RESEARCH ARTICLE

Climate and elevational range of a South African dragonfly assemblage

Contribution to EU/ALARM Project

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Abstract

Elevation and climate are interrelated variables which have a profound affect on biota. Flying insects such as dragonflies can rapidly disperse and select optimal habitat conditions at appropriate elevations. Such behaviour is likely to be especially important in geographical areas which are subject to major climatic events such as El Niño. Accordingly, we studied dragonflies and environmental variables in a series of reservoirs over an elevational range of 100–1350 m a.s.l. at the same latitude on the eastern seaboard of South Africa. The aim was to determine how elevation and climate (as regional processes), as well as local factors, influence species assemblage variability, habitat preference and phenology. Certain environmental variables strongly explained the main variation in species assemblage. These included local factors such as pH, marginal grasses, percentage shade, exposed rock, marginal forest and to a lesser extent, marshes and flow. Different species showed various tolerance levels to these variables. Elevation and climate as regional processes had very little influence on dragonfly assemblages in comparison with these environmental factors. These odonate species are essentially sub-tropical, and are similar to their tropical counterparts in that they have long flight periods with overlapping generations. Yet they also have temperate characteristics such as over-wintering mostly as larvae. These results indicate evolutionary adaptations from both temperate and tropical regions. Furthermore, most were also widespread and opportunistic habitat generalists. The national endemics *Pseudagrion citricola* and *Africallagma sapphirinum* only occurred at high elevations. However, the endemic *Agriocnemis falcifera* was throughout all elevations, suggesting regional endemism does not necessarily equate to elevational intolerance. Overall, the results suggest that many millennia of great climatic variation have led to a highly vagile and elevation-tolerant dragonfly assemblage which readily occupies new water bodies. Such an assemblage is likely to be highly tolerant of global climate change, so long as there is sufficient water to keep the reservoirs at a constant level.

Introduction

Insect phenology usually varies with topography and associated environmental factors (Wolda 1987). Interactions between temperature-dependent development and microclimate are important features of insect life-history, leading to the maintenance of considerable genetic variation in populations (Bradshaw and Holzapfel 1990; Roff 1990). Studies in insects and other arthropods suggest that microclimatic gradients sometimes can have larger effects on emergence phenology than do annual fluctuations in weather conditions (e.g. Kingsolver 1979; Weiss et al. 1993). Moreover, field evidence (Thomas et al. 2001) supports theoretical predictions (Thomas et al. 1999) that certain types of thermophilous insects have expanded to occupy broader niches, and hence larger patch sizes near their northern range margins in the northern hemisphere during some warm summers in recent years (Ott, this volume).

Small reservoirs are a characteristic feature of the South African agricultural landscape, acting as important reserves for dragonflies (Samways 1989a). These reservoirs have been shown to be important in promoting the conservation of insect diversity, but mostly of generalist species (Samways and Steytler 1996). Such reservoirs increase the area of occupancy of the local species. Thus, they are present in the local area in natural water bodies and simply move across to the reservoirs.

The topography of KwaZulu-Natal, South Africa ranges in elevation from 0–3000 m a.s.l along a 200 km E-W transect at one latitude. This area is strongly modified by montane climate at higher elevations, and has a sub-tropical/tropical climate at sea level. The study area within KwaZulu-Natal is situated at the edge of a major escarpment comprising a highly heterogeneous landscape structure with a wide variety of aquatic habitats. This elevational transect supports a high diversity of dragonfly species making up close to three-quarters of the South African odonate fauna. This provides a basis for measuring how species phenologies and distribution respond to the seasonal (temporal) and elevational changes. This information can be useful for subsequent conservation action, and for providing baseline data for future studies on the impacts of global climate change.

Using a series of five moderately-sized artificial, but well-established reservoirs (which only reach about 1400 m a.s.l.), the aim here was to determine the extent to which elevation (as a regional process), alongside local factors, influence habitat preferences and species distribution. Furthermore, as there is no information on the effects of seasonal changes on southern African odonate species, the aim was also to determine how phenology might vary with elevation.

Materials and methods

Study area

The study area was in KwaZulu-Natal between the coast and the Drakensberg escarpment (<3000 m a.s.l.). Elevation exerts a major influence on climatic features at all spatial scales, being a barrier to rain-bearing air masses, and by altering temperature through lapse rates and aspect (Tyson 1986; Schulze 1997).

Reservoirs, all of which were over 30 years in age, were selected within this elevational gradient (Fig. 1) to be at the same latitude (with 26 minutes latitude) and to be relatively comparable (Table 1). The maximum elevation that could be entertained for these comparative studies was 1400 m a.s.l, even though the mountain peaks reached 3000 m a.s.l.

Methods

Each reservoir was about 1 ha, and stratified into six sub-sites, each measuring 20 m length (along a line transect on the reservoir edge) by 2 m width (1 m on land and 1 m into water). Data were collected on 42 sampling occasions, and covered various stages of dragonfly development (adults, tenerals and young adults (together here simply called 'tenerals'), larvae and exuviae). Mating or oviposition were also recorded (mostly tandem flights and occasional dipping of ovipositors). Environmental variables were recorded twice a month from January 2001 to December 2002, except for the winter months of June, July and August when data were collected once each month.

Adult males were recorded using close-focus binoculars, and walking along the 20 m sub-sites and counting within 6 min all individuals perching or flying. Counts of Anisoptera at sub-sites can be virtually 100% accurate and that of Zygoptera exceeds 80% (Moore 1991). Counts were between 10h00 and 14h00 during sunny, high activity periods of the day.

Exuviae and tenerals were recorded as an indication of successful breeding. In this study, population changes were indicated by comparing the maximum numbers of individuals (adults, tenerals and larvae) observed each month for the whole sampling period. Unidentified tenerals from the field were collected and reared in the laboratory until their body colour (with genitalia morphology) could be used for subsequent identification.

Larvae were sampled with a dip-net (41 cm diameter × 1 mm mesh sieve). Two dips per sub-site (12 dips/site) were done within 20 min. Each dip was followed by vigorously shoving the net back and forth in water once among water weeds, along rushes and besides banks. We fully accept that no single, quantitative collection method is equally efficient for all species of larvae, and even all ages. However, the comparative efficiency of the collection method, being standardized, will be the same at different sites. Individual larvae in the net were identified using a 9× hand lens, counted and

Figure 1. The mid-elevation site (790 m a.s.l.) with reedy margins typical of all the sites.

released back into water except where individuals could not be identified in the field, in which case, they were picked out with soft, flexible forceps and placed in aerated plastic cages containing reservoir water. Usually only last-instar larvae were collected for subsequent rearing and identification in the laboratory.

Marginal vegetation (both structural and compositional) was estimated using percentages of sub-sites they covered. At all sub-sites, aquatic plants were recorded as: marginal forest stands (Mfor), marginal grasses (Mgra), floating and submerged vegetation (Fsv), marginal herbs, sedges and reeds (Mhsr).

