LIFE-HISTORY STRATEGIES IN DRAGONFLIES AND THE COLONIZATION OF NORTH AMERICA BY THE GENUS *ARGIA* (ODONATA : COENAGRIONIDAE)

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The genus *Argia* appears to have had a tropical American origin, but the range of some species now extends to Canada. This colonization of latitudes with very different seasonal regimes from those of the ancestral environments has been made possible, at least in *A. vivida*, by the selection of relatively warm habitats for oviposition, and by a larval diapause which restricts the cold-intolerant adult and egg stages to a favorable time of year. The ability of larvae to adapt their metabolism individually to different temperatures, and the habit of sun-basking in adults, are also components of a strategy which has allowed northward colonization. But it is the widespread occurrence of diapause in the Odonata which is seen as the important contributant to their success in colonizing higher latitudes, a phenomenon which contrasts with the other principal groups of aquatic insects (Ephemeroptera, Plecoptera, Trichoptera) in which diapause has only occasionally been demonstrated. The Plecoptera and Trichoptera, at least, appear to have generally taken an alternative route, namely the development of cold tolerance in all stages.

INTRODUCTION

The environment of the earliest Odonata is unknown but appears to have been tropical. Protodonata fossils are found in Middle and Upper Carboniferous and Permian equatorial beds (WOOTTON, 1981). No Paleozoic larvae are known and so we do not know whether the earliest odonates had aquatic larvae. However, the relatively high thermal thresholds for development in modern odonate larvae suggest that larvae, like adults, are a warm-adapted group. WIGGINS, MACKAY and SMITH (1980) state that "Odonata first became aquatic in cool, running waters" (p.145) and that " larvae ... were initially cool-lotic-adapted" (p.187). I believe that these statements

are a misconstruction of CORBET's (1962) statement that the most primitive extant dragonflies are found near the (cool) sources of water courses. It is quite possible that these primitive odonates have been displaced to the colder, more stable, highland water courses by more recently evolved groups. KENNEDY (1919) was of the opinion that the first zygopteran probably lived in tropical ponds, and TAI (1967) suggests that most dragonflies originated in the old-world tropics and spread from there.

There is no argument over the new-world genus *Argia;* this genus is agreed to be of Neotropical origin (WALKER, 1953) and furthermore of young phylogenetic age. KENNEDY (1919) came to this conclusion on the basis of the large number of closely related species, while KIAUTA & KIAUTA (1980) agreed on the basis of the high chromosome numbers and total chromatin levels in the North American species they studied. These latter authors point out that the extraordinary amount of variation in recombination potential suggests that *Argia* is in the midst of an intense evolutionary process.

Unfortunately the genus is poorly collected in South America and the more than 100 species that have been described are difficult to systematize. Consequently we are a long way from having a reconstructed phylogeny from which we can map the origin and spread of the genus. Nevertheless, this paper will attempt to discuss the origin of the genus and the mechanisms whereby it has colonized North America.
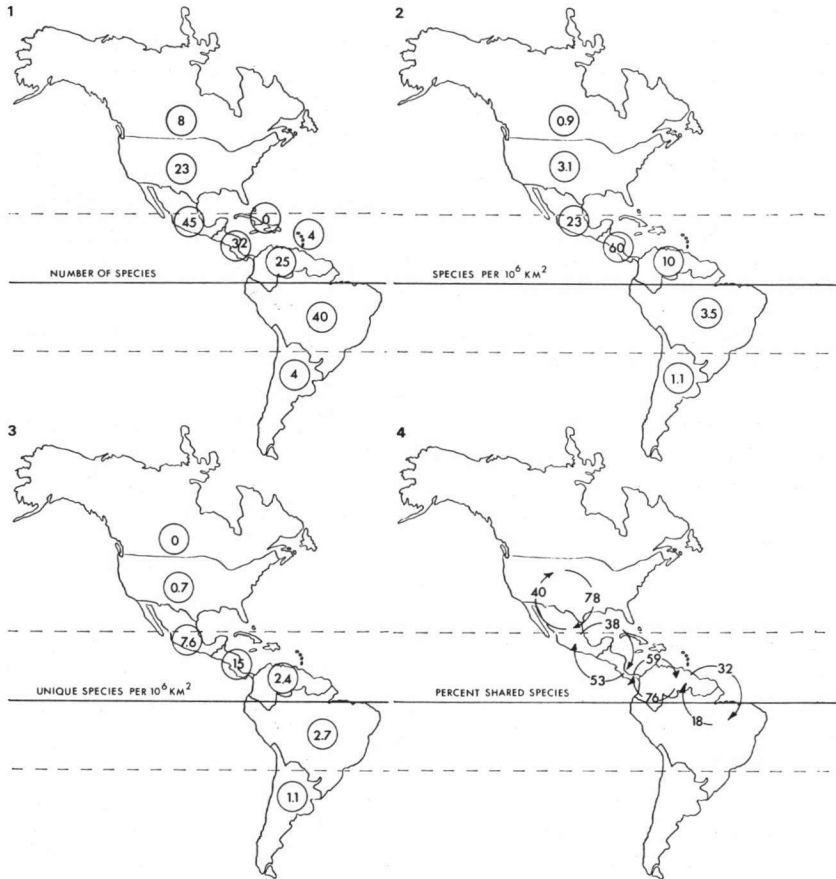
DISTRIBUTION OF *ARGIA*

