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THE ODONATA OF NUMIDIA, NORTHEASTERN ALGERIA PART II SEASONAL ECOLOGY[1]

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Abstract

This paper, a companion to Part I which treated status and distribution of Numidian Odonata, summarizes current knowledge of their seasonal ecology and identifies areas where promising research avenues exist. Annual patterns of adult occurrence and reproductive activity are used to infer life cycles, with particular reference to strategies that enable species to bridge the hot, dry summer, and to propose a phenological classification applicable to south-temperate north-African Odonata.

Introduction

Odonata are insects of tropical origin that are relatively intolerant of low temperature (Pritchard et al. 1996; Corbet 1999). Accordingly temperate species face two compelling ecological needs: to pass the winter in a cold-resistant stage and to confine reproductive activity to the warm season. In low temperate latitudes species may encounter climatic conditions resembling those found in the Tropics where rainfall is seasonal, and which impose two constraints on aquatic insects: the ephemeral nature of (aquatic) larval habitats which are restricted to the wet period, and the desiccating heat of the dry period, typically the summer (Masaki 1980). Despite the promising pioneer investigations of the aquatic fauna of Algeria and Tunisia by Gauthier (1928), ecological studies of Odonata and other aquatic insects have lagged behind faunistic studies. Recent work has shown that local populations, many at the southern limit of their geographical range, have evolved distinctive responses to cope with their environment (Samraoui et al. 1993; 1998a; Samraoui & Corbet in prep.) The climate of Numidia is typically Mediterranean, being characterized by a mild and unpredictable rainy

[1] Dedicated to the late Dr Elliot Pinhey who contributed greatly to knowledge of African Odonata.

season between October and May, and a hot, dry season exceeding four months (June to September).

Methods

The information presented here was collected within Numidia, northeastern Algeria, during a period spanning ten years (1990-1999). Details of sampling and of habitats are given in Part I (Samraoui & Corbet 2000). Certain observations, cited as 'Samraoui unpublished', are based on repeated observations by the first author, but are not yet in a form suitable for a publishable report; they have been included because they are sufficiently indicative to provide a basis for reasoned inferences regarding patterns of seasonal development in the Numidian odonate fauna, a subject that will require many years of dedicated research to investigate thoroughly.

Results

In Table 1 we allocate forty species of Numidian Odonata among six groups based on their season of flight and reproduction, namely: A, early spring (2 species); B, spring (2); C, summer (13); D, autumn (6); E, extended (15); and F, late (2).

Two rare species, *Ishnura pumilio* (Charpentier) (recorded in June and October, perhaps in group E) and *Orthetrum nitidinerve* (Sélys) (recorded in July and August, perhaps in group C) probably do not breed regularly within Numidia and so have not been allocated. Three gomphids, *Onychogomphus costae* Sélys (emergence spread from May through July; Benchallel 1994), *O. uncatus* (Charpentier) and *O forcipatus unguiculatus* (Vander Linden), have been omitted because reproductive data concerning adults are lacking.

Fig. 1 portrays the seasonal frquency distribution of flight and reproductive activity for the forty species listed in Table 1.

Discussion

Knowledge of phenology and life cycles is needed to unravel relationships between the timing of recurrent biological events and associated environmental factors (Tauber & Tauber 1976), as well as functional links between population structure and patterns of species interactions (Lawton et al. 1980; Wissinger 1988). Among the major physical constraints encountered by Mediterranean species is the alternation of wet and dry seasons.

Arthropods, especially aquatic insects and Crustacea, in north Africa can be expected to be adapted to the drying of ponds, lakes and rivers in summer (Masaki 1961; Rzóska 1984), a time when, for Odonata, all three stages of development (egg, larva and adult) may occur.

