

## CO-OCCURRENCE OF ODONATA IN THE EASTERN UNITED STATES

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The structure and dynamics of individual ecological communities reflect the frequency and intensity of interactions on a regional scale among populations mixed by dispersal. We therefore characterize and compare the distributions of 37 broadly sympatric odonate species across 201 aquatic sites in the Eastern United States to investigate these regional interactions. Since the 37 species all co-occur at a relatively well-studied site (Bays Mountain Park, Sullivan County, Tennessee USA), we are able to relate life-history characteristics and within-site distribution across habitats to between-site habitat use.

A series of statistical tests based on the chi-square statistic is used to assess the distributions of the species across broad habitat categories (stream, river, pond, lake) and the pairwise associations of species across all sites. In the 43 best-studied sites, 25.6 odonate species co-occurred on average, considerably more than would be expected if the species were distributed randomly across sites. Species occupying relatively many of the study sites tended to co-occur with fewer species per site and to have somewhat longer flight seasons than the less widespread species. Those species that were more uniformly distributed across site-habitat categories tended to occupy more total sites but did not appear to have longer flight seasons or lower co-occurrence frequencies. Negative associations of species pairs were relatively rare, perhaps because competitive exclusion is uncommon among odonates; some possible exceptions merit additional study, such as *Enallagma civile* vs *Lestes vigilax*. Niche complementarity is not apparent between species, but different degrees of specialization within vs between sites may be conspicuous in individual species like the local habitat specialists at Bays Mountain Park (*Plathemis lydia*, *Ischnura posita* and *I. verticalis*).

### INTRODUCTION

Much recent ecological research has focused on individual invert-

ébrate communities, particularly studies of insects (e.g. DAVIDSON 1980; GREENFIELD & KARANDINOS 1979; FOX & MORROW 1981) and other arthropods (e.g. ROBINSON 1981; BELL 1980, and several chapters in KERFOOT 1980). Though much has been learned and considerably more remains to be learned from this approach, the structure and dynamics of such spatially defined biological systems may often depend on interactions with other systems via dispersal of organisms or propagules (CROWLEY 1981; VANDERMEER et al. 1980; VAN DER MEIJDEN 1979). Thus it may also be important to consider the regional distribution of the metapopulations composed of partly mixed conspecific populations from neighboring communities. (In this paper the term "species" is used to refer to these metapopulations and "population" refers to the conspecific assemblage within a single community.) Species that co-occur regionally (sympatry) may or may not tend to co-occur within communities (syntopy); the frequency of syntopic co-occurrence may help to illuminate underlying mechanisms of local interaction and distribution. Since the rates and directions of both ecological responses (e.g. ecological shift – MACARTHUR & WILSON 1967) and evolutionary responses (e.g. character displacement - BROWN & WILSON 1956) to other species are clearly related to the frequency with which they encounter each other in nature (see HURLBERT 1978; CROWLEY & JOHNSON 1982), co-occurrence is often more appropriately quantified by an index of encounter frequency than by more esoteric indices of association (e.g. BARONI-URBANI & BUSER 1976; BARONI-URBANI 1980; PIELOU 1977).

A relatively well studied, stream fed, lake-pond community at Bays Mountain Park, Sullivan County Tennessee USA contains populations of about 46 odonate species (JOHNSON et al. 1980; JOHNSON & CROWLEY 1980a), most of which are widely distributed across the eastern United States. Knowing that these species can co-occur, we wondered how frequently they do so and in what types of aquatic systems. We are particularly concerned in this paper with evaluating four hypotheses about the habitat distributions and life histories of these odonate species – hypotheses suggested by ecologists studying other communities or by our own studies of the Bays Mountain odonate community:

(1) Habitat generalists (cf. fugitive species of HUTCHINSON 1951, r-strategist species of MACARTHUR & WILSON 1967, and tramp species of DIAMOND 1975) have longer flight seasons, occupy more sites, and have lower co-occurrence frequencies than habitat special-

ists (cf. competitive, K-strategist, and high-S species of the same authors).

(2) Species that specialize on habitat categories among sites (or that occupy relatively few sites) should tend to generalize on habitats within sites; between-site generalists (or widespread species) should tend to specialize on habitats within sites (cf. CODY 1974; FOX & MORROW 1981).

(3) Pairs of species that frequently co-occur should overlap relatively little in habitats within sites; pairs that co-occur infrequently should overlap more within sites (cf. niche complementarity of SCHOENER 1974).

(4) Some species may use habitats (and other niche axes) similarly enough to produce negative associations across site via competitive exclusion or selective predation (JOHNSON & CROWLEY 1980a, 1980b, 1982).

After explaining the methods to be used to consider these questions, we attempt to characterize the distribution of 37 of the 46 Bays Mountain species across broad habitat types. We then examine the relation between co-occurrence frequencies and the number of sites occupied to see if the more widely distributed species have lower co-occurrence frequencies (e.g. DIAMOND 1975, MAC-ARTHUR & WILSON 1967). Finally, we present parts of a 37x37 matrix of co-occurrence values to look for positive and negative associations among species, and we discuss the implications of the results.

## MATERIALS AND METHODS

Both published and unpublished species lists for individual aquatic systems based on larval and/or adult identifications were compiled from several sources (see below). The distributions by state of the 46 Bays Mountain species were obtained from M.J. Westfall Jr. (pers. comm.), and these were supplemented by unpublished data of H.B. White III and by interpolation in two scantily collected states (ie. Delaware was assumed to have *Cordulegaster maculata* and *Aeshna umbrosa* and West Virginia to have *Libellula incesta* and *Tramea carolina* because these species are known to be present in all of the immediately surrounding states). Then in order to include as many of the available sites and as many of the 46 Bays Mountain species as possible in the analysis, while assuming that all species have access to all sites, we reduced the number of species considered to 37

and restricted the study area to the 13 contiguous states illustrated in Figure 1.

The 201 sites included in the analysis each contain at least one of the 37 Bay Mountain species and are classified according to four broad habitat types: stream, river, pond/marsh ("pond"), or lake/reservoir ("lake"). Forty-three of these sites are considered "intensively studied": Either adults and larvae were sampled simultaneously, or the site was sampled for adults or larvae in at least three different months; and the total number of odonate populations present at the site (usually including some not found at Bays Mountain Park) is known. The other 158 sites were less intensively studied; in many cases, their species lists were compiled by an experienced collector on a single visit to the site. The total number of sites in each habitat category, with the numbers of intensively studied sites indicated parenthetically, are: 58 (8) stream, 44 (10) river, 61 (18) pond, and 38 (7) lake. Thus 102 (18) sites are lotic, and 99 (25) are lentic.

The distribution for each species across the four habitat types



Fig. 1. The distribution of study sites by state in a region of the Eastern United States. For each state, the total number of sites is indicated, with the number of these that were intensively studied shown in parentheses. The triangle marks the location of Bays Mountain Park, occupied by all species included in this study.

and the two more general habitat categories was assessed as an adjusted decimal fraction: The number of sites of each type occupied by the species is divided by the total number of such sites before calculating its fractional habitat distribution, so that a perfect generalist would be expected to occupy each of the four habitat types in the proportion 0.25 and each of the two general categories in the proportion of 0.5. If one half or more of the sites occupied by a species is in one of the four habitat categories, then the species is considered to be a specialist on that category (e.g. a stream specialist). If the adjusted habitat fractions for all four categories are less than one half, but the lentic or lotic fraction equals or exceeds two thirds, then the species is considered to be a lentic or lotic specialist. If the habitat distribution meets neither of these criteria, then the species is considered to be a habitat generalist. The 37 species are tested against the null hypothesis of random distribution across the four habitat categories using chi-square goodness-of-fit tests with three degrees of freedom. And all 666 possible pairs of the 37 species are tested against the null hypothesis of identical distributions across the habitat categories using chi-square tests of heterogeneity with three degrees of freedom.