Figures 1-4 present certain manipulations that can be made with the data in the literature. Undoubtedly the distributional records are incomplete, especially in South America, and the taxonomy may very well be incorrect, but these are the only published data that we have to work with at the present time.

These figures are based on political divisions which, nevertheless, roughly coincide with certain latitudinal belts. Some are misleading, such as the Canadian zone from which 8 species are recorded; this zone is largely unpopulated by *Argia* which reaches only 47°N in eastern Canada and 51°N in western Canada. Also 8 species whose distribution in the United States is restricted to the region around the Mexican border are, nonetheless, included in the United States total.

Note that no species are recorded from the Greater Antilles and only 4 species from the Lesser Antilles, whereas 25 per cent of all Central American odonates known to CALVERT (1908) were also

known by him to occur in the West Indies. In Canada, *A. moesta* (Hagen) and *A. fumipennis violacea* (Hagen) occur in New Brunswick and Nova Scotia, but not on Prince Edward Island which is separated from the mainland by only 10 km. A sea barrier of 45 km apparently prevents *A. emma* Kennedy from reaching Vancouver Island, although another 7 coenagrionids that occur on the S.W. mainland of

Figs 1-4. The distribution of *Argia* in geographic regions of the Americas (the regions are: Canada, United Stated, Mexico, Central America, Greater Antilles, Lesser Antilles, northern South America, central South America and southern South America): (1) number of species; — (2) of species per million square kilometers; — (3) number of species per million square kilometres recorded from each geographic region and not recorded from any other region; — (4) percentage of the species in each geographic region which are shared with adjacent regions. In this figure Canada and the United States are combined as are central and southern South America.

British Columbia all occur on the Island as well (CANNINGS & STUART, 1977). Either the genus has low vagility or perhaps suitable habitats are not present on these islands.

By far the greatest number of species per unit area and the greatest number of unique species per unit area is found in Central America (Figs 2 & 3), with a decline in both of these statistics to the north and to the south. This suggests a center of speciation in Central America, which is further reinforced when the proportions of shared species between regions are considered (Fig. 4). For example, Mexico shares many fewer of its species with the United States than does the United States with Mexico, suggesting a spread from Mexico into the United States. The differently sized areas in Central and South America and the paucity of information south of the equator make deductions for these regions difficult, but such information that is available is not totally inconsistent with a center of speciation and subsequent spread from Central America north of the Isthmus of Panama. However, the large proportion of unique species in central South America might indicate another center of speciation there.

The importance of determining where the North American species or their ancestors originated is that the time available for colonization may have been very different for origins north and south of the Isthmus of Panama. The currently accepted view (MALFAIT & DINKELMAN, 1972) of geological events in Central America appears to be that a group of volcanic islands (the Proto-Antilles) existed between North and South America in the early Cretaceous (135 mya) and these moved eastward relative to the continents and became the Greater Antilles. In the late Tertiary (20 mya) a new Central American archipelago had appeared and this consolidated to form the Isthmus of Panama only in the mid-Pliocene, about 6 mya. Given the apparent inability of *Argia* to 'island-hop', the genus would have had only 6 million years in North America if our species came from South America, but very much longer if our species or their ancestors came from north of the Isthmus. Given KENNEDY's (1919) and the KIAUTAs' (1980) views on the recency of the genus it is unlikely that *Argia* was in the Americas at the time of Pangaea, 200 mya. Therefore, either the North American or the South American species would appear to be less than 6 million years old.

