How to enter a desert –
patterns of Odonata colonisation of arid Namibia

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ABSTRACT

With a total of 75 species the odonate diversity in the Namibian desert is surprisingly
high. Based on their distribution characteristics, invasion patterns, and breeding suc-
cess, there are six well-defined categories of Odonata: widespread species – (1) per-
manently living in the desert, and desert biased, (2) permanently living in the desert,
but not desert-biased; (3) entering the desert seasonally; (4) entering from neigh-
bouring tropical or temperate regions, whose populations may breed in the desert
sometimes or locally. Category (5) consists of species with highly localised breeding
populations in the desert, which are widely isolated from potential source popula-
tions. The last category (6) consists of species restricted to allochthonous perennial
rivers. We discuss these patterns from a geographical and a temporal perspective.
On the one hand, there have been different spatial directions from where species
have entered deserts. On the other hand, Odonate distribution patterns in the deserts
have a palaeoclimatic as well as a present time perspective, the latter with seasonal
and annual fluctuations and a strong influx from neighbouring biomes. The discov-
ery of a desert-bias in several species suggests that odonates could be well adapted
to desert conditions or, in other words, some species of odonates may be promoted
by arid conditions.

INTRODUCTION

Deserts are not obvious habitats for freshwater animals such as dragonflies. Conse-
quently, books about deserts and desert organisms usually do not mention dragon-
flies (e.g. Lovegrove 1993). However, Odonata occur in deserts everywhere where
suitable freshwater habitats are available (Suhling et al. 2003). Therefore the ques-
tions where these animals came from and how they establish populations are fascina-
ting. Ecological requirements for desert dwelling Odonata have been reported in a
number of papers (Polcyn 1994; Anderson et al. 1999; Suhling et al. 2003; Borisov 2006).

A first paper considering dragonfly diversity in desert environments was by Brinck (1955), who analysed the dragonfly fauna of southern Africa. Based on the generalised knowledge of the odonate's distribution patterns in southern Africa at that time, the author assumed that odonate species diversity is correlated with average annual precipitation. This led to the broadly correct assumption that areas with a higher rainfall have higher dragonfly diversity than those with lower rainfall (cf. Suhling et al. 2009). When estimating the number of odonates existing in the Namibian deserts, i.e. for the Namib and Kalahari Deserts, thus very low species numbers derived (Brinck 1955). Assuming a lack of long-term permanant surface water in the desert, Brinck (1955) stressed that species must re-immigrate from surrounding areas from time to time and therefore that no permanent desert dragonfly fauna exists. In fact, at that time the number of known species in Namibia was low. However, recent research in the Namib Desert since 2001, illustrated that species diversity in Namibia, especially in the desert regions is much higher than expected (Martens et al. 2003; Suhling & Martens 2007). In particular, it was found that there are characteristic assemblages established at perennial waters (Suhling et al. 2006).

The first comprehensive biogeographic investigation of odonates in a desert was presented by Dumont (1982). In his analysis of the Sahara and Sahel most desert odonate populations are interpreted from a palaeoclimatic perspective, i.e. species being relicts from more humid ages. This interpretation is also figured out in discussing dragonfly faunas of Tunisia (Dumont 1977) and Darfur (Dumont 1988). In addition to these relict populations, Dumont (1982) identified a small number of species as migrants, whose distribution patterns depend on rainfall events and population outbreaks. He further stated that these species were absolutely useless in interpreting palaeoecological conditions. The problem of relictual populations was also raised in studies about the dragonflies of Morocco (Jacquemin & Boudot 1999), Algeria (Samraoui et al. 1993) and the Arabian peninsula (Waterston 1985; Waterston & Pittaway 1991).

The question "are there desert species?" was raised by Suhling et al. (2003). In their review these authors identified desert endemics as one major group of desert species. For instance, *Ischnura saharensis* Aguesse, 1958 and *Paragomphus sinaiticus* (Morton, 1929), which are widely distributed, may be true desert dwellers that evolved under arid conditions. Other desert endemics often occur in isolated habitats and may be relicts of more humid conditions. Suhling et al. (2003) mentioned also relict odonate populations of otherwise widespread Afrotropical species as another group of desert dwellers and noted striking similarities in small mountain stream odonate assemblages of the Namib Desert and the Arabian Peninsula. A third and most important group of species in the African and Arabian deserts included some generally widespread savanna species. It has been stressed that typical desert species have dispersal abilities and life history traits which allow them to colonise and successfully reproduce in desert freshwaters.

A functional approach was used to interpret macroinvertebrate faunas of Tinajas, water filled rock-pools in arid environment, in southeastern Utah, USA (Anderson et al. 1999). These authors concluded that dragonflies apply reproduction bet-hedging over time and space coupled with good dispersal ability, which are major traits in coping with variable ecological conditions including drying and refilling of those wetlands.

In this study we ask how dragonflies have managed to enter the desert by analysing the current distribution of dragonflies in the Namibian deserts, which we have surveyed during the previous years. We compare the desert odonate fauna with that of

neighbouring regions in Namibia and in adjacent countries in order to identify potential historical or recent pathways of species colonisation of desert biomes. We also provide miscellaneous observations, e.g. of sudden appearance of various species, that may help understanding these rare, but ongoing processes. We use published general ecological information, particularly about dispersal ability of species occurring in the Namibian deserts (mainly data assembled in Corbet 1999: chapter 10). When interpreting how current distribution arose historically genetic studies are a useful tool (Hewitt 2004) and can offer good insights in colonisation history and isolation of odonate populations on different geographical and phylogenetic scales; for examples concerning Odonata see Artiss (2004), Jordan et al. (2005), and Kiyoshi (2008). We thus also consider published information from molecular genetics studies pertaining to Namibian Odonata (e.g. Hadrys et al. 2006). We consider as well results from paleobiological studies concerning historic climatic variations in forming conclusions about the geographical pathways and the temporal scales of dragonfly colonisation of deserts (Brook et al. 2006). Finally, we discuss what can be learned from the Namibian studies documented here as they apply to general patterns of desert colonisation in dragonflies.

MATERIAL AND METHODS

Study area

Namibia is in the subtropical high pressure climate zone with annual rainfall broadly ranging from ca 600 mm per year in the east, i.e. the Caprivi Strip, to ca 10 mm at the Atlantic coast (Fig. 1). Two other major African climate systems influence Namibia's seasonal climate. The Intertropical Convergence Zone (ITCZ) affects most of the country during the southern summer. Thus, significant moisture bearing winds in the interior of Namibia come from north, northeast or east, i.e. from the more tropical and humid parts of Africa. The effect of the ITCZ decreases towards the south and west of the country. During winter, cold fronts from the southern temperate zone connect the southernmost part of Namibia along the Orange River with the Cape region. Namibia has two rainy seasons; the main rainy season begins in December in the northeast and as late as February/March in the southwest of the country. The early, minor rainy season begins in October.

　　Most of the country's elevation is above 900 m a.s.l. The escarpment along the Atlantic coast reaches up to ca 2,500 m. The highest summit is the Brandberg Massif at 2,579 m. The interior of Namibia east of the escarpment is mainly shaped by the Kalahari Basin, which is filled with deep sands where open waters rapidly ooze into the ground. Natural perennial waters excluding large rivers are therefore mainly situated in the escarpment where several small springs originate.

