comporte actuellement le genre, mais la conformation des pattes et des antennes constitue des caractères tout aussi discriminatoires.

RÉPUBLIQUE DÉMOCRATIQUE DU CONGO, Yangambi, en forêt, 36 exemplaires des deux sexes dans une termitière de *Cubitermes*, juillet 1960 (J. Decelle). Holotype et 35 paratypes au Musée Royal de l'Afrique Centrale, Tervuren.

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# A CONTRIBUTION TO THE ECOLOGY OF SOME ODONATA. THE ODONATA OF A « TRAP » AREA AROUND DENDERLEEUW (Eastern Flanders : Belgium)

par Henri J. DUMONT

## 1. Introduction.

There is today an overwhelming faunistical literature on the Order Odonata and the number of reports is still increasing. Many authors have brilliantly inventorized their particular environments and most tend to present some stray notes on ecology, more frequently ethology of the species encountered. True ecological approaches however are few. As some stimulating exceptions, the autecological work of ZAHNER (1959, 1960) on *Calopteryx splendens* should be cited here, together with the synecological approaches by FISCHER (1961) and MACAN (1964).

The present paper is an attempt to gain some insight into the factors that govern habitat selection in a number of species living closely together on a limited area, presenting some curious features.

These may be summarized as follows :

1) All the pools considered lay along the axis of the river Dender, an affluent of the Scheldt, over a length of not more than 3 km. They are all situated on one bank of the river and not more than a few hundreds of meters remote from it.

2) They are *all* artificial and recent (see further), and, at one exception, very shallow. All are permanent in nature.

3) Their basins belong to an area (Fig. 1), delimited by steep railroad taluds bordered by some small rivulets in the south, south-

west and west ; the river Dender in the East ; the Highway Brussels-Ostend (again bordered by rivulets) in the North. All of these might serve as artifical pathways for Odonate distribution and so, the whole territory might act as a mouse trap for any migrating dragonfly. The depression is very humid, covered with meadows, woods and swamps.

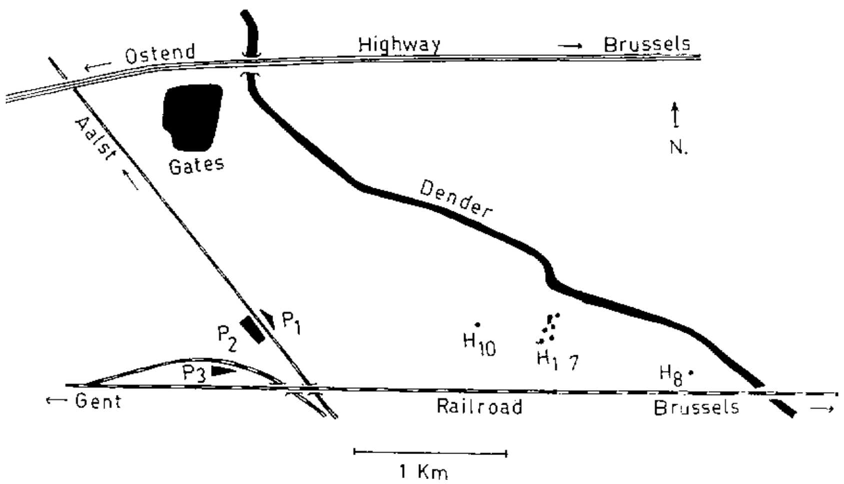


FIG. 1. — Diagram showing localization of all ponds and pools discussed in the body of this paper.

## 2. Description of the biotopes.

### a) *The three sand pools* ($P_1$-$P_3$)

They are the oldest pools in the territory, situated at the intersection of the railways Brussels-Ostend and Brussels-Gent and the shunt of the railway Brussels-Ostend to the village of Denderleeuw (Fig. 1). They were created in the beginning of the century, as a consequence of soil-extraction for raising the railway taluds. All three are situated within the limits of the village of Welle.

Pools 1 and 2 are part of the transgression area of the Dender, Pool 2 being closely apposed to the erosion talud (a rather steep accident in the landscape, 2 à 3 m. high). Pool 3 lays completely out of the alluvial plain. Its bottom is more elevated than the surface of the two others (Fig. 2). Pools 1 and 3 are triangles with largest side ca. 40 m. ; Pool 2 is a vast rectangle (120 x 50 m.).



Depth is not exceeding 3 m. Phragmites abounds on the shores, together with Carex spp. Locally, willow trees grow.

Aquatic vegetation is rich and varied : Polygonum amphibium, Ranunculus aquaticus, Hydrocharis morsus-ranae and Elodea canadensis. Since 1965, Pool I has been progressively immigrated by Sagittaria sagittifolia, Sparganium and Butomus umbellatus.

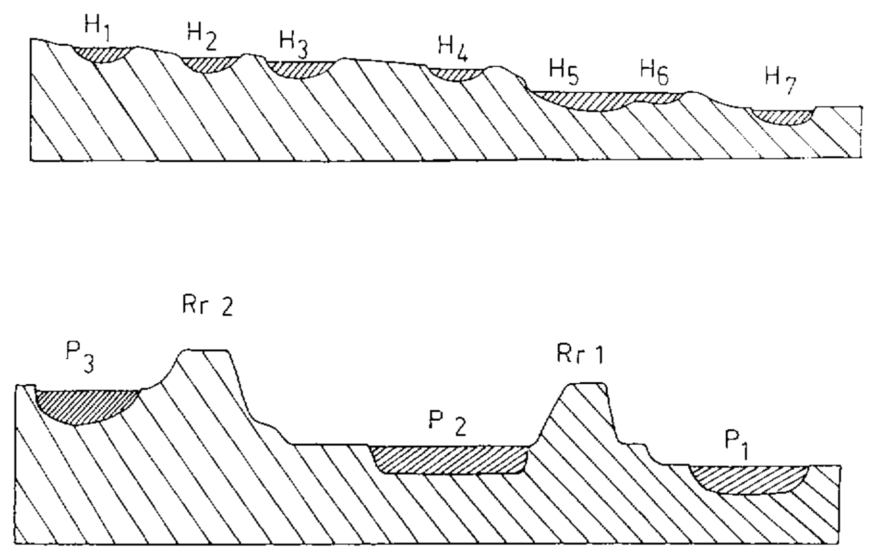


FIG. 2. — Semidiagramatic section, showing the relative position of the Bomb holes (above) and the Sand pools (below).

