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Winter survival by dragonfly adults in the Cape Floristic Region

Julia van Schalkwyk, Michael J. Samways* and James S. Pryke

Department of Conservation Ecology and Entomology, Stellenbosch University, P/Bag X1, Matieland 7602, South Africa

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Little is known about the ability of adult dragonfly individuals to survive into or over the winter in the Cape Floristic Region (CFR), a significant biodiversity hotspot in South Africa. Dragonfly species richness and abundance were recorded throughout winter and into spring in Jonkershoek Nature Reserve. Several environmental variables were also measured. Individuals of eight dragonfly species (four in the Anisoptera and four in the Zygoptera) survived into the winter as adults, even though winter conditions would seem unfavourable (wet, windy and cold) for them in this area at this time of year. Five of these species were CFR endemic or national endemic species or subspecies, illustrating local adaptation. Of the remaining three, all of which are widely distributed species in Africa, only one, *Trithemis arteriosa*, clearly appeared as old, overwintering adults into spring, indicating its versatility both in its adaptation to winter conditions as well as its well-known tolerance of biotope variability. This may partly explain its success as one of South Africa's most common and widespread species. Although many environmental variables were measured and correlated with species richness and abundance, it was only air temperature and associated low relative humidity that were highly positively significant. This emphasizes that the species were opportunistic during the winter and only took to the air on clear, sunny and warm winter days during the cold season. Unlike some other local studies conducted in the summer, these winter results indicated that water flow was a less important variable than that of the seemingly critical variable of temperature during this season. In addition, the importance of emergent vegetation also played a role and appears important for shelter on cool, wet, windy days which precluded flight activity.

Keywords: Odonata; winter survival; South Africa; endemic species; *Trithemis arteriosa*

Introduction

Phenology is the seasonal activity of a species, driven by environmental factors. Insect emergence is a vital phenological event, since the timing of insect mating is crucial to population maintenance (Corbet, 1980). Added to this, there are numerous predator–prey interactions that largely rely on the timing of insect emergence (e.g. Nakano & Murakami, 2001). Since insects are ectothermic, temperate zones expose them to the crucial period of overwintering (Chown & Nicolson, 2004; Leather, Walters, & Bale, 1993). Especially in terrestrial environments, low temperatures, dehydration, anoxia and ice crystal formation can be limiting factors (Denlinger & Lee, 2010).

Dragonflies (Odonata) are of tropical origin, and are generally intolerant of low temperatures (Corbet, 1999; Pritchard, Harder, & Mutch, 1996). Despite this, they are spread over most parts of the world, except the particularly cold areas. In dry tropical areas, dragonflies are restricted

*Corresponding author. Email: samways@sun.ac.za

by larval habitats that only exist in the wet season, and are threatened by desiccation in the dry season (Corbet, 1999). The adults of some species in these environments nevertheless remain as adults despite the drying of their habitat. This is the case in Seychelles, where both *Allolestes maclachlani* and *Teinobasis alluaudi*, and to a lesser extent, *Leptocnemis cyanops*, remain in the area and show agonistic behaviour, even after the streams have stopped flowing leaving only small muddy pools (Samways, 2003). Teneral individuals emerge as the streams dry out, indicating that the adult stage is a survival strategy honed over many years on these tropical islands with seasonal flow regimes.

As seasonal differences increase with latitude, dragonflies are faced with colder winters. Winters have to be passed in a cold-resistant stage, leading to the majority of temperate species being characterized by a partivoltine life cycle, while tropical species tend to be multivoltine (Corbet, 1999).

Dragonfly overwintering is almost entirely associated with the water environment, and predominantly involves the life cycle stages of egg and larvae (Corbet, 1999). Relatively few exceptions exist where dragonflies pass through cool or cold winters as adults (Corbet, 1999). The best known example of an overwintering adult odonate in a non-tropical climate is that of winter damselflies (the genus *Sympecma*), which, during winter, hibernate in the terrestrial environment. A study on the phenology of the dragonflies of Numidia (a Mediterranean climate) found that out of the 40 species recorded, only the adult form of one (*Sympetrum striolatum*) was present all year round (Samraoui & Corbet, 2000).

In sub-tropical regions, adult overwintering is less rare. Jödicke (2003) encountered the adults of seven dragonfly species during winter in the Tunisian oases region. Although winters there are not cold enough to significantly suppress the larval development of most species, it did result in some inhibitory effect, as emergence and abundance were lower (Jödicke, 2003)

Dragonflies are sensitive to changes in riparian and in-stream biotope conditions. They are considered excellent indicators of water margin and aquatic conditions (Chovanec & Waringer, 2001; Oertli, 2008; Sahlén & Ekestubbe, 2001; Samways & Sharratt, 2010; Suh & Samways, 2001). Dragonflies have proven to be useful as indicators of the ecological quality of aquatic habitat heterogeneity, land-water quality, the hydrological dynamics of water bodies (Chovanec & Waringer, 2001; Clark & Samways, 1996; D'Amico, Darblade, Avignon, Blanc-Manel, & Ormerod, 2004; Stewart & Samways, 1998), and of global warming (Hickling, Roy, Hill, & Thomas, 2005). This high sensitivity makes them useful in identifying biodiversity hotspots, or areas of high conservation value (e.g. Clausnitzer et al., 2012; Simaika et al., 2013). Considering that seasonal influences may be altered by habitat conditions, as well as a result of the sensitivity of odonates to their direct environment, it is important to examine the effects of smaller scale spatial influences as well as large scale seasonal patterns.

