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The dragonfly community of a communal cattle pasture in the Sava floodplain (Croatia) with special reference to the biology of *Lestes barbarus* (Fabricius, 1798) (Zygoptera: Lestidae)

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A total of 25 dragonfly species were recorded between May and September 1997 on the communal cattle pasture of Lonja village and its surrounding area in the Lonjsko Polje Nature Park. At least 10 dragonfly species were reproducing successfully in the astatic ponds. *Sympetrum* spp. were dominating the community as they accounted for 95 % of all exuviae collected. Their high productivity in astatic environment is shown by average densities of over 70 exuviae/m²/year. By employing mark-recapture techniques it was stated that after emergence, *L. barbarus* covers distances of 80 to 880m to reach the hedges surrounding the pasture, where the animals spend the entire maturation period. Suitability of hedges as maturation habitat depends on their width and the width of adjacent margins. When mature, nearly all animals observed returned to the pond where they had emerged. Densely vegetated pond habitats with vegetation heights between 20 and 50cm are preferred reproduction sites for *L. barbarus*. The highest recorded age for individuals was 69 and 68 days for males and females respectively. The importance of low-intensity pasturing systems for nature conservation is briefly discussed.

ZDRUŽBA KAČJIH PASTIRJEV VAŠKEGA PAŠNIKA V POPLAVNI RAVNICI REKE SAVE (HRVAŠKA), S POSEBNIM POUDARKOM NA BIOLOGIJI GRMIŠČNE ZVERCE *LESTES BARBARUS* (FABRICIUS, 1798) (ZYGOPTERA: LESTIDAE) - Med majem in septembrom 1997 je bilo na vaškem pašniku vasi Lonja in njegovi okolici v naravnem parku Lonjsko polje zabeleženih 25 vrst kačjih pastirjev. Najmanj 10 vrst je v občasno presušenih mlakah uspešno zaključilo svoj razvoj. V združbi kačjih pastirjev so prevladovali kamenjaki *Sympetrum* spp., saj so njihovi levi predstavljali 95% vseh zbranih. Njihova visoka produktivnost v tem nestanovitnem življenjskem okolju je razvidna iz povprečne gostote preko 70 levov/m²/leto. Z metodo označevanja in ponovnega ulova je bilo ugotovljeno, da se osebki grmiščne zverce *L. barbarus* po preobrazbi oddaljijo od izvornega bivališča 80-880m ter preživijo celotno obdobje spolnega dozorevanja v živih mejah, ki obdajajo pašnik. Primernost le-teh kot bivališča v času spolnega dozorevanja je odvisna od njihove širine in širine njihovih robov. Skoraj vsi spolno zreli osebki so se vrnili k mlaki, kjer je potekal njihov razvoj. Njihova prednostna razmnoževalna okolja so gosto zarasle mlake z 20-50cm visoko vegetacijo. Najvišja ugotovljena starost osebkov je znašala za samčke 69 in za samičke 68 dni. Na kratko je pretresen tudi pomen ekstenzivnih pašniških sistemov za varstvo narave.

Introduction

Fortunately, the last decade has seen a sharp increase in autecological studies of several odonata species. Most authors have

concentrated their work on behavioural ecology and habitat requirements at the reproduction site. This is not surprising, since the majority of the odonata life cycle is spent in the larval stage.

Only recently the habitats occupied 'away from the water', during the maturation period or while foraging, has received more attention (CONRAD et al., 1999; CORBET, 1999). Although many Coenagrionidae spend most of their life in the close vicinity of the reproduction site, most Anisoptera and Lestidae travel large distances during these periods. It is quite probable that these species exhibit distinct habitat preferences, although data is sparse. JÖDICKE (1997) suspects that European Lestidae choose their maturation habitat carefully and deliberately.

The low-intensity land use in the Sava floodplain mirrors conditions vanished in most parts of Central Europe. It is well adapted to the changing environment of a semi-natural floodplain. Together with historical reasons it has helped to conserve biotopes and ecosystem types rarely encountered in more industrialised countries (see in detail SCHNEIDER-JACOBY, 1993). The region is therefore very well suited to study the exact habitat requirements of typical floodplain dragonflies and the distinct community of astatic pond environments. Especially the pastures offers a large variety of habitat types both at the reproduction site and in the surrounding area. By this, preferences for distinct vegetation types or biotopes in the land habitat are possible to be discerned. This paper analyses the different habitat preferences of *Lestes barbarus* during its adult life in relation to the land use characteristics.

