Odonatologica 25(1): 49-58 *March 1, 1996*

DETERMINANTS OF ADULT DRAGONFLY ASSEMBLAGE PATTERNS AT NEW PONDS IN SOUTH AFRICA

R. OSBORN and M.J. SAMWAYS
Invertebrate Conservation Research Centre, Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa

Received February 27, 1995 / Reviewed and Accepted June 8, 1995

Adult Odonata species assemblage patterns were studied at 8 ponds near Pietermaritzburg, South Africa. Different ponds had different assemblages. Strong inferential evidence from multivariate analysis and correlation suggested that the main determinants of assemblage patterns were certain biotic and abiotic environmental variables. In other words, assembly 'rules' may be governed more by factors external to the taxon than by interspecific competition. Larger ponds were not necessarily richer in species than smaller ponds because factors such as water quality, vegetation type and microsite diversity overrode biotope size. Species richness was greatest at shallow, well-vegetated ponds with clear, oxygenated water. Such ponds provide suitable conditions for both larvae and adults. Sunlight/shade and marginal/submerged vegetation gradients were the main drivers of assembly patterns at the ponds. Species assemblage patterns were determined by several variables acting together. In turn, the assemblage patterns at each pond were influenced by different variables representing different ecological successional stages.

INTRODUCTION

Differences in proportionate species abundances are the result of various types of abiotic and biotic influence (DRAKE, 1990). Different species compositions and relative abundances can arise depending on the species assembly mechanics in operation at a site. For example, inter-pond variation in invertebrate assemblages may be due to competition and species dispersal or to biotope factors at a pond. These factors may in turn influence the establishment and survival of the colonists (FRIDAY, 1987). The sequence of species invasion may also result in different assemblage patterns (DRAKE, 1991). Early colonists may influence the establishment of later colonists by outcompeting them (ROBINSON & DICKERSON, 1987), and by influencing the biotope (BARNES, 1983). Early colonization however, may not necessarily guarantee successful establishment of a species, because resource use, competitive interactions and biotope suitability may also play roles.

Adult dragonflies are sensitive responders to newly-created physical conditions of both the bank and the water (CLARK, 1991). However, there is no guarantee which particular species will establish. Rather, the physical and physiognomic conditions determine which species arrive and stay (STEYTLER & SAMWAYS, 1995). Following on from this, it would be interesting to know whether there are assembly rules governing the species profile at a particular pond, i.e. whether the presence of certain species can dictate which other species may or may not establish. This paper is an investigation into whether or not there are assembly rules governing species proportions of adult Odonata at ponds. It makes no assumptions about the larvae which may or may not influence the adult rules.

MATERIAL AND METHODS

Eight ponds were selected in the vicinity of Pietermaritzburg (latitude 29°36'S and longitude 39°19'E), in Kwazulu-Natal, South Africa. Sites were at the Pietermaritzburg Golf course (altitude 640 m a.s.l.), Darville Purification Works (640 m a.s.l.), Bisley Valley Nature Reserve (650 m a.s.l.), Bird Sanctuary (650 m a.s.l.), Botanic Gardens (690 m a.s.l.), Queen Elizabeth Park (800 m a.s.l.) (two ponds), and Airton's dam (1100 m a.s.l.).

Sites were sampled on hot, sunny days between 11h00 and 13h00, when Odonata were most active (CORBET, 1962). Only adult males were considered as they are easy to recognise on the wing and they show strong biotope fidelity. The one exception was *Trithemis dorsalis* and *T. furva*, which owing to their similarity, had to be grouped as one.

Ten quadrats of 20m x 2m were measured out at each site. Males flying into or landing within, a quadrat during 15 min were recorded as present. Intraspecific and interspecific encounters were also noted in each quadrat. Abundance data were obtained from 5 December 1991 to 17 February 1992.

