

**COEXISTENCE OF THREE *SYMPETRUM* SPECIES AT DEN DIEL,
MOL, BELGIUM
(ANISOPTERA: LIBELLULIDAE)**

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In an Odonata community of the NE of Belgium 7 *Sympetrum* spp. coexist. Resource partitioning between 3 of them, *S. depressiusculum*, *S. danae* and *S. pedemontanum*, was studied. Habitat separation was found between *pedemontanum* versus *depressiusculum* and *danae* and separation in adult diurnal activity-pattern between *depressiusculum* versus *danae* and *pedemontanum*. Although the interactions between *depressiusculum* and *danae* are reduced by differences in diurnal activity and to some extent by seasonal separation, they interact frequently and aggressively. The pioneer characteristics of *S. pedemontanum* are discussed.

INTRODUCTION

Coexistence of related species in a stable environment at equilibrium is only possible when they are ecologically distinct enough that each has a particular resource on which it is able to win the competitive interaction (McNAUGHTON & WOLF, 1979). In a community of related species we, therefore, expect either instability or (and) resource partitioning, the latter not necessarily arising from interspecific competition.

Resource partitioning often is based on a spatial and/or temporal separation. In Odonata several examples are known. BENKE & BENKE (1975) showed a temporal separation in larval growth and imaginal activity in an Odonata community. Congeneric species, however, were almost identical in phenology. The authors suggested that coexistence was possible because of errors of exploitation of the dominating species of the genus. VAN NOORDWIJK (1978) documented a temporal as well as spatial separation between the seven genera in a community of eight Zygoptera species, but not between the two members of the genus

Coenagrion. He argued that, because of the annual fluctuations in the environment, no stable equilibrium is ever reached, thus allowing a "continued transient coexistence". ANSELIN (1978) found a seasonal separation between coexisting *Erythromma* species.

As congeneric species often are similar in life history, habitat preferences and behaviour, coexistence mechanisms are vital to avoid interspecific competition when they live together.

At "Den Diel" (Mol, Belgium) seven *Sympetrum* species coexist, viz. *S. danae* (Sulzer, 1776), *S. depressiusculum* (Selys, 1841), *S. pedemontanum* (Allioni, 1766), *S. sanguineum* (O.F. Müller, 1764), *S. vulgatum* (Linnaeus, 1758), *S. flaveolum* (Linnaeus, 1758) and *S. striolatum* (Charpentier, 1840). The first five are abundant (WASSCHER & MICHIELS, 1982). We searched for resource partitioning between 3 of them: *S. depressiusculum* and *S. pedemontanum* because they are rare elsewhere in Belgium (CAMMAERTS, 1979), and *S. danae* because it is the most common *Sympetrum* species in the region.

LOCALITIES AND METHODS

Den Diel (Mol, Belgium) is situated at 5°11'E and 51°15'N. It consists of (1) six large and medium-sized ponds, formed by lignite-exploitation during World War II, on an oligotrophic, sandy soil and (2) a network of irrigation ditches, fed with calcareous water from the nearby canal. Six different localities were distinguished (Fig. 1):

Beek Groesgoor (BG): a wide (1.8-2.8 m) irrigation ditch with slowly running water, the surroundings are dry, semi-open and partly cultivated; it is dredged once every year; pH ca 7.5, conductivity ca 380 micro-S;

Afvoerbeek (A): outlet ditch of a large-sized pond ("Grote Sprietput"), with slowly running water; the surroundings are dry, heath-like, and semi-open; pH ca 9.6, C ca 370 micro-S;

Westen van Plas (WP): semi-open, western part of the long, central pond; strongly overgrown with shore-vegetation; pH ca 6.7, C ca 390 micro-S;

Zuidoost Hoek (ZO): south-eastern part of the same pond with

a broad zone of shore vegetation and an adjacent glade of about 0.5 hectare; pH ca 6.7, C ca 390 micro-S; the banks between localities WP and ZO are covered with overhanging trees and, consequently, unfavourable for *Sympetrum*.

Gemeentepas (G): southwestern pond; fen-like, with a broad zone of shore-vegetation; pH ranges from 6.5 in the open water to 3.8 in the peaty parts, C resp. between 220 and 300 micro-S.

