Adv. Odonatol. 6 : 177-198 April, 1994

NICHE SPECIALIZATION IN DRAGONFLIES *

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Two organisms minimize competition and enable co-occurrence if they use their environmental requirements differentially. Niche specialization occurs at the interspecific but also at the intraspecific level, whereby we suggest that time, space and food are the three most important niche dimensions. A general aspect of the biology of dragonflies is that adults and larvae live in totally different habitats, and so they occupy different ecological niches. Climate, temperature and competition lead to different life-histories (e.g. duration of embryonic and larval development, diapause and larval growth rate) and to different diurnal and seasonal activity rhythms of adults. Spatial niche specialization occurs in all three dimensions with two-dimensional segregation being the most common one of these. It is shown that spatial niche segregation is highly dependent on the actual degree of competitive interactions. Temporal and spatial niche specialization, as well as the utilization of different diets or differentsized prey, reduce food competition. The impact of different predators (invertebrates and vertebrates) in larval habitats may be minimized by special antipredator defence strategies. Oscillating or stable predator dominances in the larval sites advance species with different migration tendencies.

INTRODUCTION

Living organisms and their abiotic (nonliving) environment are inseparately interrelated and interact upon each other. Depending on its physiological, morphological and behavioural abilities every species becomes more or less adapted to its ecological environment. The position or status of an organism within its community and ecosystem is, by analogy, its 'profession' and is termed 'ecological niche', whereby time, space and food are suggested to be the

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* Dedicated to my teacher Professor Dr Günther Osche.

three most important niche dimensions among potentially competing species (PIANKA, 1973 ; SCHOENER, 1974). Niche specialization is the result of an evolutionary process in which different species became adapted by evolving different requirements and preferences ; this enables each of them to use their environment in a different way and keeps them out of competition or, at least, minimizes it. Thus, niche specialization enables coexistence of many species.

Competition occurs wherever niches overlap even to a partial extent. Because of competition, no two co-occurring species occur in exactly the same ecological niche at the same time and place (the so-called 'competitive exclusion principle', 'Monard's principle' or 'Gause-Volterra's principle), even if closely related species (with similar morphological and physiological characteristics) may have virtually the same niche requirements. The extent of niche overlap at which one species pushs out an other is not known, but it inevitably occurs if two species occupy exactly the same niche, i.e. this leads to 'total competition'.

Organisms with similar ecological niches can only co-occur if all essential ecological factors which were used together are abundant. An ecological separation becomes necessary if two co-occuring organisms strive for the same thing(s) and if at least one of these things become sparse, which together mean that capacity treshold of the environment is obtained. Niche specialization occurs at the interspecific, but also at the instraspecific level.

A short survey of some phenomena of this nature in dragonflies is given in the following: A general aspect of niche specialization in dragonflies is that larvae and adult dragonflies have quit different modalities of life and their habitats differ totally: larval and adult dragonflies occupy different ecological niches — probably a form of intraspecific competition avoidance, e.g. in food. This is widespread within the holometabolic insects and is one of the reasons for the large ecological success of this group. Within the hemimetabolic insects 'habitat splitting' between different stages (larvae — adults) only occurs in three of 24 orders the Ephemeroptera, Plecoptera and just the Odonata.

NICHE SPECIALIZATION IN ADULTS

TEMPORAL NICHE SPECIALIZATION

Of all recent dragonfly species 70% live in the tropics and subtropics and only 30% are distributed in all the other parts of the world. This indicates that dragonflies primarily are thermophilic insects. Occurrence of dragonflies depends highly on their thermic demands, and the distribution, seasonality and also inter-habitat variation of species is strongly restricted by climatic factors, especially temperature (cf. also MAY, 1978). Larval and adult dragonflies may have little or no ability to acclimatize to changed thermic conditions (cf. LEGGOTT, 1986). Certain temperature thresholds and the extent of thermic plasticity seem to be species-specific and cause seasonality and spatial distribution of species.

Representative of other European genera, seasonal distribution patterns of European *Coenagrion*-species in Central Europe and Finland are compiled in Table I. Different seasonal distribution patterns indicate a temporal niche specialization in these ecological related species, but such patterns are only restricted to a certain geographical region because different climatical, competitive or other environmental conditions lead to a shift in seasonality. For example, compared with the western European atlantic climate with its moderater temperatures, the temperature regime in eastern Europe is characterized by larger amplitudes with higher absolute values in spring, summer and autumn due to the larger continentality. Therefore temperatures in the habitats, especially in the shallow waters, rise quicklier and to higher values in eastern than in western Europe, so that (1) temperatures suitable for larval development and emergence occur earlier in the year and (2) is appropriate to adult dragonflies for a longer time in the east than in the west (PLATTNER, 1965). Due to this, flying seasons of the species listed in Table I begin 1-5 decades of days earlier in southern Transsylvania (Central Romania) (cf. PLATTNER, 1965) than e.g. in Germany and last longer in eastern than in western Europe.

Table I

Flight periods of *Coenagrion*-species in Central Europe (left), where 10 species occur and Finland (right), where only 5 species occur (data from Finland after VALLE, 1938)

species	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep
C. hastulatum	■■■	■■■■	■■			■■	■■■■	■■■■	■■	
C. armatum	■■	■■				■■■	■■■■	■■■■	■	
C. lunulatum		■■■					■■■■	■■■		
C. scitulum		■■■								
C. ornatum	■	■■■■	■■■■							
C. mercuriale	■	■■■■	■■■■	■■						
C. pulchellum	■■■	■■■■	■■■■	■■■■	■■		■■■	■■■■	■■	
C. puella	■■■	■■■■	■■■■	■■■■	■■■■					
C. hylas		■	■■■■							
C. lindeni		■	■■■■	■■■■	■■					
C. johansonni							■	■■■■	■■■	

Compared with dragonflies from Scandinavia the seasonal phenology of Odonata from Central Europe differs as follows (Fig. 1) : — (1) increase of the number of species from north to south ; — (2) flight period of dragonflies begins earlier and ends later in the south than in the north ; — (3) the time

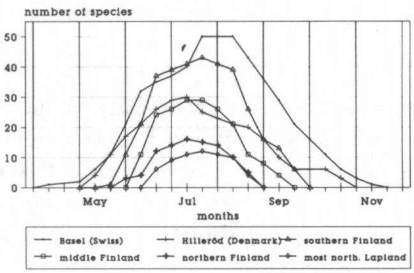

Fig. 1. Number of species during flight period in several European regions (redrawn and modified from Valle, 1938, with datas from Wesenberg-Lund, 1913 and Portmann, 1921).

with the maximal number of species shifts from the early or mid July to early August ; — (4) duration of flying season of a certain species normally is longer, but sometimes, in particular in species with more northern headquarters (e.g. the eurosibiric *C. hastulatum* and *C. armatum*), flight period is shortened in the south (Table II).

Table II

Coenagrion hastulatum : duration of flight periods (in weeks) in different parts of its distributions area ; after (1) Valle, 1938, (2) Wesenberg-Lund, 1913, (3) Schmidt, 1964, (4) original (this work) and (5) Maibach & Meier, 1987

Coenagrion hastulatum	Finland (1)	Denmark (1, 2) N. Germany (3)	Black Forest (4) Swiss (5)
duration of flight periodd	12	10-8	8-6

Seasonal regulation of development appears to be very complex. It is achieved by different diapause characteristics in the penultimate and final instar, distinct responses to critical daylength (which causes diapause) and/or temperature thresholds (within a certain species-specific extent) in the different instars (cf. Corbet, 1957a, 1962 ; Lutz, 1968 ; Norling, 1971, 1984a, b) and is influenced to some extent also by competitive interactions (e.g. Lawton *et al.*, 1980 ; Baker, 1986, 1987). As in many insects (cf. Beck, 1980), the photoperiodic responses of dragonfly populations form different latitudes are supposed to be genetically adapted to the average local conditions (Norling, 1984a, b) so that emergence and sexual maturation are synchronized (Corbet, 1962).

