Voltinism of Odonata: a review

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ABSTRACT

We classified 542 records of voltinism for 275 species and subspecies of Odonata according to three variables: geographical latitude, systematic position and habitat type. We sorted records according to voltinism – categories being three or more generations per year, two generations per year, one generation per year, one generation in two years and one generation in three or more years. We sought to correlate the voltinism of each record with latitude of the study site, thus demonstrating an overall negative correlation between voltinism and latitude. After allowing for phylogenetic similarity a negative correlation remains, although it decreases in strength after removal of taxonomic correlates, mainly between family and genus levels. A negative correlation exists at the species level within most families, with the exception of Lestidae. In genera for which we lacked data for latitudes 0-31°N/S no significant correlation between latitude and voltinism exists. In temporary waters most species complete at least one generation per year; most species in lentic perennial waters complete one generation or fewer; and the majority of species in lotic waters complete half a generation or less. We discuss the roles of exogenous and endogenous factors in influencing voltinism and identify those that may be affecting the correlation that the data reveal. We suggest projects that could improve understanding of voltinism in the context of seasonal regulation and the main types of odonate life cycle so far recognised.

INTRODUCTION

Knowledge of voltinism, i.e. the number of generations completed within one year in the field, is needed to understand how life cycles have become appropriate to environmental conditions in different regions especially with regard to latitude, and consequently how seasonal regulation has been achieved. We assume that the Odonata are primarily tropical in origin and that, while colonising temperate latitudes, they have retained components of warm adaptation. Thus, unlike the

Ephemeroptera and Plecoptera in temperate latitudes, many species of Odonata have evolved one or more diapause stages that confine cold-intolerant stages – i.e., the reproductively active adult, larvae in early stadia, and sometimes also the egg – to the warmer times of year (Pritchard 1982). Such diapause stages, commonly a feature of one or more larval stadia, occasionally occur also in the egg and/or the pre-reproductive adult. The ways in which the incidence and completion of dia-pause, be it obligate or facultative, are regulated by responses to temperature and photoperiod are manifold and complex (see review in Corbet 1999a: 230-237) and provide an essential template against which to interpret patterns of voltinism in Odonata. For example, at the highest latitudes, the constraints imposed by the brief, cool, variable summer may result in mechanisms of seasonal regulation that significantly extend (or shorten) the time needed to complete a generation as a result of cohort-splitting (Norling 1984a). This phenomenon can enable some 'out-lier' members of a hatching cohort to emerge either one year sooner (Corbet 1957c) or one year later (Norling 1984a) than the rest of the cohort. An estimate of voltinism for a given species in a given latitude (or habitat) will be subject to variation which will reflect lack of uniformity in the temporal status of members of each population, itself an expression of such variables as times of emergence, oviposition and hatching from the egg, and larval growth rate and the impact of predation. Voltinism in Odonata depends mainly on regulating mechanisms and on growth rates, which usually increase with increasing temperature up to a species-specific maximum (Krishnaraj & Pritchard 1995). We can therefore expect that, if climate does not require a diapause, ambient temperature will affect voltinism directly, and therefore at low latitudes development should be more rapid. In-creased development rate at lower latitudes has, for instance, been shown for *Onychogomphus uncatus* (Ferreras-Romero et al. 1999).

Latitude and its physical correlates probably have a major influence on voltinism. Our primary purpose in this review is to try to characterise such an influence, while making allowance for certain other variables, namely phylogeny and habitat. For tropical species in seasonal-rainfall areas, constraints imposed by obligate migration will obviously affect the voltinism of populations, though to an extent that may be almost impossible to measure. Our hypothesis in this review is that voltinism of Odonata correlates inversely with latitude.

Comparative analysis between species should take phylogeny into account because the life-history traits of a taxon may be ecologically constrained by the characters of its ancestors (Felsenstein 1985; Harvey & Pagel 1991). It has been shown, for instance, that growth rates and temperature optima are characteristic of groups of species (e.g. Krishnaraj & Pritchard 1995; Pritchard et al. 2000). Recent research indicates also that species-specific differences in ingestion rates are responsible for differences in growth rate (McPeek et al. 2001). In this article we therefore correct statistically for variation associated with phylogenetic affinity (cf. Harvey & Pagel 1991) before analysing for latitude effects.

A preliminary, broad analysis of voltinism in Odonata was presented by one of us (Corbet 1999a: table 7.2) without specifying the source data, and with the inten-tion of publishing those data, together with a more searching analysis, in due course. The present review fulfils that intention. A brief synopsis, foreshadowing, but not duplicating, parts of this review, was presented later (Corbet 1999b). Here we pre-sent an overview and analysis based on more than 250 publications on 275 species

and subspecies of Odonata. For this review we use the derivative terms 'univoltine' and 'bivoltine' to mean completing, respectively, one and two generations per year, 'multivoltine' to mean completing three or more generations per year, 'semivoltine' to mean completing one generation in two years and 'partivoltine' to mean completing one generation in more than two years.

HISTORIC OUTLINE

The earliest published record of voltinism in Odonata known to us is that of Jan Swammerdam. Referring to a species that was almost certainly *Gomphus vulgatissimus*, occupying a river in The Netherlands, he surmised that the species was semivoltine (Swammerdam 1758: 99, although the observation was made before 1669). Almost 100 years later John Bartram reported that the (exophytic) odonates he observed in Pennsylvania were univoltine: "The Eggs are soon hatch'd and the young Reptiles creep amongst the Stones and Weeds etc. and so continue [as] Water-Animals the greatest Part of the Year, until the Season comes round for their Appearance in the beautiful Fly ..." (Collinson 1750). Bartram did not (could not) assign a scientific name to the species he observed but if it was a species of *Sympetrum* his assertion about its univoltinism would have been correct. The first systematic study of the topic was by Wesenberg-Lund (1913) who investigated voltinism in Denmark by making field observations, including the inspection of two-weekly samples of larvae, and concluded that within a single population voltinism could vary from year to year. His conclusions were general, however, and he did not assign values for voltinism to any particular species, apart from correctly interpreting the univoltine life cycles of *Lestes dryas* and *L. sponsa* (Wesenberg-Lund 1913: 377). Tillyard used qualitative field observations to infer voltinism of some Australian Odonata, including *Austrolestes leda* (Selys) (Tillyard 1906), *Petalura gigantea* (Tillyard 1911) and *Anax papuensis* (Tillyard 1916). Portmann (1921) likewise used field observations to infer that *Anax imperator* in Switzerland was univoltine but did not present quantitative data to support this inference. Calvert, in his classic papers on larval development in Odonata, first (1929) considered growth rates only in the laboratory, but later (1934) used phenological data for several species of *Anax* to infer voltinism in the field. The first large-scale, systematic study of voltinism was launched by Münchberg in northern Germany in the late 1920s. He sampled larvae in nature at regular intervals throughout the year, recording their dimensions and state of development and placing these findings in the context of the flying season to infer the voltinism of several species of *Sympetrum* (1930a), Aeshnidae (1930b, 1936), Gomphidae (1932a), Corduliidae (1932b), and Lestidae (1933). Prominence was given to the topic of voltinism by the inclusion of findings by Münchberg (mainly) and Portmann in a popular book on German Odonata by Schiemenz (1953). Records of voltinism were included also in the book by Robert (1958), who reared several European species of Odonata. A new development occurred in the 1950s when information about growth rates and voltinism in the field was combined with knowledge of the temporal pattern of emergence to construct hypotheses regarding the responses controlling such phenomena as the synchronisation and seasonal placement of emergence and the contribution to voltinism of cohort splitting (Corbet 1957c). This led to an ecolo-

gical classification of Odonata based on the means they employ for achieving seasonal regulation (Corbet 1954; Corbet & Corbet 1958) and thus to a template for classifying their life cycles (Corbet 1960, 1999a: table 7.3).

Such templates for Palaearctic Odonata have been proposed by Corbet (1960: 143) and Norling (1975). Corbet recognised two main categories: spring and summer species, distinguished according to the presence or absence of a diapause in the final larval stadium. Norling (1975) likewise recognised two categories, distinguished according to the overwintering stage and voltinism. Both authors stressed the distinction between the obligatorily univoltine life cycle and the rest. Later, in a searching review of the relationship between voltinism and latitude, Norling (1984a) confirmed his recognition of two basic types of life cycle, venturing to explain the relationship between latitude and generation length in the context of the northern expansion of Odonata, with special reference to the induction of larval diapause by photoperiod. Corbet (2003), in proposing an hypothesis that would rationalise the existence of univoltinism at high latitudes, recognised three broad types of life cycle: Type 1: spring species; Type 2: summer species; and Type 3: obligatorily univoltine species.

Light was thrown on voltinism of tropical Odonata by Gambles (1960), Corbet (1962) and Kumar (e.g. 1972, 1976, 1979). Using the analogy of locust migration, elucidated by Rainey (1951), Corbet (1962: 195) hypothesised that several species of temporary-pool-breeding odonates in seasonal-rainfall zones in the Tropics (e.g. *Pantala flavescens*) were likewise travelling with the Inter-Tropical Convergence Zone (ITCZ), the rain-bearing frontal system, and were thereby being delivered to a succession of localities where rain was falling or about to fall. In this way it was hypothesised that such populations would be able to complete several generations in rapid succession, perhaps as many as five within a year, though in different localities (see Corbet 1999a: 219). This hypothesis has an important bearing on estimates of voltinism among tropical Odonata. So far this hypothesis has been sustained, evidence in support of it being persuasive (e.g. Corbet 1984) though unavoidably circumstantial. Here we assume that the hypothesis has not been falsified. Studies of non-migratory Odonata in wet/dry climates in the Tropics have also been exceptionally informative. Gambles (1960) showed that some species in Nigeria (at 9.68°N), e.g. *Lestes virgatus, Gynacantha vesiculata* and *Crocothemis divisa*, maintain a (regulated) univoltine life cycle which features a long-lived, siccatating adult and a drought-resistant egg for which the hatching stimulus is apparently wetting. Kumar (1972, 1976, 1979a), studying tropical-centred species at about 30°N, revealed similarly regulated univoltine life cycles in *Platylestes praemorsus* and *Bradinopyga geminata* and showed also that certain other non-migratory species, e.g. *Crocothemis servilia, Orthetrum sabina*, (apparently unregulated) exhibit facultative bivoltinism if suitable aquatic habitats are available during the dry season and also that the duration of larval development depends on ambient temperature, a phenomenon detected also by Jödicke (2003) in subtropical Tunisia at about 33°N. These observations by Kumar and Jödicke have provided valuable insights into the origins of seasonal regulation in low temperate latitudes, where temperature rather than rainfall serves as the dominant environmental variable. A study by Schnapauff et al. (2000) from rice fields in Greece reveals that bi- and multi-voltinism associated with habitat change from dry to wet season, e.g. in *Crocothemis erythraea* and *Sympetrum fonscolombii*, may be a general phenomenon at low temperate latitudes.

Patterns of voltinism in relation to life cycle and latitude on a global scale were discussed by Corbet (1999a: 217), citing 172 records representing 27 families. A crude analysis (making no allowance for life cycle) revealed that (as expected) tropical-centred species exhibit higher levels of voltinism than do temperate-centred species, but no attempt was made to seek a regression of latitude against voltinism among temperate-centred species, an omission we correct in this review. It is already known, from discrete observations, that several extrinsic factors, both abiotic (including latitude) and biotic, can modify voltinism within a species (Corbet 1999a: table A.7.2), but no correlation with latitude has previously been sought on a global scale.

