CURRENT TOPICS IN DRAGONFLY BIOLOGY

Transcript of discussion recorded during plenary session of the 7th International Symposium of Odonatology at Calgary, Alberta on 16 August 1983

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

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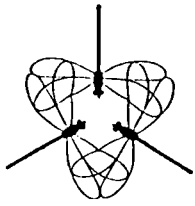

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CURRENT TOPICS IN DRAGONFLY BIOLOGY

Edited by
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C O N T E N T S

PREFACE

At the 6th International Symposium of Odonatology, held in Chur, Switzerland in August 1981, the programme included a plenary session devoted to discussion of topics of current interest to odonatologists. This session, which I chaired, proved rewarding, and it was decided to repeat the exercise at the 7th International Symposium in Calgary, Alberta in August 1983. On both occasions I had circulated beforehand to members of the Societas Internationalis Odonatologica (S.I.O.) a list of possible topics for discussion; and additional topics were suggested at the Symposium or during the session itself. At Calgary, thanks to the efforts of the Symposium Secretary, Dr Gordon Pritchard, and to the expert technical help provided by the University of Calgary, we were able to record the whole session and to do so 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 2½ hours and yielded interesting facts and stimulating ideas. To make these more accessible to the reader, I have compiled a brief bibliography, a list of contributors and their addresses, and indexes to contributors and dragonfly taxa. Citations to entries in the bibliography are indicated in the text by superscript numbers.

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It is a pleasure to thank Mrs Gillian BLYTH for valued help with the demanding task of transcribing the recorded discussion, and for producing the final typescript. My warm thanks are due also to Professor B. KIAUTA for helping to ensure that this communication has indeed been a rapid one.

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 14 and 29.

Philip S. Corbet
December 1983

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DISCUSSION

Cues for habitat selection

CORBET: The first topic that I suggest we discuss is this question: Do we know of any suspected cues for habitat selection by which males and females might be identifying the rendezvous? I have a few examples here to generate discussion.

Gerhard Jurzitza[1] noticed that in Chile *Antiagrion grinsburgi* laid eggs only in the leaves of a fern, *Blechnum chilense*, along the banks of a stream. Eberhard Schmidt has told us in this Symposium that *Erythromma viridulum* has a very close association with *Ceratophyllum*. Dennis Paulson[2], some years ago, noticed that territorial males of *Miathyria marcella* are closely associated with the water hyacinth, *Eichhornia crassipes;* and Godley[3] has recently shown that the small larvae of *Miathyria* occur amongst the roots of *Eichhornia*. Mike Parr has noted[4] that males of *Nesciothemis nigeriensis* use the grass *Echinochloa pyramidalis* predominantly as territorial perches. And according to Hassan[5] the small libellulid *Aethriamanta rezia* in Nigeria perches on the water lettuce, *Pistia stratiotes*, and oviposits on the foliage.

Now these are examples where there is a very close correlation between a plant and the choice of territory or oviposition site by a given species. There are other cases in which people initially suspected that there was a close relationship but it hasn't proved to be invariable. An example would be *Aeshna viridis* and *Stratiotes:* although *Aeshna viridis* oviposits predominantly in *Stratiotes*[6], there are instances where it lives in ponds where there is no *Stratiotes*[7]. Likewise *Aeshna mixta* oviposits in *Scirpus* in Japan and the larva lives amongst the roots[8], but in western Europe it oviposits in dead *Typha*[9]; and there are other examples such as *Lestes viridis* which sometimes lays predominantly in *Salix*[10] but in other places in a wide variety of woody plants[11].

May I then open discussion on this topic: the use of identifiable cues for habitat selection?

PAULSON: There are a number of species of *Telebasis* that you find almost always associated with duckweed, *Lemna*, and *Spirodela* and floating fern, *Azolla*[2], and I think this is the breeding habitat because you collect larvae there and it may in part just be a good place to perch out in the middle of a pond too.

MAY: Yes: I have a graduate student, Bruce MacKinnon, who has been working on this problem in *Pachydiplax*, although we don't have any specific association with a particular species of plant. He has found that first of all females appear to require some sort of submerged or slightly emergent vegetation for oviposition and he has some experimental confirmation of this based on adding floating grasses to an otherwise bare area; and they do seem to prefer that. And also males appear to select preferential areas where vegetation is denser and higher around the perimeter of the pond. I believe also Karen Sherman, who was then at Cornell, recorded at the American Institute of Biological Sciences meeting a couple of years ago similarly for *Pachydiplax* that females in her study site in South Carolina oviposited almost exclusively on floating algal mats[95].

CORBET: This raises the question of providing artificial oviposition sites for attracting ovipositing females or for experimental purposes and I think Jonathan Waage has done this for *Calopteryx maculata*[12]. Do we know of any other examples where this has been done or could be done?

SCHMIDT: Not quite in this way. I want to speak for *Aeshna viridis* as an example because its oviposition in *Stratiotes* is so pronounced compared with other substrates that we should regard this species as one of the very few in which there is a connection with a certain plant; the larvae dwell in the axils of this plant and they are well protected there from predation by fish. I ought to omit *Erythromma viridulum* because it lays not only in *Ceratophyllum* but in many other fine-leaved floating plants, like *Ranunculus* (for example *fluitans)* or *Myriophyllum*.

CORBET: So you think it's probably the physical structure of the plant rather than the species of plant?

SCHMIDT: Yes. It's true that it's not the species but the type of plant, and we have many examples that illustrate this. *Aeshna mixta* for instance oviposits in 'reeds', whether these be *Scirpus, Carex, Phragmites, Juncus* or *Typha*.

CORBET: To know this might make it easier to construct surrogate oviposition sites - artificial oviposition sites.

GARRISON: I wonder if any odonates are host-specific in terms of where they oviposit. I ask this because when I returned from the Dominican Republic this new *Protoneura* seemed to be ovipositing specifically on a particular sedge that grew along the bank of the river. This I thought was quite odd and unusual for the genus itself. In these areas quite a few specimens may be found in tandem.

PAULSON: I would like to suggest that we look at situations like that and determine whether there are plants that are similar in physical structure (but not the same species) and that are avoided, because I would agree that probably it is the physical structure in many cases that's really important: the softness of the stem or the places for larvae to hide, that sort of thing. And if you have a species that is similar physiognomically then they'll probably use that too.

MOORE: A special case of this is provided by species that breed in epiphytic plants: there are two species of *Megalagrion* that breed in *Freycinetia* and *Astelia* and apparently not in other epiphytic plants[13]. This preference presumably reflects the actual nature of the closeness of the leaves, but I don't know of any work in detail on this. It seems to be a very special case of the general one.