Meteorological data e.g. rainfall, ambient and water temperatures (At/Wt) collected at Goodhope Estate (GH), Cedara (CE) and the Botanical Gardens (BG) were compared with that collated by the weather bureau at Cedara Agricultural College. Also, rainfall and temperature data for Krantzkloof (KL) and Stainbank (SB) Nature Reserves were compared with that collated by the Durban Airport weather station.

Other measured environmental variables were percentage exposed rock in the sampling sub-site (Exrock %), percentage shade (% Sh), water depth (Wd), turbidity (Tur %), pH, flow (1 = running, 0 = still), reservoir circumference (Pcir (m)) and elevation (Elev (m)).

Data were analysed with univariate methods for species richness and abundance relationships using diversity indices, distributional models and graphical methods. Species spatial and temporal variability was analysed using Analysis of Variance (ANOVA). Spearman's rank correlation coefficients were used to measure the association between variables and species abundance and richness. These correlations were

Table 1. The five elevational sites used in this study

Site name/code	Grid reference and Elevation	Land use
Kenneth Stainbank Nature Reserve (SB) (Low elevation)	29°50'S; 30°55'E; 100 m a.s.l.	Nature reserve
Krantzkloof Nature Reserve (KL) (Mid-low elevation)	29°46'S, 30°5'E; 450 m a.s.l	Nature reserve
Botanical Gardens, Pietermaritzburg (BG) (Mid-elevation)	29°35'S; 30°25'E; 790 m a.s.l.	Botanical gardens
Cedara (CE) (Mid-high elevation)	29°61'S; 29°06'E; 1050 m a.s.l.	Low-intensity agricultural area
Mondi Goodhope Estate (GH) (High elevation)	29°40'S; 29°58'E; 1350 m a.s.l.	Extensive grassland corridors (natural state) among pine stands

calculated using the software SPSS version 6.1. MINITAB and SPSS software were used to run ANOVA, relating species to sites and site variables. In addition to ANOVA, Similarity coefficients calculated between every pair of samples helped facilitate a classification or clustering of samples into groups which are mutually similar or an ordination plot in which the samples are 'mapped' into multidimensional space in such a way that the distances between pairs of samples reflect their relative dissimilarity of species composition.

Hierarchical agglomerative clustering, using the program 'Cluster' in the computer software PRIMER (Clark and Warwick 1994) was used to compare sites. The species by sub-site (SS) data matrix was transformed using 4th root-transformation to balance rarer and commoner species. The Bray-Curtis similarity index was then used to produce a similarity matrix and then fused successively through hierarchical clustering using group-average linking, to produce a dendrogram with the x-axis defining a similarity level at which two samples or groups are considered to have fused, and the y-axis representing the full set of samples.

Correspondence analysis (CA), operates on a site and species data matrix and represents it on a two-dimensional plane (ter Braak and Smilauer 1998). It uses a site-by-species scores data matrix and summarises it such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. Conversely, from a species-by-site matrix, CA ordinates the data such that the closer two species are to one another on the same ordination plane, the greater the likelihood that they will occur at the same or similar sites and vice versa. Canonical Correspondence Analysis (CCA) was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the bi/triplot, and is therefore a measure of how much the species distribution differs along that environmental gradient. Important environmental gradients therefore tend to be represented by longer arrows than less important ones (ter Braak and Looman 1995). The software CANOCO version 4 and CANODRAW version 3.1 (ter Braak and Smilauer 1998) were used.

Results

Species phenology

A total of 47 species was recorded throughout the study (Table 2). Adults of only three species (*Ceriagrion glabrum, Lestes plagiatus* and *Crocothemis erythraea*) were recorded during winter, and then only at Mid (BG) elevation. Accumulation curves reached asymptotes for tenerals with 10–14 species, and for adults with 21–25 species, and varied with elevation (Fig. 2).

Relative proportions of adults, tenerals and larvae

Larvae stayed at about the same level all year round (Fig. 3). Tenerals and adults showed the same trends as in Fig. 2 i.e. none in July and August. However, there was trend for maximum numbers to be reached later at higher elevations, from October to December for tenerals and November to February for adults. Larval abundance varied from 20 individuals in January at Mid-low (KL) elevation to 138 in April at Mid-high (CE) elevation. Teneral counts also varied from two individuals in June at High (GH) elevation to 175 individuals in November at Mid-high (CE) elevation. Thereafter, larval abundance at all elevations was high in November for both years. No teneral individuals were recorded at any elevations during winter (July to August). Adult abundance was greatest in November for both years and at all sites except at High (GH) and Mid-low (KL) where it was in December.

Peak occurrence periods

There was continual emergence over the summer months, and there was continuous presence of two or three developmental stages between September and June. *Lestes plagiatus* and *L. tridens* probably over-wintered in the egg stage. Table 3 summarises the months for peaks in adult, teneral, larval stages, and mating/oviposition in Anisoptera and Zygoptera species. Anisoptera adults from High (GH), Mid-high (CE) and Low (SB) elevations had peak occurrences mostly from December to March, although most species peaked in November during the first sampling year at the High (GH) elevation. Species peaks in Mid (BG) and Mid-low (KL) elevation were also similar, occurring in November in both sampling years. Double peaks occurred at the Mid-high (CE) elevation for *C. erythraea,* occurring in March and November 2001, January and November 2002. *Trithemis stictica* peaked in March and November 2001, April and November 2002.

Zygoptera species had very similar peak adult occurrence periods at High (GH), Mid (BG) and Low (SB) elevations, from December to March in both years. At Mid-high (CE) and Mid-low (KL) elevations, peak adult appearance was April/May. Zygop-