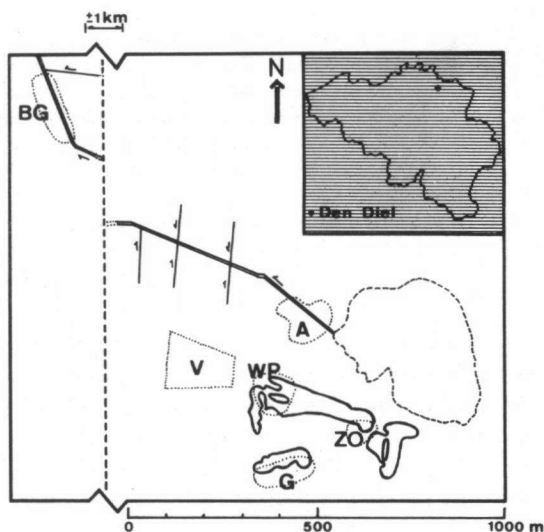


Fig. 1. Situation of the study-area and its subdivision in localities.

Veld (V): a non-grazed pasture (length: 180 m, width: 80-150 m) close to the central pond but without oviposition-sites; used as a roosting area by many species of Odonata. The grass was mown on 15 August 1983 so that this locality then lost its attraction to dragonflies.

The major part of the surroundings of these localities is wooded.

Observations were made from 3 July until 10 October 1983. During the first two months the weather was warm and dry. September was cold and rainy, except for the last 8 days, which were warm and sunny again.

Population parameters were estimated by capture, marking and recapture. The individuals were wing-marked with quick-drying paint or with a waterproof pen, using the coding technique of HINNEKINT (1974). Local reproduction was proven by the observation of freshly emerged teneral and occasional findings of exuviae (for more details, cf. MICHIELS, 1984).

Diurnal activity and aggressive interactions were studied by recording behaviour continuously, from the beginning of *Sympetrum* activity at ca 10.00 Civil Time until its end at ca 16.00. Such observations were held at locality G (8 and 15 August), locality WP (9 August), locality ZO (12 August), locality BG (12 August) and locality A (15 August). Additional observations were made at localities A (12 August) and G (6 September). As a measure of activity we used the number of tandem-pairs ovipositing or flying over, the number of inter- and intraspecific interactions, and the number of interactions in which a certain species was the aggressor. The latter were grouped into (i) aggressive and (ii) investigatory approach in flight. The first consisted of a very quick attack of the "target", in which the aggressor approached the antagonist up to less than 10 cm. If the target resisted, this often resulted in a whirling air-fight with physical contact. Sexual interactions were rarely seen or not recognised as such, and have been included in this first group. Short and moderate flights that seemed to be a cautious inquisition of unknown intruders were the most important kind of interactions in the second group; the aggressor usually returned to his perch, not having approached his target to within 50 cm. Any ambiguous observation was discarded.

All data were converted from Civil time (Mid-European Summer-time) to Solar Time, specific for 5°11'E.

RESULTS

SPATIAL DISTRIBUTION

Between 7 July and 28 September a total of 1313 different individuals were marked: 538 *S. danae* (307 ♂, 231 ♀), 520 *S. pedemontanum* (256 ♂, 264 ♀) and 255 *S. depressiusculum* (162 ♂, 93 ♀). Only 110 (8.4%) resightings of marked individuals were made: 38 (7.06%) of *S. danae* (22 ♂, 16 ♀) 51 (9.8%) of *S. pedemontanum* (34 ♂, 17 ♀) and 21 (8.24%) of *S. depressiusculum* (16 ♂, 5 ♀). This very low recovery rate must be attributed to the high numbers present and to immigration from and emigration to adjacent areas. Consequently, these data could not be used to estimate absolute numbers (SOUTHWOOD, 1978). We, therefore, analysed the number of each species relative to the total number captured in each locality.