Table 1. Flight period and reproductive activity of Odonata in Numidia during 1990-1999.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Group A												
Anax ephippiger (Burmeister)			●	●○	○○	○○	○			○		
Sympecma fusca (Vander Linden)		○○	●●	●○	○○	○○	○○	○○	○○	○○		
Group B												
Aeshna isoceles (O.F. Müller)				○	○○	●○	○					
Coenagrion puella kocheri (Schmidt)			○○	○○	●●	○						
Group C												
Acisoma panorpoides ascalaphoides					○	●●	○●	○○	○○			
Rambur												
Aeshna affinis (Vander Linden)					○	○●	●○	○○				
Boyeria irene (Fonscolombe)							○○	○○	○			
Coenagrion mercuriale (Charpentier)					●○	○○	○○	○○				
Coenagrion scitulum (Rambur)				○○	○○	●●	●					
Enallagma deserti (Sélys)					○	○○	○○	○○				
Gomphus lucasii Sélys					○	○○						
Lestes v. virens (Charpentier)				?	? ?	○●	●●	○●				
Orthetrum cancellatum (Linnaeus)				○○	○●	○●	○○	○○				
Platycnemis subdilatata (Sélys)					○	○●	○○	●○				
Sympetrum sanguineum (O.F. Müller)					●	●●	●●	●○				
Trithemis arteriosa (Burmeister)						○	○○	○○	○○	○		
Urothemis edwardsii (Sélys)					○	●●	●○	○●	○			
Group D												
Aeshna mixta Latreille					○	○○	○○	○○	○○	●●	●●	●○
Lestes barbarus (Fabricius)				○○	○○	○○	○○	○○	○○	●●	○	
Lestes cf. *virens*				?	? ?			○	○○	●●	●	
Lestes v. viridis (Vander Linden)					○○	○○	○○	○○	●●	●●	●	○○
Sympetrum meridionale (Sélys)					○○	○○	○○	○○	●●	●●	○●	
Sympetrum striolatum (Charpentier)	●●	●●		○	○○	○○	○○	○○	○○	●●	●●	●●
Group E												
Anax imperator Leach			○	○●	●●	●●	●○	○●	●●	○○	●○	○
Anax parthenope Sélys				○○	○●	○○	○○	○●	●●	●○		
Brachythemis leucosticta (Burmeister)					○○	○●	○○	○○	○○	○○	○	
Calopteryx h. haemorrhoidalis					●○	○○	●●	●○	●●	○○	○	
(Vander Linden)												
Cercion lindenii (Sélys)			○	○●	○●	○●	●○	○	○	○	○	
Ceriagrion tenellum (de Villers)				○○	○○	●●	●○	○●	●○	○●		
Crocothemis erythraea (Brullé)			○	●●	●●	●●	●●	○●	●●	●○	○	
Diplacodes lefebvrii (Rambur)				○○	○●	●●	○●	●●	●●	●●	○	
Erythromma viridulum (Charpentier)					○○	●●	○○	○○	○●	○		
Ischnura graellsii (Rambur)		○	○●	●●	●●	●●	●○	○●	●●	●●	●●	
Orthetrum chrysostigma (Burmeister)				○○	○○	○○	○○	○○	○○	○○	○	
Orthetrum coerulescens anceps					●○	●○	○○	○●	○●	○○		
(Schneider)												
Orthetrum trinacria (Sélys)					○○	○●	●●	●○	○●	○		
Sympetrum fonscolombii (Sélys)			○	●●	○○	○○	○○	○●	●○	●○	○○	
Trithemis annulata (P. de Beauvois)				○	○○	○●	○○	○○	○○	○○	○○	
Group F												
Aeshna cyanea (O.F. Müller)								○		○○		
Paragomphus genei (Sélys)						○	○○	○	○○	○		
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.

[1] Groups A-F refer to species observed to fly and reproduce during (A) early spring, (B) spring, (C) summer and (D) autumn and (E) an extended period, and (F) species observed to fly (and by implication reproduce) late. Unfilled circles, immature or mature adults; reproduction not observed. Filled circles, reproduction (i.e. copulation and/or oviposition). Because two species, *Lestes virens virens* and *L.* cf. *virens*, cannot be distinguished except as mature adults, entries for immature adults have been entered thus '?' for both species whenever a sighting of either was made.