### b) *The Gates Pool* (*Fig.* 3).

A rather regular shaped reservoir (550 x 450 m), connected with the Dender by a small rivulet. Maximum depth is about 10 m., average depth 6 m. It behaves as an eutrophic lake, with well-developed epi- and hypolimnion in summer and two complete circulations in spring and automn. The summer hypolimnion (beyond 4 m) is completely devoid of oxygen, so that production of benthos and insect life is confined to the littoral. The latter is a well developed zone, between 10 and 30 m wide, and rich in vegetation. Importantly, an invasion of Butomus umbellatus, Sparganium and Sagittaria about 1964 should be noted.

These plants now tend to dominate all others in the littoral. P h r a g m i t e s is abundant locally only. In the sub-littoral C e r a t o p h y l l u m abounds.

The reservoir was constructed right on the winter transgression limit of the Dender, so that its eastern part is still in the alluvial

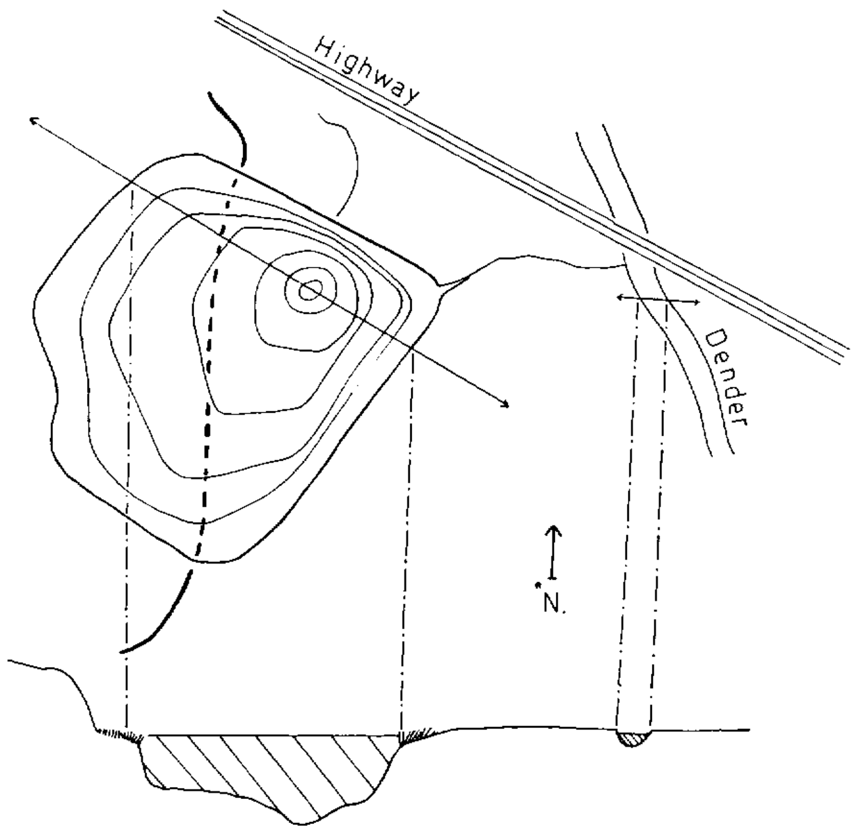


FIG. 3. — The Gates pond and its surroundings, including a cross section (semi-diagramatic) at the level of maximum depth. Position of transgression talud of the River Dender relative to the pond also indicated.

area ; its western part belongs to the erosion slope. As a consequence, the eastern shores are flat and the western ones steep, about 10 m. high, with a slope of ca. 70°.

The reservoir is fed by sources in the western talud and has a



very limited discharge to the Dender. It does not receive water from the Dender to-day. Until 1955, the year when the reservoir was finished, (dug out for raising the local highway traject), a broad artificial canal linked the reservoir to the heavily polluted river. The Dender, that used to be a mesosaprobic, slow-running river, supporting important fish and plankton stocks, has been polluted by upstream industries in the years subsequent to world-war II and became unsuitable for animal life about 1949-1950. If it may be assumed that only little polluted water from the Dender actually entered the pond, it is equally likely that remnants of the original river populations quickly moved into it, so that a rather stormy invasion may not have been improbable.

Fish stock today is still very rich, though since a few years the waters of the basin have been used as cooling water by a nearby factory. There is a limited discharge of oil that is slowly accumulating in the littoral and may lead to asphyxy-conditions in the future. No dramatic effects have been recorded until now.

3) *The Bomb holes.*

Heavy bombings on the railway station of Denderleeuw in 1944 had no other lasting effect than creating a great number of fresh biotopes for aquatic animals. The majority of these holes have been filled up since, but a certain number still persist and have rapidly reached appreciable population levels. Undoubtedly, some dramatic winter transgressions of the Dender just after the war favoured this quick population greatly.

We have been censuring 9 among these bomb holes for 15 years now (a tenth one was destroyed in 1965). Seven among them ($H_1$-$H_7$) are grouped, largely within a piece of marshy wood (alder trees, willows and poplars). $H_6$ and $H_7$ are largely outside the woods but still surrounded by willows. $H_5$ and $H_6$ are connected by a broad isthmus, to form in fact only one pool.

C a r e x spp. and P h r a g m i t e s abound. E l o d e a c a n a d e n s i s covers great parts of the water surface. The landscape presents a very gentle slope from $H_7$ to $H_1$.

The bottom is rich in limonite, which may be considered the chief source of the iron that has been detected in all pools.

In 1967, the original site was deeply changed by the owners. $H_1$ and $H_2$ were replaced by two large rectangular fish pools (40 x 20 m), and a third one, entirely new, was added. All trees and brushwood were removed (shading absent). The fishpools, inasfar as we shall be concerned with them, shall be coded $F_1$-$F_3$.

$H_8$ lays in a meadow, fully in the alluvial plain of the Dender and unshaded. It was destroyed in 1967.

$H_{10}$ is situated in the same wood as $H_1$-$H_7$ and is fully shaded by alder trees.

### 3. **List of species with years of incidence since 1957** (table I).

Clearly, table 1 is a qualitative approach, not accounting for fluctuations in the population levels. Therefore, a few comments on the rarer species should be made here.

