

**NICHE AND LIFE-HISTORY DIFFERENCES IN
FIVE HIGHLY SYMPATRIC SPECIES OF *TRITHEMIS* DRAGONFLIES
(ODONATA: LIBELLULIDAE)**

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ABSTRACT

Niche and life-history differences in five species of *Trithemis* were investigated to determine the extent of interspecific competition. Interspecific competition was mostly avoided because species favoured different habitats and microhabitats. There was the possibility of competition between larvae under conditions of lowered food concentration, where they occurred in the same habitat and microhabitat. Larvae of different species preferred specific prey taxa, but chose to feed on a different prey taxon once it was more readily available. Because species were restricted more by food size than taxon, competition for food was unlikely. Interspecific competition may have occurred between adults because the niche breadth of some species became contracted as the density of other species increased. Interspecific competition among larvae was unlikely because individuals of different sizes were present together, allowing for food partitioning. Asynchronous development therefore ensured that competition for food of the same size was reduced. Competition was also reduced by species showing peaks in abundance at different times of the year.

PREFACE

This study was conducted in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg from January 1993 to December 1994. Field work was done at the National Botanic Gardens in Pietermaritzburg. The study was supervised by Professor Michael J. Samways.

This study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work of others, it has been duly acknowledged in the text.



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CHAPTER 1

Introduction

1.1 Background

The aim of this study was to complete an ecological study on species which have shown aggressive behaviour suggesting interspecific competition. The species that were studied were: *Trithemis arteriosa* (Burmeister), *Trithemis dorsalis* (Rambur), *Trithemis furva* Karsch, *Trithemis kirbyi ardens* Gerstaecker, and *Trithemis stictica* (Burmeister). The species were strongly territorial, often abundant, and showed strong similarities in use of space for foraging and mating behaviour (Osborn, 1992). Observations on reproductive behaviour suggested that all used the same habitat for mating and oviposition. The species were very similar in size and general morphology, and may therefore have competed for the same space. Spatial and temporal partitioning was therefore investigated.

Interspecific competition was investigated in both adults and larvae. Competition between the adult and larval stages was avoided by the two stages occurring in different media. Interspecific competition could have resulted in larvae having a reduced growth rate, ultimately producing smaller adults which were less able to compete for matings. Interference competition between adults of different species could have influenced access of other species to prime sites for oviposition, egg and larval development. Egg deposition rates could have been negatively affected if there was aggressive interference between species. Competition between these different stages was interrelated with each stage indirectly influencing the competitive advantages of the other. It was therefore important to examine the possibility of competition in all life stages.

Life-history is important in interspecific competition because a species that can invade, colonise and multiply in a habitat in a short time will outcompete others, especially where conditions are unpredictable (Osborn, 1992). In more predictable conditions, a species with a longer life-cycle may be dominant

because it is better adapted to the conditions than a generalist which is tolerant of a variety of conditions.

1.2 Competition among larvae

Many laboratory and field experiments have been conducted on interference and exploitative competition among larval dragonflies. Interspecific competition among larvae is common, although it is often modified by fish predation. Fish predation may be an important influence on the occurrence, abundance, and therefore competition in larvae (Morin, 1984). Competition by interference has been shown by Baker (1981), but may be limited to species dependent on a scarce supply of perches. Exploitative competition is best shown by reduced growth rate or survivorship of a species when placed with another species, than when kept alone.

1.3 Interspecific competition in adults

Unlike the larvae, competition among adults has not often been investigated, although some work has been done on resource partitioning (Michiels & Dhondt, 1987; Dudgeon, 1989). Moore (1964) suggested that interspecific competition in adults was rare. Intraspecific competition was considered by him to be more important than interspecific competition in influencing dragonfly assemblages. However, interspecific competition may occur if conditions become adverse, resulting in resources becoming limited. Both interference and exploitative competition among adults could occur particularly if another species is already established at the site most suitable for oviposition and territories. The earliest colonist may therefore exclude later colonists from becoming established (Robinson & Dickerson, 1984). Individuals can then defend their territories, and exclude others from their space.

1.4 Aims of the investigation

This study investigates competition in species of *Trithemis* by examining the habits and habitats of species. Life-history, habitat and microhabitat preferences of species were therefore investigated. Behaviour and choice experiments were used to indicate food, substrate and vegetation preferences. The relative abundances of adults and larvae in habitats over time were used to indicate habitat and microhabitat preferences. Habitat preferences were determined for each month because they may change with seasonal changes. Mechanisms of resource partitioning were investigated, and the likelihood of competition under different scenarios, determined. Interspecific competition among larvae can influence the reproductive success of adults (Fincke, 1992), which was why it was important to investigate both life-stages.

The similarity of species' niches was investigated. Resource limitation was also determined in view of information on habitat choice and behaviour. It was important to consider how similar species' niches were to ascertain the potential for competition. Competition will be unlikely where species' niches are dissimilar enough that they can coexist. As a result, species may coexist despite overlapping a great deal along one or two niche dimensions. Species' niches do have to be different for species to coexist (Chesson, 1991). Resource limitation was also important to consider because competition will occur if species overlap on a resource which is limited. Behaviour was used to show resource use and to assess the effect of one species on another when using the same resources.

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CHAPTER 2

Habitat and microhabitat preferences of larvae and adults of *Trithemis*

ABSTRACT

Habitat and microhabitat preferences of sympatric species of *Trithemis* were investigated. Spearman's rank correlation coefficients showed that adults and larvae were correlated with specific environmental variables. Calculations based on Manly's alpha, showed that species preferred different habitats and microhabitats. Even without much habitat partitioning, species could coexist by occupying different microhabitats. Also, where they shared the same habitat, they did so at different times of the season. Adults and larvae did not always prefer the same part of the pond, which suggested territorial displacement of adults, or migration by larvae at time of emergence.

2.1 Introduction

2.1.1 *Studies on habitat and biotope preferences*

This study investigates the habitat preferences of both adults and larvae. This was done to indicate species-specific preferences. It was important to include the larval stage because competition was also being investigated in this species, and because of the longevity of the larva compared with that of the adult. The larva is also less able to move from adverse conditions, whereas the highly mobile adults can (Osborn, 1992). Studies by Barnard (1937), Harrison and Elsworth (1958), do indicate habitat preferences of larvae of some species of dragonflies. However, this is the only study to attempt a quantitative analysis of habitat preferences, in both adult and larva.

Much work has been done recently on the occurrence of adults in specific habitats (Osborn, 1992; Stewart, 1993; Steytler, 1994). This study is unique in that it investigates habitat preferences of larvae and adults over time. This was done because data from a short time may be inaccurate in showing true habitat preferences. It has been shown recently, for example, that species may favour different sites at different times of the season because of thermoregulatory requirements (Michiels & Dhondt, 1990). Habitat selection promotes coexistence between potential competitors because segregation can be achieved if species have distinct habitat preferences.

Habitat segregation is very important among larvae, especially considering that adaptive radiation has led to morphological and behavioural specialization between species (Corbet, 1962). Larvae therefore avoid exploitative and interference competition by using different niches. Habitat selection is essential in ensuring successful reproduction (Orians & Wittenberger, 1991).

2.1.2 *Aims of the study*

The objective of this study was therefore to determine species preferences for different habitats. Microhabitat preferences were determined within each habitat. Environmental factors possibly responsible for these preferences were also investigated.

2.2 **Materials and methods**

2.2.1 *Study area*

The study site was at the Pietermaritzburg National Botanic Gardens (29°35'S, 30°25'E), in South Africa. The site was located at an elevation of 690 m a.s.l. This site was selected because all five species were present in sympatry. Four of the species were also permanently resident. Breeding of dragonflies at sites is usually confirmed by emergence, the presence of larvae, exuviae and observation of oviposition (Clarke, Hewitt, Smith & Smith, 1990). The presence of exuviae and oviposition activity confirmed that species were breeding at the site. The site also represented an environmental gradient from a fast-flowing stream to a large dam and adjoining marshland. There were the following habitats along this gradient: 1.) Shaded rocky stream, 2.) Wooded rocky stream, 3.) Gravel-bed stream, 4.) Sunny river, 5.) Wooded river, 6.) Marsh, 7.) *Cyperus* marsh, 8.) Southern dam (edge of dam), 9.) Northern dam (edge of dam), and 10.) Pond. This was a useful variable against which the relative abundances of species could be measured. More detailed descriptions of these sites are given in Steytler and Samways (1995).

2.2.2 *Sampling design*

Adults and larvae were sampled using the stratified random sampling method. The principle of stratified sampling is to partition the population so that the units within each stratum are as homogeneous as possible. This ensures that the

estimate of the population mean and total is as precise as possible (Thompson, 1992). Under these conditions it is more precise than simple random sampling (Manly, 1990).

2.2.3 *Sampling of adults*

Sampling was from 4 August 1993 to 15 June 1994, to ensure the detection of changes in populations associated with seasonal changes. The site was visited from one to three times a week depending on the weather. Weekly visits are necessary for maximum accuracy of relative abundances (Moore, 1991). Bailey (1992) suggests three times a week as minimal for most accuracy. The site was visited three times a week where possible when the weather was sunny and warm. Sampling was only done on hot, sunny days when Odonata are most active (Corbet, 1962). Sampling therefore should only be done when conditions are best for dragonfly activity (Brooks, 1993). Species at the study site were in the past less abundant and active in cooler, cloudy conditions (McGeoch & Samways, 1991). There were an unequal number of visits to the site over the season because of differences in the number of sunny days. This however, did not adversely affect the results because dragonfly activity was dependent on sunshine, such that it was more accurate to sample adults on sunny days. Based on data collected at the start of the study, species occurred most abundantly at the water's edge between about 10h00 and 13h00.

Strip transects were used for sampling the adults. Spatial replication consisted of 25 m x 2 m strip transects selected in each habitat, except the rocky stream where transects were 25 m² in area. The degree of replication or number of transects was in proportion to the area of the habitat. The number of replicates was determined for 95% precision (Elliott, 1977). There were 60 transects in total. Transects were arranged around the edge of the water extending 1 m on the bank, and 1 m into the water. This method has been used before when relating Odonata assemblages to habitat (e.g. Osborn, 1992; Steytler, 1994). Optimal allocation of transects ensured that most of the study area was covered

(Thompson, 1992). The study area was divided into 10 habitats, and transects were allocated to habitats. Adults were sampled by randomly walking the 25 m and recording in five minutes, any individuals perched within a transect. Individuals flying past were not counted because they could not be shown to have territories, or to be foraging or mating in that particular transect.

2.2.4 *Within-transect sampling*

The size of each transect was 25 m x 2 m. This size was arrived at from data collected during a previous study using 20 m x 2 m transects. The best transect size for 5% variation was then determined using the formula in Krebs (1989). This allowed the determination of the transect size for maximum accuracy and for a variation of 5%. A computer program was written in Turbo Pascal 5.0, for the calculation. Transects were sampled at random, with a different transect being used as a starting point during a single sampling period. Transects were sampled in this way at different times of the day and week.

Adults were identified in each transect using a pair of 8 x 21 Minolta binoculars. Visual observation of adults often gives estimates that closely approach the absolute population size (Southwood, 1978). If the marginal vegetation is not too dense, and the species under study are not too cryptic in habit, the accuracy of counts is probably quite high. It is possible that teneral and females may be underestimated because of their more cryptic colouration. All individuals of both sexes were counted. Where identification was uncertain, a net (opening diameter 30 cm) (mesh size 0.5 mm), and 9 x hand lens were used to catch, identify adults, and then release them.

2.2.5 *Species identification*

Pinhey (1951) and Pinhey (1970) were consulted for the adult identification. Voucher specimens and the slide collection, kept in the Invertebrate

Conservation Research Centre, Department of Zoology and Entomology were referred to for identification of adults. A new reference collection was also made.

Mature adult males were identified using body colouration and wing venation. *Trithemis dorsalis* and *T. furva* are very similar. The relative development of the hamular hook on the accessory genitalia was used to check the identification between these two. The most visible difference between them was the presence of a yellow margin on the pterostigma in *T. furva*, which was absent in *T. dorsalis*. This could be seen in mature males when they perched. Immature males and mature females were recognized by colour of wing venation and thoracic markings. The thoracic markings were very easily seen and very distinctive for these species. Teneral individuals were recognized by the hyaline appearance of the wings and weak flight of the individuals. A mature adult male of *T. arteriosa* is shown in figure 1.



Fig. 1. Photograph of mature *Trithemis arteriosa* ♂. (Mag. 3x).

2.2.6 *Sampling of larvae*

Larvae were sampled twice a week over the same period as the adults, from late autumn to mid-winter. More frequent visits were not possible because of the long time taken to sample the larvae.

Larvae were sampled semi-quantitatively by pulling a D-frame net over a 1 m² area of substrate. The D-frame net is usually used for sampling aquatic insects in small streams and in ponds, where the net can be pulled along the substrate, or through vegetation to collect insects. It can also be used in rocky streams, by agitating the substrate upstream from the net. Preliminary sampling of larvae at a farm dam showed that more larvae were caught with this net than with a conventional pond net. There were 10 replicates to ensure a reasonably precise estimate. The substrate was sorted in a white sorting tray. Larvae were then identified using a 9 x hand lens. The net diameter was 41 cm, and height was 15.5 cm. The mesh size was of 1 mm diameter. Barton (1980), suggested that the mesh size of a net for sampling Odonata larvae should be at least 0.5 mm to reduce clogging.

There were 28 sampling stations in total, with an unequal number in each habitat, because of habitats being of unequal size. There were 10 pulls of the net at random in each station. Stratified random sampling was used, with stations selected at random in each habitat. The relative abundance of larvae was then estimated by counting the total number of larvae collected at each station. The very heterogeneous nature of the different habitats made it difficult to estimate densities accurately. Extrapolating the numbers collected to the area of habitat would not have been valid here because of habitat heterogeneity. Larvae were sampled on warm days, as the behaviour and therefore ease of collection of larvae could have been influenced by temperatures.

Body lengths and head widths were measured using a pair of 150 mm x 0.02 mm Vernier callipers. Body lengths were measured from the tip of the labium to the apex of the anal pyramid. Head widths were measured from the distal edge of one compound eye to the next. Only ultimate instar larvae could be sexed. Ultimate instar larvae are recognized as such by having well-developed wing sheaths extending to the third leg (Gardner, 1960). After metamorphosis, mud-dwelling larvae become easy to collect as they move towards the shore and bask in the warm shallows (Corbet, 1960). This could bias sampling results in favour of larger individuals.

2.2.7 Larval identification

Barnard (1937), Pinhey (1961, 1962), Carchini, Samways and Caldwell (1992) and Samways, Di Domenico and Carchini (1993), were used for the larval identification. Larvae were identified using abdominal shape, thoracic markings and the relative development of the dorsal abdominal spines. Certain larval characters remained constant throughout the growth and development and were therefore diagnostic for all instars.

Individuals could not be placed into separate instars because the number of instars varies according to food quantity and quality (Corbet, 1962). The only time larvae could be assigned to instars was when they were reared out from eggs in the laboratory, and each ecdysis event recorded. Larvae sampled in the field were instead assigned to size-classes.

2.2.8 Reasons for selection of environmental variables

Size and shape of water may be important in habitat selection by adult Odonata (Corbet, 1962). Shallow water may be important for larvae, because depth of water influences oxygen and prey availability. Dissolved oxygen and temperature

influence the development of dragonfly larvae (Corbet, 1962). Many Odonata also prefer water of a certain pH (Weir, 1974; Osborn, 1992). High turbidity may reduce visual detection of prey and current rate may influence oxygen concentrations in the water. Vegetation serves many important functions for Odonata (Buchwald, 1992), and along with substrate provides refuge from predators. The thermal requirements of the species results in different responses to sunlight and shade (Osborn, 1992).

2.2.9 *Measurement of variables*

There were 10 measurements taken of each variable in each habitat, unless stated otherwise. Measurements were taken on five different days in sunny, warm conditions at 12h00. Variables were only measured in one month because the aim was to relate species to habitats, not to seasonal changes in habitats. Only the correlation of species with environmental variables among habitats was of concern. The perimeter and width of the water were measured with a tape measure. Depth was measured according to the method of Wetzel and Likens (1991). Dissolved oxygen, pH and water temperature were measured using a 3405-Electrochemistry set. All probes were calibrated in August before use.

Turbidity was measured using a Secchi disc with 10 cm increments. The Secchi disc is used because of its simplicity (Wetzel, 1983). The readings were made at midday, since the results become less reliable near dawn or dusk because of reduced surface illumination (Wetzel, 1983).

Determination of oxygen in natural waters is best undertaken using oxygen-temperature probes (MacKereth, Heron & Talling, 1989). These oxygen electrodes allowed measurements to be taken quickly, and in remote places (Wetzel & Likens, 1991). Water samples were collected in a 150 ml plastic beaker. Dissolved oxygen was then measured immediately to prevent too much influence by the surrounding atmosphere. Oxygen readings were taken on calm days, to prevent wind turbulence from seriously biasing the results (Cole, 1979).

Current rate was measured using a model 201D portable current meter. The current meter readings were calibrated by checking them against the time taken for a ping pong ball to travel 1 m. Readings were recorded randomly at 10 positions along each transect, at the surface and on the substrate. This gave a better indication of the current regime, because most of the larvae were found on the substrate.

Substrate classification was based on the Wentworth scale (Wentworth, 1922). Substrate was sampled by randomly throwing a wooden 1 m² transect at each sampling station. There were ten replicates at each station. Five samples were taken from within the transect, placed in jars and transported to the laboratory. The particle size was then measured, and the frequency of particles of different size, recorded. Frequency of the boulders was estimated in the field.

Degree of shading of transects was estimated by recording the number of hours during one day that the transect received full sunshine. This was preferred to simply estimating the percentage sunshine at all transects at 12h00. This is because different species may simply move to different transects when the transect is in full sunshine, or when it is more shaded.

2.2.10 *Habitat description*

Habitats were classified based on amount of open water, and whether aquatic vegetation covered the bottom of the water body. Some habitats are shown in figures 2 to 5. Vegetation was classified into: submerged, floating-leaved, emergent and marginal vegetation. The classification used, was that of Howard-Williams (1980). The percentage of vegetation in each height category was recorded. One specimen of each plant found in each habitat was collected for identification.



Fig. 2. The rocky stream as it flows through *Eucalyptus* woodland.



Fig. 3. The dam from the western edge showing the forested southern edge.



Fig. 4. The marsh with *Typha latifolia capensis* and *Nymphaea* species.



Fig. 5. One edge of the pond showing the marginal vegetation.

2.2.11 *Data analysis*

Manly's alpha is considered the best method of assessing dietary and habitat preferences (Krebs, 1989; Schooley, 1994). A score was calculated for each month because a pattern of habitat selection may be missed if temporal changes are ignored (Schooley, 1994). A score was calculated for each month, based on the relative abundance of adults in proportion to habitat area. The frequency with which species preferred habitats was then found by the number of months with which a habitat scored the highest. Calculations were performed using a program written in Turbo Pascal 5.0.

Environmental variables were tested for normality using probability plots in STATGRAPHICS (STSC, 1989). Data were shown to be nonparametric. Correlations were therefore calculated using Spearman's rank correlation coefficients which are more powerful than Pearson's coefficients when data is nonparametric (Neave & Worthington, 1988). Species covariation was determined using Spearman's rank correlation coefficients. Schluter's variance ratio test was not calculated because the degrees of freedom were insufficient (Ludwig & Reynolds, 1988). Analyses were performed using a modified version of the program SPCOVAR.BAS (Ludwig & Reynolds, 1988).

2.3 Results

2.3.1 *Species covariation*

Trithemis arteriosa, and *T. dorsalis* adults were significantly positively correlated with *T. stictica* (Table 1a). *Trithemis dorsalis* and *T. furva* were significantly negatively correlated in their abundances. *Trithemis arteriosa* larvae were highly significantly positively correlated with the relative abundance of *T. stictica* ($r_s = 0.841^{**}$, $n = 10$, $P < 0.01$). Both adults and larvae of these two species occurred together along the environmental gradient. Larvae of *T. arteriosa* and *T. dorsalis* were not as strongly positively correlated as the adults were (Table 1a & b). Larval covariations across habitats were generally not as strong as the adults (Table 1b). Whereas adults of *T. dorsalis* and *T. furva* were very negatively correlated (Table 1a), larvae were positively correlated (Table 1b). Relative abundance of adults and larvae is given in Appendix 1 at the end of this chapter.

Table 1. Spearman's rank correlation coefficients r_s showing the covariation in the relative abundance of (a) adults and (b) larvae across the environmental gradient, from stream to pond. * Values significant at $P_{0.01}$ ($n = 10$). Values given are based on the maximum relative abundance of larvae over 10 months. Data from only 10 months were used because not all larvae were present together in the eleventh month.

(a)	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. kirbyi ardens</i>	<i>T. stictica</i>
<i>T. arteriosa</i>	*				
<i>T. dorsalis</i>	0.593	*			
<i>T. furva</i>	-0.687 *	-0.788 *	*		
<i>T. kirbyi ardens</i>	0.696 *	0.613	-0.406	*	
<i>T. stictica</i>	0.710 *	0.750 *	-0.880 **	0.522	*

(b)	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. stictica</i>
<i>T. arteriosa</i>	*			
<i>T. dorsalis</i>	0.186	*		
<i>T. furva</i>	-0.506	0.496	*	
<i>T. stictica</i>	0.841 **	0.005	-0.391	*

2.3.2 *Habitat preferences of adults*

Species had distinct habitat preferences. All species preferred at least one habitat 50% of the time. *Trithemis arteriosa* preferred the sunny, southern part of the dam to any other habitat (Fig. 6a). Another species that favoured this side of the dam was *T. kirbyi ardens* (Fig. 6d). *Trithemis stictica* showed less of a preference for any particular habitat (Fig. 6e). Whereas *T. dorsalis* preferred the pond (Fig. 6b), *T. furva* favoured the stream (Fig. 6c).