METHODS

Data base

In the Appendix we present records of odonate voltinism, published and unpublished, available to us at the time of writing and from many parts of the world (Fig. 1). We included only those records that appear to us secure, but they vary widely in rigour and quality between two extremes: from the detailed, quantitative analysis of many successive samples of larvae taken during more than one year to a strong inference based on a single sample or on temporal patterns of emergence or flight. For example, the observation of emergence from a habitat known by the observer to have been available for oviposition no more than a year previously would in our view constitute reliable evidence of univoltinism. Similarly, the developmental stage of larvae remaining in a water body when annual emergence has just ended can yield useful information about voltinism in that population. There are several other considerations that affect the strength of generalisations about voltinism drawn from field data:
  (1) Voltinism is most readily determined for species that are consistently univoltine, such as most species of *Lestes* and *Sympetrum*, because the identity of size-groups is not blurred by cohort splitting.
  (2) When emergence or oviposition continues without interruption throughout the year, as in many tropical species, it may be difficult or impossible to infer voltinism in the field, except by elaborate analytical methods (see Yule 1996).
  (3) The practical difficulty of continuing a study for several consecutive years means that records for partivoltine species with long life cycles tend to be under-represented.
  (4) Most publishable studies are conducted at habitats with large populations because they are liable to yield clear-cut results; this leads to populations in secondary and latency habitats (Sternberg 1995; Corbet 1999a: 11) being under-represented.
  (5) An investigator's personal circumstances seldom permit a study of voltinism to continue beyond one or two years; accordingly temporal variation in voltinism will be understudied, especially in partivoltine species.
  (6) Evidence for voltinism may differ widely in quality from one study to another, presenting the challenge of assigning greater weight to some records than to others when interpreting data.

Having regard to the last consideration, and though confident in the security of the data we have cited, we advise any investigator intending to use information in the Appendix for comparative purposes to consult the original sources. In some cases, e.g. when citing findings by Aguesse (1955) and Montes et al. (1982), we accepted the authors' unequivocal statements about voltinism without being provided with evidence. Some other reports, though consistent with one type of voltinism, do not explicitly exclude alternatives. For example, observations by some authors describe adults of *Uracis imbuta* leaving rain forest en masse and rapidly attaining reproductive maturity at the onset of the rains, a pattern of behaviour consistent with that of species having a regulated, univoltine life cycle of the A.2.1.2 type (Corbet 1999a: 220). However, such observations do not exclude the (unlikely) possibility that such populations might complete more than one generation in a year were larval habitats to be available. Accordingly we omitted observations of this kind from the Appendix.

On the assumption that climatic regimes are likely to result in major differences between species in different latitudes, we used degrees of latitude for the analyses (see below). Where possible we derived the latitude from the original article or from the author directly. Failing this, we tried to reconstruct the latitude from the locality information provided, e.g. the nearest town, using an atlas or the Internet. Therefore the information is variably precise; we recorded latitude to the nearest 0.01 degree, thus adopting the normal format for geographical information systems. Altitude data, though obviously relevant, could not be obtained with acceptable accuracy. This we regret, because (as expected) altitude can affect voltinism (Deacon 1979).

Beyond the primary segregation according to latitude, we classified individual records according to two other variables that we predict will impose constraints that prevent voltinism being a simple resultant of the main physical correlates of latitude. These variables are (1) systematic position and (2) larval habitat. We gave weight to systematic position (i.e. phylogenetic affinity, see below) to allow for patterns compellingly exemplified by taxa such as *Lestes* and *Sympetrum*, many members of which exhibit a univoltine life cycle (type B.2.1.2), usually maintained across a wide latitudinal range by an obligate diapause in the egg and/or the adult,
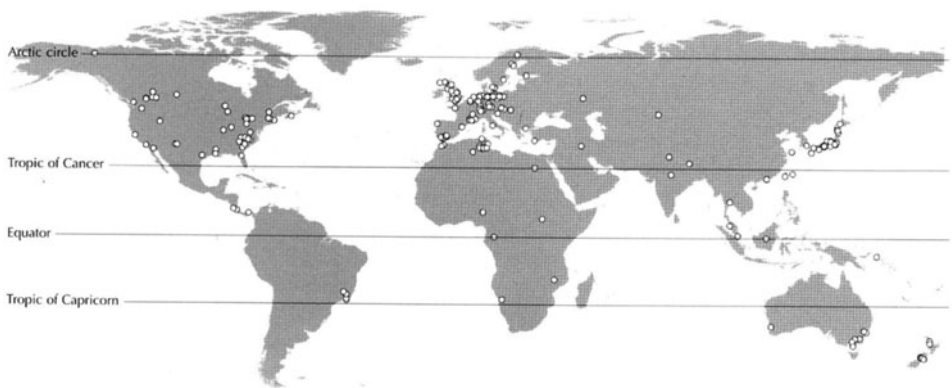

Figure 1: Distribution of localities from which data of Odonata voltinism (Table 1) were derived.

even in representatives that occur north of the Arctic Circle. Because any one species can be opportunistic in choice of habitat, we used broad habitat categories, each of which included the habitat type most representative of the one in the original account. We have identified three categories: perennial lotic, perennial lentic and temporary lentic.

Analysis of the influence of latitude

For analysing the influence of latitude on voltinism we used Spearman rank correlations because we predicted that our data are dependent and not normally distributed, particularly in respect of phylogenetic relationships, and the fact that many species have more than one entry in the database (Appendix). We used Stearns' method (1983) of directly subtracting the variation associated with phylogenetic similarity from the species' data. Because no consensual phylogenetic tree was available for all species of Odonata included in our database, we used taxonomic similarity to stand in for phylogeny. For higher taxonomy we referred to the work of Misof (2002) and Rehn (2003). The species were classified by taxonomic relatedness into suborder, family and genus. The families Corduliidae and Calopterygidae were used in the widest sense, i.e. to include Macromiidae and Synthemistidae in Corduliidae and Hetaerinidae in Calopterygidae. The study of Rehn (2003) implies that the number of zygopteran families may be combined into some recent 'superfamilies', e.g. Coenagrionoidea. However, because the zygopteran taxonomy is not yet resolved, we referred here to the families in current use. Taxa were given categorical codings to produce dummy variables for membership of suborder, family and genus. Each categorical code was used as an independent variable in a multiple regression to remove the taxonomic correlates, resulting in a set of residuals that are not correlated with taxonomy (for details on methods see Harvey & Pagel 1991: 130, box 5.1). For this kind of analysis we had to remove from the database all taxa for which no replicates were available. For example, in the Euphaeidae three genera, *Anisopleura*, *Bayadera* and *Epallage*, were each represented only once in the data set, and therefore, when removing generic relatedness, only one replicate was available for each of these genera, resulting in singularities in the regression analysis. Then, after having removed these three genera, only one genus with replicates was left within the Euphaeidae, so that the whole family had to be removed from the analysis. The same occurred with the Chlorocyphidae, Polythoridae, Platystictidae, Protoneuridae, Epiophlebiidae, Petaluridae, and Cordulegastridae. Likewise, all genera with only one entry had to be removed. Due to these statistical requirements eventually only 481 from a total of 542 entries in the database could be used.

Were phylogenetic affinity to have influenced our results, we expected the correlations based on the taxonomy-independent residuals to be weaker than those obtained using the original voltinism data. Therefore, as a first step, we correlated voltinism data, expressed as number of generations completed per year (multivoltine = 3, bivoltine = 2, univoltine = 1, semivoltine = 0.5, partivoltine = 0.3) against latitude without removing the effect of taxonomy. For the next step, to determine at which taxonomic level voltinism was most influenced, we first removed membership of suborder and family and thereafter, in another analysis, membership of suborder, family and genus.

Seven families, Calopterygidae, Lestidae, Coenagrionidae, Aeshnidae, Gomphidae, Corduliidae and Libellulidae, are represented by sufficient numbers of entries in the database to allow correlations between voltinism and latitude at the family level to be carried out. The residuals from the removal of genus membership, as well as the voltinism data without removal of other taxonomic correlates, were used (see above). Additionally, we performed correlations at the genus level for some genera. For the genus level we used the voltinism data without removing the effect of taxonomy. We also did so for two species that have enough entries in our database: *Ischnura elegans* and *Gomphus vulgatissimus*.

In the Appendix we scored for records, and not solely for species (or subspecies). A frequency table for voltinism derived directly from entries in the Appendix would be misleading, mainly because some species, e.g. *G. vulgatissimus*, have several entries, resulting in the overall voltinism frequencies for the Gomphidae being correspondingly weighted by the voltinism of *G. vulgatissimus*. Another, different, distortion resulted from the fact that entries for some species feature populations exhibiting different types of voltinism, e.g. *Pyrrhosoma nymphula* and *Anax imperator*. Hence, to avoid misinterpretations we did not summarise data at the family level.

Analysis of habitat effects

The larval habitat may constrain the duration of larval development. Temporary waters usually require rapid growth to permit successful development (cf. Wellborn et al. 1996; Suhling et al. 2005). Except for those species that siccatate, most temporary-water species may therefore be able to produce more than one generation per year. By contrast, species occurring in perennial waters, particularly riverine calopterygids and gomphids (Rüppell 2005; Suhling & Müller 1996), often have a 'slow' life style (sensu Johnson 1991) leading to low growth rates (e.g. Johansson 2000; Suhling 2001). Major differences in voltinism should therefore appear between each of (1) temporary waters, (2) perennial lentic waters and (3) perennial lotic waters. We recognised that some species exhibit opportunistic habitat occupancy within and between seasons, choices that may influence their voltinism (see Kumar 1976). We assigned such species to one of the three types of habitat by choosing the one which probably most influenced their voltinism. We tested for the effect of larval habitat by linking each habitat type to each species entry in the database (Appendix). Because of multiple entries for species, the data set was not independent. Therefore we used the Kruskal-Wallis rank test to evaluate differences in voltinism between habitat types. This operation was conducted for the raw data as in the Appendix, as well as for data corrected for taxonomic relationship at the family and genus levels (see above).

Figure 2: Scattergrams of Odonata voltinism vs latitude — (a) Correlation of numbers of generations per year with latitude. In (b) and (c) phylogenetic correlations are removed using the method of Stearns (1983). (b) Correlation of residuals of voltinism from a multiple regression with suborder and family relatedness. (c) Correlation of residuals of voltinism from a multiple regression with suborder, family and genus relatedness (see Methods). Because some cases had to be removed from the original data set due to singularities, the number of replicates was only 484 in all diagrams. Negative (southern) latitudes are multiplied by -1.
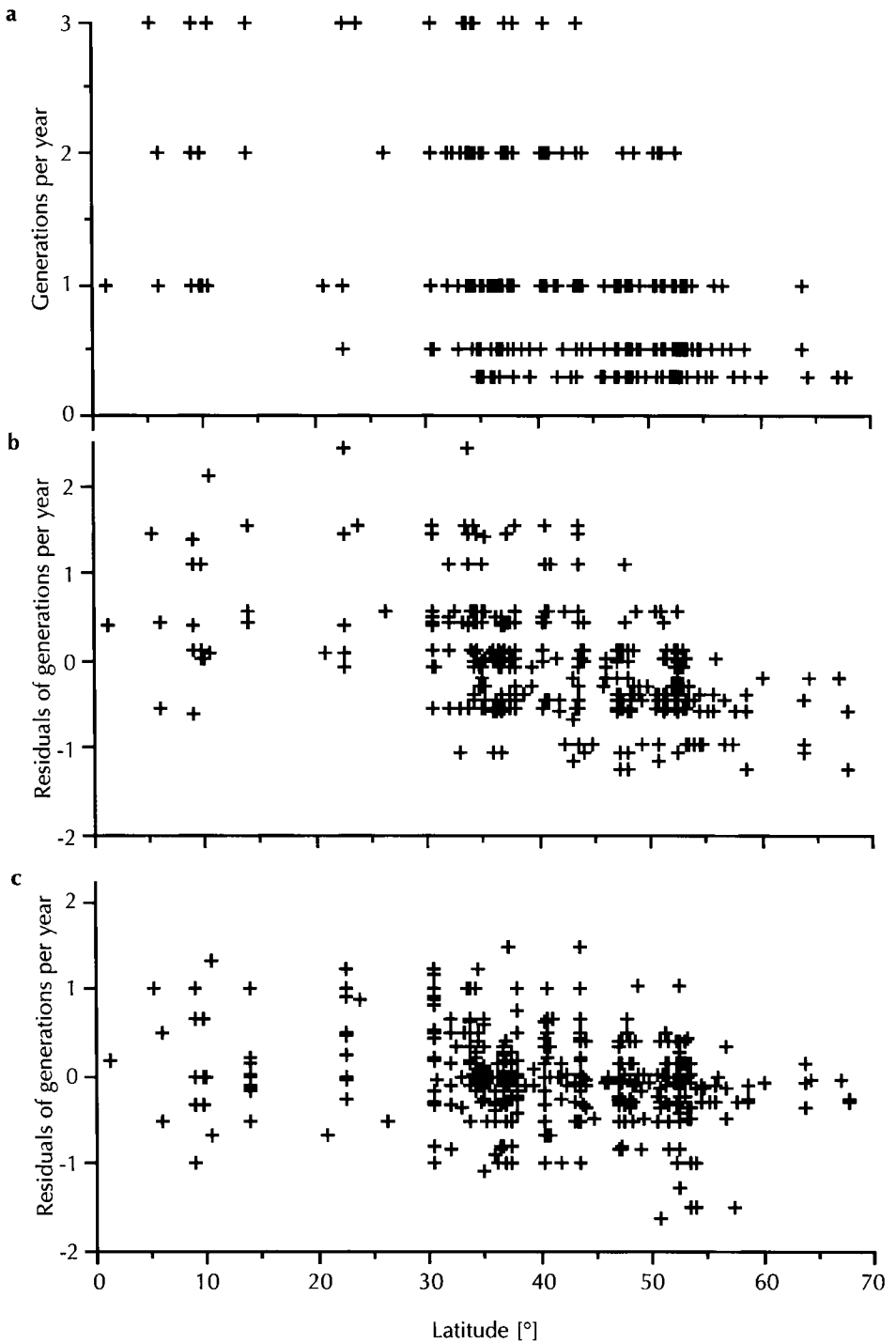
RESULTS

