CURRENT TOPICS IN DRAGONFLY BIOLOGY

Vol. 2

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The discussion was chaired, and this transcript edited, by Philip S. CORBET

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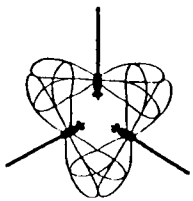

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CURRENT TOPICS IN DRAGONFLY BIOLOGY

Vol. 2

Edited by
Philip S. Corbet

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C O N T E N T S

PREFACE

At the 7th International Symposium of Odonatology, in Calgary, Alberta, Canada in August 1983, the programme included a plenary session devoted to discussion of topics of current interest to odonatologists. This session was recorded and transcribed, and subsequently published as a Supplement in the Societas Internationalis Odonatologica (S.I.O.) Rapid Communications series. At the 8th International Symposium of Odonatology, in Paris, France in August 1985 a similar plenary session was held and, thanks to the efforts of the Symposium Secretary, Dr Jean LEGRAND, and of Mr Bernard SIGWALT, we were again able to record the whole session in a way that made transcription feasible.

In editing the transcript, I have made minor changes, or corrections, needed to improve readability and comprehensibility. The discussion lasted about 2 hours and, as before, yielded interesting facts and ideas. To put these in context, I have compiled a brief bibliography and a list of contributors and their addresses. Also included are indexes to contributors and dragonfly taxa. Citations to entries in the bibliography are indicated in the text by numbers in parentheses.

In a few places the discussion repeats points that were raised during the corresponding session at Calgary in 1983. This is to be expected, and I have not attempted to exclude such repetition because I consider it desirable that each of these transcripts should present a balanced record of the contemporary discussion.

Readers wishing to cite observations reported in this publication can do so in this form.

> DAVIES, D.A.L., 1986. In *Current topics in dragonfly biology*, P.S. CORBET (ed.), p. 8. *Soc. int. odonatol. rapid Comm. (Suppl.)* : x + 33 pp.

It is a pleasure to thank Miss Margaret MITCHELL for valued help with the demanding task of transcribing the recorded discussion, and for producing the final typescript. My warm thanks are again due to Professor Bastiaan KIAUTA for helping to expedite publication.

The original tapes of the discussion have been deposited in the archives of S.I.O. The transcripts of sides 2, 3 and 4 begin on pages 8, 13 and 20.

Philip S. Corbet
April 1986

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DISCUSSION

Breeding in small containers

CORBET: Our first topic is one which I expect we can deal with fairly quickly. I should like to ask if anyone has encountered additional examples of dragonflies breeding in small containers, as a sequel to our discussion of this subject at Calgary in 1983. New examples crop up from time to time: for example Roger Kitching has recently discovered the hitherto undescribed larva of *Lyriothemis cleis* in water collecting in the stumps of palm trees in Sulawesi.

LEGRAND: Some years ago in Africa, in Gabon to be precise, I encountered a tree-hole species called *Hadrothemis camarensis*. So I bred it from the egg and I did some work on it. The species can be found to the Ivory Coast where I think its ecology would be the same.

CORBET: You had clear evidence that it was living in tree-holes did you?

LEGRAND: Yes; absolutely. I have quite a lot of information about it. I shall have to publish it, but I haven't yet! I hope to do so soon.

CORBET: Good. That observation is of particular interest to me because larvae of *Hadrothemis camarensis* were found in bamboo containers in Uganda(1) whereas the hitherto undescribed larva of *H. scabrifrons* was found by Angus McCrae and me in a pan tree-hole in Kenya in 1979(2). It does seem as though species in this genus show a preference for tree-holes. Are there any other examples please? Ola Fincke found *Rhodopygia hinei*, a sympetrine libellulid, recently in a tree-hole in Panama(3).

GAMBLES: I don't know whether this example could be regarded as a small container but I should like to mention the case of small rainwater puddles which form in depressions in granite boulders. In such a habitat in West Africa I twice observed ecdysis from one larval instar to the next (not to the final instar). This habitat offers an ideal situation for anyone wishing to make field observations in the tropics.

CORBET: May I ask what genus and species were involved?

GAMBLES: Particularly *Bradinopyga strachani* and *Pantala flavescens*. *P. flavescens* will of course breed anywhere - ditches, ponds etc.

CORBET: Thank you. It's interesting to note that a related species, *Bradinopyga geminata*, has recently been used by Anthony Sebastian and his colleagues for the biological control of the mosquito, *Aedes aegypti*, in Rangoon(4,5). Females laid eggs in large metal drums which quite possibly served as surrogate rock-pools. In

India and South East Asia the species commonly breeds in cement tanks which are used for storing water(6,7). Are there any other examples please?

MACHADO: Yes; about two years ago I found *Libellula herculea* in tree-holes(8) and I recently found it again. I should like to know if anyone else has encountered the genus *Libellula* in a tree-hole.

CORBET: Is this species close to the genus *Belonia*?

MACHADO: Yes: it's a *Belonia*.

CORBET: And it's interesting to recall here that Jorge Demarmels found it breeding in rock pools by the side of a river(9).

MACHADO: That's right.

CORBET: Are there any other examples of species of *Libellula* breeding in small containers?

GEIJSKES: I have also found larvae of *Libellula herculea* (or *Belonia*) occupying rainwater which accumulated in old boats stranded for a long time on the shore and which provided a nice breeding place for this species*.

OTT: In Teneriffe, the Canary Islands, I found a spring supplying water to cement ponds. There are *Trithemis arteriosa*, *Crocothemis erythraea* and *Anax imperator* breeding in these ponds and they are emerging on the walls. Nearly the whole fauna there is living in these ponds.

CORBET: What are the dimensions of the ponds?

OTT: About 2 or 3 metres square; or much bigger.

CORBET: Do they not have a water inlet from another habitat where larvae might occur?

OTT: No: they are supplied only by water coming out of the mountain side.

LEGRAND: This is not exactly an example but according to my observations it seems that larvae of *Hadrothemis camarensis* and larvae of a predatory mosquito** can exclude each other in tree-holes. If eggs of the mosquito hatch before those of the

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* Probably in Suriname (ed.).

** Probably *Toxorhynchites* (ed.).

dragonfly, the very small carnivorous mosquito larva (even if only one is present) can exclude the dragonfly. Where I found last-instar larvae of that mosquito I never found any dragonfly larvae. I did that work on 1 kilometre square of forest which included about 53 tree-holes. I can't tell you the percentage that contained the mosquitoes or dragonflies but it was astonishingly high. I might add that I think the *Hadrothemis* larvae were feeding on tadpoles as well as on mosquito larvae.

CORBET: I should now like to move on, still under this topic, to ask if anyone has ideas of how to construct artificial, surrogate tree-holes which could serve as traps for detecting, and making a census of, dragonflies that breed in tree-holes. Ola Fincke showed us pictures of some splendid plastic washing-up bowls which she used for attracting egg-laying females of *Megaloprepus caerulatus*, and I am wondering whether anyone else has tried to do this in forest for finding tree-hole breeders or whether anyone may be able to suggest other suitable containers. I have used sections of exotic bamboo for this purpose in Uganda(10) but the diameter of the entrance to each section was almost certainly too small for local Anisoptera to use them routinely.

KIAUTA: We are noticing here and there in Switzerland at various elevations *Somatochlora alpestris*. At Amdenerhöhe, canton St Galen, there is at an altitude of about 1500 metres a hanging bog with dug holes, the origin and purpose of which I do not know. The holes were each about 30 cm square and held water only about 5 cm deep. On 3 August 1985 adults of *S. alpestris* were nearby and in one such hole a larva was found. So I wonder if they normally breed there and if so whether it would be possible to attract them in this way, because you see adults but do not seem to find larvae in any other kind of aquatic habitat; so I would think that they breed in that sort of habitat there. This was quite recently - during very rainy weather in July.