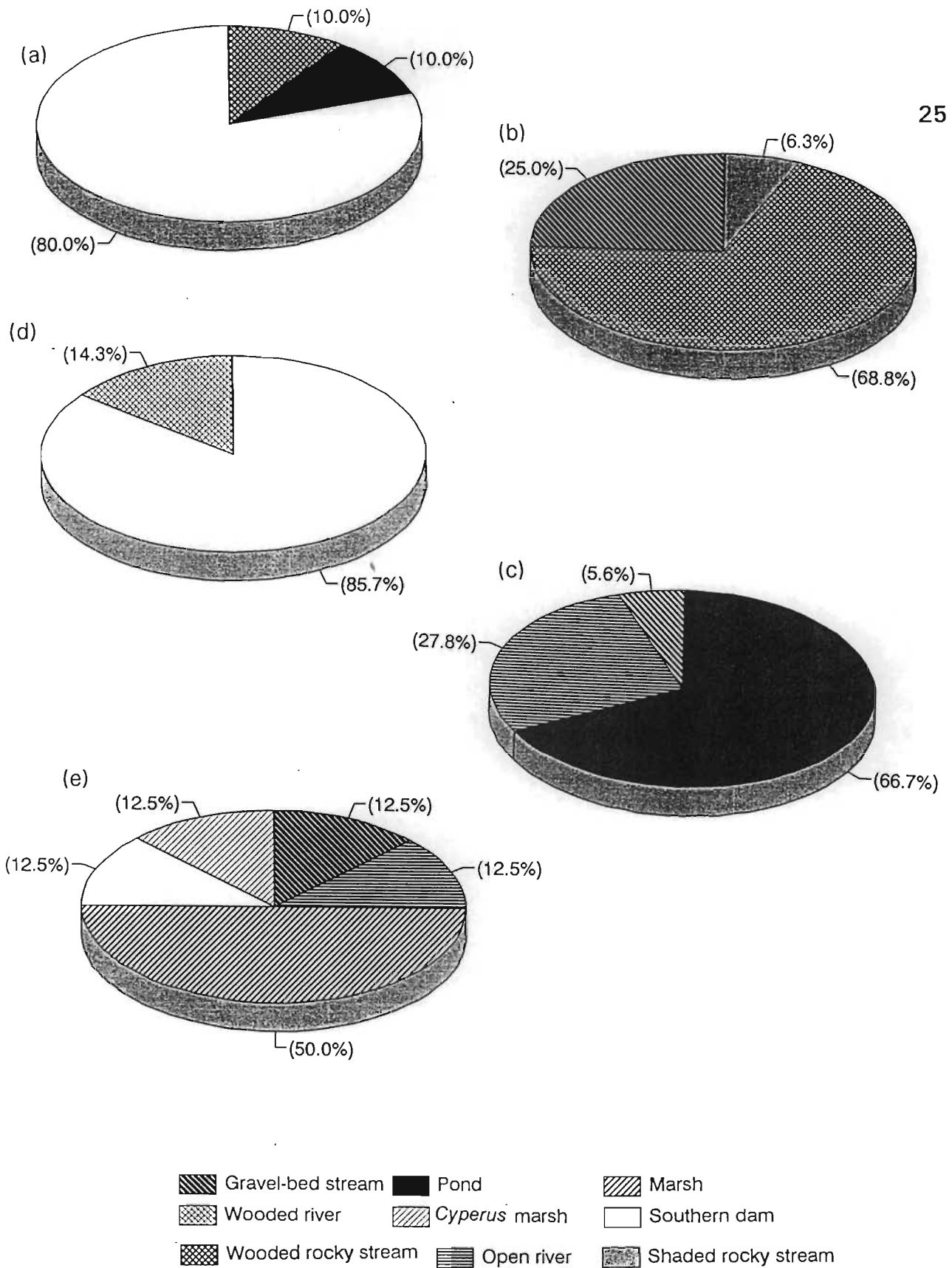


Fig. 6. Habitat preferences of adults. Percentages indicate the percentage of months that each habitat had the highest Manly's alpha score. ($n = 10$ for each month). (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. kirbyi ardens*, (e) *T. stictica*.

2.3.3 *Habitat preferences of larvae*

Trithemis dorsalis, *T. furva* and *T. stictica* had stronger preferences for one habitat, compared with *T. arteriosa* (Fig. 7). *Trithemis dorsalis* and *T. furva* preferred the pond of all the habitats (Fig. 7b & c). Although this was the case, *T. dorsalis* occurred in the pond early in the season, from spring to early summer. *Trithemis furva* was then most abundant in the pond in late summer, January to late February. The other two species preferred the open river (Fig. 7a & d). *Trithemis stictica* had a very strong preference for the open river (Fig. 7d).

2.3.4 *Larval microhabitats*

All species showed microhabitat preferences (Fig. 8). Microhabitat preferences were determined based on the number of larvae collected from different microhabitats within each habitat. Various categories of microhabitats were used (Fig. 8). The only species restricted to one microhabitat was *T. dorsalis* (Fig. 8b). This was more important than habitat preference in determining the distribution of this species along the environmental gradient. *Trithemis arteriosa* and *T. furva* were found in at least three microhabitats, and were less selective in microhabitat choice than the other species were. *Trithemis stictica*, and *T. furva* were clearly the two species most often found clinging to vegetation (Fig. 8c & d). *Trithemis arteriosa* and *T. dorsalis* most often hid under living or dead plant material.

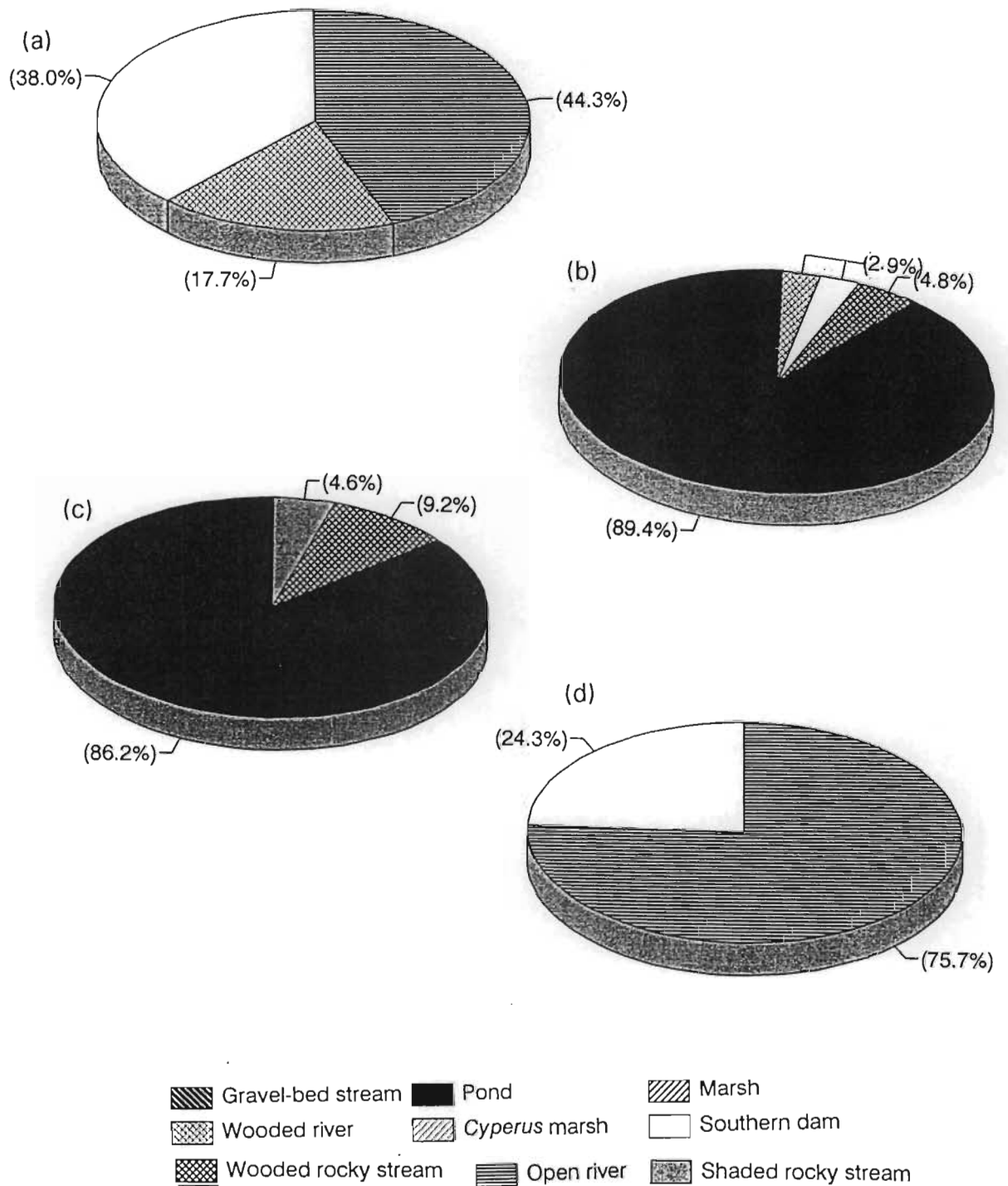


Fig. 7. Habitat preferences of larvae, of the four resident species ($n = 10$). (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. stictica*. Percentages indicate the frequency with which species preferred habitats. This was based on the frequency with which habitats had a high Manly's alpha score.

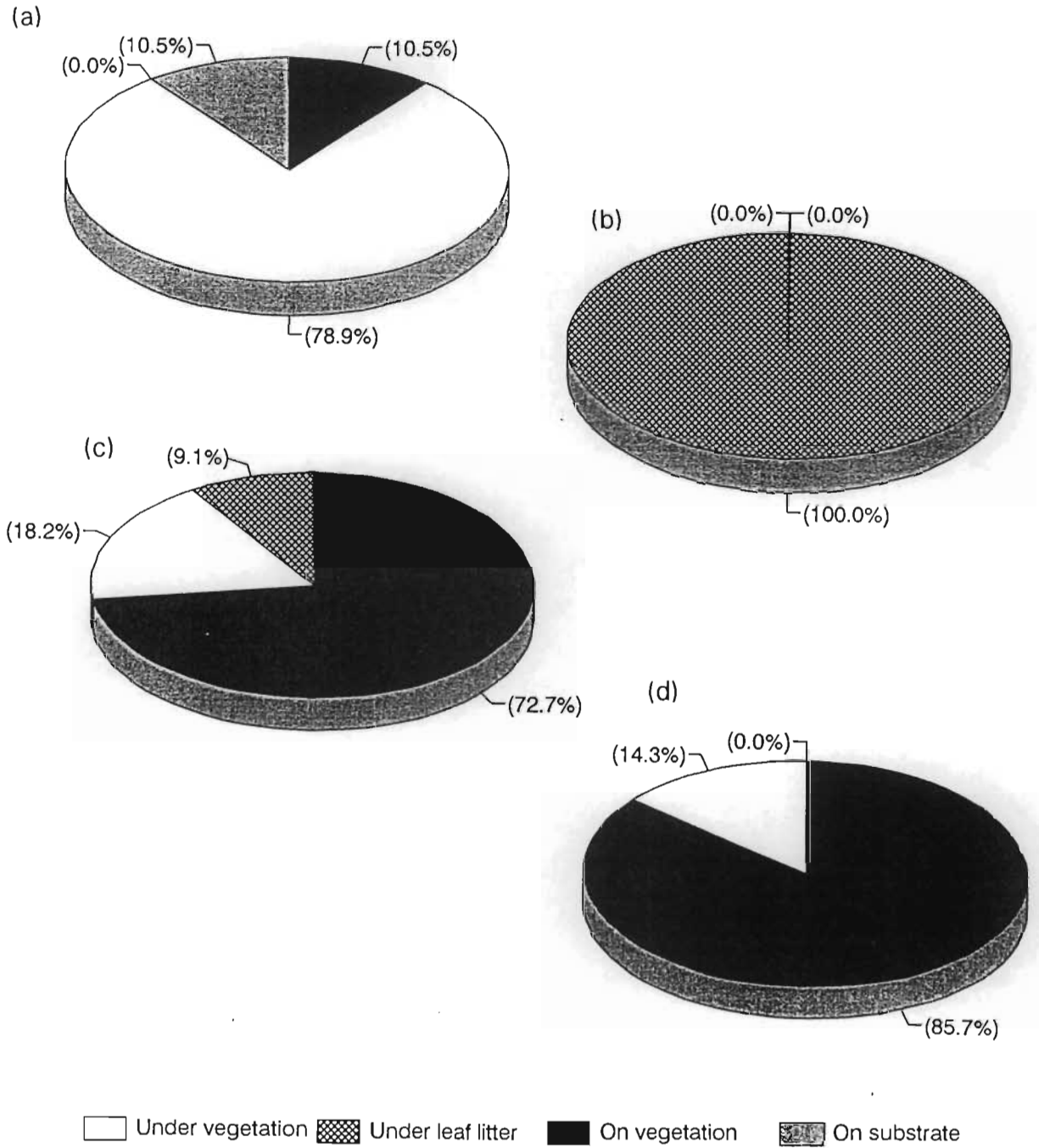


Fig. 8. The frequency with which larvae were collected from different microhabitats ($n = 4$). This was used to indicate microhabitat preferences. (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. stictica*.

2.3.5 *Adult correlations with environmental variables*

Most of the adults were significantly correlated with water area and sunshine (Table 2). However, *T. furva* was not significantly correlated with submerged vegetation ($r_s = 0.416$, $n = 10$, $P < 0.05$), and boulders ($r_s = 0.619$, $n = 10$, $P < 0.05$). Species were mainly negatively correlated with variables (Table 2).

Table 2. Spearman's rank correlation coefficients r_s for the relative abundance of adults and environmental variables. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$ ($n = 10$).

Variables	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. kirbyi ardens</i>	<i>T. stictica</i>
Water area (m ²)	0.920 **	0.612	-0.765 *	0.677 *	0.832 **
Boulders (%)	-0.332	-0.138	0.619	0.087	-0.506
Emergent vegetation (%)	0.328	0.440	-0.687 *	0.203	0.629
Floating-leaved vegetation (%)	0.161	0.452	-0.015	0.255	0.018
Submerged vegetation (%)	0.019	-0.306	0.416	0.008	-0.341
Vegetation cover (%)	0.104	-0.053	-0.385	-0.293	0.356
Open water (%)	-0.104	0.053	0.385	0.293	-0.356
Mean vegetation height (cm)	0.378	0.289	-0.533	-0.216	0.275
Vegetation height > 15 cm	0.018	-0.006	0.239	0.007	-0.166
Vegetation height 16-25 cm	-0.263	-0.352	0.401	0.007	-0.290
Vegetation height 26-50 cm	0.477	0.099	-0.500	-0.082	0.562
Vegetation height 51-100 cm	-0.128	0.105	0.007	-0.127	0.031
Vegetation height > 100 cm	0.488	0.375	-0.642	0.529	0.369
Number of hours of sunshine	0.774 *	0.782 *	-0.642	0.425	0.640

2.3.6 *Environmental variables*

Environmental variables measured among habitats are summarized in table 3. The pH was similar in most habitats. There were major differences in dissolved oxygen, current rate and substrate between habitats. There were also noticeable differences in water area, turbidity and depth. The occurrence of plant species in different habitats is shown in table 4.

2.3.7 *Larval correlations with environmental variables*

There were highly significant correlations between the relative abundance of *T. arteriosa* and water area and width (Table 5). *Trithemis furva* was highly significantly correlated with boulders and benthic current, whereas *T. dorsalis* was most strongly correlated with floating-leaved vegetation and very fine sand (Table 5). *Trithemis stictica* was significantly correlated with medium-sized sand ($r_s = 0.723^*$, $n = 10$, $P < 0.05$).

Table 3 Environmental variables of different habitats at the site. The habitats were as follows: 1 = Shaded rocky stream, 2 = Wooded rocky stream, 3 = Gravel-bed stream, 4 = Sunny river, 5 = Wooded river, 6 = Marsh, 7 = *Cyperus* marsh, 8 = Southern dam, 9 = Northern dam, 10 = Pond. Standard errors are reported to the right of mean values ($n = 10$). Values for which standard errors are not given are based on percentage cover.

Variable	1	2	3	4	5	6	7	8	9	10
Temperature (°C)	19.33 (0.03)	19.64 (0.03)	19.31 (0.03)	20.47 (0.02)	18.74 (0.01)	21.3 (0.03)	22.2 (0.07)	21.74 (0.01)	18.34 (0.02)	22.46 (0.01)
Dissolved Oxygen (%)	70.34 (0.01)	70.23 (0.01)	70.8 (0.16)	59.74 (0.17)	58.31 (0.00)	59.7 (0.14)	59.74 (0.01)	60.37 (0.02)	64.15 (0.01)	65.22 (0.01)
pH	7.77 (0.01)	7.77 (0.01)	7.75 (0.01)	7.53 (0.05)	7.52 (0.02)	6.6 (0.06)	6.61 (0.05)	7.07 (0.05)	7.07 (0.01)	7.36 (0.04)
Turbidity (cm)	10.8 (0.02)	10.82 (0.01)	11.95 (0.04)	9.78 (0.01)	12.2 (0.04)	4.1 (0.02)	4.4 (0.04)	4.25 (0.01)	4.27 (0.05)	8.21 (0.01)
Water area (m ²)	75	75	50	150	150	100	100	350	300	16
Water depth (cm)	10.1 (0.20)	12.04 (0.01)	12.4 (0.13)	44.68 (0.17)	50.58 (0.11)	3 (0.47)	5 (0.54)	138.2 (0.18)	300.2 (0.23)	60 (0.63)
Water width (cm)	95 (4.38)	111 (5.74)	96 (2.00)	320 (3.48)	415 (1.67)	197 (0.95)	213 (0.50)	3750 (0.95)	3750 (0.65)	200 (0.68)
Surface velocity (cm/s)	295 (0.39)	440 (0.47)	146 (0.68)	1470 (0.73)	1646 (0.55)	0	0	0	0	1500 (1.76)
Benthic velocity (cm/s)	292 (0.39)	442 (0.68)	203 (0.67)	1821 (0.63)	1786 (0.31)	0	0	0	0	2010 (0.42)
Mean velocity (cm/s)	293	443	175	1646	1713	0	0	0	0	1755
Boulders (%)	22	34	0	0.7	0	0	0	0.1	0	0.6
Large cobble (%)	15	30	0	0	0	0	0	0	0	0
Small cobble (%)	10	19	0	0	0	0	0	0	0	0
Large pebble (%)	22.2	15	0	0	0	0	0	0	0	0
Small pebble (%)	22	1.2	0	0	0	0	0	0.2	0	0
Coarse gravel (%)	6	0.23	24	0	0	0	0	0.1	0	0
Medium gravel (%)	2	0.2	0.8	0	0	0	0	0.1	0	0
Fine gravel (%)	0	0.13	1	0	0	0	0	0.3	0.2	0
Very coarse sand (%)	0.1	0.14	46	0	0	0	0	0.3	0.8	0
Coarse sand (%)	0.1	0.1	19	0.3	0	0	0	0.2	1.3	0
Medium sand (%)	0.1	0	0.2	36	0	0	0	11.7	8.7	0.4
Fine sand (%)	0.1	0	0	36	45	0	0	20	22	2
Very fine sand (%)	0.1	0	0	26	32	33	29	32	25	38
Silt (%)	0	0	0	0.2	23	67	71	35	42	59
Emergent vegetation (%)	0.1	0.1	38	53	34	80	65	37	16	11
Floating-leaved vegetation (%)	0	0	0	0	0	0	0	0.1	0	0.4
Submerged vegetation (%)	12	16	0.16	0.2	0.8	0	0	0.2	13	0.2
Vegetation cover (%)	8	17	54	3	53.2	85	65	40	46	17
Open water (%)	92	83	46	97	46.8	15	35	60	54	83
Mean vegetation height (cm)	26 (3.86)	42.24 (5.42)	42.26 (4.47)	55.07 (2.68)	42 (1.61)	59 (0.87)	91.83 (4.48)	53.27 (1.03)	82.34 (3.34)	80.73 (2.33)
Vegetation height <15 cm	31.1	76.87	81.08	25.3	70.31	52.34	54.51	84.94	70.2	99.62
Vegetation height 16-25 cm	24	21.2	53.4	37.8	15	6.9	0	7.8	24	11.94
Vegetation height 26-50 cm	6	13.6	1	2.3	8	30	34.3	21.6	30	0
Vegetation height 51-100 cm	2	11.1	13.2	5.6	20	42	0	4.68	10	12

Table 5 Spearman's rank correlation coefficients r_s for the relative abundance of larvae and environmental variables. * Values significant at $P_{0.01}$ ($n = 10$). Correlations were based on data collected on larvae and environmental variables across habitats, during one month.

Variables	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. stictica</i>
Water temperature (°C)	-0.184	0.380	0.335	0.242
Dissolved oxygen (%)	-0.380	-0.172	0.305	-0.230
pH	-0.165	-0.165	0.508	-0.013
Turbidity (cm)	-0.212	-0.037	0.218	-0.225
Water area (m ²)	0.868 **	0.053	-0.472	0.546
Water depth (cm)	0.696 *	0.574	0.048	0.320
Water width (cm)	0.836 **	0.404	-0.301	0.456
Surface velocity (cm/s)	-0.049	0.369	0.634	0.004
Benthic velocity (cm/s)	-0.070	0.339	0.803 **	0.103
Mean velocity (cm/s)	-0.099	0.400	0.726 *	0.004
Boulders (%)	-0.044	0.024	0.816 **	0.295
Large cobble (%)	-0.390	-0.319	0.400	-0.247
Small cobble (%)	-0.390	-0.319	0.400	-0.247
Large pebble (%)	-0.390	-0.319	0.38	-0.247
Small pebble (%)	-0.067	-0.046	0.227	0.064
Coarse gravel (%)	-0.265	-0.210	-0.008	-0.083
Medium gravel (%)	-0.265	-0.210	0.046	-0.083
Fine gravel (%)	0.246	-0.042	-0.373	0.093
Very coarse sand (%)	0.138	-0.199	-0.313	-0.046
Coarse sand (%)	0.406	-0.347	-0.081	0.367
Medium sand (%)	0.680 *	0.223	0.271	0.723 *
Fine sand (%)	0.789 *	0.439	0.102	0.464
Very fine sand (%)	0.144	0.675 *	-0.003	0.109
Silt (%)	0.000	0.234	-0.276	-0.105
Emergent vegetation (%)	0.116	-0.217	-0.473	0.278
Floating-leaved vegetation (%)	0.180	0.862 **	0.307	0.253
Submerged vegetation (%)	0.208	0.008	0.319	-0.088
Vegetation cover (%)	-0.281	-0.127	-0.808 **	-0.469
Open water (%)	0.281	-0.127	-0.808 **	-0.469

2.4 Discussion

2.4.1 Oviposition sites

Adult were probably correlated with water area because they were selecting suitable oviposition sites. Species of Odonata can respond to water area, selecting larger over smaller areas (Wildermuth, 1992). This was the case for *T. dorsalis*. Observations made at other sites also showed this species ovipositing over a large expanse of water, often far from the edge. Some species may select large areas of water because they have a large territory. This did not explain the correlation of these species with large areas of water. Their territory size was at maximum, only about 3 m (Osborn, 1992). Some species may even prefer to oviposit in small water bodies (Fox, Jones & Holland, 1992).

The length of uninterrupted shoreline may also be important to riverine species (Corbet, 1962; Parr, 1983). *Trithemis donaldsoni* (Calvert) and *Trithemis annulata* (Beauvois), for example, prefer long straight stretches of water (Corbet, 1962). *Trithemis furva* was however probably not strongly correlated with stream length, as it was not strongly correlated with area or width of water. Adults may therefore be responding to visual cues indicating the suitability of a habitat for eggs and larvae. They may be visually able to assess levels of turbidity, and the presence of fish. They may also be attracted by the reflecting surface of the water. As no tactile examination of the water, or emergent plants was noted, it was concluded that selection of oviposition sites was primarily visual. Such tactile responses however, were seen in a libellulid by Wildermuth (1992).

Larger water areas also are of greater permanence than smaller areas. The degree of permanence of a water body can influence the distribution of Odonata (Cannings & Cannings, 1987). It is important for adults to select and colonize ponds where conditions for larvae are optimal, because larvae live longer and are unable to move away from a habitat in times of adversity (Osborn, 1992).

