INTRODUCTION

Conservation of dragonflies has become increasingly important in recent years (ASAHIYa, 1974; DUMONT, 1971; MOORE, 1976, 1982; SCHMIDT, 1977; VAN TOL & VERDONK, 1988; TYAGI, 1985; WILDERMUTH, 1994a). Reserves are now being set aside specifically for them (MOORE, 1987; SUGIMURA, 1989). In South Africa, there has been considerable inadvertent dragonfly conservation through the construction of farm dams which have provided more extensive suitable biotopes for otherwise more localized species (SAMWAYS, 1989), and the creation of reserves is now underway (STEYTLER & SAMWAYS, 1995). These artificial dams vary considerably in their dragonfly assemblage patterns, depend-
ing on the vegetational and physical conditions. Determination of the influence of such conditions is important in the design of ponds for conservation (WILDER-MUTH, 1994b). This is particularly so in South Africa, where water holes are constructed for large vertebrates, and could be modified to accommodate specific dragonflies.

The aim here was to determine biotope preferences of dragonflies in a species-specific assemblage associated with a wide range of biotopes at one point location. Such a single site avoided the risk of major changes in water quality that might otherwise occur from one locality to another. Also, as the distances between biotopes were well within the flying capability of the species involved, a clear picture of biotope fidelity was likely to emerge. These biotope preferences are then used to make conservation recommendations.

SITE AND METHODS

The site was Airtons’ dam, Hilton, near Pietermaritzburg, KwaZulu Natal, South Africa (30°17'E, 29°34'S, 1050 m a.s.l.). The centre of the site was a small pond, variably about 400 m³, formed from the damming of a small stream with a concrete wall. Above the pond, the stream ran through forest and then meandered through rank grass and sedges, and formed a small riffle before entering the pond. Below the wall, the stream flowed over and between vegetated and unvegetated rocks.

The site was partitioned into four biotope subsites, A = stream (below wall), B = pond (above wall), C = stream in rank grass (above wall), D = stream in forest (above wall). A sinuous transect followed the edge of the pond and the stream above and below the dam. The transect at each of the four biotopes was divided into eight 2 m-long segments (microhabitats or sample units [SUs]) along the water’s edge. The SU quadrat was 2 m either side of this 2 m long segment, making the area of each sample unit 8 m², and 32 SUs in total.

All mature male Odonata were recorded in these quadrats. Females and teneral males were not included as they were generally difficult to recognize on the wing, and were not consistently associated with the water. All species, including the large cruising ones, were only recorded once at one sample unit on any one sample day.

After a preliminary trial period, formal recording ran approximately fortnightly from 6 April 1988 to 24 May 1989.

Several habitat variables were measured at each SU including general water current, percentage shade, rocks, bushes, sedges, long grass (> 400 mm height), short grass (< 400 mm height), herbs and water cover, added up to 100%. Percentage shade was not included in this total, as it referred to the general shading effect from large Eucalyptus sp. trees which was a blanket affect over whole forest biotope without differences between microhabitats.

RESULTS

GENERAL ASSEMBLAGE PATTERNS

A total of 23 species were sampled, 8 Zygoptera and 15 Anisoptera, viz. Synlestidae: Chlorolestes tessellatus (Burm.); Lestidae: Lestes plagiatus (Burm.); Protoneuridae: Elattoneura glauca (Selys); Platycnemididae: Allocnemis leucosticta Selys; Coenagrionidae: Pseudagrion
Dragonfly spatial patterns