A comparison of total numbers sampled (Tab. I) shows that the species composition differed markedly between localities. *S. pedemontanum* was by far the dominant species in locality BG (97%) and was the most abundant also in localities A (53%) and V (53%). In the three other sites, *S. danae* was the most

Table I

Total number of captures (new individuals plus resightings) and the percentage of the species per locality

| Species and sex | Localities | | | | | | Total |
|------------------------|------------|-----------|-----------|------------|------------|------------|-------------|
| | BG | A | WP | ZO | G | V | |
| <i>danae</i> | | | | | | | |
| males | 5 | 19 | 8 | 64 | 163 | 70 | 329 |
| females | 1 | 15 | 9 | 52 | 94 | 76 | 247 |
| total | 6 (3%) | 34 (41%) | 17 (63%) | 116 (56%) | 257 (58%) | 146 (34%) | 576 |
| <i>pedemontanum</i> | | | | | | | |
| males | 113 | 31 | 5 | 17 | 19 | 105 | 290 |
| females | 119 | 13 | 1 | 8 | 17 | 123 | 281 |
| total | 232 (97%) | 44 (53%) | 6 (22%) | 25 (12%) | 36 (8%) | 228 (53%) | 571 |
| <i>depressiusculum</i> | | | | | | | |
| males | 0 | 2 | 1 | 48 | 94 | 33 | 178 |
| females | 0 | 3 | 3 | 18 | 53 | 21 | 98 |
| total | 0 (0%) | 5 (6%) | 4 (15%) | 66 (32%) | 147 (34%) | 54 (13%) | 276 |
| Grand total | 238 | 83 | 27 | 207 | 440 | 428 | 1423 |

abundant (WP: 63%; ZO: 56%; G: 58%). Though never dominant in total, *S. depressiusculum* was abundant in localities ZO (32%) and G (34%).

Although locality BG was sampled 4 times only, it was clear that extra samples would not yield important new information, except for the dominating *S. pedemontanum*. Numerous freshly emerged teneral and exuviae indicated local reproduction. Other *Sympetrum* species were rare; on 10 August only 6 out of 150 individuals captured were *S. danae* (1 ♀, 5 ♂).

In locality A, *S. pedemontanum* dominated from August onwards. Freshly emerging teneral and many exuviae of this species were found. Two teneral and a few exuviae of *S. danae* indicated a moderate local reproduction of this species. *S. depressiusculum* was an occasional visitor only.

In spite of the limited data (Tab. I), but supported by occasional visits and one continuous observation, locality WP seemed to be mainly dominated by *S. danae* and *S. depressiusculum*, both of which reproduced here (freshly emerged teneral and exuviae). The six individuals of *S. pedemontanum* were all captured on the same day at the end of the flying season.

Locality ZO was visited with great regularity. *S. danae* dominated and freshly emerged teneral and exuviae were regularly found. *S. depressiusculum* was also common, especially so from August onwards; one teneral and one exuvium were recorded. *S. pedemontanum* was seen in low numbers only.

At locality G, *S. danae* by far outnumbered the other two species. High

numbers of teneral and exuviae pointed to an important local reproduction. *S. depressiusculum* was also abundant and even dominated in September. One freshly emerged teneral and 4 exuviae were found. *S. pedemontanum* appeared occasionally only.

Locality V was an important roosting and maturation area for all three species. Especially in July many individuals were caught here. Only two visits were made after 15 August, because then the grass was mown and the area had lost its attraction to *Sympetrum*. The relatively high numbers, including some teneral, of *S. pedemontanum* indicated a strong exchange with locality A. This was supported by the movements of marked individuals (MICHIELS, 1984) and the absence of reproduction of *S. pedemontanum* at the central pond. *S. danae* was common too, but no teneral of this species have been observed. *S. depressiusculum* was present in low numbers only.

Our results show that the three species are spatially separated at Den Diel to some extent. *S. pedemontanum* appeared to be a small-stream dweller (localities BG and A). *S. danae* and *S. depressiusculum*, on the other hand, were particularly common along the shores of ponds (localities ZO, WP and G). For the latter, this appeared to be obligatory. *S. danae* seemed to be especially attracted by locality G.

SEASONAL ACTIVITY

To study seasonal separation, the obvious means would be a comparison of the evolution of population size. But, as mentioned above, the low recovery rate did not allow population size to be estimated. We have, therefore, used the evolution of the relative abundance of each species in each sample for each locality (Figs 2-3).

The flying season started with the appearance of *S. danae* and *S. pedemontanum* during the first two weeks of July. Teneral of both species were seen resp. from 3 and 7 July onwards. After mid-July both species were common on their favourite localities. *S. depressiusculum* clearly appeared later (Fig. 3); the first individuals were seen on 21 July. At the end of July, when all *S. depressiusculum* individuals were still immature, many adults of *S. danae* and *S. pedemontanum* were present and the former was even reproducing (tandem-pairs observed).