The only detailed information on probable past events within the genus are at the level of sub-species. The KIAUTAs (1980) believe that *A. fumipennis violacea* (Fig. 5) evolved in north or central United States and spread both north and south; *A. f. fumipennis* (Burmeister) appears to be younger than central U.S. *A. f. violacea* but older than

the northernmost populations of this subspecies; *A. f. atra* Gloyd in Florida is thought to be the youngest subspecies. Also, JOHNSON (1972) attributes the origin of pattern variation amongst populations of *A. apicalis* (Say) in the south-eastern United States to habitat changes in the Pleistocene.

Eight species of *Argia* have ranges that extend into Canada (Figs 5-12), and their distributions have been much influenced by the Great Plains in that they tend to have eastern or western distributions in North America. Of the eastern species, *A. tibialis* (Rambur) (Fig. 6) and *A. apicalis* (Fig. 7) are found only north of Mexico. These 2 species have the highest known chromosome number ($n=19$) of any odonate (KIAUTA & KIAUTA, 1980) and have presumably evolved rather recently in the United States. If the KIAUTAs (1980) are correct in their assessment of the evolutionary history of *A. fumipennis*, the presence of *A. f. fumipennis* in Mexico and Guatemala is a result of a recent southward spread (Fig. 5). *A. translata* Hagen (Fig. 8) has the largest latitudinal range of any *Argia* - from Massachusetts to Brazil - but its origins are unknown. The remaining 2 eastern Canadian species have broader east-west distributions in the southern United States and also occur in Mexico. *A. sedula* (Hagen) (Fig. 9) ranges from Pennsylvania to California, while *A. moesta* (Fig. 10) occurs

Argia fumipennis violacea
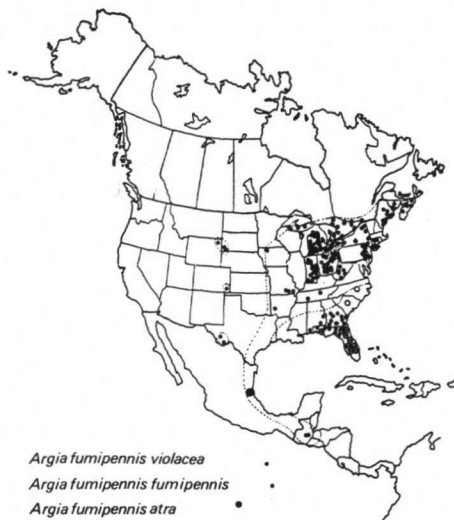
Argia fumipennis fumipennis

Argia fumipennis atra

Fig. 5. The distribution of *Argia fumipennis* and subspecies. In figures 5-12 a larger circle indicates a record for a whole area (state or country), while smaller circles indicate more precise localities (county or township).

from Nova Scotia to western Mexico and California. Of the 2 western Canadian species, *A. emma* (Fig. 11) is not found south of central California, whilst the range of *A. vivida* Hagen (Fig. 12) extends from Alberta and British Columbia to central Mexico. Nothing is known of the origins or relationships of these last 4 species, but it is probable that they have origins in the United States.

