CURRENT TOPICS IN DRAGONFLY BIOLOGY

Vol. 5

Including a discussion focusing on
survival during the hot dry season

Transcript of discussion recorded during plenary session
of the 11th International Symposium of Odonatology at
Trevi, Italy on 23 August 1991

This transcript was edited by
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DATE OF PUBLICATION

June 15, 1992

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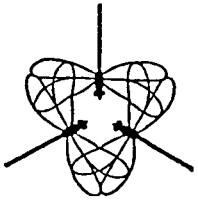

Societas Internationalis Odonatologica
Rapid Communications (Supplements)

No. 15

CURRENT TOPICS IN DRAGONFLY BIOLOGY

Vol. 5

INCLUDING A DISCUSSION FOCUSING ON
SURVIVAL DURING THE HOT DRY SEASON

Edited by
G. Pritchard

Bilthoven
1992

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PREFACE

At the 7th, 8th, 9th and 10th International Symposia of Odonatology the programme included a plenary session devoted to topics of current interest to odonatologists. Each session was recorded and transcribed, and subsequently published as a Supplement in the Societas Internationalis Odonatologica (S.I.O.) Rapid Communications series as Numbers 2, 6, 8 and 12. At the 11th International Symposium of Odonatology in Trevi, Italy in August 1991, a similar plenary session was held and, thanks to the efforts of the Symposium Secretary, Professor Carlo UTZERI, it was again possible to record the 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 two hours. During the first 45 minutes or so (Part One) several topics were briefly addressed; the rest of the session (Part Two) was spent discussing survival during the hot, dry season, this being a topic of special interest to odonatologists in the host country because it experiences a Mediterranean climate. In conformity with previous volumes, and to put the discussion in context, I have included a short 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.

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

> UTZERI, C. 1992. In *Current topics in dragonfly biology*. G. PRITCHARD (ed.). p. 11. *Soc. int. odonatol. rapid Comm. (Suppl.)* 15: viii + 29 pp.

The discussion was chaired by Professor Philip CORBET who is indebted to the Royal Society of Edinburgh and the Royal Society of London for financial contributions towards his participation in the Symposium.

I would like to thank my wife, Valerie PRITCHARD, for making the original transcript (I am sorry that I could not include the personal commentary that she inserted into the transcript!); and Philip CORBET for valuable assistance and advice with the editorial process, including the production of the bibliography.

The original tapes of the discussion have been deposited in the archives of S.I.O. The transcripts of sides 2 and 3 begin on pages 9 and 17 respectively.

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April 1992

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DISCUSSION

Preamble

CORBET: Welcome to the 6th of the SIO plenary seminars, which have been a feature of the SIO International Symposia since the one held in Chur, Switzerland in 1981.

These seminars, or discussion sessions, offer a good opportunity for us to exchange information and views on various topics in odonatology, especially those topics which may be elucidated by the exposure of chance or anecdotal observations, because such observations are unlikely otherwise to be published or shared with a large group of odonatologists; also, of course, there is the great value of interaction among ourselves during these discussions which exploit the rare opportunity of our meeting in an enquiring frame of mind.

I should like to thank Carlo Utzeri, Secretary of the Organizing Committee, and members of the Committee for having asked me to chair such a session at this Symposium and also those who submitted suggestions for topics to be discussed in it, although I wish they had been more numerous!

I propose that we allot the time this afternoon as follows: in Part One, which will probably last for about half an hour, we can focus briefly on several, diverse topics to see if pooling of the information that we possess may help to generate ideas or questions and identify future investigations of promise. In Part Two, which could last for an hour and a half, we might examine the main topic that has been chosen, namely "Strategies for survival during the hot, dry season".

Such a format in Part Two would repeat a pattern that was followed at Madurai, India during the 9th SIO Symposium in 1988, and at Johnson City, Tennessee during the 10th SIO Symposium in 1989. At both Madurai and Johnson City we devoted much of the seminar to discussing a topic of especial interest in the region where the Symposium was being held. At Madurai, the movements of *Pantala flavescens*, and at Johnson City, interference among larvae. There are obvious advantages in adopting this approach. So today, we shall focus in Part Two on strategies for survival during the hot, dry season in order to try to throw further light on the studies by Carlo Utzeri and his colleagues on adaptations shown by dragonflies to the Mediterranean climate.

Part One: diverse topics

Habitat selection

CORBET: I have five topics on my provisional list for Part One and the first one is habitat selection. In this Symposium we have had excellent contributions from Hansruedi Wildermuth on *Somatochlora*, *Leucorrhinia pectoralis* and *Perithemis mooma*, and from Ola Fincke on pseudostigmatids living in tree holes. Now for many species, the plants they choose in which to oviposit are also relevant, and there have been several contributions, both in the oral presentations and in the posters, that bear on this subject: for example, Nancy House, Andreas Martens, Peter Miller with the distribution of eggs in the tropics on the banks of ponds,

and Lutz Müller with the oviposition behaviour of *Libellula depressa*. I wonder if we could start this by my inviting anyone who wishes to identify key issues in this very challenging subject, namely the way in which first of all males and then females, choose a habitat in which eggs will eventually be laid. Would anyone like to start the discussion on this topic?

PARR: In Malawi I had examples of *Orthetrum* species come into my house when doors were open, and they would then attempt to oviposit, or they would look as if they were attempting to oviposit, on a shiny, wooden floor. Now, to my mind, these insects were responding to two main stimuli. One was a dark hole, which was the interior of the building, and the other was the shiny nature of the floor, which would presumably have reflected light like water. And so I think that those two factors may be very important in insects that are forest dwellers and are looking for water in that kind of environment. The females of *O. julia* were particularly involved here, *O. julia falsum* in fact.

CORBET: Thank you. It's interesting that two of the conspicuous factors that emerged from Wildermuth's study were the reflectivity of the surface, the broken reflective aspect of the surface, and also the dark colour (1). I wonder, Ola, if you had any of these thoughts specifically in mind when you designed your artificial tree-hole?

FINCKE: Yes, I did. I put the black plastic in because when females enter a gap area in which there is a fallen tree, what they typically do is search the dark parts of the surfaces of that tree, underneath usually, and they will investigate any place where water has dripped down, any moist place; so that's why I used the black plastic and it seemed to work well. I had one interesting experience this summer. I always assumed that the males that defend tree-holes cue in on the water surface as well, and I think they do, but there was a case this summer that led me to believe that they have a series of criteria, the first one being that they will investigate any tree gap, and in one particular case, a week after I arrived, a very large tree fell and I subsequently spent time at that tree fall. And during this time as many as five or six males per day would come in and investigate this tree-fall, and they would flutter over areas of the fallen tree where there should have been a hole, or looked like there would have been a hole. In other words, it was a little bit overgrown with vegetation, and then there would be dark areas, in particular places where the trunk had split slightly such that there was a slit and then it was dark, but there was no water there. Some of them hung around for as long as three days, but eventually they left and for three weeks this area was highly active. Males would come in, search, maybe hang around for several days, and then leave. So obviously males, like females, will cue in on places where there could be water, but what was interesting was that females were much more specific and no female ever hung around one of these areas that looked like it had water but didn't. In other words, the females were, not surprisingly, a lot harder to fool than the males.

