Odonatologica 27(2): 189-199 *June 1, 1998*

A FIVE YEAR SURVEY OF AN ODONATE COMMUNITY INHABITING A NORTH VENEZUELAN MOUNTAIN STREAM

J. DE MARMELS
Instituto de Zoología Agrícola, Facultad de Agronomía,
Universidad Central de Venezuela, Apartado 4579, Maracay 2101-A, Venezuela

Received May 12, 1997 / Reviewed and Accepted August 6, 1997

Monthly counts of adult odon. were carried out along a transect following a forested mountain stream, «Quebrada Pasaquire». 17 of the 41 spp. recorded were considered for evaluation. The average monthly abundance curve of spp. such as *Euthore fasciata* Sel., *Archilestes grandis* (Ramb.), *Philogenia cassandra* Sel., *Progomphus abbreviatus* Belle, *Brechmorhoga rapax* Calv. and *Libellula herculea* Karsch matches the climogram of the study area, e. g. these spp. are markedly seasonal, with high adult abundances in the wet season, and low numbers in the dry season. On the other hand the presence of adult *Hetaerina capitalis* Sel. and *H. cruentata* (Ramb.) did not seem to be correlated with season. *Macrothemis pseudimitans* Calv. and *Micrathyria venezuelae* De Marmels appeared to be more common in the dryer months, but their population sizes were always low. Based upon the data of this survey it can be stated that the odon. community studied has a persistent structure, relatively low variabilities of population densities, and is stable. The evidence includes persistence of the dominant taxa over at least 5 generations, typical standard deviations of the logarithm of population sizes, as well as high and significant year-to-year rank concordance. *Cannaphila vibex* (Hag.) and *Progomphus abbreviatus* became more common during this survey, while *Andaeschna rufipes* (Ris) shifted towards local extinction. However, 5 yr may not be sufficient to show such trends to be irreversible: in almost all species at least one trend reversal occurred during the survey. Some of the potential ecological mechanisms underlying the constancy and stability of this odonate community are discussed and it is suggested that abiotic factors, such as periodical floods in this lotic habitat, may be of some concern.

INTRODUCTION

It is a principal aim of ecologists and conservationists to identify the mechanisms responsible for persistence and stability of natural communities. However, the question if and how the persistence and stability can at all be assessed and measured adequately is rarely posed. CONNELL & SOUSA (1983) emphasize that for this purpose, long-term density records over at least several generations for two or more species in a community, are needed. Such studies are rare. In a recent survey JOHNSON & CROWLEY (1989) found that a larval odonate community in North America was persistent and remained stable over a ten year period.

Similar studies of neotropical odonate assemblages have not been made so far and little is known even about phenology and abundance of common species, let alone the persistence and stability of natural communities in space and time.

In this paper I shall present a five year record (for most species fragmentary data of a sixth year are available) of monthly individual counts in an adult dragonfly community inhabiting a North Venezuelan mountain stream. 17 of the 41 species recorded were considered for quantitative analysis. They represent 98 % of the total odonate population and include the most common as well as a few rare species, providing these latter were autochthonous and easily recorded with the method used. It is noteworthy that only 9 of these 17 species averaged each >1 % of the total odonate population. The taxa not analized quantitatively (2 % of the total odonate population size) are discussed separately. A special case is *Aeshna cornigera* Brauer. In this dragonfly the counting method proved unsuitable for the assessment of abundance and, therefore, this species had to be excluded from the analysis, in spite of its autochthony and relative abundance, as suggested by the exuviae found (Fig. 36). All species recorded are probably univoltine.

The first aim of this study was to establish flight periods and relative abundances of the species present. In a second term, the year-to-year variability (or constancy, including persistence) of the population sizes is interpreted as reflecting the antagonism between stability and intensity and/or frequency of environmental perturbations (i.e. resistance or insensitivity to disturbance; resilience or ability to recover from disturbances; see CONNELL & SOUSA, 1983; JOHNSON & CROWLEY, 1989, and references cited therein).

To evaluate the effectiveness of any underlying resistance and resilience in neutralizing disturbances, three different measures of year-to-year variability are applied: persistence of taxa through at least five generations, standard deviations of logarithms of population sizes, and a test of population rank-concordance across years. Several possible mechanisms which might control the apparent stability of the odonate assemblage studied are also suggested. However, evidence from field observations is not conclusive.