Environmental variables were measured at ponds during February 1992. The variables measured pertain to the larvae as well as the adults to see if adults select conditions suitable for their future larvae. Percentage cover by rocks, soil or vegetation was estimated. The percentage sun and shade at 12h00 was also recorded. Water temperature was measured with a CLIMA Hygro-Thermometer and dissolved oxygen using a 3405-Electrochemistry Analyzer. Turbidity was measured with a Secchi disc, and pH was determined with a standard pH kit. Ten readings were taken at 13h00 at each pond. Average depth, area of pond, water movement, and biotope complexity was assessed for each pond. Biotope complexity was determined by recording how many species of plants were present. Water movement was recorded as fast-flowing, slow-flowing, or still.

STATISTICAL ANALYSIS. – Data were analyzed using TWINSPAN (Two Way Indicator Species Analysis) (HILL, 1979a), DECORANA (Detrended Correspondence Analysis) (HILL, 1979b) and CANOCO (Canonical Correspondence Analysis) (TER BRAAK, 1988). Both TWINSPAN and DECORANA are indirect gradient analysis multivariate techniques, where a pattern of sites and species is produced and then interpreted in a second step. CANOCO, by comparison, combines species abundance data and environmental variables such that any relation between the two can be detected in one step (TER BRAAK, 1986).

GENERAL PATTERNS OF SPECIES RICHNESS

A total of 37 species were recorded, 14 Zygoptera and 23 Anisoptera, viz. Synlestidae: *Chlorolestes tessellatus* (Burm.); – Lestidae: *Lestes plagiatus*

(Burm.); – P r o t o n e u r i d a e: *Allocnemis leucosticta* (Selys); – C o e n a-g r i o n i d a e: *Ceriagrion glabrum* (Burm.), *Pseudagrion hageni* Karsch, *P. kersteni* (Gerst.), *P. massaicum* Sjöst., *P. salisburyense* Ris, *Enallagma glaucum* (Burm.), *Agriocnemis falcifera* Pinhey; – C h l o r o c y p h i d a e: *Platycypha caligata* (Selys); – G o m p h i d a e: *Ceratogomphus pictus* Hagen; – A e s h n i d a e: *Anax imperator mauricianus* Ramb., *A. speratus* Hagen, *A. tristis* Hagen; – L i b e l l u-l i d a e: *Notiothemis jonesi* Ris, *Orthetrum caffrum* (Burm.), *O. chrysostigma* (Burm.), *O. julia falsum* Longfield, *Nesciothemis farinosa* (Förster), *Palpopleura lucia* (Drury), *Crocothemis erythraea* (Brullé), *Brachythemis leucosticta* (Burm.), *Sympetrum fonscolombei* (Selys), *Trithemis arteriosa* (Burm.), *T. dorsalis* (Ramb.), *T. furva* Karsch, *T. kirbyi ardens* Gerst., *T. stictica* (Burm.), *Pantala flavescens* (Fab.), *Tramea burmeisteri* Kirby, and *Urothemis edwardsi* (Selys).

Some species such as *Crocothemis erythraea* and *Trithemis arteriosa* were present at six of the eight sites, whereas others, e.g. *Aeshna minuscula, Anax tristis* and *T. kirbyi ardens*, occurred at only one site. Species richness increased with increasing dissolved oxygen and clarity of water. Ponds with increasing biotope complexity, heterogeneity and proportion of rocks were rich in species. The optimal pH of water for most species was 6.8. Darville, the most species poor pond, had the lowest percentage dissolved oxygen (14.8%), highest water temperature (37.2°C) and was very turbid and acidic (pH = 5.5). This was in contrast to Airton's dam, which was rich in species and had a low water temperature (23.4°C), and was more oxygen rich (57.8%) with minimal turbidity.

DETAILED CLASSIFICATION OF SITES

The TWINSPAN analysis gave three site groups. *Tramea burmeisteri* was the indicator species for Level 1 of the division, occurring preferentially on the right side of the dichotomy at the third site group.The ponds at Queen Elizabeth Park and at Airton's dam were characteristic for the third site group of the division. *Pantala flavescens* was the indicator species for Level 2, preferring the ponds at the second site group, consisting of the Golf course, Bird Sanctuary, Bisley Valley and Botanic Gardens. Species at this site group were heliophilic and eurytopic. In contrast, the third site group had stenotopic species restricted to only a few sites.

