Seasonal ecology of Algerian Lestidae (Odonata)

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Abstract

When comparing the phenology of species within the family Lestidae in Numidia, northeastern Algeria, we found that: (1) four of five species – *Lestes barbarus*, *L. numidicus*, *L. viridis*, and *Sympecma fusca* – feature a prolonged pre-reproductive period approaching five (*Lestes* spp.) or eight months (*S. fusca*); (2) adults of *L. numidicus*, and probably of *S. fusca*, move to upland refuge sites in summer, whereas those of *L. barbarus* and *L. viridis* aestivate in alder carrs in lowlands close to reproductive sites; and (3) adults of all five species exhibit distinct spatial and/or temporal segregation.

Introduction

Knowledge of life history is crucial in shedding light on patterns of species' distributions and on how aquatic communities are organized (Wellborn et al. 1996; McPeek & Brown 2000). Odonata have been particularly good biological models from which to evaluate complex life cycles within the dual realms of ecology and evolution (Corbet 1999: 204; Cordoba-Aguilar 2009: 1). Life history constraints and predation have both been shown to shape the distribution of North American lestids along a pond hydroperiod gradient (Stoks & McPeek 2003, 2006). However, whereas much is known about the seasonal ecology of north-temperate Lestidae (see reviews by Jödicke 1997: 27-28, 188-193; Corbet 1999: 224, 263-264), little is known about their tropical counterparts (e.g. Gambles 1960; Kumar 1972, 1976; Dunkle 1976; Corbet 1999: 262; Corbet et al. 2006; Pritchard 2008). Likewise, until recently the ecology of Mediterranean Lestidae had been poorly understood, although some illuminating phenological data are known (review in Jödicke 1997). Within temperate regions certain species exhibit a latitudinal cline in the duration of their pre-reproductive period, the latter being positively correlated with mean summer temperature (Uéda 1978). Our work focused on the seasonality of Lestidae within a semi-arid environment, as part of a larger study designed to elucidate life

cycles of Mediterranean Odonata with emphasis on strategies that allow species to bridge the hot, dry season, and on latitudinal clines that may exist within their phenology. Based on previous ecological surveys (Samraoui et al. 1998; Samraoui & Corbet 2000), we hypothesized that *Lestes barbarus*, *L. numidicus*, and *L. viridis* possess a life cycle resembling that of *L. sponsa* (Uéda 1978, 1989), and my present results support and amplify this prediction.

Study area and methods

Study area

Observations spanning from 1990 to 1999 were carried out within the El Kala and Guerbes-Senhadja wetlands, northeastern Algeria (Samraoui & Bélair 1997, 1998). These study sites are situated between 36°37'N - 37°00'N and 7°15'E - 8°26'E and include temporary marshes, shallow lakes, seasonal ponds, and wadi. The climate of Numidia with an annual rainfall up to 1,200 mm and a mild to warm winter is described as subtropical and it has been instrumental in maintaining extensive wetlands and a high number of Afrotropical species (Samraoui et al. 1993a). Upland habitats include woodlands comprising cork oak, *Quercus suber*, and thick bushes of *Erica arborea*, *Pistacia lentiscus*, and *Rubus ulmifolius*. Alder carrs typically occur by the edge of lakes or marshes. 'Alder carr' is a term describing moist woodland comprising mainly *Alnus glutinosa* ca 10-15 m high and featuring a closed canopy. They maintain a shaded, relatively cool, and humid environment throughout the dry season.

Methods

I used two types of observation methods:

(1) counts of adults every two weeks, using transects at a small number of sites, mainly during 1991-1994 and also between August 1998 and August 1999;
(2) qualitative sampling of adults once a month but irregularly at 70 sites during 1990-1999.

Pre-reproductive periods were inferred from intervals between peaks of emergence and reproductive activity.

To monitor maturation during aestivation in 1993 I assigned adult individuals to one of three broad categories: teneral, assumed to be no more than 24 h after emergence; immature; and mature, exhibiting mature coloration and/or reproductive behaviour or gonad condition. Every month between May and November 10 females of each species – except *L. barbarus* of which insufficient specimens were obtained – were dissected to check for the presence of mature oocytes, i.e. eggs. 'Flight period' indicates the presence of adults, immature and/or mature. 'Reproductive season' indicates the period when adults are reproductively active.