Relationship between voltinism and latitude or phylogenetic affinity

In the Appendix we compiled voltinism data for 269 species and six additional subspecies, many of which have several entries. The types of voltinism were not equally distributed over all families. For instance, multivoltine species were recorded more often from Coenagrionidae and Libellulidae, whereas partivoltinism occurred mainly in the Anisoptera, for instance in the Cordulegastridae, though rarely in the Zygoptera.

Number of generations per year including all entries was significantly negatively correlated with latitude (Spearman rank correlations, Fig. 2). This was true for voltinism data without removal of phylogenetic correlates ($rho = -0.505$, $p < 0.001$, Fig. 2a) as well as for the residuals from such phylogenetic membership removals (Figs 2b, 2c). After removing suborder and family membership the correlation was somewhat reduced compared with that without such removal ($rho = -0.427$, $p < 0.001$, Fig. 2b). However, after also removing genus membership the correlation coefficient dropped distinctly, although still being significant ($rho = -0.203$, $p < 0.001$). This indicates that most variation attributed to phylogeny occurs between the family and the genus levels. When completely eliminating from the data set the family Lestidae, most species of which are obligatorily univoltine because the life cycle is regulated, the correlation slightly strengthened ($rho = -0.527$, $p < 0.001$). In the Calopterygidae, Coenagrionidae, Aeshnidae, Gomphidae, Corduliidae, and Libellulidae the number of generations per year was significantly negatively correlated with latitude, whereas no such correlation was found in the Lestidae (Table 1, Fig. 3). After removal of taxonomic correlates at the genus level the correlations were reduced in strength, implying effects of phylogenetic inertia at the genus level. However, the correlations were still negative and significant for the Coenagrionidae, Aeshnidae and Libellulidae, and there was a trend in the Gomphidae (Table 1).

Some genera contained enough entries in the Appendix to allow correlations of voltinism with latitude at the genus level (Table 2). Spearman rank correlations indicated negative correlations between numbers of generations per year and latitude for most genera tested, these being significant only in *Coenagrion*, *Ischnura*, *Anax* and *Orthetrum* (Table 2). However, for most of the non-significant genera we did not have data between 30°S and 30°N, which may have influenced the results. In *Lestes* there was no good evidence for variation in voltinism, all species being univoltine (cf. Appendix). For several species there were records for at least two different generation times within a single species, which sometimes revealed a high within-species variability of the duration of a generation (Appendix). The clearest example was the widespread Palaearctic species *Ischnura elegans*, which had been observed to be multivoltine (in Spain, southern France and Greece), bivoltine (in Belgium, France and Germany), mainly univoltine (in northern England, Italy and The Netherlands) and semivoltine (in Scotland) (Appendix). In this species the data revealed a pronounced inverse relation between latitude and voltinism (Spearman

rank correlation: rho = -0.867, p = 0.004, n = 12). By contrast, voltinism of *Gomphus vulgatissimus* was positively correlated with latitude, although not significantly so (rho = 0.237, p = 0.344, n = 17).

Influence of larval habitat

Most entries (56%) for species of temporary waters were multi- or bivoltine, whereas for species in lentic perennial and lotic waters most entries were uni- or semi-voltine (65%) and semi- or parti-voltine (68%), respectively (Fig. 4). Hence, the median numbers of generations per year were highest in the temporary-water
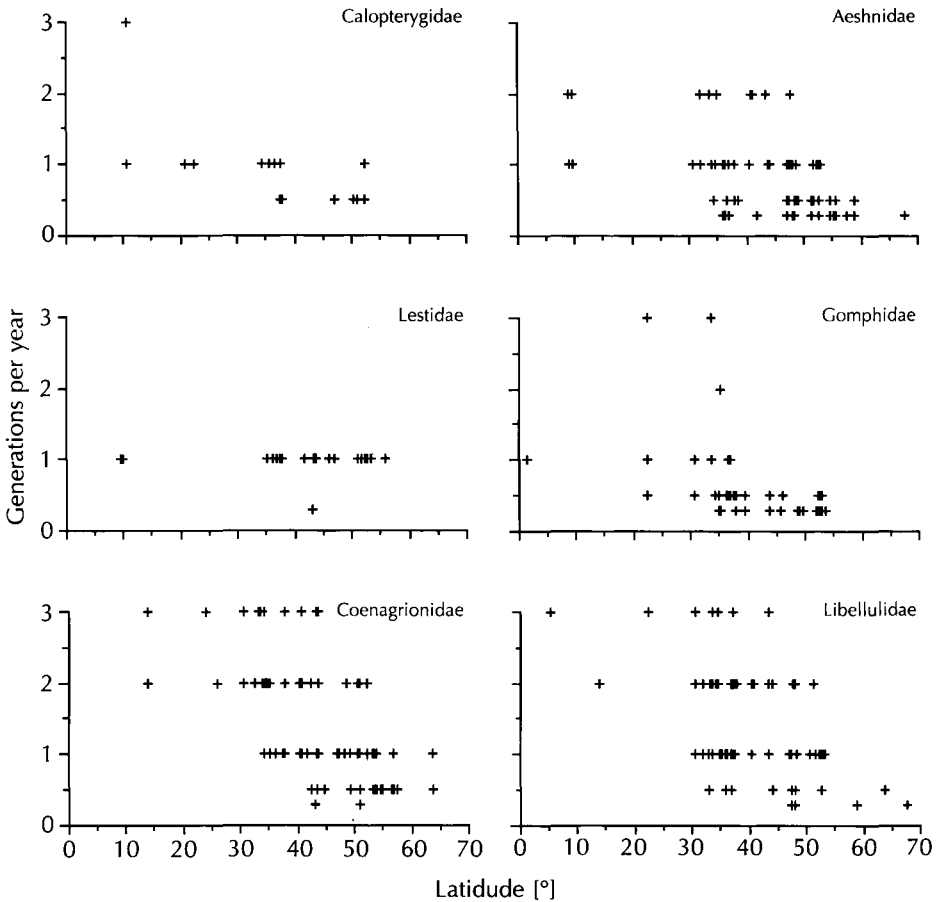
Figure 3: Scattergrams of Odonata voltinism vs latitude segregated according to family — in the Calopterygidae the multivoltine entry represents *Hetaerina capitalis* in Costa Rica; in the Lestidae the single partivoltine entry represents an upland population (579 m a.s.l.; 43.05°S) of *Austrolestés colensonis* in New Zealand; in the Gomphidae bi- and multi-voltine entries represent the predominantly tropical species *Paragomphus genei* in Namibia and Tunisia, respectively.

Table 1. Latitude vs Odonata voltinism — Spearman rank correlations for higher taxonomic groups between latitude and voltinism and between latitude and residuals of a multiple regression between voltinism and taxonomic relationship at the genus level. *n* gives the numbers of entries which could be used for analysis after removal of taxa without replicates (see Methods).

Family	*n*	Latitude vs voltinism		Latitude vs residuals	
		rho	*p*	*rho*	*p*
Aeshnidae	88	−0.462	< 0.001	−0.222	0.038
Corduliidae	30	−0.634	< 0.001	0.066	0.945
Gomphidae	69	−0.610	< 0.001	−0.218	0.072
Libellulidae	124	−0.528	< 0.001	−0.235	0.009
Calopterygidae	19	−0.524	0.026	0.021	0.929
Coenagrionidae	99	−0.694	< 0.001	−0.309	0.002
Lestidae	38	0.113	0.491	−0.171	0.297

species (2 generations per year) followed by perennial lentic species (1) and lotic species (0.5). Voltinism differed significantly between the types of habitat, which was true for voltinism data without removal of phylogenetic correlates (Kruskal-Wallis test $H = 104.56$, $p < 0.001$) as well as for the residuals after removals of the suborder and family memberships ($H = 43.9$, $p < 0.001$) and genus membership ($H = 6.4$, $p = 0.041$).

DISCUSSION

Our analyses reveal an overall negative correlation between voltinism and latitude. Certain departures from this correlation can be interpreted in terms of the factors, both exogenous and endogenous, that are known or inferred to influence voltinism and that therefore act as sources of variation in our analysis, as depicted for instance in Figure 2.

Exogenous factors

Major factors influencing development and therefore also voltinism are ambient temperature and photoperiod (Corbet 1999a: 228). Latitude is correlated with both these factors and may therefore be used as a surrogate variable, as in this study. Our results reveal that the general pattern supports our hypothesis: the number of generations per year decreases with latitude. In low latitudes (i.e. in the Tropics) most species are multi- or bi-voltine, whereas in high latitudes most species are semi- or parti-voltine. In mid-latitudes and the Subtropics the frequencies are intermediate (Fig. 5). This pattern can also be observed at the levels of most families and of some genera. However, our analysis reveals also that voltinism is influenced by phylogenetic constraints. On the one hand, this can be explained by life-cycle strategies (i.e. endogenous factors; see below) of certain taxonomic groups. For in-

stance in the Lestidae these lead to obligate univoltinism in most species (Appendix). On the other hand, the uneven representation of entries in our database has surely influenced the results. Many genera, for instance, have very few entries often deriving from a very small latitudinal range. Therefore they show little or no variation with latitude. Entries for the genera *Ischnura*, *Anax* and *Orthetrum*, of which we have examples from low to high latitudes, reveal that in genera in which the species have unregulated life cycles (sensu Corbet 1999a: 220) distinct correlations between voltinism and latitude occur. Thus, increasing temperatures and decreasing winter periods in lower latitudes often lead to increased growth rates and therefore allow completion of more than one generation per year. This is evident in *Ischnura elegans* (Table 2), which shows the clearest correlation between latitude and voltinism.