The TWINSPAN species classification ended at Level 4, with the production of eleven species groups. Species groups one, two, three, eight, ten and eleven were associated with particular biotope types (Fig. 1). Remaining species groups were not ecologically meaningful.

Group 1 species preferred open ponds (over 85% open water), which had some marginal vegetation and grassy banks. Group 2 species were associated with large open ponds (> 8000 m^2). These species were also tolerant of a wide range of physical conditions. Temporary pool-dwellers living in arid conditions clustered together to form Group 3. Group 8 species preferred well-vegetated waters (> 75% vegetation cover). Shaded biotopes with much submerged vegetation were favoured by species making up Groups 10 and 11.

CANOCO ordination

A triplot ordination diagram (Fig. 2) was produced from the CANOCO output. Most species occurred in the upper right of the diagram, but some formed clusters in the lower left and lower right. The species pattern largely matched that of TWINSPAN and DECORANA. There was a marked vegetation gradient from submerged (lower left of the diagram) to marginal vegetation (upper right of the diagram). There was also a pronounced sun/shade gradient. *Pseudagrion hageni, Allocnemis leucosticta* and *Notiothemis jonesi* occurred closest to the percentage shade plot. Species in the top right of the diagram occurred at sunlit ponds which had much marginal vegetation. Species richness declined and stenotopic species became more common towards the lower left of the diagram along both major axes. These 'top right' species preferred shady ponds high in submerged vegetation.

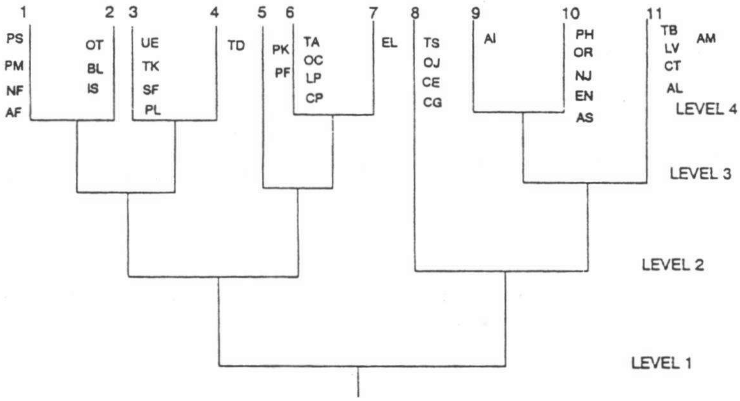

Fig. 1. TWINSPAN species classification showing biotope groups. Species abbreviations: AF = *Agriocnemis falcifera/pinheyi*; – AI = *Anax imperator mauricianus*; – AL = *Allocnemis leucosticta*; – AS = *Anax speratus*; – BL = *Brachythemis leucosticta*; – CE = *Crocothemis erythraea*; – CG = *Ceriagrion glabrum*; – CT = *Ceratogomphus pictus*; – CT = *Chlorolestes tessellatus*; – EN = *Enallagma glaucum*; – EL = *Ellatoneura glauca*; – IS = *Ischnura senegalensis*; – LP = *Lestes plagiatus*; – LV = *L. virgatus*; – NF = *Nesciothemis farinosa*; – NJ = *Notiothemis jonesi*; – OC = *Orthetrum caffrum*; – OR = *O. chrysostigma*; – OJ = *O. julia falsum*; – OT = *O. trinacria*; – PF = *Pantala flavescens*; – PL = *Palpopleura lucia*; – PH = *Pseudagrion hageni*; – PK = *P. kersteni*; – PM = *P. massaicum*; – PS = *P. salisburyense*; – SF = *Sympetrum fonscolombei*; – TB = *Tramea burmeisteri*; – TA = *Trithemis arteriosa*; – TD = *T. dorsalis*; – TF = *T. furva*; – TK = *T. kirbyi ardens*; – TS = *T. stictica*; – UE = *Urothemis edwardsi*.