*Calopteryx splendens* is by no way a regular inhabitant of the region. Twice, during hot summers, a few males were seen (July 1958 on $H_9$ and August 1969 on Gates). All specimens seen agreed in showing a very nervous behaviour. They were extremely shy and flying at a height of 2-3 m. in an anisopterous way. One specimen captured proved not to be fully adult.

It is probable that, despite the intimate linkage of this species to running waters, some degree of migration occurs, especially in hot seasons and when the normal habitats tend to be oversaturated. Consequently, it seems reasonable to suppose that the specimens seen followed one of the several dispersal ways leading to our region, but reproduction is definitely excluded here.

*Aeschna isoceles* is known in one male specimen, reared from $P_1$ (emergence on 15.VI.1964) from a larva captured in winter. It is possible that this rather rare species regularly reproduces in the biotope, but never reaches appreciable numbers and so goes easily overlooked.

*Aeschna affinis* : one exuvium on $H_6$, july 1969. In subsequent days, an adult male was seen over $F_{1-3}$. It was shy and could not be captured. *Aeschna affinis* is a mediterranean species which has been recorded in Belgium only by SÉLYS (1888). It is also known from the Netherlands, where it was re-discovered lately by LIEFTINCK (1952). Its occurence in our region is probably incidental, and though it has reproduced in the « trap », it would be too optimistical to expect it to settle here.

*Gomphus pulchellus* is known from one male, hunting along the railway track near $P_1$ on 18.VI.1964. No larvae or exuviae are on record, so that this was probably another dwelling specimen.

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**TABLE 1 — List of species**

| | 1957 | 1958 | 1959 | 1960 | 1961 | 1962 | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1969 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Calopteryx splendens | | × | | | | | | | | | | | × |
| 2. Lestes viridis | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 3. Lestes sponsa | | | | | | | | | | | | × | × |
| 4. Coenagrion puella | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 5. Coenagrion pulchellum | | | × | × | × | × | × | × | × | × | × | × | × |
| 6. Coenagrion lindeni | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 7. Pyrrhosoma nymphula | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 8. Ischnura elegans | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 9. Erythromma naias | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 10. Enallagma cyathigerum | | | | | | | | | | × | × | × | × |
| 11. Platycnemis pennipes | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 12. Aeschna cyanea | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 13. Aeschna grandis | | × | × | | | | | | | × | × | × | × |
| 14. Aeschna isoceles | | | | | | | | × | | | | | |
| 15. Aeschna mixta | | | | | | | | | | × | × | × | × |
| 16. Aeschna affinis | | | | | | | | | | | | | × |
| 17. Anax imperator | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 18. Brachytron pratense | | | | | | | | × | × | × | × | × | |
| 19. Gomphus pulchellus | | | | | | | | × | | | | | |
| 20. Libellula quadrimaculata | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 21. Libellula depressa | × | × | × | × | × | × | × | × | × | × | × | | |
| 22. Orthetrum cancellatum | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 23. Sympetrum striolatum | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 24. Sympetrum vulgatum | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 25. Sympetrum flaveolum | | × | × | | | | | | | | | | × |
| 26. Sympetrum danae | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 27. Sympetrum sanguineum | × | × | × | × | × | × | × | × | × | × | × | × | × |
| 28. Crocothemis erythraea | | | | | | | | × | | | | | |
| 29. Cordulia aenea | | | | | | | | | × | | | | |

*Crocothemis erythraea* is a well-known migrator. We have commented upon it at some length before (DUMONT, 1967). B. HINNEKINT claims to have seen a second specimen on the Gates Pool in June 1966, but this record is not certain, as it may as well have been a *Sympetrum fonscolombei*. As this however is another rare species and a good migrator, HINNEKINT's observation is of a definite interest anyway.

*Cordulia aenea* : again, only one specimen seen over $P_1$, june 1965. As one would normally expect this species to occur in the biotope, it seems rather strange that it has not been seen more often.

All other species may be regarded as regular inhabitants. Their distribution over the area is described in the next section.

In table 2, we have re-arranged all water bodies in a more « logical » order, in order to make their natural grouping better visualized. It is to be stressed that « presence » or « absence » of a species on any of the water bodies was determined by several joint criteria. They are : presence or absence of adults around the pond, records on larvae and records on exuviae. All data over a period of twelve years.

Strikingly, two groups of ponds occur, one « rich » in species, another one « poor » in species, $H_8$ occupying an intermediate position.

Further, since $H_1$ and $H_2$ have been replaced by $F_1$-$F_3$, there has been a quick faunistical change in this area. In less than two years the following species appeared : *Orthetrum cancellatum, Aeschna grandis, Aeschna mixta, Sympetrum striolatum, Sympetrum vulgatum, Sympetrum sanguineum, Sympetrum danae* and *Erythromma naias*, bringing their total up to 12 species (see further).

In the next sections, we shall try to throw some light on the causality of this peculiar distribution pattern.

## 4. **Chemical data.**

Though it is unlikely that chemical constitution of water might have an important discriminatory effect on dragonfly-larvae and their development except at the extremes of their range, very little is actually known about this and the need for some thorough investigation seems warranted.

**TABLE 2**
**Internal distribution patterns of true inhabitants**

| | Gates | $P_1$ | $P_2$ | $P_3$ | $H_6$ - $H_5$ | $H_7$ | $H_4$ | $H_3$ | $H_2$ | $H_1$ | $H_{10}$ | $H_8$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *L. viridis* | × | ×× | × | × | ××× | ××× | × | × | | | | |
| *L. sponsa* | | × | | | × | | | | | | | |
| *C. puella* | × | × | × | × | ××× | ×× | ×× | ×× | ×× | ×× | ×× | ×× |
| *C. pulchellum* | | ×××× | ××× | ×××× | | | | | | | | |
| *C. lindeni* | ×× | ×× | ×× | ×× | | | | | | | | |
| *P. nymphula* | | × | × | | ××× | ××× | ×× | ×× | ×× | ×× | | |
| *I. elegans* | ××××× | ×××× | ×××× | ×××× | ×× | ×× | × | × | × | × | × | ×× |
| *Er. naias* | ×× | ×× | ×× | ×× | × | | | | | | | |
| *En. cyathigerum* | ××× | × | | | | | | | | | | |
| *P. pennipes* | | ××× | ×× | × | | | | | | | | |
| *A. cyanea* | | ×× | ×× | | ××× | ×× | × | × | × | × | × | ×× |
| *A. grandis* | × | × | × | | × | × | | | | | | |
| *A. mixta* | × | | | | | | | | | | | |
| *An. imperator* | ×× | × | × | × | | | | | | | | |
| *B. pratense* | | × | | | × | | | | | | | |
| *L.4-maculata* | × | ×× | × | × | × | | | | | | | |
| *L. depressa* | | | | | | | | | | | | × |
| *O. cancellatum* | ××× | | | | | | | | | | | |
| *S. striolatum* | ×× | × | × | × | ×× | ×× | | | | | | × |
| *S. vulgatum* | × | × | × | × | ××× | ××× | | | | | | ×× |
| *S. flaveolum* | | | | | × | × | | | | | | |
| *S. danea* | ×× | × | × | × | ××× | ××× | | | | | | ×× |
| *S. sanguineum* | ×× | × | × | × | ××× | ××× | | | | | | ×× |
| *Number of species per pond* | 15 | 19 | 16 | 13 | 15 | 11 | 5 | 5 | 4 | 4 | 3 | 8 |