 A. alberta Kennedy and *A. lugens* (Hagen) are western United States species, which have presumably originated there, while the 8 or
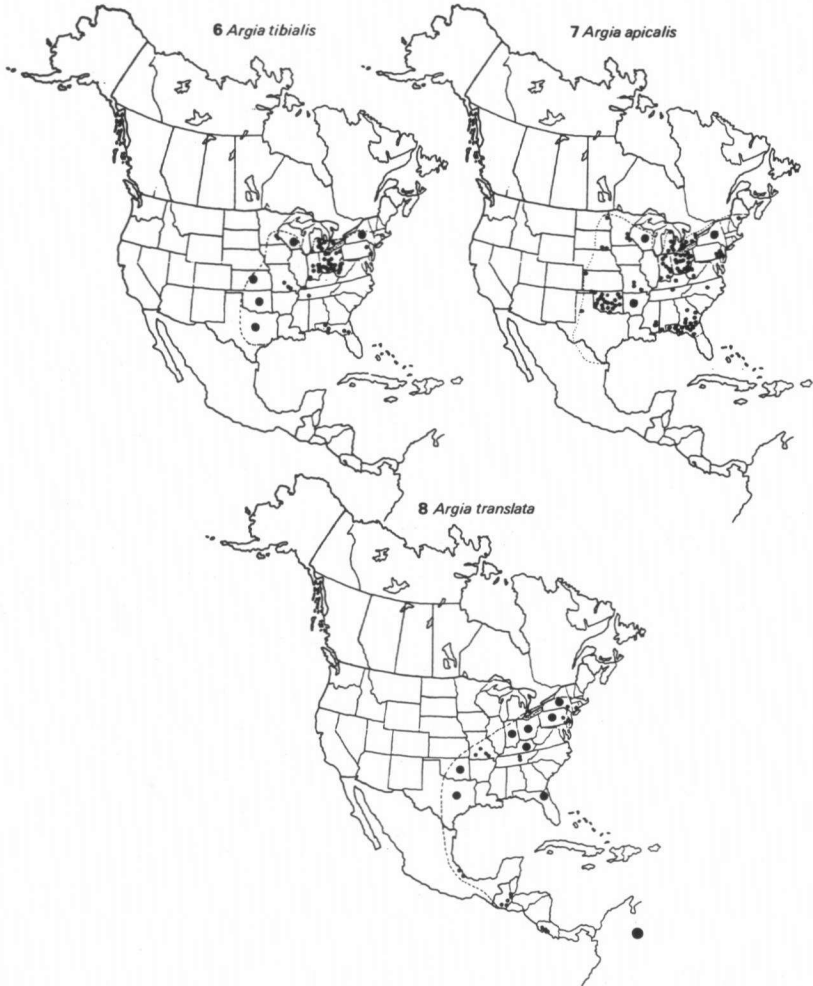
Figs 6-8. The distribution of three *Argia* species (cf. Fig. 5).

so species whose northern limit is in the south-western United States along the Mexican border have origins further south.

Thus it appears that the genus *Argia* had a tropical American origin and therefore might be expected to be warm-adapted and to show relatively little seasonality in its life-cycles. However, several species have spread into North America to about 35° N, and others have apparently rather recently evolved in North America and some of these attain 51° N. This last group of species clearly could not survive
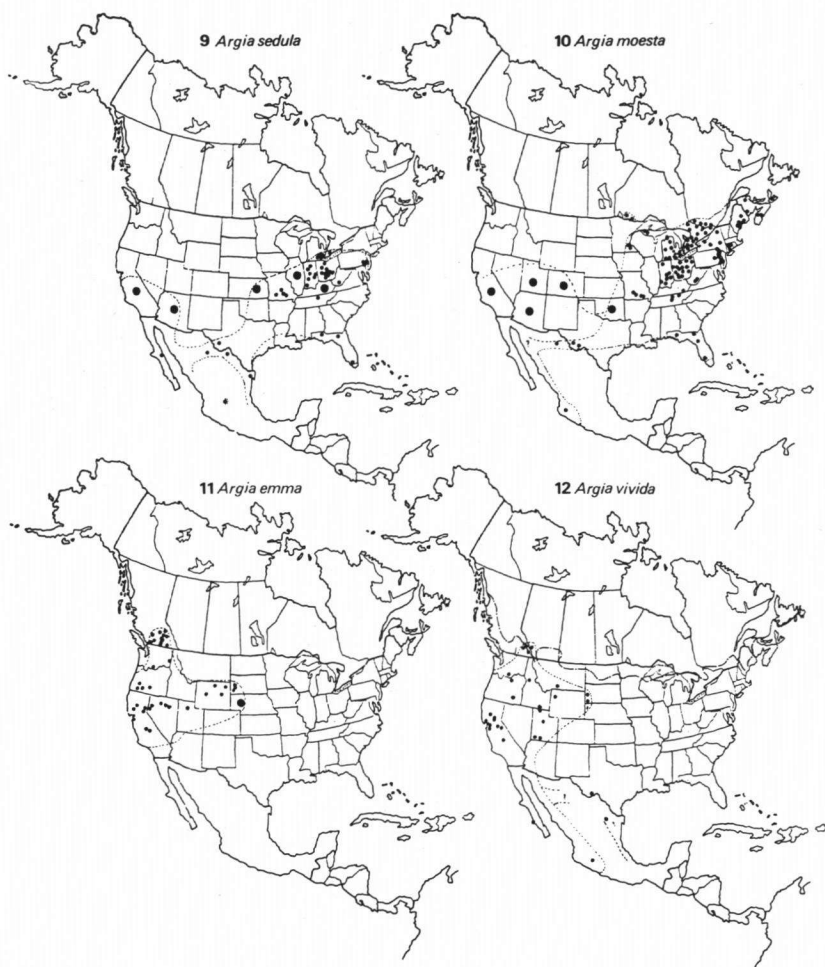
Figs 9-12. The distribution of four *Argia* species (cf. Fig. 5).