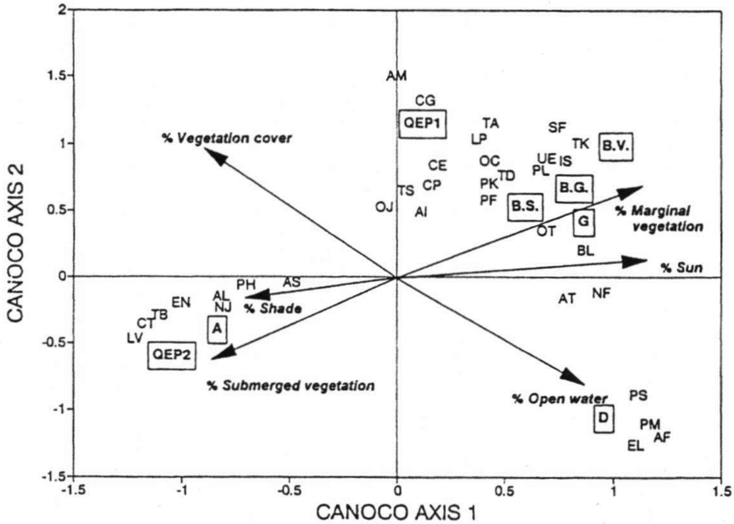

Fig. 2. CANOCO triplot ordination of sites, species and environmental variables. Species abbreviations are as for Fig. 1. – [Site abbreviations: A = Airtons' Dam; – B.G. = Botanic Gardens; – B.S. = Bird Sanctuary; – B.V. = Bisley Valley; – D = Darville; – G = Golf course; – QEP1 = Queen Elizabeth Park Pond 1; – QEP2 = Queen Elizabeth Park Pond 2].

Sites were placed along the environmental gradients that characterised them best. The Botanic Gardens, Bird Sanctuary and Golf course shared the most species. Airton's dam and Queen Elizabeth Park (lower pond) also shared many species. Darville differed from the other sites in that it had only a few species. The site groupings were similar to those produced by TWINSPAN and DECORANA.

ASSEMBLAGE CORRELATION WITH ENVIRONMENTAL VARIABLES

Inter-set correlations of environmental gradients with axes (Tab. I) showed that percentage submerged vegetation, percentage sun and percentage shade were highly correlated with axis 1. Percentage oxygen and submerged vegetation were also strongly correlated with axis 1. Percentage bare ground was mainly correlated with axis 2. Axis 1 was important in accounting for the observed species distributions (axis 1 eigenvalue = 0.838). Axes 2 and 3 were less important (eigenvalues for axis 2 = 0.575 and for axis 3 = 0.513). The environmental variables were found in some cases to be correlated. The species-environment correlation of both DECORANA and CANOCO was very strong (always greater than 0.96). The environmental variables were responsible for the main variation in species patterns (cumulative percentage variance of species data and of species-environment relation = 82.5%).

Table I
Inter-set correlation coefficients for environmental variables and ordination axes

Environmental variable	CCA axes 1	2	3	4
Temperature	715	-557	-55	-55
Oxygen	-875	236	30	-73
pH	-233	543	591	385
Turbidity	-293	194	-73	-93
% Shade	-628	-60	-51	-118
% Sun	628	60	51	118
% Rocks	-263	449	119	-254
% Bare ground	273	661	562	-202
% Vegetation cover	-505	426	-501	-308
% Open water	505	-426	501	308
% Floating vegetation	753	-583	-13	-112
% Submerged vegetation	-883	-248	166	-8
% Floating-leaved vegetation	-85	99	-400	-204
% Marginal vegetation	538	402	221	245
Average depth of water	519	-325	315	641

DISCUSSION

COLONIZATION HISTORY

Odonata species establishment at a pond depends on species dipsersal abilities and suitable physical conditions (BARNES, 1983). Successful arrival by adults at a new site does not necessarily imply successful establishment. With time, biotope conditions may no longer be suitable for the pioneer species, which then disappear. In this study, *Orthetrum julia falsum, Ceratogomphus pictus* and *T. arteriosa* were replaced by *Palpopleura lucia* and *Ischnura senegalensis* after a seasonal drop in water level at a pond.