××××× : dominating ××× : abundant
×××× : very abundant ×× : regular × : rare to exceptional

**TABLE 3 — Chemical constitution**

| | *Kations* (mg/l) | | | | | | |
|---|---|---|---|---|---|---|---|
| | $Ca^{++}$ | $Mg^{++}$ | $Na^{+}$ | $K^{+}$ | $Fe_{tot}$ | $Mn_{tot}$ | $NH_4^{+}$ |
| Gates Pool . . . . . . . | 92,7 | 8,8 | 22,05 | 15,60 | U | T | 0,640 |
| Pool 1 . . . . . . . . | 102,3 | 11,2 | 18,17 | 8,19 | T | T | 0,320 |
| Pool 2 . . . . . . . . | | 12,4 | 25,53 | 4,99 | T | T | 0,640 |
| Pool 3 . . . . . . . | 64,1 | 11.7 | 9,20 | 4,48 | U | U | 0,100 |
| Hole 8 . . . . . . . . | 40,0 | 2,8 | 9,89 | 9,55 | 4,20 | T | 2,100 |
| Hole 1 . . . . . . . . | 118,4 | 16,1 | 16,33 | 1,64 | 2,20 | T | 0,600 |
| Hole 2 . . . . . . . . | 115,2 | 16,1 | 17,48 | 0,95 | 1,60 | T | 0,760 |
| Hole 3 . . . . . . . . | 112,0 | 16,2 | | 1,64 | 1,60 | T | 0,540 |
| Hole 4 . . . . . . . . | 99,0 | 4,6 | 17,48 | 1,31 | 3,00 | T | 0,520 |
| Hole 5 . . . . . . . . | 99,0 | 8,8 | 17,48 | 1,30 | 1,40 | T | 0,460 |
| Hole 6 . . . . . . . . | 99,0 | 8,8 | 17,48 | 1,30 | 0,80 | T | 0,440 |
| Hole 7 . . . . . . . . | 99,2 | 18,2 | 17,25 | 1,38 | 0,60 | T | 0,380 |
| Hole 10 . . . . . . . . | 122,7 | 11,7 | 5,29 | 1,13 | 1,70 | T | 0,300 |

| | *Anions* (mg/l) | | | | | | | | pH | $^{16}$18°C | *C org.* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $Cl^{-}$ | $SO_4^{--}$ | $PO_4^{---}$ ortho | $PO_4^{---}$ react | $NO_3^{-}$ | $NO_2^{-}$ | $SiO_2$ | $HCO_3^{-}$ | | | |
| Gates Pool . . . . . . | 30,60 | 59,52 | 0,220 | 0,320 | 1,500 | 0,028 | 10,0 | 180,4 | 7,65 | 396,5 | 7,0 |
| Pool 1 . . . . . . . | 27,70 | 58,08 | 0,025 | 0,240 | | 0,014 | 24,0 | 313,2 | 7,50 | 555,0 | 9,0 |
| Pool 2 . . . . . . . | 33,50 | 81,60 | T | 0,220 | 2,850 | 0,023 | 28,0 | 336,0 | 7,65 | 654,2 | 7,8 |
| Pool 3 . . . . . . . | 31,04 | 61,04 | 0,010 | 0,030 | 0,100 | 0,004 | 1,5 | 163,3 | | 373,6 | — |
| Hole 8 . . . . . . . | 22,00 | 31,70 | 0,030 | 0,060 | 0,850 | 0,021 | 15,0 | 55,0 | 6,95 | 298,9 | — |
| Hole 1 . . . . . . . | 26,98 | 66,24 | 0,015 | 0,100 | 0,350 | 0,018 | 28,0 | 366,0 | 7,25 | 572,5 | 8,2 |
| Hole 2 . . . . . . . | 28,20 | 63,36 | 0,030 | 0,040 | 0,380 | 0,011 | 28,0 | 376,2 | 7,35 | 618,5 | 7,7 |
| Hole 3 . . . . . . . | 24,85 | 44,18 | 0,020 | 0,100 | 0,175 | 0,004 | 24,0 | 384,6 | 7,35 | 610,6 | 7,7 |
| Hole 4 . . . . . . . | 23,40 | 37,60 | 0,015 | 0,400 | 0,140 | 0,003 | 28,0 | 382,8 | 7,35 | 589,7 | 7,1 |
| Hole 5 . . . . . . . | 21,30 | 43,70 | T | 0,200 | 0,135 | 0,002 | 24,0 | 351,6 | 7,40 | 589,7 | 6,5 |
| Hole 6 . . . . . . . | 21,30 | 59,60 | T | 0,120 | 0,140 | 0,003 | 24,0 | 372,0 | 7,45 | 589,7 | 7,3 |
| Hole 7 . . . . . . . | 31,95 | 31,95 | — | 1,800 | 0,145 | 0,002 | 28,0 | 367,2 | 7,45 | 572,5 | 14,1 |
| Hole 10 . . . . . . . | 18,40 | 61,04 | 0,010 | 0,030 | 0,250 | 0,016 | 20,0 | 366,0 | 7,35 | 578,6 | — |

A few previous attempts by SCHOFFENIELS (1951) and FISCHER (1959) in this direction should be noted here.