STUDY AREA

«Quebrada Pasaquire» (alt. ca 900-1100 m, El Avila National Park, Miranda State, Venezuela) is one of the numerous, small, rocky streams with permanent water, which drain the southern slopes of the Central Coastal Cordillera, just north of Venezuela's capital, Caracas. The survey was carried out along this stream, the lower end of which is marked by a large drainage tube which «swallows» the stream at the «Boyacá» Highway. In the far upper course an insurmountable orographic obstacle puts an end to further access. Distance between the two ends is perhaps about a kilometer. The stream is embedded between rather steep, forested slopes, but these slopes loose tree cover at some elevation above the stream. Small cascades, pools and rocky terrasses alternate with rather plain stretches with sandy bottom and leaf litter. Only for the last thirty meters of the lower course the stream flows through open savannah. There are no lateral affluents.

The flora of «El Avila» National Park has been comprehensively treated by STEYERMARK & HUBER (1978). The forest of the study site is referable to the «residual gallery forest».

The climate of the valley of Caracas, including the lower southern slopes of the Coastal Cordillera with the study site, is characterized by a marked dry season between the end of December and the beginning of May, and a wet season with abundant precipitation during the rest of the year. Figure 1 shows the climogram (10 yr average) of San José del Avila (999 m elevation), a place situated a few kilometers west of the study area. The annual average temperature at this site is 21°C, the annual average precipitation 815.7 mm (STEYERMARK & HUBER, 1978; WALTER & MEDINA, 1971).

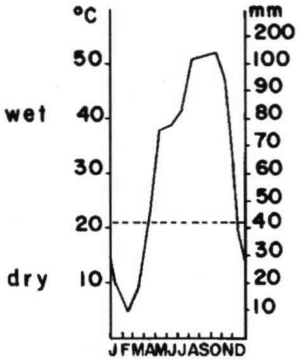


Fig. 1. Climogram (10 year average) of San José del Avila, alt. 999 m (after STEYERMARK & HUBER, 1978, modified).

METHODS

Monthly dragonfly counts were carried out during more than 5 years (part of 1980 and 1981-1985); along a transect following the stream, between 9.30 a.m. and 2.30 p.m., under reasonably good weather conditions. All odonate species observed during the ascent along the transect were listed and the adult individuals counted. The transect was interrupted whenever a cloud prevented sunshine from reaching the bottom of the small canyon for longer than one minute. Usually, after a break at the upper end of the transect, all dragonflies were counted again during the descent. In these cases, and if more than one transect had been carried out during the same month, only the count with the highest number of individuals was evaluated, for each species separately. Larvae and exuviae were also recorded, but not considered for quantitative analysis.

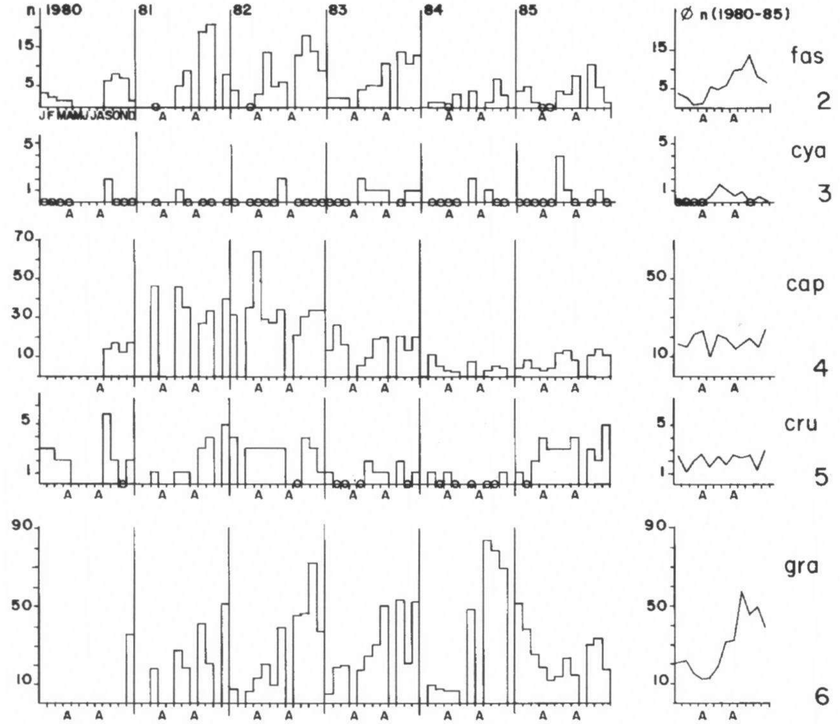
The transect method, as used in the present work has proven very successful for estimating butterfly abundances (MOORE, 1975; POLLARD et al., 1975; DOUWES, 1976; DE MARMELS, 1990a), but has rarely been applied to odonates (MOORE, 1953; DE MARMELS & SCHIESS, 1977), though many workers using «abundance classes» seem to obtain their data in a similar way.