Environmental changes over time may also cause an increase or decrease in species richness (MOORE, 1991). Anisoptera are generally more abundant at temporary ponds than are Zygoptera, because Zygoptera are less able to fly far. This was shown by the proportionately more species of Zygoptera than Anisoptera at the Botanic Gardens, which had a high and constant water level. CORBET (1962) points out that at a large spatial scale, pond size, shape, depth and vegetation cover may be important cues for potential colonists. For some species, pond shape, and the length of uninterrupted shoreline may be important cues for habitat selection. In this study, *T. arteriosa, B. leucosticta* and *O. trinacria* may have been selecting for large areas of open water. *Brachythemis leucosticta* in particular, prefers uninterrupted shores (CORBET, 1962).

POND SIZE, HETEROGENEITY AND POSITION

The Golf course and Bird Sanctuary ponds were large, but the biotope complexity and heterogeneity were low. Interestingly, species richness was also low in comparison with smaller ponds where there was more biotope heterogeneity. For example, the smaller pond at Queen Elizabeth Park was much richer in species than the larger pond at the same locality, because biotope complexity overcame the limitations imposed by a small pond. Ponds, such as the Botanic Gardens, provide complex biotopes which permit high species packing.

Territory size requirements appeared not to limit species richness at the ponds. However, species abundances may well have been affected, because it is well known that territorial clashes among rival males may result in local dispersal of species (CORBET, et al., 1960). Territory size may also be determined by density, with greater site fidelity by males, at higher densities (POETHKE, 1988).

At a larger spatial scale, ponds varied in Odonata species depending on elevation and degree of forested surroundings. Some species were limited to the ponds on the moister, forested higher elevations (e.g. *Chlorolestes tessellatus*), while others occurred only in drier savanna surrounding ponds at lower elevations (e.g. *Brachythemis leucosticta*).

ENVIRONMENTAL CUES DETERMINING ASSEMBLAGE PATTERNS

Biotope requirements of these species were important in governing the presence/absence and abundance of species along environmental gradients. Species showed preferences for certain biotope features, and assembled according to these preferences. Adult Libellulidae select suitable oviposition sites by visual assessment, and later, tactile examination of the site (WILDERMUTH, 1991, 1992). Adults react to the presence of certain types of vegetation, and to smooth surfaces, when selecting suitable oviposition sites at a site (WILDERMUTH, 1992).

The adult Odonata species here were greatly influenced by the shade/sunlight (i.e. thermal-light) conditions. Indeed, species at the Botanic Gardens' site have been shown to segregate according to thermal requirements (McGEOCH & SAMWAYS, 1991). McKINNON & MAY (1994) for instance, found that *Pachydiplax longipennis* preferred pond edges with tall vegetation and sunlight. In this study here, there were clear 'sun' and 'shade' species. *Nesciothemis farinosa* and *C. erythraea*, were never observed in the shade, whereas *N. jonesi*, and *C. tessellatus* were only found under these conditions.

Species also preferred particular substrates on which to perch. *T. kirbyi ardens* and *C. pictus* perched on rocks and bare ground, whereas *O. caffrum* and *O. chrysostigma* perched on sticks and reeds over mud, possibly because the larvae are mud-dwellers.

There are known to be other features of the biotope that are important for species establishment. For example, different-sized Zygoptera often select perches wide enough to conceal the body from predators, without impeding vision (ASKEW, 1982). Furthermore, Aeshnidae and Zygoptera select specific plants for endophytic oviposition (CORBET, 1962), and for perches (MESKIN, 1989; BUCHWALD, 1992).

Adults sometimes do not select and oviposit in ponds where conditions for the larva will be optimal, as shown by *P. flavescens*, which will oviposit in swimming pools. However, it may be that adult selection is vital for the survival of larvae that have narrow niches and/or larvae that are unable to disperse in times of adversity.