Chemical analysis of all ponds were made in winter (Feb. 1967), as it could be supposed that biochemical circadian rhythms would then be at minimum. Results are presented in Table 3. Occasional other determinations are referred to in the text.

*Remarks.*

1) pH is in all cases near to neutrality. As winter pH values may be supposed to agree closely with the true pH of the waters (i.e. unaffected by summer photosynthesis), it appears that no free strong acids or bases of inorganic nature are present.

2) Conductivity (a measure of total ionic content) shows important fluctuations in the different groups of ponds. Obviously, conductivity is largely determined by the bicarbonate ion. This is high in all ponds situated in the swampy area, but remarkably low in $P_3$ (on the diluvium) and $H_8$ (on the alluvium). As to the Gates Pool, situated on both, we have shown (DUMONT, 1968) that summer primary production greatly decreases the alkali reserve of the surface layers by photosynthesis.

3) Micronutrients (all forms of nitrogen, phosphorus, also including organic carbon) in all cases present abundant supplies. This is good proof of the *potentiel* capacity of all waters to support complicated food webs and important stocks of a variety of plants and animals.

4) $Cl^-$, $SO_4^{--}$ and $Mg^{++}$-content show no striking trends ; $Ca^{++}$ tends to vary in the same sense as $HCO_3^-$, a result that could have been predicted, as it is reasonable that $Ca^{++}$-ions should match the $HCO_3^-$-ions to a major extent.

5) The behaviour of the alkali metals, Iron and Calcium is rather peculiar. First, stress lays on the fact that it is impossible for any form of ionic iron to go into solution at the pH-values encountered. It must necessarily be in some organic or « complexed » form, and it is more than probable that some humic material is responsible for this (vide OBENAUS, 1963), especially in winter. In the Gates Pool, iron has never been detected as it will necessarily always be transferred to the hypolimnion. In the three pools, no



iron is detectable in summer. The same goes for $H_8$ and in $H_5$-$H_6$ this element is reduced to « traces » in the hot season. It is conceivable that all kations get more or less adsorbed on the humic acid-ferri-ion complex, a statement that can easily be verified from table 3.

The phenomenon is best illustrated by the alkali metals, behaving very similarly in $H_{1-7}$ (note the extreme low potassium levels). In $H_8$, it is the calcium level that seems to be most affected, indicating that maybe some different types of humic acids may be at work in the alluvial and the swamp areas.

The chemistry behind all this is no doubt complex and shall not concern us here in detail. The point is that strong interactions between the « chemical » level and the « biological » level occur. The disappearance of iron from solution in $B_{5-7}$ and to a lesser extent in the other bomb holes and most strikingly in some rivulets around these holes is always accompanied by the flocculation of a dark brown gel containing much trivalent iron-hydroxyde.

This is the well-known phenomenon of rupture of the humic-acid-iron complex by high oxygen levels.

Some oxygen determinations have shown low levels in the bomb-holes in winter and higher levels in the pools. In summer, the oxygen level in $H_{1-4}$ doubles, but it triples in $B_{5-6}$ and reaches saturation and even some supersaturation levels in all the pools. The surface levels in the Gates-pool where heavy blooms of blue-green algae occur, may be very strongly supersaturated and show a distinct diurnal rhythm.

Some winter oxygen levels are shown in table 4 (determinations of 22.XII.66).

**Table 4**

| *Code* | *Oxygen (mg/l)* |
|---|---|
| $H_1$ | 0,8 |
| $H_2$ | 0,4 |
| $H_3$ | 0,8 |
| $H_4$ | 0,8 |
| $H_{5-6}$ | 1,6 |
| $H_7$ | 2,0 |
| $P_1$ | 4,8 |

The amount of iron found is inversely corellated with oxygen levels. As oxygen levels in turn are largely determined by the biological activity of plants and before all phytoplankton and this again by the amount of light energy reaching the surface, it is clear that all pools may be classified after their ability to convert potential productivity (which is, as we have argued, rather high in all cases) to actual production.

On such a scale and regarding the degree of shading as an indicator of light energy levels, $H_{1-4}$ would be at the bottom and the large pools on top, an indication that number of dragonfly species inhabiting pools in our environment first of all depends on the primary production of their waters.

For all pools and ponds, the summer midday shading is as follows (on an arbitrary scale with 10 = fully shaded and 0 = fully unshaded).

Gates : 0 ; Pool 1 : 1 ; Pool 2 : 0 ; Pool 3 : 0 ; Hole 8 : 0 ; Hole 1 : 8 ; Hole 2 : 8 ; Hole 3 : 10 ; Hole 4 : 10 ; Hole 5 : 4 ; Hole 6 : 3 ; Hole 7 : 4 ; Hole 10 : 10.

Similarly, FISCHER (1961), in an attempt to classify some Mazurian moraine district pools after their physical features (dimensions, vegetation, water level flux) with reference to their Odonate fauna, found a number of heavily shaded forest-pools to be completely devoid of dragonfly larvae. It is conceivable that in such a bog pools reducing circumstances may have led to high levels of humic materials in suspension, creating such an unfavourable conditions that animal life was destroyed by asphyxy.

## 5. Food stocks for the dragonfly larvae.

Dragonfly larvae being predators, food supplies should be adequate and sufficient to permit them to grow.

As the first instars of both Zygoptera and Anisoptera prey upon zooplankton, and as the larger crustacea entomostraca may be considered one of the chief food sources of Zygopteran larvae throughout (demonstated by MACAN, 1964), this community should be tested on its presence and stock.

Anisopterous larvae and late Zygopteran instars eat other insect larvae, insects and fish larvae. The burrowers probably feed on aquatic oligochaeta and a variety of other benthonic animals.

A survey of possible food sources is compiled in Table 5.