Table 2. Odonata species sampled during this study with species code names

Species	Elevations					
	Code	SB	KL	BG	CE	GH
Anisoptera						
Aeshnidae						
Anax imperator Leach, 1815[3]	Aimp	AL*	AL	AL	AL	AL
A. speratus Hagen, 1867[3]	Aspe	A	A	A	A	A
A. tristis Hagen, 1867[1]	Atri	A	–	–	–	–
Gomphidae						
Ceratogomphus pictus Sélys, 1854[3]	Cpic	–	–	–	A	A
Ictinogomphus ferox (Rambur, 1842)[2]	Ifer	A	–	–	–	A
Notogomphus praetorius (Sélys, 1878) [2]	Noto	–	AT	–	–	AT
Paragomphus cognatus (Rambur, 1842) [3]	Pcog	–	–	A	–	–
Libellulidae						
Acisoma panorpoides Rambur, 1842[2]	Acis	ATL	–	–	ATL	ATL
Brachythemis leucosticta Burm., 1839[3]	Bleu	A	–	–	–	–
Chalcostephia flavifrons Kirby, 1889[1]	Chfl	A	–	–	–	–
Crocothemis erythraea (Brullé, 1832) [3]	Cery	ATL	ATL	ATL	ATL	ATL
Diplacodes lefebvrii (Rambur, 1842) [2]	Dlev	A	–	–	–	–
Hemistigma albipunctum Rambur 1842[2]	Halb	A	–	–	–	–
Nesciothemis farinosa (Förster, 1898) [3]	Nfar	AT	AT	AT	AT	AT
Notiothemis jonesi Ris, 1919[1]	Njon	–	A	–	–	–
Orthetrum caffrum (Burmeister, 1839) [3]	Ocaf	–	–	–	ATL	ATL
O. hintzi Schmidt, 1951[1]	Ohin	–	–	–	–	A
O. julia falsum Longfield, 1955[3]	Ojul	ATL	ATL	ATL	ATL	A
Pantala flavescens (Fabricius, 1798) [3]	Pfla	A	A	A	A	A
Palpoleura portia (Drury, 1773) [3]	Pluc	AT	AT	AT	–	–
P. jucunda jucunda Rambur, 1842[2]	Pjuc	–	–	–	–	AT
Diplacodes luminans (Karsch, 1893) [1]	Plum	AT	AT	AT	–	–
Sympetrum fonscolombii (Sélys, 1840) [2]	Sfon	A	A	A	A	A
Rhyothemis semihyalina Desjardins, 1832[2]	Rshy	AT	–	AT	AT	–
Tetrathemis polleni Sélys 1877[1]	Tpol	A	–	–	–	–
Tramea basilaris (Beauvois, 1817) [2]	Tbas	AL	AL	A	AL	AL
Trithemis arteriosa (Burmeister, 1839) [3]	Tart	A	A	A	AL	AL
T. dorsalis (Rambur, 1842) [3]	Tdor	–	ATL	ATL	ATL	ATL
T. stictica (Burmeister, 1839) [2]	Tsti	–	ATL	ATL	ATL	ATL
Urothemis assignata (Sélys, 1872) [2]	Uass	A	A	A	A	A
Zygonyx natalensis (Martin, 1900) [2]	Znat	–	A	A	–	–
Zygoptera						
Chlorocyphidae						
Platycypha caligata Sélys, 1853[3]	Pcal	–	–	AT	A	–
Coenagrionidae						
Africallagma elongatum (Martin, 1907) [1]	Aelo	–	–	A	–	–

Species	Elevations					
	Code	SB	KL	BG	CE	GH
A.glaucum (Burmeister, 1839) [3]	Aglm	ATL*	ATL	ATL	ATL	ATL
A. sapphirinum (Pinhey, 1950)[4]	Asap	–	–	–	–	A
Agriocnemis falcifera Pinhey, 1959[4]	Afal	ATL	ATL	ATL	ATL	ATL
Azuragrion nigridorsum (Sélys, 1876) [2]	Azn	AT	–	–	–	–
Ceriagrion glabrum (Burmeister, 1839) [3]	Cglm	ATL	ATL	ATL	ATL	–
Ischnura senegalensis (Rambur, 1842) [3]	Isen	ATL	ATL	ATL	ATL	ATL
Pseudagrion citricola Barnard, 1937[4]	Pcit	–	–	–	–	A
P. hageni Karsch 1893[2]	Phag	AT	AT	AT	–	–
P. kersteni (Gerstäcker, 1869) [3]	Pker	ATL	ATL	ATL	ATL	ATL
P. massaicum Sjöstedt, 1909[3]	Pmas	ATL	–	ATL	ATL	–
P. salisburyense, Ris, 1921[3]	Psal	ATL	ATL	ATL	ATL	A
Lestidae						
Lestes plagiatus (Burmeister, 1839) [3]	Lplg	–	ATL	ATL	ATL	ATL
L. tridens McLachlan, 1895[1]	Ltri	AT	–	–	–	–
Platycnemididae						
Allocnemis leucosticta Sélys, 1863[2]	Aleu	–	–	A	–	–

* Record of adult, teneral and/or larval stage of the corresponding species. **[1]** Common African species whose range extends south just over the border into South Africa, but are local or rare in the country, **[2]** African species that are widespread and/or locally common in South Africa, **[3]** African species that are regularly seen in the right habitats, some of these are very common throughout South Africa, **[4]** Species endemic to South Africa (i.e. South of the Limpopo River).

tera species with two peaks per year were *Ischnura senegalensis* and *C. glabrum*, each occurring at various elevations (*C. glabrum* was absent at High (GH) elevation). Also, *Africallagma glaucum* and *Pseudagrion massaicum* had two peak appearances in Mid-high (CE) elevation. *L. plagiatus* had two peaks per year at Mid (BG) and Mid-low (KL) elevation, while *L. tridens* and *P. massaicum* had two peak abundances per year in Low (SB) elevation during both years. *L. tridens* from Low (SB) elevation had four peaks at different times during the two sampling years: April and December 2001, March and November 2002, indicating more than one generation per year. The number of species per family was very similar from one elevation to the next.

Fifteen species occurred at all five elevations, while 17 species were restricted to only one elevation: eight in Low (SB); four each at High (GH) and Mid (BG) and one only occurred at Mid-low (KL). 15 species occurred over at least two elevations at all five elevations (Table 4).

The dominant species at the Low (SB) elevation site was *L. tridens* (22%), while *T. stictica* dominated in Mid-high (CE) elevation. Both elevations had relatively high percentage levels of species dominance patterns compared to the other elevations. Mid-low (KL) elevation and High (GH) elevation showed some similarity in patterns of species dominance, with *T. arteriosa* (17%) and *T. stictica* (18%) being the dominant species.
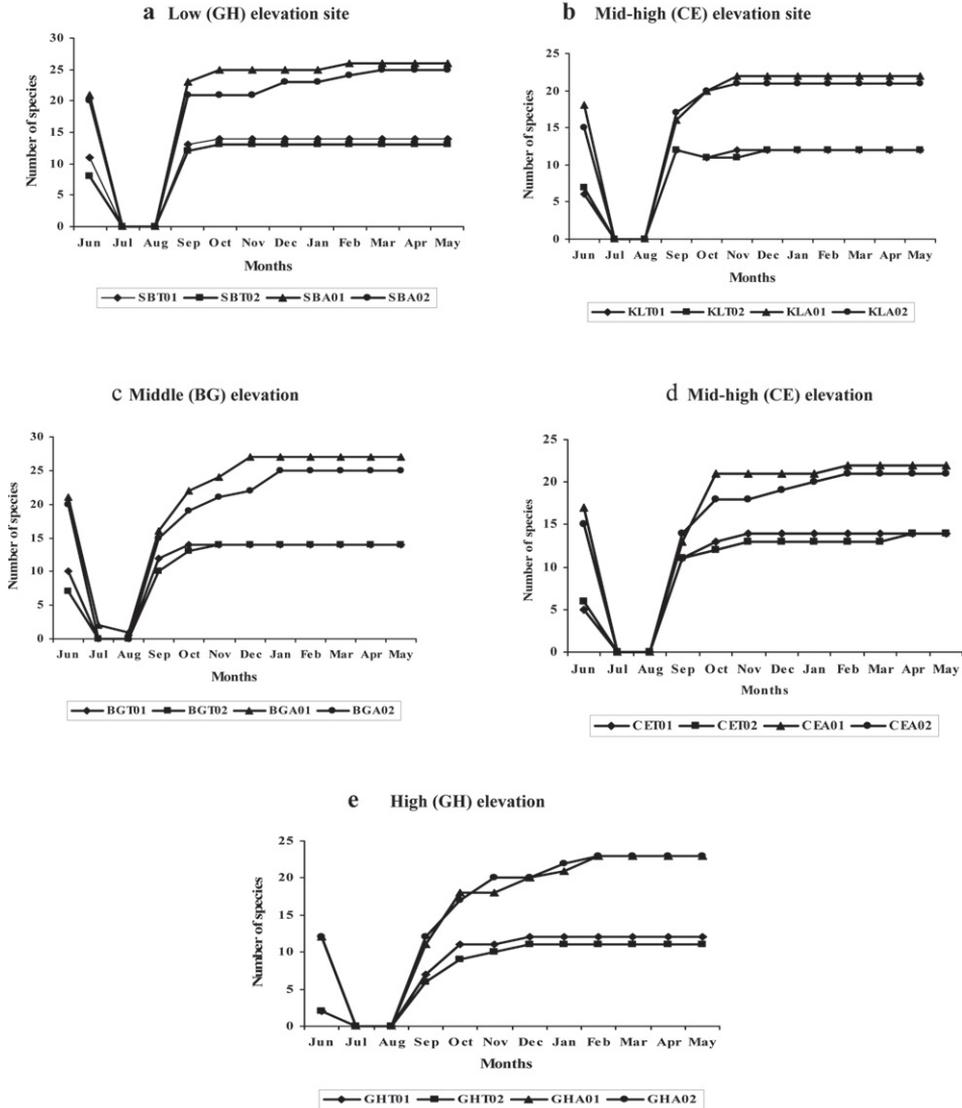
Figure 2. Accumulative dragonfly tenerals (T) and adults (A) species recorded at **a** Low (SB), **b** Mid-low (KL), **c** Mid (BG), **d** Mid-high (CE) and **e** High (GH) elevations during the first (01) and second (02) year of the study.