Lestes barbarus is a holo-mediterranean species occuring as far east as Mongolia (JÖDICKE, 1997). In parts of Central Europe, like Germany, *L. barbarus* is listed as 'threatened' in the Red Data Book (OTT & PIPER, 1998). The decline is partly due to the loss of the required reproduction sites as a result of land amelioration processes (SCHORR, 1990; STERNBERG & BUCHWALD, 1999). In Austria and Slovenia the species is relatively rare. With a few exceptions only irregular breeding and very small populations are reported from both countries, thus the species is treated endangered (RAAB & CHWALA, 1997; CHOWANEC, 1999; KOTARAC, 1997). Although the data concerning the status of *L. barbarus* in most of its distribution range are deficient, it seems unthreatened in some parts of southern Europe, like Croatia (FRANKOVIĆ & HERLJEVIĆ, 1994).

Study area

The 'Lonjsko Polje' Nature Park is located approximately 100 km south-east of Croatia capitol Zagreb between the towns of Sisak and Nova Gradiška (Fig. 1). The protected area is part of the Sava floodplain. The size of the park is about 506,5 km². The Nature Park

holds one of the largest alluvial forests and regularly inundated areas in Central Europe (SCHNEIDER-JACOBY, 1993).

Fig. 1. Location of the "Lonjsko Polje" Nature Park in Croatia

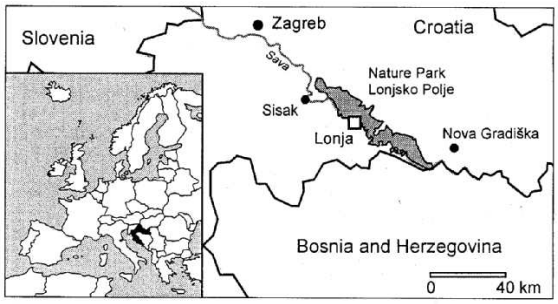
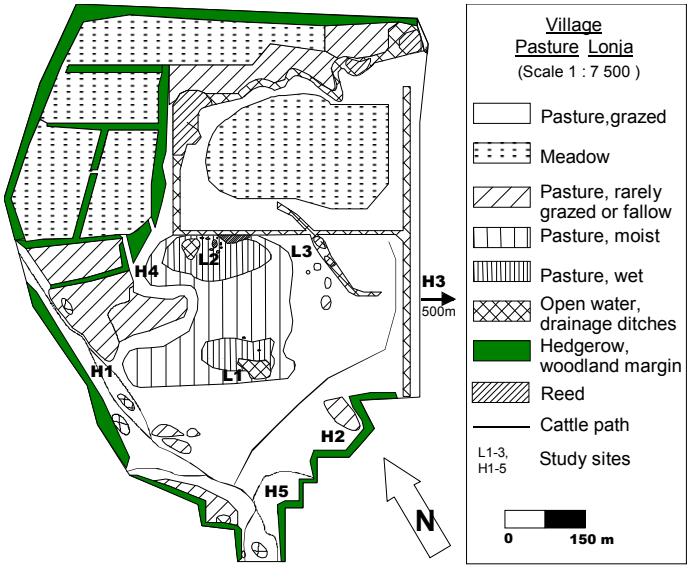


Fig. 1
Location of the »Lonjsko Polje« Nature Park in Croatia

The study was conducted on the communal cattle pasture of Lonja and its surrounding area (78 ha). It consists of a mosaic of extensively grazed pastures, meadows, fallow areas, hedgerows, drainage ditches and a large ground depression (L1 and L2) (Fig. 2).

Fig. 2. Land use and different habitats on the village pasture of Lonja, Croatia. Study sites H 1-5 are hedgerows used as maturation habitats, L 1-3 are ponds / drainage ditches used for reproduction (H 3 lies approx. 500 m in the direction of the arrow)



As groundwater levels rise this depression is regularly flooded, but it normally dries up during the summer months (July-September). The vegetation of this temporary pond is characterised by a mixture of Phragmition, Agropyro-Rumicion, Bidention and Nanocyperion plant communities. The dominant plant species are *Agrostis stolonifera, Trifolium fragiferum, Galium palustre* and *Eleocharis palustris*.