Wildermuth (1992) has already suggested that Odonata may react to visual cues when selecting an oviposition site. There is some evidence that *T. arteriosa* has an even stronger preference for large areas of water than *T. dorsalis*. This was the case in a study on assemblages at ponds (Osborn, 1992). The absence of *T. arteriosa* from the small pond at the Botanic Gardens for most of the season, also suggested this.

Trithemis arteriosa also did not occur in swamps (Pinhey, 1976), and was found in streams and a reservoir, but was more abundant at the reservoir (Miller & Miller, 1991). It occurred at running and still waters (Dumont & Al-Safadi, 1991; Miller & Miller, 1991), but was more abundant at the larger area and still waters (Miller & Miller, 1991). This agrees with the results here, with adults preferring the large dam.

Choice of oviposition site may be influenced by factors other than the quality of the site (Gibbons & Pain, 1992). The correlation of *T. furva* larvae with benthic current was possibly because of a greater need for oxygen by eggs and larvae. Oxygen availability does increase in moving water (Gibbons & Pain, 1992). Water temperature also fluctuates less in water with a high flow rate (Gibbons & Pain, 1992). The other species were negatively correlated with benthic current. Steytler and Samways (1995) also found that *T. arteriosa* and *T. stictica* were negatively correlated with flowing water. The absence of larvae in flowing water suggested that these species favoured slow-flowing or still water.

Exophytically ovipositing species are also selective in choice of oviposition site, because the placement of eggs in the environment decides the conditions under which larvae live.

The distribution of oviposition sites has important consequences for aggressive interactions. This is because the more clumped the sites, the more intense these interactions (Conrad & Pritchard, 1992), and the greater the likelihood that

individuals will be displaced. With *T. arteriosa*, it may benefit females to oviposit in sites where densities are lower. This may explain the occurrence of larvae in the river. Oviposition was only seen to occur once in the river. Females may also be able to outcompete other females for the best oviposition sites, where sites are limited (Fincke, 1992). This was unlikely to be the case for *Trithemis* because all species used different sites. Anisoptera may therefore show flexible oviposition behaviour as an adaptation to high intraspecific competition (Martens, 1991).

Copulating pairs may be at greater risk from predators because they are perhaps easier to catch than single individuals in flight. Nevertheless, recent studies have shown the opposite (Gwynne, 1989). Predation risk is not limited to copulating pairs, but is associated with all stages of reproduction (Magnhagen, 1991).

2.4.2 *Thermoregulation*

There were strong positive correlations in all species except *T. furva*, with the number of hours of sunshine per day. Stewart (1993) also found that *T. kirbyi ardens* occurred in sunny exposed conditions, and Steytler (1994) found *T. arteriosa* in sunny situations. Temperature is an important factor influencing the distribution of Odonata in South Africa (Brink, 1955), with most species preferring sunny, clear conditions (Pinhey, 1951).

Although *T. arteriosa* has a wide ecological tolerance and is widely distributed (Brink, 1955; Blackman & Pinhey, 1967), it never occurs in swamps or deep forest (Pinhey, 1976). *Trithemis kirbyi ardens* also prefers xerophilic conditions. In cloudy conditions, *T. arteriosa* and *T. dorsalis* perched on rocks and bare ground (Osborn, 1992). These species were heliophilic, and only found at sunny sites (Osborn, 1992). *Trithemis arteriosa*, *T. dorsalis* and *T. stictica* were also found by Steytler (1991), to be negatively correlated with shade. Because these species are perchers, spending less than 20% of their time in the air (Parr,

1983), they rely on postural adjustments, orientation to sunshine, and perching on an appropriate substrate to maintain body temperature (McGeoch & Samways, 1991; Osborn, 1992).

Trithemis adults need to maintain their body temperature high enough to meet the energetic demands of territorial defense (Fried & May, 1983). Being present in habitats having many daily hours of sunshine, means a longer period for reproductive activity. This is important because reproductive behaviour in Anisoptera is limited by energy requirements (May, 1984). Oviposition by females can represent a high energetic cost (May, 1984). This would especially be the case for *Trithemis*, because males hover while mate guarding females. Hovering while mate guarding was also thought to be energetically expensive by Sherman (1983). The proportion of time spent hovering may however be reduced at high temperature (May, 1987).

Selection of microhabitats suitable for thermoregulation is probably the most common form of thermoregulation in ectothermic insects (May, 1979). Species often select rocks and bare ground as basking surfaces (May, 1979). The preference of *T. stictica* for the marsh, may have been because it can better tolerate shady conditions than the other species. It may be that the species prefers dappled shade rather than completely shaded conditions. Evidence also comes from the fact that it was the only species to occur at a forested, shaded pond (Osborn, 1992). It is however, also known to favour swampy conditions (Pinhey, 1967, 1976). *Trithemis arteriosa* was positively correlated with tall grass (> 50 cm high) (Steytler & Samways, 1995), but no significant positive correlation was found here.

Territorial behaviour is limited by low environmental temperatures (May, 1987). This could be through temperature indirectly effecting food availability and female activity. *Trithemis annulata* (Palisot de Beauvois) was reproductively active at temperatures of 35°C, and could orient its body to reduce or expose the surface to the sun (Dell'anna, Utzeri & Belfiore, 1990). Observations at the site

showed that at least *T. arteriosa*, *T. dorsalis* and *T. stictica* also adopted this position. The Libellulidae are one of the most sun-loving families of Odonata (Tillyard, 1917).

2.4.3 Perch sites and territory defense

These species did aggressively defend territories. Species had to find suitable perches for establishing territories. There may have been species-specific preferences for particular perches, for example, coenagrionid damselflies selected plant stems of different diameters, according to their dimensions (Askew, 1982). Males may perch at different heights to avoid competition with other males (Cordoba-Aguilar, 1994). Most of the *Trithemis* species perched at a similar height. Only *T. furva* and *T. kirbyi ardens* established territories on rocks. All other species perched higher on emergent vegetation. Odonata adults may establish territories on specific plants. *Erythromma najas* (Hansemann), for example defended territories from floating vegetation (Fox *et al.*, 1992).

2.4.4 Microhabitats

There are probably two main factors influencing the occurrence of a species in a particular microhabitat, namely: food and protection from predators. The only species present exclusively in one microhabitat was *T. dorsalis*. This species hid under leaf litter in the dam, river and pond. The evidence suggests that this was an actual preference of this species. Perhaps because its preferred food, Chironomidae occurred most abundantly under leaf litter. Some Odonata do select microhabitats to reduce predation risk (Dionne, Butler & Folt, 1990). If species were concealing themselves from predators, this may have been because of the vegetation type. Hiding behaviour of damselflies in response to fish predators was related to habitat structure (Dionne *et al.*, 1990). The occurrence of *T. dorsalis* with *T. arteriosa* and *T. stictica* on substrate under submerged vegetation, could have suggested that there was no territorial interference between these species.

Other species were all closely associated with vegetation. There were fish (*Tilapia sparrmanii* Smith), in the dam. There was the potential for fish predation, as the *Tilapia* do prey on invertebrates (Skelton, 1993). This was possible because the fish were present in the shallows just beyond the emergent vegetation where many larvae were also found. Although larvae of these species were associated with aquatic vegetation. Rather, larvae of these species clung to submerged stems of emergent vegetation or occurred on the substrate beneath vegetation.

Trithemis furva was most often found climbing on *C. benghalensis* in flowing water. For this species, and *T. dorsalis*, microhabitat was the most important determinant of species distribution. This occurrence was not because of risk of fish predation, because although fish were found in the open river, none were present in the pond where both inhabited the same microhabitat as before. Vegetation may be selected because of a greater chance of finding food such as Ephemeroptera, Zygoptera and Culicidae. The need to attach firmly to a substrate in flowing water would also explain their selection for this microhabitat.

2.4.5 Selection for optimal conditions

Both adults and larvae were selecting conditions suitable for the larvae. The preferences of adults could be explained by a combination of thermoregulatory requirements and selection of oviposition sites. Individuals of some species may move from source (productive) habitats to less productive (sink) habitats (Pulliam & Danielson, 1991). Larvae occurred where they could obtain most of their preferred food, and be simultaneously protected from predators. There was therefore habitat and microhabitat partitioning among both stages of the life cycle. Consequently, actual competition between species was low. Rather the habitat and microhabitat partitioning evident in these species may reflect past competition.

2.4.6 *Habitat and food partitioning*

Habitat selection was determined by recognizing that species preferences may have changed with seasonal changes in habitats. The positive covariation in abundance of adults across the environmental gradient implied that species were not competitively excluded from habitats. Although some of the *Trithemis* species were partitioning the habitat and microhabitat, others which favoured the same habitat may have coexisted by partitioning prey. Species may segregate according to the size, taxon or hardness of food. Linked with food partitioning is substrate and vegetation, because prey will occur on specific substrates. Experimental tests of substrate preferences would provide further evidence of microhabitat partitioning among species.

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Appendix 1. The relative abundance of (a) adults (maximum relative abundance for 50 each month), and (b) larvae (total abundance), from September 1993 to June 1994.

(a)					
Months	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. kirbyi ardens</i>	<i>T. stictica</i>
September	27	5	11	3	6
October	38	9	14	1	3
November	54	14	17	3	16
December	66	12	15	3	15
January	45	12	6	4	13
February	57	7	7	0	11
March	64	14	7	1	17
April	71	10	10	0	6
May	28	8	1	0	0
June	8	0	0	0	0

(b)				
Months	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. stictica</i>
September	2	6	0	4
October	4	5	0	3
November	6	4	5	2
December	6	13	10	4
January	4	2	11	7
February	8	4	0	6
March	3	3	0	0
April	2	0	0	0
May	0	0	0	0
June	0	0	0	0

CHAPTER 3

Food and substrate preferences among larvae

ABSTRACT

Food and substrate preferences were investigated among larvae of species resident at the Botanic Gardens, Pietermaritzburg. Larvae were active hunters, choosing to catch and feed on particular prey species. Food preferences were investigated by behaviour choice experiments. *Trithemis arteriosa* and *T. dorsalis* showed more selectivity for prey than *T. furva* and *T. stictica*. Species fed on all the prey species provided, suggesting that they were not as selective of prey species as of size. Substrate preferences were similarly investigated in a laboratory choice experiment in which samples of substrate were provided. Vegetation and substrate preferences were analysed using the variance ratio test, Mann-Whitney test and Wilcoxon's signed rank test. There was no conclusive evidence to indicate that species preferred any specific substrate. However, when vegetation was added, species tended to occur among the vegetation, despite the underlying substrate.

3.1 Introduction

3.1.1 *Coexistence and food preferences*

Two Odonata species residing in the same habitat may occupy distinct microhabitats and feed on different prey species. This would facilitate coexistence between species. However, species may also differ in their abilities to capture the same prey such that one species feeds more on that prey taxon than the other. This would enable them to avoid exploitative competition. Food preferences may also change according to food availability such that species exploit a prey species which has rapidly increased in number. Predation is said to be selective if species consume prey species more frequently than they occur in the wild (Chesson, 1978). Unselective feeders may be better able to coexist because neither is limited to a specific prey type. Prey species that are eaten may vary depending on the season and growth of the larva (Lamoot, 1977; Blois, 1985a).

Odonata are unlikely to compete for food in productive habitats (Rehfeldt & Hadrys, 1988), particularly as they are obligate, generalist predators eating any prey taxon within a specified size range (Corbet, 1962). Food size may be important because species are morphologically limited in what they can handle and ingest. Food may differ in ease of manipulation and handling. For instance, the integument of an Oligochaeta may be harder to puncture than that of a Chironomidae. Prey species may also not be equally visible to the larvae. Feeding may also make species vulnerable to predation if they hunt where predators are abundant, and if their body movements render them conspicuous.

It was important to examine substrate preferences at the same time as food preferences because the species may live where it can easily find food, and attain camouflage from visual predators. Species will aggregate on their preferred substrate. This may lead to competition for space and for prey species concealed on the substrate. Overexploitation of the food source may intensify intraspecific

predation. Food preferences of different-sized individuals are likely to be different because of morphological constraints.

3.1.2. *Aims of the study*

The aim of this investigation was to investigate species-specific preferences for food, substrate, and vegetation, which could allow species to coexist where they share the same habitat.

3.2 Materials and methods

3.2.1 *Food preferences experiment*

The food preferences experiment was conducted during the week beginning 27 December 1993. The first test was one of size-selective predation. Some Odonata larvae are able to eat prey of different size, while others are limited to a narrow size range. *Crocothemis erythraea* (Brullé) and *Orthetrum julia falsum* Longfield for instance, will readily consume prey ranging in size from a larval *Culex* sp. (6-9 mm), to a larva of *Rana angolensis* Bocage (15-30 mm) (personal observation).

The experiment here was designed to test if *Trithemis* species were limited by the size of prey on which they fed. Three aquaria were used for the experiment. Each aquarium was 60 cm x 30 cm in size. Aquaria were filled up to 25 cm with tap water which was aerated using an electrical pump. The aquaria were left for two days to allow the water temperature to equilibrate with that of the insectary. A layer of commercial gravel (2 cm thick), was added to the base of each aquarium. Final instar larvae in the size range (16.0-18.0 mm) were used in the experiment. Larvae of *T. dorsalis*, *T. furva*, *T. stictica* and *T. arteriosa* were placed in each aquarium at different times. There were two treatments. This was necessary because the small prey species may have been preyed on by larger species, which would have biased the results.

In the first treatment, larvae of species from the following families were used: Chironomidae, Culicidae, Zygoptera, and Ephemeroptera were added. This was the smaller prey category (body length 3.5-9 mm). The larger prey category consisted of *Tubifex* sp. (Oligochaeta), *R. angolensis* (Amphibia), and *Notonecta* sp. (Notonectidae) (size 10-15 mm). These prey species were chosen for the experiment because they were found in the habitat where the larvae were present, and could have been prey of the larvae. The prey were collected outside the study area in other ponds at the Botanic Gardens, to prevent biasing the study.

Twenty individuals of each prey species were introduced into each aquarium. The larvae were starved for 24 hours before being placed in aquaria. They were then placed in the aquaria for 48 hours, after which the amount of prey remaining was noted. Nine larvae of each *Trithemis* species were used in the experiment. Three larvae of each species were placed in each aquarium. Intraspecific interference among larvae was not recorded. There were three replicates of each treatment. Individuals were chosen using a random number table. Larvae and exuviae used in the experiments were later preserved in 75% alcohol. Inter-sex differences were not tested for because there were not equal numbers of males and females.

Specific food preferences within the small size range, were investigated by means of a cafeteria experiment. In this type of experiment, individuals are provided with a choice of foods with the most preferred food being selected first. Larvae of only four of the species were present, namely: *T. arteriosa*, *T. dorsalis*, *T. furva* and *T. stictica*. The potential larval prey species found in the habitat where the species occurred, were: *Chironomus* sp., *Culex* sp., *Baetis harrisoni* (Barnard) and *Enallagma glaucum* (Burmeister). All individuals selected were about 8 mm in length. Final instar larvae were collected from various sites around Pietermaritzburg. Larvae were starved for 24 hours before the start of the experiment. Larvae were maintained in small plastic containers in aerated aquaria, until needed for the experiment.

Prey were provided in equal proportions, that is in a 1:1 ratio (with a total of four individuals being added), present in the wild. Four jars were half filled with tap water. Prey taxa were added to each jar before the larvae were added. Individuals of the different *Trithemis* species were randomly selected and placed into a jar. The time was taken, and the larvae watched until they caught and ate one of the prey. The prey species consumed at five minute intervals, until 20 minutes had elapsed, was recorded. Fifteen individuals of each species were used. There were not enough larvae in the wild to investigate differences between sexes. The sex of individuals was therefore not considered. To determine if food preferences changed when the density of prey changed, the proportion of *Culex* sp. was increased relative to the other taxa. The procedure discussed above was then repeated.

Food preferences of dragonfly larvae were investigated in the past by gut dissection, or examination of faecal material. Gut dissection has the disadvantage of the larvae having to be killed. Larvae of *T. arteriosa*, *T. dorsalis*, *T. furva* and *T. stictica* were collected from another pond at the study site. They were maintained in small containers, until expulsion of faecal pellets. These were then dissected and attempts made to identify the foods eaten. However, food was too finely fragmented to be recognized. Faecal pellet examination might also overestimate prey that have many sclerotized body parts.

3.2.2 *Substrate preferences experiment*

This experiment, and the next were conducted in the week beginning 3 January 1994. Twenty individuals of each of the four species were used in the substrate preferences experiment, 10 in the experimental and 10 in the control. Two aquaria were used for the experiment. Samples of different substrate were collected from the Botanic Gardens from all the available habitats in which larvae were found. A 10 cm² sample of each type of substrate: mud, sand, pebble, and gravel, was placed in one of the two aquaria. There was not enough time to test for species preferences for specific substrates, therefore only these four broad

categories were used. The location of each sample of substrate was randomly arranged in one aquarium. The second aquarium was used as a control for any preferences which species may have had other than for substrate. Aquaria were divided into eight numbered blocks. Aquaria were half filled with tap water and aerated using an oxygen pump. No other individuals were introduced into the aquaria, and the substrate was washed and examined for the presence of any other macro-organisms. Larvae were maintained in an oxygenated aquarium until the experiment began. Larvae were all of the late instar recognized as such by the development of the wing sheaths (Gardner, 1960). Differences between sexes were again not investigated. Substrate was classified on the basis of particle size, using the Wentworth scale as described in chapter 2.

Trials were conducted on each species separately. In each trial, one individual was randomly selected for the control aquarium and one for the experimental aquarium. Both larvae were placed in the centre of the tank to avoid biasing the results. Larvae were left for two hours, and the block in which they occurred, noted. Food was not introduced to avoid biasing the results.

3.2.3 *Vegetation preferences experiment*

This experiment was conducted in the same way as the substrate preferences experiment. Ten individuals of each species were used in the experiment. The same four species were used in this experiment, as above. Again two aquaria were used, one as a control, and one as an experimental arena. The same system of dividing the aquaria into blocks was used. There were four treatments, *Elodea densa* (Planchon), *C. benghalensis*, leaf litter from *Eucalyptus* sp., and substrate (commercial gravel). During all the experiments, room temperature was maintained at 25-26°C, and relative humidity at 60-70%. Illumination was from directly above from neon lights ensuring that there was no directional influence because of light or temperature.

3.2.4 *Trithemis* species correlations with potential prey/predator species

Relative abundances of larval *Trithemis* and prey species were determined over 11 months in the field, in order to calculate the correlation between species and food. Prey species included mainly: *Austrocaenis capensis* Barnard, *Baetis harrisoni* Barnard, *Culex* sp., *Chironomus* sp., and *Enallagma glaucum* Burmeister.

3.2.5 Analysis

The substrate preferences experiment could not be analysed using the Chi-square goodness-of-fit test because there were insufficient degrees of freedom (Ludwig & Reynolds, 1988). Preference for substrate was instead analysed using the variance to mean ratio test. The variance ratio test was used to test if the distribution of individuals among blocks in aquaria was random. A significantly nonrandom distribution would indicate a possible preference for one side of the aquarium, or one type of substrate. The analysis was conducted as described in Elliott (1977), and significance tested using the Chi-square statistic.

The Wilcoxon's test was used to substantiate if a species preferred substrate more than vegetation, and Mann-Whitney was used to test for extraneous influences, or a similar response in both control and experimental aquaria. Data on larval position on substrate was used in both these analyses. Such nonparametric tests as these, have the advantage over parametric tests by not making any assumptions about the underlying distribution of the data (Potvin & Roff, 1993). They are also more powerful than parametric tests when the distribution is not normal (Potvin & Roff, 1993). For species such as *T. arteriosa*, a significant value may not be found because the test was designed to detect only specific preferences for vegetation.

In cases where the variance ratio test was non-significant the Mann-Whitney test was used for deciding if where the variance ratio test was non-significant, that individuals responded similarly in both aquaria to an external influence. Only

T. arteriosa was tested in this way because there was no significant influence of either substrate or vegetation. This is more powerful than the *t*-test when data are nonparametric, and can be used on small samples (Zar, 1984; Neave & Worthington, 1988). The Wilcoxon's signed rank test was mainly used for species where the variance ratio test was significant. It was used to test whether the species showed a stronger preference for vegetation than substrate. The analyses for these tests were done using computer programs written in Turbo Pascal 5.0. Spearman's rank correlation coefficients were calculated between the relative abundance of larvae and other invertebrates. It could then be determined based on larval data collected in the field that larvae were changing their relative abundance according to food availability. Calculations were performed using the computer program SPCOVAR.BAS (Ludwig & Reynolds, 1988).

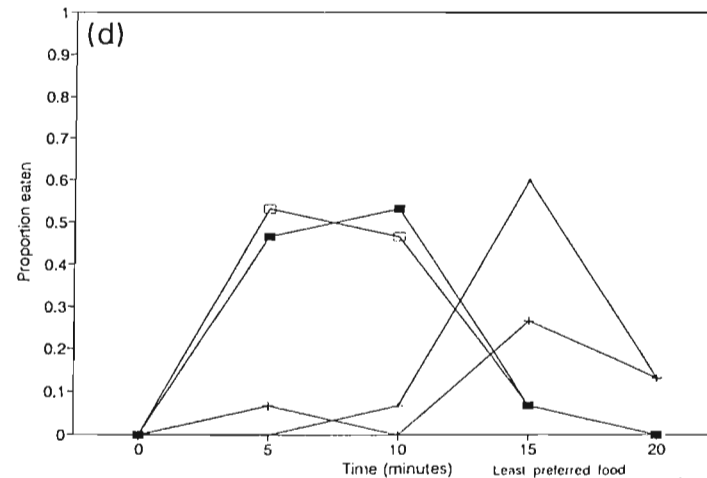
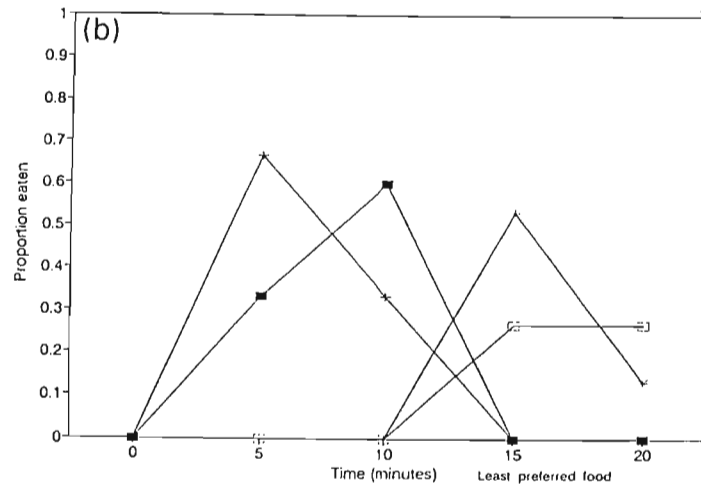
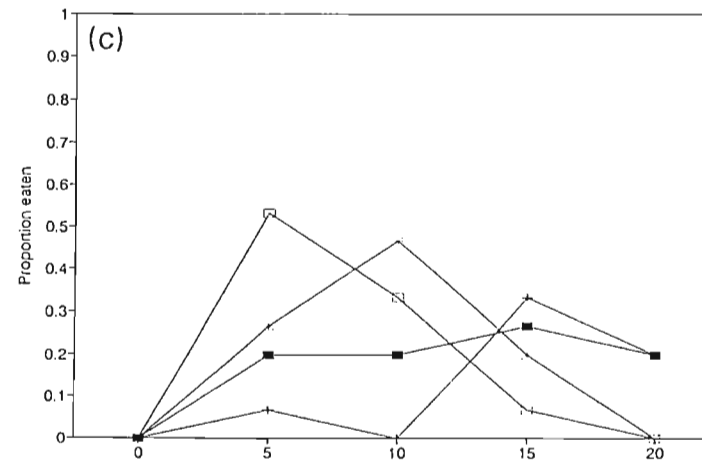
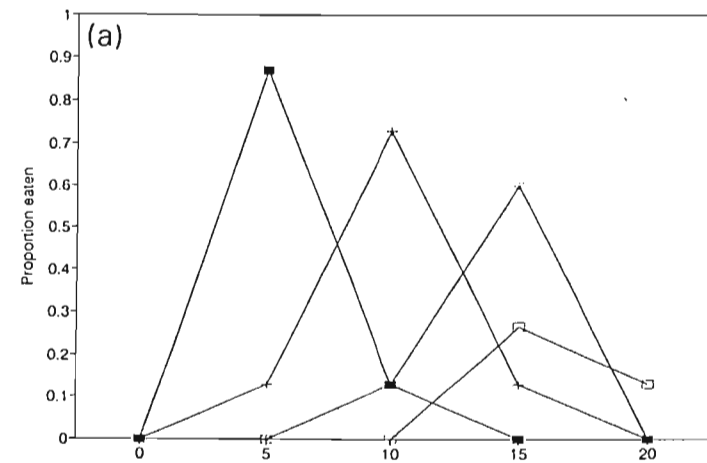
3.3 Results

3.3.1 Food preferences

Results from the size-selective predation experiment are summarized in table 1. It is clear from the table that species did not feed on large prey (i.e. greater than 10 mm in length). Species were also less inclined to feed on *E. glaucum* than the other taxa in the small size category. *Trithemis arteriosa* preferred *B. harrisoni*, while *T. dorsalis* preferred *Chironomus* sp. (Fig. 1a & b). *Trithemis furva* and *T. stictica* chose to feed on *E. glaucum* first. In both these species *Chironomus* sp. individuals were eaten last (Fig. 1c & d). These apparent preferences weakened when the proportion of *Culex* sp. was increased relative to the rest of the prey. *Culex* sp. were clearly selected first (Fig. 2). The next food to be selected by *T. arteriosa* and *T. dorsalis*, were their original choices of *B. harrisoni* and *Chironomus* sp., respectively (Fig. 2a & b). The results showed flexibility by species in their choice of food. Significant tests were not calculated because the sample size was too small, because not all larvae were present and abundant at the same time.