Spatial variations in adults, tenerals and larvae with elevation

Larval species richness and abundance was highest at Mid-high (CE) elevation. Patterns of teneral species richness across elevations ranged between 14 and 16 species per elevation during the study, with Mid-low (KL) recording lowest individual counts. Overall number of adults species varied slightly across elevations, with Low (SB) eleva-
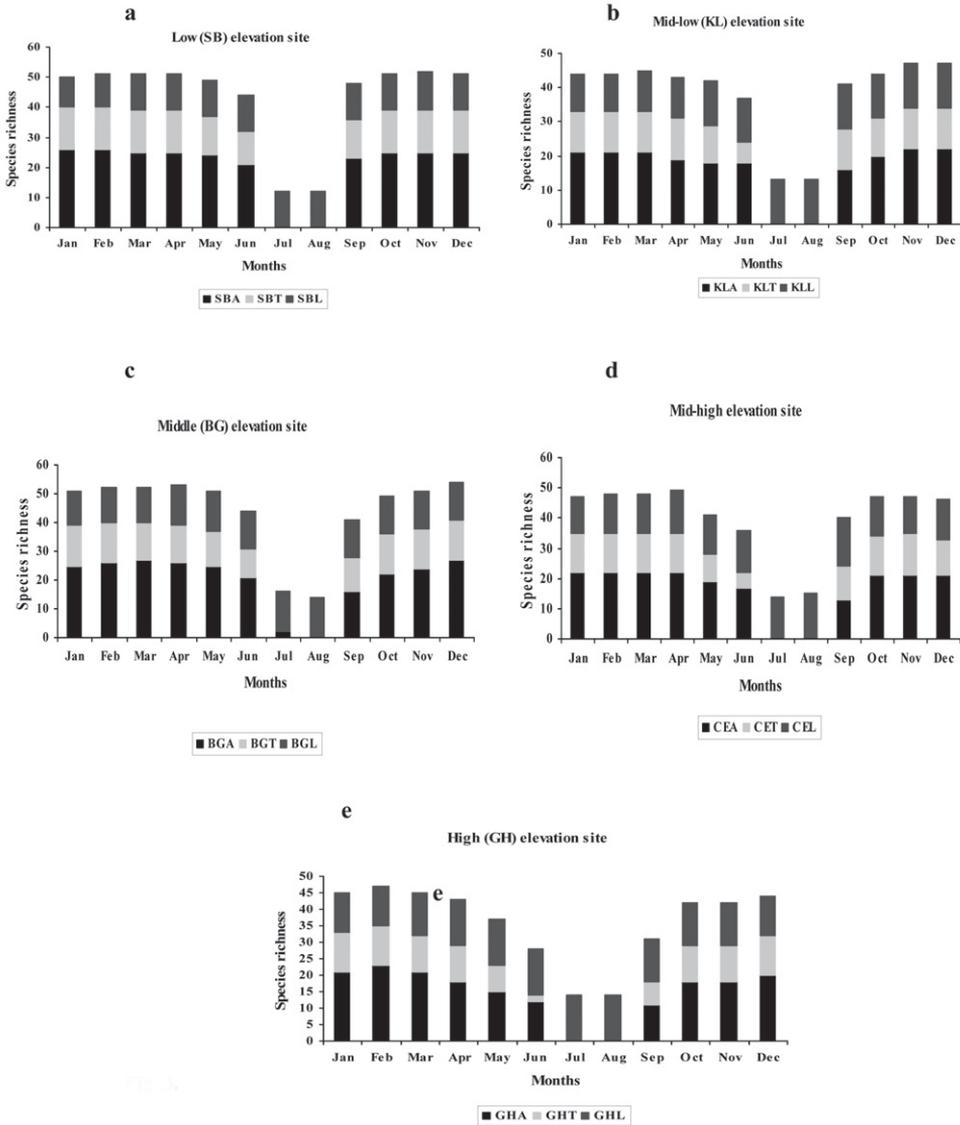
Figure 3. Dragonfly species recorded at **a** Low (SB), **b** Mid-low (KL), **c** Mid (BG), **d** Mid-high (CE) and **e** High (GH) in terms of adults (A), tenerals (T) and larvae (L), and during the two-year sampling period.

tion supporting the most species. Adult abundance was highly variable across elevations, with Mid-low elevation (KL) recording lowest abundance. Larval species richness was significantly positively correlated with elevation (F = 19.25; P = 0.002), as was abundance (F= 7.69; P=0.024). Teneral species richness was negatively correlated with elevation but not statistically significantly. There was weak, non-significant positive correlation for teneral individuals with elevation (F = 4.73; P= 0.056). Regressions of adult dragonfly species richness (P=0.27) and abundance (P=0.32) on elevation were

Table 3. Summary of species phenologies recorded during this study.