The chance of adults selecting the incorrect sites for oviposition, may depend on the nature and specificity of the cues that the species uses when selecting sites. A species that only responds to smooth surfaces, may attempt to lay in unsuitable conditions, whereas a species which uses reflective patterns of water and vegetation structure may be less likely to select unsuitable conditions for the eggs and larvae. Adults may select sites using the light patterns of reflection of the water (WILDERMUTH & SPINNER, 1991). Larval requirements are also important because of the greater longevity of this developmental stage compared with that of the adult. Large expanses of submerged vegetation provide various microsites for many weed-dwelling species, as well as their potential prey. In turn, complexity of submerged vegetation also provides concealment from their predators. In this study it appears that species richness at Airton's dam was possibly related to the highly suitable conditions for the larvae.

Nevertheless, it is still unclear, whether behavioural selection is for a biotope that is optimal for the larva or for the adult. Dissolved oxygen and temperature are important influences on larval growth rate and developments (CORBET, 1962), but it is uncertain whether the adult can detect such conditions and respond by ovipositing in the most suitable place. Warmer ponds such as Darville were too anoxic to support many species, and the adults present were mostly transient individuals, suggesting that they will generally only spend time in areas suitable for all the developmental stages. WILDERMUTH & SPINNER (1991) thought that adults are able to recognize suitable larval conditions. They thought that females are able to assess the likelihood of survival of eggs and larvae by using proximate cues such as depth, size, water current and vegetation structure of water (WILDERMUTH & SPINNER, 1991).

COMPETITION

Few agonistic interactions between species were observed. This is not to say that there was no competition or no avoidance. Nevertheless aggressive interactions among *T. arteriosa* individuals suggested that intraspecific competition for territories may be important in influencing the spatial distribution of males. The interspecific agonistic interactions observed here agree with MOORE's (1964) findings that interspecific competition among adult Odonata is relatively unimportant. In view of MOORE's (1991) findings, changes in environmental conditions over time would also influence patterns of interspecific competitive dominance. Habitat preferences of congenerics may be important in preventing aggressive interference among adults (MICHIELS & DHONDT, 1987).

ARE THERE RULES GOVERNING THIS DRAGONFLY ASSEMBLAGE?

DIAMOND's (1975) assembly rules have been extensively criticised by various authors. CONNOR & SIMBERLOFF (1979) for example, argued against claims that species distribution patterns are due mainly to competition.

In this study, which is on an assemblage rather than a community, environmental gradients, from vegetation structure to abiotic variables were the main determinants of the Odonata assemblage patterns. Species combinations at ponds were, through strong inferential evidence, the direct result of species-specific biotope preferences, rather than of competition. This is not to say that competition was not influencing the species assemblage. Cannibalism can for example, have a significant impact on abundance levels, as can predation by one Odonata species on another. In other words, there will be intra- and interspecific interactions that affect abundances of the various species. However, these interactions do not greatly influence species relative abundances, and almost certainly do not result in exclusion of a species from a pond, where other environmental conditions are optimal. In short, it appears that pond temporal succession and environmental fluxes are mostly responsible for the changing relative abundances of species.

As a general principle, species assembly is largely dependent on which species are keystone and which are not. Also, species that have increasingly similar requirements for food and space will tend to be mutually more influential. In turn, they may influence each other's abundance position in the assemblage profile, possibly irrespective of other, redundant species, or, alternatively, functionally important keystone species.

IMPLICATIONS FOR CONSERVATION

In conclusion, the results here imply that for conservation management there is little need to ascertain which species of Odonata are present and abundant, prior to colonization by, and establishment of, other species. It matters more to make sure that the biotope is suitable per se, and managed where necessary.

ACKNOWLEDGEMENTS

Financial support was provided by the Foundation for Research Development, the Gay Langmuir Fund, the University of Natal Research Fund and the Department of Environmental Affairs & Tourism.

REFERENCES

ASKEW, R.R., 1982. Resting and roosting site-selection by coenagrionid damselflies. *Adv. Odonatol.* 1: 1-8.