Our data do not allow us to determine whether the moment of maximum abundance coincides for all three species. Our observations, however, lead us to think that both *S. danae* and *S. pedemontanum* reached their maximum abundance around the middle of August. For *S. depressiusculum* this was about two weeks later. From Figure 3 it appears that *S. depressiusculum* is as least as common as *S. danae* at the end of August.

From mid-September onward *S. danae* and *S. depressiusculum* were still quite

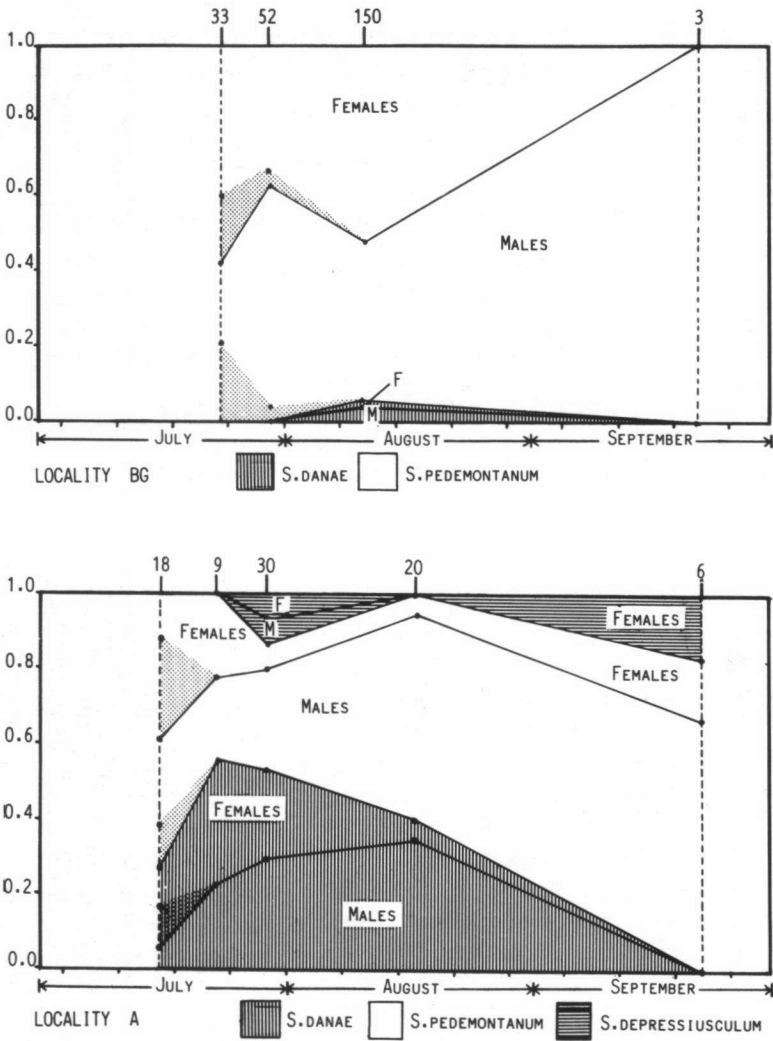


Fig. 2. Evolution of the relative sample composition (Y-axis) in time (X-axis) in the lotic habitats BG and A. Each sample is represented by a series of points in vertical direction. The interval between them stands for the relative portion of each species/sex-group in the given sample. Sample size is indicated at the top. Teneralis are shaded. Samples collected at short intervals were grouped.

numerous at their favourite localities (ZO and G), whereas *S. pedemontanum* had disappeared almost completely from localities BG and A, but maintained its (low) numbers in the other localities. The last sample was taken on 28 September.