Site Elevation (m a.s.l.)	Adults		Mating/ oviposition		Larvae	
	Zygoptera	Anisoptera	Zygoptera	Anisoptera	Zygoptera	Anisoptera
Low (SB) 100 m	Dec–Mar 2002 Dec–Mar 2001	Dec–Mar 2002 Dec–Mar 2001	Feb–Jun	Jan–Apr	Apr–May Dec	Apr–May Dec
Mid-low (KL) 450 m	Nov 2002 Nov 2001	Apr 2002 Apr 2001	Feb–Mar	Feb–Mar Oct–Nov	Apr–Jun Dec	Apr–May Dec
Middle (BG) 790 m	Nov 2002 Nov 2001	Jan–Mar 2002	Feb–Mar Sep–Nov	Feb–Mar	Mar–Apr, Jul, Nov–Dec	May, Sep– Oct
Mid-High (CE) 1050 m	Dec–Mar 2002 Dec–Mar 2001	Apr–May 2002 Apr–May 2002	Jan–May Oct–Nov	Feb–May	Mar–May Sep–Dec	Apr, Jul–Aug
High (GH) 1350 m	Dec–Mar 2002 Nov 2001	Dec–Mar 2002 Feb–Apr 2001	Jan–May	Feb–Jun	Feb–Sep	Feb–Sep

not statistically significant even though there was a generally decreasing trend in species as elevation increased.

Two-way ANOVA of the response of adults, tenerals and larvae to elevation across seasons showed no statistically significant effect on adult species (F = 1.2, P = 0.31) or teneral individuals (F = 1.6; P = 0.41). However, there were statistically significant responses for adult individuals (F = 2.9; P = 0.01), teneral species (F = 2.1; P = 0.05), larval species (F = 4.2; P = 0.002) and larval individuals (F = 10.0; P = 0.001) (Table 5).

Relationship between species and environmental conditions

Species associations with elevation were strongest on ordination plots when all Odonata were separated into their component sub-orders (Anisoptera and Zygoptera). CA results for Anisoptera (Fig. 4a) showed most open water species clumped at the centre of the ordination. Zygoptera species showed various trends as species were more dispersed from the centre of the ordination (Fig. 4b). They were more tolerant of diverse conditions of shade as well as of open water. Separate CCA ordinations were also run for species belonging to Anisoptera and Zygoptera again for better interpretation of the effects of measured variables and elevation on patterns of dragonfly assemblage composition and distribution. Species-site-variable triplots for Anisoptera (Fig. 5a) and Zygoptera (Fig. 5b) showed that most assemblages were related to a number of environmental variables, and indicated how species responded or not to gradients of these variables in space.

Accordingly, elevation, marginal grasses, pH, reservoir circumference, atmospheric temperature and percentage shade appeared on the first (horizontal ordination axis) as the most important variables, while water depth, floating /submerged vegetation and marginal forest occurred on the second axis (vertical) and were less important in determining Anisoptera species assemblage distribution patterns. Marginal forest, percentage shade, water depth and floating/submerged vegetation were the most important

Table 4. Odonata species and elevational distributiona

Elevations	Species
One elevation 100 m (SB)	Azn, Ltri, Atri, Bleu, Chfl, Halb, Dlev, Tpol
450 m (KL)	Njon
790 m (BG)	Pcal, Aleu, Aelo, Pcog
1050 m (CE)	None
1350 m (GH)	Asap, Pcit, Ohin, Pjuc
Two elevations CE, GH	Cpic, Ocaf
KL, BG	Znat
KL, GH SB, GH	Noto Ifer
Three elevations SB, CE, GH	Acis
SB, BG, CE	Pmas, Rshy
SB, KL, BG	Phag, Pluc, Plum
Four elevations KL, BG, CE, GH	Lplg, Tdor, Tsti
SB, KL, BG, CE	Cglm
All five elevations 100–1350 m	Uass, Tart, Sfon, Pfla, Ojul, Nfar, Cery, Aspe, Pker, Psal, Isen, Afal, Aglm, Tbas, Aimp

SB (Low) = (100 m), **KL** (Mid-low) = (450 m), **BG** (Mid) = (790 m), **CE** (Mid-high) = (1050 m) and **GH** (High) = (1350 m). Species codes are as in Table 2.

variables, while marginal grasses, elevation and pH were important for Zygoptera. The following Anisoptera species were also associated with marginal grasses of reservoirs at High (GH) and Mid-high (CE) elevations: *T. stictica, Palpopleura jucunda, Acisoma panorpoides, Orthetrum caffrum. N. jonesi* was associated with highly shaded conditions of sub-site three at Mid-low (KL) elevation.

Low (SB) elevation species (when the elevation gradient is projected backwards on the ordination triplot) had the typical species *Hemistigma albipunctum, Chalcostephia flavifrons, Tetrathemis polleni, Diplacodes lefebvrii, Rhyothemis semihyalina* and *Tramea basilaris,* even though the last three species were also present at higher elevations. Open reservoirs at all elevations had the following species in common, located mostly at the centre of the ordination for Anisoptera: *O. julia, C. erythraea, T. arteriosa, P. lucia, A. speratus, A. imperator, T. dorsalis, N. farinosa* and *P. flavescens.*