BARNES, L.E., 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes. *Freshw. Biol.* 13: 561-578.

BUCHWALD, R., 1992. Vegetation and dragonfly fauna - characteristics and examples of biocenological field studies. *Vegetatio* 101: 99-107.

CLARK, T.E., 1991. *Dragonflies as habitat indicators of the Sabie River in the Kruger National Park.* Unpublished M.Sc. thesis, University of Natal.
CONNOR, E.F. & D. SIMBERLOFF, 1979. The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.
CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.
CORBET, P.S., C. LONGFIELD & N.W. MOORE, 1960. *Dragonflies.* Collins, London.
DIAMOND, J.M., 1975. The assembly of species communities. *In*: M.L. Cody & J.M. Diamond [Eds]. Ecology and evolution of communities, pp. 342-344, Harvard Univ. Press, Cambridge.
DRAKE, J.A., 1990. Communities as assembled structures: do rules govern patterns? *Trends Ecol. Evol.* 5: 159-164.
DRAKE, J.A., 1991. Community assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.* 137: 1-26.
FRIDAY, L.E., 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshw. Biol.* 18: 87-104.
HILL, M.O., 1979a. *TWINSPAN - A fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell Univ., New York.
HILL, M.O., 1979b. DECORANA - *A fortran program for detrended correspondence analysis and reciprocal averaging.* Cornell Univ., New York.
McGEOCH, M.A. & M.J. SAMWAYS, 1991. Dragonflies and the thermal landscape: implications for their conservation (Anisoptera). *Odonatologica* 20: 303-320.
McKINNON, B.I. & M.L. MAY, 1994. Mating habitat choice and reproductive success of Pachydiplax longipennis (Burmeister) (Anisoptera: Libellulidae). *Adv. Odonatol.* 6: 59-77.
MESKIN, I., 1989. Aspects of territorial behaviour in three species of Pseudagrion Selys (Zygoptera: Coenagrionidae). *Odonatologica* 18: 253-261.
MICHIELS, N.K. & A.A. DHONDT, 1987. Coexistence of three Sympetrum species at Den Diel, Mol, Belgium (Anisoptera: Libellulidae). *Odonatologica* 16: 347-360.
MOORE, N.W., 1964. Intra- and interspecific competition among dragonflies (Odonata): an account of observations and field experiments on population density in Dorset, 1954-60, *J. Anim. Ecol.* 33: 49-71.
MOORE, N.W., 1991. The development of dragonfly communities and the consequences of territorial behaviour: a 27 year study on small ponds at Woodwalton Fen, Cambridgeshire, United Kingdom. *Odonatologica* 20: 203-231.
POETHKE, H.-J., 1988. Density-dependent behaviour in Aeshna cyanea (Müller) males at the mating place (Anisoptera: Aeshnidae). *Odonatologica* 17: 205-212.
ROBINSON, J.V. & J.E. DICKERSON, 1987. Does invasion sequence affect community structure? *Ecology* 68: 587-595.
STEYTLER, N.S. & M.J. SAMWAYS, 1995. Biotope selection by adult male dragonflies (Odonata) at an artificial lake providing for insect conservation in South Africa. *Biol. Conserv.* 72: 381--386.
TER BRAAK, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
TER BRAAK, C.J.F., 1988. *CANOCO-a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis (version 2.1).* Groep Landbouwwiskunde, Wageningen.
WILDERMUTH, H., 1991. Behaviour of Perithemis mooma Kirby at the oviposition site (Anisoptera: Libellulidae). *Odonatologica* 20: 471-478.
WILDERMUTH, H., 1992. Visual and tactile stimuli in choice of oviposition substrates by the dragonfly Perithemis mooma Kirby (Anisoptera: Libellulidae). *Odonatologica* 21: 309-321.
WILDERMUTH, H. & W. SPINNER, 1991. Visual cues in oviposition site selection by Somatochlora arctica (Zetterstedt) (Anisoptera: Corduliidae). *Odonatologica* 20: 357-367.