Plant material used by females to lay eggs was placed in water in the laboratory within 24 h of oviposition. Water was oxygenated and kept at room temperature (15 +/- 3°C) under natural light conditions. To monitor hatching, I inspected aquaria for the presence of larvae, weekly until 1 December and thereafter once every two or three days until mid March.

Table 1. Biweekly sightings of adult lestids in lowlands (excluding alder carrs), alder carrs, and uplands. T: teneral; A: immature or mature adult; R: reproductive behaviour. The symbol "?" denotes tenerals or immatures of either *Lestes numidicus* or *L. virens virens*.

Taxon	J	F	M	A	M	J	J	A	S	O	N	D
Lowlands												
Lestes barbarus				A A	T A	A A	A A	A A	A A	R R	A	
L. numidicus				?	? ?	?		A	A	R R	R	
L. v. virens				?	? ?	R R	R R	A R				
L. viridis					T	T T	T	A	R R	A R	R R	A
Sympecma fusca	A	A R	R R	A	A A	T T	A	A	A	A A		
Alder carrs												
Lestes barbarus					A	A	A A	A A				
L. viridis						A	A A	A A				
Sympecma fusca					A	A	A A	A A	A A	A A		
Uplands												
Lestes barbarus					A	A						
L. numidicus					?	? ?	?		A	A		
L. v. virens					?	? ?	?	R				
L. viridis										A		
Sympecma fusca						A	A A	A	A			

One-way ANOVA was performed using STATISTICA 7.0 (Statsoft inc.) with a significance level of $p \leq 0.05$, to determine whether perch height differed within and between species of lestids found perched on alders. Tukey tests were conducted to determine mean values that differed significantly.

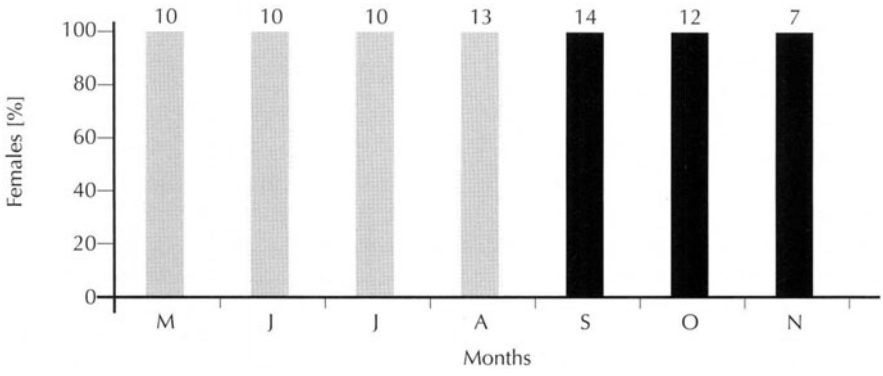

Figure 1: Maturation of ovaries in *Lestes barbarus* — seasonal changes. Numbers above bars denote sample size. (▩) immature females; (■) mature females.

Results

Monthly records of adults obtained during 1990-1999 are presented in Table 1. Synopses of the seasonal ecology of each of the five species follow.

Lestes barbarus (Fabricius)

Emergence: April to May.
Flight period: April to early November.
Pre-reproductive period: Five months.
Reproductive season: October.
Comments: An uncommon species. After emergence individuals dispersed widely; from the first half of June onwards many were found in alder carrs, where they aestivated. Although females possessed mature ovaries in September (Fig. 1), no reproductive behaviour was observed before October. In late August only males were found close to reproductive sites in a seasonal marshy site (Fig. 2) dominated by *Cladium mariscus*, *Hypericum afrum*, and *Iris pseudoacorus*, whereas only females were recorded in alder carrs (Fig. 3). This pattern of segregation persisted until reproductive activity began in early October. Females oviposited in tandem in *Juncus effusus* in temporary ponds, which held water only during the wet season. Reproduction usually finished by the end of October.