Additional data on the dragonfly community of another astatic pond is presented from the communal pasture of Mužilovčica (in the following M 1), about 4 km north-west of Lonja. In contrast to the pasture of Lonja it is grazed more intensively by herded cattle, free-ranging cattle, horses and pigs, the latter being traditional local and very robust breeds (see GUGIĆ, 1996).

Methods

The different biotopes of the pasture in Lonja were mapped. The following parameters were used to describe habitat types at the reproduction site: vegetation cover (%), water cover in July (%), average vegetation height, and dominant plant species. Water cover, in particular, is highly variable as a result of the fluctuating water table.

In order to describe the dragonfly community of the astatic pond exuviae were collected every two days between May 23rd and July 20th 1997 (pond partly dried up!) on 4 permanent transects (5 m x 0,5 m). Sampling continued until no more exuviae could be found. Material was determined using ASKEW (1988), HEIDEMANN & SEIDENBUSCH (1993) and JÖDICKE (1993; 1997). For the problems in determining *Sympetrum meridionale* see HEIDEMANN & SEIDENBUSCH (1993).

Additionally twice per week between May 23rd and September 2nd 1997 adult Odonata were sampled along random transects run for 30 minutes. Relative density was recorded in form of abundance classes (see STERNBERG & BUCHWALD, 1999).

To analyse the habitat preferences of *L. barbarus* and to gather quantitative data on the abundance of other dragonflies, a total of 20 transects (100 x 5 m) were established in the different habitat types. They were checked between June 20th and September 4th on 23 occasions. Transects were run between 10 a.m. and 16 p.m. under sunny and warm weather conditions (cloud cover < 4 / 8). This corresponds to the main activity period of *L. barbarus* (UTZERI et al., 1987).

Mark-recapture experiments were employed to study the local population of *L. barbarus*. Specimens were individually marked on the wing with an enamel pen (Edding 780). The sex of marked specimens was recorded. During 36 days we marked individuals in different segments of the pasture in order to determine any movement between habitat types. The marking effort in each segment was standardised to 60 minutes.

SPSS for Windows 6.0 and Excel 7.0 were used to analyse the data. Non-parametric data were processed using the KRUSKAL-WALLIS H-test and the MANN-WHITNEY U-test. In the case of parametric data, Student's t-test or analysis of variance (ANOVA) were applied (BÜHL & ZÖFEL, 1995).

Results

Dragonfly community of the temporary pond

Exuviae:

In all 982 exuviae of 10 species were collected (incl. 3 ind. of *Sympecma fusca*, 2 ind. of *Lestes dryas* not collected on the transects) (Tab. 1). The community is dominated by Sympetrinae, which comprise over 95 % of all exuviae. They also show the high productivity of this astatic environment in reaching an average emergence density of over 70 ind. / m² / year.

Tab. 1. Exuviae density at pond L1 (number /m² / year). The material was collected on 4 permanent transects in two-day intervals between May 23rd and July 20th 1997. The species in which the emergence period probably started before May 23rd are marked with an asterisk.

SPECIES	MEAN	MIN	MAX
Sympetrum striolatum	26	14,6	32
S. meridionale / sanguineum / striolatum	46,95	23	62
S. sanguineum	1	0,2	2,2
S. vulgatum	0,95	0,4	1,6
*Aeshna affinis**	0,9	0	3,2
*Ischnura elegans**	0,25	0	0,8
*I. pumilio**	0,45	0	1,4
Lestes barbarus	0,45	0	1,2

Imagines:

A total of 21 dragonfly species were recorded during the transects. The most common species were *Lestes barbarus, Ischnura pumilio, I. elegans* and *Coenagrion puella*. Of the Anisoptera, species like *Aeshna affinis, Libellula depressa, Orthetrum albistylum* and *Sympetrum* spp. were dominant. Nearly all species appeared in higher densities on the pasture in Lonja. Apart from this, the comparatively small amount of *Sympetrum* spp. is explained by the ending of the study period in September. By this time only few individuals had commenced with reproductive activity.

Dragonflies noted at other times at the ponds were *Sympetrum fonscolombii, S. flaveolum* (L1)*, S. vulgatum* and *S. striolatum* (L1,

M1). A comprehensive overview of the dragonflies of both pastures is given in Table 2.