　　Major parts of Namibia are covered by desert, xeric savanna, and shrubland. All perennial rivers are allochthonous, most draining the highlands in Angola and Zambia. Only along the northeastern perennial rivers that have large floodplains, namely the Okavango, Kwando, Chobe, and Zambezi Rivers, do major perennial wetlands exist. Large temporary wetlands, however, occur in the floodplain of the temporary flowing Cuvelai River as well as in large depressions forming flooded pans after seasonal rainfalls. Two other large perennial rivers, the Kunene and the Orange, which constitute borders for Angola in the north and for South Africa in the south, lack broad floodplains so that they support few lentic water habitats. For more details on Namibia's environment see Mendelsohn et al. (2002).

Definition of the desert region in Namibia

Our objective was to identify potential pathways and processes which may have allowed species to enter the desert. We first identified species occurring in the desert and defined desert for the purpose of our study. Several definitions for deserts are available, using annual average or median precipitation to water deficit and the type of vegetation. We included the following resources in defining desert regions in Namibia: maps of the biomes, vegetation structures, and average precipitation of the atlas of Namibia (Mendelsohn et al. 2002), as well as the map of the WWF African freshwater ecoregions (Thieme et al. 2005), all available electronically for use with geographic information systems (GIS). The last map defines eight freshwater ecoregions in Namibia (Table 1).

We combined three of the freshwater ecoregions defining the desert region, namely the Western Orange, Southern Kalahari, and Namib ecoregions, which overlaps broadly with the region of Namibia receiving less than 350 mm of rain per annum as well as including xeric grassland and shrubland vegetation in Namibia but excluding woodlands. All river catchments in this area drain directly or via the Orange River into the Atlantic Ocean. The region includes the Namib Desert, the Nama
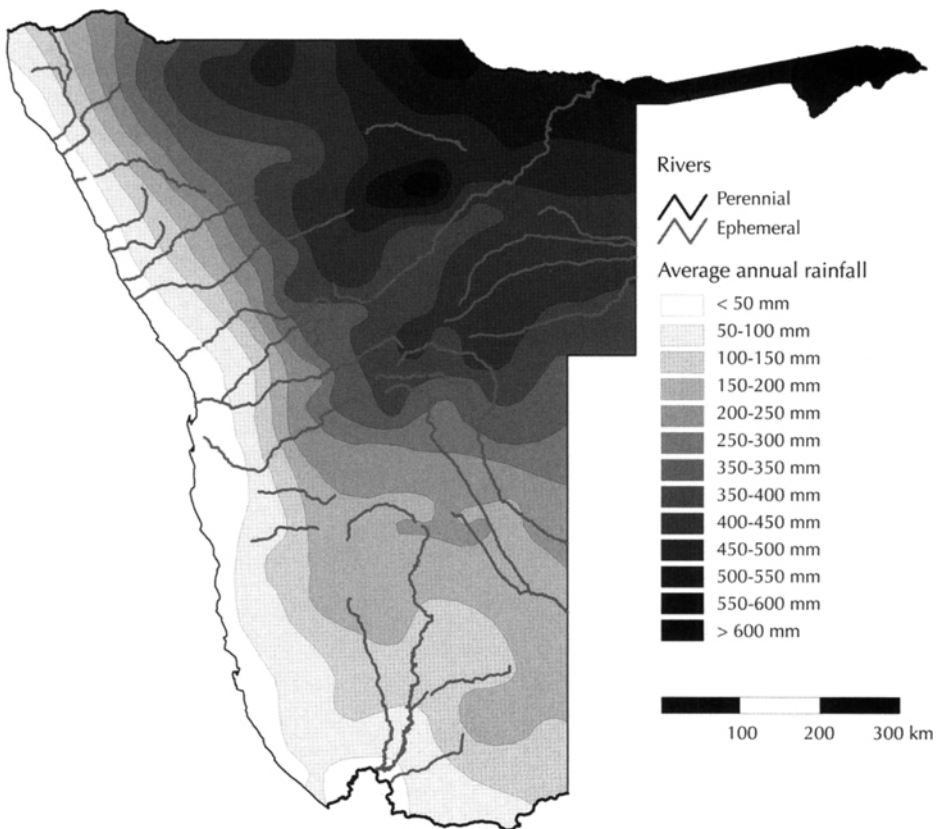

Figure 1: Map of Namibia showing the average annual rainfall.

Table 1. Basic information summarising the numbers of localities visited and the number of total odonate records in the eight Namibian freshwater ecoregions.

Freshwater Ecoregion	No.	Biome	Localities	Records	Species
Western Orange	1	Desert	15	79	23
Southern Kalahari	2	Desert	68	513	26
Namib	3	Desert	268	3126	72
Kalahari	4	Savanna	48	252	35
Karstveld	5	Savanna	32	302	49
Etosha	6	Savanna	62	255	33
Okavango floodplains	7	Floodplains	74	1392	93
Upper Zambezi floodplains	8	Floodplains	69	949	91

Karoo, and the Succulent Karoo biomes, but cuts through parts of the Acacia Tree and Shrub Savanna biome (cf. Mendelsohn et al. 2002). By defining the desert for our purpose via the freshwater ecoregions we took into account that the freshwater habitats may be better determinants for dragonfly occurrence than biomes defined via terrestrial vegetation, e.g. the WWF terrestrial ecoregions (Olson et al. 2001). The other freshwater ecoregions were combined to Savanna and Floodplain ecoregion types for comparison (Fig. 2)

Data base

Our investigation is based mainly on the Namibian Dragonfly Database, containing 6,868 records from 636 localities all over Namibia (Fig. 2), which have been made since 1903. However, 83% of the records date from surveys carried out between 2001 and early 2009, in which we spent at least 25 months on field surveys for dragonflies, traversing all major biomes. Only 8% of the records precede 1990. Not all localities have been equally surveyed; some have been regularly monitored over a number of years and others have been visited only once. Some records are occasional findings by non-odonatologists or photographic records of single species. As long as a species could be verified and georeferenced we used it in our analysis since we did not aim to compare community patterns but only species' geographical distributions. The numbers of dragonfly localities and records per freshwater ecoregion are shown in Table 1. The Namibian Odonata Database is governed by the National Museum of Namibia, Windhoek. Overviews about species' distributions as of 2006 are presented by Suhling & Martens (2007).

Analysis

We used a number of different resources to identify species occurring in the desert and to infer potential pathways by which these species entered the desert. First, we identified all species occurring in the deserts as defined above by plotting all records from the database on the freshwater ecoregions using GIS (ArcView 3.0). We thereafter noted how many of the localities surveyed in each of the three ecoregion types had at least one species record (= locality record) for all species occurring in the deserts. We divided the numbers of locality records by the total numbers of localities per type of ecoregion, which allowed us to determine a species representation

index (in %) per type of ecoregion. We were then able to identify species as over-represented or underrepresented in deserts as compared particularly to the more humid floodplain ecoregions. Representation of a species served as one criterion in defining patterns of occurrence in the deserts. Overrepresented species were considered as true desert dwellers. Species underrepresented or equally represented in the desert could have been anyhow widespread and common.

We also used distribution data of Odonata from the neighbouring regions where available, namely Botswana (J. Kipping in litt.) and South Africa (Tarboton & Tarboton 2002, 2005; Samways 2008), and the most comprehensive database of southern Africa Odonata administered by J. Kipping for the IUCN Odonata Species Specialist Group.