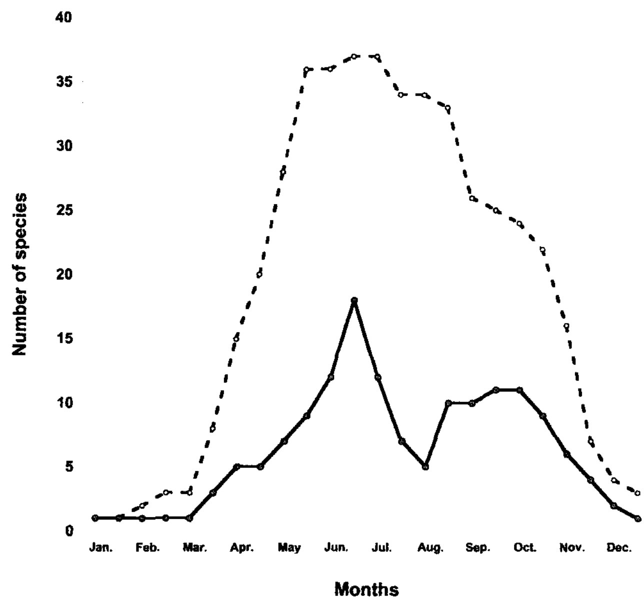

Figure 1. Frequency distributions of flight and reproductive activity of Odonata in Numidia during 1990-1999. Frequencies are summed for each half month for the 40 species recorded in Table 1, the indistinguishable records (?) for immature adults of *Lestes virens virens* and *L.* cf. *virens* having been included as scores for both species.

Developmental rate in temperate Odonata is typically controlled by responses to exogenous factors, namely: temperature, photoperiod, availability of prey, presence of free water, and density of conspecifics and predators (see Corbet 1999). Repertoires of responses possessed by different species will reflect strategies that have evolved to maintain life-cycle continuity in the face of such environmental constraints. Other factors favouring the evolution of adaptations (Mayr & Ashlock 1991) can be sought in the relative insularity of the Maghreb, surrounded as it is by sea and desert, and in the fact that for several species the region represents the southern limit of distribution.

With regard to their mode of seasonal regulation, temperate Odonata fall into two main ecological types: 'spring species' which spend the last winter before emergence in diapause in the final larval stadium and consequently typically emerge synchronously and early in spring; and 'summer species' which spend the last winter before emergence in a stadium before the final one and consequently typically emerge later and with less synchronisation than spring species (Corbet 1954). Summer species can usefully be further divided into those requiring more than one year to complete development, and those that are univoltine (life cycles B.2.1 and B.2.2 in Corbet 1999: Table 7.3). Towards the highest and lowest temperate latitudes, it appears that phenological differences between spring and summer species are less marked (Paulson & Jenner 1971; Norling 1971, 1984). In southern Europe Odonata emerge earlier and fly for longer than in more northerly latitudes, and the peak of species richness shifts from early or mid July to early August (Sternberg 1994). The warm/cool sequence characteristic of middle- and high-temperate latitudes becomes progressively over-ridden in north Africa by a climate that features a wet season from October to May and a dry season from June to September. This sequence is however subject to vicissitude in that the pattern of rainfall may vary considerably from year to year (Seltzer 1946).

Based on period of flight and adult reproductive activity, we have identified six main groups (A-F above) which we expect to reflect adaptations to local climate. That some of these adaptations (e.g. protracted duration of the prereproductive period) show a latitudinal cline (Uéda 1978, 1988; see Jödicke 1997; Samraoui & Corbet in prep.) and that they are also exhibited by insects orders other than Odonata (Masaki 1980; Samraoui 1998 in prep.) support our classification which is consistent with seasonal distributions reported for Morocco (Jacquemin & Boudot 1999) and Tunisia (Jödicke et al. 2000), and broadly similar to the classification put forward for Odonata in central Europe by Schmidt (1985), who recognised five phenological groups: early spring, late spring, early summer, normal summer and late summer species. Close similarities of phenology exist among Odonata of southern Europe and north Africa (Utzeri et al. 1984, 1988; Jacquemin 1987; Agüero-Pelegrin & Ferreras-Romero 1992; Muñoz-Pozo & Ferreras-Romero 1996; Samraoui et al. 1998a; Agüero-Pelegrin et al. 1999; Jacquemin & Boudot 1999; Samraoui & Corbet in prep.).