Although some adult dragonflies do overwinter in South Africa, most studies have focused on the warmer, summer rainfall regions of the country (Niba & Samways, 2006; Samways & Niba, 2010; Suh & Samways, 2001; van Huyssteen & Samways, 2009). The Cape Floristic Region (CFR) biodiversity hotspot is notable for its high level of dragonfly endemism (Grant & Samways, 2007; Samways, 2008). However, with the exception of Samways and Grant (2006), little is known of the phenology of the odonate species of this winter rainfall region, especially in the biologically important, yet agriculturally intensive, Hottentots-Holland Mountains. In response, this study aims to undertake a winter and early spring phenological study at natural and disturbed sites in this area, and relates this winter residency of adults to prevailing environmental conditions at this time of year, with their persistence during the winter and into spring associated with extensive wing wear, indicating their longevity. If some adult individuals, even a few, can survive the winter into spring, they are in a position to mate and oviposit early in the warm season. This would be an advantage in the CFR, as the onset of the hot, dry summer leads to rapid reduction of surface water resources and changing water conditions which may not be optimal for the larvae for long.

Methods

Study area and sites

Twenty-eight sites were selected in Jonkershoek Nature Reserve, Stellenbosch, Western Cape, South Africa (38°58′11″S; 18°55′31″E) in the CFR biodiversity hotspot. The reserve is a mountain catchment area, with the shallow, fast flowing, rocky, 2–10 m wide Eerste River flowing through it. The natural vegetation of the area is mountain fynbos and relic forests along sheltered kloofs. The climate is hot, dry summers and cool, wet winters, with prevailing cool, south-easterly winds. The reserve is relatively pristine as a catchment (Brown & Dallas, 1995), although with one small dam, the Kleinplaas Dam (storage capacity: 337,000 m^3), at the lower end of the reserve.

Of the 28 sites, 13 were located along the rim of the dam in the reserve, and the rest were upstream of the dam in the natural area. Within the river, there is a wide variety of biotopes, from riffles and glides to deposition pools. All these biotope types were included in the sampling to maximize on the potential number of dragonfly species included in the study. Sites were selected during late summer (end of March) so as later to have sites of known dragonfly activity, and to assess which dragonfly species were present in the area before winter commenced.

Dragonfly sampling

Each sampling unit was one 3 × 3 m quadrat. Some sites were along narrow rivers surrounded by riparian forests, making larger quadrats impractical. These sites were spaced at >50 m apart to reduce the risk of noting the same individuals in different quadrats. Within a 10 min period, species richness (total number of species present) and abundance (total number of individuals observed) were recorded. Species present in each quadrat (perched or flying) were visually identified using close focus binoculars and a field guide (Samways, 2008). A hand net was used to capture and verify the identity of uncertain individuals, after which they were released. Only adult males were noted, since females are more difficult to identify and not necessarily closely associated with biotopes near water (Suh & Samways, 2001). Towards the end of winter and in spring, the degree of wing wear was used to determine approximate age of individuals. Categories were as follows (van Huyssteen & Samways, 2009): (1) young – wings are clear with perfect wing margins (no wing wear); (2) middle aged – 1–5 mm of wing margin worn; (3) old – wing wear more than 5 mm of the wing margin worn. Sampling occurred about every second week, from 6 April (autumn) until 16 September 2012 (spring), which was highly dependent on weather conditions, as sunny days were required to record dragonflies on the wing.

Environmental variables were chosen to cover a wide range of possible significant variables, even if some of these finally turned out to be non-significant. These variables were measured for each quadrat during the start of each sampling period, and included: percentage water cover, based on estimated percentage of surface covered with water (referred to in the tables and figures as Water); percentage vegetation cover on land, based on estimated percentage vegetation cover on the bank in quadrats (VegL); percentage vegetation cover over water, based on estimated percentage vegetation cover over the water in quadrats, and included emergent macrophytes and winter flooded bushes (VegW); percentage sand cover, based on estimated percentage exposed sand (Sand); percentage rock cover, based on estimated percentage exposed rock (Rock); percentage shade cover, based on estimated percentage of shade (Shade); water flow rate, classified as either Pool (stationary/slow moving surface water with a minimum reflective surface), Glide (flowing water with a medium reflective surface), Riffle (flowing water with a highly reflective surface) or Dry (quadrats that lost their water body when sampled through drop in river/dam level) (Flow rate); ambient air temperature (°C) (Temp); humidity of air (% rh) (Humidity); and wind speed (km h^{-1}) (Wind sp). Bank vegetation was classified as one of open riparian forest (<30% of river bank with tree canopy), closed riparian forest (>70% of river bank with tree canopy) (Smith, Samways, & Taylor, 2007), fynbos, reeds or grass (Habitat). Time of day of sampling was also recorded (DayPeriod).