CORBET: Your supposition is supported by recent records of the larval habitat of a related species, *S. arctica*, in Britain(11,12). This opens fascinating possibilities, not the least of which is the conservation of dragonflies by habitat management and by constructing habitats which can often be done quite cheaply. Such measures could increase the size of local populations of dragonflies. I might mention in this connection that Hansreudi Wildermuth has been a successful pioneer in this area - showing local community groups how they can make ponds which are attractive to dragonflies(13,14).

If I may, I shall now pass to our second topic.

Economic importance

CORBET: Over the years attention has from time to time been directed towards the possible economic importance of dragonflies(15). (I use the expression 'economic importance' in the broad sense to mean 'value to man'.) With the pressures currently being placed

on professional biologists, their thoughts naturally turn to possible applications that work on dragonflies might have for the benefit of man. I should like to know whether anyone has any ideas of ways in which dragonflies might be used for the benefit of mankind - apart, of course, from the delight that we derive from them. At our last session in Calgary(16), and earlier today, I mentioned a successful project mounted by Anthony Sebastian and his colleagues in Rangoon which involved putting out large metal drums to collect eggs of *Bradinopyga geminata* and then rearing the resulting larvae to half size by feeding them on chironomid larvae which were easily obtained in quantity. Then local householders, who had in their houses water-storage containers which served as breeding sites for most of the population of the mosquito, *Aedes aegypti*, were encouraged to come and collect half-grown larvae of *B. geminata* and to place two of them every two weeks in each container on their premises. The local inhabitants participated enthusiastically in this venture and as a result the population of *Aedes aegypti* was quickly reduced to a low, and acceptable, level. This example is in some ways a special case, but it does nevertheless show a way in which dragonflies can be of significant applied value. Just before I ask for other examples I should also mention that in Wells County, Maine the local council is financing a project which involves buying in large numbers of dragonfly larvae from a biological supply-house and encouraging local residents to distribute the larvae in neighbouring swamps in the expectation that the mosquito nuisance will be abated by these means(17). Whether this is no more than a device for boosting the confidence of the local residents I have not been able to discover: I have not seen results of any trials which demonstrate that mosquitoes have been suppressed in this way. Nevertheless, it is a project which deserves mention.

WAAGE: In relation to this kind of question one should consider the major contribution made by studies on dragonflies to biological theory and to experimental methodology in work on predation. Quantitative studies of larval feeding, flight energetics, and attack and capture rates of adults can make a tremendous contribution, not to biological control directly, but to the theory of biological control. Recent work by the Japanese using artificial perches wired up to microcircuits has been used to record not only the coming and going of dragonflies but also the weight of the food they catch after each feeding sally.

CORBET: Are you referring to work by Higashi(18) with *Sympetrum frequens*?

WAAGE: Yes; and the work of John Lawton on foraging behaviour of larvae(19,20).

MAY: I mentioned this example yesterday, half in jest, but I really believe that it might be worth following up. I refer to the use of *Ischnura* in glasshouses to suppress whiteflies. One reason why I am encouraged to think that this approach could be of potential value for biological control in glasshouses is that

Ischnura (although not *verticalis*) is the only dragonfly which has been successfully colonised on a permanent basis. Specimens I watched appeared, on very superficial examination, to be feeding on whiteflies at a rate sufficient to control them. They were focusing specifically on whiteflies which were highly visible on the leaves. I think it possible that dragonflies that feed by gleaning could have some potential for biological control if used in this way.

CORBET: That represents a good combination of useful properties: a suborder in which adults glean on a large scale; and one in which some species at least can be reared continuously in captivity in confined conditions, as Clifford Johnson reported in 1965 and 1966(21,22).

MACHADO: I have recently described with a colleague a species of *Gynacantha** feeding on adults of a beetle which attacks the cocoa plant in Brazil(29). The dragonfly was evidently having some effect because we dissected some adults and found that they contained large numbers of small beetles. So I advised the plantation owners to maintain the habitats - or presumed habitats - of the *Gynacantha* in the forests nearby. They were intending to cut down the forest to make room for more cocoa plantations but I said: "No. Leave the forest because to remove it might destroy this equilibrium." This is one example of the economic importance of dragonflies.

CORBET: Did you find that the plantation owners were receptive to your suggestion?

MACHADO: Yes.

TYAGI: I wish to refer to remarks made by Mike May about *Ischnura* feeding on whiteflies. During my stay in Gulaghatti some years ago I saw *Ischnura forcipata* and *I. aurora aurora* feeding on mosquitoes as soon as the latter emerged from the water. When mosquitoes emerge they are very weak and often rest on some leaf nearby where *Ischnura* adults, which are waiting nearby, pounce on them and eat them. I've seen many instances of *Ischnura* feeding on emerging mosquitoes.

CORBET: Where was this observation please?

TYAGI: In a small valley near Deradun city called Gulaghatti.

CORBET: Some of you may have seen a rather touching article in *Mosquito News* some years ago by mosquito workers in Vero Beach, Florida. They have a protocol there whereby they rear many thousands of *Aedes taeniorhynchus*. They rear them so that a high

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* *Gynacantha bifida* feeding on *Xyleborus* spp. (ed.).

proportion will emerge on the same day so that they are of known age. Then they mark them and release them in their normal breeding habitat - a salt marsh. Then, by successive sampling, they are able to follow age-dependent changes in the mosquitoes. A tremendous investment of time and effort goes into rearing a batch which may consist of tens of thousands of mosquitoes. Two such workers took down a huge cage of newly marked mosquitoes to release them in a salt marsh, at sunset (because this most closely simulates natural conditions for the mosquitoes). They took the lid off the cage and (this was in Mike Wright country (23)) almost immediately huge numbers of *Anax junius* assembled over the cage and picked off the mosquitoes as they took to flight. So the hapless investigatcrs cut their losses and wrote a paper for *Mosquito News* on the feeding habits of *Anax junius*(24).

KIAUTA: I am unable to produce at the moment exact bibliographic references, but I would like to comment on information which I noticed recently in the literature that there are several thousand species of Lepidoptera associated in central Europe with spruce. Most of them are injurious in one way or another, particularly in connection with so-called 'acid rain'. In the United States research was recently carried out on dragonfly predation on insects associated with coniferous forests with spruce and so on. The investigators analysed the gut contents of several species belonging to different families; they were able to identify the species of Lepidoptera on the basis of their scales - it appeared that certain dragonfly taxa, like aeshnids and corduliids, are particularly predaceous on Lepidoptera and so I wonder whether or not enhancing their habitats in areas where coniferous forests might be endangered by air pollution wouldn't be beneficial to the forest. I could provide references later.

CORBET: Well, I can think of other respects in which that could have particular value because one of the management practices in establishing coniferous forests is to drain the land thoroughly and in the United Kingdom a lot of dragonfly habitats have disappeared because of this practice. Your suggestion would constitute an additional argument for going about it in another way and preserving interesting habitats in consultation with odonatologists.

SIGWALT: May I respond as an ecologist? When I was working on a book on regional ecology I used to calculate the key-factor in population dynamics and I would ask whether the effect of dragonflies as predators has been identified as a key-factor in a life-table.

CORBET: Has such a finding been published please?

SIGWALT: It is the classical work of Frank Morris on the spruce budworm(25)

CORBET: Are you saying the Odonata were shown to be a key-factor?

SIGWALT: No; the Odonata were not taken into account.

KIAUTA: What Bernard Sigwalt is now saying exposes a problem: feeding dragonflies are not susceptible to capture by any mechanical device for collecting insects. Most other aerial insects are collected mechanically in one way or another: either they are attracted by light or by a Malaise trap or in some other way; but because dragonflies are seldom caught by such means the odonatological component in the biotic community of an area including water is liable to be ignored. If you look at hydrobiological works you will hardly ever find references to dragonflies and if there are any they are very insignificant and unrepresentative. This is simply due to the fact that they can't be readily collected by mechanical means, unlike almost all species of Lepidoptera, Coleoptera, Trichoptera and so on.