The number of co-occurring species per site occupied by a given species is referred to in this paper as its co-occurrence frequency. The mean and standard error of the co-occurrence frequency are calculated for each of the 37 species. (The less intensively studied sites are ignored in these calculations, because of the likelihood that co-occurrence frequencies for these sites would be grossly underestimated and biased by differences in life histories.) The null hypothesis of species randomly and independently distributed across the observed numbers of sites provides a useful comparison with the observed co-occurrence frequencies: The expected co-occurrence frequency for a given species at a site is obtained by adding one (for the given species, which is necessarily present) to the summed expected values of Bernoulli variables for each of the other species that may be present; these expected values are simply decimal fractions representing the proportions of all sites occupied by each of the other species. The variance of the co-occurrence frequency for a given species at a site is the sum across all other species of these decimal fractions of sites occupied, each multiplied by one minus the same fraction. But when co-occurrence with species in addition to the 37 Bays Mountain species is taken into account, a binomial term must be added to the Bernoulli terms in the expected value and variance calculations. (This yields the same expected value but a slightly higher variance

than would be obtained if the identities of all those additional species were known, so that their co-occurrences could also be expressed using Bernoulli variables.) The expected value increases by the total number of occurrences of additional species in all sites, divided by the total number of sites. The variance is augmented by this same amount multiplied by one less than the total number of sites and divided by the total number of sites. (See e.g. BLUM & ROSENBLATT 1972 for derivations of these expressions.)

The results of these observations and calculations are plotted against the number of sites occupied per species to evaluate the hypothesis that widespread species have lower co-occurrence frequencies. (This and several following hypotheses about relations among variables are tested using the Olmstead-Tukey Corner Test of Association – see DANIEL 1978.) Co-occurrence frequencies are compared by orthogonal contrasts for groups of species differing in habitat distributions, primarily to consider the hypothesis (related to the previous one) that generalists have lower co-occurrence frequencies. The relations among co-occurrence frequency, number of sites occupied, and duration of flight season are examined by corner tests and by a three-dimensional graph.

In order to measure the pairwise intensity of co-occurrence across all sites (and thus perhaps both the results of and potential for ecological interactions within sites), we examine the conditional co-occurrence of species pairs in a 37 x 37 matrix, parts of which are presented below. Conditional co-occurrence is the proportion of all sites occupied by the row species that are also occupied by the column species. If the column species were distributed at random across sites, then the expected conditional co-occurrence would equal the proportion of all sites occupied by the column species. Pairwise associations of species across all sites are tested against a null hypothesis of independent distributions using 2x2 contingency tables, yielding a chi-square statistic with one degree of freedom. A modified version of the 2x2 test is also run using expected values derived by assuming random distributions across sites within habitat categories only; thus the new expected co-occurrence frequencies are the products of the observed habitat-specific frequencies of the two species, divided by the respective habitat frequencies, and summed over the habitat categories.

An outline of these analytical procedures, which should prove useful for studying co-occurrence in other taxa as well, is presented in Table I.

Table I  
Analytical protocol

- 
1. Classify sites by habitat.
  2. Compute species habitat distributions.
  3. Classify species by predominant habitat.
  4. Test species for uniform habitat distribution.
  5. Calculate co-occurrence frequencies.
  6. Examine relations among
    - a. predominant habitat category;
    - b. number of sites occupied;
    - c. duration of flight season;
    - d. co-occurrence frequency.
  7. Test species pairs for homogeneous habitat distributions.
  8. Compute conditional co-occurrence values; compare with expected values.
  9. Test species pairs for site association.
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## RESULTS

Table II summarizes the distribution of the 37 species across sites in this study, grouping them by predominant habitat. Nine of the species are flowing-water specialists (ie. lotic, stream or river), nine are habitat generalists, and the other 19 were found primarily in standing-water sites. The species vary widely in the numbers of sites occupied and in mean co-occurrence frequencies per site; the co-occurrence variation among sites within species is also substantial. Most of the habitat specialists differ significantly in distribution from uniform across habitat categories, and most of the generalists do not differ significantly from a uniform habitat distribution.

A graph of between-site overlap (i.e. the conditional co-occurrence of a species pair divided by the fraction of all sites occupied by the column species) vs. habitat overlap within Bays Mountain Park (CROWLEY & JOHNSON 1982) for all 55 possible pairs of the 11 dominant species in the park yielded no apparent trend (corner test; graph not shown). Most of the between-site overlap values lie between one and two; two conspicuous outliers are *Enallagma aspersum* - *E. traviatum* (between-site overlap 5.55, within-site overlap 0.02) and *E. aspersum* - *Plathemis lydia* (5.08, 3.75), the differing within-site values reflecting the near-restriction of *E. aspersum* and *P. lydia* to the pond and *E. traviatum* to the lake at Bays Mountain Park. Similar results are obtained when overlap is calculated from proportional use of between-site habitat categories (the  $L_{ij}$  index of HURLBERT 1978; see also CROWLEY & JOHNSON 1982), but in this case the highest between site habitat overlaps are only 2.15 (*E. aspersum* - *Tramea carolina*) and 2.09 (*E. aspersum* - *E. traviatum*).

Table II

The species included in this analysis, the number of sites occupied, the habitat types, and the numbers of co-occurring species per intensively studied site