Table 1. Results of the size-selection food experiment. Values indicate the number of individuals (out of 20 that were introduced), remaining after 48 hours. Taxa marked with an asterisk were larger than 10 mm ($n = 9$).

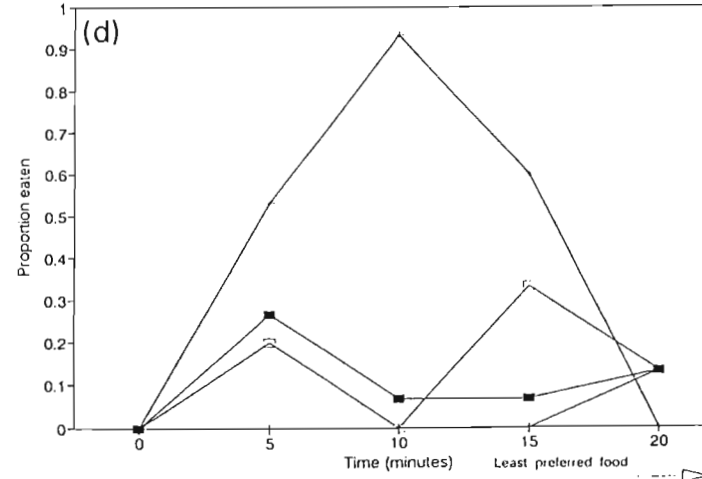
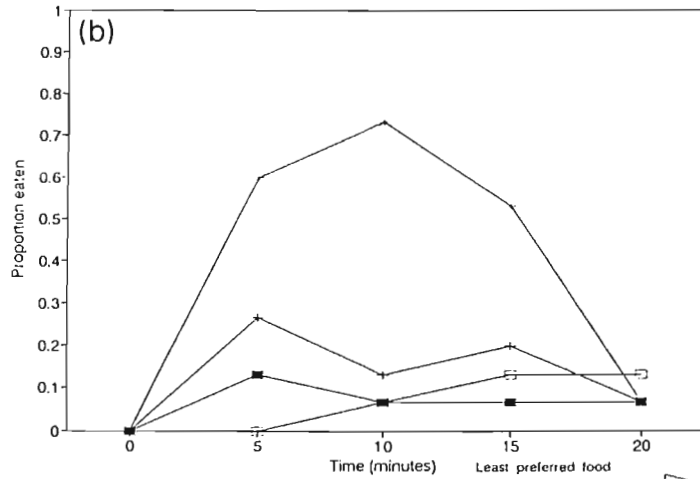
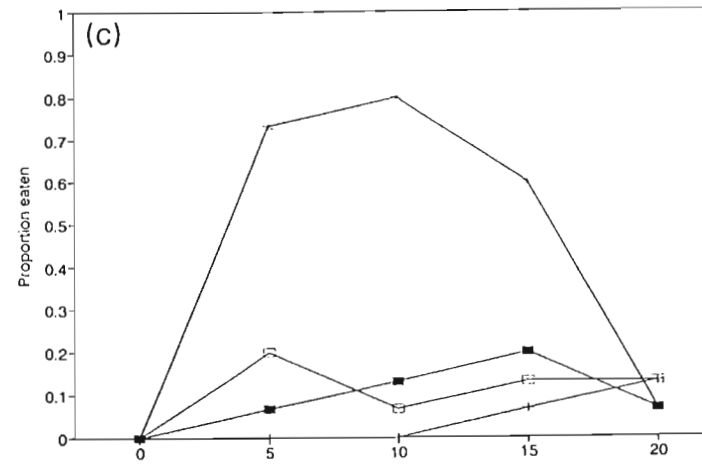
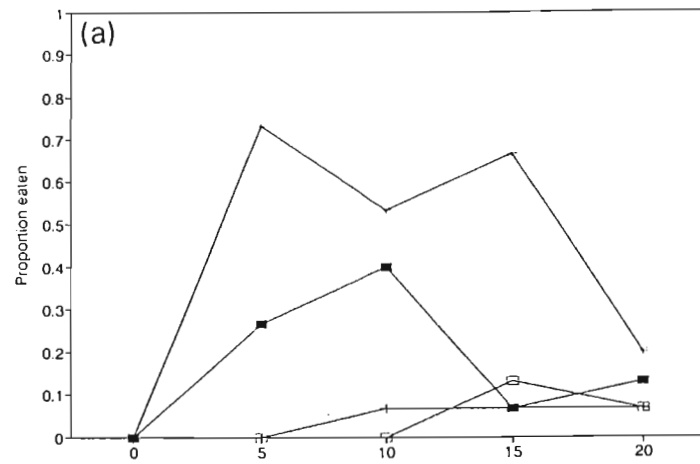
Species	<i>B. harrisoni</i>	<i>Chironomus</i> sp.	<i>Culex</i> sp.	<i>E. glaucum</i>	* <i>R. angolensis</i>	* <i>Notonecta</i> sp.	* <i>Tubifex</i> sp.
<i>T. arteriosa</i>	0	0	5	9	20	20	20
<i>T. dorsalis</i>	3	1	0	18	20	20	20
<i>T. furva</i>	0	2	0	11	20	20	20
<i>T. stictica</i>	2	0	1	6	18.5	20	20



■ *B. harrisoni* ▲ *Chironomus sp.* ● *Culox sp.* □ *E. glaucum*

■ *B. harrisoni* ▲ *Chironomus sp.* ● *Culox sp.* □ *E. glaucum*

Fig. 1. The proportion of each prey species eaten by larvae at various time intervals. The most preferred food was that of which most was eaten in five minutes. (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. stictica*. There were 15 individuals of each species used in the experiment. Prey species are shown in the legend below figures.



■ *B. harrisoni* + *Chironomus sp.* — *Culex sp.* ▴ *E. glaucum*
 Least preferred food →

■ *B. harrisoni* + *Chironomus sp.* — *Culex sp.* ▴ *E. glaucum*
 Least preferred food →

Fig. 2. The proportion of each prey species eaten by larvae at various time intervals. *Culex sp.* was the most preferred food when it was more abundant. (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. stictica*. There were 15 individuals of each species used in the experiment. Prey species are shown in the legend below figures.

3.3.2 Substrate preferences

Species preferring mud were *T. dorsalis*, and *T. stictica* (Fig. 3). This was also shown by their significantly nonrandom distribution in the experimental aquarium compared with the individuals in the control aquarium (Table 2). *Trithemis stictica* showed a highly significantly nonrandom location in the experimental tank (Chi-square = 23.6**, 7 d.f., $P < 0.01$). Although the other two species were found more often on substrates with a larger particle size (Fig. 3), the variance ratio test results were non-significant (Table 2). The Mann-Whitney test showed that *T. arteriosa* did not select the same areas in the experimental versus control aquaria (i.e. the result was non-significant) ($U = 41.50$, $n = 8$, $P > 0.05$). *Trithemis arteriosa* and *T. furva* occurred more often on gravel in the experiment than on any other substrate (Fig. 3). These two species preferred a larger particle size than the other two.

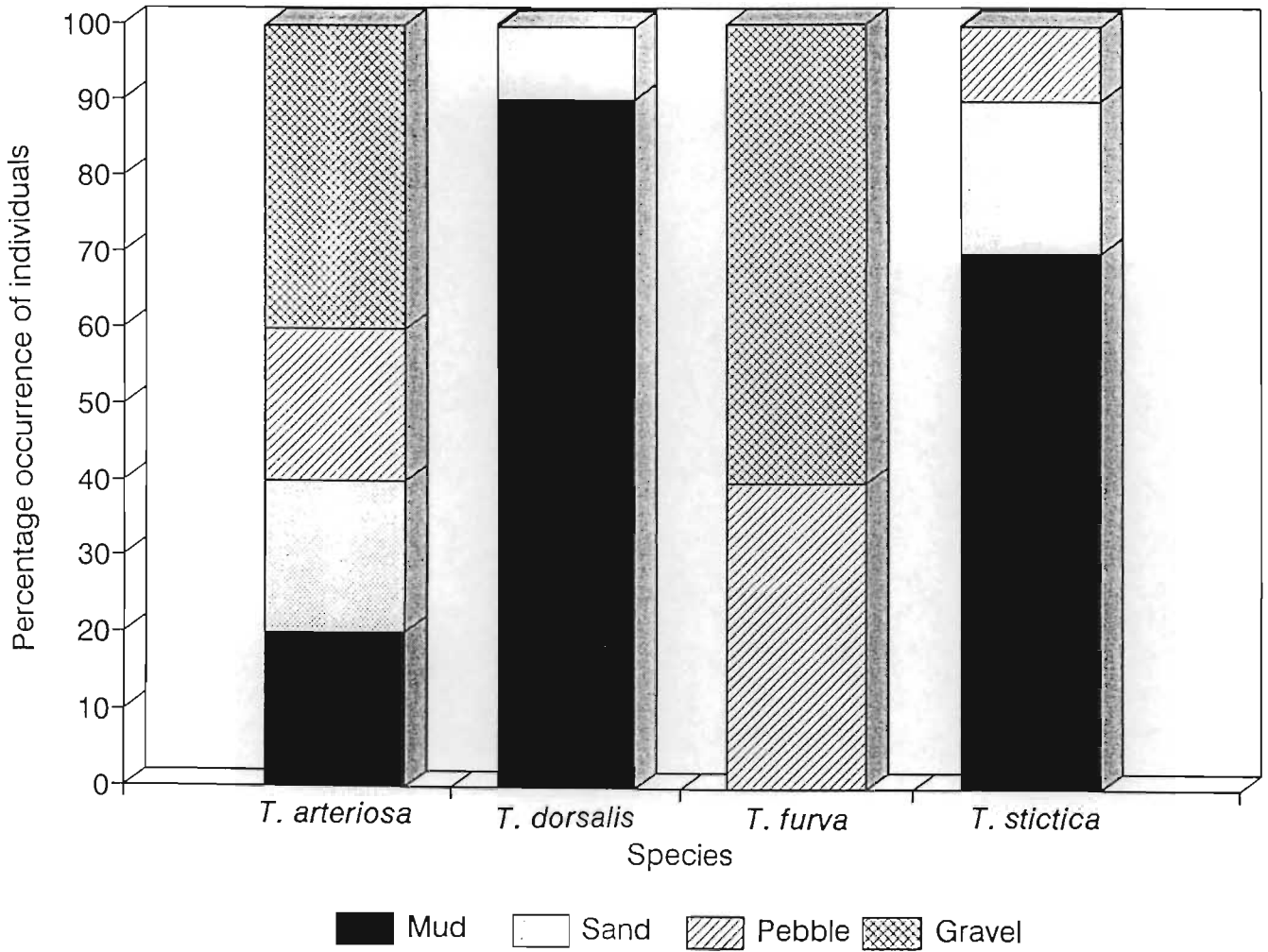


Fig. 3. The percentage occurrence of larvae on different substrates, indicating the strong preference of *T. dorsalis* and *T. stictica* for mud. Ten individuals of each species were used in the experiment.

Table 2. The substrate choice experiment results indicating the number of larvae located on each type of vegetation. The variance ratio test index and Chi-square statistic are given. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$. Ten individuals of each species were used.

Substrate	<i>T. arteriosa</i>		<i>T. dorsalis</i>		<i>T. furva</i>		<i>T. stictica</i>	
	Control	Experiment	Control	Experiment	Control	Experiment	Control	Experiment
Mud	1	2	2	4	2	0	3	2
Sand	1	1	0	1	2	0	1	1
Pebble	0	2	1	0	1	2	3	1
Gravel	3	1	1	0	1	4	0	0
Gravel	1	3	1	0	0	2	1	0
Mud	0	0	2	5	3	0	1	5
Sand	2	1	1	0	1	0	1	1
Pebble	2	0	2	0	0	2	0	0
Mean	1.250	1.250	1.250	1.250	1.250	1.250	1.250	1.250
Variance	1.071	1.071	0.500	4.214	1.071	2.214	1.357	2.786
Index	0.857	0.857	0.400	3.371	0.857	1.771	1.086	2.229
Chi-square	6	6	2.8	23.6 **	6	12.4	7.6	15.6 *

3.3.3 Vegetation preferences

Trithemis furva showed the strongest preference for *C. benghalensis* (Fig. 4). *Trithemis dorsalis* was strongly associated with leaf litter (Fig. 4). These two preferences were very distinct and considered a part of the microhabitat preferences of these species. Unlike in the substrate experiment, *T. furva* was significantly not randomly distributed with respect to vegetation (Table 3). All the species except *T. arteriosa* were significantly associated with vegetation (Table 3). Despite this, *T. arteriosa* still occurred mainly where vegetation was present (Fig. 4). This species did not appear to prefer either *E. densa* or *C. benghalensis* more. The Mann-Whitney test again indicated that there was no external influence on the distribution of this species in the control versus experimental aquarium ($U = 80.20$, $n = 8$, $P > 0.05$) (Table 3).

The Wilcoxon's signed rank test showed that species preferred living vegetation to substrate and nonliving vegetation. For *T. dorsalis* ($T_- = 8^{**}$, $n = 8$, $P < 0.01$), *T. arteriosa* ($T_- = 16^{**}$, $n = 8$, $P < 0.01$), *T. stictica* ($T_- = 18^{**}$, $n = 8$, $P < 0.01$). Although *T. arteriosa* was never significantly not randomly distributed in either experiment, it still had a stronger preference for vegetation than for substrate (Fig. 3 & 4).

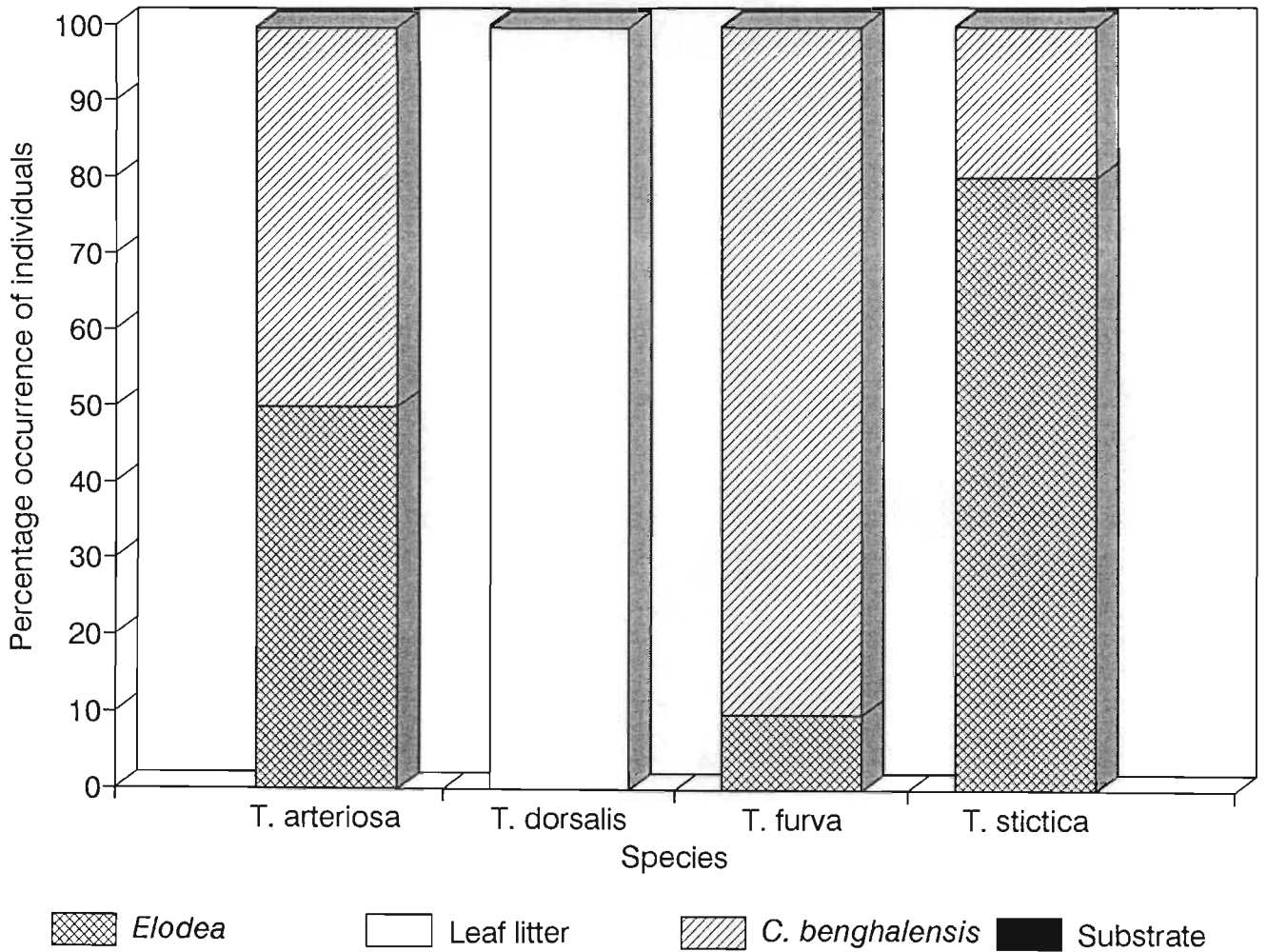


Fig. 4. The percentage occurrence of larvae near different types of vegetation, indicating the strong preference of *T. arteriosa* and *T. furva* for *C. benghalensis*. Ten individuals of each species were used in the experiment.

Table 3. The vegetation choice experiment results indicating the number of larvae located near each type of vegetation. The variance ratio test index and Chi-square statistic are given. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$. Ten individuals of each species were used.

Vegetation	<i>T. arteriosa</i>		<i>T. dorsalis</i>		<i>T. furva</i>		<i>T. stictica</i>	
	Control	Experiment	Control	Experiment	Control	Experiment	Control	Experiment
<i>E. densa</i>	2	3	1	0	1	0	0	4
Leaf litter	0	0	1	6	0	0	0	0
<i>E. densa</i>	2	2	3	0	0	1	2	4
<i>C. benghalensis</i>	1	3	0	0	3	5	2	2
Substrate	0	0	0	0	2	0	3	0
Leaf litter	3	0	2	4	2	0	1	0
<i>C. benghalensis</i>	2	2	2	0	1	4	2	0
Substrate	0	0	1	0	1	0	0	0
Mean	1.250	1.250	1.250	1.250	1.250	1.250	1.250	1.250
Variance	1.357	1.929	1.071	5.643	1.071	4.214	1.357	3.357
Index	1.086	1.543	0.857	4.514	0.857	3.371	1.086	2.686
Chi-square	7.6	10.8	6	31.6 **	6	23.6 **	7.6	18.8 **

3.3.4 Correlations of final instar larvae and food in the field

Trithemis furva was significantly positively correlated with *Chironomus* sp. ($r_s = 0.825^{**}$, $n = 8$, $P < 0.01$). The final instar larvae of *T. dorsalis* were positively correlated with the seasonally changing relative abundance of *Austrocaenis capensis* Barnard ($r_s = 0.605$, $n = 8$, $P > 0.05$). It was also positively correlated with *Chironomus* sp. ($r_s = 0.531$, $n = 8$, $P > 0.05$). *Trithemis stictica* was strongly negatively correlated with *T. sparmanii* ($r_s = -0.822^{**}$, $n = 8$, $P < 0.01$). Although not significant at the 5% level, *T. arteriosa* was positively correlated with *Culex* sp. ($r_s = 0.634$, $n = 8$, $P > 0.05$), and *E. glaucum* larvae ($r_s = 0.643$, $n = 8$, $P > 0.05$).

3.4 Discussion

3.4.1 *Prey choice and morphological limitations*

Some predators may choose a range of prey sizes to feed on, because it takes too long to search for more energetically profitable items (Krebs & Davies, 1992). Therefore, a predator should select a prey item that offers the most energy relative to handling time (Krebs & Davies, 1992). The behaviour of predator and prey influence prey choice. A prey species may for instance, be selected because it is most often encountered by the predator and not because the predator actively hunts for it (Sih, 1993). This is why it was important to perform a cafeteria experiment and not simply an experiment measuring the number of prey remaining, as was done for the size experiment.

Species may be restricted by how much food they can process to provide adequate energy (Penry, 1993). A species may be more unselective if there is no advantage to be gained by feeding on one type of prey (Krebs & Davies, 1992).