Data analyses

Generalized linear models (GLMs) with Poisson distribution (and log link functions) were used to compare all environmental variables to species richness and abundance data (O'Hara, 2009; Zuur, Elena, & Elphick, 2010) in SAS 9.3. These GLMs were used to determine changes in species richness and abundance for percentage cover at each site (water, vegetation on land and water, sand, rock and shade), certain weather variables (ambient air temperature, wind speed and humidity), bank habitat type, and different flow rates (pool, glide, riffle, dry). Canonical correspondence analysis (CCA), using CANOCO 5, was used to correlate species data with environmental variables (ter Braak & Šmilauer, 2012). CCA complements ordination with the power of regression (Lepš & Šmilauer, 2003). Environmental data were transformed to as near linear as possible, while analyses were permutated 9999 times to normalize distribution and allow comparisons of variables (Lepš & Šmilauer, 2003). The technique involves a direct gradient analysis that makes use of multiple regressions to select linear combinations of environmental variables that are responsible for the major variation observed in species scores on each axis. It is a robust method that accommodates for skewed species distributions, interrelated environmental variables and incomplete environmental variables (Palmer, 1993). Species and nominal environmental variables (non-quantitative and indicative of exclusive classes to which observations belong) are indicated by points, while quantitative environmental variables are indicated by arrows. Nominal variables included in the CCA are flow category (pool, glide or riffle), time of day (morning, early afternoon or late afternoon) and week of observation, while quantitative variables included ambient air temperature, as well as percentage cover at each site (water, vegetation on water, sand, rock and shade). Arrow lengths or distances of nominal variables from the centre of the coordinate system's origin indicate the relative importance of the variable, while direction is an indication of how the variable is correlated with a particular species (positively or negatively).

Results

Overall species results

Individuals recorded during the entire sampling period in terms of rank abundance are given in Figure 1. A total of 38 individuals in eight species were recorded in the quadrats during the study period, of which four were in the Anisoptera and four were in the Zygoptera. There was a distinct reduction in species during the middle of winter (10 June until 8 September) and an increase in spring (Figure 2). All individuals observed at the end of the study, both common and rare species, were old individuals with more than 5 mm wing wear.

The highest species richness was recorded for sites 6 and 8. These are both sites with fynbos as bank habitat. The anisopteran species recorded most often was *Trithemis dorsalis* (a widespread and common African species), followed closely by *T. arteriosa* (also a widespread and common African species), then *Orthetrum julia capicola* (an endemic subspecies to the CFR). There was also an anisopteran species that was recorded only once, *T. furva* (a widespread and common African species). The most abundant zygopteran species was *Chlorolestes conspicuus* (an endemic species to the CFR) and those recorded the least included *Pseudagrion draconis* and *Elattoneura frenulata* (both national endemic species).

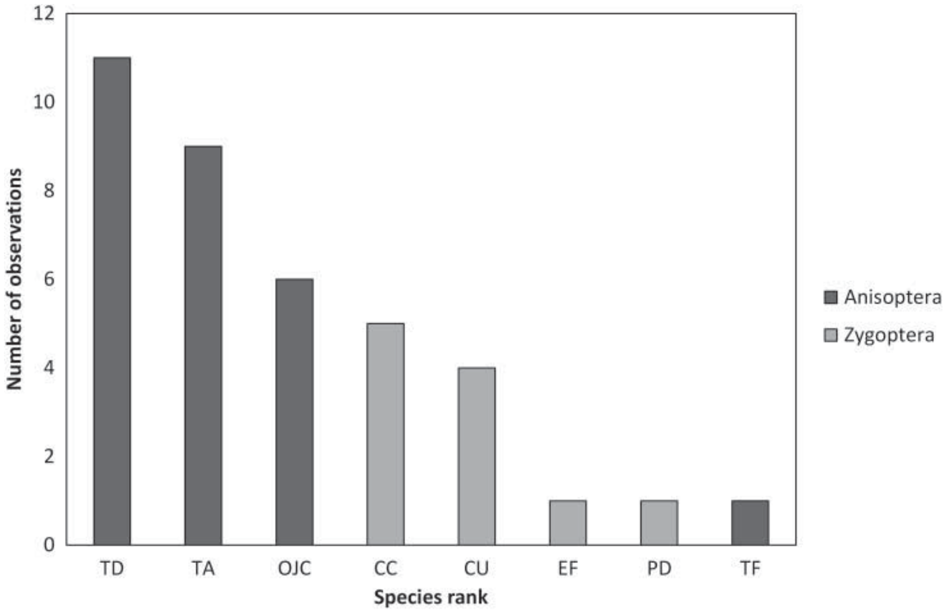

Figure 1. Number of Odonata individuals observed over entire sampling period (6 April to 16 September 2012), arranged in order of rank abundance for all sites. TD – *Trithemis dorsalis*, OJC – *Orthetrum julia capicola*, TF – *Trithemis furva*, TA – *Trithemis arteriosa*, CU – *Chlorolestes umbratus*, CC – *Chlorolestes conspicuus*, EF – *Elattoneura frenulata*, PD – *Pseudagrion draconis*.