Species <sup>1</sup>	Sites occupied <sup>2</sup>		Predominant habitat <sup>5</sup>	Co-occurring species per studied site <sup>6</sup>
	Studied <sup>3</sup>	Total <sup>4</sup>		
<i>Amphiagrion saucium</i> (Burm.)	3	7	streams	39.7 ± 30.1
<i>Cordulegaster maculata</i> Sel.	5	9	streams	24.6 ± 15.0
<i>Argia moesta</i> (Hag.)	11	39	rivers**	26.0 ± 9.5
<i>Dromogomphus spinosus</i> Sel.	10	19	rivers**	19.9 ± 8.6
<i>Hagenius brevistylus</i> Sel.	6	12	rivers**	27.2 ± 14.6
<i>Progomphus obscurus</i> (Ramb.)	4	10	rivers**	30.0 ± 21.3
<i>Basiaeschna janata</i> (Say)	10	21	lotic**	27.1 ± 10.9
<i>Calopteryx maculata</i> (Beauv.)	20	83	lotic**	26.1 ± 7.1
<i>Enallagma exsulans</i> (Hag.)	17	58	lotic**	17.4 ± 5.5
<i>Aeshna umbrosa</i> Wlk.	6	15	generalist	39.7 ± 20.2
<i>Argia fumipennis violacea</i> (Hag.)	12	63	generalist	26.0 ± 9.4
<i>Enallagma divagans</i> Sel.	6	16	generalist	27.3 ± 14.6
<i>Ischnura posita</i> (Hag.)	21	79	generalist	23.8 ± 6.5
<i>Ischnura verticalis</i> (Say)	28	101	generalist	21.3 ± 5.1
<i>Libellula cyanea</i> Fabr.	11	30	generalist	32.4 ± 11.9
<i>Pachydiplax longipennis</i> (Burm.)	24	71	generalist*	22.9 ± 5.9
<i>Plathemis lydia</i> (Dr.)	24	81	generalist	23.4 ± 5.9
<i>Tetragoneuria cynosura</i> (Say)	15	29	generalist	29.3 ± 9.1
<i>Anax junius</i> (Dr.)	23	53	lentic**	23.1 ± 6.1
<i>Chromagrion conditum</i> (Hag.)	3	11	lentic	40.0 ± 22.0
<i>Enallagma civile</i> (Hag.)	16	48	lentic	26.1 ± 8.3
<i>Enallagma signatum</i> (Hag.)	18	41	lentic*	25.6 ± 7.2
<i>Epicordulia princeps</i> (Hag.)	14	32	lentic**	22.4 ± 7.5
<i>Erythemis simplicicollis</i> (Say)	25	70	lentic**	22.0 ± 5.6
<i>Lestes rectangularis</i> Say	8	30	lentic*	33.1 ± 15.0
<i>Lestes vigilax</i> Hag.	6	22	lentic*	33.2 ± 17.7
<i>Libellula incesta</i> Hag.	8	29	lentic	28.5 ± 12.4
<i>Libellula luctuosa</i> Burm.	22	58	lentic**	23.0 ± 6.3
<i>Perithemis tenera</i> (Say)	22	51	lentic**	23.4 ± 6.0
<i>Anomalagrion hastatum</i> (Say)	8	24	lakes**	27.4 ± 13.0
<i>Celithemis elisa</i> (Hag.)	8	22	lakes**	34.1 ± 14.6
<i>Anax longipes</i> Hag.	1	2	ponds	65.0 ± 0.0
<i>Enallagma aspersum</i> (Hag.)	7	15	ponds**	33.1 ± 16.0
<i>Enallagma traviatum</i> Sel.	4	12	ponds**	38.3 ± 24.2
<i>Sympetrum vicinum</i> (Hag.)	13	34	ponds**	25.9 ± 9.4
<i>Tramea carolina</i> (Linn.)	8	13	ponds**	33.4 ± 14.5
<i>Tramea lacerata</i> Hag.	16	38	ponds**	22.4 ± 7.3

<sup>1</sup> 37 of the 46 odonate species found at Bays Mountain Park, Sullivan County, Tennessee (JOHNSON et al. 1980).

<sup>2</sup> Data for 13 contiguous states (Delaware, Indiana, Kentucky, Maryland, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Virginia and West



The number of sites occupied, a useful measure of between-site specialization, is plotted in Figure 2 against habitat specialization in Bays Mountain Park. Three Bays Mountain specialists appear to be widespread habitat generalists in the present study: *Plathemis lydia*, *Ischnura verticalis*, and *I. posita*. In contrast, the five representatives of the generalized detritus/submerged-macrophyte guild at Bays Mountain Park (*Enallagma signatum*, *Tetragoneuria cynosura*, *Celi-themis elisa*, *E. divagans*, and *E. traviatum*) occupy relatively few of the present study sites and differ markedly in habitat specialization across sites. *E. aspersum* is a specialist on both axes, and *Argia fumipennis violacea* and *Libellula luctuosa* are consistently generalized. When between-site specialization is calculated instead from proportional use of habitat categories (the  $L_{ij}$  index), the pattern is very similar to that for the number of sites occupied, except that *Tetragoneuria cynosura* and *Enallagma divagans* are then clearly generalists, corresponding to the widespread species in Figure 2.

Table III summarizes the number of sites occupied according to the predominant habitat categories of Table II. The habitat specialist species (stream, river, lake and pond specialists) occupy fewer sites than do the more generalized species (lotic, generalist and lentic) as

(Footnotes Table II continued):

Virginia) from BENKE & BENKE 1975; CROSS 1955; HARWOOD 1975, 1976; INGRAM 1976; KENNEDY 1922; KORMONDY & GOWER 1965; NESTLER 1978; ROBACK & WESTFALL 1967; WHITE 1963; WHITE et al. 1968; WILLIAMSON 1934; WRIGHT 1946; WRIGHT & SHOUP 1945; and unpublished data from T. ABRAHAMSEN, P.H. CROWLEY, R.D. CUYLER, S. DUNKLE, P.D. HARWOOD, M.L. MAY, T. SHERK, K.J. TENNESSEN, J. THORPE, E.C. WALTZ, H.B. WHITE and E.B. WILLIAMSON (via B.E. MONTGOMERY).

- 3 Simultaneous sampling of both adults and larvae, or sampling of adults or larvae in at least 3 different months.
- 4 Includes both intensively studied and briefly studied sites; these latter generally represent a single sampling of larvae or observation of flying adults.
- 5 Based on four specific types—lakes (and reservoirs), ponds (and marshes), streams, and rivers; two less specific types—lentic and lotic; and an unspecialized type—generalist. Observed proportional occupancies of site types, corrected for differences in abundance among all sites, are used to designate the predominant habitat as follows: Any specific type with a corrected proportional occupancy at or above one half is considered predominant; if none meet this criterion, and if the corrected occupancy of lotic or lentic habitat equals or exceeds 2/3, this less specific type is predominant; if neither of these criteria are met, then the species is considered to be a generalist. The distributions across habitat types are compared with an expected distribution determined by the abundances of the types using a chi-square goodness-of-fit test (3 d.f.); no asterisk on the predominant habitat type indicates that the null hypothesis could not be rejected at the 5% level of significance; one asterisk is  $0.05 > P \geq 0.01$ ; two asterisks is  $P < 0.01$ .
- 6 Mean number of species co-occurring per site occupied by the given species, plus or minus one standard error of the mean.

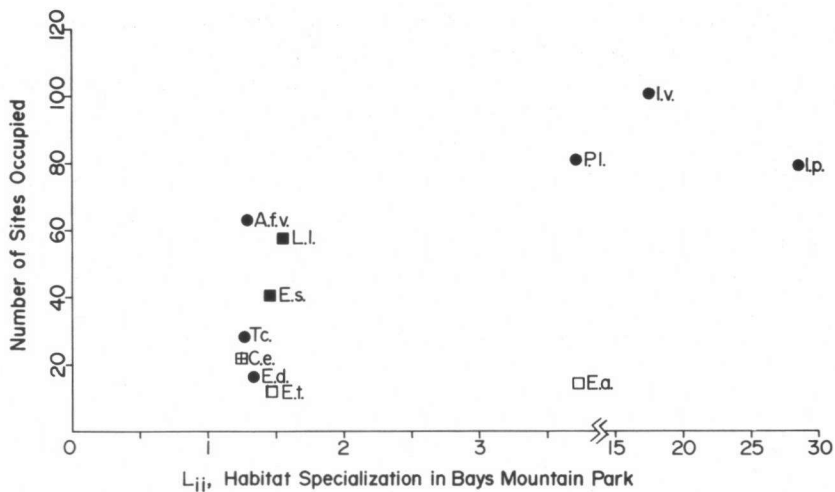


Fig. 2. The number of sites occupied in the present study vs the degree of habitat specialization by these dominant species in Bays Mountain Park. Specialization is expressed using an index  $L_{ij}$  that should be roughly proportional to the frequency of intraspecific encounter between two randomly chosen individuals (HURLBERT 1978). Species corresponding to the abbreviations are: A.f.v., *Argia fumipennis violacea*; C.e., *Celithemis elisa*; E.a., *Enallagma aspersum*; E.d., *Enallagma divagans*; E.s., *Enallagma signatum*; E.t., *Enallagma traviatum*; I.p., *Ischnura posita*; L.v., *Ischnura verticalis*; L.l., *Libellula luctuosa*; P.l., *Plathemis lydia*; and T.c., *Tetragoneuria cynosura*. Habitat specializations among sites are indicated by the following symbols: ●, generalist; ■, lentic; ⊞, lakes; and □, ponds.

might be expected, since fewer appropriate sites are available for the specialists. Dividing the number of appropriate sites available then yields an index of predominant habitat use, which appears to be somewhat lower for stream, pond and generalist species than for the others.