3.4.2 *Feeding responses*

Some species respond to particular mechanical, chemical or visual cues when selecting prey (Shettleworth, Reid & Plowright, 1993). Odonata larvae either find prey by visual stimuli (usually the weed-dwellers), or by mechanical, tactile means (often bottom-dwellers) (Corbet, 1962). The *Trithemis* species are visual predators which actively stalk their prey. The small size of the antennae and many ommatidia of the compound eyes lends support to this. Because their prey are active, larvae have to chase after their food. They are flexible feeders feeding on whatever prey is abundant and of the correct size. Species can probably switch to, or use tactile means to assist prey detection in very turbid waters. Species that are visual predators may be limited to clear waters. *Anax junius* (Calvert) for example, can distinguish between the size and form of prey

organisms by responding to small movements of the prey (Corbet, 1962). Similar cues may be used by *Trithemis* species when selecting prey. How actively they hunt for prey may also depend on their level of starvation. Odonata larvae may only actively hunt for prey when prey is scarce, or larvae are starved. This might occur in *Trithemis* species, with species adopting a sit-and-wait mode of feeding when food is abundant. Odonata larvae may also forage more if prey is less active (Harvey & White, 1990).

3.4.3 *Feeding and development*

Many Odonata are generalist feeders, preying on a variety of invertebrates from Copepoda and larval Ephemeroptera to Oligochaeta (Crowley, Nisbet, Gurney & Lawton, 1987). Prey is often eaten in proportion to their relative abundance (Crowley *et al.*, 1987). This was found to occur in *Trithemis*, with individuals selecting *Culex* sp. because they were the most abundant prey.

Odonata species feed on smaller prey during the earlier instars, than during the later instars (Crowley *et al.*, 1987). However, smaller prey may be eaten by larger individuals because they are easier to catch (Blois, 1985b). Tillyard (1917), noted that early instar larvae could catch Cladocera with ease.

3.4.4 *Size-selective predation*

Attempts to rear these larvae using larvae of Amphibia and Notonectidae, has met with limited success, which showed that these species feed within a narrow size range. *Sympetrum fonscolombei* (Selys) readily engulfs larval Notonectidae, and even smaller individuals of the same species with little effort (personal observation from rearing). This species is similar in size (between 15-20 mm) (Carchini, 1983), to *T. dorsalis*, *T. furva*, and *T. stictica* (all between 16.5-19 mm) (Carchini, Samways & Caldwell, 1992). With such similarity in size *Trithemis* could be thought of as handling larger prey, but this was not so.

Catching efficiency, foraging tactic and ease of manipulation of food will also influence food choice.

Although most Odonata are considered generalist feeders (Corbet, 1962), the species in this study were quite specialized. They specialized on prey in a certain size range, but were then generalist in their choice within that range. The two species with the most distinct preferences were *T. arteriosa* and *T. dorsalis*. In both cases, the second choice was the preferred prey species for the other species of *Trithemis*. Odonata larvae may select prey of a certain size within a species. This may occur in the *Trithemis* species, or more likely, smaller larvae will feed on smaller individuals of the same prey.

3.4.5 *Prey visibility and interference*

One factor not considered in the experiment was the visibility of the prey taxa. It could be that *B. harrisoni* are more visible than *Chironomus* sp. in certain habitats, such that they are also preferred by *T. dorsalis* in that habitat. This was probably not the case here, because *Chironomus* sp. were the most abundant invertebrates in the leaf litter microhabitat to which *T. dorsalis* was restricted. No *B. harrisoni* were found under leaf litter.

It has been found that larvae can exclude each other from areas of food concentration (Baker, 1981). The results of the experiments in this study only indicate preferences without interference by other larvae. In the wild, territorial larvae could exclude individuals of the same or other species from food. Exclusion has been found to occur among species of *Ceonagrion resolutum* (Selys) (Baker, 1981).

3.4.6 *Seasonal changes in food availability*

It may only be advantageous to be selective if a prey species becomes more abundant and easy to catch. This was the case with the *Trithemis* species which consumed more *Culex* sp. compared with their usual preferences (Fig. 2).

Although larvae of some species of *Trithemis* were correlated with prey over time, this could have been a consequence of a mutual response to seasonal changes. This is difficult to evaluate because of the diversity of prey species in any one habitat (Crowley *et al.*, 1987).

Food preferences may change with seasonal changes in the availability of prey species in the habitat. Dudgeon (1989), for instance, found that there were seasonal changes in the diet of some Odonata larvae. All four *Trithemis* species ate individuals from each prey taxon suggesting that they may easily switch prey in times of adversity.

3.4.7 *Substrate preferences*

Reice (1980), has shown that species may prefer leaf litter whatever the underlying substrate. This was the case for *T. dorsalis*, which favoured leaf litter over mud.

It may not be a question of substrate choice *per se*, but rather the attraction of prey *Trithemis*. Larvae displayed active visual hunting of prey, and could move onto a different substrate while in pursuit of prey. When food is abundant, these species may revert to being sit-and-wait predators and become restricted to one type of substrate. The habitat distribution of some Odonata larvae was determined by substrate characteristics (Dudgeon, 1989). This was also the case for *T. dorsalis* and *T. stictica*.

Larval preferences were not investigated in *T. kirbyi ardens* because there were few larvae at sites. In February, two individuals were found in the Blackboroughspruit, a small stream that flows intermittently. Both were found on pebbles where water was slow-flowing. This species could have preferred a certain type of substrate, but this could not be determined from two individuals. They were of different size which could mean that they prefer this type of substrate at all stages of development. An examination of habitat preferences of this species at various sizes may be useful for further study.

Some Odonata larvae prefer a particular substrate. *Paragomphus cognatus* (Rambur) larvae were found to prefer sandy sediments (Harrison & Elsworth, 1958; Oliff, 1960; Keetch & Moran, 1966). Harrison and Elsworth (1958) observed that *Trithemis* species occurred most often on mud and sand in the slower-flowing parts of the Great Berg River. Only very small larvae were found in the stony backwaters (Harrison & Elsworth, 1958). These were possibly early instar *T. furva* larvae. Small larvae of this species were found near the edge in the fast-flowing stream at the Botanic Gardens.

3.4.8 *Substrate choice and predation risk*

Larvae may occur less often on substrates exposed to high predation risk (Wellborn & Robinson, 1987; Pierce, 1988). This could be why *T. furva* preferred to hide under vegetation, rather than sit on exposed substrate. The negative correlation of *T. stictica* with fish (*T. sparmanii*) over the breeding season could show a greater sensitivity by this species to predation, than the other species.

3.4.9 *Flexibility in substrate choice*

It is difficult to assess substrate preferences by individual species because a preference for a substrate by a species may not be consistent (Minshall, 1984). Different stages of development can be associated with different substrates

(Minshall, 1984). Field experimental manipulations could be done to verify observed patterns of substrate preference.

3.4.10 *Preferences for aquatic macrophytes*

Species often showed a stronger preference for vegetation than substrate. The association of these species with vegetation matches their prey choices. Almost all the prey species they fed on were associated with aquatic vegetation.

Many Odonata larvae cling to, and climb on plants (Corbet, 1962). *Trithemis furva* larvae for instance, were restricted to *C. benghalensis* at the Botanic Gardens. The species in the genus *Trithemis* clearly showed this. Larvae inhabiting plant beds near the water surface are exposed to higher temperatures than bottom-dwellers, which may be necessary for rapid growth.

3.4.11 *Specificity of species for food, substrate and vegetation*

Although species favoured specific types of food, substrate, and vegetation, they were not averse to switching to other resources. Food choice may therefore be determined by availability of the prey taxa, if the prey is still small enough to enable efficient handling and ingestion. Substrate and vegetation choices are consequences of the presence of predators or prey. It was unlikely that larvae were displaced by related species, particularly as there was much substrate and vegetation heterogeneity.

3.4.12 *Food partitioning and development*

Apparent preferences for prey species changed with the availability of prey. Food partitioning with reduced intraspecific and interspecific competition may also be accomplished by species having displaced life-cycles. This is because different stages of development will feed on different species of prey. Different life-histories would ensure that the larvae of two species are not at the same stage of development, and therefore likely to compete for food.

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CHAPTER 4

Synchrony and asynchrony in the life-histories of *Trithemis*

ABSTRACT

Synchronous hatching, development and emergence were investigated using field work and laboratory studies. Synchrony can determine success in larval and adult stages under different conditions. The advantages of synchrony may be outweighed by that of asynchrony, particularly under conditions of size-selective predation and food scarcity. However, where densities are high, asynchrony can result in cannibalism of smaller individuals by larger individuals. All the species in this study had overlapping cohorts, although there was a synchronous mass emergence of *T. stictica* near the end of the season. The development rate of species was rapid in the field and laboratory. Growth rate, and ultimately development rate of individuals may be reduced by the presence of other individuals when food is limited. This would stagger the development causing different cohorts to occur together, despite synchronized hatching. Separation of life-cycles ensured that larvae of different species were not all of the same size. There was thus food partitioning which reduced interspecific competition.

4.1 Introduction

4.1.1 *Development and competition*

The wide range of sizes reached during development of dragonfly larvae can lead to interspecific and intraspecific interference (Crowley, 1984). Body size differences between species may influence the outcome of contests between larvae (Crowley, 1984), and hence determine which species is competitively superior. The competitive dominance of species may be determined by life-history responses to daily and seasonal changes (Grant & Dunham, 1990). Individuals with asynchronous development may be less adversely affected by exploitative competition than those developing in synchrony, because they will feed on prey of different sizes (see chapter 3). However, increased cannibalism among dense populations of individuals of different sizes, may negate these benefits. Cannibalism can also synchronize development by causing high mortality of small individuals (Crowley & Hopper, 1994). Seasonal temperature changes can also synchronize life-histories by influencing the degree of synchrony in development (Corbet, 1957). Synchronous emergence could be beneficial because it reduces predation, but may also cause competition for emergence-supports if many individuals emerge on the same day (Corbet, 1957, 1962).

Different life-history strategies allow species to partition resources temporally and spatially. Different generations and cohorts may be affected differently by competition, and flexible life-histories might ease survival in adverse conditions. Life-histories are therefore closely linked to competitive advantages of species. One strategy may enable one species to better exploit a habitat than another. There is enough evidence to show that different life-history strategies promote coexistence of species where they occur together (Sevenster & Van Alphen, 1993). A combination of life-history traits may therefore enable species to coexist where they occupy the same space

(Yafuso, 1994). Separation and displacement of life-cycles reduces competition for food between species (Carchini & Nicolai, 1984).

4.1.2 *Objectives of the study*

The aim of this study was therefore to examine the life-histories of the four resident species, to determine the degree of synchrony of each stage. The purpose was therefore to ascertain egg hatching, development, and emergence patterns. Oviposition behaviour, hatching of eggs, development rate, and emergence were examined. This enabled determination of voltinism, and life-history strategies.

4.2 **Materials and methods**

4.2.1 *Study area*

The Blackboroughspruit (37°10'S, 24°45'E) (650 m a.s.l.) and Dorpspruit below the Botanic Gardens site, were used for collecting larvae, and mated females. Development and emergence were investigated at the Botanic Gardens.

4.2.2 *Sampling*

Adults and larvae were sampled as discussed in chapter 2. Populations were monitored from 4 August 1993 to 15 June 1994. The incidence of oviposition by species was recorded in different habitats, and over time. The head widths of larvae were measured using a pair of 150 mm x 0.02 mm Vernier callipers. Species identification in the field was made using a 9 x hand lens, and the key by Carchini, Samways and Caldwell (1992). Identification of species was verified by rearing out of larvae collected at the Blackboroughspruit, Dorpspruit and farm dam. Weekly collections of exuviae were made. Collections of exuviae are considered one of the best ways to determine the residency and

size of a population of Odonata (Moore & Corbet, 1990; Moore, 1991). Final instar larvae were identified by the development of wing sheaths and development of compound eyes (Gardner, 1960). Exuviae were placed in vials in 75% alcohol. Exuviae were identified and sexed as described for the larvae.

4.2.3 *Laboratory investigations*

The method of Tillyard (1917) was used to obtain eggs. Mated females of *T. arteriosa* and *T. furva* were caught using a net. The abdomens were then dipped into water in a petri dish until eggs were released. This was not necessarily the actual numbers of eggs released in the wild by unconstrained females. Eggs were maintained in these dishes in distilled water. They were kept in the insectary, where temperature was kept at 25-26°C, and relative humidity at 50-60%. Egg batches were separated into petri dishes, so that about 20 eggs were present in each.

Eggs were kept hydrated, and checked daily for signs of hatching. The number of larvae hatching from eggs was recorded each day. The number of instars was recorded by noting each ecdysis. This was noticed by the presence of exuviae in the dishes. These were searched for and removed daily. Observations were made under the same stereomicroscope as before. Larvae were fed on Cladocera, Copepoda and Ostracoda, which occurred in the natural habitat of the larvae. Later instars were fed on larval Culicidae and Ephemeroptera. Feeding was observed through the microscope upon introduction of food. Survivorship of larvae was also recorded.

Exuviae and teneral adults that were reared out were placed in vials in 75% alcohol. All specimens are housed in the Invertebrate Conservation Research Centre in the Department of Zoology and Entomology.

4.2.4 Analysis

Larvae sampled in the field were assigned to size-classes rather than instars because the number of instars can only be determined by noting ecdysis (Tillyard, 1917). A further complication, is that the number of instars is known to vary according to food availability (Corbet, 1962). The number of individuals occurring in these size-classes over time was recorded. The percentage of populations emerging over time was calculated from the collections of exuviae. Although some exuviae would have been missed due to dense vegetation, rain and wind, the collection nevertheless served to indicate the numbers of each species emerging relative to the others. The presence of teneralis also showed that emergence had occurred. The development of ten individuals of *T. arteriosa* and *T. furva* were followed, and the difference between duration of instars tested for using the Mann-Whitney test.

4.3 Results

4.3.1 Eggs and hatching success

Eggs hatched after two days for *T. arteriosa* and three days for *T. furva*. A gelatinous mass developed around the eggs 24 hours after they were laid. There were 80-100 eggs per batch for *T. arteriosa*, and 150-200 for *T. furva*. *Trithemis arteriosa* deposited eggs in four or five dips of the abdomen, while *T. furva* deposited all the eggs in one dip. The eggs of *T. arteriosa* were yellow and elliptical in shape, becoming dark brown near hatching. The eggs of *Trithemis* examined by Pinhey were subelliptical in shape (Pinhey, 1970). The pale green eggs of *T. furva* also became brown when ready to hatch. Figure 1 shows prolarvae of *T. furva* escaping from eggs. Hatching occurred after the eggs were rehydrated. Hatching success was only 15% in this case. Success was 58% for eggs which did not dry out. *Trithemis furva* showed a higher hatching success of 76%.

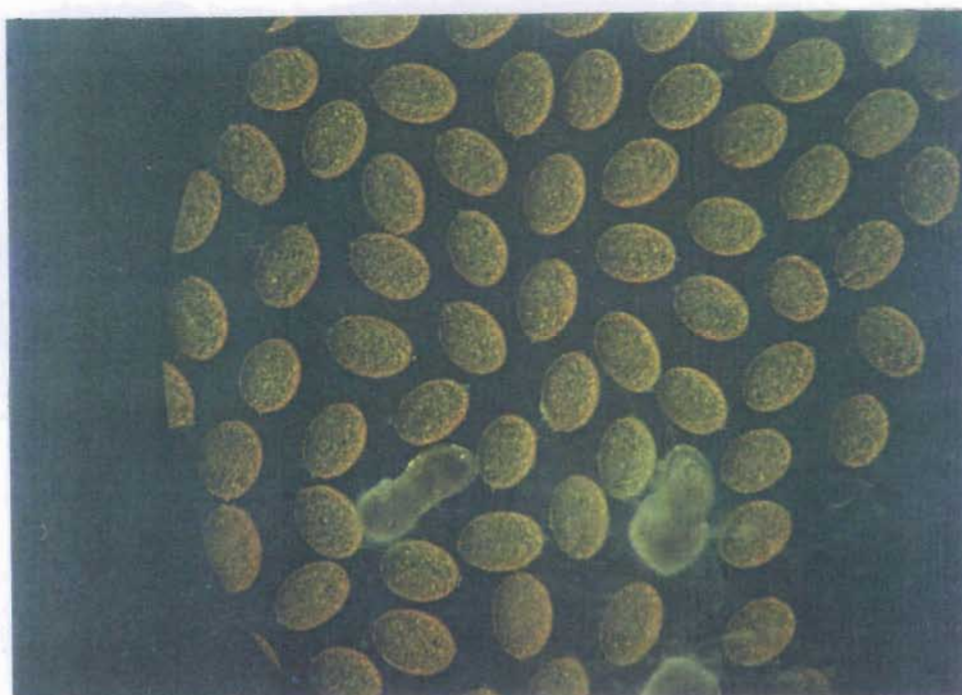


Fig. 1. An egg clutch of *Trithemis furva* showing prolarvae hatching from eggs. Each egg is about $360\mu\text{m}$ long.

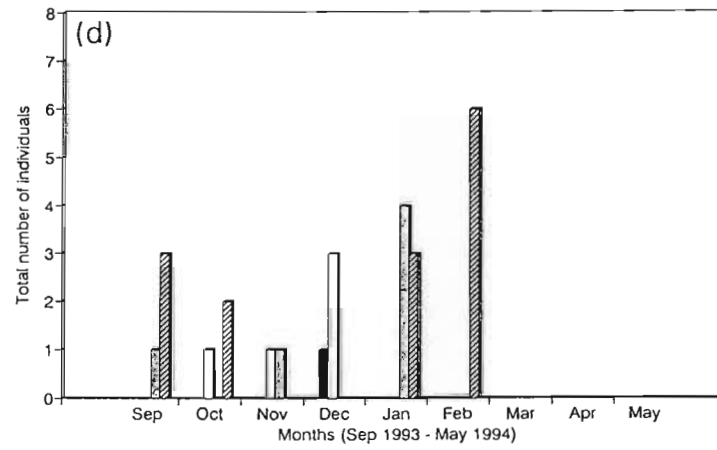
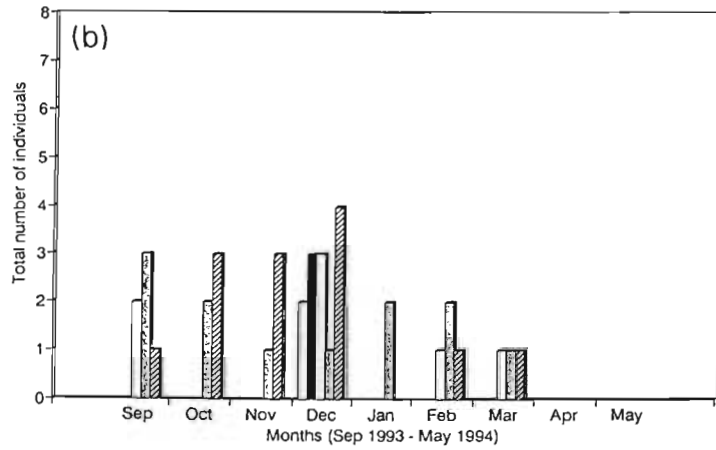
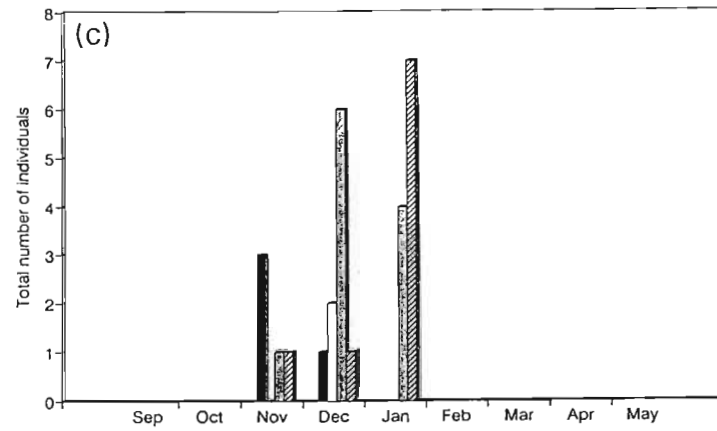
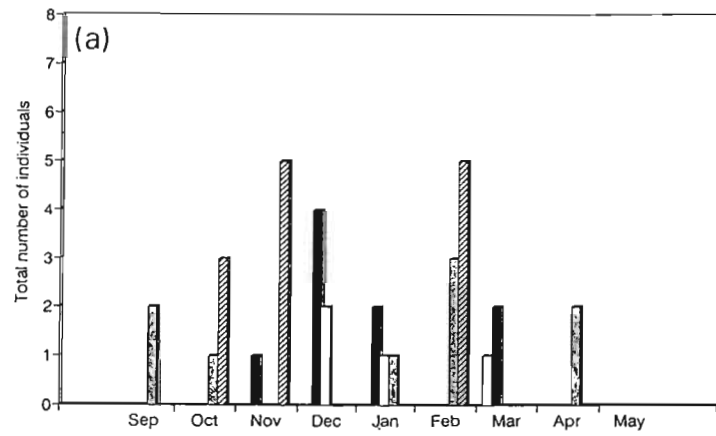
4.3.2 Larvae

Larvae of both species remained attached to the material surrounding the eggs. They moved onto algae which was later introduced into the dishes. Both species preferred feeding on Cladocera, *Simocephalus vetuloides* (Sars) to Copepoda, *Eucyclops prasinus* Kiefer. Development was rapid, with species passing through many instars in the first seven days after hatching. Instar 1 is considered here to be the prolarval stage. *Trithemis arteriosa* had 20 instars, and *T. furva*, 24 (Table 1). This may not reflect the actual numbers of instars in the wild, as the constant conditions of the insectary may have influenced the result. Development of *T. arteriosa* was more rapid than *T. furva*, lasting until 20 February 1994. *Trithemis furva*, by comparison, emerged in early March. Survivorship of larvae was different for the two species. *Trithemis furva* survived better than *T. arteriosa*, with 60-76% of larvae surviving, whereas only 40-52% of *T. arteriosa* larvae successfully emerged. The total duration of all instars of *T. arteriosa* was 59 days, compared with the 65 days of *T. furva*. The mean duration of instars for each species was similar (Table 1). The duration of instars was not significantly different (i.e. at the $P_{0.05}$ level) (Mann-Whitney $U = 4.5$, $n = 24$, $P > 0.05$).

Table 1. The duration of each larval instar (days), for *T. arteriosa* and *T. furva*. Development time until emergence was followed for the first 10 larvae that hatched in both cases. The mean duration is given with standard errors indicated in brackets ($n = 20$ for *T. arteriosa*, and $n = 24$ for *T. furva*).

Stage	Species	
	<i>T. arteriosa</i>	<i>T. furva</i>
Prolarva		
Instar 2	1 (0.25)	1 (0.16)
3	1 (0.11)	1 (0.16)
4	2 (0.20)	1 (0.17)
5	2 (0.15)	1 (0.18)
6	1 (0.16)	1 (0.11)
7	2 (0.08)	3 (0.11)
8	5 (0.13)	2 (0.20)
9	4 (0.21)	6 (0.10)
10	2 (0.22)	2 (0.22)
11	3 (0.26)	3 (0.16)
12	3 (0.17)	1 (0.17)
13	3 (0.15)	3 (0.20)
14	3 (0.16)	3 (0.23)
15	2 (0.16)	1 (0.24)
16	3 (0.17)	3 (0.11)
17	7 (0.14)	1 (0.10)
18	5 (0.12)	4 (0.10)
19	5 (0.10)	4 (0.12)
20	5 (0.15)	3 (0.11)
21		7 (0.11)
22		2 (0.12)
23		5 (0.11)
24		7 (0.11)
Total duration (days)	59	65
Mean duration	2.95	2.71

Based on field sampling, larvae of *T. arteriosa* took two and a half months to complete development from early instar larvae to emergence (Fig. 2a). Final instar larvae which were present as small larvae in December, were found in February (Fig. 2a). *Trithemis stictica* had a more synchronous development than the other species, as shown by the reduced number of size-classes found in the same month (Fig. 2b & d). Larvae of *T. furva* developed over three months before emerging (Fig. 2c). There were many late instar larvae of *T. stictica* at the start of the season (Fig. 2d), compared with the other species. *Trithemis arteriosa* was multivoltine as shown by the larval size-classes (Fig. 2a). *Trithemis dorsalis* appeared to be bivoltine (Fig. 2b). *Trithemis stictica* was also clearly bivoltine, while *T. furva* was univoltine and *T. arteriosa* was multivoltine.