High (GH) elevation zygopterans like *Pseudagrion citricola* and *Africallagma saphirinum* were strongly associated with sunny conditions, high pH and marginal grasses. Low (SB) elevation species were *L. tridens* and *A. nigridorsum* while *P. hageni* was associated with Middle (BG) to Low (SB) elevation shade conditions. *A. elongatum, P. kersteni* and *P. salisburyense* were associated with minimal flow, exposed rock and marshy conditions.
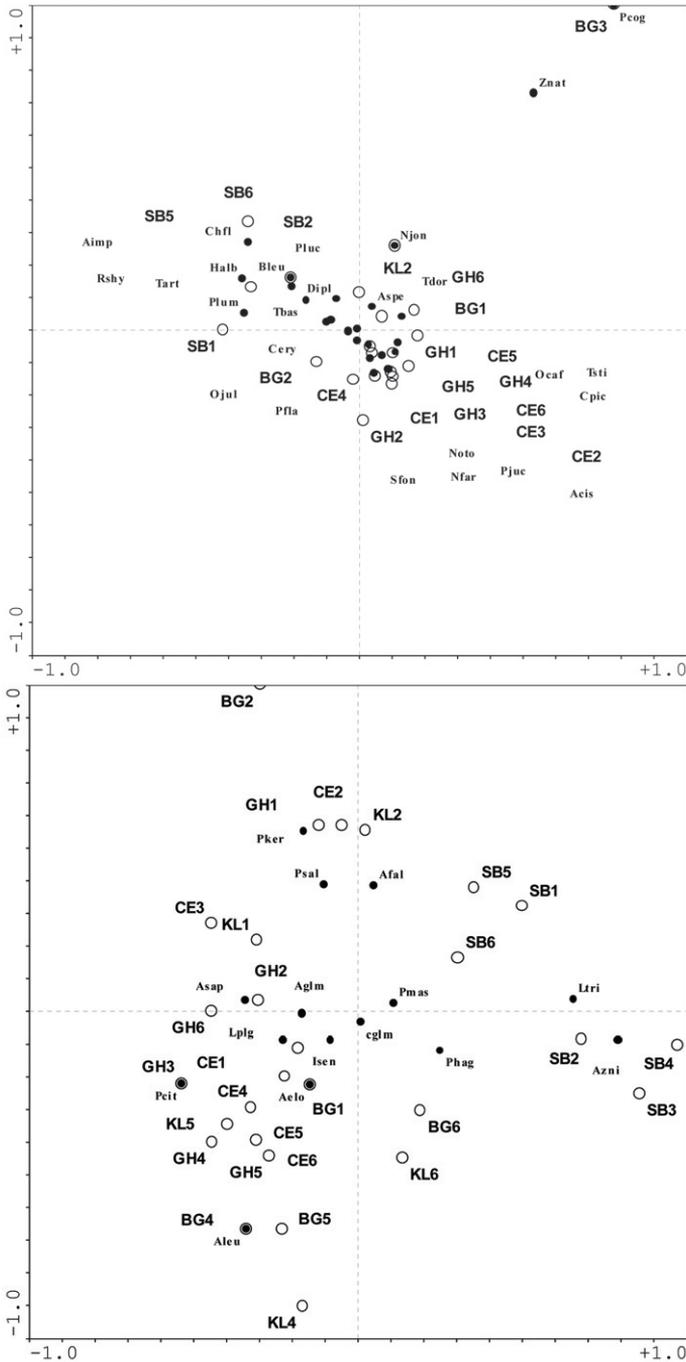
Figure 4. a CA biplot of Anisoptera species (closed circles) and sampling sites (open circles), and **b** CA biplot of Zygoptera species (closed circles) and sampling sites (open circles) for pooled 2001 and 2002 data. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Species codes are as in Table 2.
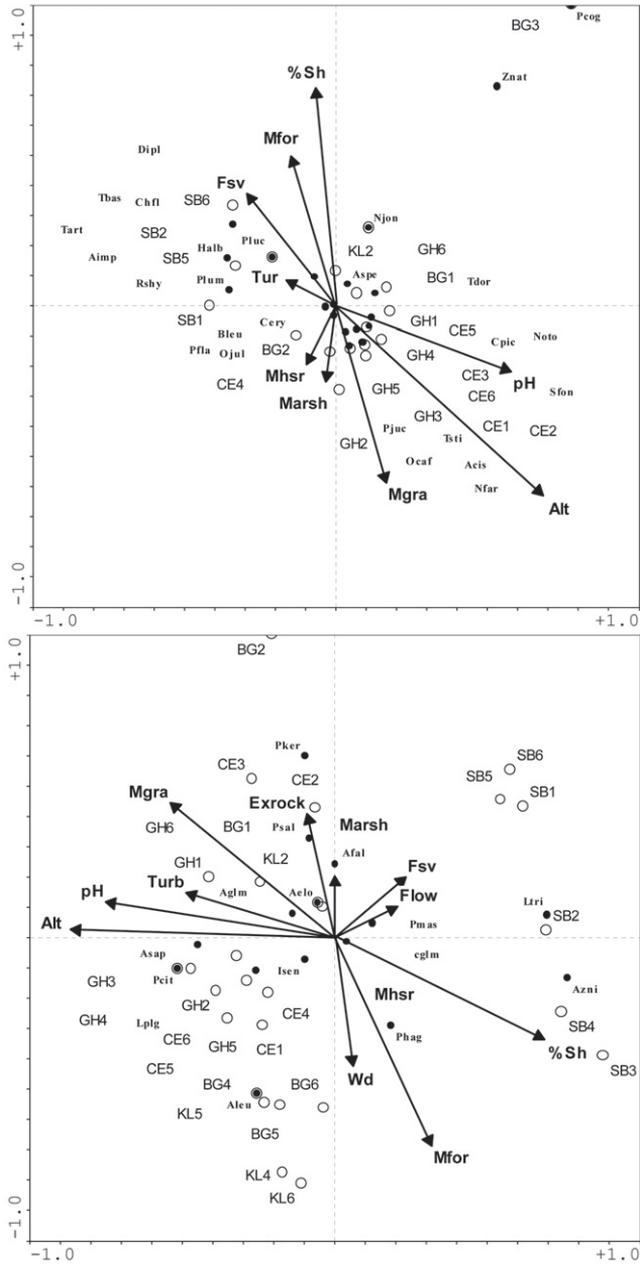
Figure 5. a CCA triplot of Anisoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) and **b** CCA triplot of Zygoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) for pooled 2001/2002 data. Axis 1 is horizontal and axis 2 vertical. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Site variables are: Alt= elevation, Mgra= marginal grasses, Mhsr= marginal herbs, sedges and reeds, Mfor= marginal forest, Tur= water turbidity, Fsv= floating and submerged vegetation, %Sh= percentage shade. Species codes are as in Table 2.

Table 5. Two-way-ANOVA results of elevation and seasonality interaction for mean dragonfly adults, tenerals and larvae richness and abundance, and measured site variables during the whole sampling period.

Site	Summer					Autumn					Winter					Spring					F	P
variable	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH		
Asp	25	21.5	24	21	21	25.5	21	26	21.5	23	20	16	20	16	12	23	21	22.5	20	19	1.2	0.31 ns
Aind	700	351	418	296	790	572	374	480	567	648	130	62	98	112	75	600	404	552	554	534	2.9	0.01
Tsp	13.5	12	14	13	11	13.5	11	13	14	11.5	9.5	6.5	8.5	6.5	2	13.5	12	14	13	11	2.1	0.05
Tind	172	94	132	230	215	122	125	137	223	200	25	15	20	19	5	216	162	190	243	200	1.6	0.14 ns
Lsp	12.5	13	13	13	13	12	12.5	14	14.5	14	12	13	14	15	13.5	13	12.5	13	16	13	4.2	0.002
Lind	124	141	84	93	77	145	120	146	193	83	83	70	89	131	135	121	75	147	134	151	10	0.001
% Sh	19	12.4	16.5	0	0	12	15.8	11	0	0	11	16	10	0	0	17	11	14.6	0	0	1.3	0.26 ns
At	24.5	30	30	29	30.4	28	29.3	29	30.5	30	17	17	18	20	21.9	26	28	26.3	28	25.5	0.8	0.59 ns
Fsv	30.8	17	24	21	11.3	30	2	28	20.5	6	18	0.6	15	14	3.7	24	1.9	21.8	16	6.8	0.7	0.6 ns
Mfor	30	40	25	0	0	30	50	25	0	0	30	50	25	0	0	30	50	25	0	0	1	0.44 ns
Mgra	27.5	16	12.5	22	21	25	4.8	12	23.4	22	11	2.2	5.5	10	8.3	22	6.2	11.7	22	26.2	1	0.46 ns
Marsh	27	27	23	12	7.5	29	29	24	14.8	7.3	12	5.5	12	6.6	4.2	26	28	15.6	11	8.2	7.4	0.001
pH	7.2	6.9	6.9	7.2	7	7	7	7.3	7.1	7.1	6	7.2	7.1	7	6.8	6	7.1	7.1	6.9	7.2	0.8	0.58 ns
Tur	18	25	20.5	23	20	15	26	24	17	25	22	28	20	19	28.8	20	21	20	19	17.4	0.5	0.86 ns
Wd	25	28	29.3	26	24	24	25	22.8	25	20	15	15	16	16	18.9	24	24	24	23.4	20.2	1.4	0.24 ns