CORBET: We might mention at this point the extraordinary instance of the protoneurid *Roppaneura beckeri* in southern Brazil which is intimately linked with one species of umbelliferous plant *(Eryngium floribundum)* in which it lives[14]; and it presumably never breeds in anything else.

GARRISON: Our studies this summer also with *Ischnura gemina* show it to oviposit primarily in two different kinds of plants. One of them is *Nasturtium officinale*. It will sometimes try to oviposit on grass or sedges which grow in the area but generally it's not successful and seems rarely to land on those plants when trying to oviposit. In this case it would seem that it might be the structure of the plant itself that's amenable for oviposition.

MAY: Perhaps someone mentioned it - perhaps I missed it - I can hardly believe it hasn't been mentioned: *Ischnura kellicotti* is, I thought well known, to be associated with, I guess both *Nymphaea* and *Nuphar* - but in any case lily pads - and I believe the larvae live on the undersides of the pads; also the adults perch on the leaves at the surface.

CORBET: Dennis Paulson mentioned that in his thesis in 1966 .

PAULSON: Can I add another species to that? *Ischnura erratica* on the Pacific coast is by no means limited to water lilies but is very common on *Nuphar* and floating *Potamogeton* - again perhaps not because these are so special but because they offer an appropriate flat place on which to perch away from the shore where they live.

JOHNSON: I'd like to raise a related question and that has to do with the ability of the adults to tell whether there are fish in a pond or not. It seems to me that fish can have such a selective effect on larvae with different behaviour types that those adults really should be able to know - if it's at all possible for them to do so. We have that impression at Bays Mountain Park but we certainly don't have many indicative observations.

CORBET: I was speaking to Truman Sherk, who has done some very extensive work on vision in Odonata, about this question a couple of years ago and he was of the opinion that they probably could do this because of their ability to handle polarised light[15,16]. They would be able to see beneath the surface of water much better than we could and they might very well be able to see things like water plants underneath the water and also fish.

JOHNSON: Karen Sherman told me that she thought her dragonflies could tell whether there were fish present.

CORBET: Well, I'd like to leave this topic now, not because there's not plenty of scope for continuing it, but because it has brought us to an interesting point where I think we can see possible field experiments involving the setting out of surrogate oviposition sites and perhaps model fish and so on. I think there are some very nice projects we could follow up here.

Breeding in small containers

CORBET: May I move now to a related topic? This is the question of dragonflies that breed in small containers. This slide shows a list[17] I compiled a couple of years ago of families and genera of dragonflies that live in the water that accumulates in cavities in plants. Now these may be the leaf-bases of plants like *Astelia*, epiphytic bromeliads or the umbelliferous plant I spoke of. They may also be tree-holes and pans in trees. Looking at the list we see that there are quite a number of Zygoptera which are specialised for this sort of thing but very few Anisoptera. In the case of Anisoptera this may be partly an artefact of collecting, because it is very difficult to collect effectively in tree-holes - and the Anisoptera larvae are probably quite capable of gripping onto the bottom of the tree-hole. So one reason why Anisoptera are not well represented may be because they are more difficult to collect. We can add to this list now: *Libellula herculea*, I think it is, which is very close to *Belonia*, has been found in a tree-hole as has also a related member of the Gynacanthini from South America[18]. But that's probably close to a complete list as regards our present knowledge.

This photograph shows a pan in some relict forest near the coast of Kenya in which were living larvae of the large libellulid, *Hadrothemis scabrifrons*[19]. And this picture shows *Mecistogaster jocaste*, an endophytic species, projecting eggs into a tree-hole in, I think, Bolivia[20].

First of all, may I ask if anyone has come across any other examples of Odonata living in small containers, beyond this list?

PAULSON: I have no such examples but in South America I have collected a fair number of long slender coenagrionids that you find in the forest away from water and I would consider all of them as candidates also.

CORBET: Do you think they don't belong to any of these genera?

PAULSON: Right. *Metaleptobasis*, for example, is one and there are others. Another thing: perhaps the Zygoptera may well be pre-adapted to breeding in those sites just because of their shape and their oviposition mode where certainly libellulids are not pre-adapted to breeding in bromeliads or other such things.

MAY: In response to Dennis' remark, I don't know whether this is true of all *Metaleptobasis*, but I know that the species on Barro Colorado Island (Panama) is: I don't know if it never oviposits in such places but it also certainly oviposits in a small, temporary surface pond.

PAULSON: It's not right that one: I've seen the larvae emerging.

CORBET: It's perhaps worth mentioning that the *Belonia (Libellula herculea)* which has recently been found to occupy tree-holes, also breeds in rock pools near rivers[21]. So it may well be that some of the Anisoptera, at least, that are occupying these habitats are a spill-over from ground pools or rock pools, which may be their normal habitat. One thing that occurred to me here which might be worth pursuing is the use of test oviposition containers that look like tree-holes. Such a technique has been used extremely effectively for many years in the study of tree-hole breeding mosquitoes in the tropics. It seems to me that there are great possibilities here for a quick census of tree-hole-breeding Odonata in an area where they are suspected to occur by putting out bamboo sections or whatever in appropriate places. These have the advantage that they can be emptied completely and then filled up again and replaced.

WESTFALL: In connection with what Dennis said, I remember that Calvert thought that the long abdomen of *Mecistogaster* was adapted for getting the eggs in between the leaves of bromeliads[22]; so I was not surprised when I was in Jamaica and got the *Diceratobasis* there (it of course has a fairly long abdomen) and raised it out of bromeliads[23]. But then when I got that little new species of *Erythrodiplax*[24] it was just not tree-adapted at all, and so I thought this must be a mistake - that it must have just by chance gotten into the bromeliads. But I searched in every pond around there dug and dug and dipped through there but never did I find that *Erythrodiplax* any place other than in the bromeliad.

CORBET: Did you find it again in another bromeliad?

WESTFALL: I found a lot of them in bromeliads, right, but why they were using that kind of habitat and not the pond which was right next to it, I don't know. But they certainly didn't have a long abdomen to get the eggs in there. I don't know how they did it.

CORBET: Well this throws a new light on the possible adaptive value of having a long abdomen, doesn't it, in *Mecistogaster*? It may be for throwing eggs into tree-holes!

BICK: Where do the eggs go in this *Mecistogaster*? Is the group not endophytic?

CORBET: Yes, and they've been seen ovipositing endophytically. Other species have been seen, yes.

BICK: But then in this one the eggs are - just free?

CORBET: They are thrown free of the abdomen and float; and they are projected towards the darkest part of the tree-hole.

BICK: Do you suppose it's that way in all the Zygoptera in small containers?

CORBET: I would be very surprised if it was. I think this is viewed as an exception. Do you have anything to add, Dennis on this?

PAULSON: No, just from the literature - and that I've seen *Megaloprepus* ovipositing right on the surface or probably just under the surface.