Voltinism differs significantly among perennial lotic, perennial lentic and temporary lentic habitats (Fig. 4). This is to be expected, particularly due to the life-cycle constraints caused by drying out of temporary waters. Temporary waters usually require rapid growth to permit successful development (cf. Wellborn et al. 1996). This pattern is especially evident in arid countries, such as Namibia (Johansson & Suhling 2004; Suhling et al. 2004, 2005). Species occupying temporary waters there develop more rapidly than those occupying permanent waters, and those occupying lentic waters there develop more rapidly than those occupying lotic waters. This correlation is not independent of latitude – seasonal rainfall and ephemeral pools are commoner at lower latitudes – or phylogenetic affinity because certain taxa, e.g. *Pantala flavescens*, oviposit by preference in ephemeral
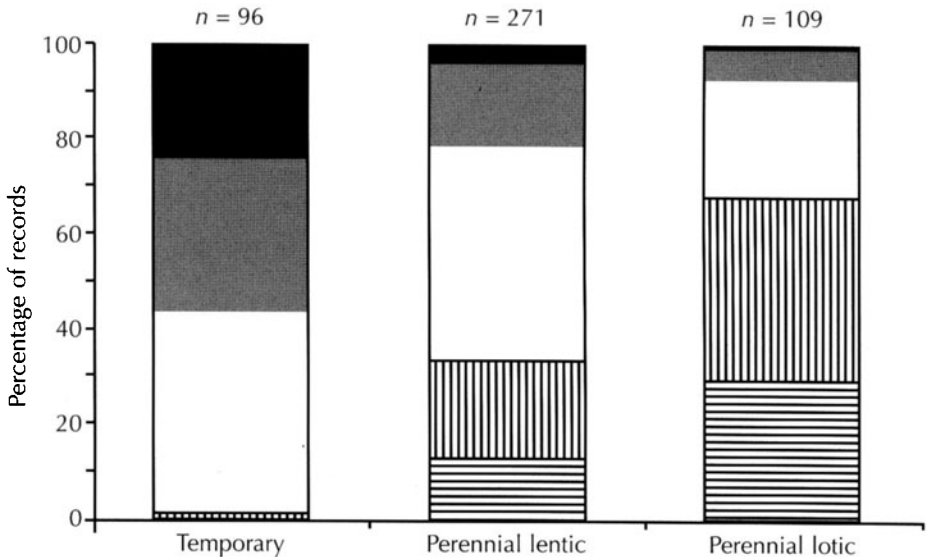

Figure 4: Percent occurrence of the different types of Odonata voltinism listed in the Appendix to habitat-type — the semivoltine entry for temporary habitats is represented by *Libellula depressa* from France (Blois 1985). — Black: multivoltine; grey: bivoltine; white: univoltine; vertical-hatching: semivoltine; horizontal-hatching: partivoltine.

Table 2.   Latitude vs Odonata voltinism — Spearman rank correlations for selected genera.

Genus	n	rho	p
Coenagrion	17	–0.504	0.044
Enallagma	15	–0.332	0.214
Ischnura	30	–0.657	< 0.001
Aeshna	44	–0.240	0.116
Anax	25	–0.516	0.004
Gomphus	25	–0.056	0.785
Orthetrum	16	–0.560	0.030
Sympetrum	32	–0.168	0.349

pools lacking surface vegetation (Weir 1974), which on that account can be expected to be warmer. With the exception of those species, e.g. Lestidae, that hibernate in the egg or adult stage or aestivate or siccatate as adults, most temporary-water species may therefore be able to be bi- or multi-voltine (cf. Suhling et al. 2003). On the other hand, species occurring in perennial waters, particularly lotic habitats, such as Gomphidae and Cordulegastridae, often have a slow life style (sensu Johnson 1991) associated with low growth rates and therefore longer generation times (e.g. Johansson 2000; Suhling 2001).

The effect of type of larval habitat on voltinism influences the relationship between latitude, taxonomy and voltinism in two major ways. First, in lower latitudes the frequency of temporary waters increases – as does the frequency of entries in our database for temporary-water species. In genera that have unregulated life cycles, such as Ischnura, Anax and Orthetrum, growth rate depends mainly on temperature, enabling them to develop rapidly in such temporary waters, which more often occur in lower latitudes. Hence, the finding that in these three genera, for instance, voltinism correlates well with latitude (see above) also reflects their ability to use these habitats at higher ambient temperatures. Second, the distributions shown in the Appendix allow the special status of several families to be highlighted as occupants of habitats that are either solely lotic (Calopterygidae, Chlorocyphidae, Euphaeidae, Platystictidae, Polythoridae, Cordulegastridae) or mainly lotic (Platycnemididae, Gomphidae). Wheras in other families several species occur in habitats that sometimes or always feature drying, such as temporary pools (Lestidae, Coenagrionidae and Libellulidae). Hence, taxonomy and habitat are often correlated, which explains some of the obvious variation caused by taxonomic relatedness in the correlation between latitude and voltinism. Besides the known differences between the habitat types chosen in our study, small-scale differences in habitat may matter also. For instance, in Gomphus vulgatissimus, which shows no significant correlation between voltinism and latitude, informative conclusions can be drawn from the larval habitat: G. vulgatissmus is semivoltine in large rivers, which can feature high summer water temperatures (> 30°C in shallow water near the banks) even at about 50°N, whereas it is usually partivoltine, requiring up to four years per generation, in smaller streams as well as in cold lakes, regardless of latitude (Müller et al. 2000).

Endogenous factors

We have considered endogenous factors only by allowing that phylogenetic affinity (sometimes reflected in life-cycle regulation) may impose constraints, examples being the obligatorily univoltine life cycles exhibited by many species of *Lestes* and *Sympetrum* under almost all circumstances, and the low voltinism exhibited by the predominantly lotic Cordulegastridae. We now consider other endogenous factors (sometimes reflecting phylogeny) that can influence interspecific variability. Many species of Odonata in temperate latitudes possess an elaborate suite of responses to temperature and daylength that result in the emergence period being placed at a time of season favourable for reproduction (Norling 1984a), a process known as seasonal regulation. Such species are described as having a 'regulated' life cycle. The better-known examples of seasonal regulation entail extending generation time, as when (in spring species, with the Type-1 life cycle) development of the
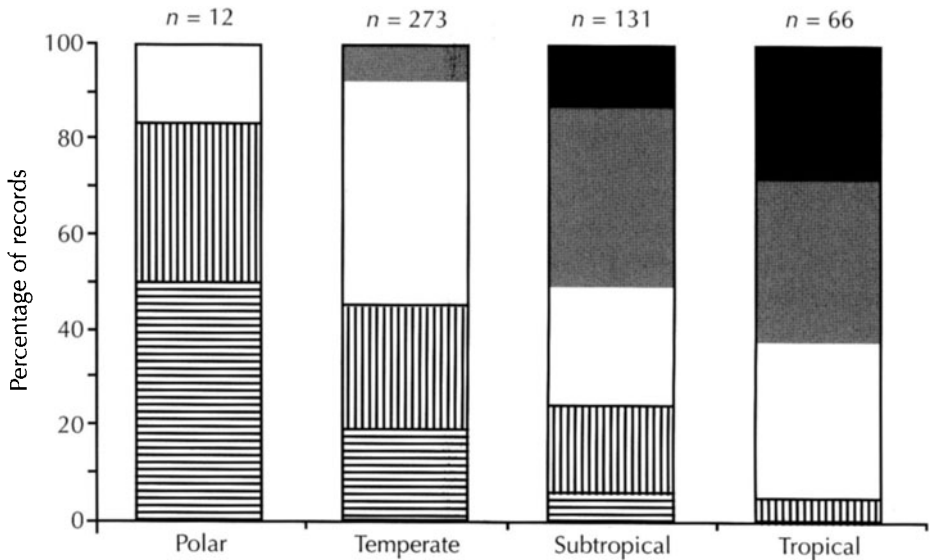
Figure 5: Percent occurrence of the different types of Odonata voltinism in the major climatic zones of the earth — tropical (latitude 0° - 23.45°N/S), subtropical (23.45° - 35°N/S), temperate (35° - 58°) and polar (> 58°) derived from all entries in the Appendix. We allow for departures from the conventional (geographical) definitions of climatic zones: in the Dehra Dun valley in India the tropics reach 30.5°; in western Europe (Mediterranean France only), reflecting local climate determined by the Gulf Stream, we consider the subtropics to extend to about 44°N; the polar zone is conventionally regarded as falling within latitudes exceeding 66.5°N/S but here, to reflect the realities of the climatic environment within which the northernmost Odonata occur, we place the southern limit of this zone at 58°N. — Black: multivoltine; grey: bivoltine; white: univoltine; vertical-hatching: semivoltine; horizontal-hatching: partivoltine.

most precocious individuals is arrested by the intercalation of a final-stadium dia-
pause, which allows retarded individuals to 'catch up' in the autumn preceding a
spring emergence. Likewise, onset of this late season diapause may oblige a larva
in summer to postpone emergence for an extra year. Or, in summer species (with
the Type-2 life cycle), a rising series of temperature thresholds for entry to succes-
sive late stadia in spring (Corbet 1957b; Lutz 1968) can enable laggards to catch
up with the most precocious individuals that are thereby held back. Another
mechanism causing univoltinism is postponed reproductive maturation of species
that emerge in spring and oviposit in autumn to avoid the drought of their habi-
tats in summer (cf. Samraoui et al. 1998). Such species, for instance *Aeshna mixta*,
Sympetrum meridionale and *S. s. striolatum* in Algeria, spend the hot summer as
immature adults away from their reproductive habitats, as does *S. sinaiticum* in
Tunisia (Jödicke 2003). Such a resting period, representing a summer diapause is
known as aestivation, as distinct from the siccatation-resting period exhibited by
some tropical species during the dry season.

There are other, less well-known, responses that can shorten generation time and,
by serving thereby to offset the effects of latitude, may obscure the direct correla-
tion we postulate. Such responses are found among most species of *Lestes* and help
to maintain the obligatorily univoltine life cycle typical of the genus. Most tempe-
rate species of *Lestes* feature a diapause in the egg (see Jödicke 1997), which pre-
vents small larvae being exposed to low (winter) temperatures and synchronises
egg hatching in spring (Corbet 1956). Thereafter the larvae, which have an intrinsi-
cally high thermal coefficient for growth (Krishnaraj & Pritchard 1995) and a high
intrinsic attack coefficient (Pickup & Thompson 1990), grow unusually rapidly and
emerge promptly in early to mid summer – early enough to complete the repro-
ductive period before the advent of autumn, whereupon the adults die. This suite
of responses alone would normally be able to maintain the univoltine life cycle of
Lestes, but in *L. congener* (Johansson and Rowe 1999) and *L. sponsa* (Johansson
et al. 2001) a mechanism exists that enables retarded larvae in spring and early
summer to grow more rapidly (under the progressively longer photoperiods that
characterise the advancing season up to the summer solstice) and thus to 'make up
for lost time'. In this case seasonal regulation is not extending generation time but
abbreviating it. This response, the so-called 'light-growth effect' (see Saunders
2002), is well known in insects and has been detected in at least ten other species
of Odonata (Danks 1987: 204). A far-reaching consequence of this photoperiod
response is that it could provide a mechanism for continuously compensating for
the retarding effects of latitude between the spring equinox and the summer solstice,
because of the relationship between latitude and daylength (Corbet 2003; see also
Corbet 1999a: 229). Any mechanism that compensates for latitude in such a way
will weaken the regression of latitude on voltinism and so weaken the correlation
we have revealed in this paper.

Another respect in which responses of odonate larvae may help to compensate
for latitude is their possession of genetic heterogeneity in regard to a photoperiod
that is critical for the induction of larval diapause. In *Leucorrhinia dubia*, for
example, populations in Sweden at different latitudes have different critical values
for the photoperiod that induces larval diapause. In this way the seasonal regula-
tion of larvae can be made appropriate to latitude (Norling 1984b). Unlike the
light-growth effect, however, such a response is likely to prolong, not abbreviate,
larval duration.