Co-occurrence frequency, the number of species occupying sites containing a particular species, was compared among the predominant habitat categories of Table II by orthogonal contrasts (GILL 1978), none of which were statistically significant. Yet Figure 3 shows a clear inverse relation between co-occurrence frequency and the number of intensively studied sites occupied (corner test,  $P < 0.01$ ). Mean co-occurrence frequencies of individual species are not statistically distinguishable from the null line (random distribution across sites), but the decreasing trend and the general tendency for frequencies to exceed the null-line values are obvious. The overall

mean co-occurrence frequency across all species and sites is 25.6; the mean percentage of all intensively studied sites occupied per species is 29.2, compared with 18.1 per cent over all sites.

The relation among the duration of flight season (JOHNSON et al. 1980), number of sites occupied, and co-occurrence frequency for 23 of the 37 species is illustrated in Figure 4. Though co-occurrence frequency, estimated from the intensively studied sites, is plotted here against the number of all sites occupied, the same kind of strongly inverse trend as in Figure 3 is again present. And flight-season duration is positively related to the number of sites occupied (corner test,  $P < 0.01$ ), restricting the points to a wedge-shaped region of the figure. The relation between co-occurrence frequency and

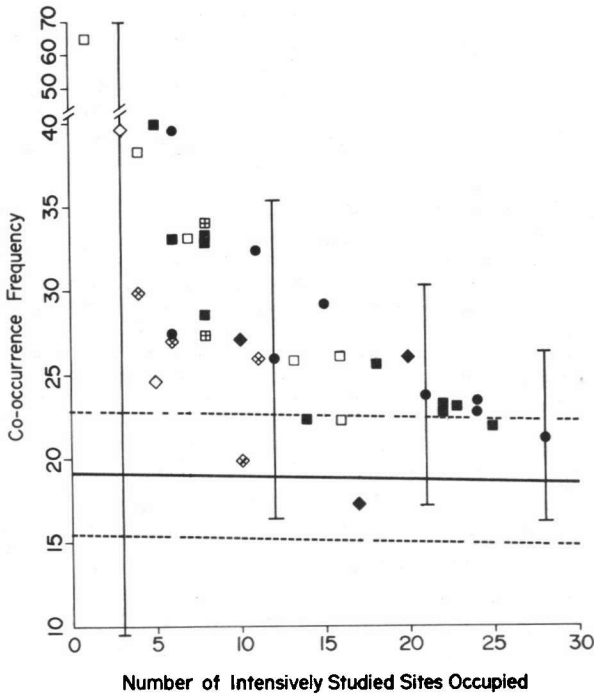


Fig. 3. The co-occurrence frequency in intensively studied sites vs the number of these sites occupied. Each point represents the mean number of species found at sites occupied by one of the 37 species included in this study. Error bars ( $\pm$  S.E.) are shown for four representative species; left to right they are *Amphiagrion saucium*, *Argia fumipennis violacea*, *Ischnura posita* and *Ischnura verticalis*. The solid line indicates the co-occurrence frequencies expected if species were distributed randomly across sites; the dashed lines are one standard deviation from these expected frequencies. Habitat specializations among sites are indicated by the following symbols: ●, generalist; ◆, lotic; ◇, rivers; ◇, streams; ■, lentic; ▣, lakes, and □, ponds.

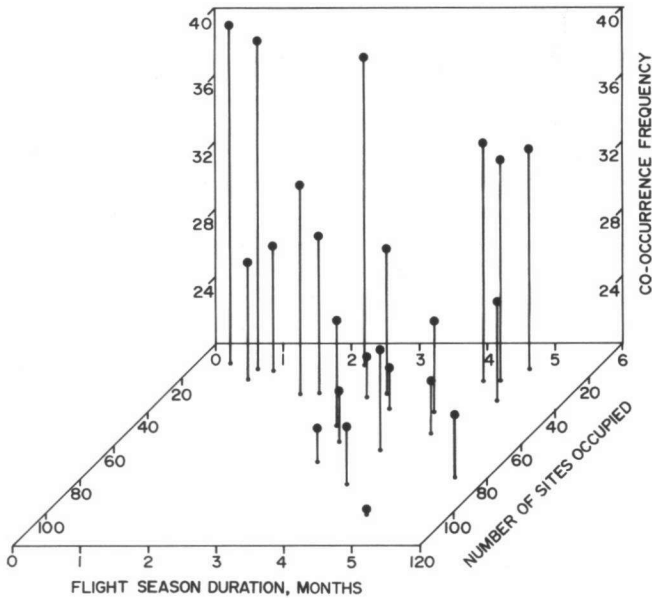


Fig. 4. A three-dimensional graph of the relation among co-occurrence frequency, number of sites occupied, and duration of flight season, for the 23 species having flight seasons well documented at Bays Mountain Park (JOHNSON et al. 1980); these include no flowing water species from Table 2 except *Basiaeschna janata*, (and they include all others in the table except *Anax longipes*, *Anomalagrion hastatum*, *Lestes rectangularis*, *Pachydiplax longipennis*, *Perithemis tenera* and *Tramea carolina*). In contrast to Figure 3, the co-occurrence frequencies determined for intensively studied sites are plotted here against the total number of sites occupied (including both the briefly and intensively studied sites). The pattern of points suggests a truncated plane intersecting the two orthogonal planes in the figure near their outer edges, and roughly parallel to the flight-season axis.

flight-season duration, however, is more complex. In two dimensions, with all points projected onto the vertical plane in the figure, there appears to be a significantly inverse relation between co-occurrence and flight season (corner test,  $P < 0.05$ ): but in the three-dimensional diagram, the points seem to fall on or near a plane (sloping toward the lower left of the figure) that approximately parallels the flight-season axis, indicating only a weak relation at best between co-occurrence and flight season. Similarly, the duration of flight season is not detectably related to predominant habitat category; generalists, lentic specialists, and pond specialists all have flight-season durations averaging 2.7-2.9 months (JOHNSON et al. 1980, and Table II).

Conditional co-occurrence values for four groups of species are presented in Table IV-VII. Since the first three of these groups each

consist of species similar in predominant habitat, negative associations (i.e. conditional co-occurrences less than expected by random distribution across sites) are rare. In Table IV, both of the underlined negative associations include species occupying less than 10 sites that predominate in different between-site habitats (Table II) – unconvincing evidence of negative interactions among the nine flowing-water species in this study. But the negative association between the generalists *Enallagma divagans* and *Ischnura verticalis* in Table V cannot be so easily dismissed, despite the lack of statistical significance.

