

## Annual Patterns of Production in a Dragonfly Community in Western Virginia<sup>1</sup>

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### ABSTRACT

The number of dragonflies emerging from five mountain ponds over a four-year period was highly variable and independent for six species. Levels of adult activity were accurate indicators of relative reproductive input to the individual ponds. There was a general lack of concordance between reproductive input and subsequent adult emergence at a pond for three of four species studied, demonstrating the existence of differential egg or larval survival among ponds and years. Emergence and subsequent adult activity were not correlated for two of four species, indicating the existence of among-pond variability in factors affecting adult distributions. *Plathemis lydia* exhibited spatially and temporally stable populations and significant correlations between reproductive input and emergence, and between emergence and subsequent adult activity.

*Keywords:* ecology, habitat selection, life history, Odonata, population dynamics, reproductive output, spatial heterogeneity.

### INTRODUCTION

It is axiomatic that the sizes of natural populations are determined by combinations of two dynamic forces: 1) recruitment of new individuals through local reproduction, and immigration from other populations; and 2) loss of individuals through mortality and emigration. Both forces may vary considerably over space and time and produce dramatic fluctuations in the sizes and distributions of populations (Andrewartha & Birch, 1954; Birch, 1957). Information on the magnitudes and underlying forces of fluctuations in size are unknown for most natural populations. Such information depends on long-term studies which use dependable census techniques on well-defined populations. Examples of such studies include work by Ehrlich et al. (1975) on butterflies, Dixon (1979) on aphids, Taylor & Taylor (1979) on moths and aphids, and Gill (1978) and Gill et al. (1983) on amphibians.

Dragonflies which breed in discrete habitat patches such as small ponds offer an exceptional opportunity to document the range of spatial and temporal variation in recruitment and mortality of critical life stages. Odonate life histories are characterized by an extended aquatic larval stage and a comparatively short terrestrial adult stage (Corbet, 1962, 1980). The points of transition between these two stages, i.e., emergence (aquatic to terrestrial) and oviposition (terrestrial to aquatic), provide excellent windows through which to view the forces controlling population size. Furthermore, comparison of emergence patterns with oviposition patterns at several ponds illuminates the possible sources of variation in rates of immigration, emigration, and local reproduction. In this paper, we report the patterns of emergence and oviposition of adult dragonflies at five mountain ponds in northwestern Virginia over a four-year period. Species-specific patterns of emergence document the importance of spatial and temporal variation in reproductive suitability of ponds. We focus on oviposition as a measure of reproductive input and a potentially important source of variation in emergence of four species. Differential survival of eggs and larvae represents the only other source of variation in emergence. Patterns of variability in the survival of these

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<sup>1</sup>Editor's note: This paper is adapted from Chapter 2 in Halverson (1983); with my approval, no effort was made to update the literature references.

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stages were evaluated by Halverson (1983). Measures of the extent of migration among ponds by adult dragonflies are reported in Halverson (1983).

The specific questions asked in this study were: 1. What are the annual patterns of variability among ponds in dragonfly emergence? 2. Are the patterns similar for different species which utilize the same set of ponds? 3. Does the number of emerging adults correlate with the size of the subsequent breeding population at a pond? and 4. Can the variation in emergence be ascribed to variation in previous reproductive input, or is it necessary to postulate variation in environmental factors affecting the survival of eggs or larvae?

### STUDY SITE AND ORGANISMS

Our study was conducted at five woodland ponds in the Shenandoah Mountains, George Washington National Forest, Rockingham County, Virginia, from 1978 through 1981. The ponds were small (5–15 m in diameter), roughly circular, and positioned along mountainous ridges varying in elevation from 1,024 to 1,114 m above sea level. None of the ponds supported fish populations but each was used for breeding by a variety of amphibians. For more detailed descriptions of the surrounding terrain and the fauna of these ponds see Fraser (1976), Gill (1978), Gill et al. (1983), and Halverson (1984). The five ponds used in this study were Pond Ridge Pond (PR), White Oak Flat Pond (WF), Cline's Hacking Pond (CH), Dictum Ridge Pond (DR), and Second Mountain Pond (SM) (Fig. 1). These ponds, along with a similar sixth pond, comprised the only permanent, aquatic habitat within a 6 km radius. Each of the five study ponds was surrounded by a drift fence of window screening 0.5–0.8 m high at a distance of 0.5–2.5 m from the pond edge. These fences were erected and maintained to study amphibian populations (see Berven et al., 1979; Berven, 1982; Gill, 1978; Gill et al., 1983), but also provided convenient supports for emergence of many of the dragonfly species.