The factors discussed above achieve seasonal regulation and find expression in the different kinds of life cycles shown by Odonata. On a global scale, twelve types of odonate life cycle have been identified (Corbet 1999a: 220), falling under two major dichotomies: tropical-centred vs temperate-centred species and regulated vs unregulated life cycles. From what has been said, we conclude that a meaningful correlation between voltinism and latitude can be expected only among species that occupy temperate latitudes and whose life cycle is not regulated so as to be invariably univoltine. Species appropriate for such an analysis are those with one of three main types of life cycle as defined by Corbet (1999a: 220), namely B.1 (unregulated; facultatively multivoltine), B.2.2.1 (regulated; facultative diapause in larva) and B.2.2.2 (regulated; facultative diapause in larva and obligate diapause in egg). Species in the second and third of these categories correspond broadly to Types 2 and 3 respectively as defined by Corbet (2003) and are appropriate for such analysis because the regulatory processes (as far as we know) relate mainly to the arrest or acceleration of larval development connected with the seasonal placement and synchronisation of emergence, and not to the temperature-dependent rate of growth during the growing season. These processes occur in two episodes: before the summer solstice, when they result in acceleration of growth before emergence; and after the summer solstice, when they result in growth being arrested in an overwintering stage (see Corbet 2003).

Having regard to the inferred effects on odonate distribution of global warming (e.g. J. Ott 1996, 2000; Hickling et al. 2005), we anticipate that in future the distributions illustrated in Figures 2 and 3 will undergo displacement towards the right.

CONCLUSIONS

We have given examples of mechanisms underlying seasonal regulation. These show that voltinism is often correlated with, but never likely to be a simple resultant of, latitude, or indeed of any other exogenous factor. Voltinism is a resultant of the interaction of exogenous and endogenous factors that, acting in concert, maintain a viable, seasonally appropriate life cycle under varying environmental conditions. Our review points up six lines of enquiry that are likely to be fruitful in clarifying the underlying causes of voltinism in Odonata. They focus especially on odonate populations in the Tropics and the far north.

(1) To determine voltinism in the Tropics, especially in perennial waters. Most existing records derive from temporary waters, which, by their nature, do not provide information about the number of generations that may be completed in other habitats.

(2) To try to obtain information that would bear on the current hypothesis regarding the migratory behaviour and voltinism of ITCZ migrants. A productive approach might be to make co-ordinated observations of adult arrivals and larval development in a region (such as India) in which the track and approximate timing of the passage of the annual monsoon rains are known. To conduct such an investigation would provide an opportunity to obtain an estimate of the voltinism of a (suspected) ITCZ migrant (such as *Pantala flavescens*) and also to test the hypothesis advanced to explain its seasonal appearance and disappearance. Odonatologists in western India are exceptionally well placed to undertake such a project because the path followed by the annual monsoon there is well known.

(3) To determine voltinism of species from habitats which are poorly represented in the Appendix – e.g. perennial waters in the Tropics and perennial water courses in a desert or semi-desert environment.

(4) To explore the effects on voltinism of habitat change. In the Mediterranean Region, multivoltinism is associated with habitat change: one generation survives the winter in the larval stage in natural ponds and swamps, whereas one or more summer generations develop in rice fields (Schnapauff et al. 2000). In central Europe such a summer generation may occur facultatively in shallow, warm ponds (cf. Inden-Lohmar 1997). Facultative bivoltinism (even sometimes multivoltinism) can occur among tropical-centred species in India when perennial habitats are used to bridge the interval between monsoons (Kumar 1976).

(5) To determine (in the laboratory) the light-growth response of larvae of the species of *Lestes* and *Sympetrum* that occur north of the Arctic Circle, namely *L. disjunctus*, *L. dryas* and *S. danae*.

(6) To determine (in the field) the voltinism of as many species as possible close to the northern limit of their distribution. Now that Cannings et al. (1991) have identified specific habitats for 24 species, representing three main types of life cycle, north of the Arctic Circle, an opportunity exists to obtain this information. Such a study could use strong inference based on the size-distribution of larvae remaining at, or near, the end of the annual emergence period. Such larvae form the cohort due to emerge one or more years sub-sequently. They could be distinguished from the current year's emergence group because the latter would be present as F-0 larvae, typically showing signs of metamorphosis.

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Appendix: Records of voltinism of 269 species plus six additional subspecies of dragonflies, varying from detailed, long-term analyses of cohorts and their growth rates to informed infe-rences based on knowledge of the flying season, ambient temperatures and growth rate deri-ved from various studies. Information on latitudes and longitudes refer to the study sites and are in decimal degrees (accuracy: 0.01 degree); negative values stand for S and W respec-tively. Multiple entries for a single species or subspecies are listed in order of increasing vol-tinism, namely partivoltine (P), semivoltine (S), univoltine (U), bivoltine (B), and multivoltine (M). The habitat type for the study site is classified as temporary (TEM), perennial lentic (PER), and perennial lotic (LOT).