PARR: Your list mentions *Taenobasis* as being a hole breeder. This could well be the reason why we failed to find that *Taenobasis malawiensis* that Elliot Pinhey first described[25]. And when we went back there we were looking in streams - around streams - and if it is really a hole breeder then that could explain it. Does anyone know about the breeding of other species of *Taenobasis*? Are they generally hole breeders, or how do they breed?

CORBET: I am afraid I don't know. Does anybody know anything about the breeding habits of *Taenobasis*?

PAULSON: No, except that the ones I've collected in southeast Asia have been on streams.

MAY: One other aspect that I know nothing about but which would be interesting to pursue in relation to tree-hole breeders, is their adaptation to what must be somewhat unusual water chemistry in that I would imagine, for example, oxygen levels may on occasion be low - especially if there are other occupants in the tree-hole. I know that A.M. Laessle[25] did a study of the limnology of bromeliads, of the water that collected in bromeliads. I don't really remember his results in detail, but I should think that many of these species might prove to have special physiological adaptations for this mode of existence.

CORBET: Before we leave this topic I would like to introduce the possibility of using tree-hole-breeding dragonflies in an attempt to culture them in the laboratory. So far very few people - in fact only Clifford Johnson[26,27] I think - have been successful in continuously culturing Odonata in the laboratory and if this could be done it would open the way for further use of what is obviously a very valuable animal as a biological model. It has been found in mosquitoes for instance that tree-hole breeders are very amenable to rearing in the laboratory because they're used to living in a

confined space and because artificial oviposition sites can be presented to them very readily. So I would suggest that if the opportunity arises some time it might be worth giving thought to this possibility. Dennis do you have something to add?

PAULSON: Just one thing: just looking at these libellulid genera we discussed this the other night. I don't know about the *Erythrodiplax* but all the others are species in which the females have a flange on the abdomen which they use for flipping eggs on to land, at least when I've seen them, and there are a lot of other libellulid genera that have those flanges and for some of them we have never found the larvae and that might give some clues toward locating them either in phytotelmata or perhaps in very tiny temporary pools or something.

WASSCHER: I want to know where have they been found - in which part of the world. Are they all tropical rainforest breeders or are they found in other parts of the world too?

CORBET: They are virtually all tropical rainforest breeders, yes.

Tolerance of larvae to pH and salinity

CORBET: I'd like to pick up a point that Mike May made just now to move on to another topic. It is often stated that aquatic animals, including Odonata, are associated with water of a certain pH. I think this is accepted as a bit of vernacular wisdom that we have without necessarily knowing how this linkage affects the dragonflies or how they are involved in this linkage. I wonder if anyone has any ideas to suggest as to how pH in a given situation can be linked with a certain species or with several species of Odonata?

LUTZ: I have had a graduate student over the last two years who used eggs of six species of anisopterans and never found a tolerance limit for egg development at the low or the high end for pH. We were using solutions as low as a pH of 2 and as high as 14 without detecting any obvious difference.

SCHMIDT: It seems that the imagines are responsible for this linkage to pH. Do you know the work of Steiner[28] who conducted some experiments on preference in *Leucorrhinia*? And the second point is that we know that *Aeshna subarctica* is confined to *Sphagnum* and some similar mosses - but maybe to *Sphagnum*[29]. *Sphagnum* effects an exchange of ions and because of this a *Sphagnum* bog may have a low pH. I don't know whether *Aeshna subarctica* reacts to the pH but it may, because the brown waters have a detectable odour. But in this case pH surely works indirectly.

CORBET: Yes, but it could be the moss which also requires water of a certain pH. Rob Cannings, do you have anything to add from your experience of *Somatochlora* breeding in bog pools?

CANNINGS: The species of *Somatochlora* that we were looking at up north and that we originally thought were living only in bogs, that is in acid conditions - and this includes *Somatochlora sahlbergi* - seemed to prefer mosses even at rather neutral values of pH and I think it is the actual presence of the moss rather than any difference in pH or low pH that was the reason for that species being there. Similarly with *Leucorrhinia patricia*, which we always considered an acidophile, mainly because it was described and best known from the Canadian Shield: it occurred in exactly the same place in the moss but in a fen which presumably was rather neutral in pH. That's all I can offer on low values of pH. As far as high pH goes, we've collected specimens of *Lestes congener*, *Enallagma clausum* etc. in these saline ponds where the ions are mainly sodium and the pH values are almost as high as 10 in some cases and there are very, very high salinities of up to 30 or 35,000 micromoles per centimetre[30]. So obviously some of these zygopterans at least can live in nature in high pH as well. Off the top of my head that's about as much information as I can offer.

GARRISON: I suggest that there may be some species which are linked to such conditions. Among those that come to mind are species like *Erythrodiplax berenice*[31] or *E. naeva* which appear to be confined to coastal marsh areas, at least along the eastern seaboard. Another one might be *Macrodiplax balteata* which seems to prefer areas near the seashore or inlets - bays, that sort of thing; and where I have collected it in the deserts it's usually found at places like the Salton Sea or the Salt River at Phoenix, Arizona; and areas where there might be extreme irrigation, leaving salt deposits. It seems to me that it might be a fairly simple matter to test this just by getting some eggs and rearing them under various conditions and different pH values and seeing whether or not they remained viable.

PAULSON: As far as I know - correct me if I'm wrong, someone - all of the saltwater, or salt-tolerant, species do perfectly well in fresh water. They are like a lot of other saltwater things: since they can take salt water they avoid competition with a lot of freshwater species; and I think that's the case for *Enallagma clausum*, for example, which can take a very high pH - a very high alkalinity - and therefore lives in places like that because it can avoid competition with other species. It's also perfectly common in sort of neutral, nice freshwater marshes.

CORBET: Does that apply to *Erythrodiplax berenice*?

PAULSON: *Erythrodiplax berenice* breeds in Florida in complete fresh water also.

SCHMIDT: Could there not have been in the last examples a mixture of pH and high salinity (or ionic concentration)? I think the examples cited just now are saline species preferring high ionic concentration. In Europe such a species would be *Lestes macrostigma;* and many Mediterranean species can tolerate high salinity.

WASSCHER: I think in Europe too. In northwestern Europe many rare species are linked to mesotrophic waters: for example *Sympetrum paedemontanum* and *Sympecma fusca*. They are very rare. And I think they manage to exist there only because they are more competitive in mesotrophic waters than in other places where they therefore cannot manage to survive. I think it is more a matter of interspecific competition.

CORBET: More than a matter of physiological tolerance?

WASSCHER: Yes.

ASAHINA: I think I remember that Patrick Buxton, who once worked on the desert fauna, must have treated some problems relating to alkaline ponds in desert conditions. Maybe he mentioned *Selysiothemis nigra*. This could be found in his book called *Animal life in deserts*[32].