CORBET: Earlier in this symposium, Angelo, you mentioned to me that in Brazil dragonflies are being blamed for the injurious effect their larvae have in fish-culture ponds. Could you tell us something about that please?

MACHADO: In Brazil there are now many large hydroelectric reservoirs where fish are supposed to be. In the big ponds used for fish culture the managers claim that dragonfly larvae are destroying the alevines, or fingerlings. So many people were writing letters to me and asking me for a solution that I think I ought to do something; but although I'm rather good at rearing larvae, I don't know how to kill them efficiently, and there is the problem! Another point is that they brought me some larvae and I recognised *Pantala flavescens* and *Anax*. On the other hand, the evidence that dragonfly larvae are really damaging the fishes is rather indirect and, since I am supposed to study this and since according to these people the dragonflies constitute a major economic problem, I would like to know if anybody has met this situation or knows what we could do about it.

TYAGI: Well, in one way I can confirm this information given by Dr Machado. Some years ago I was in a small place called Ukai in District Surat in South Gujarat where there is the inland Fisheries Research Station. The scientists working there experienced the problem of dragonfly larvae, probably *Anax*, feeding on the fingerlings or fry of the fishes they were catching in their ponds. They had in fact taken photographs of the dragonfly larvae feeding on the fingerlings and they had an exhibit on this subject. It was a problem: how to get rid of the dragonfly larvae which were feeding on the fingerlings in the small culture ponds.

CORBET: And do you know how they tried to counteract this?

TYAGI: They could not find a solution. The dragonflies were breeding there and they could not remove the fishes from those permanent tanks which were the only places where they were culturing their fishes. So they had a continuing problem.

(Side 2 begins.)

CORBET: Am I right in saying that the scientists were not able to find a way of controlling the dragonflies?

TYAGI: Yes; they could not find a way to control the dragonflies feeding on the fingerlings.

GEIJSKES: Once I heard a story of Dr Holthouse, a well-known specialist in Crustacea, who was collecting these in New Guinea where he saw that people of the Papuas were collecting large larvae of *Anax* as food; so these larvae were used by the women of the Papuas as food.

CORBET: How did they collect them please; did they have traps for the larvae?

GEIJSKES: No; they were collecting them in baskets and dragging ashore reeds and other plants in which they found them.

DAVIES: Some time ago, perhaps about the turn of the Century, someone in North America offered a prize for an essay on the use of dragonflies for controlling mosquitoes.

CORBET: This was Lamborn - Robert Lamborn(37).

DAVIES: You know about that? I think more than one essay was published; is that right?

CORBET: A book appeared in 1890 called "Dragonflies versus mosquitoes" by Robert Lamborn(37).

DAVIES: Was there anything interesting in it?

CORBET: There were 5 essays but they didn't deal crisply with the problem I'm afraid; they didn't suggest effective ways to use dragonflies to control mosquitoes.

DAVIES: I suppose there is quite a lot of information about predation on mosquitoes and, as I mentioned the other day, on *Glossina*(26,27); and I think a lot of waterfall dwellers feed on *Simulium*(28). What I do wonder (and have seen nothing about it) is whether any dragonflies are predators of *Schistosoma*; I mean predators on the cercaria on its way from snail to human. Is there a chance that perhaps the free-living cercariae could be food for dragonflies? I mention it particularly because many countries with big irrigation schemes are having trouble keeping the snails out of collecting ditches.

CORBET: On that matter there are a few dragonfly larvae which feed, preferentially it seems, on snails; these are almost all anactines - *Hemianax* and *Anax*(30,31). One of the exhibits in the posters shows how *Anax* can eat snails(32). In this connection I'd like to mention that in 1971 a paper appeared by Manning(33) who showed (I think for the first time) that dragonflies can be

intermediate hosts of a trematode which is a rather serious parasite of man. It has, of course, been known for many years that dragonfly larvae are intermediate hosts for a prosthogonomid fluke which causes impaired reproduction in poultry(34); but as far as I know this is the first instance of dragonfly larvae occupying an intermediate stage in transmitting a trematode parasite to man. The dragonfly larvae took the cercariae in with their respiratory current; then the local people fed on the (uncooked) dragonfly larvae and thus contracted the parasites. This might be an example we would wish to forget if we were talking about the applied value of dragonflies!

FINCKE: I might mention that I can show experimentally in Panama that pseudostigmatid larvae do indeed control mosquito populations in tree-holes. There are about 30 species of mosquitoes that inhabit these tree-holes. If I recall correctly, some 22 of these species are more or less confined to tree-holes or small containers; so I think this is definitely an example of effective control by dragonflies. I don't know if any of these mosquitoes are disease vectors, but there's the possibility that (I think it was Mike May who was saying that Yellow Fever is carried by arboreal monkeys) the mosquito which transmits it could be a tree-hole-dwelling species.

CORBET: The incriminated mosquitoes belong to the genera *Haemogogus* and *Sabethes*, both of which are tree-hole breeders. Ola, may I ask if you could visualise putting out surrogate containers to collect large numbers of *Mecistogaster* and thus enhance the local population of dragonflies in order to increase the pressure on tree-hole mosquitoes?

FINCKE: Certainly, I've done that. In an experimental design, I have put out large containers and I get lots of *Mecistogaster*. I assume that this increases the adult population, but I can't measure the changes in the adult population because the adults are so dispersed; but certainly all it takes is one larva in most holes of less than one litre capacity and you virtually do away with last-instar mosquitoes. In fact that's one way I determine where dragonfly larvae are. If I look into a hole and there are no mosquitoes on the surface, I suspect that there is a dragonfly larva in there and, sure enough, usually, if you look, you find one.

CORBET: While we are on the subject may I ask you if you have found any species in addition to *Rhodopygia hinei* in tree-holes since you last spoke about them?

FINCKE: No.

MACHADO: I would like to return to the matter of dragonflies causing damage to fish culture because these people are very frightened about it, and they are willing to put a lot of money towards control. Obviously chemical control is not a solution because it can cause damage to the environment. Does anybody have an idea of the kind of biological control that might be successful? Apparently nobody has experience of this problem except Dr Tyagi.

CORBET: Could I suggest for a start that it would be worth their while funding a project to find out if the dragonfly larvae really are eating the fish, and if so what sizes of fish? This can be very easily done by examining the contents of the faecal pellets of the dragonfly larvae.

MACHADO: Yes; that's a good idea.

CORBET: When that result was known, a decision could be made as to whether or not the dragonflies really needed to be controlled. Anticipating the possibility that the dragonflies are indeed serious predators, can anyone think of a way in which species like *Anax* and *Pantala* could be suppressed or prevented from eating fish in fish hatcheries?

MAY: Obviously this would depend on the exact circumstances of rearing. In some fish-rearing ponds which are basically concrete tanks it seems that it would be possible to screen the tank and thus prevent oviposition. I have seen fish hatcheries in which the hatchlings were reared in this way. In the case of *Anax* it might be possible to remove most oviposition sites by trimming or removing certain kinds of vegetation in the pond. *Pantala* might present more of a problem; but these methods seem so obvious that I'm surprised that they haven't been tried.

CORBET: The impression I got was that you were speaking about fairly large bodies of water Angelo; is that correct?

MACHADO: Fish tanks.

CORBET: Yes; well the suggestion is that they could be rendered unattractive as oviposition sites in some way.