Taxon	Voltinism	Lat	Long	Habitat	Reference
ZYGOPTERA					
CALOPTERYGIDAE					
Atrocalopteryx atrata Selys	U	36.02	140.13	LOT	Takamura (1996)
Calopteryx dimidiata Burmeister	U	34.18	-81.12	LOT	Smock (1988)
haemorrhoidalis (Vander Linden)	S	37.93	-4.87	LOT	Ferreras-Romero et al. (2000)
japonica Selys	U	36.50	137.87	LOT	Watanabe et al. (1998)
splendens (Harris)	S	52.40	12.53	LOT	Göcking (1999)
	U	52.40	12.53	LOT	Göcking (1999)
	U	52.32	10.45	LOT	C. Ott (1996)
	U	52.32	10.45	LOT	Schütte & Schrimpf (2002)
virgo (Linnaeus)	S	52.32	10.45	LOT	C. Ott (1996)
	S	52.32	10.45	LOT	Schütte & Schrimpf (2002)
	S	50.82	-1.58	LOT	Corbet (1957a)
	S	50.38	4.17	LOT	Lambert (1994)
	S	47.00	8.00	LOT	Robert (1958)
	S	37.37	-4.75	LOT	Ferreras-R. & García-R. (1995)
	U	37.37	-4.75	LOT	Ferreras-R. & García-R. (1995)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Hetaerina americana (Fabricius)	U	10.50	-85.25	LOT	Pritchard (1991)
capitalis Selys	M	10.50	-85.25	LOT	Pritchard (1991)
rosea Selys	U	20.77	-42.88	LOT	De Marco & Cardoso P. (2004)
Mnais andersoni McLachlan in Selys	U	22.42	114.18	LOT	Dudgeon (1987)
pruinosa costalis Selys	U	35.50	139.48	LOT	Taguchi & Watanabe (1993)
Neurobasis chinensis (Linnaeus)	B	30.50	78.00	LOT	Kumar (1976)
CHLOROCYPHIDAE					
Platycypha caligata (Selys)	B	-15.00	35.30	LOT	Parr (1984)
Rhinocypha perforata (Percheron)	U	22.42	114.18	LOT	Dudgeon (1987)
quadrimaculata Selys	U	30.50	78.00	LOT	Kumar (1976)
EUPHAEIDAE					
Anisopleura lestoides Selys	U	30.50	78.00	LOT	Kumar (1976)
Bayadera indica (Selys)	U	30.50	78.00	LOT	Kumar (1972)
Epallage fatime (Charpentier)	U	36.17	28.00	LOT	Norling (1982)
Euphaea decorata Hagen in Selys	U	22.42	114.18	LOT	Dudgeon (1989b)
formosa Hagen	U	23.50	121.00	LOT	Hayashi (1990)
yayeyamana Oguma	U	24.33	123.83	LOT	Hayashi (1990)
POLYTHORIDAE					
Cora marina Selys	U	10.50	-85.25	LOT	Pritchard (1996)
LESTIDAE					
Austrolestes colensonis (White)	P	-43.05	171.78	PER	Deacon (1979)
	U	-36.87	174.77	PER	Rowe (1987)
	U	-37.87	174.77	PER	Winstanley (1979)
	U	-43.45	172.63	PER	Crumpton (1979)
	U	-43.47	172.53	PER	Deacon (1979)
Lestes congener Hagen	U	52.25	-106.50	PER	Sawchyn & Gillott (1974a)
	U	43.78	-72.26	PER	Stoks & McPeek (2003)
disjunctus Selys	U	53.18	-115.42	PER	Baker & Clifford (1981)
	U	52.25	-106.50	PER	Sawchyn & Gillott (1974b)
	U	51.08	-114.12	PER	Krishnaraj & Pritchard (1995)
	U	43.78	-72.26	TEM	Stoks & McPeek (2003)
	U	35.08	-83.17	PER	Ingram (1976)
dryas Kirby	U	55.93	12.32	TEM	Wesenberg-Lund (1913)
	U	52.25	-106.50	PER	Sawchyn & Gillott (1974b)
	U	43.78	-72.26	TEM	Stoks & McPeek (2003)
eurinus Say	U	46.00	-74.00	PER	Pilon et al. (1993)
	U	43.78	-72.26	PER	Stoks & McPeek (2003)
	U	36.07	-79.78	PER	Lutz (1968)
inaequalis Walsh	U	43.78	-72.26	PER	Stoks & McPeek (2003)
rectangularis Say	U	43.78	-72.26	PER	Stoks & McPeek (2003)
	U	41.65	-80.42	PER	Gower & Kormondy (1963)
sponsa (Hansemann)	U	55.93	12.32	TEM	Wesenberg-Lund (1913)
	U	52.50	15.00	TEM	Münchberg (1933)
	U	51.47	-0.98	PER	Corbet (1956)
tenuatus Rambur	U	10.00	-84.00	TEM	Paulson (1983)
unguiculatus Hagen	U	52.25	-106.50	PER	Sawchyn & Gillott (1974b)
	U	43.78	-72.26	PER	Stoks & McPeek (2003)
vigilax Selys	U	43.78	-72.26	PER	Stoks & McPeek (2003)
	U	35.08	-83.17	PER	Ingram (1976)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Lestes virgatus (Burmeister)	U	9.68	8.70	TEM	Gambles (1960)
viridis (Vander Linden)	U	52.50	15.00	PER	Münchberg (1933)
	U	47.00	8.00	PER	Robert (1958)
	U	37.37	-4.75	TEM	Ferreras-R. & García R. (1995)
	U	37.55	-5.11	TEM	Agüero-Pelegrin et al. (1999)
	U	37.53	-5.08	TEM	Agüero-Pelegrin et al. (1999)
Platylestes praemorsus (Hagen)	U	30.50	78.00	TEM	Kumar (1976)
Sympecma fusca (Vander Linden)	U	52.50	15.00	PER	Münchberg (1933)
	U	47.00	8.00	PER	Robert (1958)
paedisca (Brauer)	U	52.25	5.40	PER	Prenn (1928)
HEMIPHLEBIIDAE					
Hemiphlebia mirabilis Selys	U	-38.92	146.28	PER	Sant & New (1988)
COENAGRIONIDAE					
Aciagrion migratum (Selys)	B	35.00	129.00	PER	Asahina (1991)
	B	34.78	135.45		Kansai Research Group (1977)
Agriocnemis dabreui Fraser	B	13.87	100.53	PER	Asahina et al. (1972)
f. femina Brauer	B	13.87	100.53	TEM	Asahina et al. (1972)
femina oryzae Lieftinck	B	34.17	131.58	TEM	Ikeda & Sawano (1965)
Agriocnemis pygmaea (Rambur)	B	13.87	100.53	PER	Asahina et al. (1972)
	B	30.50	78.00	TEM	Kumar (1972)
	M	30.50	78.00	TEM	Kumar (1976)
Amphiagrion abbreviatum (Selys)	U	51.17	-115.57	LOT	Pritchard et al. (2000)
Amphiallagma parvum (Selys)	M	23.83	78.72	PER	Srivastava & Suri Babu (1994)
Argia vivida Hagen	P	50.83	-117.92	LOT	Pritchard (1989)
	S	42.40	-112.73	LOT	Pritchard (1989)
	U	50.60	-117.87	LOT	Pritchard (1989)
Ceriagrion auranticum Fraser	B	13.87	100.53	PER	Asahina et al. (1972)
coromandelianum (Fabricius)	M	30.50	78.00	TEM	Kumar (1972)
	M	23.83	78.72	PER	Suri Babu & Srivastava (1994)
tenellum (de Villers)	S	50.82	-1.58	PER	Corbet (1957b)
Coenagrion angulatum Walker	U	52.25	-106.50	PER	Sawchyn & Gillott (1975)
armatum (Charpentier)	S	63.83	20.25	PER	Johansson & Norling (1994)
caerulescens (Fonscolombe)	U	37.37	-4.75	LOT	Ferreras-R. & García-R. (1995)
hastulatum (Charpentier)	P	67.83	21.67	PER	Norling (1984c)
	S	63.83	20.25	PER	Johansson & Norling (1994)
	S	58.70	16.52	PER	Norling (1984c)
	U	63.83	20.25	PER	Johansson & Norling (1994)
	U	58.70	16.52	PER	Norling (1984c)
	U	47.00	8.00	PER	Robert (1958)
mercuriale (Charpentier)	S	50.82	-1.58	LOT	Corbet (1957b)
puella (Linnaeus)	S	53.47	-2.38	PER	Parr (1970)
	U	53.47	-2.38	PER	Parr (1970)
	U	48.27	15.70	PER	Waringer & Humpesch (1984)
	U	47.00	8.00	PER	Robert (1958)
	U	41.73	12.40	PER	Nicolai & Carchini (1985)
pulchellum (Vander Linden)	U	47.00	8.00	PER	Robert (1958)
resolutum (Selys)	S	53.18	-115.42	PER	Baker & Clifford (1981)
	U	53.18	-115.42	PER	Baker (1982)
	U	52.25	-106.50	PER	Sawchyn & Gillott (1975)
	U	51.08	-114.12	PER	Krishnaraj & Pritchard (1995)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Enallagma aspersum (Hagen)	U	43.58	-71.67	PER	McPeek et al. (2001)
	U	35.08	-83.17	PER	Ingram & Jenner (1976)
boreale Selys	S	53.18	-115.42	PER	Baker & Clifford (1982)
	S	49.32	-122.55	PER	Pearlstone (1973)
	U	49.32	-122.55	PER	Pearlstone (1973)
carunculatum Morse	S	44.73	-63.67	PER	Paterson (1994)
cyathigerum (Charpentier)	S	56.53	-3.53	PER	Corbet & Chowdhury (2002)
	S	53.40	-2.35	PER	Parr (1976)
	U	53.40	-2.35	PER	Parr (1976)
	U	52.32	10.45	PER	Steiner et al. (2000)
	U	47.48	19.17	PER	Steinmann (1961)
	B	52.32	10.45	PER	Steiner et al. (2000)
	B	48.68	11.18	PER	Burbach (2000)
divagans Selys	U	34.18	-81.12	LOT	Smock (1988)
hageni (Walsh)	U	35.08	-83.17	PER	Ingram & Jenner (1976)
Erythromma lindenii (Selys)	U	41.73	12.40	PER	Nicolai & Carchini (1985)
	U	37.77	-5.17	PER	Ferreras-Romero (1991)
	B	37.77	-5.17	PER	Ferreras-Romero (1991)
najas (Hansemann)	U	47.00	8.00	PER	Robert (1958)
Ischnura asiatica Brauer	B	34.78	135.45		Kansai Research Group (1977)
	B	34.50	135.50	PER	Naraoka (1976)
aurora Brauer	M	30.50	78.00	TEM	Kumar (1979a)
damula Calvert	B	34.00	-106.33	PER	Johnson (1964)
elegans (Vander Linden)	S	57.43	-7.35	PER	Parr (1969)
	S	53.88	-0.72	PER	Thompson (1978)
	S	53.43	-2.37	PER	Parr (1973)
	U	53.88	-0.72	PER	Thompson (1978)
	U	53.43	-2.37	PER	Parr (1973)
	U	41.73	12.40	PER	Nicolai & Carchini (1985)
	B	50.88	4.07	PER	Dumont (1971)
	B	50.58	7.10	PER	Inden-Lohmar (1997)
	B	43.60	3.88	PER	Cassagne-Méjean (1963)
	M	43.57	4.57	TEM	Aguesse (1955)
	M	43.52	4.67	TEM	Aguesse (1961)
	M	40.68	24.73	TEM	Schnapauff et al. (2000)
fountaineae Morton	M	33.34	9.00	PER	Jödicke (2003)
graellsii (Rambur)	B	42.26	-8.38	PER	Cordero-Rivera (1987)
	M	37.77	-5.17	TEM	Montes et al. (1982)
	M	34.03	-6.84	TEM	Azzouz & Aguesse (1990)
posita (Hagen)	U	36.07	-79.78	PER	Patrick (1969)
pumilio (Charpentier)	U	52.13	-0.48	PER	Cham (1993)
	B	50.58	7.10	PER	Inden-Lohmar (1997)
	B	48.68	11.18	PER	Burbach (2000)
	B	37.77	-5.17	TEM	Aguesse (1955)
	M	40.68	24.73	TEM	Schnapauff et al. (2000)
saharensis Aguesse	M	33.45	10.13	PER	Jödicke (2003)
senegalensis (Rambur)	B	13.87	100.53	PER	Asahina et al. (1972)
	M	13.87	100.53	PER	Asahina et al. (1972)
verticalis (Say)	U	43.58	-78.33	PER	Baker & Feltmate (1987)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Mortonagrion selenion (Ris)	U	39.72	140.67	PER	Sonehara (1994)
Paracercion calamorum (Ris)	B	32.50	123.50	PER	Naraoka (1976)
hieroglyphicum (Brauer)	B	34.78	135.45		Kansai Research Group (1977)
sieboldii (Selys)	U	40.75	140.33	PER	Naraoka (1987)
	U	40.50	140.50	PER	Naraoka (1976)
	B	40.75	140.33	PER	Naraoka (1987)
	B	40.50	140.50	PER	Naraoka (1976)
Pericnemis triangularis Laidlaw	M	0.50	114.00	TEM	Orr (1994)
Pseudagrion rubriceps Selys	M	30.50	78.00	TEM	Kumar (1979b)
salisburyense Ris	B	26.12	28.12	LOT	Chutter (1961)
Pyrrhosoma nymphula (Sulzer)	S	56.73	-3.02	PER	Corbet & Harvey (1989)
	S	54.75	-1.75	PER	Lawton (1970)
	S	54.43	-2.97	PER	Macan (1964)
	S	53.82	-1.00	PER	Bennett & Mill (1993)
	S	50.82	-1.58	PER	Corbet (1957a)
	U	56.73	-3.02	PER	Corbet & Harvey (1989)
	U	47.00	8.00	PER	Robert (1958)
Xanthocnemis zealandica (McLachlan)	P	-43.05	171.78	PER	Deacon (1979)
	S	-43.47	172.53	PER	Deacon (1979)
	U	-43.45	172.63	PER	Crumpton (1979)
PLATYCNEMIDIDAE					
Copera annulata (Selys)	B	34.78	135.45	LOT	Inoue (1979)
tokyoensis Asahina	B	34.78	135.45	LOT	Inoue (1979)
Lieftinckia kimminsi Lieftinck	U	-6.00	155.00	LOT	Yule & Pearson (1995)
	B	-6.00	155.00	LOT	Yule & Pearson (1995)
Platycnemis echigoana Asahina	B	34.78	135.45	LOT	Inoue (1979)
foliacea Selys	B	34.78	135.45	LOT	Inoue (1979)
latipes Rambur	U	37.93	-4.87	PER	Agüero-P. & Ferreras-R. (1992)
pennipes (Pallas)	U	52.40	12.53	LOT	Göcking (1999)
	U	52.32	10.45	PER	Steiner et al. (2000)
PLATYSTICTIDAE					
Drepanosticta carmichaeli (Laidlaw)	U	30.50	78.00	LOT	Kumar (1976)
Protosticta taipokuensis Asahina & Dudgeon	U	22.42	114.18	LOT	Asahina & Dudgeon (1987)
PROTONEURIDAE					
Elattoneura campioni (Fraser)	U	30.50	78.00	LOT	Kumar (1972)
Roppaneura beckeri Santos	S	-19.91	-43.93	PER	Machado (1984)
PSEUDOSTIGMATIDAE					
Mecistogaster linearis (Fabricius)	U	8.95	-79.57	TEM	Fincke (1992a)
ornata Rambur	U	8.95	-79.57	TEM	Fincke (1992b)
Megaloprepus caerulatus (Drury)	U	8.95	-79.57	TEM	Fincke (1992b)
	B	8.95	-79.57	TEM	Fincke (1992b)
	M	8.95	-79.57	TEM	Fincke (1992b)
ANISOZYGOPTERA					
EPIOPHLEBIIDAE					
Epiophlebia laidlawi Tillyard	P	28.00	85.50	LOT	Asahina (1982)
superstes (Selys)	P	32.22	130.75	LOT	Tabaru (1984)

Taxon	Voltinism	Lat	Long	Habitat	Reference
ANISOPTERA					
PETALURIDAE					
Petalura gigantea Leach	P	-33.35	150.28	PER	Tillyard (1911)
Tanypteryx pryeri (Selys)	P	35.33	139.63	PER	Taketo (1971)
Uropetala chiltoni Tillyard	P	-42.95	171.57	PER	Wolfe (1953)
AESHNIDAE					
Adversaeschna brevistyla (Rambur)*	U	-33.83	151.17	LOT	Tillyard (1916)
	U	-37.87	174.77	PER	Winstanley (1979)
Aeshna affinis Vander Linden	U	52.45	16.50	TEM	Bernard & Samolag (1997)
caerulea (Ström)	P	55.13	-4.42	PER	Clarke (1994)
	P	57.67	-5.43	PER	Smith et al. (2000)
	P	47.90	8.10	PER	Sternberg (1990)
californica Calvert	U	47.00	-119.50	PER	Kime (1974)
cyanea (Müller)	P	58.70	16.52	PER	Norling (1984a)
	P	51.15	-0.93	PER	Corbet (1959)
	S	55.67	13.21	PER	Norling (1984a)
	S	51.15	-0.93	PER	Corbet (1959)
	S	48.58	7.75	PER	Schaller (1960)
	S	37.93	-4.87	PER	Ferreras-R. & Puchol-C. (1995)
	U	52.83	7.83	PER	Jödicke (1999)
	U	48.58	7.75	PER	Schaller (1960)
	U	48.08	-1.68	PER	Blois (1985)
	U	47.32	8.78	PER	Wildermuth (1994)
	U	47.00	8.00	PER	Robert (1958)
grandis (Linnaeus)	S	52.50	15.00	PER	Münchberg (1930b)
isoceles (Müller)	S	52.50	15.00	PER	Münchberg (1930b)
juncea (Linnaeus)	P	67.83	21.67	PER	Norling (1984a)
	P	54.43	-2.97	PER	Macan (1964)
	P	47.90	8.10	PER	Sternberg (1990)
	P	48.17	-88.50	PER	Van Buskirk (1992)
	P	48.17	-88.50	PER	Van Buskirk (1993)
	P	47.00	8.00	PER	Robert (1958)
	P	36.70	137.80	PER	Kurata (1980)
	P	35.98	139.08	PER	Arai & Murabayashi (1983)
	S	58.70	16.52	PER	Norling (1984a)
	S	54.43	-2.97	PER	Macan (1964)
	S	48.17	-88.50	PER	Van Buskirk (1993)
mixta Latreille	U	52.25	5.40	PER	Münchberg (1930a)
	U	47.00	8.00	PER	Robert (1958)
	U	37.88	-4.77	PER	Munoz-P. & Ferreras-R. (1996)
	U	36.85	8.38	PER	Cheriak (1993)
	U	36.85	8.38	PER	Samraoui et al. (1998)
	U	34.50	-6.00	PER	Jacquemin (1987)
multicolor Hagen	U	47.00	-119.50	PER	Kime (1974)
nigroflava Martin	P	36.70	137.80	PER	Kurata (1980)
subarctica elisabethae Djakonov	P	47.90	8.10	PER	Sternberg (1995)
tuberculifera Walker	S	38.57	-79.03	PER	Halverson (1984)
umbrosa Walker	S	38.57	-79.03	PER	Halverson (1984)
	S	36.52	-82.62	PER	Johnson et al. (1980)