Tab. 2. Overview of the dragonfly communities of two astatic ponds (L 1 and M 1) on low-intensity pastures in the Sava floodplain. EX = Exuviae or larvae present; IMA = maximum abundance of mature dragonflies at the ponds as recorded during standardised transects; REAC = data on observed reproductive activity (co = copulation, egg = egg-laying). Abundance classes: I = single Ind., II = 2-5 Ind., III = 6-10 Ind., IV = 11-20 Ind., V = 21-50 Ind., VI = > 50 Ind; X = species recorded during other times.

SPECIES	**POND L 1**			**POND M 1**		
	EX	IMA	REAC	EX	IMA	REAC
Calopteryx splendens	–	I		–	–	
Calopteryx virgo	–	I		–	–	
Sympecma fusca	X	I		X	I	
Lestes barbarus	X	IV	egg	X	III	egg
Lestes virens vestalis	–	I		–	I	
Lestes sponsa	–	–		–	I	co
Lestes dryas	X	II	co	X	II	co
Platycnemis pennipes	–	X		–	–	
Ischnura elegans	X	III	co	X	IV	co
Ischnura pumilio	X	IV	co	X	I	co
Erythromma viridulum	–	I		–	II	
Coenagrion puella	?	IV	co	?	V	co
Aeshna affinis	X	III	egg	–	I	
Anax imperator	–	II	co	–	I	co
Hemianax ephippiger	–	I		–	–	
Gomphus flavipes	–	I		–	–	
Libellula depressa	X	III	egg	X	III	co
Libellula quadrimaculata	–	X		–	–	
Orthetrum albystilum	X	III	egg	X	II	egg
Orthetrum brunneum	–	–		–	II	
Crocothemis erythraea	–	III	egg	X	II	egg
Sympetrum fonscolombii	–	X		–		
Sympetrum flaveolum	–	X		–		
Sympetrum meridionale	X	II	egg	X	X	
Sympetrum sanguineum	X	I	egg	X	X	
Sympetrum striolatum	X	X		X	X	
Sympetrum vulgatum	X	X		X	X	
NO. OF SPECIES	**12**	**25**	**12**	**12**	**19**	**10**

Also, not all species exhibiting reproductive behaviour were reproducing successfully. Especially the above mentioned Anisoptera

with a longer larval development fail to complete their life cycle under the astatic conditions.

Population biology

The emergence period of *Lestes barbarus* began on June 1st and ended on June 20th. The first individuals engaging in reproductive behaviour were caught on July 13th at the pond L1.

The estimate of the duration of the prereproductive or maturation period (DPRP, see CORBET, 1999) varies according to the applied method. Due to a rather small sample size (n = 5) the direct observation of individuals marked at emergence and subsequently caught at the reproduction site has to be treated with much caution. The specimens reappeared after 24, 32, 34, 49 and 69 days respectively. The second method uses the time between the begin of emergence and reproduction for the entire local population (see JÖDICKE, 1997) and calculates to 43 days.

Further insights provide the mark-recapture of individual dragonflies in the maturation habitat. The duration recorded varied between 6 and 22 days. Adding the period before the first capture, the minimum DPRP calculates to 11 – 30 days.

Overall, 1362 adult individuals of *L. barbarus* were marked (30 at emergence, 338 in the maturation period and 994 in the reproduction phase). The recapture rate averaged 43,5% (41,5% for females, 44,9% for males).

The sex ratio differed notably between life-history stages. It was strongly male biased at the reproduction site (0,66 : 0,34; Chi²-Test, n = 23, $p < 0{,}001$), whereas males and females were almost evenly distributed both at the maturation sites (0,49 : 0,51) and in the land habitats occupied at other times for foraging and resting (0,48 : 0,52).

Tab. 3 shows the percentage of surviving individuals between two consecutive capture sessions. Age calculation results from the direct observation through recapturing – by this we get a very conservative minimum age. Only individuals marked in the first 4 weeks following emergence were taken into account (n = 205), in order not to underestimate the age. All *L. barbarus* not recaptured are omitted from the analyses.