□ 2-2.4 mm ■ 2.5-2.9 mm □ 3.0-3.4 mm
 □ 3.5-3.9 mm ▨ 4.0-4.4 mm

□ 2-2.4 mm ■ 2.5-2.9 mm □ 3.0-3.4 mm
 □ 3.5-3.9 mm ▨ 4.0-4.4 mm

Fig. 2. The number of larvae of different size-classes present from September 1993 to May 1994. The legend above is the measured head width of live larvae in millimetres. (a) *T. arteriosa*, (b) *T. dorsalis*, (c) *T. furva*, (d) *T. stictica*.

4.3.3 *Species emergence*

Figure 3 shows the total number of exuviae collected over the season. Most species emerged from November to February. Relative abundance of teneralis showed the emergence of individuals of *T. arteriosa*, and *T. stictica* during September and February (Fig. 4). Teneralis of *T. dorsalis* showed two peaks in abundance, while teneralis of *T. furva* were only observed during September and October 1993. The emergence pattern of the species, as indicated by exuviae, is shown by Fig. 5. The emergence curve of *T. arteriosa* was multimodal, and that of *T. stictica*, bimodal (Fig. 5). Most of the *T. furva* population emerged in January, a month after *T. dorsalis* showed a peak in emergence. *Trithemis arteriosa* emerged fairly abundantly most of the time. *Trithemis dorsalis* emerged sooner and showed a broader emergence curve than *T. furva* (Fig. 5).

Over 50% of *T. dorsalis* individuals had emerged by November, while most individuals of *T. furva* emerged in January (Fig. 6). There was also a noticeable decline in the number of exuviae of *T. dorsalis* when *T. arteriosa* began emerging abundantly (Fig. 6). Although many exuviae of this species were found in March, the sum of all the exuviae collected from August to November 1993 constituted a greater percentage of the total that were collected. In the case of *T. stictica*, even though no individuals emerged in January, by January, the population had reached in total, a high percentage.

Most of the emergence of the population of *T. arteriosa* occurred in November and December (Fig. 6), while *T. stictica* emerged mainly in January. The species where most of the population emerged the soonest was *T. arteriosa*. None of these species can really be considered to be spring emergers according to Corbet's (1962) definition, where over 50% of the population emerges within a few days. The soonest that 50% of any population had emerged was November. *Trithemis dorsalis* emerged more gradually over the season, than any of the other species.

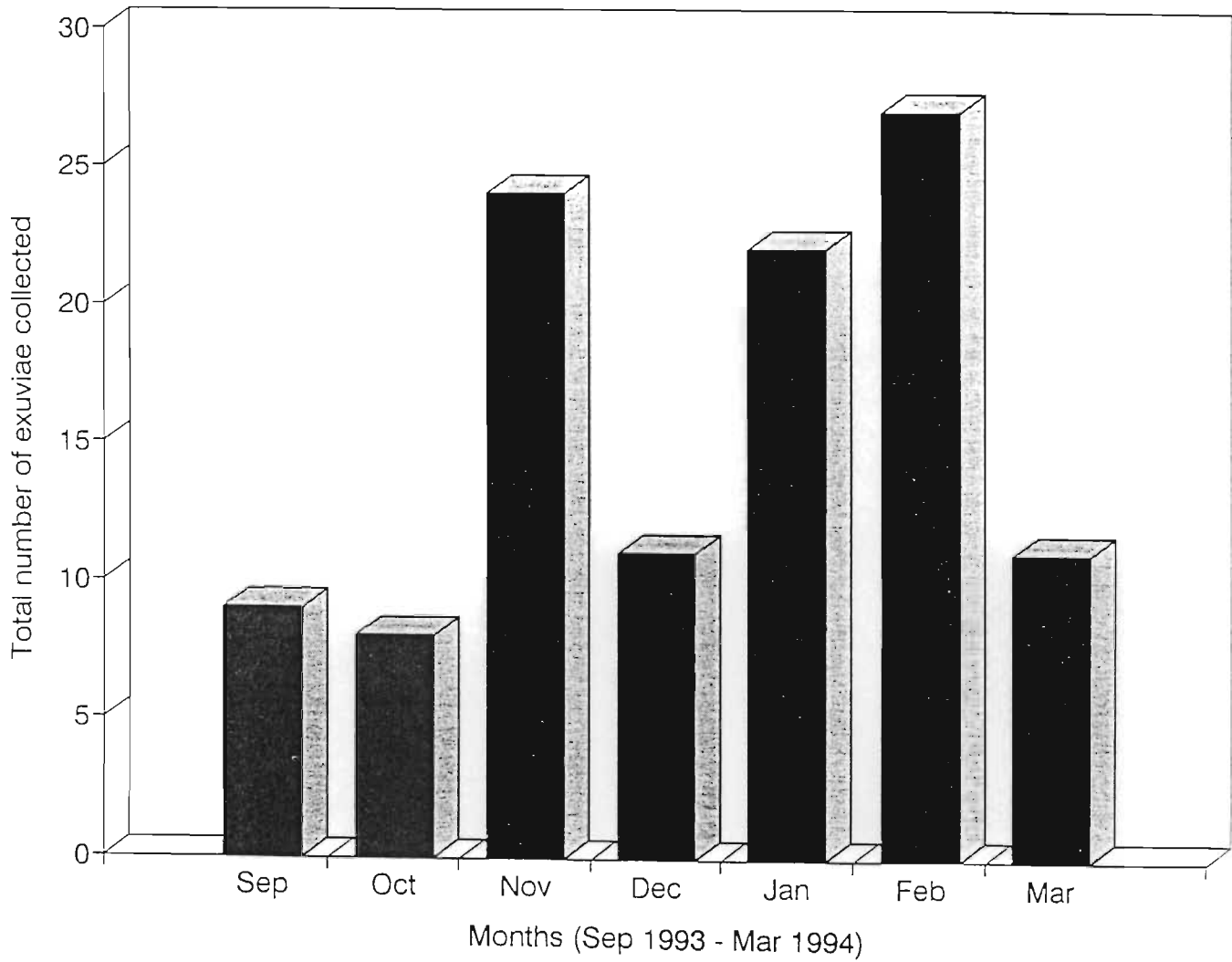


Fig. 3. The total number of exuviae of all resident species of *Trithemis* collected over the season.

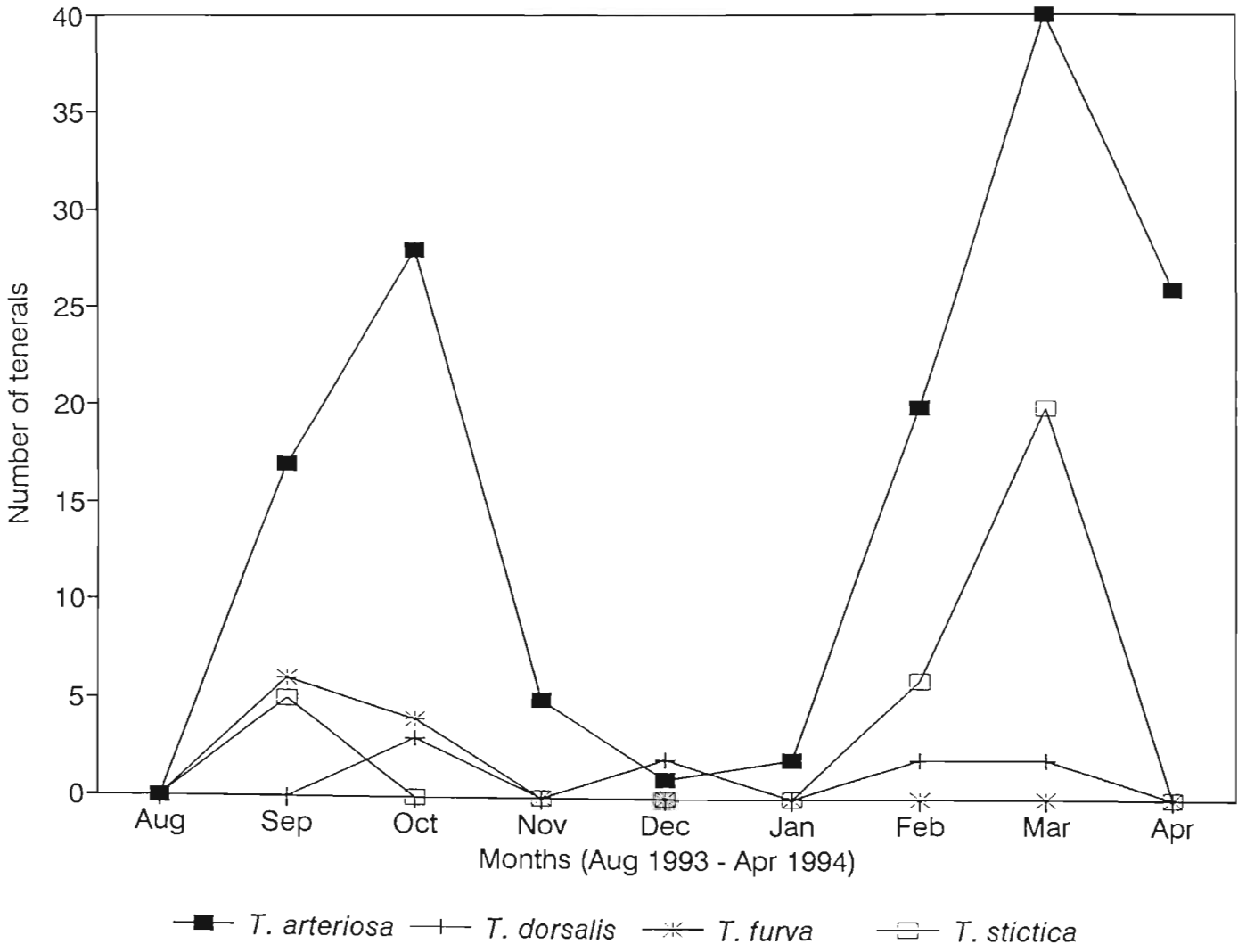


Fig. 4. Number of tenerals of all species observed during the study.

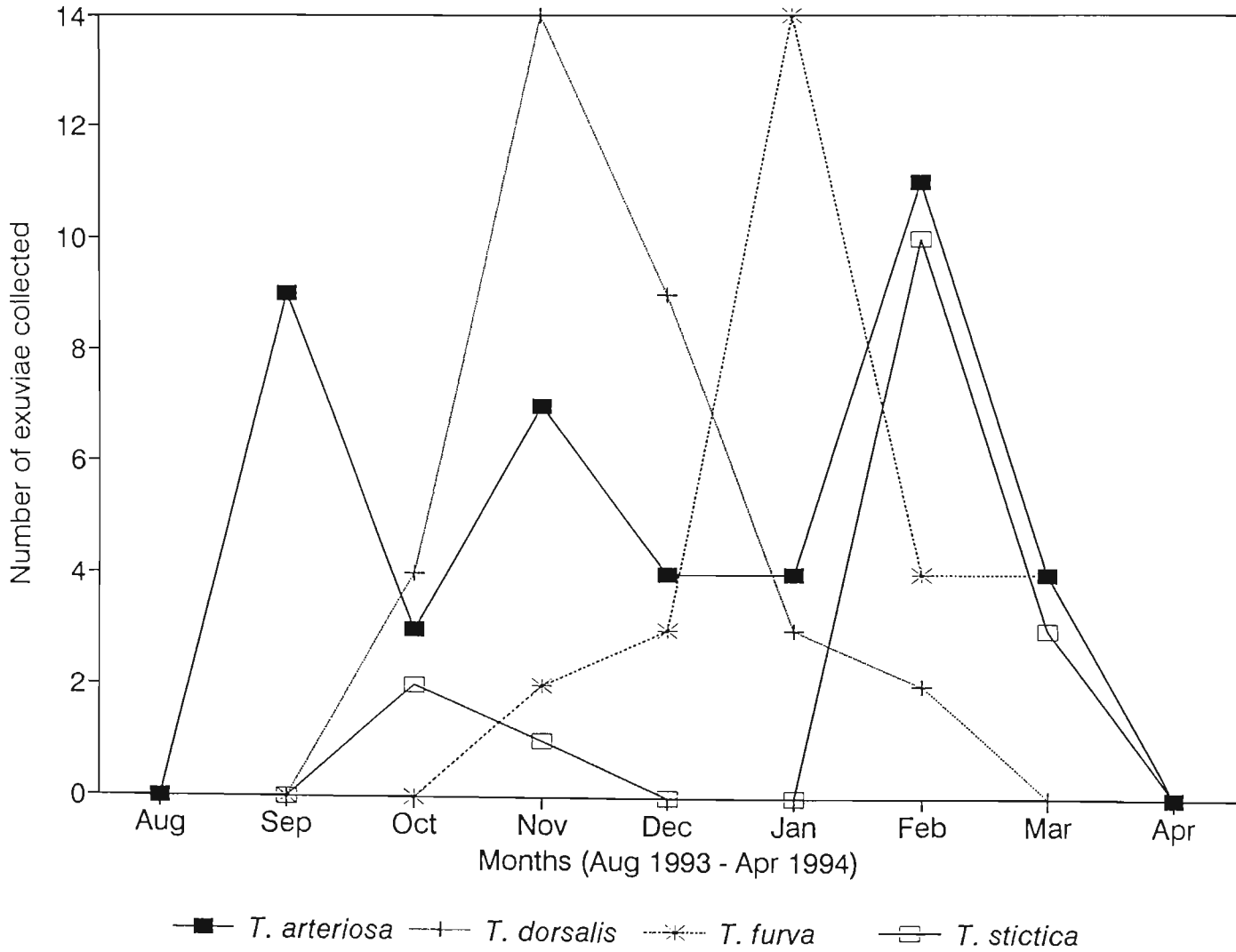


Fig. 5. The number of individuals that emerged from August 1993 to April 1994. The multimodal and bimodal emergence curves of *T. arteriosa* and *T. stictica*, are shown.

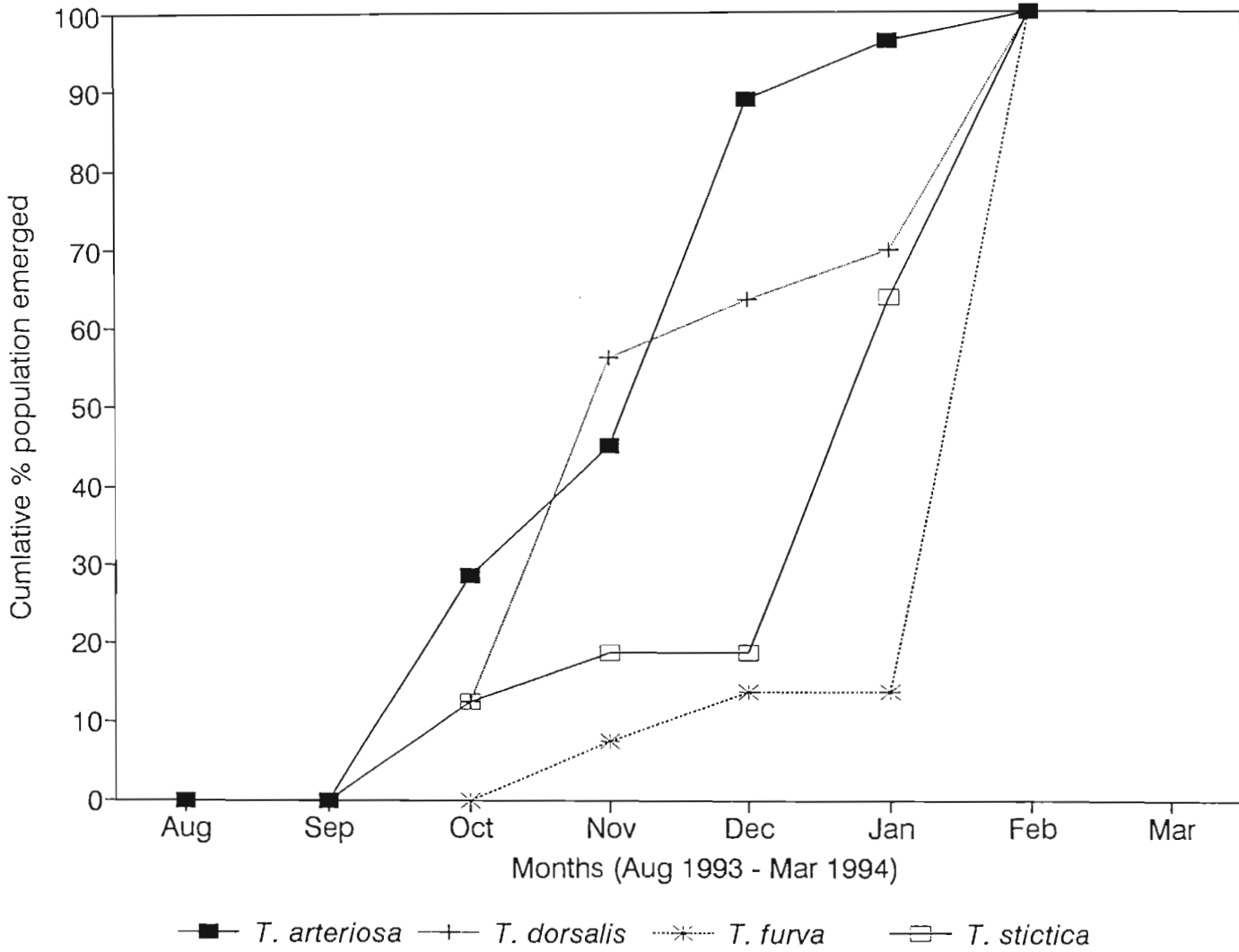


Fig. 6. The time taken for the population of each species to emerge completely at the site. Percentages are based on the exuviae collected at the site.

4.4 Discussion

4.4.1 Emergence

Asynchronous development can influence survivorship of species because species moving to shallower waters to emerge may be preyed on by other invertebrates (Wissinger, 1988). However, species with asynchronous development do not all migrate to the shore. *Trithemis arteriosa*, for instance, occurred near the edge at all stages. Asynchrony may reduce predation in two ways. The *Trithemis* species were flexible in the stage in which they overwintered. In the winter preceding the start of the study, individuals were found at other sites in the final instar. The July after the study, larvae were absent. In September 1994, only small larvae were present. Emergence only began again in mid-October. This may have been because the winter was very cold, thus delaying normal development. It seems therefore that the stage of development at which diapause is initiated depends on the weather. This is an area that requires further investigation, and should be done over more than one season.

4.4.2 The causes of synchrony

Synchronous emergence can result from synchrony during another stage of the life-cycle, such as synchronous egg hatching (Butler, 1984). This was not the case here, as both *T. arteriosa* and *T. furva* had asynchronous hatching. Synchronous entry into the final instar can be a result of larvae in the penultimate instar having been prevented from entering the final instar by long photoperiods (Corbet, Harvey, Abisgold & Morris, 1991).

The development of *Trithemis* species appeared to be affected by changes in air temperature. This was because emergence only began in November 1994 unlike the previous season, when emergence began in September 1993. July 1994 was unusually cold, colder than the previous July. In October 1994

only small larvae were found. This suggested that unlike the previous season, all the species had overwintered in the egg stage. The previous July larvae were present in the final instar, whereas in July 1994, none were present. Corbet and Harvey (1989) found a similar pattern in *Pyrrhosoma nymphula* (Sulzer), with metamorphosis being delayed by a month because of a cold winter.

4.4.3 *Asynchronous development*

Asynchronous development can cause mortality from cannibalism. Small individuals occurring at low prey densities are susceptible to cannibalism where they co-occur with larger individuals (Johansson, 1992). Among these species, *T. dorsalis* was the most unlikely to suffer from cannibalism because individuals were spatially segregated according to size, with smaller individuals present far from the shore. They also did not co-occur in microhabitats with other species and were therefore unlikely to be in competition. Species also have different vulnerabilities to cannibalism (Johansson, 1992). Larvae of *T. dorsalis* were at a greater risk from cannibalism as individuals of *T. furva* were because different instars of *T. dorsalis* were found at various distances from the shore. Increased synchrony may reduce this cannibalism, yet cause larvae to compete directly for food of the same size (Edgerly & Livdahl, 1992).

4.4.4 *Synchronous emergence*

Mass emergence may either reduce mortality by swamping the environment with more food than can be eaten by a territorial pair of birds, or increase predation if many birds are present (Corbet, 1962). Mass emergence will also make individuals more conspicuous to predators. In this way it could attract more predators and mortality could become density-dependent (Crowley, Nisbet, Gurney & Lawton, 1987). Although all the *Trithemis* species emerged around midnight, those more susceptible to predation because of mass

emergence may have been stronger fliers than others. They may therefore not have been preyed on as often as species which emerged asynchronously. This was not tested in this study, but could be possible. Other authors have suggested that mortality at emergence may not be that high (Bennett & Mill, 1993). Although mortality at emergence is often due to incomplete ecdysis or predation by birds (Corbet, 1962), *T. arteriosa* and *T. dorsalis* teneral often become entangled on the hooked trichomes and barbs of plants (Samways, 1991). *Trithemis arteriosa* is most often affected, and both mature adults and teneral become caught on plants (Samways, 1991).

4.4.5 *Possible biases with the study*

The exuvial collection was not a complete record of emergence because the area covered was large and not all parts of the vegetation, equally accessible. During heavy rainfall the water level often rose and could have washed exuviae away. During sampling very small larvae would have been missed by the net because of the mesh size. This size was chosen because it prevented clogging of the net by mud and silt. There was therefore an underestimate of the earliest instars.

4.4.6 *Suggestions for further studies*

It would be useful to obtain eggs of the species that could not be collected during this study because oviposition was rare, or females flew far from the edge and did not perch after mating. The hatching success and development rate could be similarly found. A comprehensive study could be attempted on the development of different species by using a small pond. It would be easier to search such a pond for larvae and exuviae. To better understand the factors influencing development and emergence in this species, a study needs to be completed over more than one season. Patterns of development and emergence can then be matched to changing conditions of weather, photoperiod and food availability.

4.4.7 *Development and adult success*

Different patterns of development resulting in more than one emergence could have implications for reproductive and competitive success of adults. Larvae that emerge subsequent to the first generation are often smaller (Harvey & Corbet, 1985), which could cause a decrease in clutch size in the adults (Gribbin & Thompson, 1990). This may be because of increasingly adverse conditions (Corbet & Harvey, 1989). Interspecific competition in larval stages can thus influence the reproductive success of adults and spatial and temporal distribution of teneral adults (Fincke, 1992).