In general, habitat generalists in dragonflies tend to have somewhat longer flight seasons than the less widespread species (Crowley & Johnson, 1982a) and flight period of a certain species is shorter at the periphery of its range than in the center, which can only partly be attributed to climatic factors. Other reasons presumbably are the changed competitive relationships, as can be illustrated in *A. juncea.* In the Black Forest (Baden-Württemberg, FRG) it mainly breeds in bogs, where the only co-occuring aeshnids are *A. subarctica* and *A. cyanea.* But due to autecological factors these species are too rare (Sternberg, 1985) to be serious rivals to *A. juncea,* so that *A. juncea* is able to enlarge its flight period up to 16 weeks in the Black Forest; on the other hand competition by other dragonflies, especially Anisoptera, is much greater in other parts of *A. juncea's* range, which probably leads to temporal niche specializations with a shorter flight period in *A. juncea* in Finland and Denmark/northern Germany (Table III). Cannings *et al.* (1980) stated that a lack of congeneric species (i.e., *Lestes* sp.) results in a loss of synchrony in the emergence period relative to emergence patterns where congeneric species occur.

Table III

Aeshna juncea : duration of flight periods (in weeks) and number of co-occuring frequent dragonflies in different parts of its distributions area; after (1) Valle, 1938, (2) Wesenberg-Lund, 1923, (3) Schmidt, 1964, (4) original (this work) and (5) Maibach & Meier, 1987

Aeshna juncea	Finland (1)	Denmark (1, 2) N. Germany (3)	Black Forest (4) Swiss (5)
duration of flight period	12	6-8	16
number of other frequent anisopteran species	?	about 7	0-2
number of other frequent aeshnids	1-2	3	0
number of frequent zygopteran species	4-6	3-4	0

Within dragonfly communities seasonal segregation probably reduces competition among dominant species, but habitat specialization may be more important among less abundant species (cf. for larvae Johnson & Crowley, 1980). Temporal separation occurs in species with similar microhabitats (cf. for larvae Benke & Benke, 1975). Seasonality and diurnal flight rhythms of dragonfly species depend on the activity of the adult dragonflies are often closely correlated with air temperature and intensity of solar radiation (e.g. Lutz & Pittman, 1970; May, 1977). There are also some indications that responses of adult dragonflies to temperature are age-dependent what should effect temporal separation of immatures and matures due to different diurnal flight rhythms.

Besides other characteristics (e.g. May 1976), thermal demands of certain dragonfly species can be recognized by the ambient temperature at takeoff with increasing temperature in the early morning. In figure 3 some experimental temperatures at takeoff (upper end of histograms) of several species and in both sexes are shown, if adult dragonflies were illuminated by a lamp. Three remarkable differences can be outlined here: — (1) between myothermic species (*Aeshna mixta, A. caerulea, A. cyanea, A. juncea* and *Somatochlora arctica* which all are mostly endothermic and which heat up by rapid contractions of the wing muscles ('wing-whirring')) and (mostly) heliothermic species (*Sympetrum danae, S. striolatum* and *S. sanguineum* which are mostly exothermic because in sunlight they warm up by their choice of a resting site and by their posture), — (2) between species and — (3) between sexes. It is suggested that differences between species and sexes are caused to some extent by different body colours (STERNBERG, 1990).

The lower temperature thresholds at takeoff in the mostly heliothermic *Sympetrum*-species probably results from maximizing of heat input due to special basking behaviour which cannot be found in the myothermic species.

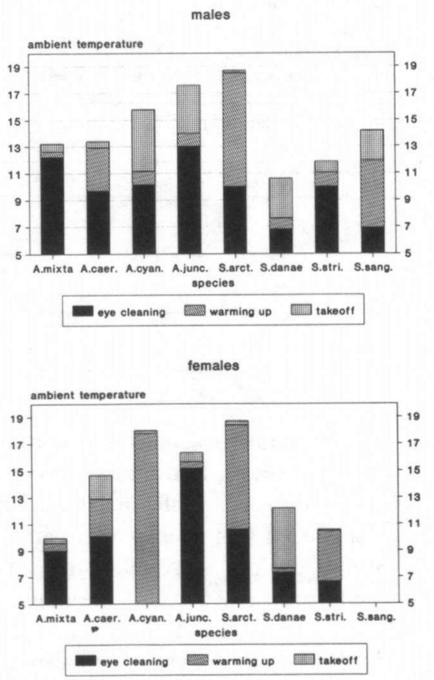

Fig. 2. Takeoff-experiments : ambient temperatures (in °C) at which males (above) and females (below) show one of three behaviour-patterns while ambient temperatures rise from 2° to 20° ; in becoming active, all dragonflies first show eye-cleaning-behaviour, then warming-up-behaviour, i.e. wing-whirring in myothermic species and raising the abdomen to maximize exposure to the lamp in heliothermic dragonflies, and then takeoff (from STERNBERG, 1990, slightly modified).

However, in a given locality, myothermic species remain active at lower temperatures than heliothermic species. The myothermic species usually remain constantly on the wings during the whole day and therefore are called 'fliers' (cf. CORBET, 1962). They are able to maintain their body temperature at a high level even at low air temperatures and are quite independent from intensity of solar radiation so they are able to become crepuscular or even nocturnal, known from the European *Aeshna cyanea, A. grandis, A. viridis* (HAMM, 1900 ; TÜMPEL, 1901 ; TIMM, 1902) and *A. juncea* (STERNBERG, unpublished) and many species of the tropics (cf. CORBET, 1962) while the heliothermic 'perchers' (cf. CORBET, 1962) are usually diunral.

Different temperature thresholds at takeoff indicate distinct adaptions to different temperature conditions in different climates and/or different seasons. Species with lower ambient temperature thresholds at takeoff are, on the one hand, able to be active earlier in the morning, maintain activity later in late afternoon or even in the evening than species which fly only at higher ambient temperatures. Or they are on their wings even at cooler days when the species with higher thermal demands are more or less inactive. Cold adapted species, on the other hand, normally do not tolerate higher temperatures, so their activity decreases or even ceases during hot hours at very hot days when the more thermophilic species still remain active. Lower temperature thresholds also enable species to live in colder microhabitats or in thermal more inmoderate environments in higher latitudes and altitudes. Thus, different temperature thresholds lead to temporal and/or spatial (micro- or macro-) segregation of species, what can be demonstrated in the *Crocothemis erythraea* and *Orthetrum cancellatum.*

In southern Germany (e.g. near Freiburg, Baden-Württemberg) the Mediterranean *C. erythraea* and the more northernly distributed *O. cancellatum* cooccur at some ponds, whereby different thermal thresholds in the two species could be confirmed (STERNBERG, 1989). This, on the one hand, causes a certain degree of diurnal segregation of two libellulid species which are rivals to some extent, e.g. on warm summer days *O. cancellatum* often is seen to be the first of the two species at the site in the morning, but is less active or even disappears during very hot hours at noon, occuring again late in the afternoon (Fig. 3d) ; on cooler days *O. cancellatum* is active during the whole day (Fig. 3b). In contrast, *C. erythraea* is less active or even inactive during cooler days (Fig. 3a), but on hot days it maintains its activity during midday (Fig. 3c). On the other hand, males of *C. erythraea* only were found in distinct parts of shore where the temperature exceeds 20°C (Fig. 3a). The lowest temperature threshold in males of *O. cancellatum* is about 16°C, so they occur in the cooler parts of shore but they disappear if the temperature rises to more than about 27°C (Fig. 3b, d). Thus, different temperature thresholds also cause a spatial separation (STERNBERG, 1989).