To show the persistence of the populations composing the odonate assemblage studied, the CONNELL's & SOUSA's (1983) principle is applied, which requires that the population be present permanently, allowing for interrupted periods that do not exceed one generation.

It is of basic interest to know whether there are any detectable trends in the abundance through time in any species. Such trends are visualized by graphing the average population size (i. e. total of individuals divided by the number of transects) of each of the 17 species, for each year.

To measure the variability in population size of each of the 17 species between 1981 and 1985 (i.e. through five generations), and to permit the comparisons with the variabilities of other natural populations, the standard deviations of the logarithms (base 10) of the total yearly average population sizes were calculated.

In stable communities a raisonable maintenance of rank for relative abundances through time of the taxa involved should be expected. Following JOHNSON & CROWLEY (1989), the persistent-structure prediction can be tested by applying Kendall's rank- concordance test (SIEGEL, 1978). Therefore, the rank-concordance coefficient W was calculated and its statistical significance evaluated to compare rank structure of the 17 analyzed taxa across the five years data.



Figs 2-18. Phenology and abundance of 17 odonate species of Quebrada Pasaquire between 1980 and 1985 (left), and monthly average abundances (right). – (2) *Euthore fasciata*; – (3) *Cora cyane*; – (4) *Hetaerina capitalis*; – (5) *H. cruentata*; – (6) *Archilestes grandis*; – (7) *Megapodagrion venale*; – (8) *Philogenia cassandra*; – (9) *Argia oculata*; – (10) *Progomphus abbreviatus*; – (11) *Andaeschna rufipes*; – (12) *Brechmorhoga rapax*; — (13) *B. vivax*; – (14) *Cannaphila vibex*; – (15) *Dythemis multipunctata*; – (16) *Libellula herculea*; – (17) *Macrothemis pseudimitans*; – (18) *Micrathyria venezuelae*. – [n = number of individuals of the highest count, for each month; – no column = no transect; – 0 = transect with no observation; – Ø n = six year average of n].

RESULTS

A total of 41 species were recorded at least once at the study site (including records from 1979 and 1980). The abundance and seasonality of 17 of them are presented, based on adult counting during at least five (occasionally six) years (Figs 2-18). A comparison of the abundance curves (monthly averages) of the 17 species with the local climogram (Fig. 1) shows that taxa, such as *Euthore fasciata* (Fig. 2), *Archilestes grandis* (Fig. 6), *Philogenia cassandra* (Fig. 8), *Progomphus abbreviatus* (Fig. 10), *Brechmorhoga rapax* (Fig. 12) and *Libellula herculea* (Fig. 16) are markedly seasonal, with high adult abundances in the wet season, but few