CORBET: Would you see there being probably a hierarchy of responses or stimuli, first of all the very general one of the tree-fall area and then perhaps

a more specific one of the reflectivity or darkness of the surface, going right down finally to the texture of the substrate in which she puts her eggs?

FINCKE: Yes, going down to the fact that before a female ever oviposits she first dips her abdomen into the water. If she doesn't detect water she won't oviposit. And in several cases I have seen a territorial male flick the water surface. Yes, I agree with you. There is a hierarchy and females require more steps of the hierarchy to be fulfilled, so to speak, before they really become localized than do males.

CORBET: Thank you. I think the invention of plastic has probably been very helpful in trying to design surrogate oviposition sites. Could I ask you, Peter Miller, if you had any thoughts when you were working on *Potamarcha congener*, of what the females were responding to when they came in to lay eggs on the bank above the water level.

MILLER: Could I redirect that question towards *Nesciothemis farinosa*? This species does a similar thing, flicking eggs onto the bank (34), and in order to collect eggs, we laid out black material along the bank and that did seem to be attractive, and the eggs stuck on it and it was a way of gathering the eggs in effect. But as you will remember some 30 years ago we also managed to catch the eggs of *Hadrothemis coacta* on a tin biscuit lid as they were scooped a metre and a half or two metres from the pool towards the jungle.

TRUEMAN: This question of dragonflies ovipositing on artificial substrates of one form or another is interesting. I've heard reports via Tony Watson of dragonflies - libellulids, but I don't know the species - ovipositing on the roofs of cars in Darwin, Australia, and causing considerable economic damage. I wonder if anyone has any information on the chemical structure of that sticky, so-called spumaline, layer on the outside of the egg, because it is this that appears to interfere with the paint.

CORBET: Does anyone have any information on the chemical structure of the spumaline surround of the egg? Peter Miller, are you in a position to comment on this? No? These eggs do have spumaline around them, the ones that are laid on car roofs?

TRUEMAN: Almost all the libellulids have some form of sticky material on the outside of the eggs; sometimes it's very thick and pronounced, sometimes it's very thin. I suspect the chemical structure is the same throughout the group, but I have no data.

CORBET: I rather think the dragonflies in this case were *Tramea*; I remember that observation by Tony Watson. Also relevant, I would think, in helping females to find oviposition sites, would be the microclimate, the humidity and temperature gradients, close to the oviposition substrate. Lutz Müller, would you care to comment on this, in the light of your observations on *Libellula depressa* laying at the surface of the water where it's particularly warm?

MÜLLER: Yes, *Libellula depressa* often prefers shallow water, and the oviposition substrate is floating water plants, maybe algae or leaves, and the eggs are laid near the surface of the water. I have measured the temperature near the eggs and at 10 cm depth, and there was a difference of more than 1°C. Because the vegetation is very sparse at this site, the sun can shine on the eggs. I saw one oviposition on an oak leaf; it was an old leaf and it was quite dark brown and black, and maybe they prefer a dark substrate too.

CORBET: Were you able to carry out any experiments? It seems to me from what you say, and from your poster, that the oviposition of *Libellula depressa* would be susceptible to experimentation.

MÜLLER: Yes, we are trying right now.

CORBET: Thank you. I wonder if we could move for a moment to the often repeated discussion topic of whether the females of any species choose particular plants, or confine their oviposition to certain plants. Of course we all know the example of *Aeshna viridis* in Europe, which is believed to concentrate on *Stratiotes* (2,3), although it is known that it is not completely restricted to it (4), and there is the remarkable example of *Roppaneura beckeri* in southern Brazil, a zygopteran which spends all of its life associated with a species of *Eryngium* (5). The larvae live in the water in the leaf bases and the adults localize around the plant. I wonder if anybody knows of any examples or suspects any example of any cases where a species is restricting its oviposition entirely, or almost entirely, to one species of plant?

MOORE: It is often thought, particularly in Britain, that *Erythromma najas* only oviposits in floating water weeds: *Potamogeton* and *Nuphar* and plants like that. I find in the fens, that in many ditches there are none of these plants and it is ovipositing in another *Potamogeton* (I think it's name is *filiformis)*, which has very thin leaves, which do not float on the surface, and it seems perfectly capable of breeding in that without any of the ones with the surface-floating weed.

CORBET: My impression is that, although originally observations may imply that a species is restricted to a certain kind of plant, it is not long before examples are shown of exceptions to this, and perhaps the microclimate of the position of the plant and the physical texture of the plant are more important than the species of the plant.

MILLER: Don't I remember Corbet describing *Aethriamanta rezia* associated exclusively with *Pistia stratiotes* (Nile cabbage)? Or is my memory wrong?

CORBET: I certainly have commented on the association between *Aethriamanta* and *Pistia*, but I think, although I've seen *A. rezia* close to *Pistia* myself, that the record that I mentioned came from Lieftinck from southeast Asia (6). There is a very strong correlation between the oviposition habits of *Aethriamanta*, and also *Urothemis*, and *Pistia* (7), and I might say that, for that reason, both those species are probably good candidates for introducing into butterfly farms when the managers express an interest in

having dragonflies as well, because one can have a little localized ecosystem with the *Pistia* plants, around which the dragonflies aggregate.

PARR: I think I've written about the association of *Nesciothemis nigeriensis* with particular grass species in Nigeria. Perhaps we don't need to go into the details of this, but my experience there was that the species was always found in association with *Echinochloa pyramidalis* (8). The males used it as perching sites and this meant that, after mating, the females would lay in that area because they would be accompanied by a male. And when I then found the species again at the original type locality that was described by Robert Gambles, which was about 800 km south of where we found it in the north of Nigeria, it again was associated with the same grass (36). They do definitely, in my experience, ignore *Cyperus* and dicotyledonous plants which may be along the shoreline of the lakes where they live. So there seems to be some association, but what it is that really ties them to the grass is difficult to say.

CORBET: Yes, I remember that very interesting example, and it's one that we have discussed in these sessions before. Am I right in saying that the females were not laying in this plant?

PARR: They don't lay in the plant, because they are like typical *Orthetrum* species; they simply lay the eggs in the water.

CORBET: They weren't laying eggs in association with the plant - near the plant bases?

PARR: As far as we can tell, they simply dip the abdomen in the water.