with a warm-adapted, aseasonal life-history strategy and it is this subject to which I shall now turn.

THE COLONIZATION OF TEMPERATE REGIONS BY DRAGONFLIES

Strategies that species of tropical origin might employ in order to survive the winter of higher latitudes will be considered under 4 headings: 1. Migration; 2. Cold tolerance in all stages; 3. Cold tolerance in some stage(s) and seasonal adjustment of the life-cycle; 4. Habitat selection and seasonal adjustment of the life-cycle.

MIGRATION

Migration as a means of escape from low winter temperatures at the same time that a species' range is extended into higher latitudes in the summer, is apparently not a common strategy in odonates. In North America it is shown to a limited extent by *Anax junius* Drury (TROTTIER, 1971) and *Pantala flavescens* (Fabricius) (TROTTIER, 1967). Weakly flying Zygoptera are unlikely to have this strategy open to them.

COLD TOLERANCE IN ALL STAGES

Eggs of some northern *Lestes, Aeshna* and *Sympetrum* can over-winter in diapause (CORBET, 1980), but odonate eggs do not normally show tolerance. *Enallagma boreale* Selys eggs from Quebec (46° N) suffered 100 per cent mortality at 15° C and 75 per cent at 20° C. The optimal temperature for egg development was 27.5° C and the lowest constant temperature at which complete development from oviposition to hatching occurred was 17° C (RIVARD *et al.*, 1975).

Larvae of some species are known to be able to survive periods of freezing (DABORN, 1971), and larvae of most temperate species can over-winter, often at low temperatures. But no larvae are known to be active or to grow at low temperatures; estimated low temperature thresholds for development appear to be about 8° C (TROTTIER, 1971; THOMPSON, 1978; PRITCHARD, unpubl.).

Adults are much less low-temperature-tolerant than larvae, Anisoptera, at least, being adapted to function at rather high body temperatures (MAY, 1978). Body temperature can be raised prior to flight by wing-whirring in anisopteran fliers, but the lowest ambient temperatures at which this is possible appear not to have been recorded

(MAY, 1976), although they are probably quite high. Mature *Argia vivida* adults do not appear at habitats in Alberta and British Columbia until sunshine is more or less continuous and air temperature approaches 20° C, and even then they perch in the sun on reflective surfaces, a characteristic *Argia* behaviour.

Therefore, dragonflies generally appear to be warm-adapted in all stages, and while many larvae, some eggs, and a few adults are cold tolerant, most eggs and adults are not. No temperate species has been able to use an aseasonal life-cycle and adult life and egg development (and perhaps adjacent larval stages) must generally be very precisely fitted into the summer.

COLD TOLERANCE IN SOME STAGE(S) AND SEASONAL ADJUSTMENT OF THE LIFE-CYCLE

This is the commonest strategy shown by the many species that have successfully colonized temperate latitudes; "the basic life-history (is) modified so as to ensure that the winter is survived by a suitably resistant stage, and that the adult coincides with the warm season" (CORBET, 1962). The resistant stage is usually the larva and the synchronization of the adult emergence with summer conditions is achieved by a larval diapause. This subject has recently been reviewed by CORBET (1980) and by DEACON (1981) and I shall not deal with it further except to raise the question: Can seasonal regulation be achieved without diapause? In order to consider this question it is instructive to consider other groups of insects with similar life--cycles.