Second, we examined a species' distribution pattern by plotting all locality records per species on a map of Namibia. Because our own entries, i.e. most entries after 2000, provide information on breeding of a species, e.g. larval or exuviae records, we were able to explore which records were based on breeding populations. We thus separated species broadly into those that definitely breed in certain desert habitats and those that may not or only very occasionally breed there.
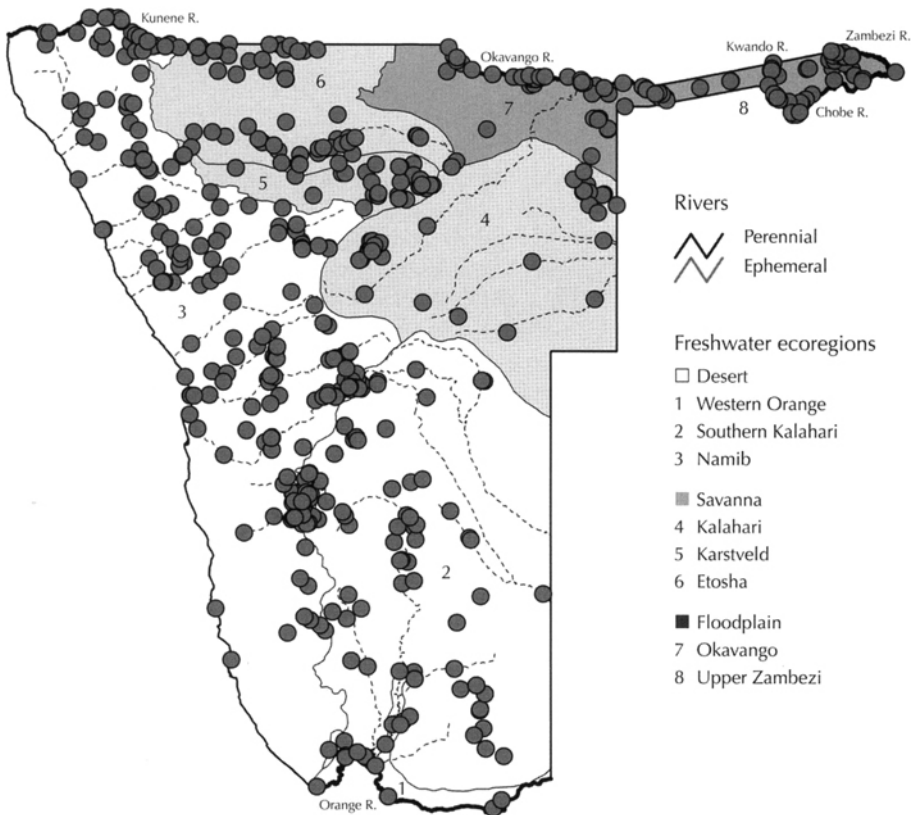

Figure 2: Map of Namibia depicting the distribution of sample localities distribution over the WWF freshwater ecoregions.

Third, we recognised ecological information gathered during our field research in Namibia. Information on phenology (seasonality) and habitats was available for records in the database. Whereas at least the month is recorded for each record, habitat is defined only in more recent records (after 2000) and only occasionally on historical records. Types of habitat distinguished were perennial and ephemeral rivers, perennial streams, springs, oxbows, swamps, perennial, and temporary wetlands, large impoundments, and farm dams.

We noted events, e.g. arrival of migrating swarms or of groups of dragonflies at certain places, during our field studies. We incorporated observations from our field station at Tsaobis at the middle course of the ephemeral Swakop River. At that locality, ponds were established each year from 2001 to 2003 between February and April (Suhling et al. 2004b). Finally, we used published information in order to identify a species' ecology, particularly the comprehensive overview on migratory species presented by Corbet (1999: 408 ff.).

Definition of species categories

We distinguished six categories of species occurring in the Namibian deserts (for examples see Fig. 3).

(1) Widespread desert biased Namibian species regularly breeding in the desert.
(2) Widespread non-desert-biased Namibian species regularly breeding in the desert.
(3) Widespread species that have been observed entering the desert seasonally — (a) seasonally breeding in the desert; (b) breeding not verified.
(4) Species which immigrate from neighbouring regions and sometimes breed in the desert locally — (a) tropical origin, i.e. from the north or the northeast; (b) temperate origin, i.e. from the south.
(5) Species with highly localised breeding populations in the desert, which are widely isolated from potential source populations.
(6) Species restricted to one of the allochthonous perennial rivers, with no breeding populations away from the river.

RESULTS

We recorded a total of 75 species of Odonata in the area as defined as desert for this study (Table 2). Ten were recorded at ca 20% or more of the localities. In descending order these were *Trithemis kirbyi, Pantala flavescens, Crocothemis erythraea, Anax imperator, Sympetrum fonscolombii, Ischnura senegalensis, Paragomphus genei, Diplacodes lefebvrii,* and *Trithemis annulata.*

Among species found in the Namibian desert, five were overrepresented in desert localities compared to other regions (category 1). Nine belonged to category 2 (fairly widespread throughout the country and in the desert). Category 3 was represented by 12 species, of which six (category 3b) could not be verified as to breeding localities in the desert. A large proportion of species belonged to those which casually immigrate from floodplain ecoregions or the Kunene River (category 4a). Some bred only or mainly at large impoundments or wetlands created by leaking impoundments, hence in artificial habitats. Examples of species breeding at impoundments are *Ictinogomphus ferox, Brachythemis leucosticta,* and *Trithemis donaldsoni.*

Table 2. List of Odonata species recorded in the Namibian deserts. The percent representation, i.e. the number of locality records divided by the number of localities surveyed ($n = 351$) is indicated and compared to the savanna ($n = 142$) and floodplains ($n = 143$). The column 'Desert bias' denotes the representation of a species in the deserts compared to the floodplains — plus: overrepresented in deserts, +++: > 6x, ++: 4-5x, +: 2-3x, (+): not found in the flood-plains; minus: underrepresented in deserts, no sign: no strong difference. The column 'River' denotes the names of the perennial rivers where a species mainly or exclusively occurs – K: Kunene; O: Orange. Sorting order is according to category and thereafter to representation in the deserts.