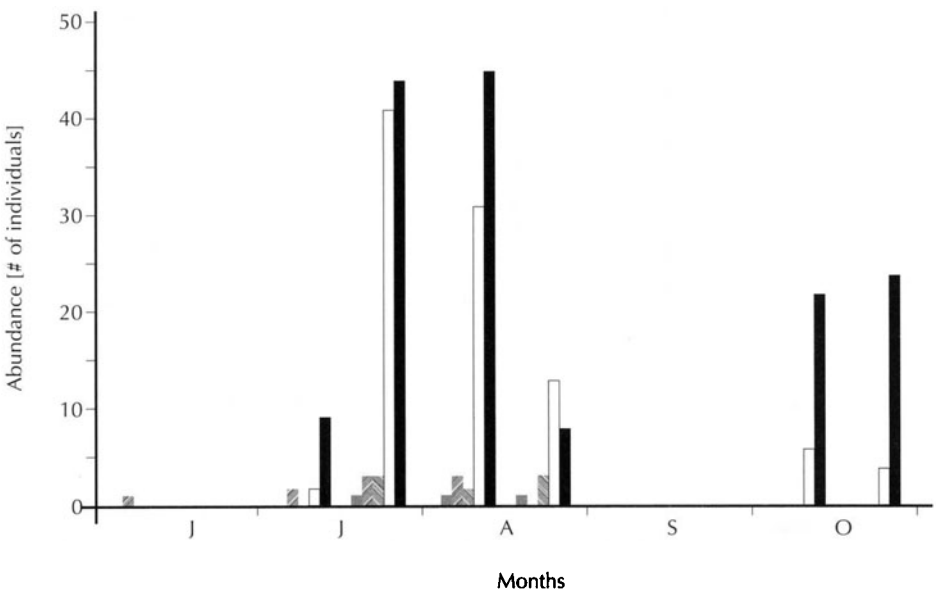

Figure 2: Abundance of three lestid species in alder carrs — seasonal changes. (■) *Lestes barbarus* males; (■) same females; (□) *L. viridis* males; (■) same females; (■) *Sympecma fusca* males; No individuals were seen in May an December, for September and November data is missing.

Lestes numidicus Samraoui, Weekers & Dumont

Emergence: Late April to June.
Flight period: Late April to November.
Pre-reproductive period: Five months.
Reproductive season: October to mid November.
Comments: I assumed that both *L. numidicus* and *L. virens* emerged concurrently because there was only one peak of emergence (late April - early June). *L. numidicus*, however, did not aestivate in the typical lestid refuges (alder carrs, dense vegetation along wadi) but sought refuge until autumn in upland forests where aestivating populations were recorded (Fig. 3).

Lestes virens virens (Charpentier)

Emergence: Late April to June.
Flight period: Late April to August (Fig. 4).
Pre-reproductive period: 4-5 weeks.
Reproductive season: Mainly June to July.
Comments: Maturation was not delayed, and was completed ca three weeks after emergence (Fig. 5). Reproductive activity in lowlands occurred mainly in June and July, whereas in upland sites it occurred mainly in August. Females oviposited, alone or more often in tandem, above water level, in *Typha angustifolia*, *Juncus acutus*, and *Scirpus inclinatus*.