The dragonfly communities of the study ponds were composed of six common species which bred at one or more of the ponds in all four years, and an additional six rare or infrequently observed species. The largest of the common species were the Black-tipped Darner, *Aeshna tuberculifera* Walker, and the Shadow Darner, *Aeshna umbrosa* Walker (common names follow DSA, 1996). These species were very similar in both their morphology and life histories: two-year life cycles, oviposition in late summer and fall, an overwintering embryonic diapause, and a 15–17 month larval period (Halverson, 1984). The Common Whitetail, *Plathemis lydia* Drury, and Twelve-spotted Skimmer, *Libellula pulchella* Drury, were moderate-sized dragonflies which

also showed morphological and ecological similarities. Both species had a one-year life cycle with a lengthy ovipositional period (mid-May to mid-August), direct embryonic development, a 10–11 month larval period, and asynchronous emergence. The remaining two common dragonflies at the study site were the Ruby Meadowhawk, *Sympetrum rubicundulum* Say, and the American Emerald, *Cordulia shurtleffii* Scudder. The former is a small species which bred from mid-July through August. Its eggs passed through an overwintering embryonic diapause but the life cycle appeared to be univoltine. Much less information is available on the life history of *C. shurtleffii*. Adults emerged early in the spring but persisted through most of the summer. The life cycle of this species may have been univoltine or semivoltine.

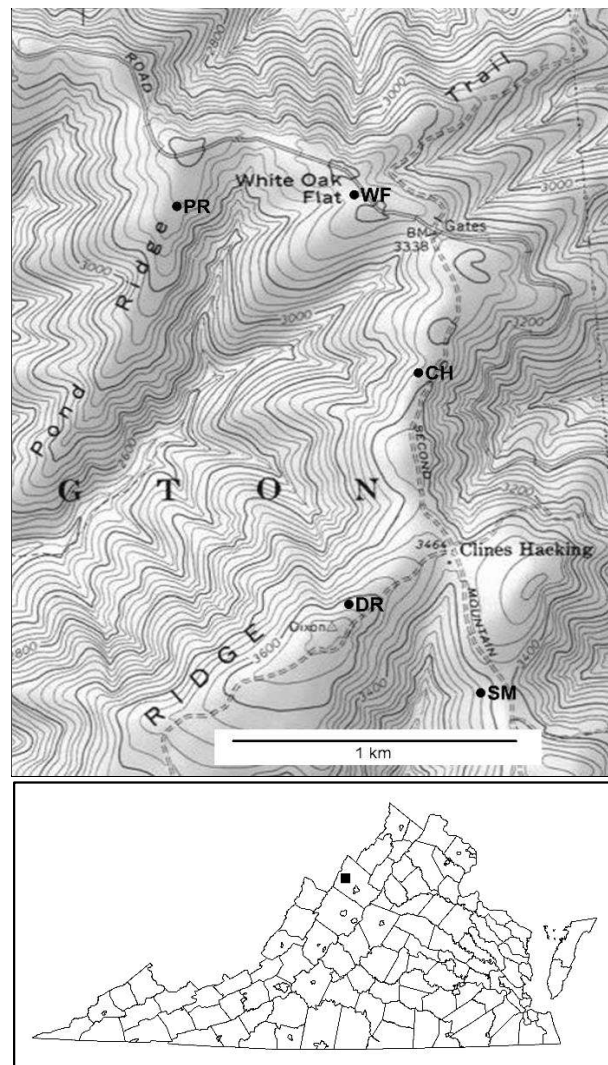


Fig. 1. Map of study ponds and location within Rockingham County, Virginia (square). See text for abbreviations.