The Plecoptera are held to have originated in the southern hemisphere in the Paleozoic and to have crossed tropical regions during the Permian Ice Age (ILLIES, 1965). The only family which has adapted to tropical environments is the Perlidae, which may have penetrated the tropics after radiation in temperate regions (ILLIES, 1965) or may have driven other families out of the tropics (RICKER, 1950). Either way, the stoneflies contrast markedly with the Odonata in that all stages, including the egg and the adult, are cold-adapted and the egg or larval diapauses that are recorded (KHOO, 1968; HARPER & HYNES, 1972) occur in the summer and presumably serve to survive warm conditions. Other photoperiodically-cued events in Plecoptera life-histories are only suppositions; HARPER & PILON (1970) suggest that synchronization mechanisms occur during larval growth in species that have synchronized adult emergence, and HYNES (1970) maintains that photoperiod must be an important factor in the life-cycles of winter stoneflies that emerge under ice.

The Trichoptera are also largely cold-adapted and the tropical groups are believed to be specialized lineages that arose from temperate ancestors (ROSS, 1967). A summer diapause occurs in some species, either as larvae, in which case metamorphosis is delayed under the influence of long days, or as adults, when maturation is similarly delayed (DENIS, 1978). A reproductive diapause occurs in *Limnephilus lunatus* Curtis in England so that the life-cycle is univoltine whether in watercress beds at a constant temperature of 10°C or in a mountain stream with fluctuating temperature (GOWER, 1967). However, *Drusus annulatus* Stephens, another limnephilid, was basically bivoltine in the watercress bed, although all stages were present throughout most of the year (GOWER, 1965), and univoltine in the mountain stream (GOWER, 1973). No diapause was recorded for this last species and temperature was considered to be the over-riding factor in determining growth rates.

The Ephemeroptera may have had a similar evolutionary history to that of the dragonflies. The Siphlonuridae are believed to be the most primitive extant family (EDMUNDS *et al.*, 1976) and they are mostly adapted to cool waters. But Ephemeroptera are common in the tropics; they were already aquatic in the Permian (WOOTTON, 1981), and of the North and Central American genera, 22 are believed to have had a tropical origin compared with 39 that are boreal (EDMUNDS *et al.*, 1976). However Ephemeroptera do not appear to go in for diapause. There is reference to a summer egg diapause in MASAKI (1980) and Landa's life-history classification (EDMUNDS *et al.*, 1976) includes an assumed winter egg diapause. CLIFFORD (1970) suggests that photoperiod affects larval growth in *Leptophlebia cupida* (Say), and implies that larvae accumulate in a late stage and thereby synchronize adult emergence.

Thus, the situation in the Ephemeroptera is puzzling and would repay further study, but the different strategies seen in the Odonata on the one hand and the Plecoptera and Trichoptera on the other, appear to be that the latter have become cold-adapted, developing at low temperatures and having cold-tolerant adults, whereas the Odonata have remained warm-adapted and require a precise mechanism for seasonal adjustment of the life-cycle. Life-cycles in Plecoptera and Trichoptera have still become adapted to seasonal changes in temperature, but precise synchronization of development is generally not critical. This is shown by observations of adults of these groups (and Ephemeroptera) emerging during the winter under unusually high temperatures (NEBE-KER, 1971; THIBAULT, 1971).

HABITAT SELECTION AND SEASONAL ADJUSTMENT OF THE LIFE-CYCLE

The life-history strategies shown by dragonflies of the genus *Argia* are completely unknown, except for some northern populations of *A. vivida* for which data are slowly accumulating (PRITCHARD, 1971, 1980; PRITCHARD & PELCHAT, 1977). In these populations seasonal adjustment of the life-cycle is necessary and is achieved by a photoperiodically induced delay in larval development (Table I; PRITCHARD & PELCHAT, 1977). Under a L:D photoperiod of 8:16 hr, I was never successful in rearing an F-1 larva through that stage. Most F-1 larvae kept under L:D 10:14 also died in that stage, but some did ecdyse after an average of 64 days. A similarly long period of time was taken in the F-1 stage by larvae under L:D 12:12, but under L:D 14:10 almost all larvae passed through the F-1 stage in an average of 23 days, as did larvae' kept under L:D 16:8. Larvae in F-2 also experienced delayed development under photoperiods of 12 hr light or less as, to a lesser extent, did larvae in F-3 (Table I). Furthermore, larvae collected in what were assumed to be the F-5 and F-4 instars (PRITCHARD & PELCHAT, 1977) attained the F-1 and F instars with one fewer molt under L:D 14:10 conditions than under L:D

Table 1

The effect of various constant photoperiod regimes on development of *Argia vivida*