KIAUTA: I would like to add four points to this discussion. First, preventing dragonflies eating the fish population. In Indonesia people eat dragonfly larvae, in particular the big ones like *Anax guttatus*. They collect them by exploiting the fact that the dragonflies emerge synchronously; so they throw tree branches into the water and the larvae climb up on the branches. They then collect them as food; so perhaps this sort of physical, manual control is one possibility in certain areas for the larger dragonflies. Second, regarding dragonflies as vectors of human disease. Some years ago a Master of Science thesis(66) was published from one of the universities of Bangkok and one of the Thai medical authorities also published a paper on dragonflies as vectors of certain parasites - trematodes - causing certain human diseases, some including fatal cases. The third thing I wish to mention is that some years ago there was constructed in Eastern Germany a light trap for collecting underwater aquatic insects. The technical description and the results of its operation have been published(35,36). I think that among the items collected were larvae of Zygoptera. So apparently at least some Zygoptera may be positively phototactic. Fourth and last, in regard to dragonflies as enemies of fish culture, on the other side of the coin is the damage that fish do to dragonfly populations. While

collecting at fish ponds in the Philippines in Luzon, we have noticed that there is a very peculiar dragonfly fauna in such ponds: it consists of a large *Anax, A. guttatus*, and then the very small *Agriocnemis femina oryzae*; and all the other species like *Orthetrum pruinosum* and *Crocothemis servilia* are immigrants, that is to say they do not breed there. So the composition of that fauna due to fish culture is rather difficult to explain if there are only those very small autochthonous species and the very large ones. This is what I noticed here and there in other tropical countries as well.

SIVA-JOTHY: I don't know, Philip, if I'm being silly here, but one rather obvious thing would seem to be to introduce insectivorous fish into these cultures. Things like *Gambusia* that will eat small, young larvae early on and that won't affect the fish population in any way.

CORBET: Are you suggesting that fish might be introduced that would selectively feed on dragonfly larvae?

SIVA-JOTHY: That's right, or on any insect larvae.

DAVIES: It seems to me that Bastiaan might have hit on the nucleus of a solution: people should be trained to eat the dragonflies instead of the fish!

PARR: The pond from which we collected the data on *Anax imperator* in Malawi was the site of quite a big trout fishery, maintained for angling. I remember seeing trout caught there which were opened and gutted: the gut was full of Zygoptera larvae. So it did appear to me, on the basis of a small sample, as though the trout were highly dependent on Zygoptera larvae. It was a site where Zygoptera such as *Pseudagrion* and *Enallagma* were exceedingly common; so there could be a useful link here in some sites between a fish population for angling and dragonflies.

CORBET: I think that one difficulty is that it is the large and spiny species of dragonfly that feed on the fingerlings; and fish are reluctant to take these as a rule.

WESTFALL: What Mike May was saying about screening those cement pools takes me back to an observation I made in Venezuela. They called me out there to where they were raising large numbers of fish for food and pointed out that they had lost a terrific number - thousands and thousands of the little fingerlings - the year before and they'd saved some of the dragonfly larvae, Hemiptera and other things they had collected from these pools. They couldn't understand why they had a problem because they had screened the pools. Indeed they did have screens all over them and yet these dragonflies were in there. We pointed out to them that they were bringing the water that was flowing into each one of these cement containers from an unscreened pond above. They had no way of keeping the small dragonflies from the upper pond from coming right on down into the cement pool. So we suggested that they try screening the water that was coming in through

those pipes by putting a filter or something over the end of them. I haven't been back to see whether they've tried that and had any success; but it was a terrific loss that they were sustaining, mostly from *Pantala flavescens* that was the greatest predator that they had there.

CORBET: In passing, Bastiaan, may I ask if I may receive from you afterwards the title of that thesis in Bangkok, because I suspect that it may be the work that I was referring to which was reported in a symposium and published in 1971.

KIAUTA: I will certainly provide it, but not afterwards; I can only do so from Holland.

CORBET: There was a question I wanted to ask you, Ola, in connection with tree-hole breeding dragonflies. From your extensive experience with *Megaloprepus*(38), could you give us an idea of what you think the sign-stimuli are to which males and females respond when they look for tree-holes - that is, when they localize on tree-holes? You mentioned that these tree-holes are in clearings - in treefall areas. What do you think happens, if you put yourself in the insect's position?

FINCKE: One point is that, although males hold territories in treefall areas, females will oviposit in a wide range of holes, both in clearings and not in clearings. So, when females are looking for a territory, I think that both males and females first cue in on large areas of light. If you imagine yourself in a tropical forest it's very dense usually and large light gaps are quite easy to focus in on. So that's one thing. Then, once they get into a gap area (I've seen this in females, though not so much in males) they orient to dark surfaces. They will flutter around treefall debris and you can see them search bark and they'll actually orient to a dark spot or dark, wet spot. So they definitely orient to dark spots, and there must be some kind of chemical reception in which they can distinguish to some extent substrate material. I say this because on the forest floor there are stone containers (grinding stones) left by Indians; these fill with water and may contain libellulids but never contain pseudostigmatids. Otherwise everything else is the same: there's leaf litter and everything else you would find in a tree-hole. So apparently pseudostigmatid females can distinguish the bark of a tree from stone. Other than that I know that males fly very closely over tree-holes; possibly they detect water either visually or by touching it. I know that *Mecistogaster* females actually hit the water surface sometimes and come up with a globule of water in their mouth and that's apparently how they make sure that there is water there.

CARON: If I may change a bit the direction of the discussion I'd like to give another example of a dragonfly being useful as an entomophagous insect. Once I observed a *Libellula julia* eating a horsefly (Tabanidae). Well that horsefly was really bugging me; so it was quite a relief for me when the dragonfly caught it. Secondly I want to draw attention to the possible use of

dragonflies in studies of the effect of acid rain on aquatic ecosystems. Dragonflies have an important place in the aquatic community and so are likely to be affected by acid rain; in fact I'm sure of it; but it's a very complex problem. I'm sure that there needs to be research on the effect of acid rain on dragonfly populations in lacustrine systems.

KIAUTA: I would like to add to remarks of Eric that a paper was published by Nilsson(39), who made observations on the effects of acid rain on dragonfly populations in the Fennoscandian lakes and found this effect to be strongly positive. The point is that the fish are much more sensitive to the chemical composition of water in the first stage of acidification than are the dragonflies; so when the fish disappear the control exercised by the fish vanishes also and certain species of dragonfly that are normally rare in that habitat become very common and these are always those species whose larvae are active during the day when the fish feed. So they expose themselves and are taken by fish. If the fish disappear, the dragonfly population increases and those *Leucorrhinia* and so on become common. Of course this persists only for a certain time - until the acidity of the water increases sufficiently to exclude them. This is a fascinating paper and I think the first and the only one so far on this subject.

CARON: Can you provide me with the reference afterwards?

CORBET: It is cited as reference 62 in the transcript of the discussion session at the S.I.O. Symposium in Calgary(40).

Aestivation of adults in temperate latitudes

(Side 3 begins.)

CORBET: Jean-Guy, I noticed recently in one of your papers with Monsieur Sylvestre that, alone among the species that you studied, *Lestes congener* emerged very late in the season with a fairly synchronised, brief emergence(41), and I thought that perhaps this might be an example of adult aestivation - a very long maturation period. Could you comment upon that for us please?

PILON: Yes; I have been thinking about it for the last few days since you mentioned it to me. I shall have to check back again in St. Thérèse. I went through all the samples again last year and noticed that we had tenerals in the catch. Now I want to go back to the Biological Station because there we had cages also. So I'm going to check to see if we didn't miss something - for example if we had early specimens in the cages and after that none until much later on. So I have to check; but from memory I will say there was no evidence for aestivation.

CORBET: On this point could I ask anyone who has experience of

Mediterranean species or species in the Southern States of the United States to reflect on this and to see if they can think of any species that would appear to have a long gap between emergence and first reproductive activity in the summer?

PARR: First of all, could you define what you mean by 'temperate' here? Do you mean south or north of the tropics (i.e. latitude $23^{o}27'$)? Is that what you're referring to?

CORBET: I think it's what I would have assumed I was referring to if I had thought about it! What I mean is animals whose reproduction is interrupted annually by a cold season.