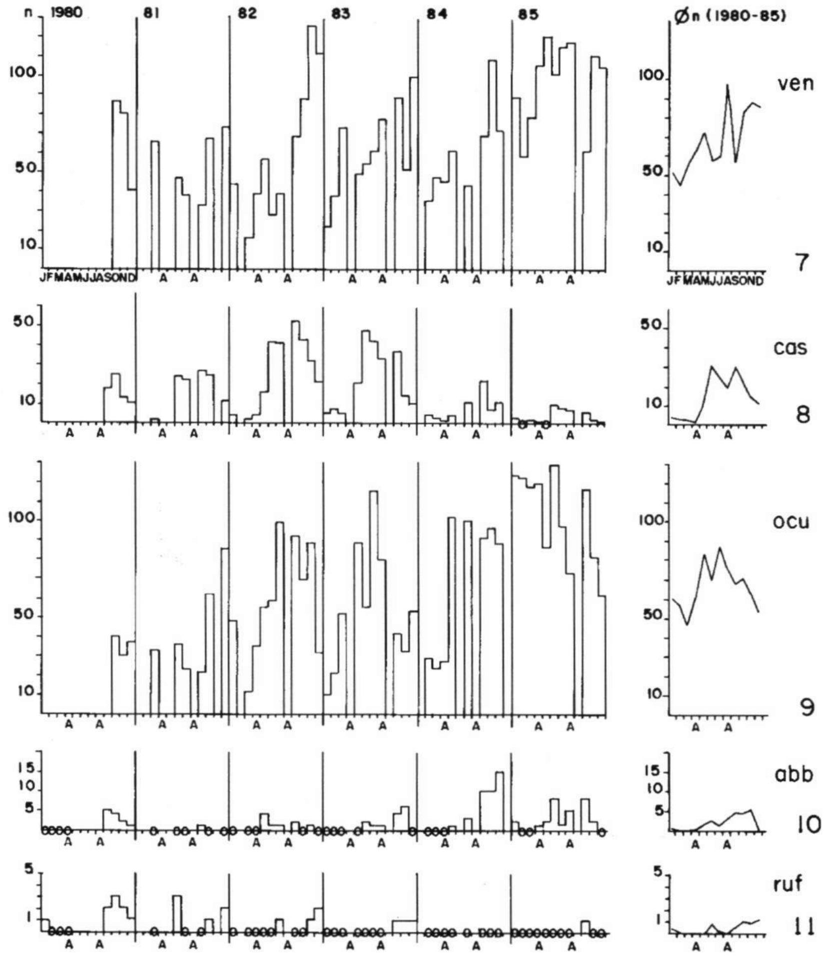


Fig. 2-18, continued

or no individuals on the wing in the dryer months of the year. On the other hand, the abundance curves of *Hetaerina capitalis* (Fig. 4) and *H. cruentata* (Fig. 5) exhibit irregular fluctuations, not correlated with the seasons. *Macrothemis pseudimitans* (Fig. 17) and *Micrathyria venezuelae* (Fig. 18) are more common in the dry season, but their overall abundances were low and the local status of the latter species is not clear beyond any doubt. Though the observed males were territorial, no females, larvae or exuviae were ever found. 15 of the 17 species were recorded during the whole period. The remaining two, viz. *Micrathyria venezuelae* and *Andaeschna rufipes*, were not observed in 1982 and 1984, respectively, but