hageni Karsch, P. kersteni (Gerst.), P. salisburyense Ris, Enallagma glaucum (Burm.); — G om ph i da e: Ceratogomphus pictus Hagen; — A e s h n i da e: Anax imperator mauricianus Ramb., A. speratus Hagen, H. ephippiger (Burm.); — L ib e ll u l i da e: Orthetrum caffrum (Burm.), O. julia falsum Longfield, Nesiothemis farinosa (Forster), Palpopleura jucunda Ramb., Crocothemis erythraea (Brullé), Sympetrum fonscolombei Selys, Thrichemis arteriosa (Burm.), T. dorsalis (Ramb.), T.stictica (Burm.), Pantala flavescens (Fab.), Tramea burmeisteri Kirby. The rank-abundance curve for the whole assemblage follows a relatively straight line, indicating high evenness (Fig. 1). However, applying PRESTON’s (1962) canonical hypothesis illustrates no clear single mode for the whole assemblage (Fig. 2), making the lognormal curve inappropriate, and suggesting that the assemblage is not in equilibrium (MINSHALL et al., 1985). More appropriate would be to analyze the dragonfly assemblage according to overall biotope, and preferably at the finer level of microhabitat (i.e. analyze the 32 SUs matrix), the species being dependent upon each other and the SUs being independent samples (LEGENDRE & LEGENDRE, 1983). Two overall types of analysis were then carried out: R-mode resemblance functions which examined species overlap and covariation, and Q-mode analysis which examined similarity and dissimilarity between SUs.

Spearman’s rank correlation coefficients were calculated to test the covariation in relative abundances of

The program SPCOVAR.BAS (LUDWIG & REYNOLDS, 1988), was used for this analysis. Petraitis niche overlap indices were calculated using the program SPOVRLAP.BAS (LUDWIG & REYNOLDS, 1988). TWINSPAN (Two way species indicator analysis), was used to classify sample units on the basis of a sharing of species (HILL, 1979). Indicator species
were determined for each microhabitat group. CANOCO (Canonical correspondence analysis), was used to determine the strength of the species-environment correlation, and the tolerance of each species to different environmental conditions.

NICHE OVERLAP AND SPECIES COVARIATION

Species which overlapped the most were: *Enallagma glaucum* and *Trithemis dorsalis* (overlap index = 0.810), and *Sympetrum fonscolombei* and *Anax imperator* (overlap index = 1.000). General overlap of all species was 0.490. The relative abundance of *Trithemis arteriosa* was positively correlated with that of *Lestes plagiatus* ($r_g = 0.771$, $n = 32$, $P<0.01$). *T. dorsalis* was also positively correlated with *L. plagiatus* ($r_g = 0.887$, $n = 32$, $P<0.01$). *L. plagiatus* was positively correlated with *P. salisburyense* ($r_g = 0.702$, $n = 32$, $P<0.01$). *Pseudagrion kersteni* was negatively correlated with all species, except *Anax speratus* ($r_g = 0.070$, $n = 32$, $P>0.05$). Both *Nesciothemis farinosa* and *Hemianax ephippiger* were negatively correlated with *S. fonscolombei*. Microhabitat overlap between congenerics was generally low. For example, for both *T. arteriosa* on *T. stictica*, and *T. dorsalis* on *T. stictica*, SO = 0.001, 31 df, $P>0.05$. The highest overlap was that of *T. arteriosa* on *T. dorsalis* (SO = 0.618, 31 df, $P>0.05$). Neither *P. hageni* nor *P. salisburyense* overlapped with *P. kersteni* in use of microhabitat. *P. hageni* overlapped minimally with *P. salisburyense* (SO = 0.006, 31 df, $P>0.05$). This was also the case for the *Orthetrum* species, with *O. julia falsum* overlapping minimally on *O. caffrum* (SO = 0.003, 31 df, $P>0.05$).

BIOTYPE PREFERENCES

The percentage of individuals occurring in each biotope was calculated to indicate preferences for certain biotopes. *E. glaucum* preferred the pond biotope (98.8%), as did *T. stictica* (90%). This biotope had a greater percentage of water cover than any other (mean = 39%, SE = 2.57). The stream biotope (A) was characterized by the highest percentage of rocks (mean = 19%, SE = 6.72), and the fastest-flowing water (mean = 1.133 m/s, SE = 0.15). Species found only in this biotope were *P. jucunda* and *C. erythroaena*. The two species, *A. leucosticta* and *C. tessellatus* favoured the stream in forest biotope (*A. leucosticta* = 80%, *C. tessellatus* = 90%). This biotope had a high percentage of shade (mean = 77%, SE = 3.53), and bushes (mean = 77%, SE = 3.40). *O. julia falsum* occurred in all biotopes except below the dam wall. *T. arteriosa*, in contrast, preferred this biotope to any other (67%). It was difficult with species which do not perch often, to show to which biotope they were restricted. Some species may only show a preference by ovipositing into vegetation in a particular transect. *L. plagiatus* preferred the pond and below-wall biotopes (80%). Both these biotopes had a high percentage of sedges and short grass present.
The TWINSPAN samples classification ended at level 6 with the production of 11 groups (Fig. 3). The indicator species for level 1, for the left side of the dichotomy were: T. dorsalis, L. plagiatus, T. arteriosa and E. glaucum. C. tessellatus was the main indicator species for the right side of the dichotomy.