PARR: Yes; and/or a dry season presumably?

CORBET: No; because I was going to deal with dry-season adaptations under a later topic. But please go ahead anyway.

PARR: Well this is my point. Just before I left Bophuthatswana I was surprised to see in Mafikeng - in fact within the confines of my own house - an adult *Lestes*; this was most surprising to me because I'd not seen them previously at that time of the year. Remember we are nearly at the end of the winter which is also the dry season. So it's cold and dry and I can't imagine that this individual had emerged recently. So I'm going to have another look when I get back to see if I can find any more and then try to determine what the species is. I couldn't catch the individual: it disappeared before the net arrived!

CORBET: It's known from the work of Robert Gambles from the late 1950s and early 1960s(42) that in tropical West Africa more than one species of *Lestes* survives the dry season as an adult and I've got a feeling that this type of life-history may well be the template, so to speak, for the adaptations to temperate regions that lestids like *Sympecma* show.

PARR: Yes; this individual could be one of the ones that Robert has observed, but without specimens we're just guessing.

CORBET: I think *Lestes virgatus* was one of the species that spent the dry season as an adult in Nigeria, was it not, Robert?

GAMBLES: Yes.

CORBET: Are there any other examples under this head?

UTZERI: I should like to say that what is occurring in *Lestes barbarus* is probably also occurring in *L. virens* and *L. viridis* in a population near Rome. I have maturation times for *virens* which are the same as for *barbarus* and for *viridis*. They ought to be the same because I don't find newly emerged individuals; and they should emerge before the ponds dry up, that is at the same time as *barbarus* and *virens* emerge. This is at the end of May or in mid-June. Then they are not seen at the ponds again before mid-August.

CORBET: What you say suggests that there may be in other lestids a pattern like the one Uéda found in *L. sponsa*; a latitude-dependent extension of the maturation period(43). I shouldn't neglect to mention here the demonstration by Uéda and Iwasaki(44) that the Japanese lestid, *L. temporalis*, spends two to two-and-a-half months away from the water after emergence before returning as a mature adult.

KIAUTA: I remember that the same case as Carlo is describing occurs in *L. macrostigma* in Dalmatia. There the situation is exactly the same but my observations are almost 30 years old; so I don't have the details now. The region features Karst limestone and there is practically no water during the summer; it disappears very early in spring. The *macrostigma* start the season very early: toward the end of May they are there. There is no water anywhere and they may reproduce only in the autumn when the rain comes again. Is this similar to your observations? *L. barbarus* also is similar in the same area.

UTZERI: Not exactly the same, because the four species of *Lestes* - *barbarus, virens, viridis* and *dryas* - all oviposit when water is still not present.

KIAUTA: And *macrostigma*?

UTZERI: I didn't succeed in finding a single population of *macrostigma*.

CORBET: Bastiaan said that in Dalmatia there are huge populations of *macrostigma*.

UTZERI: Well, it's said in Italy to breed in saline waters.

KIAUTA: Yes; brackish waters.

UTZERI: ... but I don't find any *macrostigma* in such waters.

CORBET: Are there any more suggestions for species that might be aestivating, during an extended maturation period, in temperate regions? In that case I shall pass on to our next topic.

Dimorphism in adults

CORBET: By way of introduction let me mention two examples which I find especially intriguing. The first is the difference in size that can occur between early and late forms of the same species. Sugimura has detected such a difference in six genera of Zygoptera and in four genera of Anisoptera in Japan. In the Zygoptera and in one genus of Anisoptera, the smaller forms appeared late in the season; in three genera of Anisoptera the larger forms appeared late in the season(45). We may or may not decide to regard this as a case of dimorphism; but the second example I shall mention clearly is. This is the phenomenon

described many years ago by Wenger(46) in *Boyeria irene* in which females are of two distinct kinds: those with long cerci, and those with short cerci. Recently Graham Vick has shown that the proportions of these two types can differ widely from one population to another(47). I've never seen any suggestion as to what the biological significance of this dimorphism might be, but this is one example I would be interested to have some discussion on.

KIAUTA: I can't comment upon its biological significance but upon publication of that note by Graham Vick to which you refer I received a manuscript from Morocco in which the author described a population of *Boyeria* that is apparently entirely different in constitution of 'long' and 'short' female forms. It was speculated that the proportions of females with long and short cerci might be different in different geographical regions. The paper was by a French colleague who expected to be here but isn't!

CORBET: May I ask if anyone else has had experience of dimorphism among cerci of aeshnids? In that case, may I mention the example of certain North American aeshnids - *Aeshna tuberculifera* and *A. constricta* are examples I'm told - in which there appears to be a balanced polymorphism such that many females regularly possess male coloration and behave like males. I see this as possibly being analogous to andromorphic females in *Ischnura ramburi* in that females so coloured enjoy a high degree of immunity from interference from males(48).

SIVA-JOTHY: Unless I'm much mistaken (and Leo can correct me on this) after the Calgary Symposium we went up into Banff, into the Rockies, and saw colour morphs of *Aeschna eremita* in which there were females that had very distinct male coloration and behaved just like males; in fact we mistook them for males and had to mark them with a separate colour so as to tell them apart afterwards. I'm pretty sure the dimorphism was only in *A. eremita*.

FINCKE: When you say they behaved like males, what do you mean? What were they doing?

CANNINGS: The main difference in the two species that Philip mentioned - *A. constricta* and *A. tuberculifera* - is that they are the only two species of *Aeshna* that I know of in North America in which the females oviposit in plants well out of the water; so they make no attempt to oviposit inconspicuously. They're well out in the open when ovipositing and so males have obviously plenty of opportunity to see them and to fly after them; so presumably if they look more like males, this likelihood is reduced. This is the only real behavioural difference that I know of. The only other difference is a morphological one: these two species, more than any others that I know of in North America, have very large cerci; but whether that has any importance in this whole story or not, I don't know. That's all I can offer.

BEUKEBOOM: We didn't find differences in oviposition sites between the two colour forms of *A. eremita* but the data suggest a difference in flying time during the day between the two colour forms, although the data are not strong enough for us to be sure about that. It looks as if the blue colour form - the form that looks most like the male - was flying more at the time that males were flying and that the green form was avoiding the time that the males were flying, but we cannot be sure about this. It would be very interesting to go there again and check on this.

CORBET: That's a very intriguing relationship that you mention. Are there any other points that anyone would like to raise about dimorphism?

UTZERI: May I put a question? Is it known how males behave towards these females? And is it known whether or not there is sex recognition in the species?

CORBET: I wonder, Rob, if you know from your experience how males behave towards these morphs?

CANNINGS: No; I have no experience, Philip, of them in that sort of situation; so I have very little information to add.

'INCKE: I might mention with respect to *Enallagma hageni* that there are many *Enallagma* species in which there is a dimorphism in females. I found that there was no difference in the number of copulations that either morph got. However, if you give a male a choice - if you pin a blue female and a green female in an area - you'll find that males will more readily seize the green female in tandem; it's as if they recognized more readily that female as a female, although if you look at the population as a whole you find no difference in the number of copulations by either morph. There was no difference either in mortality or longevity of the two morphs(49).

Life-history patterns in the tropics: wet and dry season adaptations

CORBET: Would anyone like to comment on experiences or findings regarding life-history adaptations to the wet/dry sequence of seasons in the tropics?

LEGRAND: I have two examples to mention concerning the wet-season adaptations of dragonflies, especially Anisoptera, Libellulidae, Tetrathemistinae. The first concerns *Malgassophlebia aequatoris* and I think that people with an interest in shade-seeking dragonflies will know that. The problem is that it's an ethological adaptation. The female only appears when rain falls, and the male too. They mate, and the female immediately begins to oviposit under the surface of leaves 20 cm to 2 m above the water of streams. The eggs are of course attached to leaves by mucus and with rain the mucus swells so that the eggs are

contained in a gelatinous mass which looks like frog spawn(50). Indeed in the same locality frogs lay eggs in the same way. A second example is another species of *Malgassophlebia*, not yet described. Adults likewise appear when the rain falls, but not at the beginning of the rains; only when it has rained enough for the water in the streams to have risen up to the banks. They only lay eggs on the banks. Now I only have one example from the dry season in the same place: Makokou, Gabon. It is a very small zygopteran, *Elattoneura*. (I don't remember the species, but I can tell you later if you wish.) It appears only during the dry season when there are hardly any other dragonflies present.