We observed six other dragonfly species infrequently as either adults or larvae at the study ponds. Twenty-six Swamp Darners, *Epiaeschna heros* Fabricius, emerged from three ponds (PR, CH, and DR) during 1978, but none was seen at the study site during the subsequent three years. Eleven Common Green Darners, *Anax junius* Drury, emerged from SM and WF ponds in 1980; we observed adults occasionally in 1979 and 1980, but only once each in 1978 and 1981. Our records for Black Saddlebags, *Tramea lacerata* Hagen, were limited to an adult observed at PR pond in 1979 and an exuvia found at the same pond in 1980. The remaining three rare species were seen only as breeding adults, with no evidence of emergence from any of the study ponds. We saw two Blue Dasher (*Pachydiplax longipennis* Burmeister) males at CH pond in 1979 and eight adults (6 males, 2 females) were observed breeding at this pond in 1980. We collected three Dot-tailed Whiteface (*Leucorrhinia intacta* Hagen) males at CH pond in 1980 and a Painted Skimmer (*Libellula semifasciata* Burmeister) male was sighted at PR and SM ponds in 1979.

#### METHODS

We collected exuviae at one- to two-week intervals during the emergence season in all four years by carefully searching the fences and enclosed vegetation at each pond. Generally, collections were taken from all five ponds on the same day, but collections spanned as many as three days on rare occasions. Collected exuviae were sorted to species and counted in the laboratory.

In 1980 and 1981, we marked 142 fresh exuviae *in situ* at two ponds, with small spots of enamel paint. These exuviae were then censused at one- to four-day intervals in order to determine the natural rate of loss of exuviae, and hence the sampling efficiency of our weekly exuvial collections. We assigned exuviae to one of two groups on the basis of morphology and emergence site, and representatives of each of these groups were marked and censused during three different portions of the emergence season. One group included large exuviae of the family Aeshnidae (*A. tuberculifera* and *A. umbrosa*), which tended to occur on reed stems or other emergent vegetation at heights of 2 to 90 cm above the pond surface. The second group included moderate-sized dragonfly exuviae (Family Corduliidae, *C. shurtleffii*) and Family Libellulidae, *L. pulchella* and *P. lydia*), which tended to occur lower in the vegetation (<30 cm) but over a wider range of horizontal distances from the pond (5-150 cm). We used the three seasonal samples as replicates to estimate variation in loss rate independently for the two morphological groupings.

We monitored adult activity of both species of *Aeshna*, *P. lydia*, and *L. pulchella* at the study ponds in 1979 and 1980 during a series of 30 min observation periods. Our observations were conducted at all five ponds on 19 days in 1979 and on 23 days in 1980. Ponds were surveyed between 1000 h and 1700 h; our observations spanned the entire breeding season in both years. During each minute of an observation period, we recorded the numbers of males and females of each species at the pond. We defined adult activity level for a given species as the total number of dragonfly minutes accumulated during the 30 min observation period. Mean activity levels during the flight season were calculated for each species at each pond in both years. The flight season for a species in any year was defined as the period between the first and last observations of a breeding adult in the study area.

Reproductive input to each pond was also evaluated directly for *A. tuberculifera* in 1978, 1979, and 1980. These data were obtainable because over 90% of oviposition by this species at the study ponds occurred in stems of the rush *Juncus effusus* L. (Halverson, 1984). At the end of the breeding season (late September or October) in all three years, we carefully examined all stems of *J. effusus* at SM and DR, and approximately 20–30% of the stems at CH, WF, and PR. We recorded the number of characteristic oviposition marks left by female *A. tuberculifera* for each clump of *J. effusus* examined. At CH, WF, and PR ponds, where 20–27 clumps of *J. effusus* of nearly equal size existed, five or six clumps were chosen randomly for exhaustive sampling. We estimated reproductive inputs at these ponds by multiplying the mean number of ovipositional marks per clump by the number of clumps at the pond.

These direct estimates of oviposition by *A. tuberculifera* during 1979 and 1980 were compared with mean adult activity for those years using Spearman rank correlations in order to verify that adult activity measurements accurately reflected reproductive input. Spearman rank correlations were also used to investigate relationships between adult activity and emergence in the same year, and between adult activity (or reproductive input) and subsequent emergence number (i.e., the number of exuviae collected one year later for *P. lydia* and *L. pulchella* or the number collected two years later for *A. tuberculifera* and *A. umbrosa*).