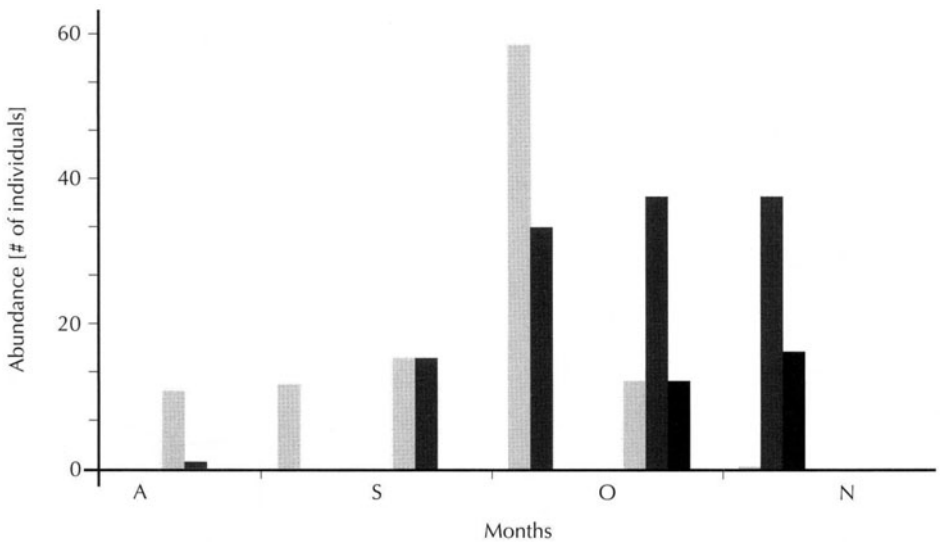

Figure 3: Abundance of three lestid species in lowland habitats, excluding alder carrs. (■) *Lestes barbarus*; (■) *L. numidicus*; (■) *L. viridis*. Data from 1998.

Lestes viridis (Vander Linden)

Emergence: Late April to early July.
Flight period: Late April to early December.
Pre-reproductive period: Five months.
Reproductive season: September to November.
Comments: Immature adults aestivated in alder carrs and in other shady, dark, cool places (e.g. streams and ravines; Figs 2, 3 7). Reproduction took place mainly in trees or bushes overhanging wadi and seasonal ponds. Females oviposited in tandem in green stems of ***Juncus maritimus*** close to water. Maturation was delayed (Table 1; Fig. 6) and its rate apparently varied markedly according to habitat/year; several males assumed mature coloration by 12 July, Bou Redim marsh, 1993. In early October most adults in alder carrs were females whereas males had already left their refuges and were distributed widely.

Sympecma fusca (Vander Linden)

Emergence: June.
Flight period: All year; adults were missing from November through January, probably hibernating.
Pre-reproductive period: ca 8 (7-9) months.
Reproductive season: Early March to April.
Comments: Mature adults were occasionally encountered in February. Adults aestivated in alder carrs (Fig. 2), although many were found in upland forests throughout summer and early autumn. It is not known whether adults from upland sites bred there or were using the sites only as aestivating refuges. By the end of February or early March females were ovipositing in tandem.

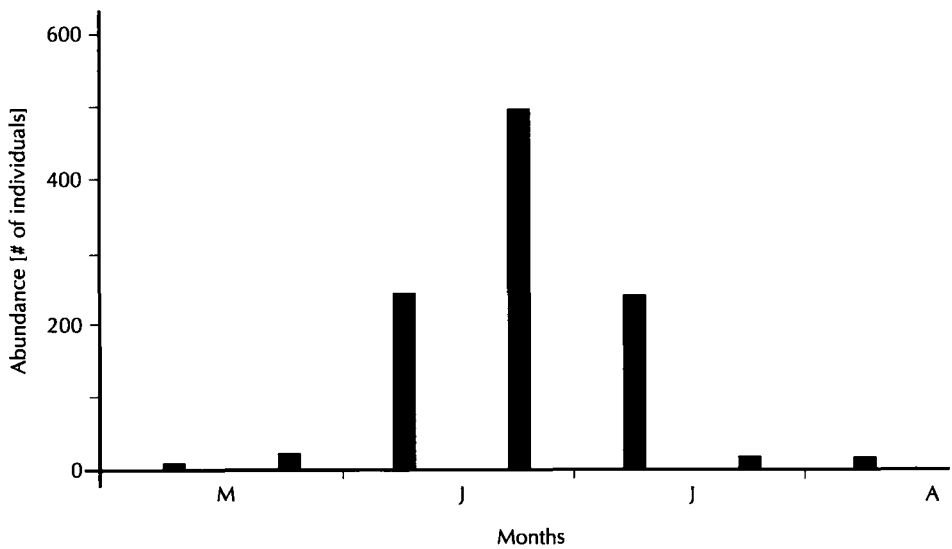

Figure 4: Abundance of *Lestes virens virens* at Mellah marsh — seasonal changes. Data from 1993.