SCHNEIDER: You are mentioning now that these females were associated with the plants, but not egg-laying in them. *Pseudagrion syriacum* is obviously also associated with *Mentha*. I don't know about the oviposition, but you only find the females at rivulets where *Mentha* is growing. That was mentioned by Dumont in one of his first papers (9); at a locality in the Middle East where there is no *Mentha*, you will not find *P. syriacum*, and the females are almost always in these plants.

CORBET: This is one of our brief topics and I would like to leave it now unless anyone has a last observation they would like to make.

PRITCHARD: This is not to do with plants, but it has to do with oviposition site selection, and it is a comment and I have no answers. I'm thinking specifically of species of *Cora*, polythorids in Central America, and in particular, *Cora marina*. All *Cora*, as far as I know, lay into water-soaked, fallen tree branches, and the adults assemble in the vicinity of these oviposition sites, perching on the ends of twigs which themselves are dead, on otherwise living trees. It may be purely coincidental, but it would be nice if there were in fact some association for the dragonflies between the perches on which they site themselves and the fact that they are going to oviposit in the same sort of structure. It may be that they are more visible on the ends of these leafless twigs, but it's

a nice association and I would appreciate knowing if anyone else has any observations or comments on species which lay into dead wood.

CORBET: Dead wood that is used as a perching site?

PRITCHARD: Well, yes. Dead wood as an oviposition site, and if anyone knows of other species that use dead wood also as perches. The perches are often some considerable distance above the oviposition sites, but there are always oviposition sites directly below them.

Biological control using dragonflies

CORBET: I would like to move now to the next topic, and it is a very different one. I decided to include this partly because Dr. Tyagi was not able to come and give his talk on the use of dragonflies in the control of mosquitoes. Since the last symposium, a full scientific account has been published of the first successful, properly monitored example of using dragonflies to suppress mosquitoes (10). I would like to mention it briefly here, because I want to draw this most valuable case to the attention of members of the Symposium. In Rangoon, about 10 years ago, a pilot field study was carried out in an attempt to control the yellow fever mosquito, *Aedes aegypti*, which, as many of you will know, breeds in small receptacles, often in people's houses, and in this area of Rangoon something like 95% of the population of *A. aegypti* was breeding inside houses, and so it was extremely accessible to the local population. Also, by virtue of this fact, it is a very effective vector of the disease dengue. By a series of fortunate accidents, and very good judgement and biological knowledge, it was discovered that eggs of *Crocothemis servilia* could easily be obtained by putting out surrogate oviposition sites. And furthermore, it was found that larvae could be reared in sufficient number and with sufficient reliability that known numbers could be placed in receptacles at regular intervals in order to carry out an experiment on control of *A. aegypti* by what is called augmentative release, using predators or parasites like an insecticide - pushing them into the system. Before this work began, the local householders were introduced to the merits of this approach by the entomologist, and they became very enthusiastic about helping and having dragonfly larvae put in the containers in their houses. In fact, when the trial finished many of them complained that dragonfly larvae were not continuing to be placed in their water containers. The trial was an outstanding success. In 2-3 weeks, it reduced the larval population of *A. aegypti* to a level so low that it was quite acceptable to public health authorities, and then suppressed it progressively until the trial ended. The adult population was also greatly reduced after about six weeks, and then progressively diminished thereafter. The trial lasted through the whole of the rainy season, the only time of year when *A. aegypti* is a health problem. Its success was ascribed to a number of things, which we should keep in mind if advising anyone to use this approach. First the virtual confinement of pre-adult stages of the target mosquito to containers accessible to control operators. Second, the oviposition behaviour, the growth rate, the survival and the ready availability of the chosen species of dragonfly, *C.*

servilia, which is a very widespread, pioneer species. And finally, the awareness and enthusiastic participation of local householders. Now this outstanding success, for which people have really been waiting for decades, will very much help the recognition of an important applied aspect of odonatology, if we publicize the example and seek out opportunities. When publicizing the example, it is important to identify the conditions under which this approach is likely to be successful and not to suggest that it will always be successful in every situation. It points up the need for more research on methodology of rearing Odonata and so we now have an excellent reason for seeking grant support for this. I have reprints of this article by Sebastian and others in Rangoon, and if any of you would like me to send you copies, please leave your name with me after the session.

That is more in the nature of an announcement, but it is something we have been waiting for for a very long time, and I would simply ask now if anyone has any comments on the way forward and the way in which odonatology might capitalize on this example.

Different modes of oviposition

We have time for one more topic briefly. In talking to members of the Symposium, and in particular Andreas Martens, I have been introduced to a phenomenon which has been described on several occasions in the past, namely the phenomenon of females of one species have a number of different oviposition modes. Now it is very common and understandable for observers to generalize (or perhaps one should say readers to generalize) after seeing a species oviposit in a certain way and to say that Species X oviposits in this way; and so a generalization becomes established and people are inclined to close their minds to other possibilities. But several observers have reported that the same species can, at different times and in different situations, oviposit in quite different ways. An example is Richard Rowe's report that the New Zealand dragonfly, *Procordulia smithii*, has at least four distinct modes of oviposition (11). I wonder, Andreas, if you would be willing to give a brief report of the similar situation you were describing to me in *Zygonyx natalensis*?

MARTENS: *Z. natalensis* has four different oviposition types (12). One type is similar to *Sympetrum* oviposition in tandem, but this will occur into the white spray of running water and into the running water. Another type of oviposition is where the female dips alone and the male is guarding, and two other modes can be observed. In both, the male is sitting in the vegetation (for example, *Juncus*), and one possibility is that the female lets her abdomen hang down, and the other possibility is that the female makes active movements with her abdomen.

MILLER: It took us two and a half weeks to get here partly because I was making some observations on *Orthetrum cancellatum* in the River Vienne in France, a tributary of the Loire. At very high densities it seems as though a different mode of oviposition sometimes appears, in which the pair, during copulation, flies around, and the male selects a pad of alga upon which

they settle. After copulation the male leaves the female there; she persists in sitting there, and then she starts jumping up and down, within only about 2-3 cm. If she oviposits in the normal way she is immediately seized by another male; so this seems to be an alternative when the density of males is very high. I don't know if anybody else has seen that. It's a very much studied species, many people have been watching, particularly Carlo, so I wonder if he's ever seen anything of this kind - jumping up and down just 2-3 cm, one wing flick and then back down. So all the eggs are being deposited in the same spot, on the same mat of alga.

UTZERI: Do you mean, Peter, that these females of *O. cancellatum* are ovipositing while perched on this vegetation?

MILLER: Virtually. It is as though they had to just free the eggs from the abdomen tip by lifting it up, and they may not release the legs and sometimes they don't, they just remain there jerking, at other times they ....

UTZERI: Are they on the wing?

MILLER: Just one beat sometimes. It's movement over 1-2 cm vertically only, at the most, or even less.