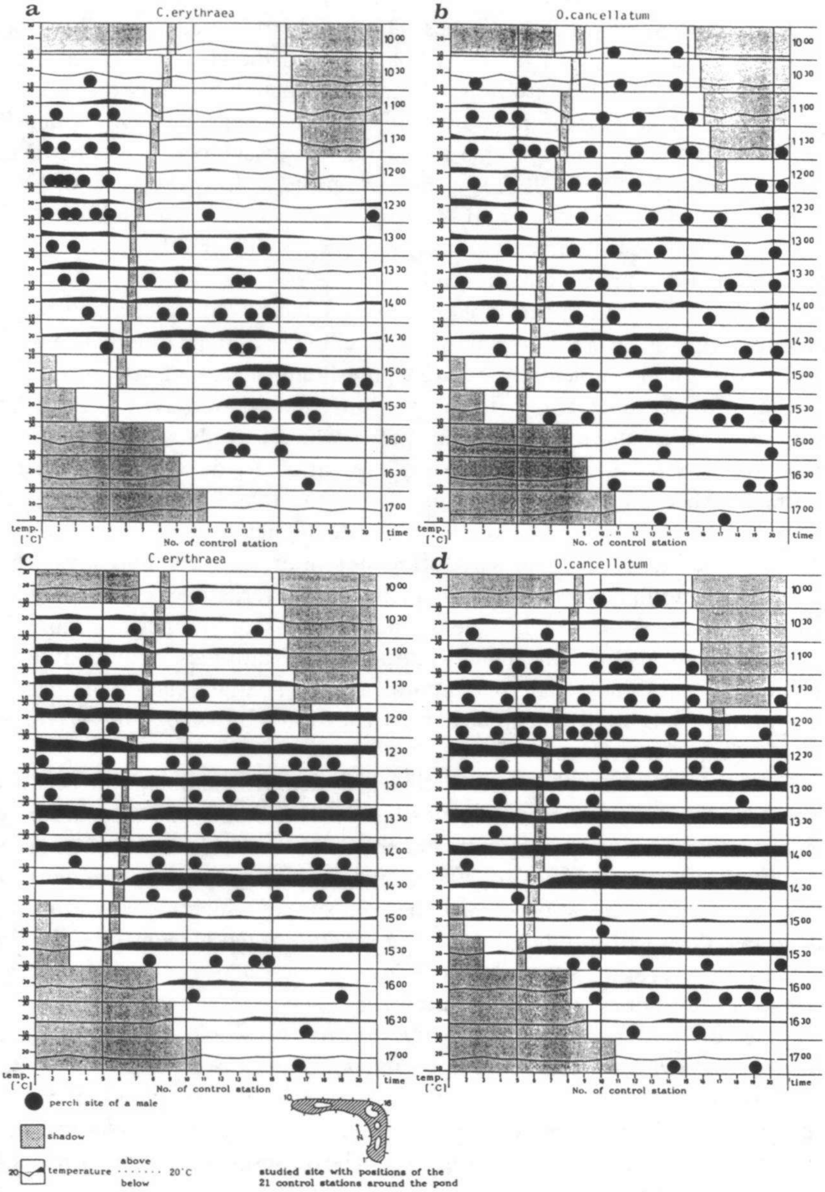

Fig. 3. Distribution of perch sites of males of *Crocothemis erythraea* (a, c) and *Orthetrum cancellatum* (b, d) and temperatures (left ordinate) in intervals of 1/2 h between 10 a.m. and 5 p.m. (right ordinate) at 21 control stations (abscissa) around the pond ; a, b : cool day ; c, d : hot day (from STERNBERG, 1989, slighty modified).

SPATIAL NICHE SPECIALIZATION

Different types of habitats are inhabited by different dragonfly species. This spatial niche specialization is well known and one of the best studied niche axes. Spatial segregation is mainly restricted to the habitat (in a more general sense) and — as a more refined type of habitat selection — to the female's oviposition sites and the male's perching sites. Only selected investigations about this subject can be represented here examplarily.

A linear distribution of closely related species could be found at flowing waters (BUCHWALD, 1988) : *Cordulegaster bidentata* settles at more or less shaded headwaters and wooded spring outlets, whereas *C. boltonii* (normally) inhabits the sunnier and lower parts of rivulets and streams (Fig. 4).

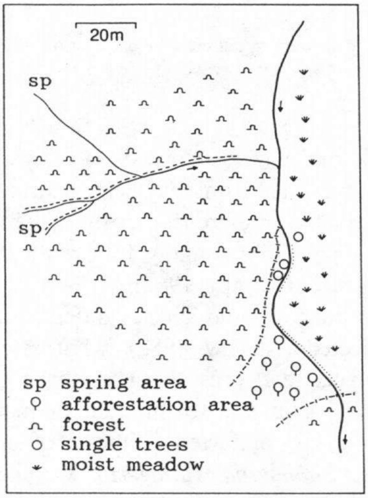

Fig. 4. Linear distribution of *Cordulegaster bidentata* (---) at the upper and of *C. boltonii* (...) at the lower part of a reverine system and in different vegetation units (southern Black Forest, Baden-Württemberg, FRG) (from BUCHWALD, 1988, slightly modified).

A two-dimensional distribution pattern is common in species which live at standing waters. For instance, KÖNIG (1990) shows that four species of the genus *Sympetrum* are spatially separated due to different oviposition sites : *S. flaveolum* and *S. sanguineum* mainly deposit their eggs on the flooded areas which dry up in summer, whereas *S. vulgatum* and *S. danae* oviposit over the water surface (Fig. 5). Niche specialization in dragonflies also occur in the third (vertical) dimension : Males of *S. flaveolum* perch lower (0.24 ± 0.15 m) than males of *S. sanguineum* (0.37 ± 0.19 m) but perch height is lower in both *Sympetrum* species in the presence of neighbouring heterospecific males

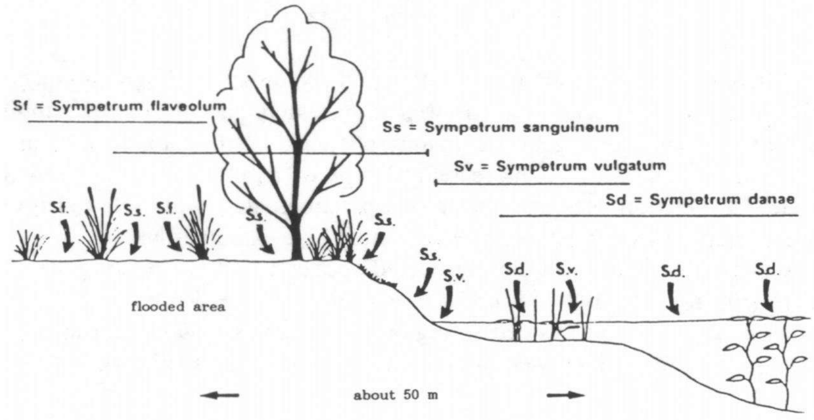

Fig. 5. Two-dimensional distribution patterns in oviposition sites of four *Sympetrum* species, shown in a schematic transect through a gravelpit (from König, 1990, modified).

than with conspecific males (Rehfeldt & Hadrys, 1988). Different heights of perch sites are also recorded from two Central American *Micrathyria*-species by May (1980). Distinctive preferences in the height of perches of members of these both genera probably roughly follow the rule that perch height is proportional to body size (Corbet, 1962).