Tab. 3. Average minimum survival rate of both sexes (BB, bb) of *Lestes barbarus* in Lonja (n = 205), as calculated by recapture data. (Q_1 - first quartil, Q_2 - median, Q_3 - third quartil)

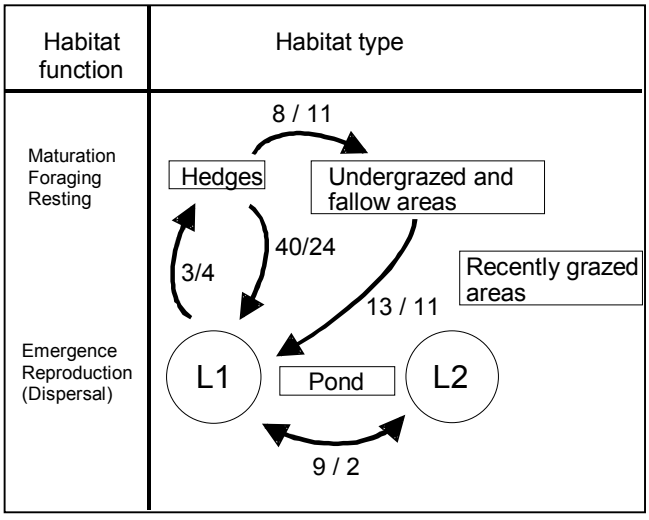
	N	**Q_1**	**Q_2**	**Q_3**	**Mean**	**SD**	**Min**	**Max**
BB	103	5	13	29	18,26	16,71	1	69
bb	102	5	12	26,25	17,53	15,73	1	68
Total	**205**	**5**	**12**	**29,25**	**17,97**	**16,18**	**1**	**69**

The picture shows a logarithmic decline with no discernible difference between sexes ($p > 0,85$). The oldest specimens reached a minimum age of 69 and 68 days, for male and female respectively. Since these individuals were first marked in the maturation period, their exact age exceeded 70 days. Bearing in mind that the emergence ended on the 20th of June, all individuals present on the pasture in September had to be at least 72 days old (unless they had immigrated).

Habitat use and movement patterns

After emergence, some individuals spent several days at the edge of ponds L1 and L2. However, most prereproductive individuals proceeded quickly to the hedges surrounding the pasture (Fig. 3), where they stayed for the entire maturation period. The distances covered between these two habitats varied from 80 - 880 m (see also Tab. 4). Apparently, individual mobility in the maturation habitat is quite restricted. Movement between hedges could only be recorded twice.

Fig. 3. Habitat use and movements associated with the phenological states of *Lestes barbarus*. The numbers describe the amount of observed movement between different habitats during the entire study period (males / females).



Mostly, mature damselflies returned directly to the reproduction site. Emergence and reproduction site were always identical. Several specimens moved from the hedgerows to other land habitats like undergrazed areas or fallows, before starting reproductive behaviour at the temporary pond. These land habitats occurred all over the

pasture. Typical plant species were *Daucus carota, Centaurea nigrescens, Lolium perenne, Melilotus officinalis, Pastinaca sativa* and *Cychorium intybus.* Especially for female damselflies, the large number of flowering plants makes these places an important foraging and resting site between successive oviposition events.

L. barbarus is highly consistent in its choice of reproduction pond. Only 11 individuals (2 females) were found at ponds other than those where they had originally been captured (Fig. 3). Males accounted for most of this observed movement (9 individuals). This is not in line with the assumption that female lestids are better dispersers (UTZERI et al., 1984, JÖDICKE, 1997, but note CONRAD et al., 1999).

Habitat preferences

Maturation period:

The five hedges analysed differ strongly in their structural characteristics and the corresponding average densities of *L. barbarus* (Tab. 4). Hedge H1, characterised by the largest width and broadest margin, had the significantly highest density of damselflies (ANOVA, $df = 4$, $p < 0{,}001$). The exposition of the hedge and the distance to the reproduction site seem less important.

Tab. 4. Characteristics of different hedges used as a maturation habitat by *Lestes barbarus*. Abundance of *L. barbarus* in the hedges (Ind. / 100 m, incl. standard deviation, n = 12)

	HEDGE (H1)	**HEDGE (H2)**	**HEDGE (H3)**	**HEDGE (H4)**	**HEDGE (H5)**
DISTANCE TO L1 (m)	240-360	80	880	200-240	280-320
EXPOSITION	E	SE	W	N-W	W
HEIGHT (m)	3-15	3-5	3-5	3-5	1-3
HEDGE WIDTH (m)	5-15	3-10	3-5	1-5	1-5
MARGIN WIDTH (m)	1-5	1-3	1-3	1-2	0
AVERAGE DENSITY	21,6	4,0	0,4	5,4	0,2
STANDARD DEVIATION	14,3	2,8	0,4	2,8	0,4

The use of hedgerows as a maturation habitat was a characteristic feature of *L. barbarus*. Although other species like *Lestes dryas, L. virens, Coenagrion puella* and *Sympetrum* spp. were recorded, none appeared in similar densities (see Tab. 5). Whereas the Zygoptera exhibited preferences for the hedge margin and even the interior under windy conditions, *Sympetrum* spp. seemed to prefer the higher strata. In warm weather they were regularly found sunbathing at a height of 3-5 m.