UTZERI: Then, I can add to this the observation of females of *O. cancellatum* which lay while perched, and this also occurs when harassment by males is very intense. I saw this several times; not very many, but several. Then I will also add the observation of at least two modes of oviposition in *Sympetrum meridionale*, which can either lay eggs in tandem with the female flicking her abdomen or just flying in a straight tandem with the female just dropping the eggs toward the ground. I would ask you, Philip, a question. Would you consider the tandem versus the female alone oviposition as two modes of oviposition?

CORBET: Yes. The examples which have been cited have included those as different oviposition modes. I was going to say, as indeed Peter has already said, that this particular difference has often been correlated with density. I think Georg Rüppell in his film of *Leucorrhinia dubia* related the two different oviposition modes to the density of males (13).

UTZERI: Can I add an observation? I also observed this in *Lestes virens* and maybe in *Sympetrum sanguineum*. In our poster paper presented in this Symposium, we have demonstrated that the time a male keeps a female in tandem is correlated with the disturbance by other males. So I think the female is let free very soon if there are no, or if there are few, males around the tandem.

MÜLLER: *Orthetrum cancellatum* females normally fly across the water surface, dipping as they go, but I have seen one female ovipositing in one place, flying over one site and dipping its abdomen in one place.

MARTENS: Whether oviposition occurs in tandem or not is, in *Zygonyx*, quite easily explained. If there is any disturbance, even only one disturbance, the pair will fly away in tandem or they will oviposit in tandem, but if they are undisturbed, they will separate and the female settles. And if in this short time, only 2-5 seconds, a rival male appears, he is able to grasp her and copulate with her.

CORBET: One of the most surprising observations I have encountered is the report by Machado and Martinez of an endophytic dragonfly, *Mecistogaster jocaste*, which has been seen throwing eggs into a tree-hole while it hovers outside the tree hole, rather like the mosquito *Toxorhynchites* (14). I would be interested to know if there are any records of *Mecistogaster* of other species throwing their eggs into tree-holes, or on the contrary, any records of *Mecistogaster jocaste* laying eggs also in the conventional way. Ola Fincke, do you have any experience that would throw light on this extraordinary observation?

FINCKE: Unfortunately not. All of the *Mesistogaster* that I have studied have done it endophytically.

CORBET: Does anyone have any observations to offer here, of examples in which one species is laying eggs in more than one mode?

MILLER: Can I just mention briefly *Phaon iridipennis*, a calopterygid in Africa which either makes long slits and packs its eggs in rows, or if it is ovipositing on a different kind of plant, lays each egg separately with separate incisions? That seems to be determined by the nature of the plant. When laying into *Cyperus* species, it is a long slit with the eggs packed like a row of soldiers, when into *Typha* it is separate holes, and I think, though I am not certain, it may be something to do with the texture of the plant which determines which mode is used (15).

CORDERO: I have some observations on *Ischnura graellsii* laying eggs in filter paper in the laboratory ...

(Side 2 begins)

... and I found that sometimes a female would lay eggs in rows and the next day the same female laid the eggs totally at random. It was the same filter paper, the same conditions of humidity and temperature; so I don't know why the female first laid eggs in rows, and the other time totally randomly. It is quite strange.

DUNKLE: I have two observations, the first of which is that I think that the pseudostigmatid that Machado described throwing eggs into tree holes was not *Mecistogaster jocaste*, but it was later described as a new species which, I think, was *martinez*, or something close to that. And another observation that I had was of a gomphid, *Hagenius brevistylus*, which oviposits in three very different modes. I think the usual one is flying fast and low over the water and just tapping the water surface over a wide area. They also rather rarely flick eggs into the vegetation much like a *Libellula* would, or *Orthetrum*. And thirdly, they may hover near the

vegetation and drop eggs from the air into the water. So that would imply very great flexibility in oviposition behaviour.

CORBET: In your observations, were you in a position to correlate tentatively these different modes with different physical conditions or the presence of other adults?

DUNKLE: I knew you were going to ask that question, and no, I don't know the correlations.

CORBET: Are there any other comments, please, on this matter of one species showing different modes of oviposition?

LOHMANN: I only want to point out that in several Aeshnidae there is an oviposition with and without tandem, for instance, in *Aeshna affinis*, *Anax parthenope*, *Hemianax ephippiger* and *H. papuensis*, and also, I think, in some *Staurophlebia* species; so several genera independently from each other, must have evolved this alternative mode of oviposition.

FINCKE: I just thought of an anecdotal thing. When I studied *Calopteryx* in the Dordogne in France I studied four species, *C. splendens*, *C. virgo*, *C. haemorrhoidalis*, and *C. xanthostoma*. Heymer had reported that some of these oviposit only under water and other species only oviposit above water, but I found that all four species did both and I'm embarrassed to say I have yet to fully analyze the data; so I can't tell you right now what the correlation is, but if I remember correctly it has to do with stream flow and the oviposition substrate.

MARTENS: There is a problem in the definition of the word oviposition. We all observe oviposition behaviour, but in order to be sure that egg-laying has occurred, we have to find the eggs directly after oviposition (16).

CORBET: I take it you are making a distinction between what we might call testing and true oviposition.

MARTENS: Yes.

FINCKE: In my particular case I was very careful. I have only called it oviposition when the eggs are laid and I can see the slits. Because they oviposit endophytically, I was sure that they were laying both above and below water.

MARTENS: One of our students in Braunschweig is now working on *Calopteryx haemorrhoidalis* in southern France and he only finds eggs if the female touches the plant under water. He cannot find any eggs at the water level.

CORBET: I would like to ask Andras Ambrus if he found, in *Aeshna cyanea*, any very unusual places where eggs were laid. This species has a reputation for laying eggs in remarkable places, like people's clothes, for instance (17).

AMBRUS: No. In the case of *Aeshna cyanea*, I haven't found any unusual egg-laying places in nature. But in the laboratory, I tried to make the females lay eggs in very different kinds of substance, including cloth, plastic, and other interesting materials, such as balsa wood. Balsa wood is very useful for getting other species, such as *Aeshna grandis*, to oviposit in the laboratory. In fact, *A. grandis* would not lay eggs in any other substrate, neither plant tissue nor wet artificial material. Females would try these other substrates several times, but didn't release eggs. *A. mixta* also tried out some different substrates, but didn't lay eggs.

MILLER: I would like to ask a question if I may, because I've observed guarded oviposition in a gomphid, *Ictinogomphus rapax*. I wonder if anybody else has observations on guarded oviposition in any gomphid, the interest being, of course, in the possibility of sperm competition.

CORBET: The question was, has anyone observed guarded oviposition in a gomphid?

DUNKLE: Yes. I have seen, I think, guarded oviposition in *Progomphus obscurus*, a North American gomphid, but I think it is rare.