Adults of several coenagrionid species differ in the mean stem diameters of roosting sites selected (Askew, 1982), what often should lead either to different roosting plants (e.g. grass, rushes, shave-grass) or distinct heights of roosting and resting sites due to different diameters at lower and apical parts of plants stems. The preferred diameter of plants stems is related to the inter-eye distance : *Enallagma cyathigerum* with a larger head width mainly roosts in the mean plant on stems with greater diameters, the small *Ischnura elegans* selects narrower stems than *Enallagma*, while the middle-sized *Coenagrion puella* prefers stems with intermediate diameters (Askew, 1982)

Microhabitat distribution between species probably results from innate species-specific habitat preferences (termed as 'ecoscheme'), which recently have been studied and discussed by Buchwald (1989) and Sternberg (1990), and can be secondarily modified by seasonally-changing (cf. Moore, 1953 ; Kormondy, 1959) and/or by locally-changing pattern of competition (cf. Buchwald, 1989 ; Sternberg, 1990).

Competition can lead to a shift in habitat selection as could be demonstrated in the ecologically related species *Somatochlora alpestris* and *S. arctica*. In a more general and superficial view both species seem to inhabit very similar microhabitats, e.g. if all known habitats of both species are compared in general (Table IV, column 1). Indeed, both species inhabit nearly the same

Table IV

Somatochlora alpestris and *S. arctica* : different (significance levels : * = $p \leq 0.05$; ** = ≤ 0.005) of interspecific (columns 1-3) and intraspecific (columns 4-5) comparisons of breeding site characteristics in allotopic and syntopic occurrences of both species ; numbers in the right most column and numbers of three undermost rows : sums of significant (*) / highly significant (**) differences of each row and column ; the breeding site characteristics are as follows : covering of aquatic moss, covering of aquatic vertical vegetation, covering of free water surface, degree of overgrowth of bottom ground, pond size, height of shore, angle of shore, depth of the pond, height of peat layer at bottom ground, height between lowest and highest water level, drought index (tendency to drought), pH (acidity), conductivity ; abbreviations : m : significances of mean-value-test (t-test, Mann-Whitney-U-test or Fisher's exact-test) ; d : significances of distribution tests (Kolmogorov-Smirnov) (from STERNBERG, 1990).

No. of column		1	2	3	4	5	
occurrence		all waters	alltop.	syntopic	syntop./ allotop.	syntop./ allotop.	
species		*S. alp./ S. arc./*	*S. alp./ S. arc./*	*S. alp./ S. arc./*	*S. alp./ S. alp./*	*S. arc./ S. arc.*	sums of parameter difference
frequency of ponds		156/259	58/161	98/98	58/98	161/98	
vegetation covering	m					*	1/0
	d					*	1/0
moss covering	m			*		**	1/1
	d			*		**	1/1
vertical vegetation	m						0/0
	d						0/0
free water	m					*	1/0
	d					*	1/0
ground overgrow	m			**	*		1/1
	d			*			1/0
pond size	m			*		*	2/0
	d		*	**		**	1/2
shore height	m			*		*	2/0
	d				*	*	2/0
shore angle	m					*	1/0
	d					*	1/0
pond depth	m	*		*		*	3/0
	d	*		*			2/0
peat height	m						0/0
	d						0/0
water level	m			*			1/0
	d			*			1/0
drought index	m			*		*	2/0
	d			*			1/0
pH	m					*	1/0
	d				**	**	0/2
conductivity	m	*					1/0
	d			*			1/0
sums of difference	m	2/0	0/0	6/1	1/0	8/1	
	d	1/0	1/0	6/1	1/1	4/3	
total sums of parameter differences		3/0	1/0	12/2	2/1	12/4	

habitat range and niche overlap is very great, if only one of these both species lives in a biotope (allotopic occurrence) (Table IV, column 2). But if both species co-occur (syntopic occurrence), a significant niche specialization occurs (Table IV, column 3) due to a dramatical habitat shift in *S. arctica*, whereas *S. alpestris* settles nearly the same habitat types as in allotopic occurrences, what can be confirmed if syntopic and allotopic occurrences within each species are compared (Table IV, column 4, 5). This indicates that the competitively weaker *S. arctica* have to withdraw into habitats which are less appropriate and which rather would be avoided if the rival *S. alpestris* is absent (for further details see STERNBERG, 1990). Further observations and investigations suggest that habitat spezialization in these two species (especially in *S. arctica*) is not due to outcompeting of larvae but due to aggressive interactions between the adults.

NICHE SPECIALIZATIONS IN LARVAE

COMPETITION AND LIFE-HISTORIES

Interspecific and intraspecific competition for space and food probably has been necessitated adaptations in functional morphology, ethology (CORBET, 1962) and development phenology which all leads to a great adaptive radiation within larval Odonata. For example, the environment of the boreo-alpine distributed *S. alpestris* is characterized by short summers and high risks due to sudden weather changes. Therefore, it may be high of adaptive value that with proceeding season the proportion of diapause eggs of each clutch increases from 0% in July up to 37% in September (Fig. 6) and the time of egg development decreases from 40 days in July to less than 20 days in September, whereas in *S. arctica* and *L. dubia* developmental time is (nearly) constant (Fig. 7). It is suggested that the developmental rate and proportion of diapause-eggs

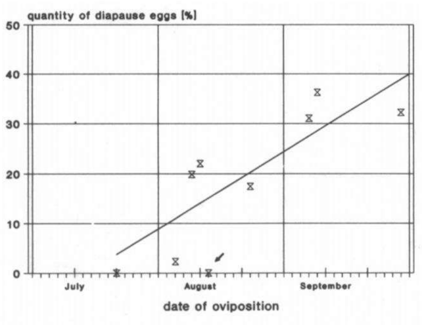

Fig. 6. Proportion of diapause eggs in females of *Somatochlora alpestris*, which were caught on different dates ; notice the value for the "special female" below the arrow which was very young an whose clutch contained no diapause eggs at all, what is quite unusual in mid August (from STERNBERG, 1990, slightly modified).

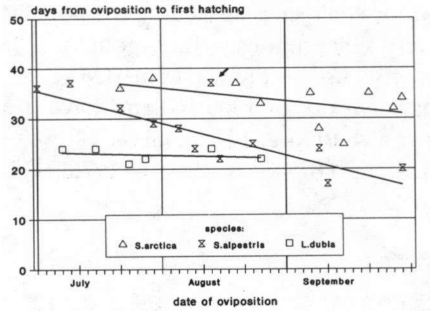

Fig. 7. *Somatochlora arctica, S. alpestris* and *Leucorrhinia dubia*: hatching begin (in days) of nondiapause eggs laid on different dates after development at 16°C; in *S. alpestris* notice the value of the "special female" below the arrow eggs needed exceptionnally long time for development, which is the same as in eggs laid 6 weeks earlier (cf. also Fig. 6) (from Sternberg, 1990, slightly modified).

in *S. alpestris* possibly depend on the age of the female (for further details see Sternberg, 1990).