Table III

The number of sites occupied by species differing in predominant habitat, relative to the number of such sites available

Predominant habitat (number of species)	Mean number of sites occupied ( $\pm$ 1 S.E.) $\bar{S}$	Number of appropriate sites available, A	Sites occupied per site available, $\bar{S}/A$
streams (2)	8.0 $\pm$ 1.0	58	0.138
rivers (4)	20.0 $\pm$ 6.6	44	0.455
lotic (3)	54.0 $\pm$ 18.0	102	0.529
generalist (9)	53.9 $\pm$ 10.6	201	0.268
lentic (11)	40.5 $\pm$ 5.2	99	0.409
lakes (2)	23.0 $\pm$ 1.0	38	0.605
ponds (6)	19.0 $\pm$ 5.7	61	0.311

Table IV

Conditional co-occurrences of flowing-water specialists. Main diagonal entries are the fractions of all 201 sites occupied by the given species. Off-diagonal entries are the fractions of all sites occupied by the row species that are also occupied by the column species

	A.s.	A.m.	B.j.	C.m.	C.m.	D.s.	E.e.	H.b.	P.o.
<i>Amphiagrion saucium</i>	0.035	0.429	0.143	1.000	0.143	0.000	0.286	0.000	0.000
<i>Argia moesta</i>	0.077	0.194	0.256	0.590	0.051	0.282	0.564	0.128	0.103
<i>Basiaeschna janata</i>	0.048	0.476	0.104	0.762	0.143	0.333	0.619	0.095	0.095
<i>Calopteryx maculata</i>	0.084	0.277	0.193	0.413	0.072	0.072	0.361	0.096	0.072
<i>Cordulegaster maculata</i>	0.111	0.222	0.333	0.667	0.045	0.333	<u>0.222</u>	0.111	0.000
<i>Dromogomphus spinosus</i>	0.000	0.579	0.368	0.316	0.158	0.095	0.737	0.263	0.263
<i>Enallagma exulans</i>	0.034	0.379	0.224	0.517	<u>0.034</u>	0.241	0.289	0.086	0.103
<i>Hagenius brevistylus</i>	0.000	0.417	0.167	0.667	0.083	0.417	0.417	0.060	0.417
<i>Progomphus obscurus</i>	0.000	0.400	0.200	0.600	0.000	0.500	0.600	0.500	0.050

Underlined conditional co-occurrences are less than the value expected by chance alone, which is the main diagonal entry in the same column, and the species do not differ from each other in their distribution across habitats. Neither of the indicated negative associations is significant at the 5% level, according to  $\chi^2$  tests of  $2 \times 2$  contingency tables.

In Table VI, negative associations between *Epicordulia princeps* and *Lestes rectangularis*, *E. princeps* and *L. vigilax*, *L. rectangularis* and *L. vigilax* and *Libellula luctosa* all merit additional attention, as does the *Enallagma civile* - *E. divagans* interaction of Table VII. But first note that most entries in Tables IV-VII represent positive associations, many very strongly positive; but the rare negative associations,

Table V

Conditional co-occurrence of habitat generalists having distributions not significantly different from uniform across habitats. Cf. Table IV

	<i>A.u.</i>	<i>A.v.</i>	<i>E.d.</i>	<i>I.p.</i>	<i>I.v.</i>	<i>L.c.</i>	<i>P.l.</i>	<i>T.c.</i>
<i>Aeshna umbrosa</i>	0.075	0.533	0.067	0.600	0.733	0.200	0.467	0.333
<i>Argia f. violacea</i>	0.127	0.313	0.159	0.508	0.524	0.413	0.413	<u>0.143</u>
<i>Enallagma divagans</i>	<u>0.063</u>	0.625	0.080	0.688	<u>0.313</u>	0.375	0.563	0.375
<i>Ischnura posita</i>	0.114	0.405	0.139	0.393	0.658	0.253	0.506	0.228
<i>Ischnura verticalis</i>	0.109	0.327	<u>0.050</u>	0.515	0.502	<u>0.149</u>	0.485	0.188
<i>Libellula cyanea</i>	0.100	0.500	0.200	0.667	<u>0.500</u>	0.149	0.767	0.367
<i>Plathemis lydia</i>	0.086	0.321	0.111	0.494	0.605	0.284	0.403	0.259
<i>Tetragoneuria cynosura</i>	0.172	<u>0.310</u>	0.207	0.621	0.655	0.379	0.692	0.144

None of these species differ significantly from each other in their distributions across habitats. Underlined conditional co-occurrences are less than the value expected by chance alone, which is the main-diagonal entry in the same column. None of the indicated negative associations are significant at the 5% level according to  $\chi^2$  tests of  $2 \times 2$  contingency tables.

Table VI

Conditional co-occurrences of lentic specialists having distributions significantly different from uniform across habitats. Cf. Table IV

	<i>A.j.</i>	<i>E.s.</i>	<i>E.p.</i>	<i>E.s.</i>	<i>L.r.</i>	<i>L.v.</i>	<i>L.l.</i>	<i>P.t.</i>
<i>Anax junius</i>	0.264	0.321	0.264	0.623	0.245	0.189	0.566	0.396
<i>Enallagma signatum</i>	0.415	0.204	0.390	0.610	0.195	0.171	0.463	0.585
<i>Epicordulia princeps</i>	0.438	0.500	0.159	0.625	<u>0.125</u>	<u>0.063</u>	0.563	0.531
<i>Erythemis simplicicollis</i>	0.471	0.357	0.286	0.343	0.200	0.186	0.557	0.486
<i>Lestes rectangularis</i>	0.433	0.267	<u>0.133</u>	0.467	0.149	<u>0.100</u>	0.467	0.267
<i>Lestes vigilax</i>	0.455	0.318	<u>0.091</u>	0.591	<u>0.136</u>	0.109	<u>0.136</u>	0.318
<i>Libellula luctuosa</i>	0.517	0.328	0.310	0.672	0.241	<u>0.052</u>	0.289	0.500
<i>Perithemis tenera</i>	0.412	0.471	0.333	0.667	0.157	0.137	0.569	0.254

None of these species differ significantly from each other in their distributions across habitats. Underlined conditional co-occurrences are less than the value expected by chance alone, which is the main-diagonal entry in the same column. None of the indicated negative associations are significant at the 5% level, according to  $\chi^2$  tests of  $2 \times 2$  contingency tables.

Table VII

Conditional co-occurrence of *Enallagma* species. Cf. Table IV

	<i>E.a.</i>	<i>E.c.</i>	<i>E.d.</i>	<i>E.e.</i>	<i>E.s.</i>	<i>E.t.</i>
<i>Enallagma aspersum</i>	0.075	0.533	0.133	0.133	0.467	0.333
<i>E. civile</i>	0.167	0.239	<u>0.042</u>	0.292	0.479	0.146
<i>E. divagans</i>	0.125	<u>0.125</u>	0.080	0.375	0.500	0.125
<i>E. exsulans</i>	0.034	0.241	0.103	0.289	0.241	0.069
<i>E. signatum</i>	0.171	0.561	0.195	0.341	0.204	0.146
<i>E. traviatum</i>	0.417	0.583	0.167	0.333	0.500	0.060

Underlined conditional co-occurrences are less than the value expected by chance alone, which is the main diagonal entry in the same column, and the species do not differ from each other in their distribution across habitats. The indicated negative association is not significant at the 5% level, according to a  $\chi^2$  test of a 2 X 2 contingency table.