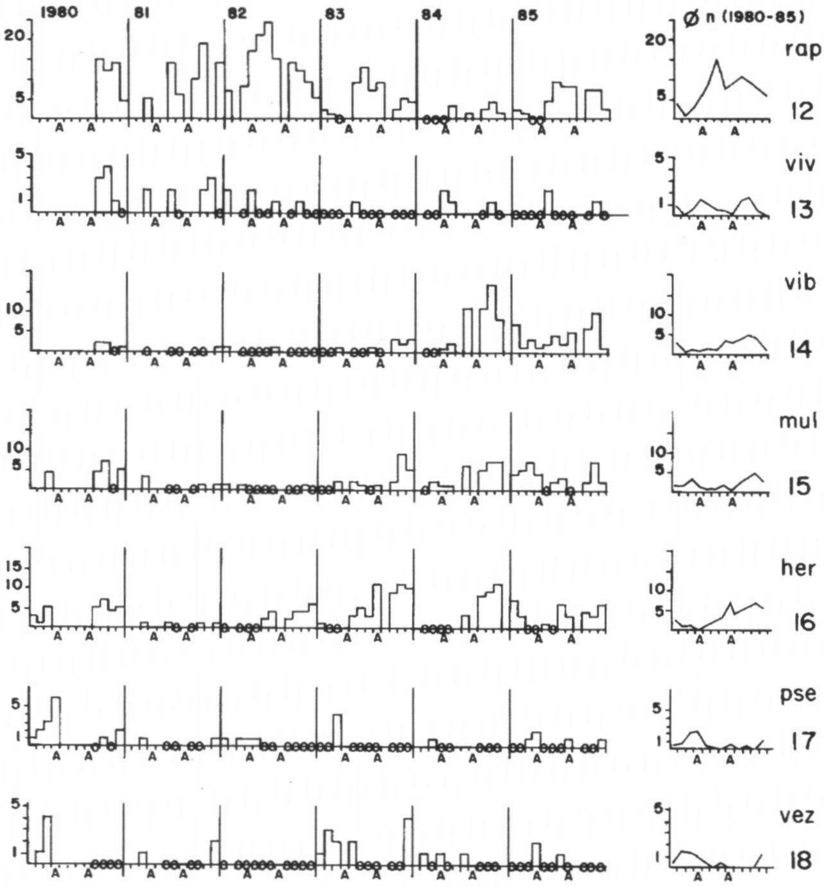


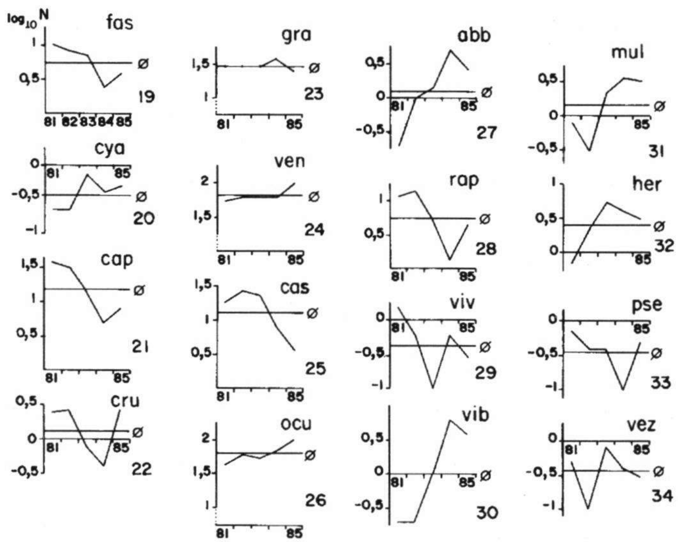
Fig. 2-18, continued

each «returned» in the following year. As the adults of «rare» species might occasionally fail to be sampled by chance alone, an eye should be kept on their larvae and/or exuviae as well. Indeed, the presence of at least *A. rufipes* could be demonstrated also for 1984, through the record of exuviae. Nevertheless, this species appeared to be on the verge of local extinction (Fig. 37). On the other hand, *Cannaphila vibex*, which was rather scarce during 1980-1983, became more common in the years to follow (Fig. 30). In general terms, the adult odonate population of Quebrada Pasaquire can be considered persistent: it is composed of essentially the same set of species year after year, with no (if any) species absent for longer than one generation (CONNELL & SOUSA, 1983).

A glance at Figures 19-34 and 37 shows rather diverse trends of abundance through time in the populations studied. Noteworthy is the occurrence of at least one apparent trend reversal during the five year survey in about half of the 17 species.

Figure 35 compares the standard deviations of logarithms of adult odonate population sizes separated by one generation to the frequency distribution reported by JOHNSON & CROWLEY (1989, fig. 14 B) of a larval odonate population in North America. The Venezuelan taxa exhibit generation-to-generation variabilities in population size closely similar to those reported by these authors [$\chi^2_4 = 5.5$, $P > 0.05$, when comparing the 9 dominant species; and $\chi^2_4 = 4.7$, $P > 0.05$ when comparing all 17 species analyzed]. The species which was most variable (*Cannaphila vibex*) shows a considerable increase from close to zero in the first years to high abundances in the last years of the survey (Fig. 30). Among the other four most variable species, *Progomphus abbreviatus* (SD = 0.527) and *Dythemis multipunctata* (SD = 0,461) show an almost identical trend (Figs 27, 31). *Andaeschna rufipes* (SD = 0.438) was slipping into local extinction (Fig. 37), and *Brechmorhoga vivax* (SD = 0.438) was rare (Fig. 29).

There is highly significant concordance of ranks for relative abundance: Kendall's W = 0.825, P < 0.001, for the 9 dominant species; W = 0.73, P < 0.001, for all 17



Figs 19-34. Trends of abundance along five years of survey (1981-1985) for 17 odonate species of Quebrada Pasaquire, based on the logarithms of the yearly average abundances: (19) *Euthore fasciata*; – (20) *Cora cyane*; – (21) *Hetaerina capitalis*; – (22) *H. cruentata*; – (23) *Archilestes grandis*; – (24) *Megapodagrion venale*; – (25) *Philogenia cassandra*; – (26) *Argia oculata*; – (27) *Progomphus abbreviatus*; – (28) *Brechmorhoga rapax*; – (29) *B. vivax*; – (30) *Cannaphila vibex*; – (31) *Dythemis multipunctata*; – (32) *Libellula herculea*; – (33) *Macrothemis pseudimitans*; – (34) *Micrathyria venezuelae*. – [N = yearly total of individuals divided by number of transects, Ø = five year average of N].

species analyzed. Thus, the adult odonate assemblage of Quebrada Pasaquire retains detectably persistent rank structure, despite the undoubted importance of environmental disturbance.