Vertical stratification of lestids perching on alders

Vertical partitioning of perch sites by the three species of lestids which used alder carrs was observed to be highly significantly different ($F2, 66 = 6.21$, $p = 0.003$). The small lestid *S. fusca* used the lower strata (< 50 cm), the larger *L. viridis* perched across the higher strata with a mean of 81.5 cm, whereas the medium sized *L. barbarus* occupied an intermediate range (Fig. 7).

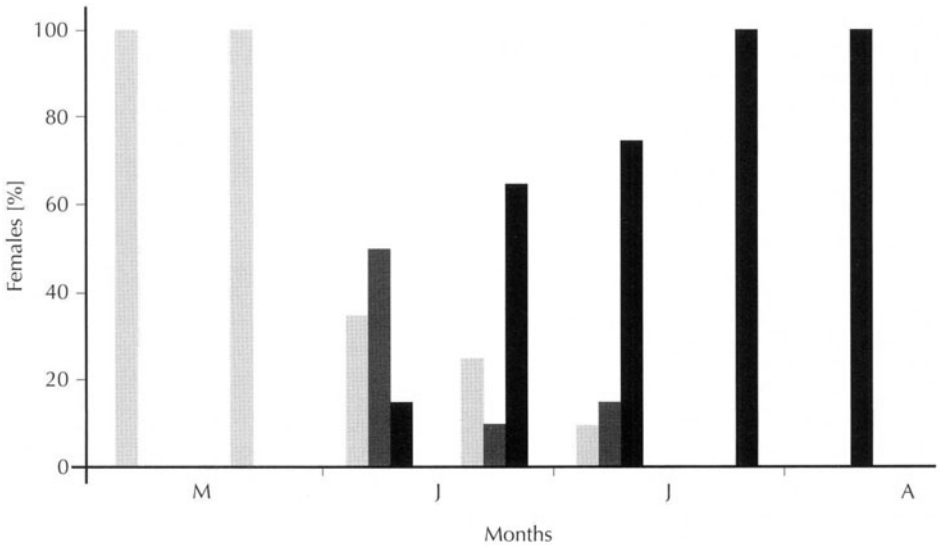

Figure 5: Colour maturation in female *Lestes virens virens* — seasonal changes. Data from 1993. (▦) teneral; (■) immature; (■) mature.

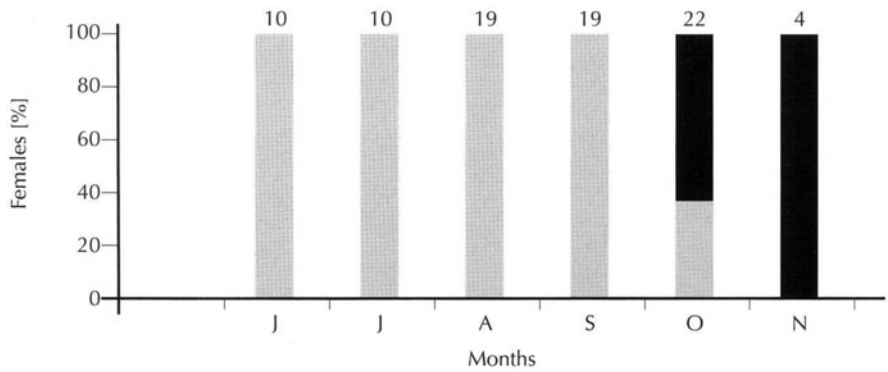

Figure 6: Maturation of ovaries in *Lestes viridis* — seasonal changes. (▦) immature females; (■) mature females.

Table 2. Duration of embryonic development in Numidian Lestidae. Hatching was recorded in the laboratory, when larvae of the first three stadia were first observed. Two separate hatchings of *Lestes barbarus* seemed to have occurred, the first event seems to have been prompted by wetting.