Table VIII

*Enallagma*  $\chi^2$  statistics for tests of homogeneous distribution of two species across habitats (upper right triangle, 3 degrees of freedom), uniform distribution of a species across habitats (main diagonal, 3 d.f.), and independent distribution of two species across all sites (lower left triangle, 1 d.f.)<sup>1</sup>

	<i>E.a.</i>	<i>E.c.</i>	<i>E.d.</i>	<i>E.e.</i>	<i>E.s.</i>	<i>E.t.</i>
<i>Enallagma aspersum</i>	18.20**	10.23*	13.38**	34.45**	9.31*	0.77
<i>E. civile</i>	7.74**	7.35	3.64	20.43**	0.37	6.64
<i>E. divagans</i>	0.64	<u>1.24</u>	1.51	3.62	5.30	10.31*
<i>E. exsulans</i>	<u>1.90</u>	0.00	0.63	20.07**	22.14**	29.09**
<i>E. signatum</i>	<u>6.89**</u>	29.40**	9.38**	0.70	9.94*	5.90
<i>E. traviatum</i>	21.62**	8.33**	1.32	0.12	6.89**	12.39**

<sup>1</sup> Asterisks indicate statistical significance: \*, 0.05 > P ≥ 0.01; \*\*, 0.01 > P

Underlining identifies negative associations.

where not confounded by habitat differences, may prove to be especially useful in implicating particular ecological mechanisms at work (e.g. competition, predation). Results of tests designed to remove any residual effects of distributional differences among habitat categories are presented below.

Table VIII summarizes for the *Enallagma* species the results of three different tests based on the chi-square statistic but are intended to evaluate the distributions of species across sites and habitats. On the main diagonal, only *Enallagma civile* (a lentic specialist) and *E. divagans* (a generalist) are indistinguishable from a uniform distribu-

tion across habitats. Eight of fifteen species pairs differ significantly from each other in habitat distribution; all differ from the lotic specialist *E. exsulans* except *E. divagans*. The 2x2 contingency tables testing for independence of distribution across sites find seven significantly positive associations but none significantly negative.

When the modified contingency test (removing the effects of differences in distribution across habitat categories) is used, the negatively associated pairs of Table IV-VII all remain negatively but non-significantly associated. Seven species (including some from Tables IV-VII) having the most frequent negative associations according to

Table IX

$\chi^2$  statistics for standard (upper right triangle) and modified<sup>1</sup> (lower left triangle) tests of independent distribution across all sites (1 d.f.)<sup>2</sup>

	<i>D.s.</i>	<i>E.c.</i>	<i>E.d.</i>	<i>I.p.</i>	<i>I.v.</i>	<i>L.l.</i>	<i>L.v.</i>
<i>Dromogomphus spinosus</i>		0.07	0.19	7.28**	2.93	1.75	0.70
<i>Enallagma civile</i>	0.52		1.24	14.22**	18.16**	23.05	2.97
<i>Enallagma divagans</i>	0.21	1.20		6.32*	2.51	2.27	19.19**
<i>Ischnura posita</i>	4.35*	10.49**	7.58**		12.63**	6.84**	11.57**
<i>Ischnura verticalis</i>	1.53	13.33**	2.23	8.61**		21.39**	1.27
<i>Libellula luctuosa</i>	0.15	14.86**	2.04	2.88	14.36**		2.79
<i>Lestes vigilax</i>	0.21	5.03*	20.11**	7.92**	0.42	5.65*	

<sup>1</sup> Expected values are calculated by assuming that species are distributed as observed among four habitat categories but randomly among sites within each category. This removes the effects of any similarities or differences between species in the distribution among categories on the test of independence.

<sup>2</sup> Asterisks, indicate statistical significance: \*, 0.05  $P \geq 0.01$ ; \*\*, 0.01  $> P$ .

Underlining identifies negative associations.

this modified test are presented in Table IX. Note that in all of these cases the negatively and positively associated pairs remain the same for both tests, but the magnitudes of the chi-square statistics may shift considerably. Of 666 pairs examined using the standard contingency tables, only one negative association was statistically significant (*Dromogomphus spinosus* – *Ischnura posita*) and this could possibly be attributed to habitat differences alone. By the modified method, however, this association remains significantly negative, and two others are also significantly negative (*Enallagma civile* – *Lestes vigilax*, and *L. vigilax* – *Libellula luctuosa*). (In contrast to the rarity of negative associations 209 of the 666 pairs in the modified test are significantly positive, indicating that the overall bias toward positive



association within the sites does not simply reflect similar distributions across habitat categories—cf. Fig. 3.) In Table IX, note the similar association patterns of *Lestes vigilax* and *E. divagans* on one hand, and of *E. civile*, *I. posita*, *I. verticalis*, and *L. luctuosa* on the other.

Of the pairs from Tables IV-VII not included in Table IX, *Epicoridulia princeps* – *Lestes vigilax* is a strong negative association ( $\chi^2 = 2.21$ , 1 d.f.;  $0.2 > P > 0.1$ ), *E. princeps* - *L. rectangularis* ( $\chi^2 = 0.42$ ) and *L. rectangularis* – *L. vigilax* ( $\chi^2 = 0.37$ ) are weak ones, and *Enallagma aspersum* – *E. exsulans* ( $\chi^2 = 0.05$ ) seems to have depended almost entirely on habitat differences.

## DISCUSSION

### EVALUATING THE HYPOTHESES

Three of the four hypotheses presented in the Introduction received limited support in the results of this analysis. First, certain life-history and distributional characteristics do seem to be associated among odonates (i.e. duration of flight season, co-occurrence frequency, number of sites occupied), in general agreement with a continuum from fugitive/tramp/r-strategist species to competitive/high-S/K-strategist species (see also VOSHELL & SIMMONS 1978). But no consistent relation between these characteristics and a tendency for the species to specialize or generalize in the use of broad habitat types was detected. Second, of the eleven dominant species at Bays Mountain Park, three habitat specialists in the park are widespread generalists across all sites studied here, and five habitat generalists in the Bays Mountain detritus/submerged-macrophyte guild occupy fewer sites with varying degrees of habitat specialization—in general agreement with the notion that niches broad on one dimension tend to be narrow on another. Third, there is no evidence from niche overlap estimates for complementarity between the use of habitats within a site (i.e. Bays Mountain Park) and the use of habitat types among sites. And fourth, some negative associations across sites were found, despite a clear tendency for species to be underdispersed. Though intense competition offers a plausible explanation for at least one of these (i.e. *Enallagma civile* – *Lestes vigilax*), this analysis certainly does not seem to provide a sensitive means of detecting competitive or predatory interactions for these particular species and sites, assuming that such interactions are actually present.

Despite the apparent correlations among life-history and distributional characteristics, the dominant pattern emerging from the

data is the substantial ecological flexibility and variability of these odonate species. Most of the 37 species were found in all four habitat types, indicating some ability by most odonates to tolerate a broad range of environmental conditions. There also appear to be striking variations in duration of flight season across sites for individual species that are not attributable to climatic differences. Flight seasons recorded at Bays Mountain Park (JOHNSON et al 1980) were used in Figure 4, but these values contrast with many of those observed for the same species at other sites within the study area (cf. CROSS 1955; WHITE 1963; and WHITE et al. 1968). Such apparent flexibility in both habitat and season, coupled with widespread dispersal among sites (CORBET 1962), suggests an explanation for the rarity of negative associations between species in this study. Ecological mechanisms like competition and predation, though generally important among odonates (e.g. LAWTON 1971; BENKE 1972; KIME 1974), may often fail to completely exclude vulnerable species from individual sites. By ecological shift or character displacement, the population may successfully adjust (though perhaps at low density) to a particular community, or else a marginally viable population may be continually replenished by dispersal from neighboring sites. It may also be possible that the dominant odonate species are simply unable to exploit the available resources efficiently enough to exclude competitively inferior species (ISTOCK's 1973 "errors of exploitation" concept).