CORBET: Does anyone else have any observations of guarded oviposition in gomphids. Kiyoshi Inoue, are there any examples that you know of from Japan, of observations of guarded oviposition in gomphids?

INOUE: As far as I can remember, no cases are reported in Japan.

CORBET: Carlo did you wish to contribute?

UTZERI: Yes, but I wish to speak about observations on two modes of oviposition. I observed two populations of *Cercion lindeni*, in one of which females oviposited under water, while in the other they laid only at the water surface, eventually laying just a bit under water (18). I think I can correlate the two modes with the behaviour of mates and with the vegetation in which they laid. I think in particular that the thickness of the plant was important. Both oviposited into species of *Potamogeton*;, one was *P. pusillus*, which is very thin, the other *P. perfoliatus*, which is thicker. I observed that females always tended to submerge and tried to drag males with them, but males never submerged and attempted to pull females out of the water. So if females have a thicker plant, they can combat the male and the male releases them, and so they can submerge. I think in this case that they actually oviposit because they stay under water for several minutes.

Part Two
Survival during the hot, dry season

CORBET: Well I would like to leave this topic now, and time is moving fast; so I will move onto Part Two, our main topic, which you will remember is strategies for survival in the hot, dry season. A word or two of background. In much of the tropics, and in lower temperate latitudes,

including the Mediterranean region, a major constraint placed on Odonata is the existence of a prolonged dry season. In the tropics this can regularly last for seven months or more. In the Mediterranean region the rainless period commonly occupies the months of July, August, and September, a time during which dragonflies, many of which have recently emerged as adults, have to find a means of surviving and postponing reproduction. Other species may have to survive the dry season as eggs or larvae. We have talked before in these discussion sessions about the strategies adopted by tropical dragonflies to survive the dry season, and I hope we can explore this topic again later in this session. But because of where we are holding this Symposium, I wish to start by considering the strategies shown by dragonflies here in the Mediterranean region. Two species in particular which seem to illustrate well adaptations needed by species occupying ponds liable to dry up in summer are *Lestes barbarus* and *Lestes virens*. These species have been studied from this point of view since the early 1970s by Carlo Utzeri and his colleagues, especially Elisabetta Falchetti, Gianmaria Carchini and Carlo Belfiore (19,20). So I would like to ask Carlo Utzeri if he would kindly open the discussion by summarizing the relevant parts of the life history of these lestids in Italy and identifying problems that, in his opinion, merit attention. And I wonder if I might ask you, Carlo, to speak to three questions in the course of your response. The first is, how do occupants of temporary ponds survive July, August and September? How do they make the bridge? The second is, how does their strategy for this bridge enable them to respond to unusually wet or unusually dry years? And thirdly, where do they go during the time when the ponds are dry? I hope that isn't too demanding a set of questions.

UTZERI: Thank you Philip. I think I will ask you to put your questions again afterwards, but I can begin by replying to your third question. I work with the species in a forest, in which they breed in small ponds, relatively small ponds, ovipositing in reeds and other plants, like *Mentha*, *Polygonum*, and several other plants. Since the forest is a mixed Mediterranean bush, there is very little open area around the ponds, and it is impossible to walk through the forest for the most part; so I cannot say where these damselflies spend their prereproductive period. I just know they emerge from mid-May to mid-June and then they stay near the pond for a few days, not more than two weeks maybe, until the pond is completely dried up, and then they disappear. They come back in the beginning of August, the first week of August generally, the males a few days before the females.

CORBET: Excuse me, may I ask you a question at this point? When they return in early August is there water in the pond?

UTZERI: No. They typically oviposit in temporary ponds whose water cycle is as follows. When there is much rain, the ponds may fill with water in September, sometimes September-October, but they may also stay dry up to the end of January. And then, in central Italy, there is generally enough rain to fill the ponds, and they remain filled with water until May, June, and sometimes July in wet years. I think that eggs hatch in early February, and emergence takes place in May and June. So in these ponds,

although the water cycle is very short, larvae still develop. These are species with diapause eggs, as you know, and I think that diapause might be a means of surviving the dry period. Uéda (21) pointed out that diapause in *Lestes sponsa* could serve to survive the cold season, but I think that in our case, it could also permit the species to survive the dry period. As a matter of fact, when water is very scarce a pond might not fill at all, and the population disappears, of course.

CORBET: You have answered two of my questions. Thank you. You have indicated that the dry season is survived first as adults, and then possibly as eggs, particularly in dry years, and you have said that you do not know where the adults go during the maturation period, but from your remarks I would conclude that, as a possibility, they go into woodland. And the third question was, do they have a strategy for responding to very wet years when there are many ponds, and very dry years when the ponds dry up very quickly and are not numerous?

UTZERI: There is a marked variation according to the amount of rain in the year. The forest where I studied these species is something over 4000 hectares, and I know some 40 temporary ponds and some other semi-permanent ones, in the sense that they have a temporary zone at their periphery while in the centre of the pond the water can stand all the year, albeit having a marked variation of level. *Lestes* is particularly abundant in the temporary ponds, but can also be found in the others. I can think of three situations which relate the density of the populations to the amount of water. If water is very scarce, and ponds don't fill at all, of course the population disappears, and I observed this two or three times in the last 10-15 years. When water is of medium abundance, there are some temporary ponds which are convenient for the completion of the life cycle of this species, and some others which are not because they dry up too quickly or fill with water too late. In this case, we of course found populations only in the appropriate ponds, but also these populations show a particular phenomenon which we described some years ago. That is, homing, after the dispersal period, to their native ponds (19,20).

CORBET: Is that the process you termed philopatry?

UTZERI: Yes. I would say that philopatry is the phenomenon of being tied to the original place, while homing is the behaviour to come back to that place. Over several years, as you have reminded me before, we have marked about 500 specimens, and I found not even one at a pond other than the native pond.

CORBET: So, you are saying - if I could just recapitulate to make sure I've understood - that a few days after emergence these adults, and you marked adults so you knew what they were doing, left the pond and at the end of the maturation period every one of your marks .....

UTZERI: ..... every one comes back to its native pond, where I marked it and where it had emerged.

CORBET: ..... and no marked specimens were found anywhere else?

UTZERI: No. This is zero percent of over 500 or so, so it's a good percentage.

CORBET: Now in a wet year, when they encounter many ponds, what would these adults do?

UTZERI: In years with much rain, dispersal is much higher, and this permits recolonization of ponds which have become void of populations. So there must be a population which survives in a very dry year. I observed that the young specimens, not precisely tenerals but some days old, attend their native pond, but also day by day they can disperse further from their pond and return to it; the young population gravitates around the pond, I think because they feed there, because other insects are also emerging at the same time. If there is not much water, they are tied to their pond, to their water body. But when there is much water they can move to a nearby pond and they can also begin gravitating around that pond. In the same way that I believe they form ties with their native pond, in the second case they can also become tied to another pond, although this occurs only in wet years of course, because they must find another pond with water.