#### RESULTS

The loss rate of marked exuviae was significantly greater for the corduliid-libellulid group than for the aeshnid group (Fig. 2). Differences among the three

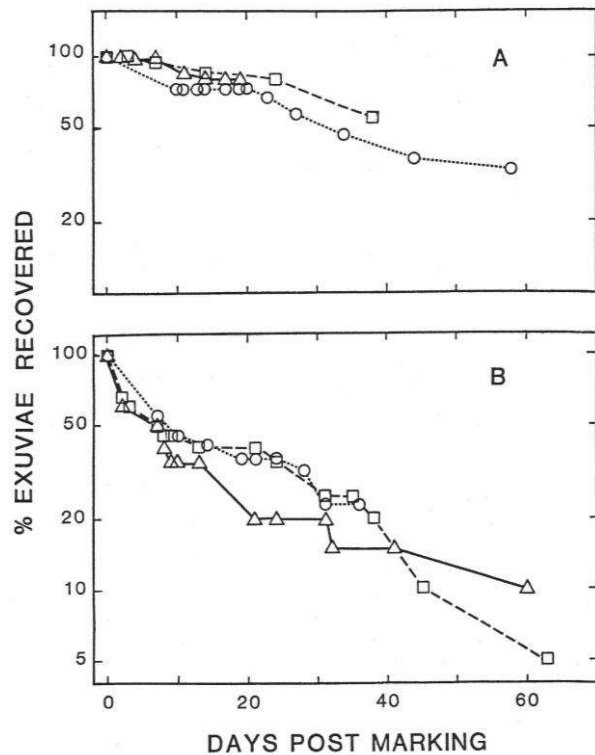


Fig. 2. Loss rate of exuviae of the aeshnid group (A) and the corduliid-libellulid group (B). Each of the three separate cohorts of exuviae monitored at different periods of time are represented by a different symbol (see methods).

seasonal samples within each group were small. Estimates of the mean sampling efficiency of weekly exuvial collections (i.e., percent of total exuviae discovered) were 89% for the aeshnid group and 49% for the corduliid-libellulid group.

Spatial variability in adult production was conspicuous for all six species (Fig. 3). Within any given year, some ponds were more productive than others. Only one species (*A. umbrosa*) emerged from all ponds in a single year, and even in this case there was an order of magnitude difference in numbers of exuviae collected at the most productive and the least productive ponds. Ponds which were the most productive for one species were not necessarily the most productive for all species. For example, while CH produced the most *S. rubicundulum* it produced relatively few exuviae of

the other species.

Dramatic annual fluctuations were also apparent for five of the six species. Many species appeared and disappeared irregularly at ponds (e.g., *A. tuberculifera* at CH pond, *L. pulchella* at WF pond). Even at ponds which consistently produced exuviae over the four years, the numbers collected frequently shifted by an order of magnitude between successive years (e.g., *A. umbrosa* or *A. tuberculifera* at WF pond). Independence among ponds in annual patterns of variation was the rule for these species. The eleven-fold increase in the number of *A. umbrosa* exuviae collected at WF (from 1979 to 1980), for instance, was accompanied by a decrease in numbers of this species at the other four ponds, including an apparent extinction at DR. The irregular appearance and disappearance of other species at the various ponds also demonstrates independence among ponds in the effects of annual fluctuations.

*Plathemis lydia* exhibited greater spatial predictability and less temporal variation in emergence than any of the other species at these ponds. No *P. lydia* exuviae were ever discovered at DR or CH during the study, but they were present in every year at SM and WF. Low temporal variation for *P. lydia* is illustrated by a comparison of variation around the mean emergence population size for the three species which emerged at WF in all four years. The coefficient of variation for the number of exuviae collected was considerably lower for *P. lydia* (34.8) than for *A. tuberculifera* (99.6) or *A. umbrosa* (105.9). In spite of the relative predictability for this species, the different trends in population size at SM (steady increase), WF (rise and fall), and PR (decline to extinction) indicate a level of independence among ponds similar to that found for the other species.

Adult activity levels varied for all species both among ponds and between years (Table 1). Mean adult activity levels were positively correlated with the number of adults emerging at a pond earlier in the same year for *P. lydia* and *L. pulchella*, but not for either *Aeshna* species (Table 2). However, only *P. lydia* yielded a significantly positive correlation between reproductive input one year, and number of exuviae (representing their offspring) collected as a cohort either one or two years later (depending on the life cycle of the study species) (Table 2). For *A. tuberculifera*, there was also a highly significant positive correlation between the number of oviposition marks at a pond and mean adult activity level (Fig. 4).