Asp = Adult species, **Aind** = Adult individuals, **Tsp** = teneral species, **Tind** = teneral individuals, **Lsp** = larval species, **Lind** = larval individual. **SB** (Low) = (100 m), **KL** (Mid-low) = (450 m), **BG** (Mid) = (790 m), **CE** (Mid-high) = (1050 m) and **GH** (High) = (1350 m). **% Sh** = percentage shade, **At** = atmospheric temperature, **Fsv** = floating and submerged vegetation, **Mfor** = marginal forest, **Mgra** = marginal grass, **Tur** = turbidity, **Wd** = water depth. (ns = non-statistically significant at the 5% level of probability)

Table 6. Intra-set correlations between each of the site variables and Canonical Correspondence Analysis axes 1 and 2 for adult Anisoptera and Zygoptera species and site variables sampled over two years across all five elevations.

Odonata/ Environmental Variables[a]	Anisoptera		Zygoptera	
	CCA axis1	CCA axis 2	CCA axis 1	CCA axis 2
Eigenvalues	–	0.319	0.318	0.127
Mfor	-0.1912	0.3923	-0.5049	0.3524
Fsv	-0.279	0.3370	0.2001	0.0900
Mgra	-0.6625	0.1082	-0.5586	0.2150
Erock	0.1777	-0.0413	-0.0947	0.5153
Marsh	-0.2967	-0.1065	0.0274	0.2826
%Sh	-0.5394	-0.3895	0.5454	-0.2373
Wd	0.1248	-0.1075	0.0642	-0.2924
Tur	0.0261	-0.2375	-0.5051	-0.0390
pH	-0.5495	0.2382	-0.7604	-0.0177
At	-0.1793	-0.0333	0.0526	-0.0476
Mhsr	0.1714	0.0286	0.0490	-0.1449
Flow	0.0776	0.1496	0.2145	-0.2579
Alt (Elev (m))	0.7523	-0.3495	-0.8522	0.0251
Pcir (m)	-0.2418	-0.3889	-0.29990	0.0141

SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = Cedara (1050 m) and GH (High) = (1350 m). [a]Variable abbreviations as in Methods.

Intra-set correlations of environmental gradients with axes (Table 6) showed that elevation, pH, percentage shade and marginal grasses were highly correlated with axis one for both odonate sub-orders, with marginal forest being an additional correlate to this axis for Zygoptera. Reservoir circumference for Anisoptera and exposed rock for Zygoptera were the only important correlates with axis two in both ordinations. Axes three and four were not important. A summary of weightings attributed to the first two axes of ordinations for Anisoptera and Zygoptera showed that species-environment correlations using CANOCO were strong. The respective eigenvalues, cumulative species variances and Monte-Carlo tests for CCA are given in Table 7. With a cumulative percentage variance for species data and for species-environment relations of 89%, it meant that measured site variables were probably responsible for the main variation in species patterns for Anisoptera. A Monte Carlo permutation test of probability further strengthened this inference as the first axis (Ax1: $F= 5.98$; $P< 0.005$) and all four axes (global: $F = 3.140$; $P< 0.005$) were highly significant. A cumulative species variance for species data and for species-environment relations of 39.9% for Zygoptera suggests that measured site variables accounted for little variation in species assemblage distribution patterns for this taxon. Although a Monte Carlo permutation test of probability showed that the first axis (Ax1: $F = 1.99$; $P< 0.01$) was significant, the overall test using all four ordination axes (global: $F = 1.75$; $P< 0.4$) was not significant.

Table 7. Summary of weightings of the first two axes of CA and CCA for both Anisoptera and Zygoptera adults sampled during the study in terms of variances accounted for by the two axes. Monte Carlo probability tests of significance are given for the first canonical axis (AX1) and all four axes.

Axes weightings	Anisoptera					Zygoptera				
	CA		CCA		All 4 axes	CA		CCA		All 4 axes
AXES	AX1	AX2	AX1	AX2		AX1	AX2	AX1	AX2	
Eigenvalues	0.457	0.343	0.358	0.319		0.352	0.186	0.318	0.127	
SP-ENC[1]			0.949	0.905				0.954	0.897	
CPVS[2]	28.9	50.6	22.7	42.9		31.7	48.3	28.5	39.9	
CPVS-EN[3]			27.5	52.1				39.9	55.8	
F-Ratio			5.989		3.140			1.992		1.759
P-value			0.005		0.005			0.01		0.4 ns

[1] Species-environment correlations; [2] Cumulative species variance of species data; [3] Cumulative species variance of species-environment relationship. (ns= statistically non-significant at the 5% level).

Discussion

Phenology

Seasonal rhythms with dormant (over-wintering) periods during winter are an integral part of the life history of temperate dragonflies (Corbet 1999). A similar trend was observed in this study, larvae generally being the only developmental stage sampled in winter (June and July). There were no adult and/or teneral species at any elevation except at Mid (BG), where adults of three species (*Ceriagrion glabrum*, *Lestes plagiatus* and *Crocothemis erythraea*) overwintered. Larvae of the dragonfly species sampled throughout this study, occurred (at various stadia) throughout the year at all elevations, but varied in diversity, richness and abundance. This was also the case for temperate regions where the larval stage is the most common over-wintering stage in Odonata (Norling 1984a; Corbet 1999).

Some species e.g. *I. senegalensis, L. plagiatus, C. erythraea*, and *T. stictica* appeared to have several distinct generations per year. This may be the case when the larval population is provided for by the synchronised return of adult residents, and oviposition occurring early enough to allow more than one generation in a year (Corbet 1999). Other species appeared to have a general overlap of larval cohorts. Nevertheless, there were still noticeable peaks in adult emergence for some species, with three distinct seasonal categories of species peaks appearing at all five elevations: 1) Spring peak (September–November), 2) Summer peak (early: December-March), and 3) Autumn peak (April-May).

Species with adult occurrence peaking in spring and/or summer probably overwintered between June and August as final-instar larvae or intermediate stadia, resuming growth to subsequent higher-instar larvae as favourable climatic conditions

and food became available from September. Autumn species perhaps over-wintered as eggs e.g. members of the family Lestidae (Corbet 1999; Norling 1984a), or as early-instar larvae. The subtropical Anisoptera species studied here were generally elevation-tolerant, univoltine, yet had prolonged emergence. In contrast, most Zygoptera were multivoltine, although also highly elevation tolerant.