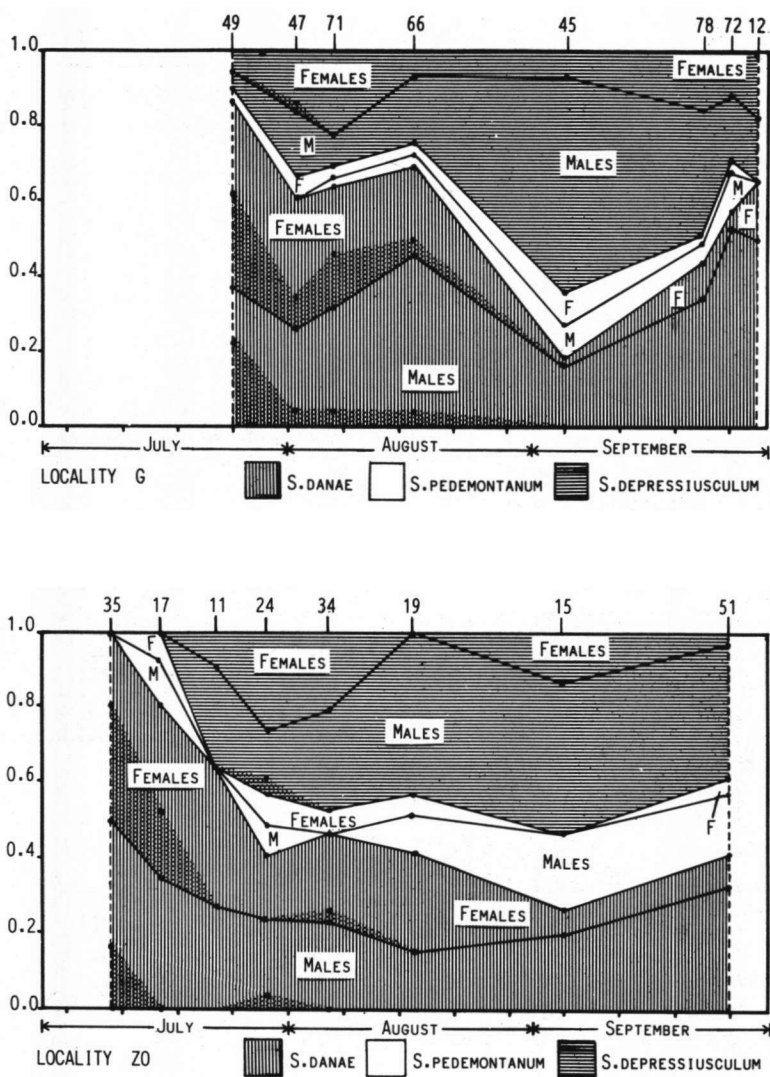


Fig. 3. Evolution of the relative sample composition (Y-axis) in time (X-axis) in the lentic habitats ZO and G; see also legend of Fig. 2.

During a final visit on 10 October, when no captures were made, all three species were still present, though in low numbers only.

DIURNAL ACTIVITY

The data on diurnal activity, collected during continuous observations, are summarized in Figure 4. Those for *S. danae* and *S. depressiusculum* result from the observations on localities G, WP and ZO. The *S. pedemontanum* data originate from localities BG and A. They were all made within the period of 8-15 August.

Because 87% of the individuals involved in interactions and all aggressors were males, the diurnal distribution of interactions can be considered as a measure of male activity.

The reproductive activity of *S. depressiusculum* (Fig. 4A) started at 9.00 (Solar Time) and remained rather constant until it came to an end at 13.00, without a clear maximum. Male activity was especially high between 9.30 and 11.00. A second, lower, peak was found between 12.30 and 13.30.

S. danae (Fig. 4B) reproduced between 10.30 and 14.00, with a clear maximum at noon. Most of the interactions were displayed between 10.00 and 14.00. They increased gradually and reached a maximum at about 12.30.

Reproductive activity of *S. pedemontanum* (Fig. 4C) was seen between 10.00 and 14.30, and showed a distinct maximum at 12.00-12.30. *S. pedemontanum*