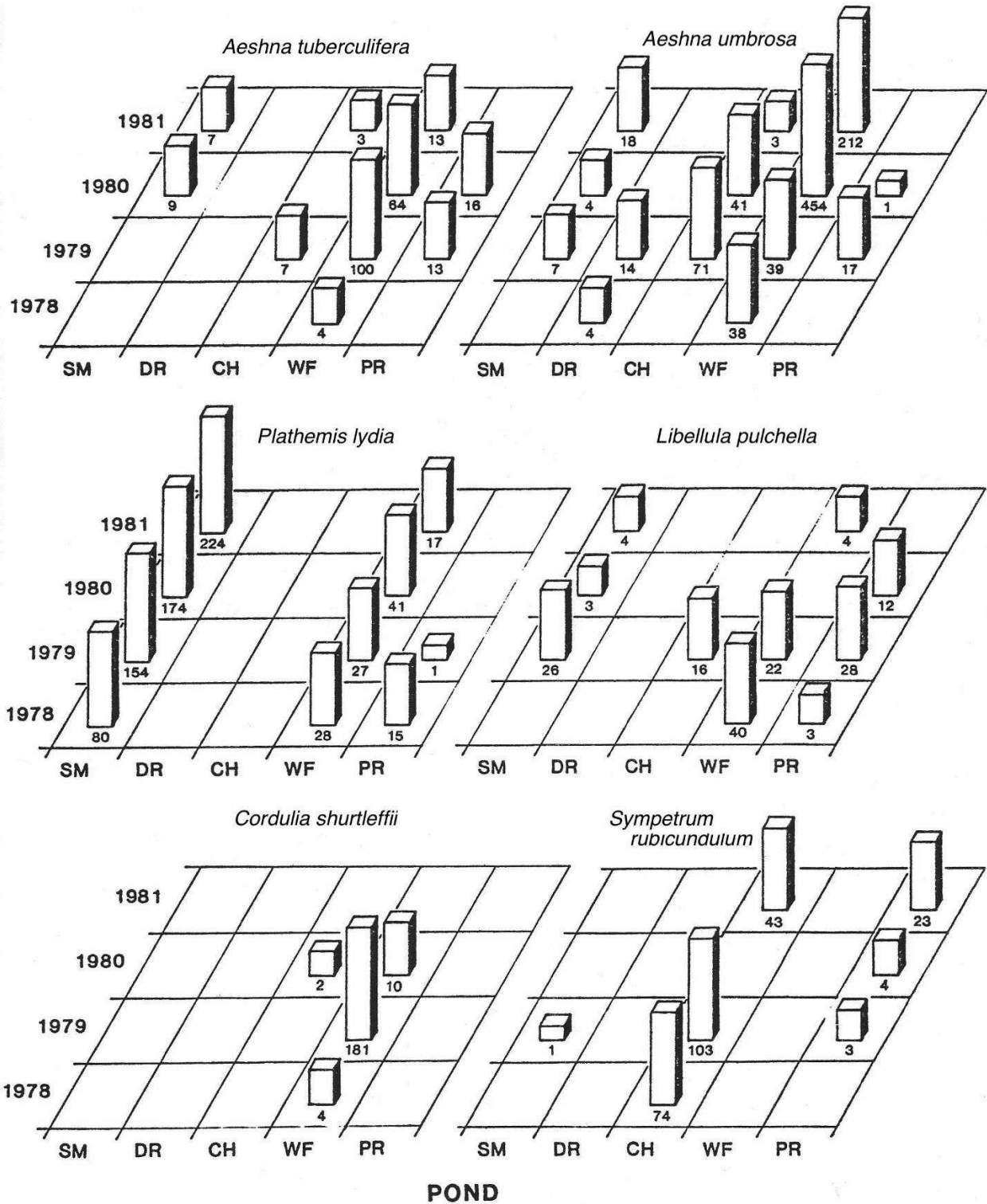


Fig. 3. Annual emergence records for six species of dragonflies at each pond during the four-year study. The height of each block represents the number of exuviae collected on a logarithmic scale; actual numbers collected appear under each block.