Taxon	Oviposition	Hatching	Minimum duration
Lestes barbarus	14 x 1998	End of xi 1998	1.5 months
		and i 1999	3 months
L. numidicus	03 xi 1998	02 ii 1999	3 months
L. virens virens	vi - vii 1998	19 i 1999	~ 6.5 months
L. viridis	03 xi 1998	08 iii 1999	~ 4 months
Sympecma fusca	08 iii 1999	18 iii 1999	10 days

Duration of embryonic development

Based on sampling of 26 temporary ponds over seven hydrological cycles, no larva of any species of lestid was found in Numidia before the end of December. Results of tests of length of embryonic development showed that only *S. fusca* had eggs followed immediately by hatching. By contrast, all four species of *Lestes* exhibited dormant eggs with diapause lengths varying markedly among species (Table 2).

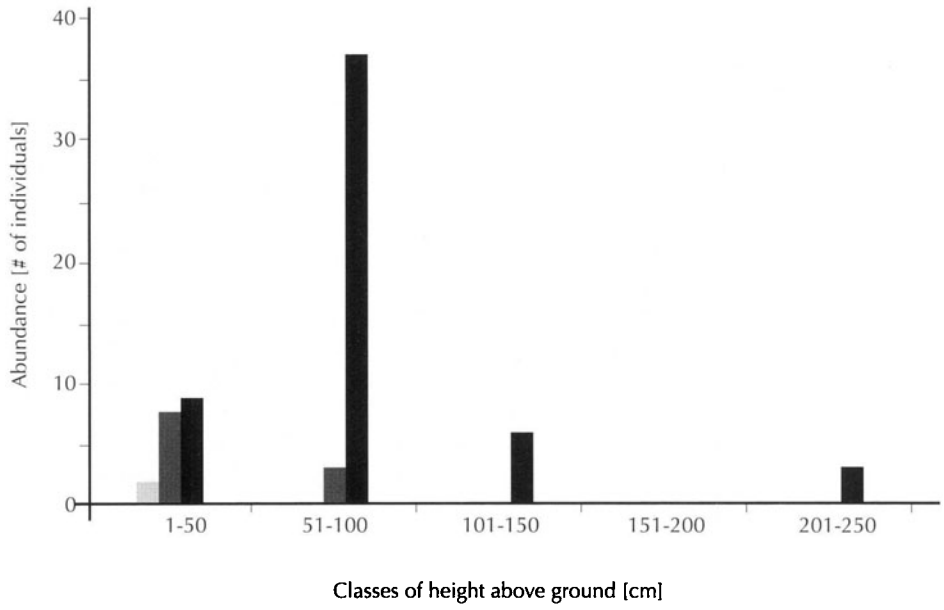

Figure 7: Aestivation of adult lestids in alder carrs — vertical stratification. Symbole hier erklären: *Lestes barbarus*; *L. viridis*; *S. fusca*.

Discussion

My results are consistent with all species of local Lestidae being univoltine, a situation expected from current knowledge of the family (Corbet 1999: 224; Corbet et al. 2006). Indeed, most known species of the cosmopolitan genus *Lestes* are reported to be univoltine (Corbet et al. 2006; Pritchard 2008). One possible exception is the tropical *L. plagiatus* (Burmeister), which inhabits permanent streams and is not known to siccatate (Gambles 1960). Siccatation as defined by Corbet (1999: 261) describes the state of suspended development exhibited by adult dragonflies in tropical regions during the dry and hot season, which cannot correctly be labelled as summer.

Most species of *Lestes* seem to exhibit a fast larval life style combining associated traits of temporary habitats, restricted microhabitat use, high vulnerability, and high activity leading to a short larval period and univoltine life cycle (Johansson 2000). Seasonal regulation in North Africa, i.e. maintenance of univoltinism while bridging the dry and desiccating summer fatal to the aquatic stages, is achieved in local populations of *Sympecma fusca* through aestivohibernation of the adult. In contrast to European populations (Jödicke 1997: 117, 175; Dijkstra & Lewington 2006: 88), North African populations of *S. fusca* emerge earlier, because they inhabit temporary water bodies, and must first aestivate in cool habitats before hibernating (Jacquemin 1987; Samraoui & Corbet 2000).