*Syn. *Aeshna b.*

Taxon	Voltinism	Lat	Long	Habitat	Reference
Aeshna viridis Eversmann	P	55.67	13.18	PER	Norling (1971)
	S	55.67	13.18	PER	Norling (1971)
	S	52.50	15.00	PER	Münchberg (1930b)
Anax ephippiger (Burmeister)	B	47.67	7.52	TEM	Hunger & Schiel (1999)
	B	43.52	4.67	TEM	Katzur (1998)
	B	40.68	24.73	TEM	Schnapauff et al. (2000)
	B	33.54	8.09	PER	Jödicke (2003)
	B	9.68	8.70	TEM	Gambles (1960)
immaculifrons Rambur	U	30.50	78.00	TEM	Kumar (1976)
imperator Leach	S	51.47	-0.98	PER	Corbet (1957c)
	U	52.30	10.78	PER	Martens (1986)
	U	51.47	-0.98	PER	Corbet (1957c)
	U	51.45	-2.58	PER	Holmes & Randolph (1994)
	U	48.08	-1.68	TEM	Blois (1985)
	U	47.55	7.58	PER	Portmann (1921)
	U	47.00	8.00	PER	Robert (1958)
	U	36.85	8.38	PER	Cheriak (1993)
	B	41,10	0,92	PER	R. Jödicke (pers. comm.)
julius Brauer	B	34.78	135.45		Kansai Research Group (1975)
junius (Drury)	U	47.00	-119.50	PER	Kime (1974)
	U	43.87	-80.87	PER	Trottier (1971)
	U	40.33	-86.10	PER	Wissinger (1988)
nigrofasciatus Oguma	U	35.97	139.08	TEM	Arai (1991)
papuensis (Burmeister)	U	-36.25	147.00	LOT	Hawking & New (1996)
	U	-31.93	115.83	TEM	Hodgkin & Watson (1958)
	B	-31.93	115.83	TEM	Hodgkin & Watson (1958)
parthenope Selys	S	52.50	15.00	TEM	Münchberg (1936)
	S	47.00	8.00	TEM	Robert (1958)
	S	49.00	11.50	TEM	Werzinger & Werzinger (2001)
	B	47.67	7.52	TEM	Hunger & Schiel (1999)
	S	47.17	8.07	TEM	Wuest-Graf (2003)
	B	43.52	4.67	TEM	Katzur (1998)
	B	40.68	24.73	TEM	Schnapauff et al. (2000)
	B	33.52	9.56	PER	Jödicke (2003)
tristis Hagen	B	9.68	8.70	TEM	Gambles (1960)
Austroaeschna unicornis (Martin)	U	-36.25	147.00	LOT	Hawking & New (1996)
Basiaeschna janata (Say)	S	36.52	-82.62	PER	Johnson et al. (1980)
Boyeria irene (Fonscolombe)	S	37.93	-4.87	LOT	Ferreras-Romero (1997)
vinosa (Say)	S	34.18	-81.12	LOT	Smock (1988)
Brachytron pratense (Müller)	P	52.50	15.00	PER	Münchberg (1930b)
	S	52.50	15.00	PER	Münchberg (1930b)
	U	51.45	-2.58	PER	Holmes (1984)
Coryphaeshna perrensi (McLachlan)	U	-22.93	-42.83	PER	Carvalho (1992)
Dendroaeschna conspersa (Tillyard)	U	-33.83	151.17	LOT	Tillyard (1916)
Gynacantha membranalis Karsch	U	8.95	-79.57	TEM	Fincke (1992b)
	B	8.95	-79.57	TEM	Fincke (1992b)
vesiculata Karsch	U	9.68	8.70	TEM	Gambles (1960)
Indaeschna grubaueri (Förster)	B	0.50	114.00	TEM	Orr (1994)
Limnetron debile (Karsch)	S	-22.45	-42.93	LOT	Assis et al. (2000)

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Taxon	Voltinism	Lat	Long	Habitat	Reference
Nasiaeschna pentacantha (Rambur)	U	29.90	-82.32	LOT	Dunkle (1985)
Oplonaeschna armata (Hagen)	P	34.05	-106.88	LOT	Johnson (1968)
Planaeschna milnei (Selys)	P	36.00	139.50	LOT	Arai (1988)
	P	41.70	140.45	LOT	Yokohama (2001)
GOMPHIDAE					
Anisogomphus maacki (Selys)	P	34.80	137.78	LOT	Fukui (1982)
	S	34.80	137.78	LOT	Fukui (1982)
Asiagomphus melaenops (Selys)	S	36.50	137.87	LOT	Kurata (1971)
	S	34.80	137.78	LOT	Fukui (1982)
pryeri (Selys)	P	35.02	135.17	LOT	Aoki (1999)
	P	34.68	135.17	LOT	Aoki (1993)
Austrogomphus cornutus Watson	S	-36.25	147.00	LOT	Hawking & New (1996)
ochraceus (Selys)	S	-36.25	147.00	LOT	Hawking & New (1996)
Davidius nanus (Selys)	P	34.80	137.78	LOT	Fukui (1982)
	S	34.80	137.78	LOT	Fukui (1982)
Dromogomphus spinosus Selys	S	36.52	-82.62	PER	Mahato & Johnson (1991)
	U	36.52	-82.62	PER	Mahato & Johnson (1991)
Gomphus flavipes (Charpentier)	P	52.83	14.78	LOT	Müller (1995)
	P	52.50	15.00	LOT	Münchberg (1932a)
	P	51.93	46.00	LOT	Popowa (1923)
	S	52.83	14.78	LOT	Müller (1995)
lividus Selys	S	34.18	-81.12	LOT	Smock (1988)
pulchellus Selys	P	52.27	10.52	LOT	Suhling (1994)
	S	52.27	10.52	LOT	Suhling (1994)
	S	37.37	-4.75	LOT	Ferreras-R.& García-R. (1995)
vulgatissimus (Linnaeus)	P	53.47	13.10	LOT	Müller et al. (2000)
	P	53.43	12.92	LOT	Müller et al. (2000)
	P	52.83	14.78	LOT	Müller (1995)
	P	52.62	8.88	LOT	Kern (1999)
	P	52.62	8.88	LOT	Müller et al. (2000)
	P	52.50	15.00	LOT	Münchberg (1932a)
	P	52.47	10.93	LOT	Müller et al. (2000)
	P	52.43	10.38	LOT	Müller et al. (2000)
	P	52.11	7.54	LOT	Artmeyer (1997)
	P	52.10	7.68	LOT	Müller et al. (2000)
	P	49.73	10.95	LOT	Müller et al. (2000)
	P	48.52	12.08	LOT	Müller et al. (2000)
	P	48.50	7.84	LOT	Foidl et al. (1993)
	P	45.80	4.98	LOT	Müller et al. (2000)
	S	52.83	14.78	LOT	Müller (1995)
	S	52.68	14.78	LOT	Müller et al. (2000)
	S	52.25	7.47	LOT	Müller et al. (2000)
Hagenius brevistylus Selys	P	32.17	-91.88	LOT	Wright (1944)
Heliogomphus scorpio (Ris)	S	22.42	114.18	LOT	Dudgeon (1989a)
	U	22.42	114.18	LOT	Dudgeon (1989a)
Hemigomphus gouldii (Selys)	S	-36.25	147.00	LOT	Hawking & New (1996)
Ictinogomphus decoratus melaenops (Selys)	U	1.36	103.48	PER	Lieftinck (1978)
pertinax (Selys)	S	34.68	135.17	PER	Aoki (1997)
	U	33.55	133.55	PER	Ishida et al. (1988) cited in Aoki (1997)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Ictinogomphus rapax (Rambur)	S	30.50	78.00	PER	Kumar (1985)
	U	30.50	78.00	PER	Kumar (1985)
Lanthus vernalis Carle	P	39.28	-89.10	LOT	Folsom & Manuel (1983)
	S	39.28	-89.10	LOT	Folsom & Manuel (1983)
Nihonogomphus viridis Oguma	S	34.80	137.78	LOT	Fukui (1982)
Onychogomphus f. forcipatus (Linnaeus)	P	49.04	7.77	LOT	Herden (1990)
f. unguiculatus (Vander Linden)	P	43.57	4.83	LOT	Suhling (2001)
	S	43.57	4.83	LOT	Suhling (2001)
	S	37.37	-4.75	LOT	Ferreras-R. & García-R. (1995)
modestus Selys*	U	30.50	78.00	LOT	Kumar (1976)
uncatus (Charpentier)	P	43.57	4.83	LOT	Schütte et al. (1998)
	P	37.93	-4.87	LOT	Ferreras-Romero et al. (1999)
	S	43.57	4.83	LOT	Schütte et al. (1998)
	S	37.93	-4.87	LOT	Ferreras-Romero et al. (1999)
viridicostus (Oguma)	S	34.80	137.78	LOT	Fukui (1982)
Ophiogomphus australis Carle	S	30.60	-92.05	LOT	Carle (1992)
cecilia (Fourcroy)	P	52.83	14.78	LOT	Müller (1995)
	S	52.83	14.78	LOT	Müller (1995)
	S	52.50	15.00	LOT	Münchberg (1932a)
colubrinus Selys	S	46.08	-87.50	LOT	Cornelius & Burton (1987)
howei Bromley	S	36.65	-80.98	LOT	Kennedy & White (1979)
sinicus (Chao)	S	22.42	114.18	LOT	Dudgeon (1989a)
	U	22.42	114.18	LOT	Dudgeon (1989a)
Paragomphus genei (Selys)	U	36.78	-6.37	LOT	Testard (1975)
	B	35.00	10.63	PER	Jödicke (2001)
	M	33.52	7.52	PER	Jödicke (2003)
	M	-22.42	15.73	TEM	Suhling et al. (2004)
lineatus (Selys)	U	30.50	78.00	LOT	Kumar (1976)
Phyllogomphoides duodentatus Donnelly	P	32.42	-115.08	LOT	Novelo-Gutiérrez (1993)
Progomphus obscurus (Rambur)	U	30.00	-97.00	LOT	Phillips (2001)
Sieboldius albardae Selys	S	34.80	137.78	LOT	Fukui (1982)
Stylogomphus suzukii (Oguma)	S	34.80	137.78	LOT	Fukui (1982)
CORDULEGASTRIDAE					
Cordulegaster bidentata Selys	P	51.53	8.08	LOT	Dombrowski (1989)
	P	47.97	7.95	LOT	Salowsky (1989)
b. boltonii (Donovan)	P	51.67	14.00	LOT	Donath (1987)
	P	46.17	14.30	LOT	Kiauta (1964)
boltonii immaculifrons Selys	S	43.60	4.83	LOT	Schütte (1997)
	S	37.93	-4.87	LOT	Ferreras-R. & Corbet (1999)
dorsalis Hagen	P	37.33	-121.93	LOT	Kennedy (1917)
CORDULIIDAE s.l.					
Apocordulia macrops Watson	S	-36.25	147.00	LOT	Hawking & New (1996)
Cordulia aenea (Linnaeus)	P	60.17	24.97	PER	Halkka (1980)
	P	52.50	15.00	PER	Münchberg (1932b)
	P	47.00	8.00	PER	Robert (1958)
	S	52.50	15.00	PER	Münchberg (1932b)
	S	47.00	8.00	PER	Robert (1958)
amurensis (Selys)	P	43.05	141.35	PER	Ubukata (1981)
shurtleffii Scudder	P	46.00	-74.00	PER	Caron & Pilon (1992)