**TABLE 5 — Food sources**

| FOOD SOURCE | *GATES* | | $P_1$ | | $P_2$ | | $P_3$ | | $H_6$ - $H_5$ | | $H_7$ | | $H_1$ - $H_4$ | | $H_{10}$ | | $H_8$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | Stock | N | Stock | N | Stock | N | Stock | N | Stock | N | Stock | N | Stock | N | Stock | N | Stock |
| 1. *Crustacea* | | | | | | | | | | | | | | | | | | |
| Cyclopids | 18 | H | 12 | H | 17 | H | 17 | H | 14 | H | 11 | H | 5 | M | 3 | M | 8 | H |
| Harpacticoida | 2 | M | 3 | M | 4 | M | 4 | M | 4 | M | 3 | M | 4 | L | 1 | M | 4 | M |
| Cladocera | 26 | H | 22 | H | 25 | H | 23 | H | 21 | H | 16 | H | 1 | M | 2 | M | 10 | H |
| Ostracoda | 6 | M | 5 | M | 5 | M | 6 | M | 6 | H | 6 | H | 6 | M | 2 | M | 5 | M |
| Asellids | 1 | M | 1 | M | 1 | H | 1 | M | 1 | H | 1 | H | 1 | M | 1 | M | 1 | M |
| 2. *Insecta* | | | | | | | | | | | | | | | | | | |
| Chironomids | M | M | M | M | M | M | M | M | H | H | M | M | M | M | L | L | M | M |
| Ephemerids | 1 | L | 2 | M | 2 | M | 2 | M | 2 | M | 1 | M | 0 | 0 | 0 | 0 | 2 | H |
| Hemiptera | M | M | H | H | H | H | H | H | H | H | M | M | M | M | L | L | M | M |
| Trichoptera | M | M | H | H | H | H | H | H | H | H | M | M | 0 | 0 | 0 | 0 | M | M |
| | M | M | H | H | H | H | H | H | H | H | M | H | M | M | L | L | H | M |
| 3. *Chelicerata* | | | | | | | | | | | | | | | | | | |
| Hydracarina | H | M | H | H | H | H | H | H | H | H | M | M | L | L | 0 | 0 | M | M |
| 4. *Oligochaeta* | 5 | H | 3 | M | 5 | H | 5 | H | 5 | M | 5 | M | 5 | M | 2 | L | 5 | M |
| 5. *Hirudinea* | L | L | M | M | H | H | H | H | H | L | M | M | M | M | L | L | M | M |

N : Approximate number of species. M : Moderate.
L : Low. H : High.

It is of course a crude approximation and so only a rough guide to the trophic levels of the ponds, as all quantitative indications were derived from net-catches. With respect to the dragonfly larvae, some elements may as well be prey as predator, dependent among other things on the time lag between life-cycles. So, the idea is only to estimate whether both young and adult dragonfly larvae can virtually get enough to eat. Evidently, some among them will be eaten themselves. A tentative conclusion from table 5 could be that in all ponds supporting « many » dragonfly species, there is a very diversified plankton, micro-nekton and benthos community, suggesting a complex food web having niches available for different types of Odonate larvae.

The $H_{1-4}$ environments conversely have a poor fauna and low standing crop. $H_8$ again takes an intermediate position. This implicates that any verdict from water-chemistry considerations does not necessarily apply directly to Odonate larvae. It would indeed be sufficient for a chemical factor to be distributive at the basis of the food pyramid to have repercutions on all higher levels, and that is probably what happens.

As we shall try to point out, only the oxygen factor might be directly distributive on all levels though in our area there is no good proof of its limiting action, a variety of other factors strongly interfering with it (see sub 7).

## 6. **Physical features.**

Corbet (162) has commented at some length upon the importance of a set of physical features on habitat selection in adult dragonflies. His conclusions embrace several aspects that may be relevant to the case under study. It is argued that habitat selection in some species is determined by the surface of open water available and the case of Mwalukwa, Dam, Tanganyika is presented, where a remarkable internal distribution was noted. Small-pool breeders gathered along the western drying-up river bed ; some eurytopic species had a tendency to occur everywhere but more commonly along the irregular sandy margins ; riverine and lacustrine species were confined to the straight dam wall.

So, both surface and circumference seem to have an attractive or inhibiting influence on some species. Both criteria can moreover



very well be evaluated by imago's who are visually well-equipped for this purpose. Corbet (1962) further lists some additional sensory means by which they can confirm or reject this visual verdict.

We have listed hereafter all ponds and pools, arranged in order of decreasing surface. Circumference was estimated too.

| *Name of Pool* | *Surface* ($m^2$) | *Circumference* ($m$) |
|---|---|---|
| Gates | 200.000 | 2.000 |
| $P_2$ | 3.000 | 380 |
| $P_1$ | 2.300 | 300 |
| $P_3$ | 2.000 | 260 |
| $B_{5-6}$ | 725 | 112 |
| $B_1$ | 280 | 59 |
| $B_7$ | 228 | 54 |
| $B_3$ | 211 | 51 |
| $B_{10}$ | 204 | 49 |
| $B_2$ | 194 | 49 |
| $B_4$ | 191 | 49 |
| $B_8$ | 70 | 29 |

Again, there is good qualitative corellation between both circumference and surface and number of species encountered, which increases the degree of overlap with previous parameters still further. Hower, it should be borne in mind that this criterium may again not offer a direct clue.

Only in the case of the large Aeschnids (*Anax imperator, Aeschna grandis, Aeschna mixta*) one could defend the standpoint that large surfaces are needed to provide « elbow room » for powerfull flyers. Importantly, these three species were among the first colonizers of the large and open fishponds created in replacement of $H_1$-$H_2$. *Aeschna cyanea,* though sometimes seen here, never selected this site as a hunting or mating territory. Further, a teleological interpretation is possible in the case of *Orthetrum cancellatum.* This species, hunting along straight shores with stony or sandy soils nearby, was restricted to the large pools, and before all the Gates pond. It invaded the newly impounded fishponds from the first year on and very commonly.

### 7. Biological phenomena.

Apparantly no single of the foregoing parameters alone offers a satisfactory explanation for the type of distribution met with. An additional fruitfull approach is in the interrelations between species and in their biological specializations themselves.

So, *Lestes viridis* occurs in all places were willows grow near water, regardless from all other features of the pool, an implication of its particular oviposition habits.

But if, as we have stressed before, the whole area may favour immigration to a high degree, it is justified to think of competition between « settled » species and « newcomers » as an important distributive agent.

Several phenomena have been observed in the course of the twelve years that point into that direction.

1) the case of *Coenagrion pulchellum* : first observed in 1960 on $P_1$, in small numbers. Since greatly expanded and also invading $P_2$ and $P_3$. Simultaneously, *Coenagrion puella* decreased in numbers, especially on $P_1$ where *pulchellum* is extremely abundant in may and june. Now, only isolated specimens of *puella* are found on $P_1$ in July and August. It is conceivable that *puella* was outcompeted by *pulchellum,* but the mechanism is unknown. Anyway, *puella* lost part of its areal and is now restricted to $H_{1-10}$.