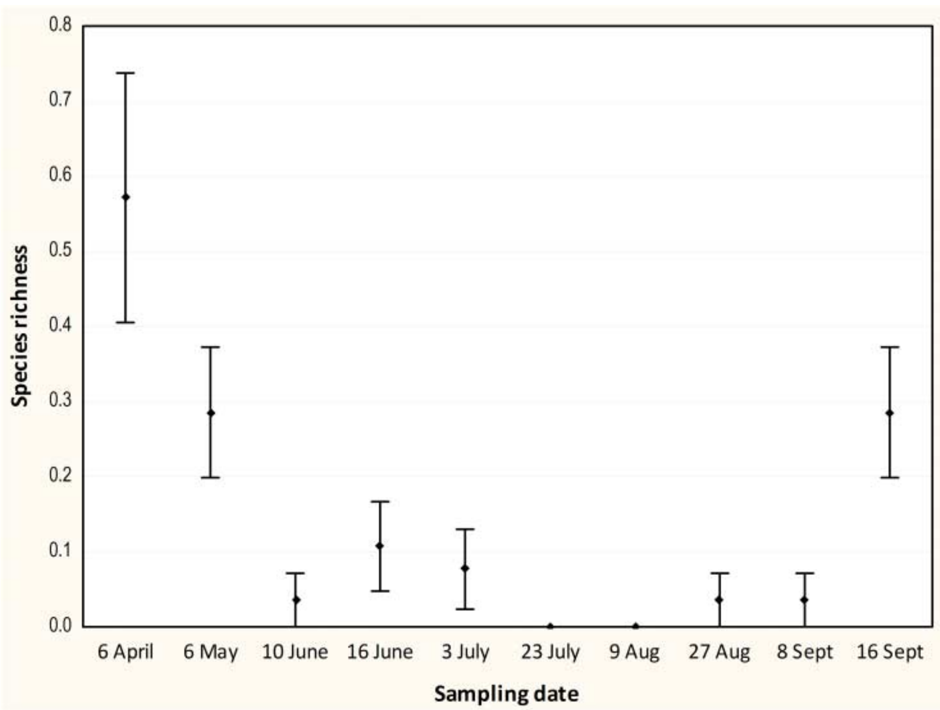

Figure 2. Mean species richness (boxes) over the entire sampling period. Bars represent standard errors. Boxes represent mean. Note the lower number of observed species during winter months (June–early September).

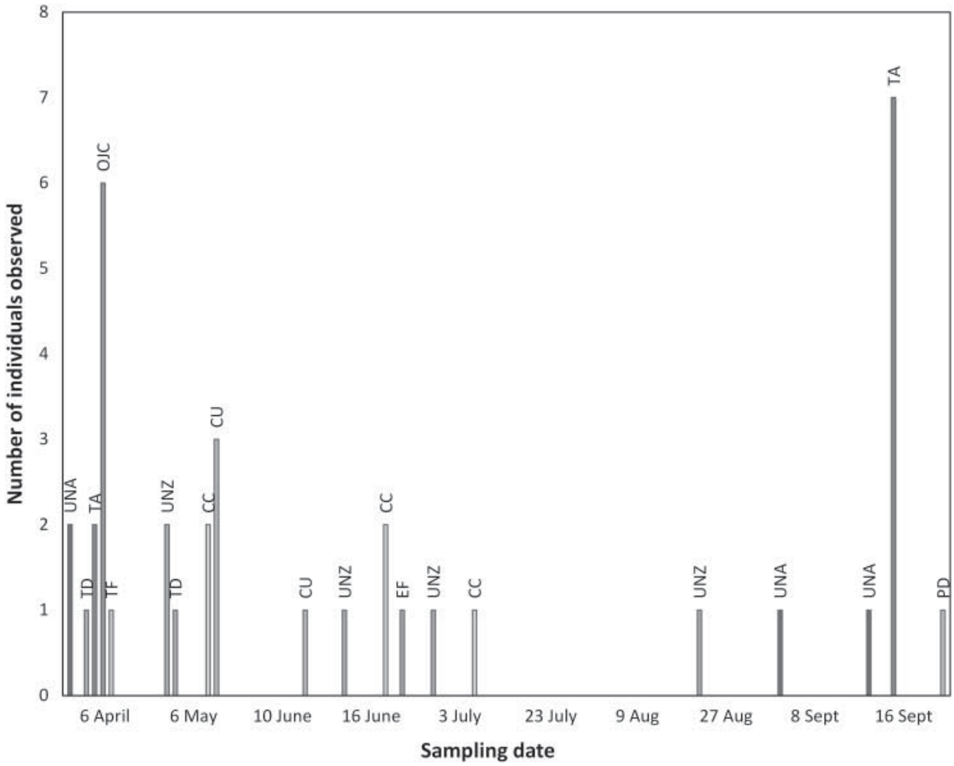

Figure 3. Changes in abundance of different Odonata species during the study period. UNA – unidentified Anisoptera species, UNZ – unidentified Zygoptera species, TD – *Trithemis dorsalis*, OJC – *Orthetrum julia capicola*, TF – *Trithemis furva*, TA – *Trithemis arteriosa*, CU – *Chlorolestes umbratus*, CC – *Chlorolestes conspicuus*, EF – *Elattoneura frenulata*, PD – *Pseudagrion draconis*.

Phenology of the most common species

As with all the other species, *T. arteriosa* was not recorded in the quadrats mid-winter (July–August). It must have survived the winter as an adult because all individuals in spring had extensive wing wear. When it appeared in spring, it was the first species to be active in high numbers of individuals at this time of year (Figure 3), which was about one month before the recorded emergence of young individuals (Grant, 2005). At the end of the previous summer, *T. dorsalis* was abundant, but one month later, it was encountered less often (Figure 3). *Orthetrum julia capicola* was recorded during late summer, but not encountered again during the sampling period. *Chlorolestes conspicuus* was recorded often during May, June and July; *C. umbratus* (another endemic species to the CFR) was recorded in highest numbers in May and for the last time in June. *Pseudagrion draconis* was the only species recorded, but only as a single individual, in spring, also with extensive wing wear, suggesting that it had survived the winter as an adult.