**Sample Unit Classification**

The TWINSPAN samples classification ended at level 6 with the production of 11 groups (Fig. 3). The indicator species for level 1, for the left side of the dichotomy were: T. dorsalis and L. plagiatus. Indicator species for level 2 were: for the right side of the dichotomy: C. tessellatus, and for the left side of the dichotomy: T. arteriosa and E. glaucum. Sampling units were at first divided into sunlit (left side of the dichotomy), and shaded (right side of the dichotomy). At level 3, the sample units were further divided into those having still water, and flowing water.

**Species-Environment Correlation and Tolerances**

Species which were the least tolerant of a range of conditions were: C. tessellatus and A. leucosticta (for AX1, best fit = 0.1191), tolerance was = 0.000. Species tolerances are shown in Figure 4. The tolerance measure was calculated using CANOCO. It shows the niche width of the species, and is based on the standard deviation of the species distribution (TER BRAAK, 1988). The cumulative percentage variance of the species-environment relationship (CCA) was 29.7 (eigenvalue for axis 1 = 0.201), and therefore very weak. This indicated that axis 1 was the most significantly associated with the species and environmental variables. Enallagma glaucum was a better indicator than T. dorsalis, having a tolerance of only 0.3679, compared with T. dorsalis, which was 1.3138. The tolerance index for axis 1 was used as it was the most significant of the four axes (eigenvalue = 0.1191).

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**Fig. 3.** TWINSPAN sample units classification showing indicator species and individual sample units comprising each of the 11 end groups. Indicator species for the left side of the dichotomy were: T. dorsalis, L. plagiatus, T. arteriosa and E. glaucum. C. tessellatus was the main indicator species for the right side of the dichotomy.
INTERSPECIFIC COMPETITION

Overlap between pairs of species was high, with the highest being between *E. glaucum* and *T. dorsalis*, and *S. fonscolombei* and *A. imperator*. These species were unlikely to be competing because they had different habits and behaviour. The rank abundance curve indicated that species were mainly partitioning the site. The fact that congenerics of *Pseudagrion*, *Trithemis* and *Orthetrum*, overlapped least in microhabitat was probably the result of interspecific competition in the past. *O. caffrum* and *O. julia falsum* had separate microhabitat preferences as shown by their negatively correlated relative abundances. They also showed more general microhabitat overlap than any other species. Interspecific interference competition among adult Odonata is common (MOORE, 1964). Yet among species of *Trithemis* and *Orthetrum* it has been found to be unimportant (OSBORN & SAMWAYS, 1995).
Territorial interference has been found to occur between Zygoptera species, e.g. *P. kersteni* and *P. hageni* (MESKIN, 1989), and influences the spacing of individual males within the microhabitat.

**THERMOREGULATION**

Sample units were clearly divided into those which were shaded and those which were sunlit. The results suggested that adults were divided into those which preferred sunshine or shade. This seems to be a common trend in adult Odonata assemblages, as have been found previously to assemble along a sunlit/shade gradient (CLARK, 1992; OSBORN, 1992; STEYTLE & SAMWAYS, 1995). Air temperature is important in ectothermic perchers such as the Libellulidae, although less important for the Aeshnidae which can generate heat endogenously (CORBET, 1980; MAY, 1984). Preferences for sunshine and shade also affects species at the biotope level. For example, *C. tessellatus* only occurred in forested, shaded habitats, while *C. erythraea* occurred in sunlit habitats (OSBORN & SAMWAYS, 1996). In this study, *C. tessellatus* was also found to occur exclusively in shaded conditions.