CORBET: And so this results in dispersal over a wider area, the populations extending over a wider area, when there are many ponds in a wet season.

UTZERI: Yes.

CORBET: Thank you very much. Can I just recapitulate and say that in both *Lestes barbarus* and *Lestes viridis* there is a long maturation period of 2-3 months and this falls during the hot, dry summer. Now that is the case at this latitude, but as one goes further north the hot, dry season becomes shorter and it becomes cooler. As one goes further south it becomes longer and hotter. And many of us will be familiar with the work on *Lestes sponsa* by Uéda in 1978 (21), in which he showed that the interval between emergence and oviposition, which is one measure of the maturation period, showed a regression on latitude or, more correctly, mean summer temperature. At the southern limit of the range of *Lestes sponsa* there was a very long maturation period of 100 days. But going further north it became shorter and, finally, in the higher temperate latitudes it was reduced to about 15 days, which is what we are familiar with in Britain. So here we have a latitude regression, a correlation between latitude and the maturation period, and I believe, if I remember correctly from some of your publications and those of others, that there is a similar regression in *Lestes barbarus* - that in the northern part of its range it has a short maturation period and in the southern part it has a long one. Are you able to confirm that Carlo?

UTZERI: Yes, I guess so. Actually I don't know many populations of *Lestes barbarus* or *virens* in the range between central Italy and central Europe say. But I know that near Rome, central Italy, the maturation period takes 2-3 months, with some individuals not returning to their pond until 120 days - four months. But I think you asked me the same question in Paris, and afterwards I talked with Eberhard Schmidt from Germany and I also checked some literature about *Lestes barbarus* versus some other

lestids. Eberhard Schmidt gave me some dates from his notebooks. And from them I can deduce that the situation in these lestids is like in *Lestes sponsa* in Japan. I think that in central Europe, as in Germany, the maturation period of *Lestes barbarus, virens* and also *viridis* is of 15-30 days, not more. And also Loibl in her classic work of 1958 (22) in central Germany, reports maturation periods for several lestids that are much briefer than in central Italy. Now I cannot say what is the situation in northern Italy or in Austria or in the places between these two extremes, but it's very probable that the situation is similar to that of *Lestes sponsa*.

INOUE: I should like to add one thing to the maturation period problem. Dr. Uéda found that in the southern lower latitudes, the maturation period of *Lestes sponsa* increases, it is true. But in Japan we do not have a dry summer. So the variation is not connected with dryness in Japan. Our summer is rather humid, so we must separate hot and dry from hot and humid. If we think only of temperature, we should mention the other famous species, that is *Sympetrum frequens*. Generally, in central Japan, they emerge at the end of June to the beginning of July, and they go up to higher mountains where the climate is cool (23).

CORBET: How high do they go, how many metres?

INOUE: The altitude is often above 1000 m, and they spend the summer in cooler places and in the autumn they come back to lower altitudes. There they mate and lay eggs. The distance covered in some cases was 60 km. We have many examples of a hot summer affecting the reproduction period, extending it into autumn. But I repeat we do not have a dry summer.

CORBET: Your point is well taken. Thank you. It might be useful to mention at this point that recent work by Uéda (23) has shown that *Sympetrum frequens* behaves differently where the summer is cooler. Is that correct? [Yes.] And that in the north of Japan, in Hokkaido, there is no resting period, no long maturation period in the summer, so that, rather like *Lestes sponsa*, there is a gradient related to latitude or, as you say, the temperature, the summer temperature. All the species we have been talking about are univoltine, and we have a pattern here of the hot or the dry season being bridged by the adult stage, and the bridge being accomplished by an extended maturation period. Now there are two things which come out of this, which I would like to use as discussion points. The first is that if we are looking for examples of such species which have a prolonged maturation period, we need to know whether the specimens we see are mature or not. Now that is very easy at the beginning, in the first day or two of the maturation period, but it is less easy later on. And Uéda (24) has recently shown that in *Lestes sponsa* the colour matures quite quickly after emergence in males and females. In the males, spermatogenesis follows quite quickly, that is to say the males soon become reproductively mature. The females do not, and oocyte development, development of the ovaries, is suppressed until mid-August. So here we have both sexes with a prolonged period when reproduction is not occurring, and during which the males are already sexually mature, but the females are not until much later. Now that is of great interest biologically, but one would like to

know how we can recognize other than by dissection whether adults are immature or mature during this reproductive diapause.

That is the first point I would like to draw to your attention in case any comments can materialize. The other is, I would be very interested to know what examples we have available to us of species in temperate regions which have a very long maturation period. I mean there are other examples. There is *Lestes praemrosa* in northern India, for instance, which Kumar (25) tells us has a maturation period of 7-8 months. And immediately we think of some of the hibernating species, like *Sympecma fusca*, for example. Obana, in 1969 (26), reported that *Sympetrum striolatum imitoides* spent several months as a maturing adult, in this case also in the mountains. George and Juanda Bick, in 1970 (27), mentioned *Archilestes grandis* as having a maturation period of 42 days, which it spent in woodland. Now there are examples like this, but very few of them are associated with observations at different latitudes, which might provide us with some more examples of latitude regressions of this kind. One final point before I ask for comments, is that at the last Symposium we were discussing examples where the time of emergence, and the time of the beginning of the flying season, were different in the north of North America and the south of North America. And it's possible that some of these differences according to latitude are caused not by a different time of emergence so much as a different length of maturation period. May I ask, please, if anyone knows of interesting examples of dragonflies in temperate regions (we'll come to the tropics in a minute) which, during a hot or a dry season have a long maturation period which they spend in a cool, humid environment?

PARR: I think I may have mentioned this to you Philip, but perhaps we should put it on record here. Last year in the United Kingdom, as many people know, it was an exceptional summer; it was very sunny, it was hot, it was very dry. So we frequently had temperatures in the 30s Celsius, which is exceptional. And in one pond that I observed, the *Sympetrum striolatum* started emerging on the 4th of June, which as far as I know is an early date for Britain, and they continued emerging right through June, July and August. But the thing that puzzled me was that although these apparently immature (well in fact they were immature because they were teneral) specimens, which were seen around the pond during that middle part of the summer, were common, not a single red, apparently mature male, appeared until towards the end of July. Now this seemed to me an inordinate length of time, a great gap between the first emergence and the first apparently reproductive individuals coming back to the pond. I did make some enquiries, I did ask people whether they had noticed this before, but I haven't had any kind of positive reply back. So I don't know what the answer to this is.

CORBET: Kiyoshi Inoue - can you tell us please, are there, in southern Japan where the summers are hot, other examples among *Sympetrum* of long maturation periods?