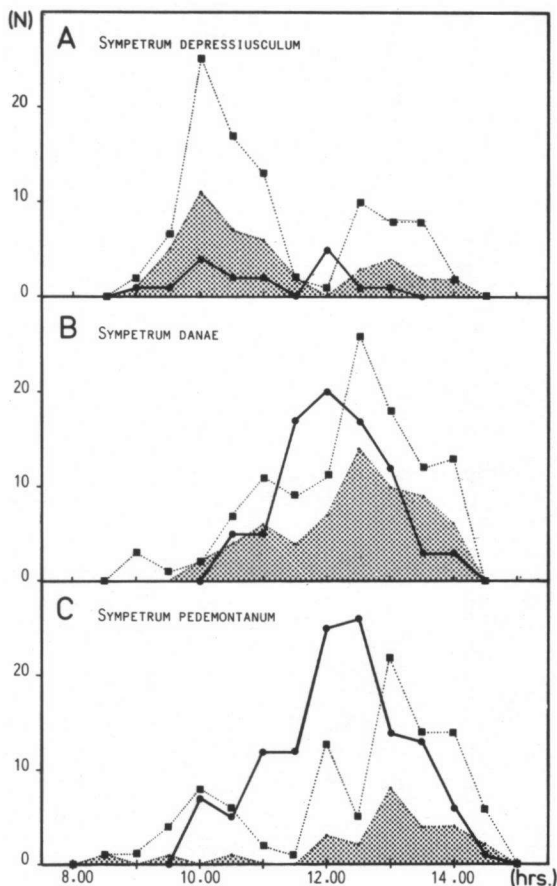


Fig. 4. Daily activity of *Sympetrum depressiusculum* (A), *S. danae* (B) and *S. pedemontanum* (C) expressed as the frequency of observations per half hour. — [Solid lines and dots: number of tandem-pairs observed; — Dotted lines and squares: number of interactions in which the species was involved; — Dotted areas: interactions in which it was the aggressor].

was seen interacting from 8.30 onwards. Most interactions, however, occurred between 12.00 and 14.30.

The data indicate that *S. depressiusculum* is especially active before noon, with a possible maximum between 9.30 and 10.30, whereas *S. danae* and *S. pedemontanum* reach peak activity between 11.30 and 13.00.

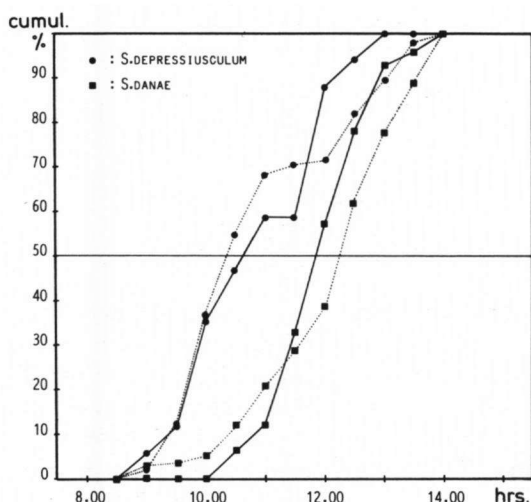


Fig. 5. Cumulative percentage of activity during one day in *Sympetrum depressiusculum* (dots) and *S. danae* (squares). — [Solid lines: number of tandem-pairs; — Dotted lines: number of interactions].

depressiusculum and 86 for *S. pedemontanum* (Tab. II). The proportion of interactions with other species was significantly lower in *S. pedemontanum* (55%) than in *S. danae* (77%, $G=11.9$, $P<0.001$) or in *S. depressiusculum* (75%, $G=9.3$, $P<0.01$). The difference between the latter two species was statistically not significant ($G=0.02$, $P>0.50$).

A comparison between the number of interspecific interactions initiated by another species against one of the three *Sympetrum* spp. and that initiated by the *Sympetrum* sp. in question, again showed statistical differences: *S. danae* attacked relatively more than it was being attacked, whereas in *S. pedemontanum* the situation was reversed, *S. depressiusculum* being intermediate. (*S. danae* — *S. depressiusculum*: $G=4.8$, $P<0.05$; *S. depressiusculum* — *S. pedemontanum*: $G=18.9$, $P<0.01$).

These observations suggest that *S. pedemontanum* either recognised conspecifics better or it had a smaller chance to encounter other species because of its habitat preference, or both.

As *S. depressiusculum* and *S. danae* largely co-occur in the same habitats, we have compared their activity patterns in Figure 5 by plotting the cumulative percentage activity of the two species. *S. depressiusculum* had displayed 50% of its activity by about 10.30, when *S. danae* had only reached ca 10%. *S. danae* did not reach 50% until noon. This represents a shift of 1.30 hours.