Different environmental conditions may lead to distinct ecological types. Thus it is suggested that in adaptation to different ecological circumstances populations of *A. juncea* evolved different development patterns in the Alps than in the Black Forest: The larvae of alpine populations only need 12 instars until completion of their development; diapause development (always ?) occur in the 8th and 12th instar and lasts 259 to 302 days (Robert, 1959). Nearly 71% of all larvae of Black Forest-populations complete their development not before the 16th and about 29% not before the 17th instar. Duration of most instars varies within a wide range (Fig. 8) and leads to an asynchrony in larval development, what is one reason for the long flight period in the Black Forest. Diapause development is absent in most cases, and if it occurs sometimes, duration is not longer than 100 days (Fig. 8) (Sternberg, 1990).

Interesting observations on an asymmetric competition are given by Gribbin & Thompson (1990). Small, younger larvae of *Ischnura elegans* develop quicklier, but their rate of increase is significantly smaller if they co-occur with large conspecific larvae, while development of the latter is 'normal' (compared with development phenology of larvae of only one age or size). The cost of this accelerated development is that the 'speeded up' younger larvae produce smaller adults. This is of some sociobiological relevance because, on the one hand, reproductive success depends directly not on the body size but on the length of reproductive lifespan; on the other hand, large adults survive for longer than small adults, thus, selection should favour large size in females (e.g. Fincke, 1982; Banks & Thompson, 1985, 1987a).

High densities of larvae raise the question of interspecific and intraspecific interactions and niche specialization. Corbet (1957b) recorded a severe intraspecific competition for emergence space in a big population of *Anax imperator* which emerge very synchronously. In Zygoptera (*Pyrrhosoma nymphula*) larval densities can rise up to 1400 ind./m² (MACAN, 1964) and in larval Anisoptera maximal densities of 1300 ind./m² have been recorded for *Celithemis fasciata* (BENKE & BENKE, 1975) ; larvae of both suborders may reach numbers of 1700 ind./m² (BENKE & BENKE, 1975). Odonate standing stock

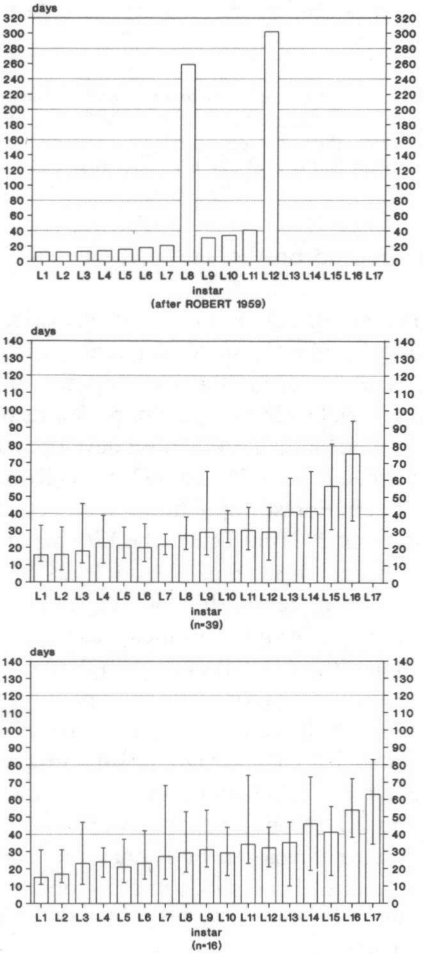

Fig. 8. *Aeshna juncea* : developmental phenology of larvae from the Alps (above) (after ROBERT, 1959) and the Black Forest where larvae either need 16 (middle) or 17 (below) instars for completion of development ; abscissa, number of larval instars ; ordinate, duration of instars (redrawn and modified from STERNBERG, 1990).

biomass was often 2-3 times as high as the biomass of their prey (Benke, 1976) which yields a strong competition in food (see e.g. Merril & Johnson, 1984).

One way of minimizing competition in such situations may be temporal separation, as could be confirmed in larvae of the co-occurring *Lestes barbarus* and *L. virens* (Carchini & Nicolai, 1984 ; cf. also Johnson & Crowley, 1980 ; Johnson *et al.*, 1980 ; Crowley *et al.*, 1987a). In *L. barbarus* egg development is quicker than in *L. virens*, and first-instar larvae of *L. barbarus* presumably occur eight weeks earlier (in January) than larvae of *L. virens*, whose egg-hatching takes place in early April. Due to this displaced life cycle larvae of *L. barbarus* are always significantly larger than larvae of *L. virens* at any given time (Fig. 9). In general, diet of larvae of both species is nearly identical, but it is affected conspicuously with larval age and size because the prey of each instar is proportional to its size (cf. also Chutter, 1961). Thus it is suggested that differences in the timing of life cycles produces size differences between the coexisting *Lestes* larvae, reduces interspecific food competition and leads to a food-resource partitioning, all of which probably faciliates coexistence of both species. So, conspecific and/or hetero-specific food competition can be reduced by changes in diet during larval development. Thompson (1978a), Shelly (1981), Merril & Johnson (1984) and Blois (1985) showed positive correlations between predator size and prey size of certain dragonfly species and/or species-specific or size-specific dietary spezializations. The latter is accurately recorded by Dombrowski (1989), who showed an alteration in selectivity of prey species at different stages of development (i.e., *Cordulegaster bidentata*, cf. Fig. 10). In contrast, in other species

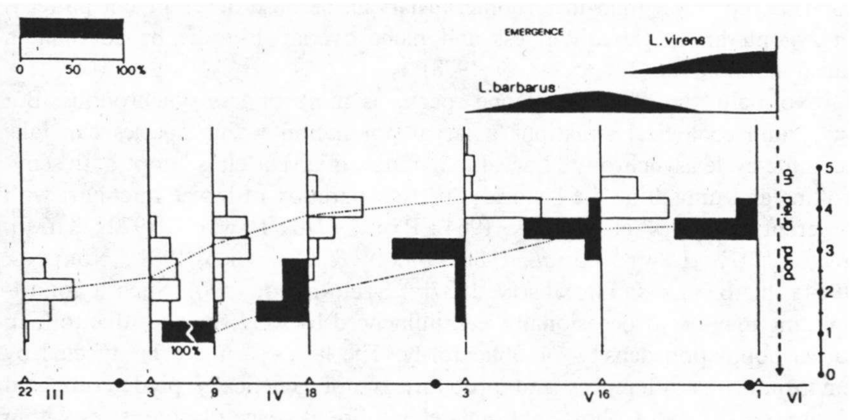

Fig. 9. Growth of *Lestes virens* and *L. barbarus* : dark histograms, *L. virens* ; white histograms, *L. barbarus* ; dashed line, mean larval sizes in each sample ; abscissa, relative frequencies per sample ; ordinate, head width in mm ; emergence, semi-quantitative description (after Carchini & Nicolai, 1984).