In the rest of this Discussion, designations of phenological groups refer to those that we have identified as applying to Numidian Odonata, namely groups A-F above. We emphasise that these groups, as shown in Table 1, are based only on the time(s) of flight and reproductive activity and do not necessarily reflect modes of seasonal regulation. Indeed some groups at least (e.g. A and E) are known to contain species with different life cycles. We hope that the arrangement of data in Table 1 will help to point up some of the more obvious gaps in phenological knowledge, besides providing a template against which future records of larval size, metamorphosis and emergence can be compared when life cycles and strategies for seasonal regulation are being inferred. We note, for example, that reproductive activity is seasonally segregated among groups A through D, all of which, on the basis of preliminary field data (Samraoui unpublished), we provisionally assume to be univoltine in Numidia, at least in lowlands.

Group A. Early spring breeders comprise the Inter-Tropical Convergence Zone migrant, *Anax ephippiger,* and the resident *Sympecma fusca.* The biology of *A. ephippiger* has been reviewed by Corbet (1999: 414-417). This species apparently reproduces in December through March in Morocco (Jacquemin 1987; Jacquemin & Boudot 1999) and in March and April in northeastern Algeria (Samraoui & Corbet 2000). The appearance of reproductively active adults of *A. ephippiger* right at the beginning of the flight period in Morocco and (slightly later) in Numidia invites comparison with the seasonal ecology of *Anax junius* Drury in mid-temperate latitudes in North America where many such adults are assumed, and some are known, to arrive from the south in early spring (Corbet 1999: 414-417). Likewise, the records by Jacquemin & Boudot (1999: 81) of emergence in Morocco during June and the absence of adults thereafter until December conforms well with the life cycle of immigrant *A. junius* in north-central U.S.A and southern Canada where, however, resident populations (exhibiting a different life cycle) also exist. It would be informative to pursue this comparison further and determine whether *A. ephippiger* overwinters as larvae in Morocco and Algeria.

The resident species in group A is *Sympecma fusca*, adults of which aestivate and hibernate and are then the first to reproduce in early spring. Larval development is rapid, and emergence, in late spring and early summer, is followed by movement to aestivating sites in alder carrs and upland woodland where a protracted maturation period ensues (Samraoui & Corbet in prep.). Reproductive activity of *S. fusca* near the Atlantic coast of Morocco (Jacquemin 1987), though similar in pattern, seems to occur distinctly earlier than in Numidia, a probable correlate of the lower latitude in Morocco (ca 34°30' vs ca 36°N). Both species occupy temporary water bodies in which larvae grow rapidly so that emergence typically precedes the disappearance of free water. Species in group A can be expected to exhibit the simplest ('unregulated') type of larval development (Corbet 1999: 225), in which growth is a function solely of temperature and exogenous constraints such as availability of prey and presence of predators, including conspecifics. Univoltinism in *S. fusca* is maintained by aestivohibernation of the adult.

Group B. Spring breeders oviposit in permanent or semi-permanent habitats. From observations in Europe, we know that both *Aeshna isoceles* (Gardner 1955) and *Coenagrion puella* (Waringer 1982) exhibit direct embryonic development, a fact confirmed for Numidian *C. puella kocheri*, eggs of which, kept in the laboratory (at 18 +/-2°C) hatched within two weeks of oviposition (Samraoui unpublished).

Group C. Preliminary data (Samraoui unpublished) show that in Numidia some (e.g. *Lestes v. virens* and *Sympetrum sanguineum*), though not all, summer breeders lay eggs that undergo embryonic diapause. Such data indicate also that eggs of these two species are drought resistant and overwinter. From the work of Ando (1962) it can be assumed that embryos of *L. v. virens* and *S. sanguineum* complete katatrepsis before winter and overwinter as fully formed embryos (type 1 of Ando). Three other species in group C (*Acisoma panorpoides ascalaphoides, Trithemis arteriosa* and *Urothemis edwardsii*) are primarily Afrotropical in distribution. It is therefore likely, though yet to be established, that their larval development is unregulated (life-cycle type A.1 of Corbet 1999: 220)