Table 1. Adult activity for each pond in 1979 and 1980. Activity is listed as the mean number of dragonfly minutes per 30 min observation period. Number of oviposition marks is also given for *Aeshna tuberculifera* (estimated numbers are indicated by an asterisk).

Year	Pond	<i>Aeshna tuberculifera</i>		<i>Aeshna umbrosa</i>	<i>Plathemis lydia</i>	<i>Libellula pulchella</i>
		Adult Activity	Oviposition Marks			
1979	SM	0.2	256	0.0	134.5	4.4
	DR	0.0	0	0.0	1.2	0.0
	CH	8.0	4375*	0.8	16.0	4.3
	WF	6.0	3723*	0.6	78.2	5.0
	PR	19.4	9196*	2.0	34.8	7.0
1980	SM	9.8	2262	7.6	56.2	5.9
	DR	0.0	673	4.8	0.2	0.0
	CH	6.6	2654*	1.0	8.4	2.5
	WF	25.6	34056*	15.3	61.5	0.1
	PR	0.0	61*	0.6	7.3	3.6

Table 2. Spearman rank correlation coefficients for the relationship between the number of exuviae collected and (1) previous reproductive input, or (2) subsequent adult activity.

Correlation between number emerging and:	<i>Aeshna tuberculifera</i>			<i>Aeshna umbrosa</i>			<i>Plathemis lydia</i>			<i>Libellula pulchella</i>		
	N	rs	p	N	rs	p	N	rs	p	N	rs	p
Previous reproductive input	10	.21	NS	10	-.10	NS	10	.81	<.01	10	.54	NS
Subsequent adult activity	10	.44	NS	10	.18	NS	10	.85	<.01	10	.83	<.01

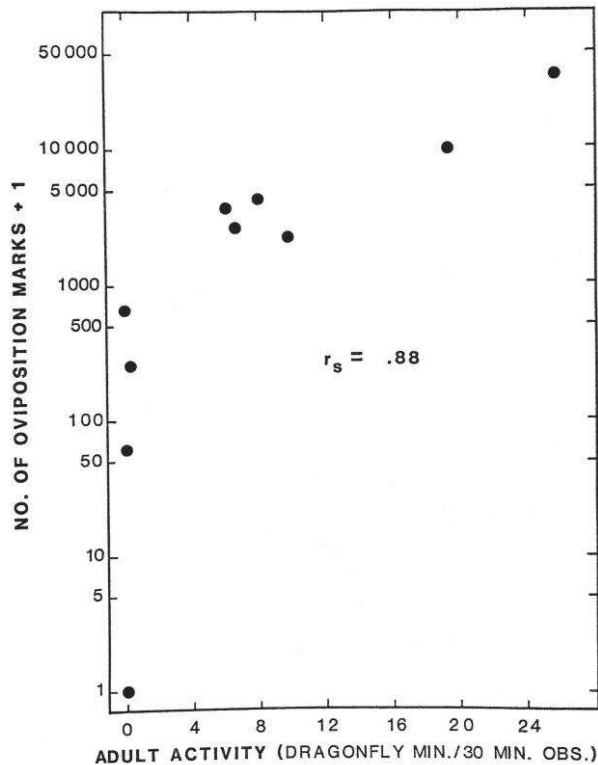


Fig. 4. Correlation between adult activity measurements and direct measures of reproductive input to ponds for *Aeshna tuberculifera*.

## DISCUSSION

### Patterns of Heterogeneity in Adult Production

Environmental heterogeneity clearly affected populations of all six dragonfly species investigated in this study. There were striking differences in adult production among ponds for all species and among years within ponds for all but *P. lydia*. In addition, annual fluctuations affected ponds independently, adding an important dimension to the heterogeneity of this system. Not only did ponds behave independently, but the various species also showed independent patterns of variability under the same set of environmental circumstances. The different responses by species as closely related as *A. tuberculifera* and *A. umbrosa* emphasizes the difficulty of relating arbitrary measurements of physical, chemical, or biotic factors in the environment to variation in environmental quality for a given species.