#### SPECIALISTS AND GENERALISTS

The habitat distributions of several species in this study differ sufficiently from information in the literature to merit emphasis here. *Aeshna umbrosa* found in seven lotic and eight lentic sites, is considered a generalist in the present study, though the genus *Aeshna* is consistently associated in the literature with lentic habitats (e.g. GARMAN 1927; CUMMINS & WESTFALL 1978). *Enallagma divagans* is also a generalist here (9 lotic, 7 lentic sites), despite its reported preference for small streams (GARMAN 1927; PAULSON & JENNER 1971). GARMAN (1927) classifies *E. traviatum* as a stream species, but nine of its twelve sites in the present study were ponds. Similarly, *Chromagrion conditum* was found in six ponds out of eleven sites (see also NEEDHAM & HEYWOOD 1929), in contrast to its "lotic" designation by CUMMINS & WESTFALL (1978). The latter authors also consider the genus *Perithemis* to favor lotic habitats; though this conclusion may be appropriate for *P. seminole*

(NEEDHAM & WESTFALL 1955), it does not appear to fit *P. tenera* (38 lentic and 13 lotic sites). Finally, *Plathemis lydia* is well represented in all four habitat categories in the data presented here (13 lakes, 35 ponds, 20 streams and 13 rivers) and is therefore classified as a generalist, though it is widely considered in the literature to be lentic (e.g. NEEDHAM & WESTFALL 1955, CUMMINS & WESTFALL 1978).

Herbivorous insects often have generalized diets over their entire geographic range but are much more specialized at individual sites (FOX & MORROW 1981). Figure 2 suggests that *Plathemis lydia*, *Ischnura posita*, and *I. verticalis* may represent analogous specialists in the habitats at Bays Mountain Park, despite their generalized distribution across habitat categories for all study sites. We have speculated that either fish predation by Bluegill Sunfish (*Lepomis macrochirus*) and Largemouth Bass (*Micropterus salmoides*) or the presence of superior odonate competitors may restrict the habitat distributions of these odonate species within the park (JOHNSON & CROWLEY 1980a). In contrast, the species of the detritus/submerged-macrophyte guild appear generalized in the park because they occupy a widespread and productive habitat; but this habitat is certainly not universally available. Thus even though *Tetragoneuria cynosura* and *Enallagma divagans* are considered generalists across the four habitat categories, an apparent preference for detritus (JOHNSON & CROWLEY 1980a; CUMMINS & WESTFALL 1978) may be responsible for restricting the total number of sites they occupy.

Regional (i.e. between-site) habitat generalists certainly need not be inferior competitors within individual communities, as exemplified by *T. cynosura* and *P. lydia*, which dominate the lake and pond respectively at Bays Mountain Park (JOHNSON & CROWLEY 1980a). Even if generalists are often less efficient than specialists within particular habitats, generalists may often be better able to take advantage of perturbations and new or temporary aquatic habitats (see CODY 1974). Habitat generalists are more widespread than specialists (see Table 3), though their lower number of sites occupied per site available than for lotic and lentic species suggests some reduced ability to persist within any particular site. Low values of this ratio for pond and stream specialists may reflect a much greater susceptibility of these sites to such severe perturbations as drought or flooding.

In contrast to the Anisoptera noted in the preceding paragraph,

the Zygoptera dominating the lake and pond at Bays Mountain Park are pond specialists—*Enallagma traviatum* and *E. aspersum*, respectively. And though the members of each pair are almost entirely restricted to separate bodies of water in the park, they are positively associated across the sites in the present study (both  $P < 0.01$ ). Perhaps the explanation for these contrary observations lies in the phrase “almost entirely restricted”, since larvae of *T. cynosura* and *E. traviatum* have occasionally been found in the pond, and *P. lydia* (but not *E. aspersum*) has very rarely been found in the lake. (See the previous section of the Discussion).

#### A TREND AND SOME POSSIBLE BIASES

The strong and consistent inverse trend in Figures 3 and 4 between co-occurrence frequency and number of sites occupied could have one or more of the following explanations:

- (1) The low co-occurrence species are superior dispersers, exploiting new or temporary sites inaccessible to the poor dispersers, which tend to reach sites only after they are already colonized by many other species (see MACARTHUR & WILSON 1967).
- (2) There is a hierarchy of site desirability, such that the most desirable sites attract the most species, and the least desirable sites attract only the widespread species (see FRETWELL 1972).
- (3) The largest and most diverse sites provide additional niches for habitat specialists that are unavailable in the smaller, less diverse sites exploited by a few generalists (see DIAMOND 1975).
- (4) Some species may require or at least benefit from the presence of certain other species (see BENKE et al. in prep.), increasing their co-occurrence frequencies but decreasing the number of sites available to them.
- (5) Many species are consistently rare or consistently common across sites. The rare species are thus found only in the few most thoroughly sampled sites, but the common species are more likely to be noticed and recorded.

This list illustrates how difficult it can be to derive simple and testable explanations for distributional data of the sort considered here. At least the first three seem likely to be important in the trends of Figures 3 and 4, but none can be strongly supported or conclusively rejected by the present results. The last statement in the list suggests that a sampling bias may be responsible for the observed trend. It is particularly important to be aware of this and some other possible sources of bias in these data, so that the limitations of the ap-

proach (and thus some possible ways of improving it) are clear. Possible sources of bias include the following:

- (1) Certain species are easier to identify (correctly) than others, particularly as larvae; the difficult species may therefore be under-represented in the data.
- (2) Species with shorter flight seasons may more often be overlooked—even with larval sampling, since synchronous development generally implies that larvae will be too small to find or to identify during much of the year.
- (3) The sites chosen by those contributing data to this study certainly do not represent a random sample of aquatic habitats and may be unrepresentative of all available sites in various ways. An obvious possibility is a bias toward sites with unusually large numbers of species present.
- (4) Neither the sites nor the species are uniformly distributed across the region illustrated in Figure 1, perhaps distorting the co-occurrences and the numbers of sites occupied.
- (5) Species with widely dispersing adults may be over-represented in the data.

Of these five possible sources of bias, 1 and 4 would be very difficult or impossible to assess: 2 is likely to be a factor in the tendency of species with long flight seasons to be more widespread (Fig. 4); 3 certainly increases the co-occurrence frequencies and may make tramp species more difficult to recognize; and 5 may apply to species like *Anax junius* and *Tramea lacerata* but it may partly cancel the bias in 3 against tramp species.