Co-variation of environmental variables

A significant negative correlation was found between temperature and humidity ($R = -0.647$), percentage shade ($R = -0.207$) and pools ($R = -0.193$). Wind speed showed a significant negative correlation with shade ($R = -0.272$) and riffles ($R = -0.191$) and a significant positive correlation with sand ($R = 0.122$) and pools ($R = 0.196$). Riffles and still water, in particular, were significantly correlated with numerous environmental variables (Supplementary Table 1; Supplementary content is available *via* a multimedia link on the article webpage).

Table 1. Generalised linear model (GLM) with Poisson distribution showing the response of the environmental variable to species richness and abundance.

	Species richness		Abundance	
	Wald χ^2	p	Wald χ^2	p
Air temperature	13.97	**0.0002**	18.82	<**0.0001**
Relative humidity	4.05	**0.0441**	6.28	**0.0122**
VegW	0.00	**0.0251**	0.00	0.0854
Sand	0.00	0.0358	0.00	0.7349
Habitat	9.12	0.1044	10.65	0.0587
Flow rate	5.49	0.1394	6.81	0.0783
Water	0.00	0.1543	0.00	0.2371
Shade	0.64	0.4225	0.74	0.3903
Wind speed	0.05	0.8313	0.20	0.6524
VegL	0.00	0.8796	0.00	0.8675
DayPeriod	0.15	0.9267	0.17	0.9188

Abbreviations: VegW = percentage vegetation cover by vegetation trees over water surface, Sand = percentage sand cover, Habitat = vegetation type, Flow rate = rate of water flow, Water = percentage of site covered by water, Shade = percentage of site shaded by overhanging vegetation, VegL = percentage vegetation cover on land at sites, Rock = percentage rock cover. DayPeriod = time of sampling during the day.
Note: Bold refers to statistically significant variables at the 5% level.

Environmental variables and species richness and abundance

There were significant correlations between species richness and temperature, humidity, and percentage vegetation over water (see Table 1 for the GLM results). There was a significant positive effect on species richness by temperature and percentage vegetation over water (Table 1, Figure 4). Species richness and humidity were negatively correlated (Figure 4).There was no significant difference in species richness and abundance between the different bank habitat types (Table 1). Abundance was, however, significantly correlated with temperature and humidity (Table 1).

Canonical correspondence analysis

The most important variables influencing species composition were temperature ($F = 3.1$, $p \leq 0.01$), time of day (late afternoon: $F = 3$, $p \leq 0.01$; early afternoon: $F = 2.8$, $p \leq 0.01$; morning: $F = 2.3$, $p \leq 0.01$), sampling period (time of year) ($F = 2.7$, $p \leq 0.01$), and whether flow rate was a glide ($F = 2.2$, $p \leq 0.05$) or a pool ($F = 2.5$, $p \leq 0.01$) (Table 2).

Trithemis arteriosa showed a strong positive correlation with temperature, while *P. draconis* showed a moderate positive correlation with temperature. Species most active early in the day were *T. dorsalis*, *T. furva* and *O. julia capicola*, while those most active in early afternoon were *C. umbratus*, *E. frenulata* and *C. conspicuus*, and the species most active in late afternoon was *T. arteriosa*. *Pseudagrion draconis* was less influenced by time of day than the other species. The species that were positively influenced by sampling period (time of year) included *T. arteriosa* and *P. draconis*, while *O. julia capicola*, *T. furva* and *T. dorsalis* responded negatively to sampling period. *C. umbratus*, *E. frenulata* and *C. conspicuus* did not show a strong positive or negative correlation with sampling period.

Chlorolestes umbratus, *C. conspicuus* and *E. frenulata* showed a strong preference for flowing over still water. Whether water was glides or riffles was not here significant for these species; *O. julia capicola*, *T. furva* and *T. dorsalis* had a strong preference for still water. *T. arteriosa* and *P. draconis* showed little preference for either still or moving water, and were associated with sites without water.

The percentage cover at each site (water, vegetation on land or water, rock or sand) had a relatively weak influence on species composition. Percentage sand and water were the strongest of these variables, while percentage rock was the weakest.