Photoperiod	Time (x days ± S.E. in a stage at 20°C)		
	F-3	F-2	F-1
8 HR*	21.5 ± 2.4	30.2 ± 3.7	—[1]
	(N = 4)	(N = 4)	
10 HR+	24.4 ± 1.2	31.1[2] ± 2.8	64.3 ± 12.0)
	(N = 15)	(N = 8)	(N = 3)
12 HR+		28.8 ± 4.1	68.2 ± 3.82)
		(N = 5)	(N = 13)
14 HR+	13.4 ± 0.43	15.7 ± 0.34	22.9[3] ± 0.80)
	(N = 11)	(N = 45)	(N = 44)
16 HR*	18.8 ± 2.3	18.2 ± 2.5	24.0 ± 1.0)
	(N = 6)	(N = 5)	(N = 3)

* Fed AEDES; + Fed ENCHYTRAEUS.
[1] 12 larvae survived 30-90 days without molting.
[2] Excludes 1 individual: 45 days.
[3] Excludes 4 individuals: 44, 48, 66, 67 days.

12:12 or 10:14. The effect of this photoperiodic influence is, there-
fore, to slow development after the autumnal equinox such that adult
emergence during the winter is impossible. Data for F-stage larvae are
incomplete at this time but it appears that the length of time spent in
this stage is very long under long days.

A. vivida also has another strategy for colonization of the temper-
ate zone - it appears to show habitat preference for geothermally heat-
ed streams. All of the known Canadian populations and many of the
populations throughout the species' range occur in warm springs.
Furthermore, individual larvae can acclimate to different temperatures
between 15° C and 40°C through qualitative and quantitative changes
in certain enzymes (SCHOTT & BRUSVEN, 1980). With this habitat
selection, cold tolerance need not be developed in any stage if adult
life is synchronized with the summer season. But A. vivida does occur
in cold streams (KENNEDY, 1915), including some that have ice-
-cover for a part of the year (NIMZ, 1978). The details of the life-his-
tory in these cold streams are unknown, although there is some evi-
dence that the life-cycle is extended (PRITCHARD, 1980). The pre-
ference of Argia for running water, especially near to springs, would
generally avoid exposure to freezing temperatures, and I suspect that
members of this genus are not as cold-tolerant as those coenagrionids
that live in ponds. Therefore, habitat selection by ovipositing females
has perhaps been an important feature of this genus' ability to colon-
ize temperate regions as perhaps, on a smaller scale, has the habit of
sun-basking by mature adults.

CONCLUDING REMARKS

My hypothesis is that species of Argia have been aided in their col-
onization of temperate North America by habitat-selection behaviour
and, most importantly, the elaboration of a larval diapause. I say the
elaboration of a larval diapause because, while it appears that odonates
in the tropics do not show diapause, the virtual universality of dia-
pause in temperate odonates suggests that the potential, at least, for
diapause was present in their tropical ancestors. Indeed, it has been
suggested that diapause in insects in general had a tropical origin
(TAUBER & TAUBER, 1981). The component parts of this scenario
are shown by other groups of insects. For example, NORRIS (1959)
has shown that the acridid Nomadacris septemfasciata (Serv.), can cue
in to an annual photoperiod change of as little as 1 hr at 8° S in Africa,
and there are many records of clinal change in critical daylengths with
increasing latitude (DANILEVSKY, 1965). Indeed, such a case of ad-

aptation to the photoperiods of different latitudes has now been demonstrated in an odonate (NORLING, 1981).

The eastern North American mosquito *Wyeomyia smithii* (Coquillett) arose, like the temperate *Argia*, from a tropical ancestor (ROSS, 1964), and its colonization of temperate regions has surely been facilitated by a photoperiod-cued larval diapause in which it passes the winter (EVANS & BRUST, 1972). A closer parallel with the proposed *Argia* scenario is provided by DINGLE *et al.*, (1980) who have shown that no tropical or subtropical species of *Oncopeltus* (Heteroptera) shows a substantial reproductive diapause, whereas the only species to invade temperate North America (*O. fasciatus* (Dallas)) goes into diapause in Iowa on short days (L:D 11:13) at 23°C (but not at 27° C) and this is coupled with a southward migration. Populations of *O. fasciatus* from Florida and California show considerable variation in the length of the preoviposition period, while populations from Mexico, Puerto Rico and Guadeloupe do not generally show diapause, although it can be induced in some individuals.

Similar studies are planned for *Argia*.

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