INTERACTIONS

We recorded 123 interactions in which *S. danae* was involved, 127 for *S.*

Table II

Number of intra- and interspecific interactions in which *S. danae*, *S. depressiusculum* or *S. pedemontanum* were involved — [All interspecific interactions were taken into account, also those where a non-Sympetrum species was involved]

| Interactions | Species involved | | |
|-----------------------|------------------|-----------------|------------------|
| | <i>danae</i> | <i>depress.</i> | <i>pedemont.</i> |
| Total number observed | 123 | 127 | 86 |
| Intraspecific | 28 | 32 | 39 |
| Total interspecific | 95 | 85 | 47 |
| Number initiated | 51 | 37 | 6 |
| Number not initiated | 32 | 46 | 38 |
| Number unknown | 12 | 12 | 3 |

As *S. pedemontanum* was spatially separated from *S. danae* and *S. depressiusculum*, it rarely interacted with them (only 3 occasions noted). Therefore we confined our further analysis to a comparison between the latter two species. Table III shows that *S. danae* was significantly more aggressive towards *S. depressiusculum* (26 out of 34 occasions) than vice versa (8/34) ($G=4.1$, $P < 0.05$). When comparing the nature of the interactions, it is striking that *S. danae* males behaved even more aggressively towards *S. depressiusculum* than towards members of their own species ($G=8.0$, $P < 0.01$). This was not the case in *S. depressiusculum* ($G=0.03$, $P > 0.80$).

Table III

Total number and result of the intra- and interspecific interactions within and between *S. danae* and *S. depressiusculum*

| Interactions and their results | Aggressor | | | |
|--------------------------------------|----------------------------|-----------------|--------------------------------------|--------------|
| | <i>danae</i> Antagonist | | <i>depressiusculum</i> Antagonist | |
| | <i>danae</i> | <i>depress.</i> | <i>depress.</i> | <i>danae</i> |
| Total number | 28 | 26 | 32 | 8 |
| Nature | | | | |
| Violent | 17 | 24 | 23 | 6 |
| Non-violent | 11 | 2 | 9 | 2 |
| Result | | | | |
| Antagonist displaced | 10 | 22 | 11 | 3 |
| Aggressor displaced | 5 | 1 | 2 | 1 |
| None displaced | 10 | 3 | 11 | 4 |
| Both disappeared | 1 | 0 | 3 | 0 |
| Other results | 2 | 0 | 5 | 0 |

The results of interspecific encounters were similar for *S. danae* and *S. depressiusculum*; displacement of the antagonist or no displacement at all were equally likely as outcome. In interactions with *S. depressiusculum*, *S. danae* was able to displace its antagonist in 85% of the attempts. *S. depressiusculum*, on the contrary, was successful in 38% of the occasions only. These latter interpretations, however, are tentative, as frequencies are low.

CONCLUSIONS AND DISCUSSION

Our observations indicate a distinct resource partitioning between the three species investigated: they are separated by habitat (*S. pedemontanum* versus *S. danae* and *S. depressiusculum*), by diurnal activity (*S. depressiusculum* versus *S. danae* and *S. pedemontanum*) and, to some extent, by adult season (*S. pedemontanum* and *S. danae* versus *S. depressiusculum* in July; *S. danae* and *S. depressiusculum* versus *S. pedemontanum* in September). We cannot, however, exclude that competition at the larval level exists between *S. depressiusculum* and *S. danae*, since the temporal shifts found in this study have a bearing upon adults only.

From the analysis of the interaction data we conclude that, in comparison with *S. danae* and *S. depressiusculum*, *S. pedemontanum* is involved in fewer interspecific interactions, probably so because of its different habitat and/or better recognition of other species. When comparing *S. danae* and *S. depressiusculum*, the former is the most aggressive.

IS *SYMPETRUM PEDEMONTANUM* A PIONEER SPECIES?

The typical habitat of *S. pedemontanum* consists of ponds with a broad transition zone of shore vegetation or marshy pastures. Recently, however, it has been also found near running water in other localities. In 14 consulted publications and in the archives of the Belgian Dragonfly Study Group, 17 lotic (L) and 24 stagnant (S) localities are mentioned and 17 localities are undescribed, viz. BEUTLER (1977): L; — BEUTLER & BEUTLER (1981): S; — GEIJSKES & VAN TOL (1983): L, S; — HUIJS & PETERS (1983): L, S; — MARTENS (1983): S; — MÜNCHBERG (1938): S; — ROBERT (1958): S; — SCHIEMENZ (1953): S; SCHMIDT (1967): S; — STARK (1980): L; — STÖCKEL (1974): L, S; — TAMM (1982): S; WILDERMUTH (1980): S; — ZIEBEL & BENKEN (1982): L. The 9 lotic localities where it was seen reproducing were mainly man-made, often new or regularly dredged ditches and canals (cf. locality BG at Den Diel). The seven stagnant reproduction sites were shallow water bodies with a varying annual water level and sometimes recently made. In other words, *S. pedemontanum* seems to prefer new, highly dynamic breeding habitats. At most occasions, however, it was seen as a solitary wanderer,

from 58 localities mentioned, 23 concern incidental observations and 20, reproduction sites. The 15 localities from which the observations were not described in detail, probably also concern incidental records only.