The restriction of *pulchellum* to $P_{1-3}$ may be related to a need for large, or at least continuous (as in the case of canals, along which this animal is often found) productive waters, and its abscence from Gates may by due to competition with *Enallagma cyathigerum.*

2) the case of *Enallagma cyathigerum* : in 1966, this species was very abundant on Gates, indicating that it must have occured here earlier. A large stock of it has remained stationary since. One or two isolated males were seen on $P_1$ and $P_3$ every year since 1966. This invader, that may justly be termed a recent one, has driven out *C. puella* from Gates where it formerly occured in appreciable numbers. Though *pulchellum* has never been recorded on Gates, it seems reasonable to suppose also that *E. cyathigerum* has ruled out the limited population that may have existed here, or, at least, prevents any new settling attempts now.



The few specimens seen on $P_1$ and $P_3$ may indicate a tendency towards further expansion, but so far no significant colonies have been built up. Future developments are however expected and further census of the situation seems warranted.

3) The case of *Pyrrhosoma nymphula* : over the whole period of observations, there has been no indication of changes in the habitats occupied by this zygopteran. It should be noted however that its occurence on $P_1$ and $P_2$ is accidental and very few exuvia have been collected here. In practice, it is restricted to $H_{1-7}$, so, generally speaking, to the least favourable ponds.

There is overwhelming evidence that this is by no way the only type nor the most common type of waters in which *Pyrrhosoma* breeds. It has been found on clear, sometimes running waters and in standing waters with a very diversified physico-chemical spectrum, ranging from eutrophic to dystrophic (cfr. the tarn studied by MACAN, 1964).

So, in our « trap » it must have been outcompeted from all places except the bomb holes by *C. pulchellum, E. cyathigerum,* perhaps also *Platycnemis pennipes.* It co-occurs with *C. puella* and *I. elegans* only.

MACAN (1964) has shown a case in which *Pyrrhosoma* and *Enallagma* co-occured, but there was a different habitat selection in the larvae (*Pyrrhosoma* in C a r e x, *Enallagma* in M y r i o p h y l u m ) and a distinct time-lag in developmental instars.

4) The case of *Platycnemis pennipes* : though by no means exceptional, the occurence of *Platycnemis* on ponds is rather unusual. It breeds in great numbers in $P_1$, emerging a few weeks after *C. pulchellum.* It selects sunny spots in the reedlands surrounding the pond for hunting and mating and is found rarely if ever mixed up with other zygopterans except in the teneral state.

Newly emerged specimens are found along the railway track and wood's edges up to several hundreds of meters remote from the pond.

As *Platycnemis* frequently occurs on current waters of medium and low speed, it probably favours the three large ponds on account of their good aeration, and low humic acid content.

They probably cannot survive in the H-environment. As they have maintained themselves very well on the ponds during the last twelve years, they must, on the other hand, be fit enough to respond to the challenge of other zygopterans.

Yet, they have not succeeded in colonizing the Gates pond, though this would seem to be another acceptable site for them. Maybe the lack of reedlands around this pond offers a sufficient explanation, and it is still possible that *Platycnemis* has never actually discovered this rather « new » biotope. The whole population may indeed have originated from one accidentilly « imported » female (by a train or so) and has not yet succeeded in covering the distance (ca. 2 km) that separates it from Gates.

Anyway, future developments with regard to a possible expansion of *Enallagma* and its implications have to be awaited here too.

5) The case of *Erythromma naias* : found on all large pools, in the sublittoral zone of floating macrophytes. Is missing on the extremely small $H_6$ and on $H_{1-4}$ and $H_7$. Yet, it quickly invaded the newly impounded fishpools. Being a very territorial species, it is conceivable that physical factors predominate its habitat selection, and that the H-environment is actively avoided. Indeed, tenerals occur over the whole area. It is noteworhty that *Erythromna* occurs till end august, i.e. its life span is rather long here. This is probably the reason why *E. viridulum* is absent, as both species normally show a different incidence period, with *E. naias* coming first and being relayed by *E. viridulum* end July. This succession was found on a lake some 20 km. north of Denderleeuw (Lake Donk). It is not clear what factor permits *E. naias* to lengthen its life span in the former and not in the latter biotope.

6) The case of *Coenagrion lindeni* : normally restricted to pure waters, rich in oxygen, this species is frequently found on or near running waters. On evidence of this distributive factor alone, it could be predicted that *C. lindeni* would occur in the most productive waters only, i.e. on the large pools.

Colonies are never large but apparently in steady state on all four pools where they occur.

In Gates, they occupy a zone between *Erythromma* (sub-pelagial) and *Ischnura* (littoral), selecting floating reed stems as settling places. Territoriality is not very pronounced. On Gates alone, *lindeni* is mixed with *Enallagma,* and though no physical interference between both has been recorded, some competition might nevertheless exist.



On $P_{1-3}$, *C. lindeni* occupies the sub-pelagial, while *E. naias* dominates the pelagial.

7) The case of *Ischnura elegans* : this is no doubt the most successfull of all dragonfly species in the biotope. It was found to occur and reproduce on all pools examined, but enormous stocks of it exist on the three large pools and Gates only. There are normally two generations per year, with a certain degree of overlap.

The zone occupied is before all the *C a r e x-girdle,* where at night thousands of *Ischnura* gather, sometimes occupying all stems available. They also frequently dwell among reedlands and in meadows.

8) The case of *Lestes sponsa* : so far, only very few males were recorded on $P_1$ and $B_{5-6}$. They probably also occur on the Gates pool, but in so small numbers that they have escaped our attention till now.

*Lestes sponsa* is the most recent appearance in the biotope, and has been seen to suffer severe competition from *Lestes viridis.* Whenever a *sponsa* tries to approach the water, it is severely attacked by *Lestes viridis* males who invariably succeed in driving it away. This does not mean that *sponsa* will not manage to conquer a habitat ultimately, because probably both species' niches are not identical. Yet, some degree of overlap appears to exist and *viridis* may be expected to loose part of its prerogatives if *sponsa* ever gets firmly implanted.