Group D. Among the autumn breeders, marked differences occur between life-cycle patterns in northern European populations and Numidia. In Numidia, seasonal regulation (i.e. maintenance of univoltinism while avoiding mortality of the aquatic stages during the dry period) in *Aeshna mixta, Lestes* cf. *virens, Sympetrum meridionale* and *S. striolatum* is achieved by immature adults moving to upland refuges and undergoing a prereproductive diapause for about four months before maturing and returning to lowland sites to reproduce (Samraoui et al. 1993, 1998a; see also Muñoz-Pozo & Ferreras-Romero 1996). In north-temperate latitudes, eggs of *Aeshna mixta* hatch in late spring after overwintering in diapause, and reproductive activity occurs in late summer and early autumn (Gardner 1950; Schaller 1968); temperature influences the duration of embryonic development and the number and duration of larval stadia (Schaller & Mouze 1970). We lack conclusive data regarding the presence or absence of embryonic diapause in Numidian populations of *Aeshna mixta*. Eggs collected in the field in November at the time of oviposition and kept at laboratory temperature (16+/-2°C)hatched after 39 days (Samraoui unpublished), a period sufficient for low temperature to allow completion of diapause development (Schaller 1968); and larvae in ca stadia 5-7 have been collected in the field in February, suggesting that hatching had occurred in January (Cheriak 1993). Because embryonic diapause is probably completed most rapidly at intermediate temperatures (e.g. ca 10°C) (see Corbet 1999: 57-58), we see here a repertoire of responses able to fit the life cycle to latitude in an elegant way: at the southern limit of the species' geographical range diapause would be completed most rapidly, enabling larval development to begin as early as January and emergence to follow in April or May, enabling adults to leave the reproductive sites before the latter become dry.

Elsewhere in the Mediterranean region (see Jödicke 1997) the pattern of adult maturation is similar in *Lestes barbarus* (middle Italy: Utzeri et al. 1984, 1988) and *Lestes v. viridis* (southern Spain: Agüero-Pelegrin & Ferreras-Romero 1992; Agüero-Pelegrin et al. 1999) in that several months are spent in the prereproductive condition. A similar pattern exists in Numidia where both species aestivate in alder carrs and where *L. v. viridis* does so also in other cool places such as ravines (Samraoui & Corbet in prep.). The phenology of *L. v. virens* and *L.* cf. *virens* in Numidia is less readily inferred because these two taxa can at present be distinguished only by coloration of the mature adult. Because prereproductive adults cannot be distinguished, corresponding entries in Table 1 must be provisional, although the life cycle of *L. virens vestalis* in middle Italy, where maturation lasts for ca 84 days (Utzeri et al. 1988), may provide an informative model for at least one of the Numidian taxa. From Table 1 it is evident that *L. v. virens* reproduces much earlier than does *L.* cf. *virens*, from which we infer that the prereproductive period of *L. v. virens* is considerably shorter, probably lasting a month or less (Samraoui & Corbet in prep.).

Most of the autumn breeders reproduce in temporary pools which contain water in autumn or winter. We have witnessed females of *Aeshna mixta, Sympetrum meridionale* and *S. striolatum*, as well as the three species of *Lestes*, ovipositing in such habitats *before* the onset of rain. For *Sympetrum striolatum* reproducing in temporary pools, larval development of progeny arising from eggs laid at the end of the reproductive period (February) would need to match the speed of species in group A.

Group E. Species with an extended flight and reproductive period include two that are known to be bivoltine at similar or higher latitudes, namely *Crocothemis erythraea* (Mediterranean region; Aguesse 1968) and *Ischnura graellsii* (northwestern Spain; Cordero 1988). However we recognise the possibility, yet to be confirmed, that some species in group E are usually univoltine even though reproductive activity continues from spring to autumn. At the height of the dry period, reproductive activity seems to be interrupted or diminished in six species (*Anax imperator, A. parthenope, Ceriagrion tenellum, Crocothemis erythraea, Erythromma viridulum* and *Ischnura graellsii*), a phenomenon largely responsible for the discontinuity in the frequency profile of reproduction during June through August in Fig. 1. Reproductive activity of *A. imperator* and *A. parthenope* then increases markedly in autumn. The same sequence (featuring an extended flight period and a drop in activity or abundance in late summer) has been recorded in several Moroccan species on the Atlantic coast (Jacquemin 1987). Sternberg (1994) has shown that, for European Odonata, different temperature thresholds correlate with species displacement in time and/or space and that, for some species, the flying season is longer in the southern part of their range.

