *P. latipes* Rambur, and *P. pennipes* (Pallas), which were observed as adults;
** including *O. f. forcipatus* (Linnaeus) from the Aveyron River system and *O. f. unguiculatus* (Vander Linden) from the Gardon de Mialet.

In "sand" and "sand covered with leaves" larvae of *G. graslinii* were usually found buried. In the other substrate types they were recorded sitting on the gravel or hiding under root material. Larvae of *O. curtisii* were found clinging to root material or sitting under it. In the other substrate types they hid in gravel interstices or under leaves, but they were never found buried.

Discussion

In our field study we have found differences in the microdistribution of *Gomphus graslinii* and *Oxygastra curtisii*. Whereas *G. graslinii* occurs mainly in sand covered with leaves or detritus, *O. curtisii* is found almost exclusively amongst alder roots. Experiments confirm the substrate selection of *G. graslinii* in its natural habitat. In contrast, *O. curtisii* selects not only alder roots but also sand with leaves. On the latter substrate only one larva was found during our field survey.
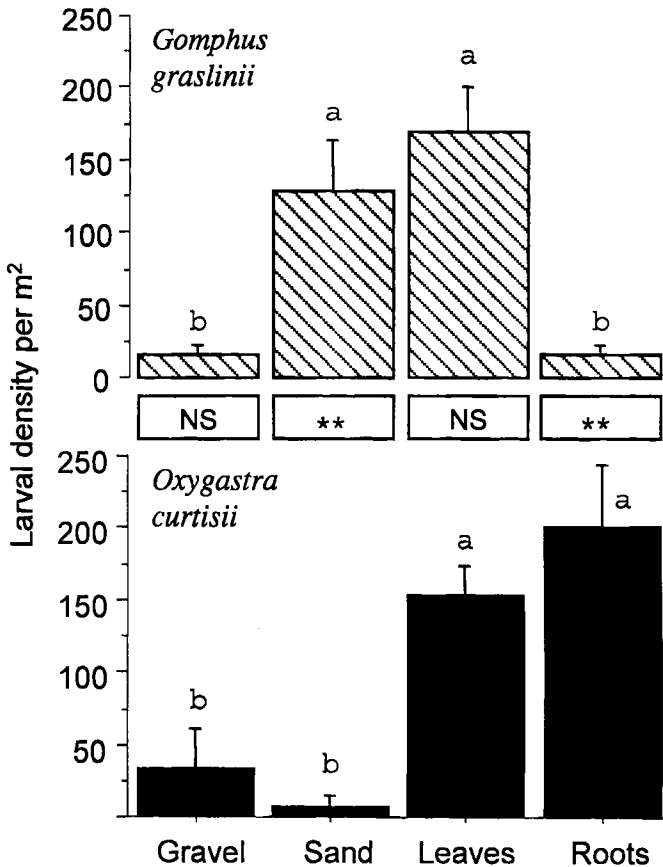
Figure 2. Substrate selection of *Gomphus graslinii* and *Oxygastra curtisii* in choice chamber experiments. Bars indicate mean densities of larvae per m² (+ s.e.) in four substrate types. Differences between the species and substrates were tested by *a posteriori analyses* (Fischer's PLSD): NS: not significant, **: $p < 0.01$; significant differences between the substrates within a species are indicated by a and b on the bars: a > b ($p < 0.05$).

Gomphus graslinii

A number of studies shows that *Gomphus* species live predominantly in sandy to muddy substrates (Huggins & DuBois 1982) and that the occurrence of detritus plays a major role in substrate selection (Suhling 1994; Müller 1995). These findings correspond to our results for *G. graslinii*: The larvae are found mainly in sandy substrate covered with leaves both in habitat selection experiments and in the field. The distribution among the three substrate types at the Aveyron River is very similar to that at the Vère River. At the Gardon de Mialet the species is too rare to allow comparisons. Whereas *G. pulchellus* and *G. vulgatissimus* clearly prefer sand covered with a layer of detritus over bare sand

under experimental conditions (Suhling 1994; Müller 1995), *G. graslinii* shows only a slight preference (see Fig. 2).

Until now, no differences in larval substrate selection were known between the four *Gomphus* species occurring sympatrically in rivers of southwestern France. According to our survey *G. vulgatissimus* coexists with *G. graslinii* in the same substrate type. Differences in phenology (see Suhling & Müller 1996) – *G. vulgatissimus* being a typical spring species sensu Corbet (1954), *G. graslinii* being a summer species – may reduce interspecific competition.

Oxygastra curtisii

In *O. curtisii* the experimental results differ from the microdistribution found in the field. Whereas in the habitat selection experiments the larvae prefer both "alder roots" and "sand covered with leaves", in the field most larvae were recorded amongst alder roots. Only at the Gardon de Mialet did we collect one larva on sand covered with detritus. We suppose that this difference could be explained by the influence of various factors like (a) predation by fish, (b) current, (c) interspecific competition, (d) intraspecific competition, or (e) food availability.