CORBET: And you think *Selysiothemis nigra* is one such species?

ASAHINA: Yes.

MOORE: An interesting case in Britain is provided by places where *Aeshna cyanea* and *A. juncea* overlap. *Aeshna juncea*, which is a smaller species, only seems to be able to survive in acid waters when it comes into competition with *A. cyanea*. I don't know if this shows us anything about what's happening; its larvae as far as I know are living in very similar conditions, but it's certainly an interesting case in which pH seems to be really quite important in determining the distribution of a species.

CORBET: But you think this might nevertheless be a reflection of the competition?

MOORE: I suspect it probably is, but in rather a subtle form. I entirely agree with Eberhard (Schmidt) about *Sphagnum*. I think it is probably nearly always the case that it is the actual vegetation which is dependent on pH and that this determines the larval population.

TENNESSEN: I was involved in a survey of the aquatic insects of a whole bunch of pools that were formed by strip-mining in coal beds, and the ponds, although they were close together, were extremely variable in their water quality: the pH would vary from 5 to about 8. I have a lot of data, 5 years' worth, on the Odonata nymphs that were living in these pools. I don't want to try to draw any conclusions from memory but when I get back I'll look at the data and if there are any correlations I can send them to you.

Drought resistance in larvae

CORBET: I'd like to move now to another topic - again dealing with larvae - and that is drought resistance in larvae. And may I emphasise that I am not talking about terrestrialism in larvae? There is a small number of Odonata that appear to have completely terrestrial larvae[33-35]. But I am not talking about these. I'm talking about species that have larvae which are normally aquatic and apparently reliant on water but which appear to be able to survive extended periods of withdrawal of free water - that is, extended periods of drought. As an introduction I'll mention one or two observations which lead us to suppose that this ability exists in a few Odonata. Henri Dumont[36] noticed in the Sahara larvae of *Trithemis arteriosa* and *Orthetrum chrysostigma* in the beds of drying-out or dried-out pools. He found clusters of larvae just below the surface of almost dry mud, in one case 30 cm below the surface of the mud. But they were alive. Paul Robert, in his book *Les libellules*, reports *Libellula depressa* larvae as being able to survive a period of drought[37]. Tony Watson tells us that in Australia *Synthemis leachi* and *Austrocordulia refracta* can tolerate the withdrawal of free water[38]; but he says that they need moist sand and that in this respect they are quite unlike the temporary-pool breeders that migrate with the rain belt, *Hemianax papuensis* and *Hemicordulia tau*, which are very vulnerable indeed to drying up. These species are unable to survive even quite a short time of withdrawal of water and this seems to be true of temporary-pool breeders in the tropics in general. And then we have observations of larvae that have been found in dried-up pools, like *Aeshna sitchensis* which has been reported by Rob Cannings in highland pools[39] (perhaps you'll speak to this in a moment, Rob?), *Somatochlora semicircularis* found by Willey and Eiler in alpine pools which were dry[40] and *Erythrodiplax berenice* at low tide[41]; and in all of these cases the larvae were under stones or logs which would preserve for them a moist cool environment underneath. And there's *Oplonaeschna amata* which Dr Tinkham worked on many years ago[42] and he pointed out there that they were able to survive periods of the drying up of the river and its associated pools, when the river ran low in the desert. Also there is *Lyriothemis*, a small libellulid which lives in bamboo sections and tree-holes in Taiwan and which can resist dryness[43]. Someone here tonight, Steven Valley, has something to add on this. Could I ask you to give us an account of some of your findings, Steven?

VALLEY: I have been studying a pond near Albany, Oregon for the last 15 years, and the last 7 or 8 years it has dried every summer - completely - and usually for a period of from 30-60 days before the rains come; and I found there quite a number of species that were in the mud and under dried vegetation and completely dry: they floated when I put them in water. I found *Anax junius, Aeshna palmata, A. multicolor, A. californica, Libellula pulchella, L. forensis*, and a number of *Sympetrum* that I couldn't identify for sure. I'd wondered why I was finding full-grown nymphs every spring after the pond had dried up and there was no way for them to be there! The

nymphs that I found were almost all aeshnids and almost all *Anax junius*. They totally wiped out the population of every other nymph; they seemed to be concentrated in fairly localised areas and there was not very good feed for anything else; so they were the final competitor for the space. I didn't have access to very much literature and I couldn't find anywhere where anybody had written anything about this so I just enquired and it seemed that no one had really observed it before. I have tried to duplicate it myself but haven't been able to do so in experiments in my own home.

CORBET: Is it your opinion, or your observation, that most of these larvae would survive the dry season?

VALLEY: Yes. I'd find them after the rains came and there'd be some water in the pond. There would be quite a number of nymphs. But then the competition for food just wiped most of them out.

CORBET: Rob, would you care to comment on your findings with *Aeshna sitchensis*?

CANNINGS: Yes. Not only *Aeshna sitchensis*, Philip, was in these ponds that I looked at on the west coast of Vancouver Island[39], but a number of other species occurred in the very same locality and under the same rocks. This is a situation in an acid bog within a few hundred metres of the Pacific Ocean and the pond, during this period in August, dried completely up. I doubt if this happens every year; this was after a particularly hot, dry spell and perhaps may only happen one in every two years, I'm not sure. But at any rate, these ponds would be dry for at least two months, I would expect, and maybe even three, until the autumn rains filled them up again. The mud surface of the pond was completely dry - large cracks appeared in the surface mud. There were a few boulders 6 to 10 inches in diameter, embedded in the mud. When turned over these revealed active but very dry larvae of *Aeshna sitchensis*, *A. juncea*, *Leucorrhinia hudsonica* and *Somatochlora albicinta* - these four species at least; and the *Aeshna sitchensis* larva at least was sitting right beside a recently shed exuvia; so it had actually managed to shed its exuvia from the last instar in that position. The surface of the mud under the rock was only very slightly damp but when the larvae were picked up they were very active. That's about all I can add; I really don't know if they would have survived until October or November but I suspect that they would.

LEE: That answers a question which I have often pondered over: How can *Aeshna juncea* survive on Dartmoor in southern England in the acid bogs which generally dry up for at least a few days if not a few weeks every summer? You can find *Aeshna juncea* larvae in these bogs in very small pools even down to only a few feet across. And if they can survive drying up regularly that explains what I have always considered rather puzzling.