Species	Desert	Savanna	Floodplains	Desert bias	River
Category 1					
Trithemis kirbyi Selys, 1891	55.6	27.5	5.6	+++	
Orthetrum chrysostigma (Burmeister, 1839)	39.6	17.6	6.3	+++	
Anax imperator Leach, 1815	32.8	16.9	13.3	+	
Paragomphus genei (Selys, 1841)	25.9	4.9	3.5	+++	
Pseudagrion massaicum Sjöstedt, 1909	13.4	2.1	0.7	+++	
Category 2					
Crocothemis erythraea (Brullé, 1832)	41.0	22.5	37.8		
Ischnura senegalensis (Rambur, 1842)	27.9	27.5	24.5		
Diplacodes lefebvrii (Rambur, 1842)	22.2	15.5	37.8		
Trithemis annulata (Palisot de Beausvois, 1807)	19.4	21.1	39.2	-	
Orthetrum trinacria (Selys, 1841)	18.5	16.2	10.5		
Trithemis arteriosa (Burmeister, 1839)	16.0	12.0	15.4		
Lestes pallidus Rambur, 1842	14.2	27.5	25.9		
Pseudagrion sublacteum (Karsch, 1893)	7.7	0.7	18.9	-	
Category 3a					
Pantala flavescens (Fabricius, 1978)	49.6	38.7	36.4		
Sympetrum fonscolombii (Selys, 1840)	30.5	26.1	7.7	++	
Tramea basilaris (Palisot de Beauvois, 1817)	10.5	24.6	23.1	-	
Anax ephippiger (Burmeister, 1839)	8.5	10.6	16.8	-	
Diplacodes luminans (Karsch, 1893)	8.5	17.6	21.0	-	
Zygonyx torridus (Kirby, 1889)	5.1	0.7	3.5		
Tholymis tillarga (Fabricius, 1798)	4.3	4.9	21.0	-	
Category 3b					
Olpogastra lugubris Karsch, 1895	3.1	0.0	21.7	-	
Rhyothemis semihyalina (Desjardins, 1832)	2.0	2.1	14.7	-	
Palpopleura deceptor (Calvert, 1899)	1.7	0.0	4.2	-	
Palpopleura lucia (Drury, 1773)	1.4	4.2	2.8	-	
Trithemis hecate Ris, 1912	1.4	4.9	16.1	-	
Tramea limbata (Desjardins, 1832)	0.8	0.0	1.5		
Category 4a					
Orthetrum brachiale (Palisot de Beauvois, 1817)	10.3	12.7	24.5	-	
Brachythemis leucosticta (Burmeister, 1839)	9.7	8.5	39.2	-	
Ceriagrion glabrum (Burmeister, 1839)	4.0	2.1	22.4	-	
Ictinogomphus ferox (Rambur, 1842)	4.0	2.1	21.0	-	
Agriocnemis exilis Selys, 1872	2.6	2.8	7.7	-	
Phyllomacromia picta (Hagen in Selys, 1871)	2.6	0.0	12.6	-	
Trithemis donaldsoni (Calvert, 1899)	2.3	0.0	2.1		

Species	Desert	Savanna	Floodplains	Desert bias	River
Category 4a (continued)					
Nesciothemis farinosa (Förster, 1898)	1.7	1.4	18.2	-	
Urothemis edwardsi (Selys, 1849)	1.4	2.8	23.1	-	
Bradinopyga cornuta Ris, 1911	1.1	2.1	0.8		
Acisoma panorpoides Rambur, 1842	0.9	0.7	15.4	-	
Hemistigma albipunctum (Rambur, 1842)	0.9	0.7	24.5	-	
Orthetrum machadoi Longfield, 1955	0.9	0.7	4.2	-	
Pseudagrion glaucescens Selys, 1876	0.6	0.0	16.1	-	
Trithemis monardi Ris, 1931	0.6	4.2	7.7	-	
Category 4b					
Africallagma glaucum (Burmeister, 1839)	7.4	3.5	0.0	(+)	
Pseudagrion salisburyense Ris, 1921	4.8	0.0	0.0	(+)	
Ceratogomphus pictus Hagen in Selys, 1854	4.0	0.0	0.0	(+)	
Trithemis furva Karsch, 1899	3.1	0.0	0.0	(+)	
Category 5					
Orthetrum julia falsum Longfield, 1955	6.8	7.7	0.0	(+)	
Anax speratus Hagen, 1867 [1]	5.1	0.8	0.0	(+)	
Crocothemis sanguinolenta (Burmeister, 1839) [2]	3.4	4.2	0.0	(+)	
Azuragrion nigridorsum (Selys, 1876)	2.6	4.9	0.0	(+)	
Palpopleura jucunda Rambur, 1842	2.6	4.2	0.0	(+)	
Aeshna minuscula McLachlan, 1896 [2]	2.0	0.8	0.0	(+)	
Trithemis stictica (Rambur, 1842)	2.0	0.0	0.0	(+)	
Pseudagrion kersteni (Gerstäcker, 1869) [2]	1.4	4.9	0.0	(+)	
Pseudagrion nubicum Selys, 1876	1.1	0.8	0.0	(+)	
Orthetrum abbotti Calvert, 1892	0.9	2.8	0.0	(+)	
Urothemis assignata (Selys, 1872)	0.6	0.0	0.0	(+)	
Crocothemis divisa Baumann, 1898	0.3	0.0	0.0	(+)	
Category 6					
Brachythemis lacustris (Kirby, 1889)	2.6	0.0	23.1	-	K
Mesocnemis singularis Karsch, 1891	2.6	0.0	16.1	-	K
Pseudagrion acaciae Förster, 1906	1.8	0.0	20.3	-	K
Pseudagrion vaalense Chutter, 1962	1.8	0.0	0.0	(+)	O
Elattoneura glauca (Selys, 1860)	1.1	0.0	11.2	-	K
Paragomphus elpidius (Ris, 1921)	1.1	0.0	4.9	-	K
Zygonoides fuelleborni (Grünberg, 1902)	1.1	0.0	8.4	-	K
Phaon iridipennis (Burmeister, 1839)	0.9	0.0	8.0	-	K
Phyllogomphus selysi Schouteden, 1933	0.9	0.0	4.2	-	K
Phyllomacromia contumax Selys, 1879	0.9	0.8	18.5	-	K
Pseudagrion hamoni Fraser, 1955	0.9	0.0	6.3	-	K
Trithemis werneri Ris, 1912	0.9	0.0	0.0	(+)	K
Paragomphus cognatus (Rambur, 1842)	0.6	1.4	0.8		K
Zygonyx natalensis (Martin, 1900)	0.6	0.0	6.3	-	K
Crenigomphus hartmanni (Förster, 1898)	0.3	0.0	0.0	(+)	O
Lestinogomphus angustus Martin, 1911	0.3	0.0	14.8	-	K
Paragomphus cataractae Pinhey, 1963	0.3	0.0	2.8	-	K
Trithetrum navasi (Lacroix, 1921)	0.3	0.0	4.9	-	K