INOUE: In the southwestern island we have no *Sympetrum*, but when we compare the *Sympetrum* of the northern part of Japan to those of the middle and

southern parts, the maturation period increases at the lower latitudes. We have many examples.

CORBET: Of long maturation periods?

INOUE: Yes. Most *Sympetrum* species emerge in late spring and they begin their reproductive period in early autumn at lower latitudes. Almost all species of *Sympetrum*.

CORBET: Well, it sounds to me as though a long maturation period in an area with a hot summer is probably a common phenomenon. What about *Aeshna mixta*? Does that have a long maturation period?

UTZERI: I would say yes. Both swarms and isolated individuals of *A. mixta* can be seen in the forest for quite a long time between May and September, in central Italy at least. *A. mixta* is a typical autumn species, or late summer species, which follows *A. affinis*. *A. affinis* flies until August and then it is followed by *A. mixta*. But *A. mixta* emerges earlier, much earlier, so it has a longer maturation period also.

MOORE: Just going back to *Sympetrum striolatum*, my own observations last year were very similar to those of Mike Parr's, and this year, with a terrible June and less good weather, mature males of *striolatum* appeared much earlier.

UTZERI: Our *Sympetrum*, at least *meridionale* and *sanguineum*, breed in the same temporary ponds as *Lestes* .....

(Side 3 begins)

..... so they must emerge before the ponds dry up, that is June, mid-June normally, but they begin mating in late July or August. They have a maturation period similar to *Lestes*. Normally also *S. striolatum* emerges in the same period in early summer, but doesn't mate before mid-September; so it has a maturation period even longer than the other two.

CORBET: Thank you. Sid Dunkle, do you have any experience of dragonflies with a long maturation period in the south of the United States?

DUNKLE: No.

CORBET: Thank you. I would like to move from temperate regions, where I think we now have a pretty good idea of the way in which some species at least, survive the dry season or the hot season. I would like to move now into the tropics. It is fairly well known that several species that have been studied in the tropics spend the dry season, which may last up to eight months, as adults, frequently in the shade of woodland. Two examples which are among the early cases to be placed on record are *Lestes virgatus* and *Acanthagyna vesiculata* in Nigeria, studied by Robert Gambles (28). Both of them inhabit temporary pools. The emergence takes place in September or October and the adults stay on the wing until May or June, *Lestes* possibly in a state of aestivation or diapause, that's not known,

but *Acanthagyna* apparently being active every day. Both of them retire to woodland, which is obviously a protected site in the dry season, and *Acanthagyna* follows the very characteristic and dramatic pattern of behaviour where it feeds in the woodland during the day, and at sunrise and sunset emerges from the woodland for a brief frantic feeding period for about half an hour while there is enough light to see the food, and presumably it is relatively cool and humid. And then oviposition begins in May before water accumulates in the ponds, *Lestes* laying in the plants, and *Acanthagyna* laying in mud. Then as soon as water collects, eggs hatch. There are several other examples which are now well documented in different parts of the tropics, and I don't think anything will be particularly served by cataloguing them at this point. The question I would like to focus on, because it's a very difficult matter to study, is how the adults that survive the dry season in woodland are stimulated to end their reproductive diapause. I'm thinking of genera like *Erythrodiplax* or *Uracis* in South America, which remain in woodland with immature coloration until the first rains come and then leave the woodland, very abruptly, and change colour, and start their reproduction. I think, Sid, you have had something to say about this in the past (29). Would you like to put us in the picture a bit better than my remarks do?

DUNKLE: Well I have little to add beyond the general observation that, as far as I know in my brief visits to tropics, it's the actual beginning of the rains which usually starts this process. At least the air has to be more humid and that would be the cue that they would respond to.

CORBET: Do you notice a very rapid response?

DUNKLE: I certainly did near Mazatlan, Mexico (29) where many dragonflies appeared as soon as there was a hard rain, and apparently they came from the forest where they had been widely scattered. I saw only scattered individuals before they suddenly appeared in droves. At that time I thought that they did not suddenly change colour, like so many people have said. I'm unsure that they do that, that they suddenly change colour as soon as it rains. I think that the colour change is more gradual.

CORBET: Ola Fincke, you were mentioning, in the course of your talk, a colour change in *Mecistogaster*, I think at the end of the dry season. Could you make some comments, please, on what you see in the pseudostigmatids in this regard?

FINCKE: I would agree with Sid, in that in *Mecistogaster ornata*, the ventral portion of the male's wings changes from bright yellow to black, but before it turns absolutely black it gets sort of dark brown; and likewise the female's wings become sort of tinged with brown on the edges, and this is a process that probably takes several weeks. But they do seem to break reproductive diapause quite quickly and start to mate if - well I have some observations of them mating just before the first heavy rains, and then certainly lots after the first heavy rains. And that break seems very abrupt, but the colour change is slower. Unlike perhaps the species Sid was describing, these things remain in the forest throughout the dry season, actively foraging, and they don't hang out in different places,

they simply break reproductive diapause. I know they are in reproductive diapause because I've dissected females throughout the year. You dissect a female in the dry season and she has no eggs and no sperm in her spermatheca. Likewise you see no matings and I've never seen a mating unless the male's wings have at least begun to change.

CORBET: Have you dissected any males during this long maturation period? I'm thinking of the case of *Lestes sponsa* in which it has recently been shown that the males actually mature quite early, but the females delay reproductive maturity (24).

FINCKE: Frankly I don't remember. I'd have to check my notes. I think most of what I did was just record the colour change. In any event, whether they do mature early or not, there is no-one around to mate with.

CORBET: There is evidence from other sources that the adult stage in many Anisoptera is used to survive the dry season, because the condition of adults at the beginning of the rainy season shows clearly that they are old and battered. And the young, fresh specimens don't appear until 3-4 months after the rains in some Anisoptera. I'm thinking of observations in Trinidad some years ago (30). Gordon Pritchard, would you be in a position to comment, from your recent experience in Costa Rica, on how the dry season is spent by Odonata there.

PRITCHARD: Actually Philip, I don't really have anything to add. I have some formalin-fixed material which I have yet to look at. I have some *Erythrodiplax* and *Uracis* of both sexes and perhaps when I have done that I shall have a little more to report. I think I can agree with what both Sid and Ola have said with regard to these two genera. I was working in a sort of transition dry forest-premontane forest site, which is not, therefore, very, very dry, but at the same time it does have a six-month dry season, without any significant rainfall. At this site, both of these genera, and both sexes of these genera, stay in the area. You find them quite readily along paths outside of the evergreen forest, and they maintain their teneral coloration pretty much throughout the dry season, which makes them very difficult to see and they are very difficult to catch. They are cryptically coloured and they take flight very easily. And the colour change occurs, I think, as both Sid and Ola have said, over a matter of a few weeks, which, sitting it out through six months of the dry season, I interpreted as being fairly rapid. But I'm sorry, that's the only positive stuff that I can add at this time.