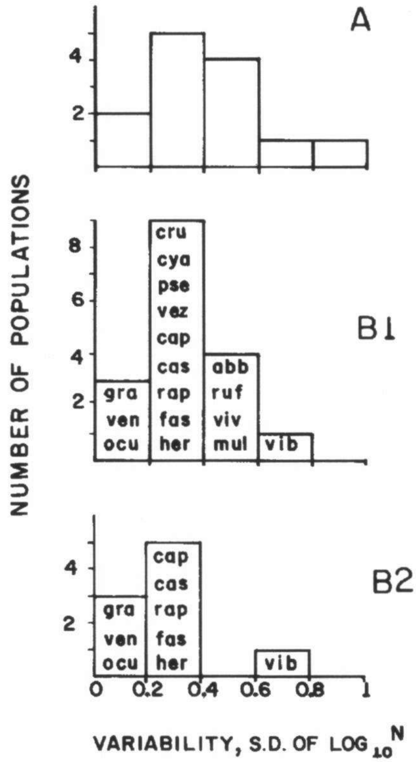
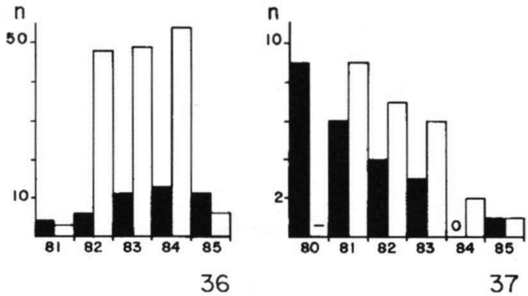


Fig. 35. Comparison of generation-to-generation variability in population sizes for (B2) the 9 dominant odonate taxa of Quebrada Pasaquire (1981-1985), and (B1) all 17 taxa of the same community, with (A) the odonate population of Bays Mountain Lake, Tennessee (USA) studied by JOHNSON & CROWLEY (1989): abb = *P. abbreviatus*; – cap = *H. capitalis*; – cas = *P. cassandra*; – cru = *H. cruentata*; – cya = *C. cyane*; – fas = *E. fasciata*; – gra = *A. grandis*; – her = *L. herculea*; – mul = *D. multipunctata*; – ocu = *A. oculata*; – pse = *M. pseudimitans*; – rap = *B. rapax*; – ruf = *A. rufipes*; – ven = *M. venale*; – vez = *M. venezuelae*; – vib = *C. vibex*; – viv = *B. vivax*.

DISCUSSION

Why are most of the species of this lotic habitat highly seasonal, with their larval stages concentrated in the dry season, in spite of the permanently tropical climate? One possible explanation lies in the violent floods, which occur in the wet season and may considerably decimate the larval populations. It is interesting to see that most of the savannah species inhabiting the Orinoco plains («llanos») have a shifted life cycle, with the adults on the wing during the whole of dry season, when the savannah is drying out completely. The adults can then be seen in gallery forest, even far from their breeding habitats in mountainous areas, where they aestivate. At the beginning of the rains they move back to the now flooded savannah, for oviposition, hence passing their larval stages exclusively in the wet season. The aestivating adults of various savannah species were recorded during dry season in the Quebrada Pasaquire then and when (see below).

The present study suggests that the adult odonate community of Quebrada Pasaquire meets three main criteria for stability and persistence: (1) The 17 analyzed species, representing 98 % of the total of individuals counted in this assemblage during 1981-1985, were present in all years, or reappeared after one season of absence (*Micrathyria venezuelae*). – (2) Their population sizes seemed to fluctuate (if at all) within some sort of extreme limits, a fact which may indicate



Figs 36-37. Relation between number of adults (solid columns) and number of exuviae (empty columns) recorded in the years 1980 (1981)-1985 for two species of Aeshnidae: (36) *Aeshna cornigera*; – (37) *Andaeschna rufipes*. [0 = sampled, but not recorded; – n = number of individuals].

«stable limit cycles» (CONNELL & SOUSA, 1983). Only few populations suggest any definite trend in status change, although the comparatively short time span (5 or 6 years) may be insufficient to interpret these as irreversible. – (3) The apparently stable populations form an assemblage with a highly concordant structure of ranked abundances among years (Kendall's W = 0.825 for the 9 dominant species; 0.73 for all 17 species analyzed). These values match the value found by JOHNSON & CROWLEY (1989; W = 0.753) for their North American larval community, a value which was shown by these authors to be among the highest published for any aquatic assemblage.