[1] Savanna records doubtful
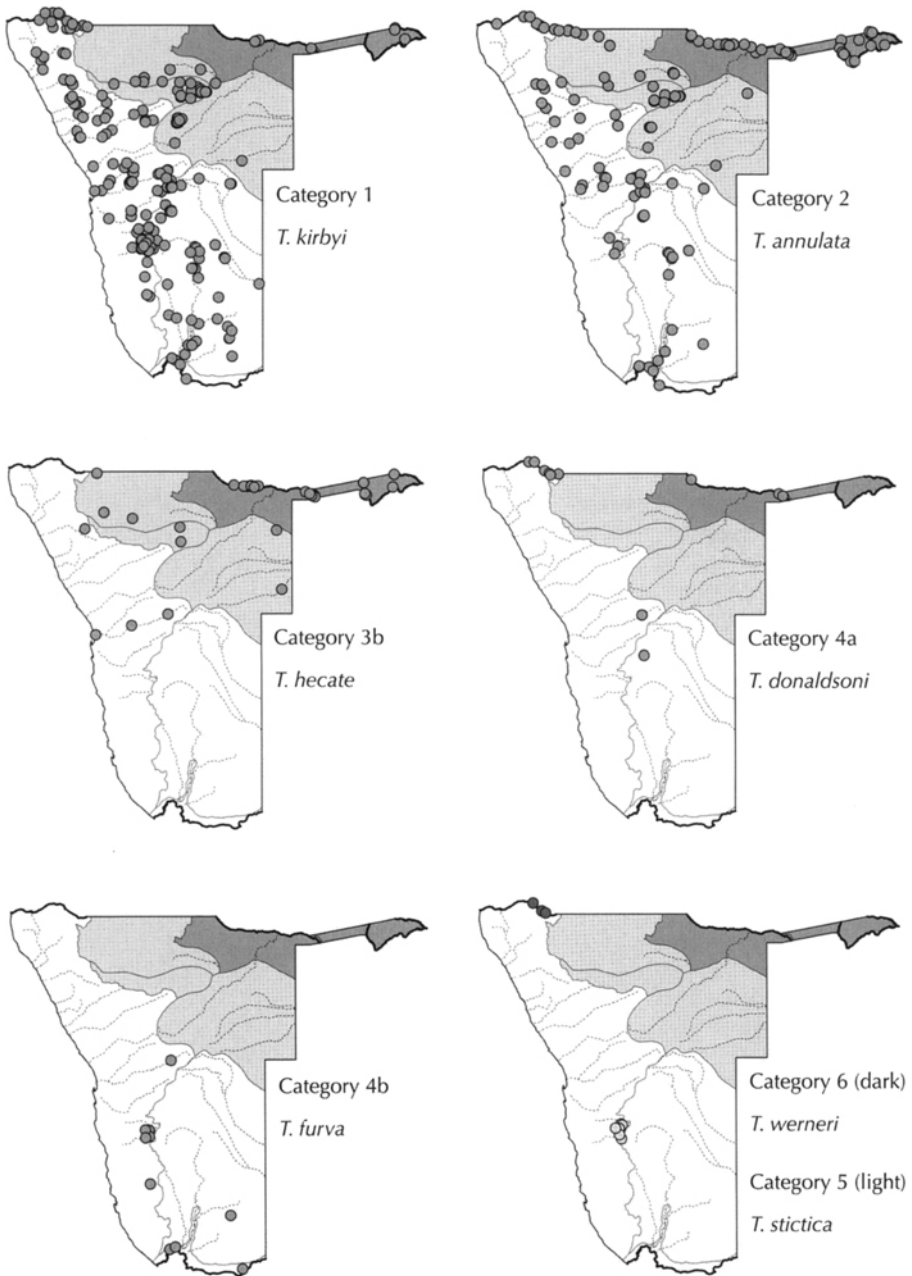[2] All savanna populations extinct before year 2000

Figure 3: Patterns of distribution of various species of *Trithemis* in Nambia, as examples for different categories of Namibian desert species. For definition of the categories see text. Category 2 would also be represented by *T. arteriosa*, category 4 by *T. monardi*. Five more species of *Trithemis*, namely *T. aconita*, *T. aequalis*, *T. morrisoni*, *T. palustris* and *T. pluvialis* have only been recorded in the floodplains in NE Namibia. Freshwater ecoregions are according to Figure 2.

Another large proportion included species that were recorded only very locally (category 5) and widely isolated from main distribution ranges outside Namibia. For most, breeding locations could be verified. The largest proportion of the species belonged to those recorded only along the two perennial rivers, the Kunene and Orange, bordering the desert (category 6). While most of these species (Table 1) had their main range along the other perennial rivers in Namibia, e.g. the Okavango, in Namibia *Trithemis werneri* has been recorded exclusively at the Kunene, and *Pseudagrion vaalense* and *Crenigomphus hartmanni* at the Orange River. Thus, 56 true desert dwelling species remain.

Comparing the total desert species list to that of some selected sites in Namibia indicates that at the deep desert sites not all species categories were present. The list of species recorded at artificial ponds at Tsaobis (Table 3) in the valley of the ephemeral Swakop River included species of four categories, while in the upper Swakop valley more species of more categories occurred. At Tsaobis adults were arriving at different occasions, including onset of the rains or of adiabatic winds, but not all species reproduced and some not every year (Table 3).
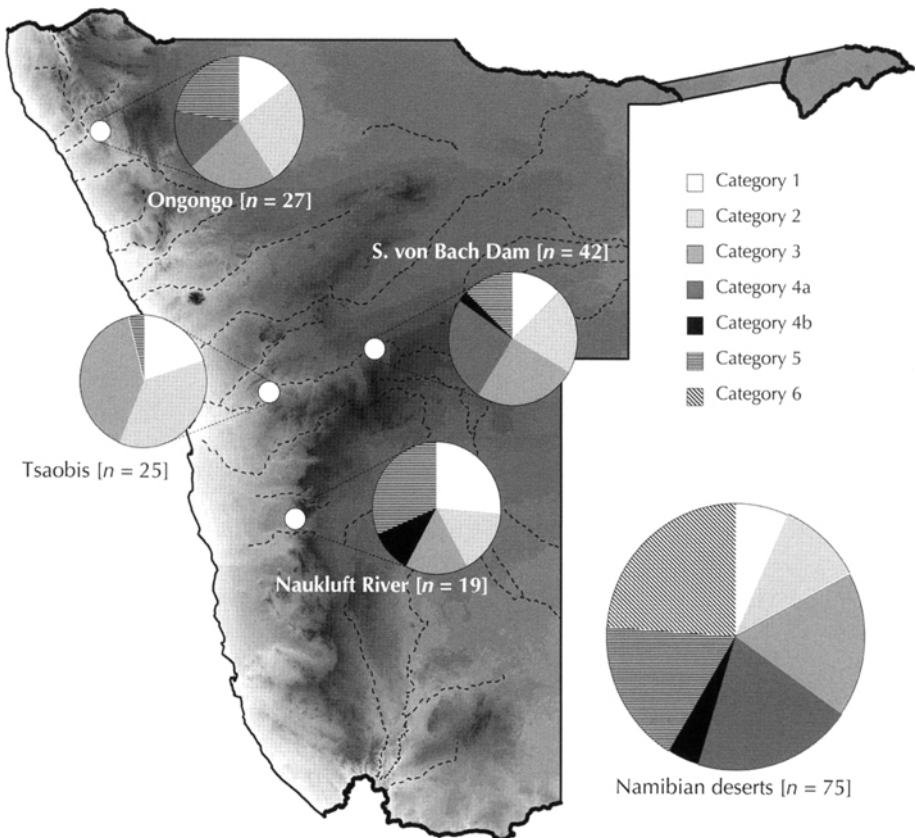

Figure 4: Composition of Odonata categories of the Namibian deserts and of four localities frequently sampled. Ongongo and Naukluft Rivers were perennial streams, at Tsaobis artificial temporary ponds were established between 2001 and 2003, and von Bach Dam is a large impoundment with a wetland below the dam.

DISCUSSION

We found that the dragonfly fauna of the Namibian deserts is quite diverse compared to former estimates of desert dragonfly faunas of southern Africa (19 species, Brinck 1955) and also of the much larger Sahara (38 species, Dumont 1982). However, Dumont (1982) used a 100 mm average annual precipitation line to define desert. His number would likely increase when applying our desert definitions to the Sahara.

Which mechanisms cause such high desert diversity in Namibia? We have shown dragonfly distribution patterns in Namibia to be variable, ranging from widespread, overrepresented desert species, to those whose ranges touch the desert marginally and others that have highly isolated desert populations. In determining how these species successfully entered the desert biomes, we consider spatial (where species emmigrated from) and temporal (chronological sequences of immigration) perspectives as detailed below. It is apparent that all assumptions we make to infer from current distribution patterns to potential historical distribution or to directions of immigrations lack comprehensive evidence and may therefore be interpreted differently. However, the results published from the disciplines paleobiology and molecular genetics provide some additional hints (see below).