CORBET: Are there any further comments, please, on strategies during the dry season in the tropics?

FINCKE: I should have added this earlier. *Mecistogaster linearis* is quite different from *ornata*. These things remain reproductively active throughout the dry season. You dissect females and they have sperm in their spermatheca, they have eggs and they will oviposit in any hole that has at least a little bit of water in it. And I hypothesized that they are laying eggs that are in diapause then and until the holes refill with water, and I'm wondering if anyone else has any observations of tropical

odonates going through a dry spell in the egg stage. This seems a very susceptible stage, but I have no other explanation for why females would yolk up eggs and keep ovipositing them in the dry season. I don't think they are just throwing these eggs away.

CORBET: Yes, well this brings us to the other theoretical possibilities of surviving a dry season, and those are either surviving it as laid eggs or as larvae. Could we look for a moment at any examples we know of, of Odonata that survive the dry season in the tropics as eggs.

WASSCHER: I don't actually have any information on this, but I think that *Uracis ovipositrix*, from the neotropics, has a very long ovipositor and the abdomen of the females is often covered with mud. And it occurs in places which become dry in the dry season, and this suggests to me that the eggs are put in the mud and they may survive there during the dry season. But I have really no facts on this.

CORBET: Could I put alongside your statement that Gamble's observations (28) on *Acanthagyna vesiculata* included the observation that females would lay eggs just before water appeared in the habitat? They had actually survived the dry season as adults, and then a week or two before the rains fell, they were laying eggs in mud. Now if they had been caught by you, for instance, during that two weeks, the abdomen would have been muddy, but it would not have meant they laid eggs during the main dry season. Can you remember when you encountered these females? Was it early in the dry season?

WASSCHER: Well, actually it was during the short dry season in Surinam. And first I can say that the dry and wet seasons are not very well defined in Surinam. They perhaps exist only statistically. So it was during the short dry season in Surinam and there was still water in the creek, which is supposed to become dry.

CORBET: Any other examples of species surviving the dry season in the tropics as eggs? What about larvae? I would think it's extremely unlikely in hot, dry climates that any Odonata would survive the dry season as larvae, except perhaps in forests.

CORDERO: I have some observations on *Cordulegaster boltonii* in northern Spain. In this area there are some smaller streams that dry up during the hot season. I have found that the larvae of *C. boltonii* survive in the bottom: one month after the stream dried up I found some live larvae under the dry leaves and detritus in the river. So this species survives in this way in very small streams, and I think this species needs at least two years to complete larval development in this area. So it is very likely that this species survives as larvae in some areas in northern Spain. It is very common in permanent rivers, but it is also found in temporary rivers.

FINCKE: I just wanted to say that I have done some unpublished experiments with *Megaloprepus* larvae and drying, and they can't withstand more than three weeks completely dry. But in nature in some years, as many as 10% do

survive in tree-holes. If it's a particularly wet year, and the hole is deep, there are some that survive. They do quite well if the drying is only temporary, and since even during a dry season in Panama sometimes you get intermittent rain, sometimes this is enough to keep them alive longer. But the bulk of the population doesn't pass the dry season this way.

CORBET: Are they are any other comments, please, on how species survive the dry season in the tropics?

KOMNICK: When they really survive the dry season, then they must get some water-proofing protection from the cuticle, which must act more effectively compared to when they live in water. So it would be very interesting to study the cuticle in these different periods. I would suggest that the lipid composition should change; there should be more lipids which are crystalline and insoluble.

MILLER: Not that this is likely, but perhaps I could remind you of *Polypedilum vanderplanki*, the chironomid larva which desiccates totally and thus has no problem with its cuticle, and can survive in this state for many years, and will revive in water within 20 minutes (31). I don't imagine that any odonate has got that far. That's a dipteran of course.

CORBET: Well, can we move to the temperate regions now? There are a number of examples which are being reported with increasing frequency, particularly of Anisoptera larvae, that can survive upon drying up in temperate regions. I'm thinking of work by Arai recently (32), in which he observed something like 25 species in a pond that regularly dried up, species that were not univoltine, or if they were univoltine, the eggs hatched before the dry period and they had obviously survived in the bottom of the pond. Kiyoshi Inoue, are you in a position to comment on the ability of any Japanese dragonflies to survive the dry season as larvae, the hot season as larvae?

INOUE: As Philip Corbet indicated, Arai has been working on this problem for four years and has discovered larvae of many species in the dry, cold winter. These durable larvae are hidden underground where the soil is almost dry. And I should like to add this. We have three species of Zygoptera that hibernate as adults: *Aciagrion migratum*, *Indolestes peregrinus*, and *Sympecma paedisca* or maybe *braueri*. I consider that these three 3 hibernating species have strategies for tolerating the dry, cold winter as adults. They avoid spending the egg stage or larval stage in such severe conditions.

CORBET: Well we're getting near the end of the session now. Are there any other comments that anyone would like to make on the main topic of survival of the hot or the dry season in temperate latitudes or in the tropics? Or are there any problems that people would like to draw to our attention as meriting study in the future?

CORDERO: I have just published a short observation about *Calopteryx haemorrhoidalis* in northern Spain. In this area most of the smaller streams dry up and then the adults from these streams try to find another

stream with water; there are many, many streams in this area and some flow all the year. There is, then, a dispersal of the adult population after streams dry up. I have found that some specimens are able to reach another stream and to reproduce successfully in the other population. So I think that this is the mechanism that allows this species to survive in temporary streams in northern Spain.

SCHNEIDER: What are the distances between these streams?

CORDERO: Two kilometres.

CORBET: And before we leave the subject of survival in temporary streams, we should not forget the strategy which has been reported from France (33) and Ontario, Canada (35), whereby larvae move down to the hyporheic zone, the top of the water table, particularly in stream beds. Manuel, I think you suspect this in some of the dragonflies you have studied in Andalusia.

FERRERAS-ROMERO: In southwest Spain, *Cordulegaster boltonii* never occurs in rivers that dry up in the summer. But *Gomphus pulchellus* and *Onychogomphus forcipatus* are in this type of stream. I think, in southwest Spain, both species are semivoltine, and I think it is very possible that the strategy is similar to *Cordulegaster boltonii* in northwest Spain [see CORDERO, p. 20].

CORBET: Has no-one any examples of finding larvae a metre or more below the river-bed in summer? We don't know whether it's common or rare, because samples are hardly ever taken in that situation, but we should be alert to that possibility.

In closing this session, allow me to thank you all very much for your participation in this seminar.

APPENDIX I

BIBLIOGRAPHY
(Compiled by Philip S. Corbet)

Listed here are publications which, in the chairman'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 (OA) are included for some citations.

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APPENDIX II

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INDEX TO CONTRIBUTORS

Names listed below are those 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.

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