KIAUTA: I wonder whether or not this has created the need for an additional category in the list you have shown on the slide[17]: rock pools. We found in Taiwan in small rock pools the larvae of *Planaeschna risi*. I estimate that the pools did not contain more than a few litres of water. They were at least 5 m from the river, higher up, and at a distance of perhaps 20 m from the flowing water. The larvae were nearly adult, in the penultimate stage, and they probably fed there on mosquitoes which were also in the pools and we reared them and obtained adults. I don't know whether this must constitute an ability to survive under dry conditions because I guess such a pool would dry occasionally; or was this a permanent pond? The species was *Planaeschna risi*.

CORBET: Yes: one would like to know whether they could survive the eventual drought. In this connection, if I remember rightly, you told me once that the temperature of the water was very high indeed in those pools. Am I remembering this correctly?

KIAUTA: I estimated that the temperature was at least between 35 and 40°C. It was an extremely hot day, in summer - white rock, no shade anywhere - but I didn't measure the temperature.

CORBET: Of course rock pools would give the larvae no opportunity for burrowing underneath the very hot surface. These pools had a rock bottom did they?

KIAUTA: No. It was a rock pool but there was some detritus or something and leaves in it.

CORBET: So the larvae could have gained some protection?

KIAUTA: But there was no more than, I would say, a maximum of 5 litres of water. Probably less.

ASAHINA: The species which Dr Kiauta is discussing is the species I named[44], and it is a running-torrent species. So it is possible that sometimes the water disappears and the remaining larvae can move to a cooler position. As soon as the water dried up and the water temperature rose then they could move to other cooler places. So they do not qualify for consideration under this topic.

KIAUTA: Would they move over the land?

ASAHINA: I believe so. Even *Epiophlebia* can move over land[45].

MAY: A number of years ago I did some experiments with *Pachydiplax* larvae in response to Minter Westfall's observations that some of the larvae that he was trying to rear had climbed out of the container and dried up and he popped them back in and they swam around. It turned out that *Pachydiplax* had a very poor ability to resist drying: if you didn't allow them access to water, they died fairly rapidly but they were able to survive and transform in 100% humidity. I kept them with a saturated paper towel in a closed container. Furthermore if they were placed in a dry container with something

like a damp paper towel they would immediately make for it; that is, they walked towards it. And I never followed that up but I think it would be amenable to fairly easy examination to see what the ability of many of these larvae is to detect gradients of humidity and to move in the direction of a moisture source, but this would certainly explain, say, Rob Cannings' finding that the larvae aggregated under rocks and that sort of thing and I suspect that that's a fairly common ability, although I don't know of any information to prove it.

CORBET: We might note here Robert Trottier's observations[46] some years ago that the height which *Anax junius* climbed when they emerged depended on the humidity.

WESTFALL: You mentioned the work that Willey did on *Somatochlora semicircularis*[40]. I was out there one summer and saw those things drying up but she took probably about a 2-inch strip of that dried mud from the bottom of the pond and took it back to Chicago and put it out on the banister outside her house where it was freezing and cold - dry as could be. It had been there all winter long and I went there for some meetings and she showed them to me out there and the things were still alive. I just couldn't believe it! But they certainly went a long time; no damp . . . . . just that little strip of mud she had picked up and put on her banister there. And they went right through the winter and didn't die. It was amazing, I couldn't believe it.

BICK: In Chicago?

WESTFALL: Yes, Chicago. Snow and everything. Maybe they got some moisture from the snow.

ASAHINA: Recently I sent an abstract to *Odonatologica* summarising my friend Arai's paper[47]. In midwinter Arai found plenty of larvae of *Anax parthenope julius* and *Lyriothemis pachygastra*, and even *Ceriagrion melanurum*, under the dead leaves of weed in a big swampy place. They were found under dead leaves, not in a wet place; it was almost dry. Some of the larvae, he said, had died but many survived. In this connection do you remember you asked me about my short note[48] . . .

CORBET: Yes, on *Orthetrum triangulare?*

ASAHINA: . . . which was walking on dry land?

PAULSON: For people who don't know the taxonomy of these species: one of the species just mentioned was a zygopteran. That's the first zygopteran, I think, we've heard mentioned here in this connection. I was wondering if drought resistance occurred in that suborder, and the *Ceriagrion* you mentioned is a coenagrionid.

CORBET: I think the view is held[49] that Zygoptera are not, on the whole, resistant to desiccation and that such a capability is much more likely to be found in Anisoptera. Yes, that makes it an interesting observation.

DUNKLE: You made a statement that temporary pool breeders don't resist drying very well. I have found *Gynacantha nervosa* larvae under logs in a dried-up pool and I have often thought that the speed with which the larvae die has a lot to do with the terrestrial predators that advance as the pool dries - ants and spiders - and I think that may be the main thing limiting their survival, rather than burrowing in the mud.

MOORE: I have been working on some experimental ponds for some years. In 1976 we had a very bad drought in Britain and *Lestes sponsa* survived very considerable drought in these ponds. The mud was still just damp and there was no surface water at all and they got through all right. Whereas all the species of *Aeshna* and many other species didn't.

(Side 2 begins.)

CORBET: Eberhard, have you seen the account of drought resistance by larvae in the thesis by Adolf Portmann[50]? Yes? Could you describe the experiments for us?

SCHMIDT: He took it in the lab. and dried it.

CORBET: And how long did it survive?

SCHMIDT: Oh that I don't know. I read it twenty years ago! But I could give you the reference.

CORBET: It seems to me as though drought resistance in larvae, especially of Anisoptera, is probably more common than we've been led to suppose from the literature. Perhaps I might add to that, taking up Sid Dunkle's point: it may be that such larvae are not very often found because they immediately become very vulnerable to predators in a drying-up pool. Are there any other examples that anyone would like to mention for us before we leave this topic?

PAULSON: Just a brief one - and probably this doesn't need belabouring - is found in the experiences of people doing life-history studies. I did a tremendous project with emergence traps in eastern Washington. One pond was temporary and dried up every year, and from it *Aeshna constricta* emerged in good numbers; I have actually already written about this in a manuscript. Very interesting: an *Aeshna* with a one-year life cycle in this pond, and I see now probably what was happening. I don't remember anything from the literature that described this sort of thing, but obviously we shall all need to think about that now.

CORBET: It occurred to me also that this is going to change some of the rather hasty interpretations of life histories in temporary pools because people have tended to assume that larvae there weren't able to survive the dry period.

SCHMIDT: May I make a more general remark? If you look at the habitats which have a rich dragonfly fauna, and I now think mainly of the temperate zones, then we can see that dragonflies are best represented where there are fewest fish. That means that we have a very rich and specific dragonfly fauna in all types of bogs with acid waters, from which fish are excluded because of the acidity; and fish are excluded also from temporary water bodies and we find many strategies for living in such waters. I think that being able to resist drought is one such strategy.