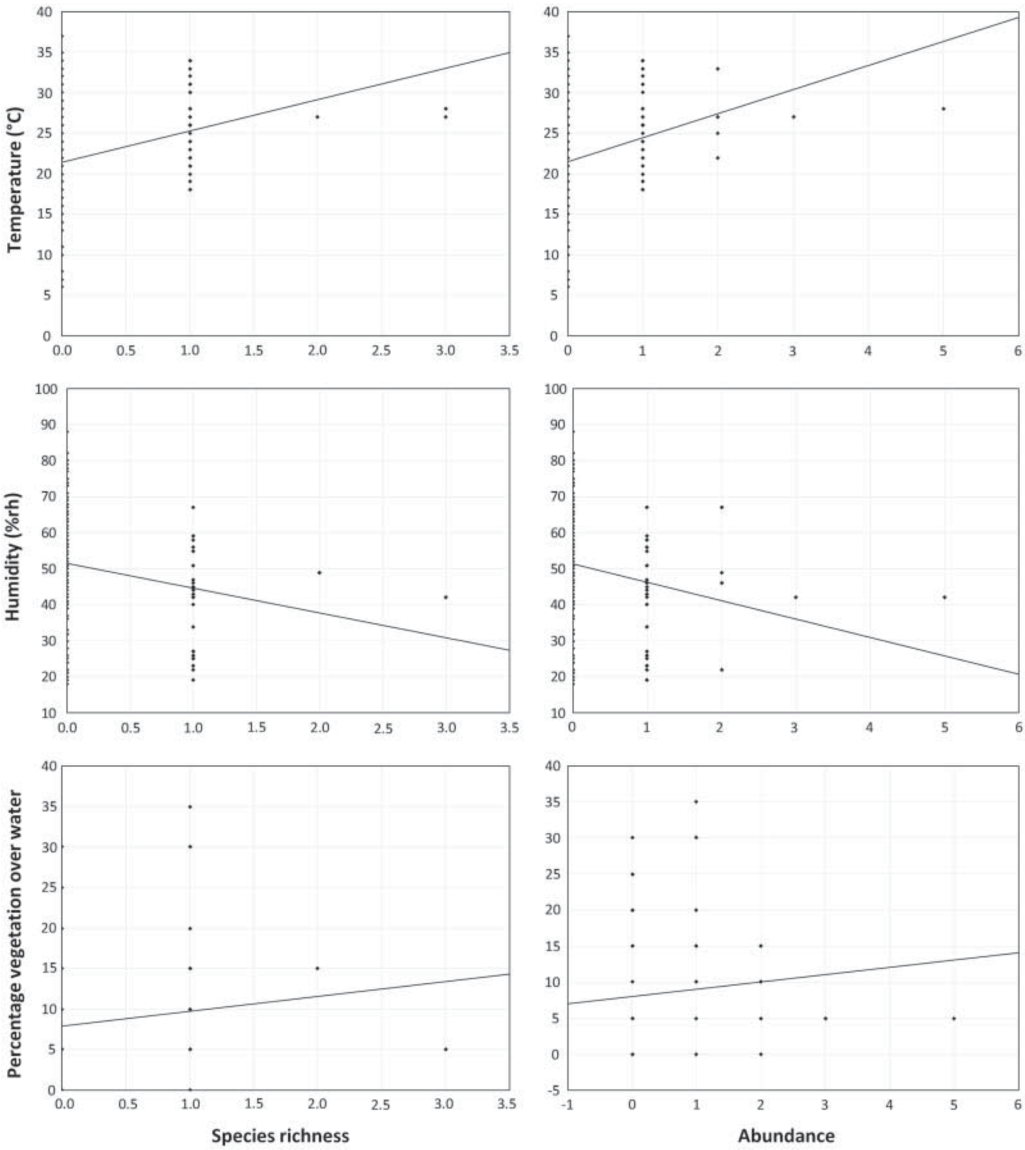

Figure 4. Scatterplots of species richness against temperature, humidity and percentage vegetation over water, as well as abundance against temperature, humidity and percentage vegetation over water.

Discussion

Implications of environmental variables for overwintering Odonata

Winter conditions in the Cape Floristic Region (CFR), including the study area here, appear to be highly demanding of Odonata. Surviving the winter as an adult in the CFR involves tolerating several months of an unfavourable environment of low temperature, high wind speeds, and heavy rain, with occasional brief snow falls. Several species were able to do this, most of which were CFR endemic or national endemic species and a subspecies, and two common and widespread

Table 2. Multivariate CANOCO results used in construction of CCA.

Name	Explains %	pseudo-*F*	*p*
Air temperature	8.5	3.1	**0.0001**
DayPeriod.Late afternoon	8.4	3.0	**0.0001**
DayPeriod.Early afternoon	7.9	2.8	**0.0001**
Sampling date	7.5	2.7	**0.0007**
Flow rate.Pool	7.0	2.5	**0.0007**
DayPeriod.Morning	6.5	2.3	**0.0025**
Flow rate.Glide	6.1	2.2	**0.0103**
Flow rate.Rif.	4.2	1.4	0.1830
Flow rate.Dry	1.8	0.6	0.6223
Rock	2.0	0.7	0.6693
VegL	1.8	0.6	0.7202
Sand	1.3	0.4	0.8468
VegW	1.0	0.3	0.9570

Temp = air temperature, DayPeriod = time of sampling during the day (morning, early afternoon, late afternoon), Flow rate = rate of water flow (still [Pool], medium water movement [Glide], fast movement [Riffle], and sites which dried out [Dry]), Rock = percentage rock cover, VegL = percentage vegetation cover on land at sites, Sand = percentage sand cover, VegW = percentage vegetation cover by vegetation trees over water surface.
Note: Bold refers to statistically significant variables at the 5% level.

African species, *T. arteriosa* and *T. dorsalis*. However, it was only *T. arteriosa* which survived and thrived, appearing in high numbers at the onset of spring.

Since dragonflies are ectothermic, their level of activity will depend on the temperature of their immediate surroundings. To maintain their body temperature within a certain range, Odonata species have developed various behavioural and physiological adaptations (Corbet, 1999) that involve body temperature control either through endogenous means (by increasing metabolic heat production) or exogenous means (through posture adjustments and selecting thermally ideal microhabitats) (May, 1976). Those species which find it too physiologically costly to endure the cold winter conditions of the CFR would either have to migrate or perish. Here, temperature on a daily basis (as opposed to average through the winter) was highly significant for both species richness and abundance, indicating that the various species responded to these marginal conditions during this period by not taking to the air when too cold (hence the change in species numbers), and only flying on warm, sunny days. The high level of wing wear during and at the end of winter for all species, coupled with the fact that they were not recorded in the quadrats, suggests that these species retreated into the bushes (see below) or elsewhere on the most unfavourable days.