This independence among species also demonstrates the improbability that the observed variation was the result of systematic sampling biases. Although weekly

exuvial collections underestimated actual adult production at ponds (and did so to varying degrees for the two family groups), this bias could not have produced the large spatial and temporal variations observed. For instance, the absence of *L. pulchella* exuviae from 1980 WF samples cannot be explained by a low sampling efficiency at this pond in that year because *P. lydia* exuviae were found in their greatest abundance at WF during the same period. Similarly, the low number of *A. tuberculifera* exuviae at CH in 1979 contrasts with a high number of *A. umbrosa* exuviae at that pond in the same year. Similar arguments can be constructed for differences in the relative abundances of *C. shurtleffii* or *S. rubicundulum*.

A number of workers have reported significant spatial or temporal variations in dragonfly population size (Moore, 1964; Kurata, 1971; Lutz & McMahan, 1973) but none has examined these two components of variability simultaneously. For example, relative temporal stability of odonate populations such as was found for *P. lydia* in this study, has been reported for other species from studies of individual ponds, but these do not provide information on spatial heterogeneity among ponds (Macan, 1977; Ubukata, 1981).

### Patterns of Heterogeneity in Adult Activity

There was extreme variation in adult activity among ponds for all species. For *P. lydia* and *L. pulchella*, this variation was related to the number of adults emerging at a pond, and deceptively suggests a functional relationship between the emergence population and the breeding population at a given pond. However, this correlation is not causative. Long-distance dispersal of adults, which is presumed to occur in odonates in general (Jacobs, 1955; Corbet 1962, 1980; Moore, 1964), has been demonstrated specifically in this system (Halverson, 1983). Such dispersal necessarily disassociates the adult breeding population from the emerging population at a pond. We interpret the observed variation in adult activity among ponds as representing behavioral responses of adults to varying environmental conditions at each pond. Some ponds attracted adults which accumulated there and elevated adult activity levels (e.g., *P. lydia* at SM), while other ponds failed to attract adults (e.g., DR). Consistent attraction of adults over several years to particular ponds which were also highly productive, resulted in the correlation of adult activity and emergence for *P. lydia* and *L. pulchella*.

Mean adult activity at a pond was a very accurate indicator of relative reproductive input at least for *A. tuberculifera*. This was demonstrated by the highly significant positive correlation between activity and the

number of oviposition marks at a pond (Fig. 3). Furthermore, mean adult activity should have been a less accurate measure of reproductive input for *A. tuberculifera* than for the other three species because a significant portion of oviposition by *A. tuberculifera* was performed by solitary females near dusk (Halverson, 1984), a time of day when adult activity was difficult to monitor. In contrast, nearly all oviposition by the other species (particularly *P. lydia* and *L. pulchella*) occurred during the middle of the day (Campanella & Wolf, 1974; Pezalla, 1979; T. G. Halverson, pers. obs.). Thus, we are confident that mean adult activity level provided a very accurate indicator of relative reproductive input for the species in this study.

#### Causes of Variation in Adult Production

Variation in production of adult dragonflies may result from variation in the number of eggs which are deposited in a pond, or from variation in the survival of those eggs or resulting larvae. Our data indicate that both factors were important in causing the differential patterns of emergence in this system.

In spite of the fact that variation in adult activity was observed for all species, this variation did not provide a general explanation for variation in the production of adults. Correlations between adult activity (= reproductive input) and subsequent emergence were generally low and not statistically significant for three of the four species examined. These results indicate that other environmental factors (i.e., those affecting survival of eggs and larvae in the ponds), must have been important in determining patterns of adult production in these species. The high correlation between reproductive input and subsequent emergence which was found for *P. lydia*, on the other hand, implies that most of the observed variation in emergence for this species can be explained by differential reproductive input. Nevertheless, direct observation and experimental evidence has shown that these same ponds were, in fact, variable in their ability to support larvae of *P. lydia* as well as the other three species (Halverson, 1983).

#### CONCLUSIONS

The number of dragonflies emerging from the five study ponds was highly variable and independent over the four-year period. Only *P. lydia* showed spatial and temporal predictability in emergence and adult activity. Variation in population size was the result of factors acting independently at both the aquatic and terrestrial stages of the dragonfly life cycle. We contend that variation in egg and larval survival is the major factor affecting emergence population size in this system, while

behavioral responses of adults, leading to immigration and emigration, are the major cause of variations in the size of breeding populations. The dynamics of the dragonfly populations at the individual ponds can be explained by these parameters of individual recruitment and loss.