9) The case of *Libellula depressa* : the predilection of *depressa* for small, open standing waters is widely recognized. In our biotope, it was exclusive of the small $H_6$ so far, and with the destruction of this pool (1966), *Libellula depressa* apparently co-disappeared. I would however like to attract the attention upon the peculiar chemical nature of $H_6$, having a remarkably low total ionic content. If this might be of any distributive value, the only pool where one might expect to re-discover *depressa* would be $P_3$, the ionic spectrum of which is rather closely related to that of $H_6$.

10) The presence of *L. quadrimaculata,* an ubiquist, merits no special attention, while *Orthetrum cancellatum* has been commented before. *Brachytron pratense,* though appearing every year, is too rare to warrant any discussion. One Aeschnid, *A.cyanea* seems to select the H-environment specifically, though it was occa-

sionnally seen on the P-environment (including some larvae and exuviae). This may be related to the hunting habits of *cyanea*, that never actually selects territories in the pelagial. It is a well-known dweller that one may virtually encounter everywhere, frequently far from water. Hunting territories and oviposition sites are always marginal. When *cyanea* and *grandis* were seen co-occuring as on $B_{5-6}$, *grandis* always occupied the pelagial and *cyanea* covered the C a r e x-zone.

The larva however should be physiologically well-equipped to live in poorly oxygenated, humic waters. Perhaps the chemical nature of water is first tested by the female dipping her antennae, provided with olfactory sense organs (STEINER, 1948) into it.

11) Five species of *Sympetrum* co-occur, greatly in the zone around $H_{1-7}$, including the surrounding marshes and grasslands. In the course of time, important fluctuations in their respective populations have been recorded.

*Sympetrum danae,* during the first five years of observations, occured in isolated specimens only, increasing greatly in numbers in subsequent years to constitute about half of the *Sympetrum* stock in 1964-65. Afterwards, a decrease occured, so that in 1969 *danae,* though still being common, was no longer the dominating species.

*S. sanguineum* was low throughout the first 8 years of observations, increasing steadily afterwards to become the dominating species in 1969.

*S. vulgatum* is probably the only species that remained stationary over the whole period, never being abundant but always common.

*S. flaveolum* shows a very peculiar incidence cercle. It was rather common during the summers of '58 and '59, though it was never seen ovipositing on any other pool than $H_7$. Rather strangely, $H_7$ was drying up fastly at that time, owing to long periods of drought. It lost approximately 2/3 of its bed. Oviposition took place over dry weed beds exclusively. Followed a complete disappearance of *flaveolum* for a period of 9 years, but it suddenly reappeared in appreciable number during summer 1969, hunting over some marshy meadows near $H_7$. Oviposition was not observed, but many females were present, so it is certain that mating took place. Remarkably, there was again an appreciable water-loss in august 69, though by no way as critical as 10 years before.



With reference to STEINER's (1948) report on the chemoreceptors on the antennae of *flaveolum,* it may be of interest to note that the decaying weed beds spread a strong and specific smell.

Finally, there is a curious antagonism in the appearances of *flaveolum* and *striolatum*. Numbers of the latter were always high when the former was absent and vice versa. In 1969, only a single male *striolatum* was captured, near $F_3$, i.e. there was a distinct separation in space between it and the *flaveolum* population.

*Sympetrum*-populations on other pools than the H-series were always low to exceptional, so that some degree of preference for humic waters may be acceptable. This agrees well with the fact that most *Sympetrum* species tend to be the dominating dragonfly fraction of moor environments where humic materials abound.

## Conclusive discussion

Apart from a few very exceptional observations, all species inhabiting the « trap triangle » discussed, appear to be species normally inhabiting standing waters. Yet, an attempt to throw some light upon the causality of their internal distribution shows that there is no parameter that can alone account for all the variation encountered.

Crudely speaking, two kinds of chemical environments are involved : productive ones, showing a very diversified fauna, and not-productive ones, showing a much poorer fauna. Production (i.e. basically phytoplankton photosynthesis and production of oxygen) is here however governed up to a high degree by physical factors, chemicals factors not being limiting. It so was sufficient to remove trees and enlarge some bomb holes to provoke subite immigration of several species typical of productive ponds.

The group favouring non-productive, humic pools consists of the *Sympetrums* and *Aeschna cyanea,* though they are by no means exclusive of them. The group favouring productive environments, regardless of their size, is difficult to evaluate, as both criteria go generally combined. Yet, *Platycnemis pennipes and Coenagrion lindeni* may almost certainly be included. *Coenagrion pulchellum* is a more doubtfull case, while *C. puella* and *Pyrrhosoma nymphula* are probably refuted into their actual breeding sites by interspecific competition.

A peculiar case is offered by *L. depressa,* having a very restricted habitat selection, but more information is needed from other breeding sites before anything definite can be said about it. The group needing a large pelagial consists of *Anax* and all *Aeschna*'s except *cyanea,* while *O. cancellatum* needs straight, rather long shore lines with appropriate perching possibilities.

*Erythromma* selects a medium sized to large pelagial, and *Enallagma* cannot be validly discussed as long as one may suppose that it is still expanding. It certainly is a strong competitor to most other zygopterans, and it is not excluded that it will rule out some among them in the future.

In general, it appears that when congeneric forms (or forms with similar specializations) co-occur, there is always some indication that competition acts as a strong distributive agent.

The group of ubiquists of two species only : the omnivalent *Ischnura elegans,* that is however most successfull in productive environments and *Libellula quadrimaculata.*

The distribution of *L. viridis,* within the range of biotopes covered, is entirely governed by oviposition possibilities, while the success or failiure of *Lestes sponsa's* immigration attempt is still to be awaited.

Finally, from a faunistic point of view, attention should be focused upon the fact that the spacially limited biotope has acquired in about half a century a rather rich dragonfly fauna, where before that time it was probably very poor.

The artificial « mouse trap » has even retained two species that are very rare in Belgium (*Crocothemis erythraea* and *Aeschna affinis*) for some time. It may thus be expected that the list given is by no means a complete one, as from time to time new immigrants will appear, while other species, now still present, may disappear through competition.

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*Note on* 1970.

The prediction on *L. depressa* has been confirmed : it was found in May and June, on P3 but also on P2. Further, a new record on *Cordulia aenea* was made (15.VI.1970, P2). Also *Sympetrum flaveolum* was abundant again, rot only near H7 but also in a swampy area on the right bank of the River Dender, exactly opposite H1-H7.