JOHNSON: It occurred to me when Eberhard was speaking that one of the frequently cited disadvantages of using dragonfly larvae as biological control agents for mosquitoes is that mosquitoes prefer temporary habitats whereas dragonflies prefer permanent water. If we've got dragonflies that could be put into temporary habitats and survive to be there the following year that would be quite a remarkable advantage when trying some biological control.

Use of larvae for biological control

CORBET: This might be a good time to mention that there has been one successful test of dragonflies as a biological control agent just recently in Rangoon, Burma[51]. The species used was *Bradinopyga geminata* which breeds in shaded pools and in which the adult aestivates during the dry season. It was found that larvae could be fairly easily obtained in the field from large jars and barrels put out for this purpose, and from small pools. In that locality the *Aedes* were breeding in domestic water containers and transmitting dengue haemorrhagic fever. It was required to control the *Aedes* if possible but very difficult to do so with conventional chemicals. The entomologist who was responsible for this control programme conducted a very good public relations exercise with the local people and persuaded them that it would be a good idea if each household were to put one larva of *Bradinopyga geminata* in their domestic water pot and that this would then suppress the mosquito larvae in the pot. The householders agreed to do this and it resulted in the complete elimination of *Aedes aegypti* larvae and pupae within 4-9 days after putting in the *Bradinopyga* larva, depending on the density of the mosquito larvae beforehand. This was a scientifically conducted experiment which has been reported in the literature and I think this is of great interest to us because, more and more, people who are concerned with biological control as an effective substitute for chemicals are thinking in terms of using agents in inundative release programmes, that is to say, propagating the agents in very large numbers and then releasing them, much as one would a biological insecticide. And it does look as though in certain circumstances dragonflies may be appropriate for this kind of approach. Now if they are, then this focuses once again on the value of developing culture methods for dragonflies because this would open the way for mass propagation of dragonflies in certain circumstances.

Dragonflies as indicators for environmental-impact assessment

CORBET: I'd like to move to another topic now and ask if any of you have any ideas on the use of dragonflies as indicator species in environmental-impact work. What we are thinking of here is the known effect on dragonfly faunas of certain types of human activity - certain types of habitat modification or environmental impact - and also whether we know of any species which are particularly useful as indicators of habitat quality. Tony Watson has drawn our attention to the possibility of using dragonflies in this way in Australia[52,53], because some species at least are sensitive at a fairly early stage in habitat modification, or habitat simplification. Does anyone know of cases which would be relevant to this question?

WASSCHER: Well I think *Calopteryx* is a very good example of this. In Europe *Calopteryx splendens* and *C. virgo* can occur only in places with submerged roots under water. When the brook is clean and suitable in this respect these species can occur there but when there are too many water plants and when the water body is changing, more euryvalent, widely distributed species take their place. So there are two effects of canalization: more water plants grow there and attract more euryvalent species and fewer rheophiles like *Calopteryx*. *Somatochlora metallica* also likes clean brooks, and probably *Aeshna cyanea* too, but it can occur also where there are many more water plants. I think there are good ways of using dragonflies as indicators in running waters. I am working on this at this moment.

CORBET: In this connection I might mention the work of Hansreudi Wildermuth in Switzerland[54,55]. He's been very active in the field of conservation using Odonata as examples. I think largely through his initiative a local Rotary Club has started a community project which entails the building of pools which the whole community has helped to make. Then they've watched the colonisation of these pools, as ecological succession proceeds. Wildermuth and his colleagues have developed detailed protocols that show how to build such a pond, how to put the water palnts in, where the shallows should be, and so on - actually to manufacture a habitat that is suitable for colonisation by Odonata. The obverse of this is to make small modifications in habitats which have been diminished in quality in some way in order to rehabilitate them and make them suitable once more for Odonata. I wonder if anyone here has any examples in mind which we could share, because I am sure that in the future, as conservation grows in importance, we're going to want to make such suggestions from time to time.

MOORE: A remark about the previous point first: quite a lot of work has been done on the toxicity of pesticides to dragonflies and on the whole it looks as if they are not very good indicators. They are not bad indicators but they are nothing like as good as Ephemeroptera. But of course there's no doubt that species like *Ischnura elegans* can take a lot of all sorts of pollutants - much more than other species - and I would add to the list *Platycnemis pennipes*. I've got definite evidence that when you get slight eutrophication and increasing silt and so on, this species disappears from rivers.

WASSCHER: Even earlier than *Calopteryx splendens*?

MOORE: I would say earlier. I would say that it's more sensitive than *Calopteryx splendens*.

WESTFALL: For a number of years the Florida State Department of Health informed me that they were using species of *Argia* in streams in Florida. Each year they would check and if they found these *Argia* larvae (nymphs!) in the water they would say "This stream's fine!" But if they found that the *Argia* were missing then they started taking water samples. They felt that these dragonfly larvae were really good indicators of pollution in the streams of Florida and used them repeatedly for this purpose.

CORBET: Was *Argia* officially recognised as an indicator?

WESTFALL: Yes, it was in a publication too.

MAY: I have read indirectly into an interesting complication of this general question however. I have a colleague who was involved in a general survey of the aquatic fauna in the pine barren streams in New Jersey which typically feature highly acidic, starkly stained, streams. Members of the survey examined three streams in which they considered the watershed to be virtually completely undisturbed, and three in which the watershed had been in some way disturbed. I don't know the details of what pollutants might have been there and so forth, but they found that there was relatively little difference in the odonate fauna. Their general finding was that, if anything, disturbed streams had a more diverse fauna (now let's not exclude the possibility of certain indicator species being eliminated), because in that case they felt that disturbance tended, if anything, to raise the pH (to get back to our previous point). That was their interpretation. Now none of these streams was severely polluted, obviously, but this introduces the notion that a moderate degree of disturbance in some circumstances might have the reverse of the expected effect.

CORBET: There has been some interesting work done by Balinsky[57,58] on the colonisation of Lake Kariba after the dam was formed, and I think Mike, you have an example from Africa in *Nesciothemis nigeriensis* which you think tends to colonise recently man-modified habitats. Is that right?

PARR: Yes, all of the known habitats for *Nesciothemis nigeriensis* are man-made[59], bar one and that is the one in which it was discovered by Robert Gambles[60] and in that case the lake might be taken to be man-made in that, as far as we can tell, it was formed as a result of a land slip which was caused by erosion - gully-erosion - which was presumably due to man's mismanagement of the agricultural land around. But certainly it is very much a coloniser of man-made dams and it is spreading to those dams in the savannah of West Africa wherever the grass that you mentioned, *Echinochloa*, appears[4]. If

the grass doesn't appear, even though the lake may be near to another one where they exist, they don't colonise it. Now I've seen them flying on and around lakes where it looks superficially suitable for them but the grass is not present, and there they don't show any kind of territorial behaviour - they're not reproductively active. They simply fly past and don't stop.