Spatial perspective

As figured out above, Namibia experiences two major climatic systems. This is reflected in some odonate species experiencing northern or southern limits of their ranges just within Namibia. However, the largest number of species entering the Namibian deserts are tropical (category 4a), and only a few southern, temperate species have their northern limits in Namibia (category 4b, some of category 5).

Immigration from the humid tropics

A majority of species we recorded in the Namibia deserts are likely of tropical origin entering the region from the north or northeast, where major rivers with large wetlands like the Okavango Delta are situated. This comprises all species of category 3, which enter the desert seasonally, and most species of category 4, that immigrate occasionally. Most species of category 6 are tropical, but do not really enter the desert (see below). Most of these species may be translocated by directional winds into the desert during the rainy seasons (see discussion by Corbet 1999: 383 ff.).

While some of the invaders have the ability to breed in the desert, others will probably not be seen again for some years. Examples for the latter include *Olpogastra lugubris*, *Trithemis hecate*, and *Urothemis edwardsii*, which we observed sparingly in the Swakop River valley. Species of category 3a (seasonal desert emigration) seem to exhibit this strategy as an obligate part of their life cycle. All other species may occasionally breed by chance through fortuitous arrivals of fertilised females or enough individuals that mate in the desert, which result in breeding populations for some years; *Nesciothemis farinosa* may be a good example which has isolated breeding populations in the northwest (Suhling et al. 2004a). Founder populations at isolated desert habitats can result in different odonate assemblages, depending on which species arrived there at the right time (Suhling et al. 2006) and on interactions with other species resulting in intraguild predation (Padeffke & Suhling 2003).

Table 3. List of odonate species recorded at artificial ponds at Tsaobis in the Swakop River valley between 2001 and 2003. Symbols – ++: successful reproduction, i.e. larvae and/or exuviae have been recorded; +: ovipositions observed, but no larvae or exuviae recorded, (+): the species has been recorded, usually in single or few specimens, but no reproduction behaviour observed, -: not recorded. Sorting order as in Table 2.

Species	2001	2002	2003	Notes
Category 1				
Trithemis kirbyi	++	++	++	Always present during the year
Orthetrum chrysostigma	++	++	++	Always present during the year
Paragomphus genei	++	++	++	Always present during the year
Anax imperator	+	+	+	After ponds were filled
Pseudagrion massaicum	(+)	-	-	After adiabatic winds
Category 2				
Crocothemis erythraea	++	++	++	After ponds were filled
Ischnura senegalensis	-	(+)	-	Single specimen
Diplacodes lefebvrii	-	(+)	(+)	Arrival with rainfalls
Trithemis annulata	++	++	++	After ponds were filled
Orthetrum trinacria	(+)	++	(+)	After ponds were filled
Trithemis arteriosa	-	(+)	-	Single specimen
Lestes pallidus	-	(+)	-	Single specimen
Pseudagrion sublacteum	(+)	-	-	After adiabatic winds
Category 3a				
Pantala flavescens	++	++	++	Arrival with rainfalls
Sympetrum fonscolombii	++	++	++	Arrival with rainfalls
Tramea basilaris	-	+	(+)	Arrival with rainfalls
Anax ephippiger	-	+	(+)	Arrival with rainfalls
Diplacodes luminans	-	+	+	Arrival with rainfalls
Zygonyx torridus	-	(+)	-	Arrival with rainfalls
Tholymis tillarga	-	+	+	Arrival with rainfalls
Category 3b				
Olpogastra lugubris	-	(+)	-	Arrival with rainfalls
Palpopleura deceptor	-	(+)	-	After adiabatic winds
Palpopleura lucia	(+)	(+)	-	After adiabatic winds
Trithemis hecate	(+)	-	-	Arrival with rainfalls
Category 4b				
Africallagma glaucum	++	-	(+)	After adiabatic winds

Colonisers from the temperate winter rainfall region

Two patterns exist for populations of the few species occuring mainly in southern Namibia: some likely entered Namibia historically and have now relict distributions, while others are still connected to South African populations via the Orange River system. The southern African endemic *Aeshna minuscula* has entered Namibian deserts from the south because it is, besides of the few Namibian records, endemic to South Africa (Samways 2008). Namibian populations may be isolated from those in the Cape today – the closest South African record is ca 550 km distant from the southernmost Namibian record.

Africallagma glaucum, Ceratogomphus pictus, and *Trithemis stictica* (see also below) come likely from the south since they do not occur in the neighbouring regions to the north and east. The distributions of *A. glaucum, Pseudagrion salisburyense, C. pictus,* and *Trithemis furva* in Namibia suggest that they entered the country via the Orange and the Fish Rivers. This may also be true for the breeding population of *Phyllomacromia picta* in the Oanob Dam in the northernmost part of the Fish River system. All these species occur in the Orange system also in South Africa (Samways 2008). It is surprising that *P. salisburyense* and *T. furva* have not been encountered in northern Namibia since both are recorded from southern Angola (Longfield 1947; Pinhey 1975).

Colonisation from the south and the north?

Molecular studies on *Pseudagrion kersteni* have indicated two genetically distinct populations in Namibia, and the same seems to be true for *Anax speratus* (Hadrys et al. 2006; Rach et al. 2008). This may be due to divergence of desert populations as documented for spring-dwelling amphipods in North American deserts (Thomas et al. 1997, 1998). On the other hand, distribution of the two species in Namibia suggests a northern and a southern population for both, each separated by a big gap in highlands of the Namibian escarpment (Fig. 5). Since both occur in southern Angola as well as in the Eastern Cape in South Africa (Pinhey 1975; Samways 2008), the genetic differences may be due to northern as well southern founders along the escarpment where their habitats, small perennial streams, occur, and to their populations being isolated from one another by the escarpment gap where no suitable habitats occur.

Down by the river – following allochthonous river lines into the desert

The Orange and the Kunene Rivers pass the desert since the desert landscape continues into South Africa and Angola. The rivers are allochthonous – most of their water derives from source regions hundreds of kilometres distant. Both rivers are habitats for species that would otherwise not occur in a desert landscape. The Orange River yields restricted populations of *Pseudagrion vaalense* and *Crenigomphus hartmanni*. This distribution pattern may also apply to those species that have colonised Namibia via the Orange system. In case of the Kunene system the list of species is much longer, comprising 16 species that are all typical of the large perennial rivers in the region, such as the Okavango and Zambezi Rivers, including species restricted to lotic water such as *Phaon iridipennis, Mesocnemis singularis*, several gomphids, *Phyllomacromia contumax, Zygonoides fuelleborni*, and *Zygonyx natalensis*. Compared to the Okavango (J. Kipping, FS unpubl.), the odonate assemblage of the Kunene is poor. Moreover, individual abundance of these dragonflies is surprisingly low in the Kunene, and abundance is even much lower (with the exception of *P. vaalense*) in the Orange than in the Kunene. We suggest that these rivers allow species to enter desert regions from more favourable landscapes upstream.