CORBET: Are they in forest?

LEGRAND: Yes; of course; only in forest. And during the wet season the species disappears.

CORBET: So the implication in all those species - *Elattoneura* and the two species of *Malgassophlebia* - would be that the adult survives the dry season? Is that what you would expect?

LEGRAND: No; I don't know but I don't think so. I don't think they survive the dry season.

CORBET: In that case how can it be that the adults are reproductively mature immediately after the rains break? Is it not necessary to infer that they must have spent the dry season as adults?

LEGRAND: No; I think they appear at the very beginning of the wet season. Concerning *Malgassophlebia*, I can't tell how long they need to mature: information about that species is very fragmentary, because they can be observed only when it rains.

CORBET: I have in mind examples from tropical South America. You mentioned *Mecistogaster* I think, Ola; and Mike you know of examples such as *Erythrodiplax umbrata* and *E. funerea* in which at the beginning of the rains adults suddenly assume mature coloration and show reproductive activity. I'd be interested to hear your comments on this. Ola, would you like to say something?

FINCKE: *Mecistogaster ornatus* undergoes adult reproductive diapause during the dry season and in April, with the advent of the rains, it breaks this diapause and females mature eggs while males undergo a change from yellow to black in their wing-tip coloration. The wing-tips in females remain yellow. This is in contrast to *M. linearis* in which females contain mature eggs throughout the dry season, although mating occurs only at the onset of the rains. So in both of these cases the species passes the dry season as adults.

CORBET: Do you know the situation in *M. ornatus*? I think the Beattys(51) described this species as occurring in Mexico in "roosting aggregations." Are you familiar with such behaviour in *M. ornatus*?

FINCKE: I looked for it. The only evidence I have for it is that if you put adults in an insectary they will aggregate in the sense that three or four will perch on the same stem, but I never found any very large aggregations in nature.

MAY: As far as the *Erythrodiplax* are concerned, what observations I have are in agreement with the short note that Eugene Morton published some years back(52). Basically, both of these species - *E. umbrata* and *E. funerea* - can be seen fairly frequently, very widely dispersed in the forest, throughout the dry season. At the beginning of the wet season they, in a fairly short period of time and certainly in a few weeks at most, change colour. During the dry season they have an immature coloration; then when the change occurs the males in particular become darker bodied and their wings acquire dark banding. In addition, they seem to undergo a local migration out of the forest, in the case of Barro Colorado Island to breeding sites which are unknown to me but which are probably marshy areas along the shore of Gatun Lake (in which the Island is). There are also several other species that I believe pass the dry season as adults: *Gynacantha tibiata* is one that comes to mind. There's a small temporary pond on Barro Colorado Island where a certain amount of reproductive activity by *G. tibiata* can be seen when there's water in the pond. But both males and females of *G. tibiata* remain there, somewhat aggregated, even when the pond has dried up. I've also found small and not at all spectacular aggregations of *G. tibiata* during the dry season in other low, muddy areas that I suspected had held water in the wet season. It was as though throughout the dry season they were hanging around potential larval sites - places where their larvae might develop. One other possibility which I mentioned to you earlier, I think, is something that's worth keeping in mind when thinking about wet/dry season adaptations. That is not the problem of drying up but the problems inherent in the fact that many stream-dwelling species must face irregular, large increases in streamflow during the wet season. This thought is prompted by the fact that I have observed that some stream-dwelling species of *Argia* are present as adults during the dry season and that their disappearance as adults seems more or less to coincide with the onset of the wet season. Now whether there's some direct effect of either cloud cover or streamflow on the adults I don't know, but another possibility is that, since adult activity is presumably in some way related to larval development throughout the year, this could be related to the eggs or larvae being in some stage that is more resistant to these freshets which occur fairly regularly. I think that for some stream species this must be an important factor to which they have to adapt.

CORBET: One can of course draw inferences about the way in which a species spends the dry season by finding adults in dry bush conditions during the dry season. There was a paper by Dr Asahina in *Tombo* a couple of years ago(53) in which he records finding adult Odonata in the dense bush of forest during the dry season in Thailand. The genera represented were *Ceriagrion, Vestalis, Neurothemis* (three species), *Tholymis* and *Pantala*.

These findings suggest to me that all of the species involved are able to survive the dry season as adults.

(Side 4 begins.)

DAVIES: What you've just said, Philip, is I think true for several species of *Austrolestes* in Australia: when their patch dries up they just sit around there, and there's no doubt they're there for a very long time. I haven't been there long enough to see if they were still waiting when the rains came but it seemed obvious that they are doing just that, as lestids do in Africa; and at least several species are involved.

CORBET: Are there further comments on this topic please? I think it would be worthwhile for people who visit seasonal rainfall areas in the tropics to keep their eyes open for the odd instance which may give us a clue. Norman, did you wish to say something?

MOORE: I want to follow up a point Mike raised just now about this change of flow of water because I think it's one of the most significant things in Scotland where there are an enormous number of water bodies which look very good for dragonflies. Indeed, many areas are good for most of the time but then you get these catastrophic floods - and we've had plenty this year - when it becomes quite impossible for the larvae to hold onto the substrate. I think this may be one of the main factors determining the distribution of many species in streams in Scotland. I think this is an important point that Mike made.

Seasonal regulation at different latitudes

CORBET: I should like to move on now to our sixth topic which is one which Eric Caron suggested. This subject concerns species which occur over a wide range of temperate latitudes in all of which they show seasonal regulation. The question being addressed is: "Do populations have different responses, appropriate to the latitude where each occurs?" Now we know from recent work by Ulf Norling(54) that this is certainly the case in *Leucorrhinia dubia* in Sweden where he's studied the critical photoperiod that can induce diapause in the penultimate larval instar and that can determine the intrastadial overwintering stage of the final instar in southern and northern populations of *L. dubia*; and he has shown that southern and northern populations each have a different critical photoperiod. It's not that they each have the same response to all photoperiods, but they have a different response to the same photoperiod, which means that they have a different response to critical photoperiods. I've always thought that continental North America would offer an ideal place to study this kind of question because one has species like *Epitheca cynosura*, for instance, that has a very crisp seasonal regulation, and yet covers a wide latitudinal range. I don't

know what the southern limit of this species is but it's certainly at least as far south as North Carolina.

MAY: It's found in Florida.

CORBET: Is it? Well that covers a wide range of photoperiodic and temperature regimes. I wonder if we have any examples before us of other work that shows that there are different responses to photoperiod or temperature at different latitudes?

SCHALLER: I have made observations on *Aeshna cyanea* over a period of twenty to thirty years(55,56). I have observed that larvae in the last instar after 31 July always go into diapause and do not metamorphose. On the other hand, I have observed that this is correlated with photoperiod. I have also observed that temperature has great importance for larval development. I have made observations for four years at one pond where I collected larvae on 15 August, 15 September and 15 October - an average of 100 larvae per collection. The four years had different mean temperatures. One of the years was a cold one. Another was a warm year compared with the mean temperature in this region of Strasbourg; and the other two years were close to the long-term mean for the region. In the warm year in early autumn I observed a high percentage of last-instar larvae. In the cold year at that time I found no last-instar larvae. In the 'normal' years most larvae in early autumn (October) were in the antepenultimate instar and they entered diapause. In this region of Strasbourg and on the same pond over the four-year period, the photoperiod is of course the same each year, but the temperature differed. I therefore think that these differences can be attributed only to the effect of temperature. In a cold year there were a few larvae beyond the antepenultimate instar that were overwintering; and in a warm year there were many larger larvae. This is an example of the influence of temperature on seasonal regulation.