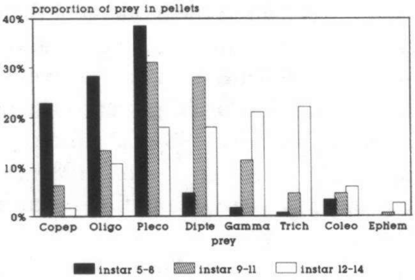

Fig. 10. *Cordulegaster bidentata*: larvae of different age prefer distinct prey species (found in feacal pellets after Sternberg, in prep.; calculated from Dombrowski, 1989).

there exist considerable dietary niche overlap in different sized coexisting larvae because bigger larvae could handle larger prey but still ate small prey as well (Thompson, 1978b; Merril & Johnson, 1984).

Spatial niche specialization also would minimize interspecific food competition, and the same mechanism may also reduce intraspecific food competition. The latter reduction is necessary if conspecific and heterospecific larvae of different ages occur in high densities, if prey spectrum is similar in many (or all) larval size classes and/or if food-resources are limited. Spatial separation is possible by their vertical and horizontal habitat separation (e.g. Robert, 1959; Huggins & Dubois, 1982; cf. also Kormondy, 1959) or if they favour distinct temperatures (Sternberg, 1990).

In larval Zygoptera there may be more potential for interspecific (especially food) competition than in anisopteran larvae, because development patterns in zygopteran species differ less and niche overlap is more broad than in anisopteran larvae (Johannsson, 1978).

Normally the life-cycle of one species is more or less synchronous. But in certain ecological situations a larval population within species can take on a life-cycle asynchrony: Larval individuals in a year-class adopt both semivoltine and univoltine life-histories due to separation of larvae in cohort with different life-cycles (cf. Macan, 1964; Parr, 1970; Lawton, 1972; Kharitonov, 1977; Lawton *et al.*, 1980; Baker & Clifford, 1981; Norling, 1984a, b; Banks & Thompson, 1987b; Sternberg, 1990). Such a cohort-splitting may occur occasionally, e.g. influenced by food shortage due to high larval population density, or obligatorily. The latter seems to be affected by environmental differences and probably is not genetically predeterminated (Norling, 1984a). Cohort-splitting yields a broad range of body sizes within species, which may increase diet niche breadth (Crowley & Johnson, 1982b). This, on the one hand, makes intraspecific and interspecific separation between different age- and size-classes more difficult, but on the other hand intensity of food competition within one age-class is diminished (cf. also NORLING, 1984a). This strategy would be advantageous if resources are limited and/or depletable and if different-sized larvae differ in diet (CROWLEY & JOHNSON, 1982b). Thus asynchrony of larval development in *A. juncea*-populations in bogs of the Black Forest (see above) probably indicates a food limitation in these habitats. Moreover, splitting of larvae in one population into two (or more) cohorts with different growth rates (with the consequence that larvae of different cohorts emerge in different years) enables genetic exchange between populations or generations of different years and also may be seen as one modality of larval 'risk spreading' (cf. STERNBERG, 1990).

PREDATORS AND STRUCTURE OF ODONATE COMMUNITIES

Dragonflies must be seen as polyphagous predators as well as common prey. Intra-odonate predation (cannibalism and mutual predation) can be considered as an extreme expression of interference competition, because killing obviously denies the victim access to resources (CROWLEY *et al.*, 1987a). Biomass of early-emerging dragonflies is mainly limited by prey availability, but early emerging odonates have a highly significant influence on the abundance of smaller, late-emerging odonates due to outcompeting for prey or simply due to predation by large larvae on small larvae. Total biomass of the smaller dragonfly larvae can be reduced significantly (BENKE, 1978 ; BENKE *et al.*, 1982 ; MERRIL & JOHNSON, 1984 ; MORIN, 1984 ; JOHNSON *et al.*, 1985 ; ROBINSON & WELLBORN, 1987 ; WISSINGER, 1987, 1988a, b) but extent of reduction highly depends from population density (e.g. FISCHER, 1961). So larval interactions play an important role in odonate population regulation (e.g. BENKE, 1978) and even may inhibit colonization of smaller species, especially Zygoptera (BENKE *et al.*, 1982 ; MORIN, 1984). Species first colonizing a pond may influence conspicuously the establishment of species that successively arrive. The increase of mutual predation among odonate larvae "may be a more important consequence of seasonal segregation of life histories than reduced 'exploitation' competition due to reduction of dietary niche overlap" (MERRIL & JOHNSON, 1984).

In order to reduce the impact of predators (invertebrates and vertebrates), dragonfly larvae as prey have to evolve 'antipredator defense strategies', i.e. morphological, physiological and behavioural traits (MCPEEK, 1990a). However, these strategies are not universally effective, because an antipredator defense that is effective against one type of predator may be quite ineffective against another type of predator. Prey species and predators only may coexist if the antipredator defenses of the first are effective against the latter, otherwise prey would be outspaced by the predator and distribution of prey would be limited due to predatory (cf. HENRIKSON, 1988).

McPeek (1989, 1990a, b) examined the influences of different antipredator defenses on distributions of *Enallagma*-species among habitats with different sets of predators. One group, with *Enallagma aspersum* and *E. boreale* (and *E. cyathigerum*, whose larvae are morphologically indistinguishable from the latter), are found as larvae only in fishless lakes also containing large active odonate larvae (*Anax junius, Aeshna mutata, Tramea lacerata*) as predators, while the other group, with *E. hageni, E. ebrium, E. vesperum* and *E. geminatum*, is found as larvae only in lakes containing fish (*Lepomis macrochirus, L. gibbosus* (Centrarchidae), *Umbra limi* (Umbridae)), where odonate predators are absent or inabundant. When simultaneously offered *Enallagma*-species of both groups in the laboratory, each of the two predator types (fish, large odonate larvae) imposes much greater mortality on *Enallagma*-species with which they do not coexist than on coexisting *Enallagma*-species (McPeek, 1990b). The *Enallagma*-species generally become less active but differentially altered their behaviour in the presence of the two predators (see Table V). This flexible decrease in activity in the presence of predators is common in other dragonflies (e.g. see Heads, 1985 ; Convey, 1988 ; Dixon & Baker, 1988) and appears to be a short-term response by the *Enallagma*-larvae to decrease the probability of their being detected by an imminently threatening predator. However, larvae of *Enallagma*-species from fishless lakes apparently hardly recognize fish as predators (as agents of natural selection) at all and only respond to the presence of odonate predators (e.g. *Anax*) (McPeek, 1990a).

Table V

Responses between the presence of no predator and presence of *Anax* larvae and/or fish ('bluegill') treatments as reducing (–) or increasing (+) of behavioural aspects or unchanged (.) behaviour for four *Enallagma* species which originate from fishless lakes with dominant anisopteran larvae as predators or from fish-containing lakes where fish is dominant but where aeshnid larvae also occur (after McPeek, 1990a).

Species of the genus *Enallagma* (Zygoptera)	*aspersum* *boreale*		*geminatum* *versperum*	
origin of larvae	fishless lakes with anisopteran larvae		fish-containing lakes with aeshnid larvae	
predator treatment	*Anax*	fish	*Anax*	fish
duration of the inactive period	+	.	+	+
number of abdominal bend	.	–	.	.
number of walks	–	.	–	–
orientation toward prey	–	.	–	–
number and duration of advances toward prey	–	.	–	–
duration of advances toward prey	.	.	–	–
number of prey captured	–	.	–	–

Adult of *Enallagma*-species inhabiting fishless lakes cannot discriminate between fishless and fish-containing lakes and apparently limit their dispersal between lakes by remaining at their natal lakes. Remaining at natal lakes where ecological conditions are relatively stable should be favoured by natural selection because costs of dispersal are potentially high due to high mortality in dispersing *Enallagma*-adults which often settle at lakes of the wrong type. In contrast, *E. ebrium* disperses large numbers of adults away from natal lakes. It is found in winterkill lakes where dramatic ecological changes occur periodically. This causes a permanent change of predator pressure: fish-containing conditions in which fish predators dominate alternate with years of fishless conditions in which large dragonfly predators dominate, because fish populations are periodically reduced to very low numbers or go extinct due to low winter oxygen concentrations. Dispersers of *E. ebrium* may recolonize lakes in which populations of this species have been greatly reduced or become extinct due to an increase of predator pressure, while nondispersers would have difficulty recolonizing these lakes after becoming extinct (McPeek, 1989).