Since climatic changes associated with seasons act locally and its effects are most apparent on the level of populations and metapopulations (McCarty 2001), many factors may have accounted for species temporal variations e.g. 1) mean annual precipitation as it affects the long-term quality and quantity of water available (Dent et al. 1989; Pinhey 1978) with rain in this study falling in summer, 2) as there are temperature irregularities usually attributed to topographical variation (Schultze 1997) in this study area, this may have resulted in warm coastal climate with high precipitation levels versus the cooler climates at higher elevations, or, 3) simple chance migrations could also have caused variation.

Aspects of dragonfly species adaptations in the sub-tropics

The centre of biogeographical distribution of a dragonfly species is very important in determining the number of generations the species can go through in a year (Corbet 1999). Most dragonflies colonising the temperate zone for example, have evolved a life cycle where winter is spent in the larval stage.

Usually a large number of stadia is a means of resisting cold (e.g. Paulson and Jenner 1972; Norling 1984b). It is possible that the first step in the colonisation of the temperate zone has been to evolve a mechanism where the larval stage coincides with the adverse season. According to Corbet (1957a,b; 1964) and Norling (1984a), two important ecological demands are imposed upon aquatic insects like dragonflies in temperate climates. These include the need for all members of a population to pass the winter in a stage resistant to cold, and the need for the adult, reproductive stage to be restricted to the warm season. Also, there is the subsidiary need for the adult stage to be restricted to a certain period in the warm season so that competition with sympatric species may be reduced. All these demands involve conspecific synchronisation and the reduction of temporal variation at certain stages of development. Larval photoperiodic responses, interacting with temperature, also provide the framework for seasonal regulation (Norling 1984b; Suri Babu and Srivastava 1990).

Although this study was carried out in a sub-tropical region, relatively close to the tropical centre of species distribution, species temporal trends reflected some aspects of synchronisation, as with their temperate counterparts. Both the temperate and sub-tropical regions are characterised by four seasons with cold or cool winters. In contrast, the larval lifespan is very short in the tropics, where growth is usually rapid and the adult life often fairly long, bridging the dry season (Happold 1968; Gambles 1960; Corbet 1999; Hassan 1981; Van Huyssteen and Samways 2009). This is perhaps because of reduced fluctuations in environmental conditions (especially temperature)

leading to unsynchronised odonate emergence, and the fact that long-lived dispersal stages are probably a prerequisite for species which inhabit temporary pools in the tropics.

Most odonate species sampled here were on the wing for about nine months of the year, from September to May/June, and showed marked monthly variations in richness and abundance during this flight period. Thus in these sub-tropical species, the overlapping generations show similarity to their tropical counterparts by long adult flight periods (Parr 1984), yet like the temperate species in overwintering as larvae.

Furthermore, species that regularly move between habitats may need to adjust to climate changes that are occurring at different rates in different areas, such as between high, medium and low elevations (Inouye et al. 2000). Overall, the subtropical species studied here are characterised by wide elevational tolerance, as well as long flight period with overlapping generations. However, this does not mean that these species are tolerant of the full 3000 m elevational range, with the Alpine zone being very species poor (Samways 1989a, 1992).

Biogeographical implication of elevational tolerance

Overall, odonate species richness ranged from 24 to 27 species between 301 and 1350 m a.s.l. However, below this (<300 m (SB)), richness increased to 31 species. Factors that may account for the high numbers of species at low elevations include high primary productivity (Connell and Orias 1964), increasingly benign, less variable and predictable environments (MacArthur 1975; Thiery 1982) and increased resource diversity (Gilbert 1984). Other processes (competition, predation and evolutionary time) may have also influenced species richness. Also, besides the advantages of a warm climate promoting larval development, the Low (SB) elevation site also, predictably, had a wide range of habitat types. Additionally, there are no mountain chains that might otherwise prevent either temporary or permanent movement south from the species-rich northern areas, thus maximising regional recruitment.

The influence of elevation on distribution patterns can also be highly dependent on latitude (Corbet 1999; MacDonald 2003; Koleff et al. 2003). This is illustrated by species which are found at progressively narrower elevations farther south. For instance, the intolerance of low temperatures by tropical species (e.g. *Tetrathemis polleni* in southern Africa) causes them to contract their southern range into a narrow lowland strip, extending down the eastern seaboard of southern Africa which is warmed by the south-moving Agulhas current.

Most species sampled were widespread and common African species. However, three (6.4%) of species sampled were national endemics, accounting for just 13.6% of the total South African odonate endemics. *Pseudagrion citricola* and *Africallagma sapphirinum* occurred only at the High (GH) elevation, while *Agriocnemis falcifera* was across all elevations, suggesting that regional endemism does not necessarily equate to

elevational intolerance (Fig. 7). Interestingly, like the non-endemics, two of these are relatively common, with only *A. sapphirinum* being rare.

Although climate is important to odonate development, assemblage variation and geographical distribution, local factors (e.g. vegetation structure and composition) are also significant in this geographical area as well as elsewhere (Steytler and Samways 1995; Samways and Steytler 1996; Osborn and Samways 1996; Niba and Samways 2001). Furthermore, water depth is also important for larval stages (Samways et al. 1996). Most adult species here responded to sub-sites reflecting pH, open sunny versus shady and waterfall (flow) versus still water conditions. Influence of regional and local conditions were seen for example in *Notiothemis jonesi* which occurs only at the shady lower elevation gradient of Mid-low (KL).

Zygoptera species were more strongly elevation dependent than Anisoptera species. *A. sapphirinum, A. elongatum, P. citricola, L. tridens* and *Azuragrion nigridosum* were highly elevation-sensitive species. Elevation-tolerant species were *L. plagiatus, I. senegalensis, C. glabrum, A. falcifera, Pseudagrion massaicum, P. salisburyense* and *P. kersteni*. As well as this regional response, there was also a local response. Zygoptera species mostly showed a higher degree of habitat specificity than the Anisopteran species. *Allocnemis leucosticta,* a South African endemic, for example, was restricted only to SS4 and 5 at the Botanical Gardens. One reason for this appears to be that Zygoptera are generally less vagile than Anisoptera.

Implications of results for dragonfly response to global climate change

South African dragonflies are extremely sensitive to fluctuations in water levels, with great fluctuations being impoverishing to the odonate assemblage (Osborn and Samways 1996). Furthermore, the geographical area where this study was undertaken is subject to great variations in rainfall from one year to the next. Floods can be severe, yet the odonate assemblage can recover within a year (Samways 1989c), indicating its great resilience in this El Niño-prone area. This means that the effects of global climate change will possibly be two-fold. Firstly, changes in temperature per se would appear, from these preliminary findings, not likely to have a great affect upon the assemblage. This is because the species involved, even the endemics, are vagile and opportunistic, and will simply colonize the habitats at the appropriate elevations. Secondly, but in contrast, the colonization process will depend greatly on the constancy of the water levels in the water bodies. While increased rainfall and flooding are likely not to be detrimental, any prolonged dry period is likely to be harmful. However, unless there is a prolonged and extreme drought, coupled loss of all local water bodies, there will almost certainly be remnant pools. Such pools would act as source habitats from which these resourceful species will disperse to new pools once the rains have returned (see Samways, this volume).

Acknowledgements

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