4.4.8 *Life-history and spatial overlap*

Asynchronous development reduced intraspecific competition among larvae, although cannibalism may have increased. Species which emerged synchronously, such as *T. stictica*, did so during different months. Interspecific competition among the adults of these two species was consequently reduced. Body size is an important determinant of competitive and reproductive success in dragonflies. Different stages of development may be spatially separated. Adults of these species may overlap spatially although the larvae occupy separate habitats, or occur in the same habitat at different times.

4.5 References

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CHAPTER 5

Spatial overlap, population movements and competition

ABSTRACT

Niche overlap and niche breadth of five sympatric species of *Trithemis* were investigated. Morosita's index of niche overlap was used to investigate habitat and microhabitat overlap between larvae and adults. Niche breadth was calculated using Smith's measure. *Trithemis stictica* became increasingly dispersed with increasing density, suggesting the possible effect of intraspecific competition. Populations which became more aggregated with increasing density had reduced niche breadths. Niche expansion would be expected to occur where the density of a species increased and the population was more strongly influenced by intraspecific competition, rather than interspecific competition. Displacement of individuals to sink habitats resulted from the increasing number of teneral emerging after the population had become crowded in the source habitat. Aggressive interference by mature males may have resulted in a temporary displacement of individuals to less profitable habitats.

5.1 Introduction

5.1.1 *Niche differences and coexistence*

Niche space of Odonata may be partitioned along a habitat or microhabitat axis, though seasonality and food may be important (Johnson & Crowley, 1980; Crowley & Johnson, 1982). Species may be separated in vertical habitat rather than horizontal habitat (Askew, 1982; Rehfeldt & Hadrys, 1988; Sternberg, 1994). Odonata species can also be segregated according to food, oviposition sites or perch sites (Brownnett, 1994). Species may compete for space where thermal niches are reduced later in the day. This occurred in *Libellula fulva* Müller, and *Calopteryx splendens* (Harris) (Winsland, 1991).

Niche differences are important in allowing species to coexist (Giller, 1984; Schoener, 1986). Species occupying the same niche would be expected to compete if the resources they are using are limited. If the resource is abundant compared with the number of individuals and species using it, then the likelihood of competition is reduced. Niche breadth of a species may be important in indicating the tolerance of a species to a range of conditions. However, niche breadth may be influenced by the presence of a competitor, rather than by adverse conditions. Niche breadth and overlap can be influenced by the density of the same or different species. For example, increased densities can result in changes in niche breadth. With increasing intraspecific competition, the realized niche breadth will be expected to increase such that individuals emerging later occupy less favourable (sink) habitats. Interspecific aggression and habitat selection may lead to spatial separation of adults of different species (Rehfeldt & Hadrys, 1988). Under conditions of interspecific competition the niche breadth of a species would be expected to contract, such that the population becomes more aggregated in time or space (Giller, 1984). Niche breadth therefore could be limited by the combined effects of intraspecific and interspecific competition.

5.1.2. *Aims of the investigation*

The aims of this study were therefore to determine the niche breadth of larvae and adults across an environmental gradient. The potential for competition was assessed after taking into account resource limitation. Spatial niche overlap of species was also determined. This was then compared with changes in the density of populations to test if species could be responding to increasing numbers by expanding or contracting their niche.

5.2 Materials and methods

5.2.1 *Study site and sampling*

The study site was the same as previously mentioned in chapter 2. Adult and larval sampling are also discussed in chapter 2. Densities of adults were calculated as the number of individuals per area of habitat. This was done for each habitat. Movement of individuals in relation to density were only tested for adults. This was because adult movements and densities were easier to determine than those of the larvae.

5.2.2 *Analysis*

Habitat and microhabitat overlap was assessed using Morosita's index, because it is the measure most free of bias and can be used for number of individuals (Smith & Zaret, 1982; Krebs, 1989). Habitat overlap of adults was computed for each month, because there may have been shifts in the competitive advantage of a species later in the season. Unless otherwise stated, computer programs for the analyses were written in Turbo Pascal 5.0.

The overlap in microhabitats of larvae was assessed as before. Indices were only calculated for large larvae. This was more accurate than finding out overlap

of larvae of different sizes because different stages can occur in separate microhabitats.

Niche breadth was calculated using Smith's measure of niche breadth. This method was also the most free of bias for niche breadth (Krebs, 1989). The variance ratio measure of Elliott (1977) was used for measuring the aggregation of the population. It was chosen for the simplicity of calculation (Krebs, 1989).

It is very difficult to measure resource limitation in the field, because it is normally best shown in situations where the conditions are modified, with a resultant increase in growth. Resource limitation was here based on the likelihood of interspecific interference among species in habitats of known area. Aggressive interactions among rival adult males were quantified in different habitats. Individual space requirements were assumed to be the same, as the species were similar in size. Other studies also showed that these species defended areas of similar size (Osborn, 1992). The spatial limitation of the habitat was assessed by dividing the area of the habitat by the frequency of aggressive interactions. This was then multiplied by 100 to produce an index between zero and two. The closer the value to two, the more limiting the resource. This was calculated for each species.

The similarity of species' niches were investigated using data on oviposition sites, perch sites, habitat, microhabitat and food preferences. Direct observations on behaviour and the relative abundance of species in habitats, provided a more accurate way of assessing the total species niche. Use of a resource by a species was scored with a one. The proportion of all resources shared by each pair of species was then calculated. This was taken as a measure of similarity of the niche and was calculated for all pairs of species.

Spearman's rank correlation coefficients were calculated to find out if the population was becoming more dispersed with increasing density. This was done using the data on relative abundance of adults of different species and

correlating this with the index of aggregation. This method was used because the data were nonparametric. Correlations were also calculated to find out if species were becoming more aggregated in response to increasing densities of potential competitors. The computer program SPCOVAR.PRN, a modification (to print out results) of SPCOVAR.BAS (Ludwig & Reynolds, 1988), was used for the calculations of Spearman's rank correlations between relative abundance and aggregation.

5.3 Results

5.3.1 *Habitat and microhabitat overlap*

Habitat and microhabitat overlap of larvae are summarized in table 1. Whereas *T. arteriosa*, and *T. dorsalis* overlapped greatly in habitat ($C_h = 0.949$), they occupied separate microhabitats ($C_m = 0.000$) (C_h = Morosita's index of habitat overlap, C_m = Morosita's index of microhabitat overlap). The same pattern was found for *T. dorsalis* and *T. stictica* ($C_h = 0.949$; $C_m = 0.000$). A similar pattern was found for *T. furva* and *T. dorsalis*, except that in this case overlap was greatest along the microhabitat axis (Table 1). All species overlapped to some extent in their use of habitat, whereas only some overlapped in microhabitat.

Table 1. Habitat and microhabitat overlap indices (Morosita's index), for larvae. Habitat overlap values are given in the lower half of the table, and microhabitat overlap values are given in the upper half of the table ($n = 10$). Data used for calculating overlap was based on the maximum relative abundance of adults for each month, when all larvae were present together.

	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. stictica</i>
<i>T. arteriosa</i>	*	0.000	0.440	0.670
<i>T. dorsalis</i>	0.949	*	0.670	0.000
<i>T. furva</i>	0.285	0.003	*	0.660
<i>T. stictica</i>	1.160	0.949	0.285	*

Overlap of adults did not remain constant over time (Fig. 1). Whereas, *T. dorsalis* overlapped a great deal with *T. arteriosa* and *T. stictica* (Fig. 1a & c), it did not overlap much with *T. furva*. Adults of *T. stictica* and *T. dorsalis* were the only two that overlapped with this species during some months (Fig. 1d & f). Overlap between most pairs of species was highest during October and December. The *T. arteriosa* and *T. stictica* pair always had high values of overlap (Fig. 1e). The three species which therefore overlapped most of the time in choice of habitat were *T. arteriosa*, *T. dorsalis* and *T. stictica*.

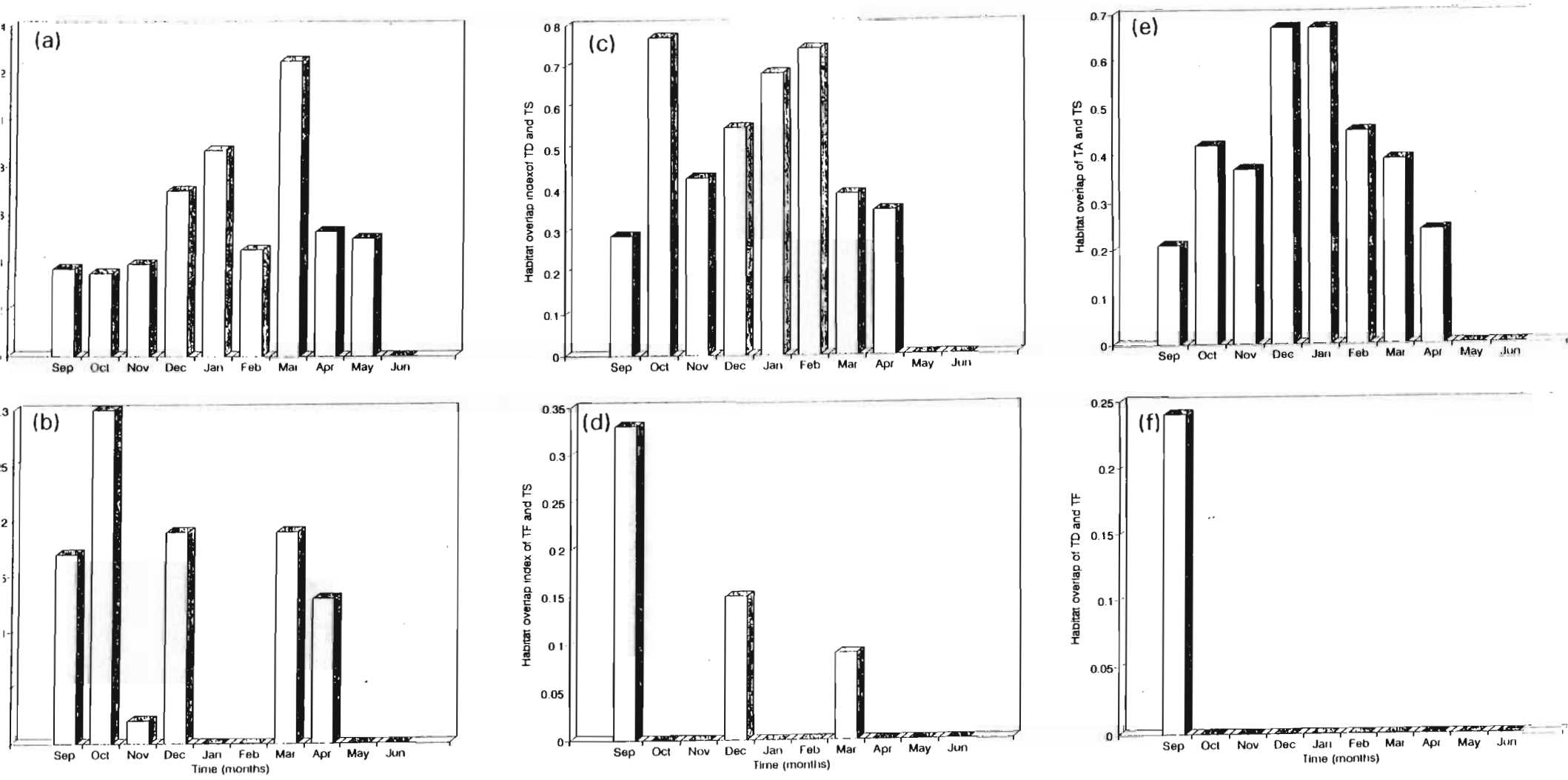
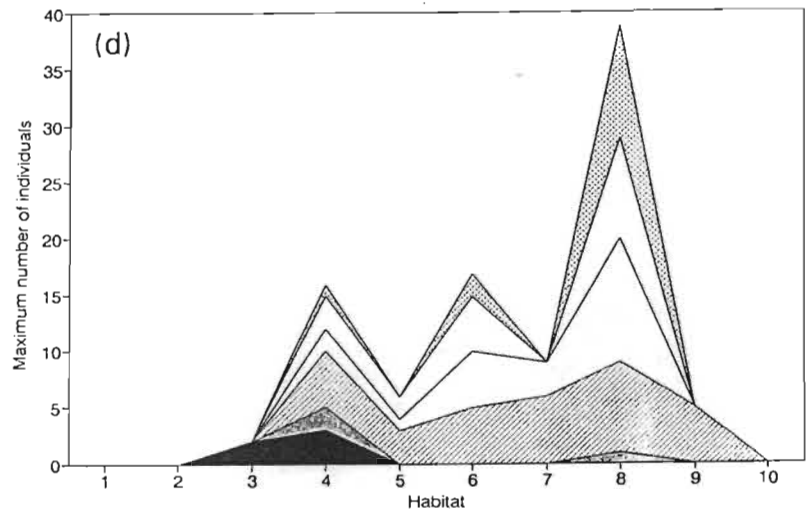
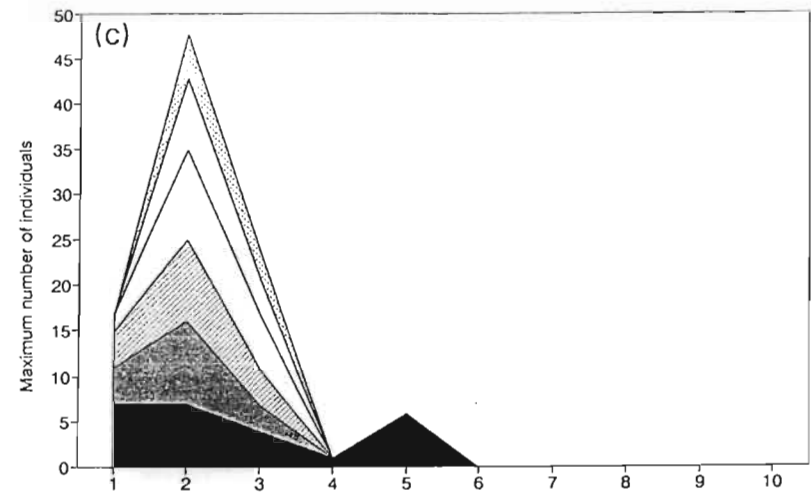
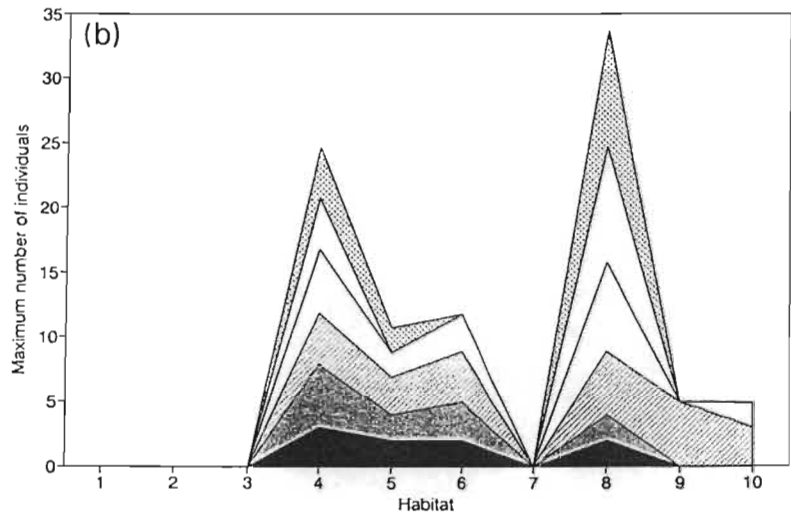
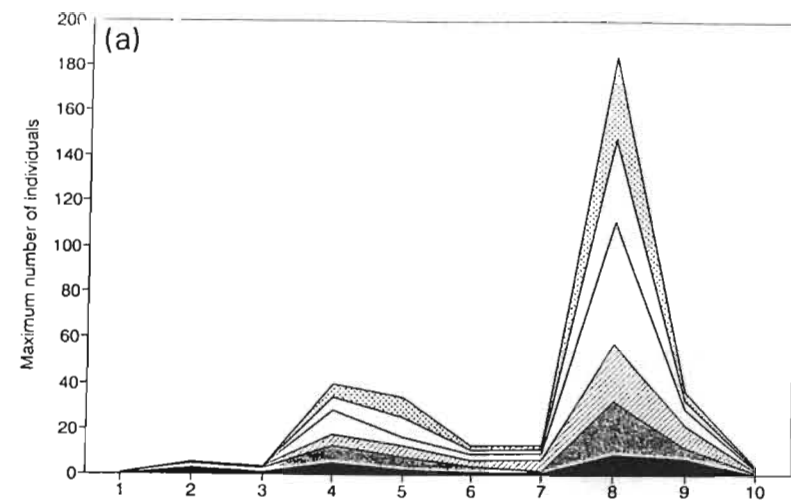


Fig. 1. Morosita's habitat overlap indices for adults over time. (a) Overlap of TA and TD, (b) TA and TK, (c) TD and TS, (d) TF and TS, (e) TA and TS, (f) TD and TF. TA = *T. arteriosa*, TD = *T. dorsalis*, TF = *T. furva*, TK = *T. kirbyi ardens*, TS = *T. stictica*. Figures are not to the same scale.

5.3.2 *Habitat overlap, niche breadth and aggregation of adults over time*

Relative abundance of individuals became concentrated in particular habitats at different times during the season (Fig. 2). The populations of all species, except *T. stictica* (Fig. 2d), became increasingly aggregated over time. Whereas *T. furva* became clustered around one habitat (Fig. 2c), *T. dorsalis* gathered around the open river and southern dam (Fig. 2b). *Trithemis arteriosa* also tended to gather around this section of dam (Fig. 2a). January and February were always the months of greatest aggregation of individuals.

Niche breadth of all species but *T. arteriosa*, increased until February. In the latter case, niche breadth remained almost the same throughout. *Trithemis arteriosa* increased in niche breadth over time (Fig. 3a). Niche breadth of *T. dorsalis* and *T. stictica* both increased until February, and then decreased rapidly (Fig. 3b).



■ Sep ■ Oct ■ Nov
 □ Dec □ Jan □ Feb

■ Sep ■ Oct ■ Nov
 □ Dec □ Jan □ Feb

Fig. 2. Increased numbers of (a) *T. arteriosa* and (b) *T. dorsalis* in favoured habitats. Contrasting patterns of relative abundance of (c) *T. furva* and (d) *T. stictica*. The habitats were as follows: 1 = Shaded rocky stream, 2 = Wooded rocky stream, 3 = Gravel-bed stream, 4 = Open river, 5 = Wooded river, 6 = Marsh, 7 = *Cyperus* marsh, 8 = Southern dam, 9 = Northern dam, 10 = Pond. Figures are not to the same scale.

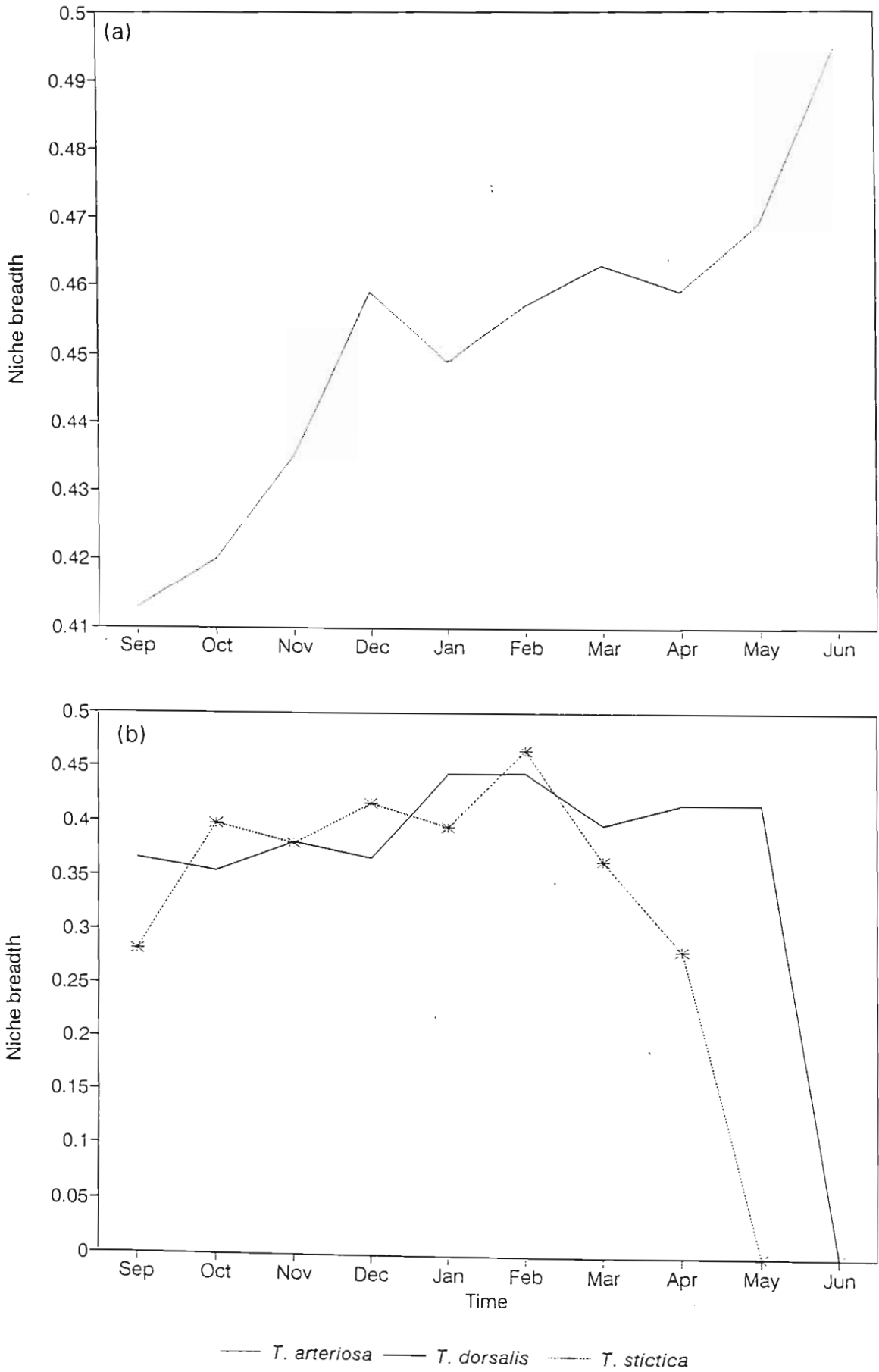


Fig. 3. Smith's niche breadth values for (a) *T. arteriosa*, (b) *T. dorsalis*, and (c) *T. stictica*.

5.3.3 *Niche breadth and density*

Correlations of adult niche breadth of a species with density were sometimes highest at the species own density (Table 2). In *T. stictica* for example, there was a highly significant positive correlation between niche breadth and its own density ($r_s = 0.941^{**}$, $n = 10$, $P < 0.01$). The niche breadth of *T. dorsalis* was also more strongly correlated with its own density, although not significantly so ($r_s = 0.341$, $n = 10$, $P > 0.05$). The niche breadth of *T. arteriosa* was negatively correlated with the density of all species (Table 2). Niche breadth of *T. furva* was positively correlated with its own density ($r_s = 0.395$, $n = 10$, $P > 0.05$).