**VEGETATION PREFERENCES**

Species were not grouped on the basis of vegetation taxon or height. Species were apparently flexible in the type of vegetation on which they perched. The height of vegetation on which adult Odonata species perch is known to be influenced by air temperature, such that species perch closer to or on the ground in cold weather (McGEOCH & SAMWAYS, 1991). However, radical changes in vegetation associated with succession changes can cause a change in Odonata assemblages (MOORE, 1991). Vegetation has important functions for adults, from concealment from predators (ASKEW, 1982), to mating and feeding perches (BUCHWALD, 1992). The use of different types of vegetation and perch height may allow species to coexist (STERNBERG, 1994), thus enabling higher species packing. In this study, vegetation would have been more important for species having endophytic oviposition.

**BIOLOGICAL INDICATORS**

Species that are restricted to a narrower range of conditions are better indicators of change, than species that are able to proliferate or breed in various situations. For example, *C. tessellatus* and *A. leucosticta* were not tolerant of a range of conditions, whereas *O. julia falsum* and *P. flavescens* were. *C. tessellatus* and *A. leucosticta* are sensitive indicators, particularly of changes in habitat quality. In this study, the stenotopic species were better indicators, being more likely to be af-
fected by changing conditions. What should be borne in mind is that this study only considered the adults and it has been found that larvae of other common species have specialized microhabitat requirements (OSBORN, 1995).

MICROHABITAT AND BIOTOPE PREFERENCES

This study showed that species may not be present in a biotope if particular microhabitat requirements are not fulfilled. Interestingly, species had stronger biotope (i.e. larger scale) than microhabitat (i.e. smaller scale) preferences. Being very mobile, the adults may simply move to different microhabitats in response to changing biotope conditions. This occurred especially in response to sunshine.

Species may prefer certain biotopes because of the presence of types of vegetation for oviposition sites. This may especially be the case for *L. plagiatus*, which oviposits into grass on the banks, and other species which have endophytic oviposition. Species such as *T. dorsalis*, which are very opportunistic may be able to colonize many different biotopes. Even adults of common species of Odonata can show biotope preferences (OSBORN, 1995). How suitable the biotope is for a species will influence the population sizes and thus interspecific interactions, which could affect assemblage structure. The large number of species at the dam, was probably because of the many biotopes that were present. The stream was important because many stenotopic species are stream species (BALINSKY, 1967).

CONSERVATION IMPLICATIONS

Common species of aquatic insects can be used to identify the type of biotope, and rarer species can be indicative of relict or undisturbed conditions and used to rate the importance of any site within its biotope group (EYRE et al., 1986). When creating ponds specifically for Odonata, as has been done before (MOORE, 1987; SUGIMURA, 1989; USHER & JEFFERSON, 1991), preferred biotope features can be incorporated into the design of the pond. It will not be practical when designing a pond for conservation, to accommodate the requirements of all lentic species, because some may be restricted to similar sites but where there are subtle differences in variables. *Bradinopyga cornuta* Ris for instance, is restricted to small, often temporary, pools in rocks (CLARK, 1992).

Inappropriate management of pre-existing ponds can lead to a 50% reduction in the Odonata species present (FRY & LONSDALE, 1991). Reducing water flow or amount of shade at the dam may for instance, result in species such as *A. leucosticta* and *C. tessellatus* disappearing from the site. Being able to predict types of invertebrate communities at a site has strong conservation value (WRIGHT, et al., 1984). Classification of running water sites has applications for conservation, biological surveillance and pollution control (FURSE, et al., 1984). Classification of still waters will also be of value, particularly as many species are restricted to lentic habitats.
Above all, what this study has shown is that it is essential to provide a wide range of biotopes (with various microhabitat conditions) so that rare stenotopic species are catered for, yet at the same time, being generally suitable for the eurytopic species. This being done, there does not seem to be any risk of "overpacking species". More microclimatic conditions probably make conditions suitable for more larvae too (OSBORN, 1995), which in turn conserves a richer local assemblage. The successful conservation of species require detailed knowledge on requirements for all life stages, as adults and larvae can occur in different biotopes (OSBORN, 1995). Despite the fact that this study focused on the adults, it does show the importance of providing and maintaining a wide range of biotope and microhabitat conditions for increasing species richness and/or for conserving rare species.

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