Shade was negatively correlated with wind speed (due to the protection offered by surrounding vegetation). An association with shade may be an indirect preference to avoid high wind speeds. High wind speeds can result in increased mortality by dislodging adults, leading them to drown or to receive irreplaceable wing damage through impacts with surrounding vegetation (Blood, 1986; Gribbon & Thompson, 1990). In the rough and spiny fynbos, this can be problematic (Grant, 2005), and it may especially be so for the lighter Zygoptera which are also weaker fliers.

Rain, particularly when heavy, can also reduce dragonfly population numbers (Gribbon & Thompson, 1990). Our study area receives an annual rainfall of around 1400 mm year^{-1} (Smith & Scott, 1992) (relatively high compared to the rest of South Africa), most of which falls during the winter, and also, being cold rain, makes overwintering relatively risky in terms of precipitation. Nevertheless, several species did survive well into the winter under these conditions.

Other environmental correlations and synergisms

Temperature was found here to have significant influence on odonate species richness. Other cues that are related to temperature, and which may be covariate, are photoperiod and inclination of the

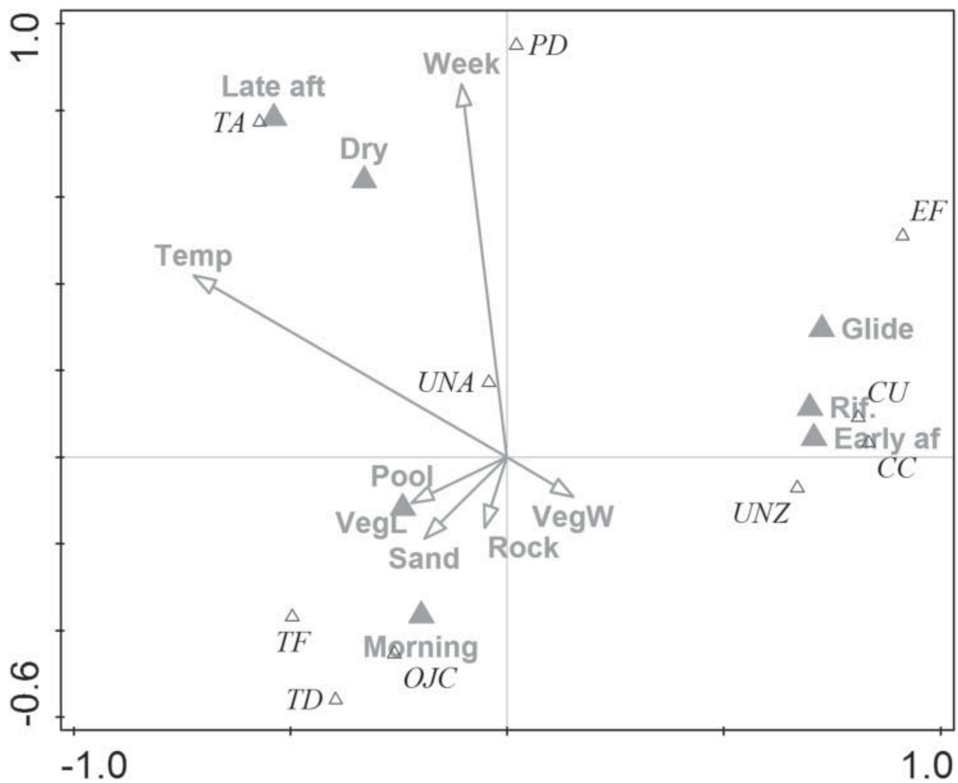

Figure 5. Canonical correspondence analysis (CCA): TD – *Trithemis dorsalis*, OJC – *Orthetrum julia capicola*, TF – *Trithemis furva*, TA – *Trithemis arteriosa*, CU – *Chlorolestes umbratus*, CC – *Chlorolestes conspicuus*, PD – *Pseudagrion draconis*, UNZ – unidentified Zygoptera, UNA – unidentified Anisoptera. Temp = air temperature, WindSp = wind speed, VegL = percentage vegetation cover on land, VegW = percentage vegetation cover by vegetation mover water surface, Sand = percentage sand cover, Rock = percentage rock cover. LateAft = late afternoon, EarlyAft = early afternoon and Morning refer to time of day. Rif. = riffle, Glide and Pool refer to flow rates. Dry = no water at site. Week = sampling period (time of year).

sun (Grant, 2005). Light levels (and possibly direction) have an effect on dragonfly movement, as certain individuals have been captured in light traps (although this may be more due to confusion rather than attraction) (Umar, Mainov, Schorr, & Chapman, 2012). These factors may explain why time of day also had an influence on the presence of particular species (Figure 5), as found by Lutz and Pittman (1970).

Species richness was significantly positively correlated with percentage vegetation over water. Aquatic macrophytes and neighbouring riparian bushes (which can become flooded in the CFR in winter and also become emergent macrophytes) are known to be an important support for many dragonfly species, including in South Africa (Bass, 2003; Clark & Samways, 1996; Ormerod & Edwards, 1987; Stewart & Samways, 1998). The strong influence of emergent cover is not surprising, as macrofloral assemblages provide important aquatic nurseries for insect life (Ormerod & Edwards, 1987; Rutt, Weatherly, & Ormerod, 1989), provide concealment from predators (Askew, 1982), act as mating and feeding perches (Buchwald, 1992; Stewart, 1993) and are oviposition sites for adults such as the endemic *Chlorolestes* spp. Importantly here for these winter fliers, when conditions are wet, windy and cool, there is immediate shelter when conditions become too adverse, which can occur suddenly in this area. These winter retreats appeared to be very important for all species as they declined according to the quadrat results (i.e. an indication of flight activity) yet were present in the local area during at least part of winter, as shown by the fact that all individuals had extensive wing wear.