Table 2. Spearman's rank correlation coefficients r_s between the niche breadth and density of adults. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$ ($n = 10$).

Density	Niche breadth				
	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. kirbyi ardens</i>	<i>T. stictica</i>
<i>T. arteriosa</i>	-0.091	0.165	-0.314	0.501	0.661 *
<i>T. dorsalis</i>	-0.101	0.341	-0.171	0.651 *	0.630
<i>T. furva</i>	-0.608	0.036	0.395	-0.350	-0.262
<i>T. kirbyi ardens</i>	-0.759 *	0.167	-0.081	0.084	0.590
<i>T. stictica</i>	-0.546	0.136	-0.404	0.144	0.941 **

5.3.4 *Species aggregation versus density*

Trithemis arteriosa was negatively correlated with all species, except *T. stictica* (Table 3). By comparison, *T. stictica* became more aggregated as the density of *T. arteriosa* decreased. The other two species both became more aggregated as the densities of all species increased (Table 3). *Trithemis stictica* showed a highly significant positive correlation with the density of *T. furva* ($r_s = 0.866^{**}$, $n = 10$, $P < 0.01$). *Trithemis stictica* became more aggregated as the density of its own population increased, although not significantly so ($r_s = 0.451$, $n = 10$, $P > 0.05$). It was also negatively correlated with the density of *T. arteriosa*. The aggregation of *T. dorsalis* was positively correlated with the density of *T. furva* ($r_s = 0.698^*$, $n = 10$, $P < 0.05$).

5.3.5 *Overlap and niche breadth*

In the *T. arteriosa* and *T. furva* pair, correlation was greatest with the niche breadth of *T. furva* ($r_s = 0.821^{**}$, $n = 10$, $P < 0.01$). Where species overlapped with *T. furva*, correlations with niche breadth were all positive (Table 4). Habitat overlap of *T. arteriosa* and *T. dorsalis* decreased as their densities increased.

Table 3. (a) Density of adults across different habitats. (b) Spearman's rank correlation coefficients r_s between the index of aggregation and density of adults. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$ ($n = 10$). An index of aggregation was not calculated for *T. kirbyi ardens* because it was present in very low densities.

(a)	Habitat									
	1	2	3	4	5	6	7	8	9	10
<i>T. arteriosa</i>	0.000	0.962	0.258	0.175	0.220	0.204	0.055	0.250	0.244	0.316
<i>T. dorsalis</i>	0.792	0.626	0.714	0.558	0.382	0.415	0.542	0.530	0.530	0.000
<i>T. furva</i>	0.503	0.443	0.397	0.404	0.406	0.511	0.612	0.451	0.100	0.000
<i>T. stictica</i>	0.721	0.812	0.619	0.421	0.499	0.344	0.380	0.394	0.000	0.000

(b)	Index of aggregation				
	Density	<i>T. arteriosa</i>	<i>T. dorsalis</i>	<i>T. furva</i>	<i>T. stictica</i>
<i>T. arteriosa</i>		-0.360	0.128	0.134	-0.187
<i>T. dorsalis</i>		-0.061	0.244	0.340	0.155
<i>T. furva</i>		-0.237	0.698 *	0.413	0.866 **
<i>T. kirbyi ardens</i>		-0.308	0.407	0.277	0.537
<i>T. stictica</i>		0.228	0.265	0.320	0.451

Table 4. Spearman's rank correlation coefficients r_s between species overlap and niche breadth. * Values significant at $P_{0.05}$. ** Values significant at $P_{0.01}$ ($n = 10$). TA = *T. arteriosa*, TD = *T. dorsalis*, TF = *T. furva*, TK = *T. kirbyi ardens*, TS = *T. stictica*.

Niche breadth	Species pair						
	TA/TD	TA/TF	TA/TK	TA/TS	TD/TF	TD/TS	TF/TS
<i>T. arteriosa</i>	-0.321	0.489	-0.110	-0.329	0.058	-0.286	0.127
<i>T. dorsalis</i>	-0.370	0.470	-0.136	-0.451	0.290	-0.286	0.112
<i>T. furva</i>	0.122	0.821**	-0.162	-0.153	0.175	-0.091	0.411
<i>T. kirbyi ardens</i>	0.267	0.714*	-0.240	-0.116	0.175	-0.043	0.337
<i>T. stictica</i>	0.172	0.557	-0.230	-0.211	0.177	-0.068	0.114

5.3.6 *Resource limitation and similarity of niches*

Territorial behaviour of males suggested that space was not limiting. The southern dam was more strongly contested ($R_L = 1.68$) ($R_L =$ Resource limitation index), than the sunny river ($R_L = 0.94$). $R_L \geq 1$ is considered limiting for the species. At the dam, space was no more limiting for *T. arteriosa*, than for *T. dorsalis*. This is because, under the same density, *T. dorsalis* would be as likely to have as many aggressive interactions. *Trithemis arteriosa* and *T. dorsalis*, and *T. arteriosa* and *T. stictica* had the most similar niches overall (Fig. 4). *Trithemis furva* had the niche that was most dissimilar to other species.

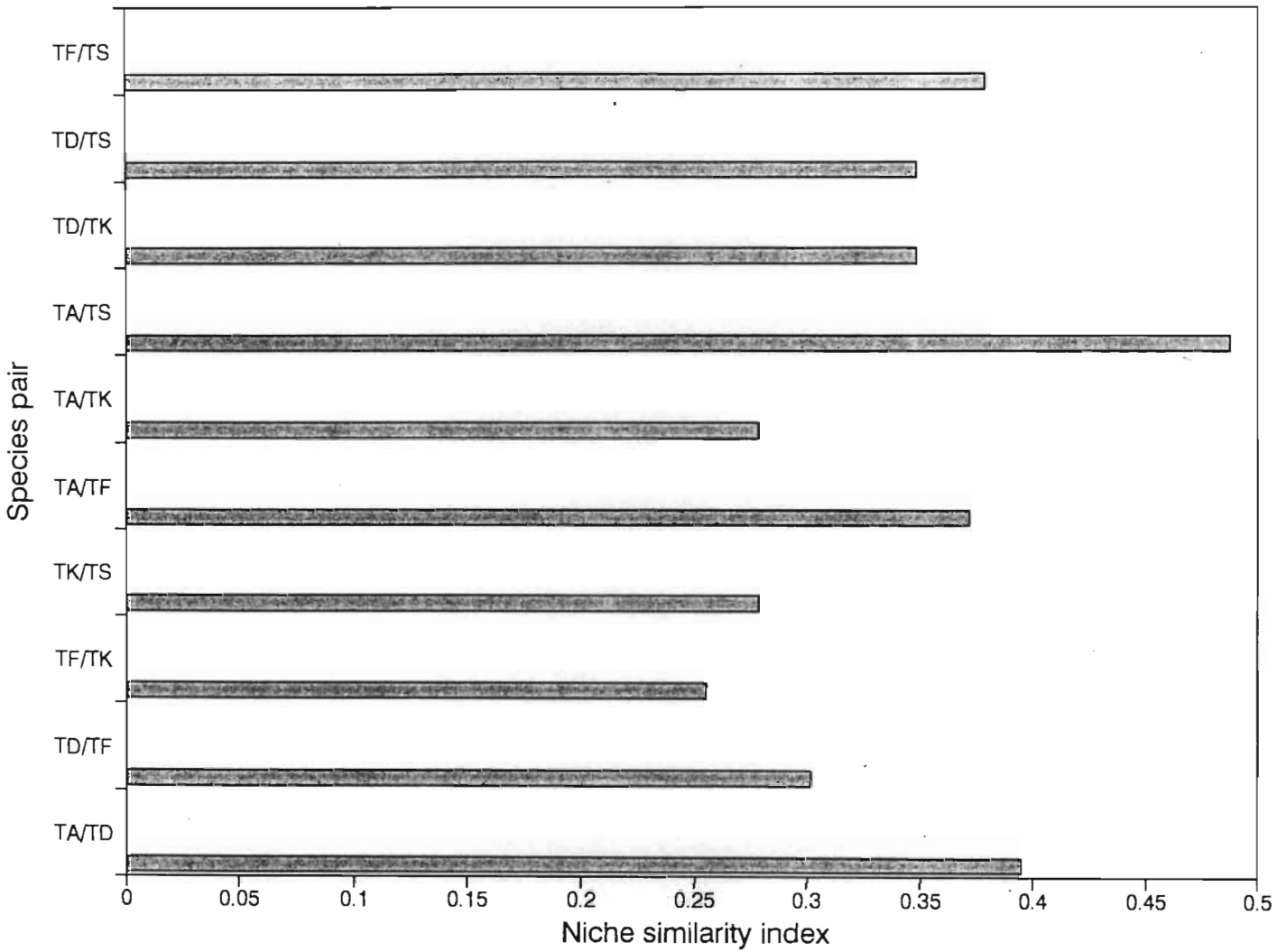


Fig. 4. The degree of similarity between species pairs based on all life-stages. TA = *T. arteriosa*, TD = *T. dorsalis*, TF = *T. furva*, TK = *T. kirbyi ardens*, TS = *T. stictica*.

5.4 Discussion

5.4.1 *Habitat overlap and availability*

The effect of overlap on populations depends on how strongly species prefer the habitat on which they overlap. Interference and exploitative competition may be intense if both species have narrow ecological tolerances, consequently being limited to the same habitat. All species in this study, except perhaps, *T. furva*, had a rather wide ecological tolerance. Intense competition was therefore unlikely. Complete habitat and microhabitat overlap does occur in these species where habitat heterogeneity is reduced, such that they inhabit the same space. The growth rate of one species may then be negatively affected, but is unlikely to be excluded if densities do not become too high.

5.4.2 *Niche breadth and competition*

According to Price (1984), strong competitors will have broad niches, and weak competitors, narrow niches. A species may however have a broad niche because it is easily displaced into sink habitats by other species, rather than because it is a strong competitor. Species with narrow niches may be able to monopolize a few resources well, in this way excluding potential competitors. *Trithemis furva* may be such a competitor, in that it maintains and defends large circular territories from rocks positioned in the middle of the stream. This species is able to patrol large areas, copulate in the open and oviposit over wide areas of water with little interference from other species. Such specialization, as in this species, could also be interpreted as resulting from past interspecific competition, with this species having been excluded from other habitats (Price, 1984). This species may however prefer this habitat because it is more favourable than the other habitats, and not because of exclusion from other habitats.

5.4.3 *Habitat overlap and emergence*

High niche overlap may be temporary, especially where there has been a sudden large emergence of individuals, which subsequently move away from water. This was the only reason *T. dorsalis* and *T. furva* overlapped in habitat use in September. Daily movements of adults should also be allowed for when examining niche overlap. This is because males overlap at the water, as congeners have a similar mating system. Away from the water overlap for habitat and foraging space may be minimal. The extent of spatial overlap may also be the result of past competition (Kneidel, 1985 ; Ives, 1991).

5.4.4 *Aggregation and coexistence*

Coexistence may be made possible by individuals aggregating on resources (Atkinson & Shorrocks, 1984; Kneidel, 1985; Shorrocks & Rosewell, 1987; Ives, 1991; Mogi & Yong, 1992). Aggregation as a way of reducing interspecific competition may be more important in populations using ephemeral resources (Kneidel, 1985). While increasing aggregation leads to decreased interspecific competition, intraspecific competition increases (Shorrocks & Rosewell, 1987). Because most insect populations aggregate on patchy resources it has been suggested that this is the main way of coexistence in insects (Atkinson & Shorrocks, 1984). However, the influence of aggregation on competition will depend on how limited species are to a resource. That is whether or not they can use sink habitats in addition to source habitats. Species may also aggregate on resources in the absence of interspecific competition (Hildrew & Townsend, 1987). Aggregation may not always reduce interspecific competition (Giller & Doube, 1994). This may be the case if two species aggregate on the same resource.

All populations, except *T. stictica* aggregated around their preferred habitat, as the season progressed. It has been suggested that aggregation may be density-

dependent. For example, adults of *Aeshna cyanea* (Müller) became more localized, and showed stronger site-attachment when density was high (Poethke, 1988). Corbet (1962) thought the opposite more likely, with populations becoming more dispersed and adults abandoning territoriality altogether at high densities. *Trithemis stictica* certainly became more aggregated at higher densities. In the Odonata it seems that adults may be attracted to areas of high density (Michiels & Dhondt, 1991). However, interspecific interactions among adults are common (Rehfeldt & Hadrys, 1988), and can cause exclusion of individuals from areas of high density (Moore, 1964).

5.4.5 *Specialization and competition*

The extent to which species overlap spatially may depend on densities, such that a species which would normally specialize on one type of habitat (its source habitat) occurs in sink habitats (Keddy, 1989; Danielson, 1992). Adult dragonflies may move to sink habitats when intraspecific densities increase, resulting in intense interference competition. In *Trithemis* adults, interference of teneral by older males may cause them to be displaced into sink habitats.

5.4.6 *Resource partitioning*

Although species overlapped a great deal along one niche axis, they all coexisted because they were separated along another axis. For instance, larvae overlapped in habitat use, but used different microhabitats. This was shown by larvae of *T. dorsalis* which overlapped with other species in habitat use, but occurred in a separate microhabitat. The only time these larvae might have occurred with others was when they moved near to the shore to emerge. Exploitative or interference competition with other species was therefore unlikely. *Trithemis arteriosa* and *T. stictica* would have competed at the larval stage because they overlapped along both spatial dimensions. Adults were seasonally separated because the amount of habitat overlap changed over time. Species were therefore not continually subject to high overlap. This may have

occurred in response to competition between species, or because one clustered around a preferred resource. This resource being one which was not strongly preferred by the other species with which it co-occurred. Evidence suggests that this was a more likely reason for the pattern.

5.5 References

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CHAPTER 6

General discussion

6.1 Investigating interspecific competition

An investigation of interspecific competition should be performed using information on how much species overlap along particular niche dimensions, and how restricted they are to the niche on which they overlap. Habitat, microhabitat, food and substrate preferences thus become integral to an investigation of competition. Because individuals of similar size will be more likely to compete for the same size food, it also becomes important to know the size distribution of larvae of different species in the habitat.

Knowledge of the life-history then becomes essential for a better understanding of competitive interactions. A fundamental concept for investigating competition, is determining how limiting resources are. This is difficult to determine, especially as resources change seasonally in abundance. How limiting space was for individuals to maintain territories with minimal interference was determined. The assumption was made that all individuals were similarly negatively affected when chased from an area by a male of another species. Using behaviour would give a better indication of how limiting space was, because estimating territory requirements on the basis of perched individuals could be deceptive. This is because territory size can change according to perch availability and density. The question becomes then to what degree territory size can become contracted before species begin invading each others' space. This is where interspecific behaviour observations become useful.

A combination of field work and laboratory studies are useful for examining competition. The laboratory experiments could not only be used to indicate food and substrate preferences. Even though species were not present in the same microhabitats and habitats, elsewhere they may be present together. They could affect each other if they overlapped completely in habitat and microhabitat. It is

also important to incorporate overlapping stages into experimental designs for populations that develop asynchronously because staggered hatching may affect survivorship, development time and fecundity (Edgerly & Livdahl, 1992).

6.2 Niche differences and evolution

Diamond (1986) suggested that niche differences evolved in a set sequence beginning with spatial separation, with separation of diet occurring afterwards. Size differences can also be important in spatial segregation of species, but are not as important as spatial differences (Diamond, 1986). It would be useful to investigate competition at times of resource limitation because this would be when competition would be more likely to occur (Grant, 1986).

6.3 Life-histories and competition

Species such as *T. arteriosa* which have many generations per year, will outcompete a species such as *T. stictica* where conditions change unpredictably, because *T. arteriosa* has many overlapping cohorts. This means that at least some individuals will survive if there is a change in conditions. This species also has the added advantage of having drought resistant eggs and larvae. *Trithemis stictica* is a species which would be favoured in situations where food availability is good. It also does not show as great a likelihood of intraspecific competition for food as *T. dorsalis* does. Probably it prefers more stable, or predictably changing conditions, where it can occur in great abundance. Different stages of development in insects will not necessarily be equally susceptible to cannibalism (Agarwala & Dixon, 1992). This can have strong implications for intraspecific competition because the relative abundances of different-sized larvae will be altered.

6.4 Species traits and competitive ability

Differences in life-history traits can determine the number of species that can coexist (Chesson & Case, 1986; Tilman & Pacala, 1993). Species that become specialized on a resource may be competitively dominant under one scenario, but a change in season or a disturbance could cause the species to become competitively displaced. Such species are more k-selected. In a situation of disturbance, a more adversity or r-selected species will thrive, possibly displacing the specialist. Hence, a species such as *T. arteriosa*, could displace a more specialized species such as *T. stictica* in such a situation. This may have explained the dominance of *T. arteriosa* at the site, where water level fluctuations were frequent. Wilson and Yoshimura (1994) also thought that environments with great temporal variation will favour generalists.

6.5 Competition among larvae

Although many studies have investigated interactions, density dependence and competition in larval dragonflies (Benke 1978; Carchini & Nicolai 1984; Johnson, Crowley, Bohanan, Watson & Martin 1985; Johnson, Pierce, Martin, Watson, Bohanan & Crowley 1987; Van Buskirk 1989; Baker 1989), few have focused on competition in the adults (Moore 1964). Ontogenetic niche shifts are an important part of life-histories (Ludwig & Rowe, 1990). Smaller instars may for instance occupy different microhabitats to larger instars. The early instar larvae of *T. dorsalis* for example, occurred in deeper water than those nearer to emergence. Microhabitat use may also be dictated by contest competition between species (Gorman, 1988). This could negatively affect the inferior competitor, by exposing it to a higher risk of predation. Different species may have different life-history traits controlling the time of peak emergence. Different stages of development of larvae can have implications for intraspecific competition because there are changes in aggression between instars (Schaffer & Robinson, 1993).

6.6 Habitat structure and competition

Habitats with spatial variability may reduce the effects of interspecific competition by allowing different species to inhabit patches independently of one another. Corbet (1962) believed that interspecific competition for food and space was the main reason for the adaptive radiation in larval morphology. It is believed that habitat structure represents niche dimensions which can be partitioned to allow the coexistence of species. A heterogenous environment means that more resource partitioning is possible (Giller & Gee, 1987), and more species can coexist

6.7 Interspecific competition among adults

Odonata males are conspicuous, usually easily identified in the field and readily interact with other individuals and species. They are therefore well suited for studies of intraspecific and interspecific competition in the field (Moore, 1964). It is believed that in order for two species to coexist they have to have distinct ecologies (Chesson, 1991). Others have argued on the basis of modelling, that ecologically identical species can coexist (Chesson, 1991). Strong interactions between species are typical of interactive communities where the niche space is almost full and coexistence becomes a problem (Cornell & Lawton, 1992). Although this depends on if a species needs the same niche as another, and how similar the niches are. Two competitors may coexist because of priority effects (Shorrocks & Bingley, 1994). That is to say, a species resists invasion of a patch which it colonised first (Shorrocks & Bingley, 1994). This could explain why *T. arteriosa* was numerically dominant over the entire season. It was the first species to emerge and establish territories.

Previous studies on competition in insects have found differing results. Lawton and Strong (1981) found that competition among different species of folivorous insects is too rare to be important in structuring communities. Connor and Simberloff (1979) concluded that competition was not a major force in

structuring communities. Ridsdill-Smith (1991) found that competition was important in dung beetles.

6.8 Niche axes

Environmental differences between habitats provide axes for niche differentiation by species. This was the case for these species, with adults partitioning the environmental gradient. Substrate structure and roughness also provide niche axes for aquatic insects (Patrick, 1975). Here, substrate structure was measured in terms of particle size. Species of *Trithemis* did prefer different particle sizes. Niche limits of aquatic insects often reflect a compromise between environmental factors within the levels of tolerance of the species, and the effects of interspecific competition (Patrick, 1975). Exploitative competition for food can occur if a species has an included niche. That is if the species only relies on one type of food, and that food is also eaten by another species (Chase & Belovsky, 1994). The inferior competitor therefore has to share resources (Chase & Belovsky, 1994). Taking this viewpoint, *T. furva* could outcompete *T. stictica*, because at least *T. furva* did not have to share habitat space. Sternberg (1994) found that spatial segregation among dragonflies depended on the degree of competitive interactions. Sternberg (1994) also suggested that time, space and food were the most important niche dimensions for Odonata.

6.9 Feeding preferences and coexistence

Food differences allow coexistence between species in a community, and enable invasion by other species (Roughgarden, 1986). Johnson *et al.* (1987), found that certain prey taxa were more vulnerable to predation by Odonata larvae, yet the prey did not decrease when larval density increased. Therefore competition for food among larvae does not appear to be important (Johnson *et al.*, 1987). Competition for food might only become intense when species are subject to adverse environmental conditions that are more energetically demanding. For example, if a number of larvae are present in a stream and the

water level drops, species would become aggregated. Individuals can become cannibalistic if there are many different instars present. This would at least ensure that larvae near emergence would emerge before the water dries up. However, if all the individuals are similar in size, they could experience competition for food resulting in reduced growth rate.

6.10 The effect of past competition

It has been suggested that current patterns of resource partitioning among coexisting species can be attributed to competition in the past (Schoener, 1974; Ricklefs, 1979; Connell, 1980; Keddy, 1989; Schluter & McPhail, 1993). Connell's (1980) 'ghost of competition past' theory, suggested that interspecific competition resulted in the evolution of ecological differences between sympatric species, enabling coexistence. However, it may be that species became adapted to the environment without the influence of interspecific competition (Strong, 1982; Begon & Mortimer, 1986; Keddy, 1989). Some recent studies suggest that habitat partitioning results from interspecific competition (Repasky & Schluter, 1994). It has further been suggested that life-history traits may have evolved under different conditions of competition (Keddy, 1989). This could lead to species having more r-selected, k-selected or adversity-selected traits (Greenslade, 1983; Southwood, 1988). Traits of species in different kingdoms may also result from past competition (Hochberg & Lawton, 1990).

6.11 Conclusions

To conclude, the species under investigation were not in much competition at the adult or larval stage. Even where they overlapped a great deal spatially, species-specific preferences for habitats and microhabitats ensured that resource partitioning and coexistence was possible. Life-history differences also ensured that species were seasonally separated, with no two species emerging in great abundance at the same time. Interspecific competition among first instar larvae was reduced by adults of different species ovipositing in specific and different

sites. Asynchronous development of larvae and species-specific differences in body size at the same instar also ensured that competition was reduced. Because larvae were mainly generalist feeders within a certain size range and not taxon restricted in prey choice, competition for food if a preferred prey item suddenly became scarce, was unlikely. Only under conditions of food scarcity and habitat homogeneity would species suffer from asymmetric competition. Nevertheless, other factors such as predation and changes in abiotic factors will cause a change in the competitive ability of species. Where two species did use the same resource, they used it at different times. *T. dorsalis* and *T. furva* were such an example. The larvae of both were found in the pond. They did so at different times of the flight season, with *T. dorsalis* having all emerged before *T. furva* became established in the pond. Besides which they occupied separate microhabitats in the pond, so that even if they had occurred together coexistence would have still been possible.

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