Tab. 5. Use of hedgerows with (HWM) or without (HSM) adjacent margins as prereproductive and / or foraging habitat by dragonflies on the pasture in Lonja.

SPECIES	HWM	HSM
Calopteryx splendens	X	
Lestes barbarus	X	
Lestes dryas	X	
Lestes virens vestalis	X	
Platycnemis pennipes	X	
Coenagrion puella	X	
Aeshna affinis	X	
Anax imperator	X	
Libellula depressa	X	
Libellula quadrimaculata	X	
Orthetrum albystilum	X	
Crocothemis erythraea	X	X
Sympetrum meridionale	X	
Sympetrum sanguineum	X	X
Sympetrum striolatum	X	

Reproduction period:

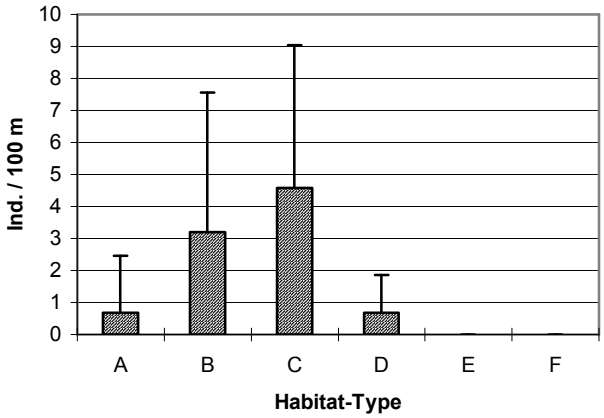
The ponds L1 and L2 on the pasture in Lonja (reproduction site) were characterised by six different habitat types (Tab. 6). Except for type F (scattered reed stands composed of *Sparganium erectum*) the different habitats mainly result from the moisture gradient between the perimeter and the centre of the pond.

Tab. 6. Description of the structural parameters characterising the different habitat types at reproduction site L1 and L2. Parameters: VC = vegetation cover (%), OW = open water (%), AHV = average height of vegetation (cm), CF = Cattle footprints (+/-), DPS = Dominant plant species. Plant species: TF = *Trifolium fragiferum*, AS = *Agrostis stolonifera*, GP = *Galium palustre*, EP = *Eleocharis palustris*, MA = *Mentha aquatica*, APA = *Alisma plantago-aquatica*, GO = *Gratiola officinalis*, MQU = *Marsilea quadrifolia*, GF = *Glyceria fluitans*, SE = *Sparganium erectum*

	TYPE A	TYPE B	TYPE C	TYPE D	TYPE E	TYPE F
VC	75-95	95-100	75-95	25-75	5-25	75-95
OW	0	0	0-10	5-50	25-95	5-25
AHV	0-10	20-50	20-50	20-50	20-100	100-150
CF	+++	++	+	-	-	-
DPS	AS, TF	GP, TF, EP	EP, MA, APA	EP, APA, GO	GF, EP, MQU	SE

The highest mean density of *Lestes barbarus* was recorded from habitat type C (U-Test, n = 23, p < 0,001) (Fig. 4).

Fig. 4. Average density of *Lestes barbarus* in the different habitat types at reproduction site L1 (n = 23). For the description of the habitat types see Table 2.



Habitat type C was composed of short and dense stands of vegetation. *L. barbarus* avoided reed stands and areas without or with sparse amount of emergent vegetation.

These preferences are confirmed by direct observations of the reproductive behaviour (tandem, wheel formation and oviposition). Such behaviour was solely recorded at pond L1 from habitat type B or C, although the latter was significantly preferred (Chi²-Test, n = 94, p < 0,01). Eggs were laid independent of the presence of water. The main oviposition plants were *Mentha aquatica* (n = 9), *Alisma plantago-aquatica* (n = 6) and *Eleocharis palustris* (n = 4). Furthermore, plants rarely used were *Bidens frondosa* and *Juncus articulatus*.