CORBET: I'm reminded of a recent study by Ulf Norling in Sweden, in which he studied a population of *Aeshna cyanea* for several years in a pond which was surrounded by trees(57). He was able to show that this species took three years, I think it was, to complete its larval development before somebody cut the trees down and exposed the pond to much more sunlight. Then *A. cyanea* shortened its life-history to two years, instead of three. Ulf attributed this to temperature also.

SCHALLER: I have observations on laboratory rearings in relation to latitude. In southern France *Aeshna cyanea* predominantly is univoltine. The egg has a diapause, and then larval development is completed after hatching in the same year. In Strasbourg I have observed that 10-15% of the population is univoltine. The rest show a larval diapause, and are semivoltine. I think latitude and photoperiod influence this phenomenon, like temperature. Have you some explanation for this?

CORBET: There was a time when I thought that it might be possible that a single species that has a wide latitudinal range, like

A. cyanea or *Epitheca cynosura*, might be able to regulate seasonally without changing its responses at all: to have the same response but to be regulated appropriately by photoperiod and temperature at each latitude. There is very little work that tests this hypothesis, but it now seems from Ulf Norling's findings as though the first comparison we have between two populations of the same species at different latitudes (*Leucorrhinia dubia*) shows that the populations have different responses to photoperiod. Perhaps they have the same responses to temperature but different responses to photoperiod, like many other insects which have been studied from this point of view.

CARON: I did find your comment, Monsieur Schaller, very interesting. Between the south of France and the north of France is quite a significant latitudinal difference and this is the kind of comparison that I'm looking for. As I mentioned this morning, *Cordulia shurtleffi* in our latitude - in the lower Laurentide region - shows a three-year life-cycle; but I wonder if it still retains the same life-cycle further south and further north? Perhaps the constant feature is the final-instar diapause, in which case temperature alone would determine its voltinism. This is the main question that I'm raising. I would invite colleagues, especially in the United States and Canada, to study the larval development of species like *C. shurtleffi* - species that may have a mosaic life-cycle through north-south latitudinal gradients. We should then be better able to discuss the question of whether species show the same, or a different, response to seasonal cues at different latitudes.

CORBET: A useful way of following your suggestion, Eric, might be for someone to do detailed work on *Epitheca cynosura* in Canada, because there is already detailed work in North Carolina on that species(58,59) and it would be instructive to carry out comparable work in Canada. May I ask you, Mike, if you know how far south *C. shurtleffi* occurs in North America?

MAY: Well I know that Frank Carle has records of it from Virginia in the mountains. I would like to ask you a question in return: I know that you and Paul Lutz at one time intended to study *Epitheca* (or is it *Tetragoneuria*?) *cynosura*; whatever came of that?

CORBET: Well, I planned my project and then I was assigned to control the insect nuisance at Expo '67 in Montreal and that took me out of circulation for two or three years after which I changed jobs. So I'm afraid nothing came of it. But it would be good if that work could be taken forward sometime.

WAAGE: I think that there are two places that are fairly famous for studies that have already shown many changes in life-cycles that go north/south. One of them is Japan. A lot of work has been done on cricket life-cycles, which show univoltine, through semi-voltine, to multivoltine patterns. The other is the eastern coast of the United States along the Appalachians where in the region between North Carolina and New York State quite a number

of species, ranging from crickets and katydids to frogs and some other insects, change from having univoltine to bivoltine life-cycles. So perhaps there are other comparable regions in the world that people know about that might be good places to focus on.

SCHALLER: I should like to mention an observation of *Aeshna cyanea* also. In my experimental and laboratory rearings of *A. cyanea*, *ab ovo*, using eggs from only one female - I find four development types: those that complete development in 10 instars, in 11 instars, in 12 instars and in 13 instars.* In the main example, when there is no larval diapause, all larvae belong to the 10-instar type. But when the larvae belong to the 13-instar type, the environmental conditions can determine whether or not there is diapause. When the conditions are very favourable, then the larvae go without diapause. This applies to the 10-, 11- and perhaps the 12-instar types, but not to the 13-instar type.

CORBET: Can you tell us please, whether your experiments showed that the conditions experienced during the egg determined which of the development types of larvae resulted?

SCHALLER: I think this is the problem. The different development types are genetically programmed I think. I am not a geneticist, but I think this is so. I have no proof, but perhaps in southern regions types with a low number of instars are in a majority and perhaps in northern regions types with a high number of instars are in a majority; and in intermediate regions (like Strasbourg, because I come from this town and this region!) I found that the two extremes exist, there being a low number of the 10-instar type and a large number of the 12-instar type of larvae.

CORBET: May I take this opportunity to ask you whether you know what life-cycle *Aeshna mixta* has at the southern limit of its range? Does it still have a diapause egg there?

SCHALLER: *A. mixta* is an autumn species and I think has no 13-instar type in its development. *A. mixta* has nine instars; the last larval instar is the ninth.

CORBET: Does it always have a diapause egg, even at the southern limit of its range?

SCHALLER: Yes. They only have a diapause in the embryo(60). *Aeshna isosceles* is an aeshnid which does not (have a diapause in the embryo) but its really in another genus - *Anaciaeshna*.

CORBET: Yes; it's more like *Anax*.

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* When comparing the reported findings of different authors, readers should keep in mind that some odonatologists do, and some do not, regard the prolarva as an instar (ed.).

PILON: I would like to comment on Dr Schaller's remarks because we did some rearing too, and I completely agree with him. I think that what he encountered in the different types of larval development is genetic, because we took eggs from one female and followed the development of each larva individually and found that the different types were evident right from the beginning(61). Now there might be some departure from this pattern if your larva is not well fed for some reason or another - I don't know - but I can say that right from the beginning you got different types. And in relation to that, we reared *Ischnura verticalis*(62), for example, and found, if I remember well, at least five different development types, with 9, 10, 11, 12 and 13 instars - something like that. I'm sure of one thing, although it's difficult to prove: in Canada when you have an exceptionally hot summer *I. verticalis* follows the 9-instar pattern and you get adults in August. Now in relation to photoperiod, we had an accident in the first rearing we did. We had *Enallagma* larvae in the third instar and there was a violent storm which caused a power-cut. So our 16-hour photoperiod was no more! Then all the larvae entered diapause when they reached the seventh instar. So diapause can be initiated at a certain instar and can come into effect later on. I don't have formal proof because this was learnt from an accident, but I think that, at least with summer species, the explanation lies along these lines.

KIAUTA: I also would be inclined to confirm what Jean-Guy says. First, there is too little variation between the number of instars in different biotopes. If you compare the tropics with the north there is a small variation but it's not fixed and it's too small to account for the phenotypic variation. If you take for instance the life-history of *Ceriagrion coromandelianum*, which has been studied recently several times independently by various workers(63) in India and Bangladesh, it has been found that there are 11 and 12 instars in different populations and in very different climatic conditions, and that there is no correlation between the climatic conditions and the number of instars; so I think the genetic basis of this would have to be tentatively assumed. If this were not so then species having a very long larval development, such as *Cordulegaster*(64) or *Epiophlebia*(65), would have to have a much larger number of instars than is actually the case. Actually they differ little from other species having a life-history lasting only one or two years

CORBET: Our time is now up and I must bring this session to an end. Thank you all for your participation in what has proved to be a very informative discussion.

APPENDIX I

BIBLIOGRAPHY

Listed here are publications which, in the editor's opinion, document or amplify certain facts or ideas mentioned in discussion and which in some cases can provide points of departure for the reader who wishes to pursue a topic further.

Numbers refer to numbers in parentheses in the text. References to Odonatological Abstracts are included for some citations thus: '(OA 1234.).'