PILON: I am watching a gravel pit in my home town and I have found in it four species which are really thriving. These species include *Sympetrum costiferum* and *Enallagma carunculatum* (this is the first place in Quebec where I have found the latter species in quite a nice population); and you also have there *Chromagrion conditum*. This is a clean gravel pit and the water in it is just coming from underneath because it is about 120 feet deep now. There are mosses and so on, and so I guess those species are well fitted to this habitat which is not rare around a city like Montreal because they are making excavations for road construction and suchlike.

CORBET: Can we make any generalisations about 'first colonisers' among Odonata? What sort of species are they? They are species with a wide ecological valency, that's for sure.

WASSCHER: I think *Ischnura pumilio* is a very good example. In warm summers and in very new, shallow waters it can be very abundant and then it is very widespread, not only at the place itself, but up to a distance away of 10 km it is spreading in the surroundings. I think it must be something of an early coloniser - a species that within a short time multiplies rapidly and then disperses widely in the surroundings or even further afield.

HILTON: A number of years ago, when I was investigating the effect of pulp-mill effluents on aquatic insects inhabiting rivers, I remember from perusing the literature that there was one person[56] who made the comment that in his view there was no such thing as an indicator species. He said something like this: the presence or absence of a species means nothing more than the bald fact that that species is present or absent. So it would be much more useful to think in terms of indicator assemblages rather than indicator species. And in that regard, I am wondering whether there is any indication that the acidification that's taking place due to acid rain is creating indicator assemblages of odonate species that would be similar to what now exists in, for example, acidic *Sphagnum* bogs. I have no information about this. I am asking if anyone has any idea about it.

CORBET: Does anyone know of examples where the effects of acid rain are changing the Odonata fauna?

WASSCHER: In Holland mesotrophic species, like *Sympecma fusca*, are becoming very, very rare[61], I think because of acidification on the one hand, and because of eutrophication due to farming on the other. So mesotrophic waters are becoming very rare in northwestern Europe and such species are disappearing very rapidly. In the years around 1915 *Sympecma fusca* was fairly common but now it's rather rare.

HILTON: In that connection I recall reading an abstract of a paper, I believe it was from Norway, in which the author found that the population of Odonata increased because the acidification caused the fish population to die and therefore there were no predators to reduce the Odonata.

CORBET: Henrikson[62], yes.

SCHMIDT: We should separate pollution itself and its consequences. Many dragonfly species suffer heavily, though indirectly, from the destruction of substrates by pollution. As indicators of specific conditions dragonflies may not be so reliable. For instance, I know a very good pond with a rich dragonfly fauna which is on sands derived from a disused lead mine. I don't know the concentration of lead in the dragonflies, but there the sands must contain a lot of lead; fish are few but the dragonfly fauna is optimal; that means that the dragonfly fauna is not a useful indicator for this heavy metal. And acid rain should be separated from other pollution. The acidity as shown in Norway may not have a severe effect on the dragonfly fauna; indeed it may favour some species.

Adult feeding by gleaning

CORBET: I'd like to change the topic now, looking at the adults for a moment, and to introduce the question of feeding by gleaning in dragonflies. This is a remarkable photograph by Curtis E. Williams from Marlin, Texas which shows a male *Perithemis tenera* over the floating algae which form its oviposition site and territory: it's picking up small water bugs. There's a large bug in the picture also, but the dragonfly is picking up small ones from the surface of the algal mat. It's gleaning by hovering. This type of feeding has been recorded in Odonata sporadically from many years: Tümpel reported it in his *Die Geradflügler Mitteleuropas*[63]. He mentioned there that Zygoptera would pick aphids off leaves (this was somewhere around the turn of the century) and I myself have watched *Pseudagrion nubicum* in Tanzania[64] trying to pick little galls off a leaf which shows that movement *per se* is not a necessary stimulus for gleaners to try and feed on sessile objects. Pseudostigmatids, including *Mecistogaster* and *Megaloprepus*, in tropical South America will try to pluck spiders out of webs[65-67]. These are all examples of feeding by gleaning. I'd like to ask if anyone knows of any other examples - particularly in the Anisoptera, in which this type of feeding appears to be very uncommon?

MAY: Well this is a very casual observation, and I haven't actually seen the prey items taken, but I have noticed a number of aeshnids, including some sort of *Aeshna* on campus this morning, flying in and out of vegetation around, say, a particular bush and I have always more or less assumed that this was what they were doing. I have also seen *Coryphaeschna ingens* in Florida do this on a number of occasions. They seem to fly in and inspect the foliage. As I say, I haven't actually seen them take prey and so I don't know for sure that this is what they're doing, but maybe someone else has better information.

CORBET: I might mention the remarkable record by Geest[68] in 1905 of an *Aeshna grandis* picking up small frogs from the ground!

CANNINGS: Philip, I have two records of species of *Aeshna* picking up stationary prey. One was recorded in that same note[39]: *Aeshna sitchensis* flying low over the dried mud of ponds, picking up dolichopodid flies that were sitting on the mud. The second one occurred just this past month up at Old Crow in the Yukon. We saw an *Aeshna eremita* swoop down and pick up a male *Coenagrion resolutum* off the floating moss on a lake. We subsequently caught the *Aeshna* and were able to identify the prey as *Coenagrion resolutum*. Those are the two records that I have.

GARRISON: Not in the Anisoptera, but in the Zygoptera again: from our study with *Ischnura gemina* earlier this summer we have records of interesting behaviour. While what I would call 'horizontal cycling on the surface of the water, gerrids normally prey on *Ischnura gemina*. But we also have a verified record of a male damselfly taking a young gerrid off the water and consuming it.

PARR: Do you know of the attempted control of the Red Locust *Nomadacris septemfasciata*, by the use of dragonflies - *Diplacodes*?

CORBET: No, I don't know about this.

PARR: This was work which was attempted by Jim Berreen who is at Birmingham now, and he was supported by the Overseas Development Agency I think, or whatever it was called then. I think the venture was a total failure, and an enormous amount of money was spent on it. It was a case where they believed *Diplacodes* was acting in this way and was picking up hoppers of the young locusts from the ground and from the vegetation.

CORBET: Do you know how they went about trying to make this into a control venture after having made that observation?

PARR: No, I think you'll find that the whole thing is a total mess and you probably won't get any details. I've tried, and I can't get much out of them.

CORBET: Well, that's worth remarking upon because in 1967 a very interesting and extensive report appeared by C.W. Stortenbeker[69] .

PARR: Yes, it's related to that . . .

CORBET: . . . I see, and he found that asilids (robber-flies) and certain species of temporary-pool-breeding Anisoptera were imposing a very heavy mortality on Red Locust hoppers in southwest Tanzania. This was a descriptive, and quantitative, observation of what went on in the field, showing how heavy this mortality was, and it sounds to me as though somebody has tried to take that further and manipulate the situation using *Diplacodes*.