Other common species like *Ischnura pumilio* and *Aeshna affinis* showed preferences for other habitat types. However, these were not as obvious as with *L. barbarus*. The coenagrionid *I. pumilio* appeared in a wider range of habitats types as long as emergent vegetation and surface water were present. It exhibited no statistically significant preference. However, reed stands (type F) were avoided (U-Test, n = 23, p < 0,01).

A. affinis occurred mainly in habitat types with bare soil and lacking open water. Also, higher densities were recorded from *Sparganium erectum* stands. A significant preference for the Types A

and F could be partly detected (U-Test, n = 23, p < 0,05). The eggs were always laid in cattle-footprints (n = 6). Male individuals were present in all observed oviposition incidences. Twice they were undertaken in the tandem position.

L. barbarus was the only dragonfly species on the pasture for which a significant preference of the temporary ponds (L1, L2) was detected. Overall, 98% of reproductive activity was recorded there (Chi²-Test, n = 129, p < 0,001). In comparison, reproductive behaviour of *Lestes dryas* occurred mainly in summer-dry drainage ditches (L3) and in small ponds adjacent to hedgerows (south-western part of the pasture). *L. dryas* is normally described as a typical inhabitant of temporary ponds (SCHORR, 1990; JÖDICKE, 1997).

Discussion

The observed species assemblage is typical for eutrophic ponds with broad, shallow eulitoral zones and a large amount of emergent vegetation (LANDMANN, 1985; WARINGER, 1989). The community is dominated by species showing the best adaptations for inhabiting temporary ponds. Members of the Lestidae and Sympetrinae both have an obligate diapause in the egg-stage, in which they are protected against desiccation (CORBET, 1999). The following species were only recorded at the astatic ponds (although not in all cases statistical significant preferences were obvious): *Lestes barbarus, L. dryas, Sympecma fusca, Ischnura pumilio, Aeshna affinis* and *Sympetrum meridionale*. They require high water temperatures for their fast larval development. These conditions are met by the shallow and in parts sparsely vegetated pond. These species can be described as typical inhabitants of astatic pond environments (e.g. KUHN & BURBACH, 1998).

In comparison to other studies of the dragonfly communities of astatic ponds the species richness on the Lonja village pasture has to be seen as high. Whereas KRAMER (1964) could not find any odonate larvae, LANDMANN (1985) found 11 species in a larger wetland area in Austria. FISCHER (1961) had between 1 – 7 species as a result of differing water regime in small ponds in Poland.

The last decade has shown a sharp increase in studies of habitat preference and behavioural ecology of dragonflies. But, they have mainly been restricted to larval habitats (CONRAD et al., 1999). However, land habitats provide very important environmental qualities for most species. Between their short visits to the reproduction site, females in particular need habitats providing a stable food supply (CORBET, 1999). The importance of land habitats as hunting grounds was also shown by STERNBERG (1993), who found that mowing caused a decrease in damselfly densities.

Although UTZERI et al. (1984) intensively studied the philopatric abilities of *L. barbarus*, they were left to speculations with respect to

the maturation habitat. They suggested thick bushes next to the reproduction site as the potential maturation habitat. On the village pasture of Lonja *L. barbarus* exhibited a distinct preference for the margins of hedges rich in flowering plants. Responding to the direction of the wind, individuals were found on both sides of the hedges. During rainy weather, they also used the hedge interior as a shelter. The importance of sunny and wind protected maturation and foraging habitats have been emphasised by other authors (JÖDICKE, 1997; STERNBERG & BUCHWALD, 1999). Moreover, the presence of flowering plants with insect pollinators assures a rich and constant supply of food for dragonflies.

In our study plot, *L. barbarus* covered at least 800 m between different habitats. This agrees with data from other damselfly species (*Lestes virens, Sympecma fusca*), who are both capable of bridging more than 1.000 m between different habitats (JÖDICKE, 1997; WILDERMUTH, 1997). AGUESSE (1961; *cit. in* STERNBERG & BUCHWALD, 1999)) found *L. barbarus* to cover up to 2.000 m in the maturation period. Movement of *L. barbarus* between several land habitats coincides with findings on the behaviour of *Sympecma paedisca* (SCHMIDT, 1993).

Maturation and foraging habitats for lestid species therefore have to incorporate habitats not cultivated too intensively. They probably have to be not much more than 2.000 m from the larval habitat. Typical examples are forest margins, clearings, fallows or heathlands (see JÖDICKE, 1997; STERNBERG & BUCHWALD, 1999).