1. CORBET, P.S., 1961. *Trans. R. ent. Soc. Lond.* 113: 356-361.

2. CORBET, P.S. & A.W.R. McRAE, 1981. *Odonatologica* 10: 311-317.

3. FINCKE, O.M., 1985. Personal communication.

4. SEBASTIAN, A., MYAT MYAT THU, MAY KYAW & MYINT MYINT SEIN, 1980. *SEast Asian J. trop. Med. publ. Health* 11: 104-107. (OA 3195.)

5. CORBET, P.S., 1986. *Waterlines, London* 4(3): 10-11.

6. FRASER, F.C., 1936. *The fauna of British India. Odonata.* Vol. 3. Taylor & Francis, London.

7. KUMAR, A., 1973. *Gurukul Kangri Vishwa Vidayalya J. Sci. Res.* 5: 50-57.

8. MACHADO, A.B.M., 1983. *Resum. 10 Congr. brasil. Zool., Belo Horizonte*: 196-197. (OA 4106.)

9. DEMARMELS, J., 1982. *Bol. Ent. Venezolana (N.S.)* 2: 94-101, and *in litt.*

10. CORBET, P.S., 1961. *Trans. R. ent. Soc. Lond.* 113: 275-283.

11. BUTLER, S., 1983. *J. Brit. Dragonfly Soc.* 1: 4-5.

12. CORBET, P.S., S.A. CORBET, & K.A.K. CORBET, 1983. *J. Brit. Dragonfly Soc.* 1: 25.

13. WILDERMUTH, H., 1981. *Libellen, Kleinodien unserer Gewasser.* Schweizer Naturschutz So-Nr 1/81, Basel. (OA 3336.)

14. WILDERMUTH, H., 1981. *Lebensraum Kiesgrube.* Schweizer Naturschutz So-Nr 2/81, Basel. (OA 3468.)

15. WRIGHT, M., 1946. *J. Tenn. Acad. Sci.* 21: 60-71.

16. CORBET, P.S., 1984. In *Current topics in dragonfly biology*, P.S. CORBET (ed.), p.15. *Soc. int. odonatol. rapid Comm. (Suppl.).* 2: x + 46 pp.

17. MARSTERS, S., 1977. *York County Coast Star, Maine* 11 May 1977: 1, 16. (OA 1912.)

18. HIGASHI, K., 1973. *Rep. Ebino Biol. Lab. Kyushu Univ.* 1: 119-129.

19. LAWTON, J.H., 1970. *J. Anim. Ecol.* 39: 669-689.

20. LAWTON, J.H., 1971. *Freshwater Biol.* 1: 99-111.

21. JOHNSON, C., 1965. *Can. Ent.* 97: 321-326.

22. JOHNSON, C., 1966. *Texas J. Sci.* 18: 179-183.

23. WRIGHT, M., 1944. *Florida Ent.* 27: 35-39.

24. EDMAN, J.D. & J.S. HAEGER, 1974. *Florida Ent.* 57: 408.

25. MORRIS, R.F. (ed.), 1963. *Mem. ent. Soc. Can.* 31: 1-332.

26. CARPENTER, G.D.H., 1920, *A naturalist on Lake Victoria.* Fisher Unwin, London.

27. CAMPION, H., 1921. *Ann. Mag. nat. Hist.* Ser. 9, 8: 240-245.

28. PETERSON, B.V. & D.M. DAVIES, 1960. *Can. J. Zool.* 38: 9-18.

29. SORIA, S. de J. & A.B.M. MACHADO, 1982. *Rev. Theobroma, Bahia* 12: 257-259.

30. SIEVERS, D.W. & A.C. HAMAN, 1973. *Proc. Iowa Acad. Sci.* 79: 105-106.

31. ROWE, R.J., 1982. Personal communication.

32. BLOIS, C., 1985. *Biology of Behaviour* 10: 183-214.

33. MANNING, G.S., 1971. *Rep. 1st Internat. Seminar, SEATO Med. Res. Lab., Bangkok*: 43-46.

34. MACY, R.W., 1934. *Univ. Minnesota Agric. exp. Sta. Tech. Bull.* 98: 71 pp.

35. ENGELMANN, H.-D., 1973. *Ent. Abh.* 39: 243-246. (OA 1025.)

36. ENGELMANN, H.-D., 1974. *Fol. ent. Hung.* 27 (Suppl.): 173-176. (OA 1110.)

37. LAMBORN, R.H., 1890. *Dragonflies versus mosquitoes. Can the mosquito pest be mitigated?* Appleton, New York.

38. FINCKE, O.M., 1984. *Adv. Odonatol.* 2: 13-27.

39. NILSSON-HENRIKSON, B.-I., 1981. *Verh. Internat. Verein. Limnol.* 21: 1612-1615.

40. CORBET, P.S. (ed.), 1984. *Soc. int. odonatol. rapid Comm. (Suppl.)* 2: x + 46 pp.

41. PILON, J.-G. & C. SYLVESTRE, 1984. *Notul. odonatol.* 2: 38-44.

42. CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

43. UEDA, T., 1978. *Tombo* 21: 27-34.

44. UEDA, T. & M. IWASAKI, 1982. *Adv. Odonatol.* 1: 281-291.

45. SUGIMURA, M., 1983. *Tombo* 25: 31-34.

46. WENGER, O.-P., 1959. *Bull. Soc. ent. Suisse* 32: 304-311.

47. VICK, G.S., 1984. *Notul. odonatol.* 2: 69-70.

48. ROBERTSON, H.M., 1985. *Anim. Behav.* 33: 805-809.

49. FINCKE, O.M., 1983. *Lifetime mating patterns and reproductive success in the damselfly* Enallagma hageni *(Walsh) (Odonata: Coenagrionidae).* Ph.D. thesis, Univ. Iowa.

50. LEGRAND, J., 1979. *Rev. fr. Ent. (N.S.)* 1: 3-12.

51. BEATTY, G.H. & A.F. BEATTY, 1963. *Proc. N. Centr. Branch Ent. Soc. Amer.* 18: 153-155.

52. MORTON, E.S., 1977. *Proc. ent. Soc. Wash.* 79: 273.

53. ASAHINA, S., 1983. *Tombo* 26: 11.

54. NORLING, U., 1984. *Odonatologica* 13: 529-550.

55. SCHALLER, F., 1960. *Ann. Sci. Nat. Zool.* 2: 751-868.

56. SCHALLER, F., 1962. *Bull. Ass. philomath. Als.-Lorr.* 11: 128-137.

57. NORLING, U., 1983. Personal communication.

58. LUTZ, P.E., 1974. *Ecology* 55: 370-377.

59. LUTZ, P.E., 1974. *Ecology* 55: 630-637.

60. SCHALLER, F., 1972. *Odonatologica* 1: 143-153.

61. MASSEAU, M.J. & J.-G. PILON, 1982. *Adv. Odonatol.* 1: 129-150.

62. FRANCHINI, J. & J.-G. PILON, 1983. *Annls Soc. ent. Québec* 28: 13-18.

63. KUMAR, A., 1980. *Rec. zool. Surv. India* 76: 249-258.

64. KENNEDY, C.H., 1917. *Proc. U.S. nat. Mus.* 52: 483-635.

65. ASAHINA, S., 1950. `*Proc. 8th Internat. Congr. Ent., Stockholm*: 337-341.

66. CHANTACHUME, K., 1979. *Survey of dragonfly from certain parts of Thailand.* M.Sc. thesis, Mahidol Univ., Bangkok. (OA 4129.)

APPENDIX II

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INDEX TO CONTRIBUTORS

Names listed are those of persons (excluding the chairman) who contributed to the discussion.

INDEX TO CITED AUTHORS

Names listed are those of persons cited by name during the discussion or those of authors of publications listed in Appendix I.

INDEX TO ODONATA

Species are listed under the generic name only.