#### ACKNOWLEDGMENTS

We thank J. Dimuzio, C. Pals, A. Pabst, D. Parr, and L. Rouch for assistance in the field and L. Douglas, E. Russek, and the Washington Computer Center for help with statistical analyses. We are also grateful for the many discussions with members of the ecology group at the University of Maryland, especially D. Allen, K. Berven, R. Denno, R. Fritz, B. Mock, D. Morse, and W. Walton. This research was supported in part by NSF grants DEB 76-20326, DEB 77-04817, DEB 78-10832, and DEB 80-05080, and in part by the Department of Zoology, University of Maryland.

#### LITERATURE CITED

- Andrewartha, H. G., & L. C. Birch. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago. 793 pp.
- Berven, K. A. 1982. The genetic basis of altitudinal variation in the Wood Frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution* 36: 962–983.
- Berven, K. A., D. E. Gill, & S. J. Smith-Gill. 1979. Countergradient selection in the Green Frog, *Rana clamitans*. *Evolution* 33: 609–623.
- Birch, L. C. 1957. The role of weather in determining the distribution and abundance of animals. *Cold Spring Harbor Symposium of Quantitative Biology* 22: 203–218.
- Campanella, P. J., & L. L. Wolf. 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) I. *Plathemis lydia* (Drury). *Behaviour* 51: 49–87.
- Corbet, P. S. 1962. *A Biology of Dragonflies*. H. F. and G. Witherby Ltd., London. 247 pp.
- Corbet, P. S. 1980. Biology of Odonata. *Annual Review of Entomology* 25: 189–217.
- Dixon, A. F. G. 1979. Sycamore aphid numbers: the role of weather, host and aphid. Pp. 105–121 *In* R. M.



- Anderson, B. D. Turner, & L. R. Taylor (eds.), Population Dynamics. 20th Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford, England.
- Dragonfly Society of the Americas. 1996. Common names of North American dragonflies and damselflies. Supplement to *Argia* 8(2): 4 pp.
- Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechnie, & L. E. Gilbert. 1975. Checkerspot butterflies: a historical perspective. *Science* 188: 221–228.
- Fraser, D. F. 1976. Coexistence of salamanders in the genus *Plethodon*: variation of the Santa Rosalia theme. *Ecology* 57: 238–251.
- Gill, D. E. 1978. The metapopulation ecology of the Red-spotted Newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48: 145–166.
- Gill, D. E., K. A. Berven, & B. Mock. 1983. The environmental component of evolutionary biology. Pp. 1–36 *In* C. E. King & P. A. Dawson (eds.), Population Biology: Retrospect and Prospect. 41st Annual Biology Colloquium, Oregon State University, Corvallis.
- Halverson, T. G. 1983. The evolution of dragonfly life histories in heterogeneous environments. Unpublished Ph. D. thesis, University of Maryland, College Park. MD. 134 pp.
- Halverson, T. G. 1984. Autecology of two *Aeshna* species (Odonata) in western Virginia. *Canadian Entomologist* 116: 567–578.
- Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36: 566–586.
- Kurata, M. 1971. The life history of *Gomphus melaenops* (Gomphidae). *Tombo* 14: 6–11.
- Lutz, P. E., & E. A. McMahan. 1973. Five year patterns of emergence in *Tetragoneuria cynosura* and *Gomphus exilis* (Odonata). *Annals of the Entomological Society of America* 66: 1343–1348.
- Macan, T. T. 1977. A twenty-year study of the fauna in the vegetation of a moorland fish pond. *Archives für Hydrobiologie* 81: 1–24.
- Moore, N. W. 1964. Intra- and interspecific competition among dragonflies (Odonata). An account of observations and field experiments on population density control in Dorset, 1954–60. *Journal of Animal Ecology* 33: 49–71.
- Pezalla, V. M. 1979. Behavioral ecology of the dragonfly *Libellula pulchella* Drury (Odonata: Anisoptera). *American Midland Naturalist* 102: 1–22.
- Taylor, R. A. J., & L. R. Taylor. 1979. A behavioral model for the evolution of spatial dynamics. Pp. 1–27 *In* R. M. Anderson, B. D. Turner, & L. R. Taylor (eds.), Population Dynamics. 20th Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford, England.
- Ubukata, H. 1981. Survivorship curve and annual fluctuation in the size of emerging population of *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Japanese Journal of Ecology* 31: 335–346.