Ecological versatility of **Trithemis arteriosa**

Relative to the other recorded species, *T. arteriosa* was more resilient in its reaction to changes in flow rate, as can be seen in the CCA. *T. arteriosa* showed a strong association with sites that lost their water. These were sites located along the Kleinplaas Dam, which periodically experienced dramatic fluctuations in water level. *T. arteriosa* also did not show such a strong positive or negative reaction to flow rate as did the other species. Since percentage rock, sand and vegetation on land and water at each site were each significantly influenced by flow rate, the relatively weaker influence of flow rate on *T. arteriosa* may be an indirect indication of its versatility in habitat selection.

Van Huyssteen and Samways (2009), working in the warmer savannah in the north of South Africa, recorded eight species overwintering, seven of which were libellulids which started to breed early in the following spring. Similarly, we found here a libellulid (*T. arteriosa*) to be the first to appear in great numbers at the end of the winter (Figure 3). Extensive wing wear indicated that *T. arteriosa* truly overwintered despite the trying weather conditions, even though we did not record it in the quadrats in mid-winter. Perhaps it spent time away from water and/or remained inactive among vegetation. Winter conditions in the northern savannah area are low rainfall (if any), low humidity and a reduction in stream flow rates. These conditions are exactly the reverse of the winter conditions in the CFR, indicating the remarkable versatility of this species.

Trithemis arteriosa showed a strong positive association with temperature (and concurrent negative association with humidity), suggesting this species has an affinity with sunshine or higher ambient temperatures. Most libellulids are too small to make use of endothermic means of thermoregulation (McGeoch & Samways, 1991) and attempt to regulate their body temperature by basking on warm surfaces (van Huyssteen & Samways, 2009), indicating that the ability of *T. arteriosa* (and to some extent also *T. dorsalis*) to overwinter is notable among local Odonata species.

Considering the great risks of surviving the winter as adults, the associated benefits should be mentioned. Within a population, the size differences among individuals can have a strong effect on ecological interactions such as intraguild predation (Ebenman & Persson, 1988; Holt & Polis, 1997; Wissinger, 1992). For odonate larvae, individuals of similar size can be potential competitors while those of larger and smaller sizes can be potential predators and prey, respectively (e.g. Benke, 1978; Paine, 1965; Polis & McCormick, 1986; Werner, Gilliam, Hall, & Mittlebach, 1983; Wilbur, 1972). Because of limited resources, competition among dragonfly larvae tends to be highest in spring, while for adults, it is lowest in spring, and tends to increase as the season progresses (Crumrine, Switzer, & Crowley, 2008). In the case of *Sympecma* spp., overwintering is associated with an increased risk of mortality and reduced risk of competition for adult niches in spring (Harabiš & Dolný, 2010). While some studies cite cannibalism to be highest early in larval development (Fox, 1975; Polis, 1981), others suggest it is greater late in the season when there are greater differences in larval sizes (Wissinger, 1988). Either way, the benefits of getting a head start as well as being able to locate optimal nursery sites, seem to outweigh the risks associated with adult-overwintering, both in this study and farther north (van Huyssteen & Samways, 2009).

Representativeness of the study

This study is not necessarily representative of the whole region. However, the influences of predation risk (Johansson, Englund, Brodin, & Gardfjell, 2006; McCauley, 2007; Thompson, 1990), dispersal and other factors (Remsburg, Olson, & Samways, 2008) are difficult to estimate at a regional scale. Furthermore, certain species not being recorded during this study does not exclude the possibility of those species surviving the winter as adults at other sites in the region. Accuracy of observed flight periods can vary for different species, since population size, apparency (visibility to a recorder), behaviour and ease with which a population can be determined are key factors in determining the presence of a species. For example, a large population of *Anax imperator* can be determined with more accuracy than a small population of *Chalcolestes viridis*, since it is a more apparent species that is easily identifiable on the wing (Hardersen, 2004). In short, more species may actually be present in the study area during the winter than were noted in this study.

Concluding remarks

We have shown here that certain species can survive into the winter as adults in the CFR, including several narrow range endemics. As physical conditions appear to be highly unfavourable for their survival, there must have been/be strong selection pressure that has led to them being present at this time of year. But only the libellulid, *T. arteriosa*, could be considered to truly overwinter as an adult, and it was the first odonate to appear in great numbers in spring, a situation similar (but involving more species) in the warmer savannah (van Huyssteen & Samways, 2009). This seems to be a strategy to be first to breed early in the season. In the case of *T. arteriosa*, arguably South Africa's most widespread, abundant and versatile odonate (Samways, 2008), this suggests that this is indeed a successful strategy. Here, the most important environmental variables influencing dragonfly species composition were temperature, time of day, flow rate and time of year. The strong influence of flow rate on the species assemblage was both direct on the species and indirect via its effect on vegetation (Grant & Samways, 2007). For the CFR, where most cold rain falls during winter, this has a great influence on the dragonfly assemblage both directly and indirectly, with only a few species able to survive these challenging conditions as adults.

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