The phenology of Algerian populations of *L. virens virens* that breed in lowlands differs markedly from the phenology of individuals from SW Spain (Ferreras Romero & Puchol Caballero 1984), whereas *L. numidicus* follows a temporal pattern similar to that of *L. virens vestalis* Rambur in Italy (Utzeri et al. 1988). Among the three species of *Lestes* that aestivate, pre-reproductive periods of *L. barbarus* and *L. viridis* are longer than values reported for southern Europe. Indeed, such prolonged pre-reproductive periods exceed in length those reported for *L. barbarus* (Utzeri et al. 1984, 1987), *L. v. vestalis* (Utzeri et al. 1987, 1988), and *L. viridis* (Agüero-Pelegrin & Ferreras-Romero 1992). They also exceed the durations recorded for *L. sponsa* and *L. temporalis* Selys in Japan (Uéda 1978, 1989; Uéda & Iwasaki 1982). Although precise data are lacking for Numidia, and although its duration may vary from year to year and from habitat to habitat, my results are consistent with the existence of a geographical cline along which pre-reproductive period of certain odonates progressively lengthens south of 40°N (see Uéda 1978). Among Odonata, this phenomenon is not unusual (Corbet 1999: 264; see also Muñoz-Pozo & Ferreras-Romero 1996; Samraoui et al. 1993b, 1998) and it also occurs in several other orders of insects (Rivnay 1956; Masaki 1961), e.g. Hemiptera (BS unpubl.), and Lepidoptera (García-Barros 1988; Samraoui 1998). Masaki (1980) notes disappointingly scattered and fragmentary documentation of this phenomenon in the Mediterranean region. Perhaps reproductive clinal patterns will be shown to be more widespread from further study.

Our life history and phenology data strongly suggested that two sympatric but reproductively isolated sibling species were present. DNA analyses were performed which confirmed the discovery of a new species, *L. numidicus*, which coexists with *L. v. virens* (Samraoui et al. 2003). However, taxonomic and phylogenetic questions surrounding the *L. virens* complex remain unresolved.

Compared with their counterparts in central Europe, Algerian species of *Lestes*, several at the southern edge of their distribution, seem to have evolved four strategies to regulate their life cycle that bridge the dry season:

— breeding much earlier and aestivating as eggs (*L. v. virens*);
— aestivating as adults in lowland alder carrs and in other cool, shady places, and thus postponing reproductive activity until after the end of summer (*L. barbarus* and *L. viridis*; Fig. 6);
— aestivating as adults in upland refuges (*L. numidicus*);
— aestivating and then hibernating as adults, which then reproduce in early spring (*S. fusca*).

Lestids of temperate and tropical latitudes differ fundamentally in phenology, pre-reproductive adults aestivating in the former and siccatating in the latter (Corbet 1999: 261). In the tropical species *L. p. praemorsa* Selys, for example, pre-reproductive adults siccatate and then lay eggs, which hatch about one week later (Kumar 1972), allowing larvae to complete development during the brief rainy season. In contrast, an aestivating lestid in temperate latitudes, if not adopting strategy (4), needs to lay eggs that overwinter in diapause. Indeed, Uéda & Iwasaki (1982) interpreted the life cycle of *L. temporalis* in Japan (at ca 35°N), which features an aestivating pre-reproductive adult and a diapausing egg, as a means of maintaining obligatory univoltinism. I lack incisive data regarding egg hatching and larval development in Algerian lestids, although preliminary data (Table 2) are consistent with all other species except for *S. fusca*, which show some degree of delayed development. Wetting, or perhaps complete immersion in water, may stimulate hatching of eggs in the field as it does in laboratory experiments with eggs of *L. barbarus* (BS unpubl.). If egg diapause enhances survival during winter in northern latitudes, the behaviour of adults in cool, moist refuges during the summer seem to perform the same role in southern latitudes: adults with much reduced flight activity are found hanging almost motionless on vegetation,.

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