The western ephemeral rivers in Namibia constitute as well a kind of transport system allowing for the appearance of exotic species into the deep desert, such as *U. edwardsi* or *T. hecate* in the deep Namib Desert near the coast at Swakopmund. We assume the species follow linear oases (Kok & Nel 1996) formed by these rivers (see also below under seasonal events). Schneider (1987) described diffusion of odonates along wadi systems in Arabia as mechanism of long-term dispersal.

Temporal perspective

We contrast very recent processes, such as regular annual invasions, from long-term processes, such as changing climate systems leaving behind relict species populations.

Bless the rain in Africa: obligate seasonal migrants

As already stressed above, most odonate species in the desert originate from the tropics, among them in particular several species that enter the deserts every rainy season, following the movement of the ITCZ and by this the rain fronts into the country. This is a very recent colonisation process that occurs annually. Most frequent in the deserts are (in order of frequency): *Pantala flavescens*, *Sympetrum fonscolombii*, *Anax ephippiger*, and *Tramea basilaris*. Particularly in *P. flavescens* and *S. fonscolombii* we have observed large aggregations of individuals flying into broadly western or southwestern direction. One such aggregation, mainly of *P. flavescens* and some *A. ephippiger* and *T. basilaris*, was so immense that it needed several hours to fly by at our field station at Tsaobis. Following the definition given by Corbet (1999: 408) these species are typical migrants. They are adapted to fly over long distances, as described for *A. ephippiger* (Burbach & Winterholler 1997; Corbet 1999: 409), *P. flavescens* (Feng et al. 2006; Anderson 2009), and *S. fonscolombii* (Barnard 1937, Lempert 1997) and enter the Namibian deserts with the rainy season. We have observed that many of these species are able to reproduce, i.e. complete one generation, in almost all habitats in the desert (Suhling et al. 2004b) and that, after the rainy season, they disappear again. Although the seasonal migration is a rather short-time event, it quite predictably happens every year and has great influence on the communities (cf. Padeffke & Suhling 2003). Thus, besides the short time scale there is also a long time scale involved, i.e. in which migrant species evolved their specific life cycle.

Several other species we pooled in category 3 also appear seasonally in the deserts, but their reproduction has never been observed (category 3b). Thus, it is likely that the dispersal is incidental and not a regular part of their life cycle. These species may be swept along in the desert by the huge aggregations of true migrants appearing with the rainfronts of the ITCZ. For instance, the arrival of some individuals of the riverine *O. lugubris* at Tsaobis occurred together with that of a large aggregation of *P. flavescens*. Therefore the species pooled under category 3b may well also belong to category 4.

Blowin' in the wind – and other seasonal events

Besides the air masses of the ITCZ bringing migrant species into the desert, some other circumstances also cause annual dispersal into the desert. Adiabatic winds falling down the escarpment, when temperatures in the highlands drop in autumn, translocate dragonflies directionally into the desert. We have seen several species arriving with these winds at Tsaobis (Table 3). Another mechanism is following the ephemeral rivers which are vertical oases (see above). Species may follow tree lines providing at least suitable feeding habitats and shade for the adults. We also observed *Trithemis annulata* and *Zygonyx torridus* in dry riverbeds after floods. Thus, these species may travel downstream with the floods and by that enter the desert. However, compared to the migrants in which seasonal migration into the desert is a regular part of the life cycle, the processes described here happen more irregularly and species arrival is thus rather accidental. Anyhow, such an fortuitous event may cause the establishment of a breeding population, for which *N. farinosa* mentioned above may be a good example.

Modern times: recent colonisations of man-made habitats

A historical but relatively recent change of aquatic habitats in the Namibian desert occurred in the 20th century when anthropogenic influence increased (Jacobson et al. 1995). First the number of farm dams increased with numbers of farms having been established even in very arid parts of the country. These, being mostly temporary water bodies, did not affect the dragonfly community significantly since they are colonised mainly by species of categories 1 to 3, which are common at all desert habitats (Suhling et al. 2006). However, particularly in the second half of the 20th century, large perennial impoundments were created. These impoundments are the only or main breeding habitats of a number of species that otherwise breed in perennial rivers, namely *C. pictus*, *Ictinogomphus ferox*, *P. picta*, *Brachythemis leucosticta*, and *Trithemis donaldsoni*. Other species that are widespread in Namibia but underrepresented in the desert may have taken advantage of these impoundments as well, for instance *Orthetrum trinacria* and *T. annulata*, which occur in high abundance at impoundment lakes.

Another group of species that benefits from dams corresponds to swamp dwellers that can be observed at wetlands that originate from the leaking dams of impoundments. A good example is the von Bach Dam near Okahandja, where we recorded 46 species of dragonflies so far, among them typical swamp dwellers in the Okavango and Kwando Floodplains such as *Acisoma panorpoides*, *Hemistigma albipunctum*, *Orthetrum machadoi*, *Rhyothemis semihyalina*, and *U. edwardsi* (Suhling & Martens 2007). Most of these species would probably not be able to establish populations in the desert without these impoundments, or would at least be much less common.

Winds of change: remnants of a wetter climate?

A number of species occurring in the Namibian deserts have highly isolated populations. Particularly, the area of the Naukluft and Tsaris Mountains just at the edge of the Central Namib Sand Sea, is of special interest since it harbours quite a variety of species of category 5, including *P. kersteni*, *A. minuscula*, *A. speratus*, *Crocothemis sanguinolenta*, *Orthetrum julia falsum*, and *T. stictica*. The latter does not occur elsewhere in Namibia and its closest further records are more than 1,000 km south of the Naukluft Mountains in the Western Cape Province of South Africa (Samways 2008). Interestingly, despite its wide isolation the Naukluft population is not diverging genetically from south and east African populations, while Okavango populations formerly recognised as *T. stictica* turned out to be true species (Damm & Hadrys 2009). We have already discussed above that *A. minuscula* as well as *P. kersteni* and *A. speratus* (cf. Fig. 5) have very likely colonised the Naukluft from the south. It is quite unlikely that regular exchanges between the Naukluft and the Cape populations still occur when recognising that most of the intervening area is extremely arid with very little suitable perennial stream habitats present. Thus, it seems likely that *T. stictica* and the other species in the Naukluft are remnants of former times in which Namibia experienced a more humid climate than today, which occurred at ≈ 25,000, 15,000, 9,000-5,000, and 900-300 years (see review in Brook et al. 2006). During those periods today's gap between the Cape and the Naukluft populations may have been widely reduced.

Do desert conditions promote evolutionary adaptation and speciation?