For these and other reasons we agree with TAMM (1982) that *S. pedemontanum* possesses the characteristics of a pioneer species:

- (1) It wanders extensively (cf. above). In Den Diel it showed a high mobility (MICHIELS, 1984).
- (2) It shows a high ability to colonize new habitats: the highest numbers of recent records in Western Europe come from new or artificially renewed habitats (MICHIELS, 1984; STÖCKEL, 1974; TAMM, 1982). STÖCKEL (1974) reports that in most places it appeared suddenly, reached high numbers during 1 or 2 years, subsequently declined sharply, and finally disappeared.
- (3) It is one of the smallest Anisoptera in Europe (Den Diel: abdominal length ♂ 21.7 mm, ♀ 21.4 mm; MICHIELS, 1984).
- (4) The larva develops very rapidly: after hibernation of the egg, the adult stage can be reached in 65 days MÜNCHBERG, 1938). Only *S. flaveolum*, which is very well adapted to desiccating ponds, shows a shorter development time (TAMM, 1982).
- (5) Adult life span is shorter, but sexual maturation is reached earlier than in *S. danae* and *S. depressiusculum* (MICHIELS, 1984). The decrease of *S. pedemontanum* at Den Diel in September, relative to the other two species, can be seen as a consequence of this (cf. above, and TAMM, 1982).
- (6) Finally, *S. pedemontanum* is less involved in interspecific interactions.

Assuming that *S. pedemontanum* adopts the strategy of a pioneer species in order to avoid interspecific interactions does not explain how it avoids congeneric species, since they all, in some way, show similar features (1, 2, 3 and 4).

However, the rheophile character of *S. pedemontanum* and its features listed under (5) and (6) distinguish it from other *Sympetrum* species in Western Europe. Only *S. danae* can be found breeding in running water occasionally (this study).

IS *SYMPETRUM DEPRESSIUSCULUM* ADAPTED TO LOWER TEMPERATURES?

Dragonfly activity is highly related to solar radiation and air temperature (MAY, 1976). Several morphological and behavioural features of *S. depressiusculum* suggest that it is better adapted to lower radiation and/or temperature than *S. pedemontanum* and *S. danae*. Firstly, *S. depressiusculum* is the largest of the three species under study (MICHIELS, 1984). Secondly, in the morning the males made fluttering flights between the stems of the vegetation on the shore. MILLER & MILLER (1984) observed that during these flights males are searching for mates. This probably leads to an increase in body temperature as well. Thirdly, *S. depressiusculum* rarely sat flat on the ground, and never was attracted by white surfaces, as observed in *S. danae* from the beginning of September onwards. This could indicate that *S. depressiusculum* has a lower optimal body surface temperature. Finally, two observations suggested that the optimal body temperature is exceeded earlier than in e.g. *S. danae*: (i) we found a temporal decrease of activity at solar noon (Fig. 4), and, (ii) very

often, we observed prolonged flights with frequent soaring intervals in the open air above the water, especially on warm and sunny afternoons. The later could last for more than five minutes, which was never observed in the smaller *S. danae* and *S. pedemontanum*. Compared with the early-morning flight, this flight type gives more air current at the body surface and, consequently, can be considered a cooling-mechanism by convection (MAY, 1976).

IS THERE COMPETITION BETWEEN *S. DEPRESSIUSCULUM* AND *S. DANA*E?

Whether the observed shift in activity between *S. danae* and *S. depressiusculum* is due to interspecific competition in the past, or is a reflection of competition at this moment, or is not caused by competition at all, cannot be implied from our field data. It is clear, however, that the observation differences help to reduce interspecific interactions anyway. These interactions do indeed exist. Their frequency and vehemence even suggest that an interference of species with each other's reproductive behaviour is not unlikely. If this leads to a reduction of the reproductive success of the males involved, interference competition is taking place between these two species. This hypothesis, however, will remain unproven, and is probably even untestable, as the progeny of an individual dragonfly is virtually untraceable.

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