Although presenting data on the emergence period for most other European Lestid, JÖDICKE (1997) gives no information for *L. barbarus*. The duration of 19 days falls in line with values known for the closely related *L. dryas* (13 – 34 days). For other species, the period is markedly longer.

The sex ratio was not determined through the counting of exuviae, but during the marking of teneral and mature individuals in different habitats. Since a sex-dependent mortality during emergence is rather unlikely, these results seem to be reliable. The small excess / overhang of females lies within the range of similar studies (overview in JÖDICKE, 1997). Noteworthy is the large percentage of males encountered in the foraging / resting habitats on the pasture.

JÖDICKE (1997) also offers overviews on the DRPR and the individual life span of mature *L. barbarus*. Whereas the former ranges from 41 days in Switzerland to approx. 75 days in Italy, the latter also lies within the range observed in this study.

L. barbarus is often described as a “pioneer species”, capable of utilising even very small water bodies with very sparse vegetation (e.g. SCHORR, 1990). However, given a wider range of habitat types, *L. barbarus* prefers the densest stands of vegetation with little or no surface water present (see also STERNBERG & BUCHWALD, 1999). In the Sava floodplain the reproduction site consists of a pond with highly fluctuating water levels, high water temperatures, and a

broad, shallow eulitoral zone with dense stands of short emergent vegetation (e.g. *Eleocharis* spp., *Juncus* spp.).

A preference for oviposition substrates of the '*Juncus*-type' generally has been assumed for the genus *Lestes* (JÖDICKE, 1997). We found that 65% of all ovipositions occurred in plants with other growth forms (e.g. *Mentha*). Therefore, we argue that '*Juncus*-type' vegetation primarily serves as a proximate cue (sensu BUCHWALD, 1989) to indicate suitable conditions for larval growth (e.g. high water temperatures, absence of fishes).

L. barbarus apparently requires the combination of suitable reproduction sites together with sheltered and sunny maturation habitats rich in food resources. The presence of broad hedge margins, undergrazed areas, and fallows rich in flowering plants directly results from the low-intensity pasturing system. This kind of land use can lead to the close proximity of different regeneration and degeneration stages of vegetation (ASSMANN & FALKE, 1997). By this, the patchiness of floodplain grasslands is further enhanced.

Although actual grazing may temporarily have a negative impact on *L. barbarus* (see HILL et al., 1999) the overall impact of large-scale grazing regimes proves to be beneficial. This kind of land use guarantees the existence of the required habitat mosaic. Stochastic disturbance slows down or even disrupts succession on the grazed areas and at the astatic pond. Therefore the survival of *L. barbarus* and of other merolimnic species is possible.

The successful emergence of *Ischnura pumilio* and *I. elegans* could be explained by a bivoltine life cycle. Such behaviour has been reported from Germany (INDEN-LOHMAR, 1997) and seems to occur regularly in the Mediterranean area (KUHN & BURBACH, 1998).

Unclear are the adaptations exhibited by *Aeshna affinis*. The development of the larvae is supposed to take 1 or 2 years (KUHN & BURBACH, 1998), but no adaptations for the survival of dry periods are mentioned. Other authors have reported reproductive behaviour at dried-up ponds (BERNARD & SAMOLAG, 1994, UTZERI & RAFFI, 1983) and observed oviposition which took place exclusively in holes dug by wild boars in the hardened ground of the dried-up pond (UTZERI & RAFFI, 1983).

Our study gives insights into the changing habitat preferences shown by *Lestes barbarus* during its adult life. The dependence on a diverse set of land habitats might imply that high-intensity land use is detrimental to the continued survival of this species on at least two levels. Uniform land use, a typical feature of modern agricultural practices, reduces the amount of habitat diversity. Hereby, the loss of flowering plants is induced and possible foraging and maturation habitats are degraded. Also, the eutrophication of larval habitat due to fertilisers could lead to changes in vegetation types.

Compared with this, the low-intensity pasturing even enhances the habitat diversity. The beneficial effects shown for other animal groups

(e.g. SCHNEIDER-JACOBY, 1993, BIGNAL & McCRACKEN, 1996, ASSMANN & FALKE, 1997, ELLIGSEN et al., 1997), seem to apply also for dragonflies. Therefore, large-scale grazing systems like the one under investigation are very well suited for the integration of nature conservation goals with land use in cultural landscapes. This is true especially in areas at risk of being abandoned by traditional farming (RIECKEN et al., 1997).

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