We raise the possibility that some species (e.g. *Anax imperator, A. parthenope*), or some individuals of those species, may at the height of summer take refuge in uplands (while briefly suspending reproductive activity); and indeed we have often encountered adults there. If confirmed, such behaviour might throw light on the evolution of the postponed reproductive maturation that characterises the life cycle of species in group D. Regular summer drought could be a powerful selective force inducing delayed maturation in species lacking drought-resistant eggs or larvae. In the recent past, much of northern Africa has endured persistent summer drought (Verschuren et al. 2000), a condition placing a premium on reproduction occurring either very early or very late, thus avoiding the desiccation of mid and late summer. Siccatation (suspension of development during the hot, dry season) among tropical Odonata may have foreshadowed the responses needed to aestivate among temperate Odonata, even though the dry season in the Tropics corresponds to the winter rather than to the summer of temperate regions.

Cercion lindenii, presently placed in group E, is suspected of being bivoltine, as it is in southern Spain (Ferreras-Romero 1991). *Sympetrum fonscolombii* combines a migratory habit with two generations per year. This phenology has already been noted in southern Europe (Aguesse 1968) and Morocco (Jacquemin 1987): emergence followed by reproduction is completed in spring and rapid larval development allows a second emergence before habitats dry up in late autumn, yielding a generation that reproduces at the end of summer and beginning of autumn. In southwestern Spain, in ricefields that retain water all year, *S. fonscolombii* can be trivoltine (Montes et al. 1982).

Group F. We place two species in this group, pending more information about their life cycles. Although *Aeshna cyanea* in Numidia is apparently confined to upland streams, we suspect that some adults at least may undergo prolonged maturation (albeit not so protracted as that exhibited by members of group D) when its habitats are reduced to residual pools. Consistent with this possibility are records of its presence in autumn among travelling aggregations of *A. mixta* in southern Europe (Cassagne-Méjean 1966) and the gradual increase in duration of the prereproductive period as emergence proceeds in central Europe (Inden-Lohmar 1997), although the latter phenomenon is susceptible to other interpretations. In a population of *A. cyanea* in southern Spain, the final larval stadium was confined to August and September (Ferreras-Romero & Puchol-Caballero 1995), unlike the situation in southern England where this stadium was encountered throughout the year except in August and September, immediately after emergence (Corbet 1959).

Our records for *Paragomphus genei*, such as they are, are not consistent with the more extensive observations by Testard (1975) in southwestern Spain, where it was univoltine, and they differ from those by Jacquemin & Boudot (1999) in Morocco, where the possibility of aestivation was raised. In Numidia mass emergence was recorded in September but not at other times of year during weekly, year-long exuvia counts (Benchallel 1994). Thus the possibility of bivoltinism in Numidia is not supported on present evidence.

About 25% of the odonate species recorded from Numidia are tropical centred. The co-existence of tropical- and temperate-centred species resident within a single biogeograpical region offers exciting opportunities for identifying the kinds of life cycles that may throw light on the transition from unregulated to regulated development and, especially, those that may show how life cycles appropriate for a wet/dry seasonal sequence evolved into those adapted to a warm/cold sequence. The Afrotropical relict fauna of Numidia may be derived from an influx across the Sahara Desert during a pluvial ca 12 000-10 000 B.P. (Samraoui et al. 1993, 1998b). Most such Afrotropical species (*Acisoma panorpoides ascalaphoides, Brachythemis leucosticta, Diplacodes lefebrvrii, Orthetrum chrysostigma, O. trinacria, Trithemis annulata, T. arteriosa* and *Urothemis edwardsii*) have been assigned to groups C and E and, as far as we know, all show direct embryonic development. If this proves to be the case, they would be ill adapted to occupy the temporary pools that are widespread and frequent in the region. As expected, some of these species (*A. panorpoides ascalaphoides* and *U. edwardsii*) are confined to the northeast in Algeria (Samraoui & Menaï 1999) and possibly to the north in Tunisia (Jödicke et al. 2000) where rainfall is highest (Selzer 1946) and where these species are restricted to permanent habitats. All the Afrotropical species show interruption of flight and reproductive activity during the winter, a discontiuity that may merely reflect the seasonal fluctuation in temperature and need not indicate regulated development. When more is known about the life cycles of Odonata in groups C and E in Algeria, Morocco and Tunisia, it will be informative to compare them with the repertoire of life cycles among tropical species studied by Kumar (1976) at a low temperate latitude in northwestern India (see Corbet 1999: fig. 7.8). By analogy with Kumar's findings, Afrotropical species can be expected to complete a generation in one year or less in Algeria and Tunisia. Differences in life cycles exist between tropical-centred and temperate-centred species of Odonata in Morocco (Jacquemin & Boudot 1999).