(a) It is possible that larvae of *O. curtisii* are not able to react to the presence of fish and therefore, in the field, fish may simply feed on (almost) all larvae living between the leaf litter. This could be caused by substrate-specific predation by fish (cf. Suhling 1999). On the other hand – if larvae of *O. curtisii* are able to recognize the presence of fish – they may select alder roots as residence as a direct response in the field. It is known that some odonate species are able to alter their behaviour as a direct response to the presence of predators (Pierce 1988; Suhling 1996; Claus-Walker et al. 1997; Koperski 1997), e.g. presence of fish is detectable by the latter's scent (Chivers et al. 1996; Koperski 1997). Roots can be assumed to offer a good shelter from bottom-feeding fish like *Barbus* and *Gobio*; furthermore due to their high structural complexity, they may also constitute an effective refuge from all other fish species. A layer of leaves may be an insufficient shelter from predation by fish, because fish feeding on benthic macroinvertebrates can detect prey by stirring-up loose substrate materials (Keenleyside 1979). In Odonata the presence of submerged macrophytes can reduce proneness to predation by fish (Dionne et al. 1990; Henrikson 1993); alder roots may have the same effect.

(b) The occurrence in sand with detritus may be caused by artificial experimental conditions which have not simulated the conditions in the field in a proper way. Compared to the field situation in the habitat selection experiments there has been no current. In the presence of current, larvae of *O. curtisii* may actively select alder roots which could be a protection against being dislodged by the current. Although the larvae lack thigmotactic behaviour (K.G. Leipelt unpubl.), it is not easy to remove them from the roots. So it is conceivable that larval *O. curtisii* by clinging to alder roots may withstand the current even during a flood or heavy spate.

(c) Another factor explaining the discrepancy in experimental results and the findings in the field may be interference competition: in the field, larvae of *O. curtisii* living in sandy reaches covered with leaf litter may be affected by the presence of larval *Gomphus* and thus be forced to move to another substrate type. Such an

interspecific asymmetric interference competition has been observed in two gomphid species (Suhling 1996). Competitive effects between a gomphid and a corduliid are referred to by Mahato & Johnson (1991).

(d) It cannot be completely ruled out that in the habitat selection experiments larval density of *O. curtisii* could have affected microdistribution: in the presence of conspecifics some larvae may be forced into a suboptimal substrate type. But according to Butler (1985) larvae of *O. curtisii* show no noticeable intraspecific aggression and in the field in some patches larval density is even higher than in the experiments. So we may suppose that intraspecific interference competition probably does not play a major role in this case.

(e) Table 1 shows that there is in general a very high number of odonate larvae between alder roots, which may indicate a good availability of food resources. Indeed, we have observed many more mayfly and caddisfly larvae in this substrate type than in any other. But we have not recorded the food items systematically.

It has to be kept in mind that larval *O. curtisii* may be evolutionarily adapted to dwell in microhabitats of high structural complexity like roots and that they may not select them actively in direct response. Some of the factors like predation by fish, current and/or food availability could have caused this affinity. This would mean however that the larvae under experimental conditions have not behaved as they would do in the field.

According to other authors (Schmidt 1944; d'Aguilar & Dommanget 1998) larvae of *O. curtisii* are considered to be mud-dwellers. In this study, in all three rivers *O. curtisii* mainly inhabits alder roots. However, it is possible that this species occupies a wide range of habitats and that there are regional or local differences in microdistribution depending on the presence and distribution of suitable substrates and on other factors such as e.g. presence of competitors. The root system of alders appears to be a better refuge in which to avoid fish predation (see above). Larvae of *O. curtisii* do not themselves burrow in coarse sand, but particles of mud fasten to them when they walk over a muddy surface resulting in a coating serving presumably as a camouflage that protects against predation. Furthermore, larvae of *O. curtisii* are able to let themselves sink into a muddy substrate by moving the legs, resulting in their becoming buried (K.G. Leipelt unpubl.).

Larval microdistribution has been studied in only a few corduliid species (e.g. Johnson & Crowley 1980; Crowley & Johnson 1982; Wildermuth 1998) and there is little information about habitat selection. But some macromiid species are exclusively or partly associated with submerged roots (Lieftinck 1950, 1953; Wilson & Theischinger 1996). *Macromia arachnomima* Lieftinck in particular resembles *O. curtisii* in some behavioural traits (cf. Lieftinck 1953; Butler 1985).

Corbet (1999) divides larval Anisoptera into four types according to their behaviour, morphology, and microhabitat occupancy. Our results showed that larvae of *G. graslinii* can easily be classified as shallow burrowers sensu Corbet (1962), a category in which all European *Gomphus* species fit (Suhling & Müller 1996). *O. curtisii* could very probably be assigned to the sprawler type: this group contains species that "use the long, laterally extended legs to support the body on or among a matrix, usually of detritus or macrophytes" (Corbet 1999); like species of the subcategory 2.2.1. (Corbet 1999: 149)

larvae of *O. curtisii* have a scoop-shaped labium and a sedentary life style and occur in slow running waters.

Acknowledgements

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