JOHNSON & CROWLEY (1983) identified interference competition among larvae, mutual predation (incl. cannibalism), and predation and competition by insectivorous fish as the mean mechanisms responsible for the apparent stability and constancy of the North American species assemblage they studied.

In the present work only adult dragonflies were considered. It can be assumed that several predators (e.g. spiders, frogs, birds) take a toll on emerging and ovipositing odonates, but their impact on population size of any particular species is not known. Probably, the factors acting upon the larvae are far more important.

At the Venezuelan study site only three species of fish were recorded, viz. *Poecilia reticulata* Peters, *Rivulus bondi* Schultz (DE MARMELS, 1978) and *Trichomycterus mondolfii* (Schultz) (MAGO LECCIA, 1968). Only the first of these was moderately common. Additional taxa may be present, but have escaped the observation. As to the aquatic Heteroptera and the odonate larvae themselves, especially the Aeshnidae and Libellulidae are probably more important predators.

The abiotic factors should not be neglected. Occasional floods, following heavy rainfall at the peak of the wet season (August-November), may wash out the whole stream bed. On the 2nd and again on the 18 September 1980, a sudden rainstorm turned the peaceful stream into a wild torrent, which led to considerable modifications of its bed. Curiously, the abundances of most species remained seemingly unaffected in the following year (Figs 2-18). Only *Progomphus abbreviatus*, *Libellula herculea* and *Dythemis multipunctata* exhibited a breakdown of their populations, but if these collapses were a consequence of the floods is not known. Again, in October 1984, in the wake of the hurricane «Klaus», the Quebrada Pasaquire flooded. Nevertheless, the sizes of most populations seemed unaffected in 1985. As most species are on the wing in the wet season, they probably manage to assure their offspring for the following year, ovipositing after the floods.

REVIEW OF THE 24 NOT-ANALYSED SPECIES

Hetaerina occisa Sel.; stray. – 1979: X (1 ♂); – 1983: V, VI, X, XI – and 1985: I, V (1 specimen resp.).
Lestes tenuatus Rambur; stray. – 1979: X (1 ♂).
Acanthagrion dichrostigma DeMarmels; stray. – 1984: X (1 ♀).
A. fluviatile (De M.); aestivating. – 1984: III (1 ♀, pale form; see DE MARMELS, 1990b).
A. vidua Sel.: pioneer species, restricted to extreme inferior portion of stream in open savannah exposed to frequent human intervention (fire, pollution, trampling), therefore not persistent, and marginal. – 1980: II, IX (2 specimens resp.); X (1), XI (2), XII (3); – 1982: V (1); – 1983: III, VIII (1 specimen resp.).
Anisagrion inornatum Sel.; stray. – 1980: I (1 ♀, immature).
Argia cupraurea Calvert: stray. – 1980: II, IV, IX (1 ♂ resp.); – 1983: III (1 ♂); – 1984: VII (2 ♂).
Leptobasis vacillans Sel.; aestivating. – 1984: III (1 ♂, pale form; see DE MARMELS, 1990b).
Aeshna cornigera Brauer.: autochthonous and persistent. The total of adults recorded did not reach 0.5% of the total adult odonate population, but the exuviae found indicate that the actual percentage is considerably higher (Fig. 36). The (larval) predatory impact of this aeshnid on the larvae of the remaining species of the assemblage may therefore be a controlling factor of some concern.
Andaeschna andresi (Racenis); stray. – 1979: IX (1 ♀); – 1982: X (1 ♀).
Coryphaeschna diapyra Paulson; stray. – 1980: X (1♂).
Gynacantha membranalis Karsch; crepuscular, local status not known. – 1982: IX (1 ♂).
G. nervosa Ramb.: crepuscular; local status not known. – 1979: X (2 specimens); – 1980: I (1), XI (3); – 1982: XII (2 ♂); – 1984: III (1), XI (2); – 1985: X (1).
Triacanthagyna septima (Sel.); crepuscular, local status not known. – 1985: II (1 ♀).
Progomphus phyllochromus Ris: both records from exuviae. – 1979: VIII (1); – 1984: X (1).
Brechmorhoga nubecula (Ramb.): similar status as *A. vidua*. – 1979: IV, V (several); – 1980: II, III, IV (1 ♀ resp.); – 1981: XII (1); 1983: III (1), XII (1); 1985: III (1), V (1).
Erythrodiplax fusca (Ramb.); same status as *A. vidua*, but more common. The total of recorded specimens approached 0.5% of the total adult odonate population. The species was rare in 1984 and altogether absent in 1985.
E. melanorubra Borror; same status as *A. vidua*, but rarer. – 1979: II (1); – 1980: I, III (at least 1 specimen, resp.); – 1981: XII (1); – 1983: II (1♂).
E. umbrata (L.): aestivating. – 1980: II (1 ♀); – 1982: XII (1 ♀).
Erythemis vesiculosa (Fabr.); stray. – 1985: X (1).
Orthemis discolor (Burm.); same status as *A. vidua*; the total of counted adults did not reach 0.25% of the total adult odonate population. The species was not recorded in 1984.
Pantala flavescens (Fabr.); vagrant. – 1982: V (9 specimens); – 1984: IV (1).
Perithemis domitia (Dru.); autochthonous, but not persistent. – 1979: VI (1 ♂); – 1980: III (2 ♂); – 1981: III (1 ♂), X (1 ♂); – 1983: XII (3 ♂).
Tholymis citrina Hag.; crepuscular, local status not known. – 1979: VIII (1 ♀).