ACKNOWLEDGMENTS

I thank Dr. R. Buchwald for valuable comments on the manuscript and Dr. R. Cassada for careful proofreeding the manuscript.

REFERENCES

Askew, R. R., 1981. Roosting and resting site selection by coenagrionid damselflies. *Adv. Odonatol.* 1 : 1-8.

Baker, R. L., 1986. Effects of density, disturbance, and waste products on growth of larval Enallagma ebrium (Hagen) (Odonata : Coenagrionidae). *Can. Ent.* 118 : 325-328.

Baker, R. L., 1987. Development of Ischnura verticalis (Coenagrionidae : Odonata) : Effects of temperature and prey abundance. *Can. J. Fish. aquatic Sci.* 44 : 1658-1661.

Banks, M. J. & D. J. Tompson, 1985. Emergence, longevity and breeding area fidelity in Coenagrion puella. *Anim. Behav.* 33 : 1175-1183.

Banks, M. J. & D. J. Tompson, 1987a. Lifetime reproductive success of females of the damselfly Coenagrion puella. *J. Anim. Ecol.* 56 : 815-832.

Banks, M. J. & D. J. Tompson, 1987b. Regulation of damselfly populations : the effects of larval density on larval survival, development rate and size in the field. *Freshw. Biol.* 17 : 357-366.

Beck, S. D., 1980. *Insect photoperiodism.* Academic Press, New York.

Benke, A. C., 1976. Dragonfly production and prey turnover. *Ecology* 57 : 915-927.

Benke, A. C., 1978. Interactions among coexisting predators — a field experiment with dragonfly larvae. *J. anim. Ecol.* 47 : 335-350.

Benke, A. C. & S. S. Benke, 1975. Comparative dynamics and life histories of co-existing dragonfly populations. *Ecology* 56 : 302-317.

Benke, A. C., P. H. Crowley & D. M. Johnson, 1982. Interactions among coexisting larval Odonata : An in situ experiment using small enclosures. *Hydrobiologia* 94 : 121-130.

Blois, C., 1985. The larval diet of three anisopteren (Odonata) species. *Freshw. Biol.* 15 : 505-514.

Buchwald, R., 1988. Die gestreifte Quelljungfer Cordulegaster bidentatus (Odonata) in Südwestdeutschland. *Carolinea* 46 : 49-64.

Buchwald, R., 1989. Die Bedeutung der Vegetation für die Habitatbindung einiger Libellenarten der Quellmoore und Fließgewässer. *Phytocoenologia* 17 (3) : 307-448.

Cannings, R. A., S. G. Cannings & R. J. Cannings, 1980. The distribution of the genus Lestes in a saline lake series in Central British Columbia, Canada (Zygoptera : Lestidae). *Odonatologica* 9 : 19-28.

Carchini, G. & P. Nicolai, 1984. Food and time resource partitioning in two coexisting Lestes species (Zygoptera : Lestidae). *Odonatologica* 13 : 461-466.

Chutter, F. M., 1961. Certain aspects of the morphology and ecology of the nymphs of several species of Pseudagrion Sélys (Odonata). *Arch. Hydrobiol.* 57 : 430-463.

Convey, P., 1988. Competition for perches between larval damselflies : The influence of perch use on feeding efficiency, growth rate and predator avoidance. *Freshw. Biol.* 19 : 15-28.

Corbet, P. S., 1957a. The life histories of two summer species of dragonflies (Odonata Coenagrionidae). *Proc. zool. Soc. Lond.* 128 : 403-418.

Corbet, P. S., 1957b. The life history of the Emperor Dragonfly Anax imperator Leach (Odonata : Ansioptera). *J. Anim. Ecol.* 26 : 1-69.

Corbet, P. S., 1962. *A biology of dragonflies.* Witherby, London.

Crowley, P. H. & D. M. Johnson, 1982a. Co-occurrence of Odonata in the eastern United States. *Adv. Odonatol.* 1 : 15-37.

Crowley, P. H. & D. M. Johnson, 1982b. Habitat and seasonality as niche axes in an odonate community. *Ecology* 63 ; 1064-1077.

Crowley, P. H., P. M. Dillon, D. M. Johnson & C. N. Watson, 1987a. Intraspecific interference among larvae in a semivoltine dragonfly population. *Oecologia* 71 : 447-456.

Dixon, S. M. & R. L. Baker, 1988. Effects of size on predation risk, behavioural response to fish, and cost of reduced feeding in larval Ischnura verticalis (Coenagrionidae : Odonata). *Oecologia* 76 : 200-205.

Dombrowski, A., 1989. *Ökologische Untersuchungen an Cordulegaster bidentatus* Sélys, 1843. Dipl.-Arbeit Univ. Göttingen.

Fincke, O. M., 1982. Lifetime mating success in a natural population of the damselfly Enallagma hageni (Walsh) (Odonata : Coenagrionidae). *Behav. Ecol. Sociobiol.* 18 : 405-412.

Fischer, Z., 1961. Cannibalism among the larvae of the dragonfly Lestes nympha Sélys. *Ekol. pol.* (B) 4 : 304-309.

Gribbin, S. D. & D. J. Thompson, 1990. Asymmetric intraspecific competition among larvae of the damselfly Ischnura elegans (Zygoptera : Coenagrionidae). *Ecol. ent.* 15 (1) : 37-42.

Hamm, A., 1900. Aeschna grandis on the wing at dusk. *Entomologist* 33 : 88-89.

Heads, P. A., 1985. The effect of invertebrate and vertebrate predators on the foraging movements of Ischnura elegans larvae (Odonata : Zygoptera). *Freshw. Biol.* 15 : 559-571.

Henrikson, B. I., 1988. The absence of antipredator behaviour in the larvae of Leucorrhinia dubia (Odonata) and the consequence for their distribution. *Oikos* 51 : 179-183.

Huggins, D. G. & M. B. DuBois, 1982. Factors influencing microdistribution of two species of burrowing dragonfly larvae, with notes on their biology (Anisoptera : Gomphidae). *Odonatologica* 11 : 1-14.

Johannsson, O. E., 1978. Co-existence of larval Zygoptera (Odonata) common to the Norfolk Broads (U.K.). *Oecologia* 32 : 303-321.

Johnson, D. M. & P. H. Crowley, 1980. Habitat and seasonal segregation among coexisting Odonata larvae. Odonatologica 9 : 297-308.

Johnson, D. M., C. C. Coney & M. J. Westfall, 1980. The Odonata of Bays Mountain Park., Sullivan County, Tennessee. *J. Tenn. Acad. Sci.* 55 : 73-76.

Johnson, D. M., P. H. Crowley, R. E. Bohanan, C. N. Watson & T. H. Martin, 1985. Competition among larval dragonflies : A field enclosure experiment. *Ecology* 66 : 119-128.