In an earlier paper it has been asked: "are there desert species?" (Suhling et al. 2003) and the conclusion was that deserts are colonised by endemics, often relicts of former periods, or by typical savanna dragonfly species. After some more years of studying Namibian Odonata we have to modify the answer. Looking at the data we assembled, there are species that are common and widespread in the desert and also clearly overrepresented in the Namibian desert compared to the savanna and floodplain areas. In Namibia these are in order of abundance: *Trithemis kirbyi*, *Orthetrum chrysostigma*, and *Paragomphus genei*. Although these species are not exclusive to xeric areas, as *Paragomphus sinaiticus* is in the Sahara and Arabian deserts (Suhling et al. 2003), we suppose that the former could be true desert dwellers that may have
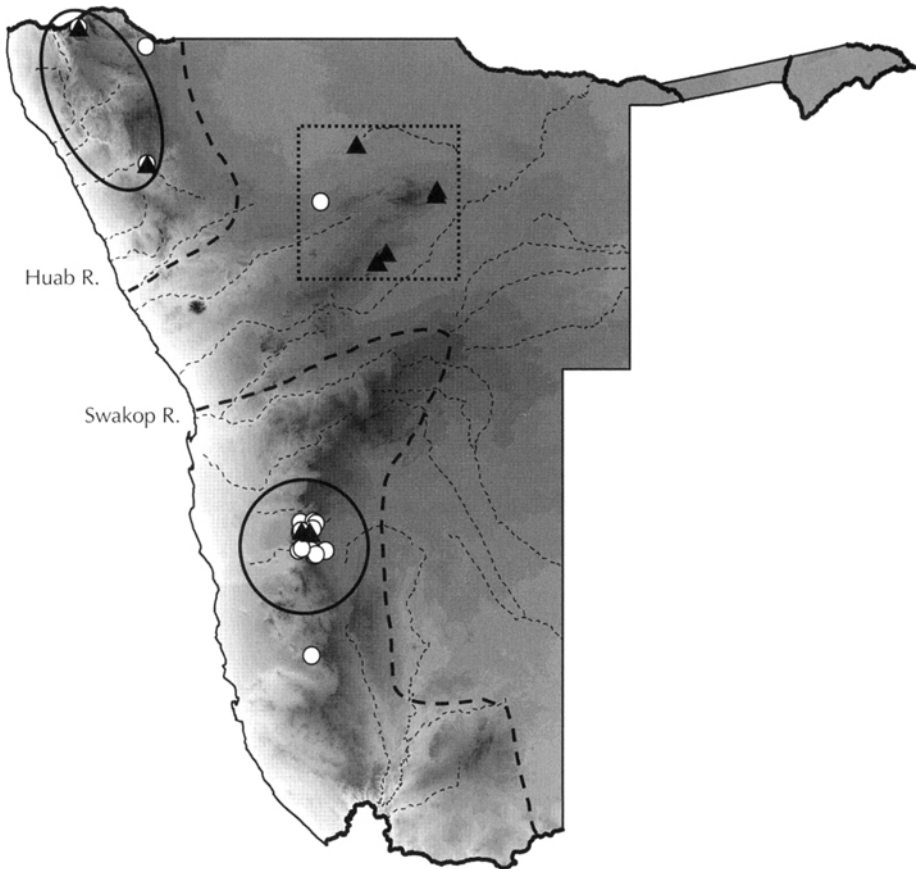
Figure 5: Distribution patterns of *Pseudagrion kersteni* (▲) and *Anax speratus* (O), which both have genetically different northern and southern populations in Namibia; the eastern populations in the karstveld (rectangle) are extinct. Circles enclose the respective northern and southern populations investigated. Note the big gap in the escarpment between the northern and southern populations. Information on genetic data from Hadrys et al. (2006) is combined with own collection information.

evolved traits allowing them to live in this environment. All three can be seen regularly on the wing in dry riverbeds even in the dry season, which suggests that they survive the dry season as adults. In *T. kirbyi* mark-recapture experiments revealed that fully mature males and females survived over at least two months (unpubl. data). The species is likely well suited for adult aestivation of the dry season, as some Algerian Anisoptera are (Samraoui et al. 1998). Circumventing drought has been identified as one of the major traits of desert dwelling odonates (Suhling et al. 2003). It is likely that desert odonates do this mainly in the adult stage. Circumventing drought as larvae, for instance by digging in wet sand, was rarely observed. Reports of living larvae of some species in dry mud of seasonal pools (Dumont 1982; Van Damme & Dumont 1999), may indicate that these species were able to survive as larvae until the end of the dry season, but does not constitute full evidence of it (Corbet 1999: 191).

Larvae of *P. genei* are perfectly suited to exist in the very unpredictable ephemeral river courses. Their larval development is short (Suhling et al. 2004) and their larvae show a sand-swimming behaviour allowing them to survive the strong flood without being submerged by shifting sands. It seems likely that *P. genei* has the same drought-escape behaviour reported for *Progomphus borealis* (McLachlan in Selys, 1873), i.e. swimming and burrowing upstream, which is interpreted as an adaptation to highly variable flow regime of desert rivers (Lytle et al. 2008).

Migrants are overrepresented in the deserts, namely *P. flavescens* and *S. fonscolombii* (category 3a). Their major traits are migratory behaviour (Corbet 1999: 408 ff.) and short development periods (Johansson & Suhling 2004). This makes those species rather part-time desert-dwellers and clearly separates them from those aestivating the dry season (see above).

Rapid development is a trait shared by all common desert species (Suhling et al. 2004; Suhling et al. 2005). Other ecological traits of desert dwellers, such as salinity tolerance, have been discussed before (Suhling et al. 2003). An important characteristic of overrepresented desert species is exophytic oviposition (for overview cf. Martens 2003). Another migrant, *A. ephippiger* is underrepresented in the Namib and Kalahari. This may be because the species oviposits endophytically – although it was observed to use also wet clay as substrate (FS unpubl.). Fish, otherwise an important factor shaping communities and causing adaptations (e.g. Stoks & McPeek 2003), play a minor role in the deserts of Namibia since no indigenous fish are present in most habitats.

As shown particularly from the results at Tsaobis, the species mentioned above are commonly accompanied by other widespread species which are however only slightly overrepresented in the desert, such as *Ischnura senegalensis* and *Crocothemis erythraea,* or as common as in other ecoregions (category 2). These may indeed be typical savanna species that are flexible enough to colonise deserts as well as suggested before (cf. Suhling et al. 2003).

What do we learn from the patterns observed in Namibian deserts?

As stated above, diversity of Odonata in the Namibian deserts is surprisingly high. We conclude that this high diversity is a consequence of several different processes in time and space that historically, and in some cases currently, allowed dragonflies to enter the area. These patterns were comparatively easy to recognise in the Nami-

bian deserts because the area to consider is not as large as that of other deserts such as the Sahara and Arabian deserts, Australian deserts or central Asian deserts. Since the fauna of the neighbouring regions, with the exception of Angola, is relatively well known (Suhling et al. 2009), interpretation of patterns was more straightforward.

We suggest that all processes summarised here may also apply to other desert regions, however to different extent. For instance, perennial rivers may contribute less to the Sahara total. On the other hand, several species recorded from Egypt very likely occur there due to the role of the Nile River transporting them from tropical Africa (Dumont 1980; Dumont 2009), i.e. *N. farinosa* (cf. Boudot et al. 2009), which in correspondence occurs along the Kunene and may have colonised habitats in the Namib Desert from there. Indeed, the fauna of the Nile River in Egypt is very similar in being poor in species and individuals, and it even shares many species with the Kunene and the Orange Rivers (unpubl. observ.). Other processes that leave behind remnants at isolated spots, such as changing climate, which have already been reported in detail for the Sahara (Dumont 1982), are corroborated by our study, although it did not yet lead to species endemism in the Namibian deserts as it did in the Sahara.

Distribution patterns of the dragonfly fauna of Namibian deserts seem to be well suited for identifying spatial pathways into the desert by means of phylogeographical methods. Further analyses may show that a number of species have colonised Namibia from different directions, having still separate populations there today due to the rarity of suitable habitats and the thus limited exchange between populations. Finally, distributions of localised species may serve as excellent examples for metapopulation studies.

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