Inspection of phenology along phylogenetic and biogeographic lines reveals that, among Numidian Odonata, it is temperate species of *Aeshna*, *Lestes* and *Sympetrum*, all in group D, that display the most elaborate seasonal regulation, thus maintaining their obligatory univoltinism. With respect to strategies that maintain a univoltine life cycle in (temporary) vernal pools, striking similarities exist among species of Lestidae and *Sympetrum* in southern Ontario, Canada (Wiggins et al. 1980), southern Europe (Utzeri et al. 1984, 1988; Agüero-Pelegrin & Ferreras-Romero 1992; Muñoz-Pozo & Ferreras-Romero 1996) and north Africa (Jacquemin 1987; Samraoui et al. 1993, 1998a; Samraoui & Corbet in press).

It has long been known that many species that bridge the dry season, the winter or both in the Mediterranean region exhibit embryonic diapause and oviposit endophytically, either in plants, as in *Aeshna* and *Lestes*, or in depressions lacking free water, as in *Sympetrum sanguineum* (see Corbet 1962), *S. meridionale* and *S. striolatum* (Samraoui et al. 1998a), where they are apparently able to resist prolonged desiccation. A common feature of species of *Lestes* and especially *Sympetrum* in vernal pools is that they are often hosts of water mites (Hydrachnida: Arrenuridae) that are themselves adapted to life in seasonal habitats. This relationship obtains in southern Ontario, Canada (Wiggins et al. 1980) and in Numidia, where *Lestes barbarus* and *Sympetrum meridionale* typify such hosts.

A powerful adaptation to life in temporary pools is evident in those species that survive the drying up of their aquatic biotopes as larvae, by burrowing and surviving close to the water table (see Corbet 1999: 189-192). Dumont (1979) found larvae of *Orthetrum chrysostigma* (group E) and *Trithemis arteriosa* (group C), not yet in the final stadium, in bottom sediment in dry or drying Saharan pools; and Van Damme & Dumont (1999) report the collection of a small larva of *Pantala flavescens* (Fabricius) in dried pond mud in Brazil. We have been unable to find evidence of this type of drought resistance in Numidia but by its nature it may be difficult to detect.

Although the ecology of north-African Odonata is coming to be better known, further research is needed to clarify the voltinism and habitat requirements of several species. In particular there is a need to document the seasonal occurrence of larvae, metamorphosis and emergence to give perspective to the information we have presented about the adult stage. This task has assumed added urgency because of the need to assess the impact on local Odonata of the recent introduction of exotic fish such as the Common carp, *Cyprinus carpio* Linnaeus and the Mosquito fish, *Gambusia affinis* Baird & Girard. Many local Odonata, especially those in lentic habitats, may not have evolved antipredation responses to fish (see Henrikson 1988; McPeek 1989, 1990a, b).

Knowledge of the status and ecology of Odonata has important implications for conservation policies because these insects can be useful for evaluating and monitoring the health of wetlands (Schmidt 1985; Corbet 1993; Wildermuth 1994; Sahlén 1999). Work of this nature can highlight the role of vegetation (in terms of both composition and structure) in providing essential habitat attributes and in drawing attention to long-neglected ecosystems like alder carrs (a scarce and threatened habitat in north Africa), temporary pools, and upland forests (now under heavy pressure from burning and overgrazing) as important dry-season refuges for Odonata and other invertebrates. The reliance of some species on two or more spatially separated ecosystems to maintain seasonal continuity needs to be taken into account when land is managed for conservation and development.

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