König, A., 1990. Ökologische Einnischungsstategien von vier Arten der Gattung Sympetrum (Anisoptera : Libellulidae). *Libellula* 9 (1/2) : 1-11.

Kormondy, E. J., 1959. The systematics of Tetragoneuria, based on ecological life history, and morphological evidence (Odonata : Corduliidae). *Misc. Publs Mus. Zool. Univ. Mich.* 107 : 1-79.

Leggott, M. & G. Pritchard, 1986. Thermal preference and activity thresholds in populations of Argia vivida (Odonata : Coenagrionidae from habitats with different thermal regimes. *Hydrobiologia* 140 : 85-92.

Lutz, P. E., 1968. Effects of temperature and photoperiod on the larval development in Lestes eurinus (Odonata : Lestidae). *Ecology* 49 : 637-644.

Lutz, P. E. & R. Pittman, 1970. Some ecological factors influencing a community of adult Odonata. *Ecology* 51 : 279-284.

Macan, T. T., 1964. The Odonata of a moorland fishpond. *Int. Revue ges. Hydrobiol.* 49 (2) : 325-360.

Maibach, A. & C. Meier, 1987. Verbreitungsatlas der Libellen der Schweiz (Odonata) (mit Roter Liste). *Doc. faun. hel.* 4 : 1-30.

May, M. L., 1976. Thermoregulation and adaption to temperature in dragonflies (Odonata : Anisoptera). *Ecol. Monogr.* 46 : 1-32.

May, M. L., 1977. Thermoregulation and reproductive activity in tropical dragonflies on the genus Micrathyria. *Ecology* 58 : 787-798.

May, M. L., 1978. Thermal adaptions in dragonflies. *Odonatologica* 7 : 27-47.

May, M. L., 1980. Temporal activity patterns of Micrathyria in Central America (Anisoptera : Libellulidae). *Odonatologica* 9 : 57-74.

McPeek, M. A., 1989. Differential dispersal tendencies among Enallagma damselflies (Odonata) inhabiting different habitats. *Oikos* 56 (2) : 187-195.

McPeek, M. A., 1990a. Behavioral differences between Enallagma species (Odonata) influencing differential vulnerability to predators. *Ecology* 71 (5) : 1714-1726.

McPeek, M. A., 1990b. Determination of species composition in the Enallagma damselfly assemblages of permanent lakes. *Ecology* 71(1) : 93-98.

Merril, R. J. & D. M. Johnson, 1984. Dietary niche overlap and mutual predation among coexisting larval Anisoptera. *Odonatologica* 13 : 387-406.

Morin, P. J., 1984. Odonate guild composition : Experiments with colonization history and fish predation. *Ecology* 65 (5) : 1866-1873.

Norling, U., 1971. The life history and seasonal regulation of Aeshna viridis Eversem. in southern Sweden (Odonata). *Ent. scand.* 2 : 170-190.

Norling, U., 1984a. The life cycle and larval photoperiodic responses of Coenagrion hastulatum (Charpentier) in two climatically different areas (Zygoptera : Coenagrionidae). *Odonatologica* 13 : 429-449.

NORLING, U., 1984b. Photoperiodic control of larval development in Leucorrhinia dubia (Vander Linden) : A comparison between populations from northern and southern Sweden (Anisoptera : Libellulidae). *Odonatologica* 13 : 529-550.

PIANKA, E. R., 1973. The structure of lizard communities. *Ecol. Syst.* 4 : 53-74.

PLATTNER, H., 1965. Betrachtungen über die Flugzeiten der Odonaten in Südsiebenbürgen (SR Rumänien). *Faun. Abh. Mus. Tierk. Dresden* 6 (20) : 231-238.

PORTMANN, A., 1921. *Die Odonaten der Umgebung von Basel. Beitrag zur biologischen Systematik der mitteleuropäischen Libellen.* Inaug.-Diss. Univ. Basel.

REHFELDT, G. E. & H. HADRYS, 1988. Interspecific competition in sympatric Sympetrum sangiuneum (Müller) and S. flaveolum (L.) (Anisoptera : Libellulidae). *Odonatologica* 17 : 213-225.

ROBERT, P.-A., 1959. *Die Libellen (Odonaten).* Kümmerly & Frey ; Bern.

ROBINSON, J. V. & G. A. WELLBORN, 1987. Mutual predation in assembled communities of odonate species. *Ecology* 68 : 921-927.

RÜPPELL, G., R. RUDOLPH & H. HADRYS, 1987. Argia moesta (Coenagrionidae) — Verhalten bei der Eiablage in der Gruppe. *Publ. Wiss. Film*, Sekt. Biol. (19) Nr. 20 : 1-9.

SCHMIDT, E. 1964. Biologisch ökologische Untersuchungen an Hochmoorlibellen (Odonata). *Z. wiss. Zool.* 169 (3-4) : 313-386.

SCHOENER, T. W., 1974. Recource partitioning in ecological communities. *Science* 185 : 27-39.

SHELLY, T. E., 1981. Selective predation by nymphs of the dragonfly Paltothemis lineatus Karsch. Program Abstr. 29th An. Meet. N. Am. Benthol. Soc. p. 56.

STERNBERG, K., 1985. *Zur Biologie und Ökologie von sechs Hochmoorlibellenarten des südlichen Hochschwarzwaldes.* Dipl-Arb. Univ. Freiburg.

STERNBERG, K., 1989. Beobachtungen an der Feuerlibelle (Crocothemis erythraea) bei Freiburg im Breisgau (Odonata : Libellulidae). *Veröff. Nat-Schutz Landschaftspfl. Bad.-Württ.* 64/65 : 237-254.

STERNBERG, K., 1990. *Autökologie von sechs Libellenarten der Moore und Hochmoore des Schwarzwaldes und Ursachen ihrer Moorbindung.* Inaug.-Diss. Univ. Freiburg.

THOMPSON, D. J., 1978a. The natural prey of larvae of the damselfly Ischnura elegans (Odonata : Zygoptera). *Freshw. Biol.* 8 : 377-384.

THOMPSON, D. J., 1978b. Prey size selection by larvae of the damselfly, Ischnura elegans. *J. Anim. Ecol.* 47 : 769-785.

TIMM, W., 1902. Dämmerungsflieger unter den einheimischen Libellen. Insektenbörse 19 : 180.

TÜMPEL, R., 1901. *Die Geradflügler Mitteleuropas.* Wickens, Eisenach.

VALLE, K. J., 1938. Zur Ökologie der finnischen Odonaten. *Ann. Univ. turku.* (A) 4 (5) : 1-76.

WESENBERG-LUND, 1913. Odonaten-Studien. *Int. Revue ges. Hydrobiol. Hydrograph* 6 : 155-422.

WISSINGER, S. A., 1987. Predation between anisopteran and zygopteren larvae and its effect on the remainder of the prey communuty in experimental ponds. *Bull. N. Am. benthol. Soc.* 4 (1) : 71 [Abstract].

WISSINGER, S. A., 1988a. Effects of food availability on larval development and interinstar predation among larvae of Libellula lydia and Libellula luctuosa (Odonata : Anisoptera). *Can. J. Zool.*, 66 : 543-549.

WISSINGER, S. A., 1988b. Comparative population ecology of the dragonflies Libellula lydia and Libellula luctuosa. *Can. J. Zool.*, 67 : 931-936.