*Syn. *Nepogomphus m.*

Taxon	Voltinism	Lat	Long	Habitat	Reference
Epitheca bimaculata sibirica Selys	S	35.98	138.38	PER	Sonehara (1967)
cynosura (Say)	S	36.52	-82.62	PER	Johnson (1986)
	U	36.52	-82.62	PER	Johnson (1986)
marginata Selys	S	35.98	138.38	PER	Sonehara (1967)
princeps Hagen	S	40.33	-86.10	PER	Wissinger (1988)
	U	40.33	-86.10	PER	Wissinger (1988)
Hemicordulia australiae (Rambur)	S	-36.87	174.77	PER	Rowe (1987)
tau Selys	U	-31.93	115.83	TEM	Hodgkin & Watson (1958)
	U	-36.08	148.75	PER	Faragher (1980)
Macromia amphigena Selys	P	34.80	137.78	LOT	Fukui (1982)
	S	34.80	137.78	LOT	Fukui (1982)
daimoji Okumura	S	34.80	137.78	LOT	Fukui (1982)
illinoiensis georgina (Selys)	S	34.18	-81.12	LOT	Smock (1988)
moorei Selys	U	30.50	78.00	LOT	Kumar (1976)
splendens (Pictet)	S	44.12	3.93	LOT	Leipelt & Suhling (2005)
Procordulia smithii (White)	P	-42.67	171.33	PER	Deacon (1979)
Somatochlora alpestris (Selys)	P	64.42	19.50	PER	Johansson & Nilsson (1991)
	P	47.90	8.10	PER	Sternberg (1990)
	S	47.90	8.10	PER	Sternberg (1990)
arctica (Zetterstedt)	P	47.90	8.10	PER	Sternberg (1990)
flavomaculata (Vander Linden)	P	52.50	15.00	PER	Münchberg (1932b)
metallica (Vander Linden)	P	47.00	8.00	PER	Robert (1958)
	S	47.00	8.00	PER	Robert (1958)
sahlbergi Trybom	P	67.10	-137.00	PER	Cannings & Cannings (1985)
Synthemis leachi Selys	S	-31.93	115.83	LOT	Watson (1967)
LIBELLULIDAE					
Acisoma p. ascalaphoides Rambur	U	36.85	8.38	PER	Cheriak (1993)
p. panorpoides Rambur	B	13.87	100.53	PER	Asahina et al. (1972)
	M	30.50	78.00	PER	Kumar (1976)
Brachythemis contaminata (Fabricius)	B	13.87	100.53	PER	Asahina et al. (1972)
leucosticta (Burmeister)	B	34.50	-6.00	PER	Jacquemin (1987)
Bradinopyga geminata (Rambur)	U	30.50	78.00	TEM	Kumar (1973)
Celithemis elisa (Hagen)	U	40.33	-86.10	PER	Wissinger (1988)
fasciata Kirby	U	33.00	-82.00	PER	Benke & Benke (1975)
ornata (Rambur)	U	33.00	-82.00	PER	Benke & Benke (1975)
Crocothemis divisa Karsch	U	34.80	137.78	TEM	Fukui (1982)
erythraea (Brullé)	B	44.00	5.00	TEM	Aguesse (1960)
	B	43.52	4.67	TEM	Aguesse (1961)
	B	43.52	4.67	TEM	Katzur (1998)
	B	37.00	-6.00	TEM	Montes et al. (1982)
	B	36.85	8.38	PER	Cheriak (1993)
	B	33.54	8.09	PER	Jödicke (2003)
	B	32.00	-5.00		Jacquemin & Boudot (1999)
	M	-22.42	15.73	TEM	Suhling et al. (2004)
servilia (Drury)	B	34.35	45.37	PER	Sage (1960)
	B	13.87	100.53	PER	Asahina et al. (1972)
	M	30.50	78.00	TEM	Kumar (1976)
Diplacodes bipunctata (Brauer)	U	-31.93	115.83	TEM	Hodgkin & Watson (1958)
haematodes (Burmeister)	U	-36.25	147.00	LOT	Hawking & New (1996)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Diplacodes lefebvrii (Rambur)	B	33.54	8.09	PER	Jödicke (2003)
nebulosa (Fabricius)	B	13.87	100.53	PER	Asahina et al. (1972)
trivialis (Rambur)	B	13.87	100.53	PER	Asahina et al. (1972)
	M	30.50	78.00	PER	Kumar (1976)
Erythemis simplicicollis (Say)	U	40.33	-86.10	PER	Wissinger (1988)
	B	40.33	-86.10	PER	Wissinger (1988)
	B	33.67	-117.85	PER	Morin (1984)
Erythrodiplax berenice (Drury)	B	43.08	-70.08	PER	Kelts (1979)
Leucorrhinia caudalis (Charpentier)	U	53.23	13.58	PER	Mikolajewski et al. (2004)
dubia (Vander Linden)	P	67.83	21.67	PER	Norling (1984b)
	P	58.70	16.52	PER	Norling (1984b)
	P	47.90	8.10	PER	Sternberg (1990)
	S	63.83	20.25	PER	Johansson (2000)
	S	36.70	137.80	PER	Kurata (1980)
intacta (Hagen)	U	-43.53	80.02	PER	Deacon (1975)
	U	40.33	-86.10	PER	Wissinger (1988)
pectoralis (Charpentier)	P	47.32	8.78	PER	Wildermuth (1994)
	S	47.32	8.78	PER	Wildermuth (1994)
Libellula deplanata Rambur	S	33.00	-82.00	PER	Benke & Benke (1975)
depressa Linnaeus	S	48.08	-1.68	TEM	Blois (1985)
	U	52.83	14.78	PER	Weisheit (1995)
	U	52.30	10.78	PER	Martens (1986)
	U	51.45	-2.58	PER	Holmes & Randolph (1994)
	U	47.33	8.23	PER	Winsland (1991)
	U	47.00	8.00	PER	Robert (1958)
fulva Müller	S	44.00	6.00	PER	Aguesse (1960)
incesta Hagen	S	33.00	-82.00	PER	Benke & Benke (1975)
luctuosa Burmeister	U	40.33	-86.10	PER	Wissinger (1988)
pulchella Drury	U	40.33	-86.10	PER	Wissinger (1988)
quadrimaculata Linnaeus	U	52.30	10.78	PER	Martens (1986)
	U	47.32	8.78	PER	Wildermuth (1994)
Lyriothemis cleis (Brauer)	M	0.50	114.00	TEM	Orr (1994)
Malgassophlebia aequatoris Legrand	B	0.56	12.86	LOT	Legrand (1979)
Neurothemis intermedia atalanta (Ris)	B	13.87	100.53	PER	Asahina et al. (1972)
tullia feralis (Burmeister)	B	13.87	100.53	PER	Asahina et al. (1972)
t. tullia (Drury)	U	30.50	78.00	TEM	Kumar (1988)
	M	5.13	100.50	TEM	Che Salmah et al. (1999)
Orthetrum albistylum (Selys)	U	47.33	8.23	TEM	Wildermuth et al. (1986)
	B	40.68	24.73	TEM	Schnapauff et al. (2000)
brunneum (Fonscolombe)	U	30.50	78.00	LOT	Kumar (1976)
	B	30.50	78.00	LOT	Kumar (1976)
caledonicum (Brauer)	U	-36.25	147.00	LOT	Hawking & New (1996)
cancellatum (Linnaeus)	S	52.50	13.42	PER	Schmidt (1982)
	B	43.52	4.67	TEM	Katzur (1998)
chrysostigma (Burmeister)	B	34.23	7.55	PER	Jödicke (2003)
	M	-22.42	15.73	TEM	Suhling et al. (2004)
coerulescens anceps (Schneider)	U	37.37	-4.75	LOT	Ferreras-R. & García-R. (1995)
	B	34.23	7.55	PER	Jödicke (2003)
japonicum (Uhler)	U	36.72	136.52	PER	Watanabe (1986)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Orthetrum pruinosum (Burmeister)	M	30.50	78.00	PER	Kumar (1988)
sabina (Drury)	B	30.50	78.00	TEM	Kumar (1976)
	B	13.87	100.53	PER	Asahina et al. (1972)
trinacria (Selys)	M	34.50	-6.00	PER	Jacquemin (1987)
Pachydiplax longipennis (Burmeister)	S	35.90	-79.05	PER	Eller (1963)
	U	35.90	-79.05	PER	Eller (1963)
	B	40.33	-86.10	PER	Wissinger (1988)
	B	33.67	-117.85	PER	Morin (1984)
Palpopleura lucia (Drury)	M	7.28	30.90	PER	Hassan (1976)
Pantala flavescens (Fabricius)	U	40.33	-86.10	PER	Wissinger (1988)
	U	-37.23	145.92	PER	Hawking & Ingram (1994)
	M	30.50	78.00	TEM	Kumar (1984)
	M	-22.42	15.73	TEM	Suhling et al. (2004)
Perithemis tenera (Say)	U	40.33	-86.10	PER	Wissinger (1988)
	B	40.33	-86.10	PER	Wissinger (1988)
	B	33.67	-117.85	PER	Morin (1984)
Plathemis lydia (Drury)	U	40.33	-86.10	PER	Wissinger (1988)
Sympetrum commixtum (Selys)	B	30.50	78.00	TEM	Kumar (1979a)
danae (Sulzer)	U	48.23	15.68	PER	Waringer (1983)
depressiusculum (Selys)	U	47.00	8.00	TEM	Robert (1958)
	U	43.52	4.67	TEM	Katzur (1998)
flaveolum (Linnaeus)	B	47.83	16.75	TEM	Schmidt (1982)
fonscolombii (Selys)	B	43.52	4.67	TEM	Aguesse (1961)
	B	32.00	-5.00		Jacquemin & Boudot (1999)
	B	34.50	-6.00	TEM	Jacquemin (1987)
	B	33.25	8.48	PER	Jödicke (2003)
	B	47.67	7.52	TEM	Hunger & Schiel (1999)
	B	40.68	24.73	TEM	Schnapauff et al. (2000)
	M	43.52	4.67	TEM	Katzur (1998)
	M	37.00	-6.00	PER	Montes et al. (1982)
internum Montgomery	U	43.38	-80.48	TEM	Peterson (1975)
meridionale Selys	U	36.85	8.38	PER	Cheriak (1993)
	U	36.85	8.38	PER	Samraoui et al. (1998)
pedemontanum (Müller in Allioni)	U	52.50	15.00	PER	Münchberg (1930a)
rubicundulum (Say)	U	43.38	-80.48	TEM	Peterson (1975)
sanguineum (Müller)	U	51.47	-0.98	TEM	Clausnitzer (1974)
	U	47.00	8.00	TEM	Robert (1958)
	U	36.85	8.38	PER	Cheriak (1993)
sinaiticum Dumont	U	33.54	8.09	PER	Jödicke (2003)
striolatum imitoides Bartenef	U	35.08	135.75	TEM	Matsura et al. (1995)
s. striolatum (Charpentier)	U	50.47	-1.45	PER	Corbet (1956)
	U	47.00	8.00	TEM	Robert (1958)
	U	36.85	8.38	PER	Samraoui et al. (1998)
	B	51.30	6.27	TEM	Jödicke & Thomas (1993)
vicinum (Hagen)	U	40.33	-86.10	TEM	Wissinger (1988)
	U	35.90	-79.05	TEM	Boehms (1971)

Taxon	Voltinism	Lat	Long	Habitat	Reference
Sympetrum vulgatum (Linnaeus)	U	47.48	19.17	TEM	Steinmann (1961)
Tramea lacerata Hagen	U	40.33	-86.10	PER	Wissinger (1988)
	B	33.67	-117.85	PER	Morin (1984)
virginia (Rambur)	U	30.50	78.00	TEM	Kumar (1989)
Trithemis annulata (Palisot de Beauvois)	B	37.27	-6.95	PER	Hartung (1985)
	B	37.37	-4.75	PER	Agüero-P. & Ferreras-R. (1992)
	M	33.54	8.09	PER	Jödicke (2003)
kirbyi ardens (Gerstäcker)	M	33.52	7.52	PER	Jödicke (2003)
	M	-22.42	15.73	TEM	Suhling et al. (2004)
pallidinervis (Kirby)	B	13.87	100.53	TEM	Asahina et al. (1972)
Urothemis assignata (Selys)	M	7.28	30.90	PER	Hassan (1977)
Zygonyx iris insignis (Kirby)	U	22.33	114.17	LOT	Dudgeon & Wat (1986)
Zyxomma petiolatum Rambur	U	30.50	78.00	PER	Kumar (1972)