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#### REFERENCES

- BARONI-URBANI, C. 1980. A statistical table for the degree of coexistence between two species. *Oecologia (Berl.)* 44: 287-289.
- BARONI-URBANI, C. & W.M. BUSER 1976. Similarity of binary data. *Syst. Zool.* 25: 251-259.
- BELL, S.S. 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol. Monogr.* 50: 487-505.
- BENKE, A.C. 1972. An experimental field study of the ecology of coexisting larval odonates. Ph.D. thesis, Univ. of Georgia.
- BENKE, A.C. & S.S. BENKE 1975. Comparative dynamics and life histories of coexisting 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. *Hydrobiologica* 94: 121-130.
- BLUM, J.R. & J.L. ROSENBLATT 1972. Probability and statistics. W.B. Saunders, Philadelphia.
- BROWN, L.L. & E.O. WILSON 1956. Character displacement. *Syst. Zool* 5: 49-64.
- CODY, M.L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, N.J.
- CORBET, P.S. 1963. A biology of dragonflies. Quadrangle Books, Chicago.
- CROSS, W.H. 1955. Anisopteran Odonata of the Savannah River Plant, South Carolina. *J. Elisha Mitchell Sci. Soc.* 71: 9-17.
- CROWLEY, P.H. 1981. Dispersal and the stability of predator-prey interactions. *Am. Nat.* 118: 673-701.
- CROWLEY, P.H. & D.M. JOHNSON, 1982. Habitat and seasonality as niche axes in an odonate community. *Ecology* 63: 1064-1077.
- CUMMINS, K.W. & M.J. WESTFALL Jr. 1978. Summary of ecological and distributional data for Odonata (dragonflies and damselflies). p. 94-98 in: R.W. MERRITT & K.W. CUMMINS (eds) An introduction to the aquatic insects of North America. Kendall/Hunt Publ. Co., Dubuque, Iowa.
- DANIEL, W.W. 1978. Applied non-parametric statistics. Houghton Mifflin Co. Boston, Mass.
- DAVIDSON, D.W., 1980. Some consequences of diffuse competition in a desert ant community. *Am. Nat.* 116: 92-105.
- DIAMOND, J.M. 1975. Assembly of species communities. p. 342-444 in: M.L. CODY & J.M. DIAMOND (eds). *Ecology and evolution of communities*. Harvard Univ. Press. Cambridge, Mass.
- FOX, L.R. & P.A. MORROW 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.
- FRETWELL, S.D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, N.J.
- GARMAN, P. 1927. Guide to the insects of Connecticut, V. The Odonata or dragonflies of Connecticut. *Conn. State Geol. & Nat. Hist. Surv. Bull.* 39.
- GILL, J.L. 1978. Design and analysis of experiments in the animal and medical sciences, 1. Iowa State Univ. Press, Ames, Iowa.
- GREENFIELD, M.D. & M.G. KARADINOS 1979. Resource partitioning of the sex communication channel in clearwing moths (Lepidoptera : Sesiidae) of Wisconsin. *Ecol. Monog.* 49: 403-426.
- HARWOOD, P.D. 1975. Dragonflies of Ritchie County, West Virginia. The Redstart—January 1975: 18-21.
- HARWOOD, P.D. 1976. Dragonflies of Raleigh County, West Virginia. The Redstart—January 1976: 49-53.
- HURLBERT, S.H. 1978. The measurement of niche overlap and some relatives. *Ecol.* 59: 67-77.
- HUTCHINSON, G.E. 1951. Copepodology for the ornithologist. *Ecology* 32: 571-577.
- INGRAM, B.R., 1976. Life histories of three species of Lestidae in North Carolina, United States (Zygoptera) *Odonatologica* 5: 231-244.
- ISTOCK, C.A., 1973. Population characteristics of a species ensemble of waterboatmen (Corixidae). *Ecology* 54: 535-544.
- JOHNSON, D.M., CONEY, C.C. & M.J. WESTFALL Jr. 1980. The Odonata of Bays Mountain Park, Sullivan County, Tennessee. *J. Tenn. Acad. Sci.* 55: 73-76.
- JOHNSON, D.M. & P.H. CROWLEY 1980a. Habitat and seasonal segregation among coexisting odonate larvae. *Odonatologica* 9: 297-308.
- JOHNSON, D.M. & P.H. CROWLEY 1980b. Odonate "hide and seek": habitat-specific rules? P. 569-579 in: W.C. KERFOOT (ed.) *The evolution and ecology of zooplankton communities*. University Press of New England, Hanover, N.H.
- KENNEDY, C.H. 1922. The ecological relationships of the dragonflies of the Bass Islands of Lake Erie. *Ecology* 3: 325-336.

- KERFOOT, W.C. (ed.) 1980. The evolution and ecology of zooplankton communities. University Press of New England, Hanover, N.H.
- KIME, J.B. 1974. Ecological relationships among three species of aeshnid dragonfly larvae (Odonata : Aeshnidae). Ph.D. thesis, University of Washington.
- KORMONDY, E.J. & J.L. GOWER 1965. Life history variations in an association of Odonata. *Ecology* 46: 882-886.
- LAWTON, J.H. 1971. Maximum and actual field feeding rates in larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Freshwat. Biol.* 1: 99-111.
- MACARTHUR, R.H. & E.O. WILSON 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.
- NEEDHAM, J.G. & M.J. WESTFALL Jr. 1955. A manual of the dragonflies of North America (Anisoptera). Univ. of California Press, Berkeley, Cal.
- NESTLER, J.M. 1980. Niche relationships of the Anisoptera of Lake Isaqueena. Ph.D. thesis, Clemson Univ. Clemson, S.C.
- PAULSON, D.R. & C.E. JENNER 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 51: 96-103.
- PIELOU, E.C. 1977. Mathematical ecology. Wiley & Sons, New York.
- ROBACK, S.S. & M.J. WESTFALL Jr. 1967. New records of Odonata nymphs from the United States and Canada with water quality data. *Trans. Am. ent. Soc.* 93: 101-124.
- ROBINSON, J.V. 1981. The effect of architectural variation in habitat on the spider community: An experimental field study. *Ecology* 62: 73-80.
- SCHOENER, T.W. 1974. Resource partitioning in ecological communities. *Science* 185: 27-39.
- VANDERMEER, J., J. LAZARUS, C. LUDWIG, J. LYON, B. SCHULTZ & K. YIH 1980. Migration as a factor in the community structure of a macroarthropod litter fauna. *Am. Nat.* 115: 606-612.
- VAN DER MEIJDEN, E. 1979. Herbivore exploitation of a fugitive plant species: Local survival and extinction of the Cinnabar Moth and Ragwort in a heterogeneous environment. *Oecologia* 42: 307-323.
- WHITE, H.B. 1963. Seasonal distribution and abundance of Odonata at a large pond in central Pennsylvania. *Proc. N. cent. Brch. Am. Ass. econ. Ent.* 18: 120-124.
- WHITE, H.B., G.H. BEATTY & A.F. BEATTY 1968. The Odonata fauna of Bear Meadows, a boreal bog in Central Pennsylvania. *Proc. Pa Acad. Sci.* 42: 130-137.
- WILLIAMSON, E.B. 1934. Dragonflies collected in Kentucky, Tennessee, North and South Carolina and Georgia in 1931. *Occ. Pap. Mus. Zool. Univ. Mich.* 288: 1-20.
- WRIGHT, M. 1946. Dragonflies collected in central Tennessee during 1945. *J. Tenn. Acad. Sci.* 21: 268-280.
- WRIGHT, M. & C.S. SHOUP 1945. Dragonfly nymphs from the Obey River drainage and adjacent streams in Tennessee. *J. Tenn. Acad. Sci.* 20: 266-278.