ACKNOWLEDGEMENTS

I feel deeply indebted to Dr ZURHILMA NARVÁEZ for her reiterated and friendly help with the solution of the statistical problems. Mr MARCO GAIANI gave linguistic support. He, Dr ARMANDO NOTZ and Dr AQUILES MONTAGNE, revised the manuscript. Mr JOAQUÍN SALCEDO realized the graphs. Financial support was received from the "Consejo de Desarrollo Científico y Humanístico"

(CDCH) of the Universidad Central de Venezuela. Last, but not least, Mrs MARÍA CONTRERAS offered her kind hospitality, including feeding and bathing facilities, every time I visited «my» odonate population in the Quebrada Pasaquire.

REFERENCES

CONNELL, J. H. & W. P. SOUSA, 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121 (6): 789-824.

DE MARMELS, J., 1981. Caballitos del Diablo del Parque Nacional El Avila. *Natura, La Salle* 1981 70/71)\: 26-29.

DE MARMELS, J., 1990a. Trockenstandorte als Habitatinseln für Schmetterlinge und Heuschrecken. *Ber. Eidg. Anst. forstl. Versuchswes.* 322: 3-57.

DE MARMELS, J., 1990b. Nota sobre dos «formas» en Acanthagrion fluviatile (De Marmels, 1984) y una descripción de la náyade (Odonata: Coenagrionidae). *Boln. ent. venez.* (N.S.) 5 (15): 116-122.

DE MARMELS, J. & H. SCHIESS, 1977. Zum Vorkommen der Zwerglibelle Nehalennia speciosa (Charp., 1840) in der Schweiz (Odonata: Coenagrionidae). *Vjschr. naturf. Ges. Zürich* 122 (3): 339-348.

DOUWES, P., 1976. An area census method for estimating butterfly population numbers. *J. Res. Lepid.* 15 (3): 146-152.

JOHNSON, D. M. & P. H. CROWLEY, 1989. A ten year study of the odonate assemblage of Bays Mountain Lake, Tennessee. *Adv. Odonatol.* 4: 27-43.

MAGO-LECCIA, F., 1968. Notas sobre los peces del Río Guaire. *In*: Estudio de Caracas, Vol. I, Ecología vegetal y fauna, cap. 5, pp. 229-256. Ediciones Biblioteca Univ. centr. Venezuela, Caracas.

MOORE, N. W., 1953. Population density in adult dragonflies (Odonata-Anisoptera). *J. Anim. Ecol.* 22: 344-359.

MOORE, N. W., 1975. Butterfly transect in a linear habitat 1964-1973. *Ent. Gaz.* 26: 71-78.

POLLARD, E., D. O. ELIAS, M. J. SKELTON & J. A. THOMAS, 1975. A method of assessing the abundance of butterflies in Monkswood National Nature Reserve in 1973. *Ent. Gaz.* 26: 79--88.

SIEGEL, S., 1978. *Estadística no paramétrica aplicada a la ciencia de la conducta.* Trillas, Mexico.

STEYERMARK, J. A. & O. HUBER, 1978. *Flora del Avila.* Soc. Venez. Cienc. Natur. Caracas.

WALTER, H. & E. MEDINA, 1971. Caracterización climática de Venezuela sobre la base de climadiagramas de estaciones particulares. *Boln. Soc. venez. Ciencias natur.* 29: 211-240.