PARR: Asilids and what?

CORBET: Temporary-pool-breeding Anisoptera, particularly *Hemianax ephippiger*.

PARR: It doesn't really add up to *Diplacodes* at all. I think they spent something like £13,000 on that project and they got nothing out of it.

CORBET: It would have been much better spent on S.I.O.!

MAY: I recall one other observation, and one non-observation. The observation again is not mine, but when I was on Barro Colorado Island there was a student there from Seattle named Tom Abrahams who was observing feeding behaviour in some of the forest damselflies. And he was actually looking at species of *Argia* which did a fair amount of gleaning, as I recall his reporting it to me verbally. There were two species of *Argia* that were quite commonly encountered: one was *A. oculata*. I can't remember the other one. They were encountered frequently in the forest, and in his observations Tom Abrahams found that they gleaned fairly often. The non-observation is on Protodonata and was suggested to me by Frank Carpenter. I talked to him in connection with my efforts to reconstruct thermoregulation of Protodonata[70] and he suggested that they may well have fed on cockroaches, which of course constituted another extremely abundant group of insects at the time, quite possibly by gleaning them from surfaces rather than waiting for them to fly, because cockroaches presumably were not very good fliers then, just as they are not now.

ROBERTSON: I have, in the last couple of months, been watching *Ischnura* and *Enallagma* and I have noticed a lot of gleaning by the adults, both females and males, who go up one blade of grass and down the next one and up the next one and so on. They'll do the same thing on reeds or anything that's available like that. And you can see them picking up insects off the surface and if there's, say, a scar on the blade they will repeatedly try to pick that up and then give up. My other observation is of *Ischnura verticalis* females who will pick up freshly emerged *Lestes* of any species and eat them. The *Lestes* are often twice the size of the *Ischnura verticalis* females which are pretty motionless when they are picked up.

CORBET: Incidentally, on the subject of culturing Odonata, I remember that Clifford Johnson[26] in his successful attempt to culture *Ischnura* was using fruit-flies and the *Ischnura* would take them off the wall of the cage.

PAULSON: I would like to turn the question around and ask how many people have seen coenagrionids and small hovering damselflies feed in mid-air, because, like Hugh, I've watched them for hours and about all I ever see them doing is gleaning. I was going to ask a question about *Argia* which Mike May may or may not have answered here. I don't think *Argia* have the ability to hover very well, or at least they don't seem to do it when you see them on territory. And I've been racking my brains: Do they hover or don't they? If someone wants to answer that, definitively, go ahead, but I've always thought

that they probably couldn't feed that way because their flight seems to be sort of 'fast forward' and it may be that they change their behaviour when they are away from water. I'm not sure about that, but mostly it's the things that hover very well that seem to have this ability to glean because they can move very slowly and grab something; and, as an aside, that's my idea of why damselflies have widely spread innocent eyes, because that perhaps gives them more depth perception and allows them to feed more successfully. A dragonfly can just shoot through the air, aim at something and hit it, but a damselfly doesn't want to fly too fast at a trunk of tree or something like that.

ROBERTSON: I would just follow up on that by saying that certainly the ones that I've seen gleaning also spend a lot of time catching insects in the air, especially the *Ischnura verticalis*. They're good at both kinds of feeding.

CORBET: Yes, in that connection I might mention a paper by McCafferty[71]. He watched *Hetaerina* in the evening, a settled swarm of males, if one can talk of that, on a rock near a stream, picking off mayflies that were swarming nearby. They'd make quick sallies out into the swarm and back onto the rock; so these were feeding in mid-air.

DUNKLE: My impression has always been that gleaning is quite a common behaviour in Anisoptera because down in the southeast I've seen many aeshnids such as *Coryphaeschna ingens*, *Nasiaeschna* and *Epiaeschna*, going up tree trunks and branches and also *Neurocordulia* and *Somatochlora georgiana*. It may function in either of two ways: they might pick up stationary prey or they might flush prey, like gnats, from below a surface and then catch the insects as they leave.

CORBET: There are one or two cases that your remarks put me in mind of where Anisoptera have been observed hovering in front of vegetation and the consequence of this is that small insects will fly out[72,73]. They'll be disturbed or blown out and of course one doesn't know whether this is a linked behaviour pattern - whether they're actually flushing them, so to speak - or whether it just happens as a consequence of their proximity, but in one or two cases it looks very much as though this is a type of flushing behaviour that the Anisoptera engage in.

DUNKLE: Yes: it's easy to see how natural selection could select for those dragonflies that closely approach the substrate and flush prey.

CORBET: Dr Higashi, in your work on feeding of *Calopteryx cornelia*[74] did you ever see the *Calopteryx* picking prey up from the ground? You report many times that they flew up into the air and caught the prey and came back to the perch. Did you also see them pick up prey from the ground?

HIGASHI: I did not see them pick up prey.

CORBET: Are there any more observations on sessile feeding or gleaning in Anisoptera?

Adaptive significance of synchronous emergence

CORBET: One point that came up today - Dan Johnson spoke about it - was the adaptive significance of synchronous emergence. Now, it's been suggested in the past[75] as well as today that one adaptive consequence of synchronous emergence would be that relatively short-lived adult insects would be more likely to meet - that is, the sexes would be more likely to meet in time - but that doesn't of course help us very much with the species that don't have a synchronous emergence unless we find that they live much longer, which may well be the case. I wonder if anyone has any suggestions to make as to what the ecological consequence of synchronous emergence might be that might be of adaptive value to dragonflies.

GARRISON: Well one is that there is something about there being strength in numbers as well of course as getting together to have an optimum chance of encountering mates.

CORBET: A thought occurred to me recently when we were talking about the benefit to the female of multiple mating which we often discuss nowadays. We ask why it should be desirable for a female to mate again if we know that a single insemination is adequate to fertilise all the eggs she will ever lay. It occurred to me that in species that have a non-synchronised emergence in which the emergence curve is a rather flat, normal curve, a female mating early in the flying season would be mating with a male that hadn't had to compete hard for a space at the rendezvous. He would therefore not necessarily be a vigorous or competitive male. It might therefore be in her interests - or the interests of her offspring - on these grounds alone, to mate again when competition was more severe and when she was likely on that account to mate with a more vigorous male. This wouldn't apply in spring species with an early synchronised emergence. With that thought in mind, do we know of any cases which might correlate with this difference related to the emergence curve?

SCHMIDT: I don't know whether it is appropriate to seek for an explanation of this kind. The successful *Anax imperator* is very synchronised and has a long life-span. Again *Leucorrhinia rubicunda* is rather well synchronized, and *L. dubia* is not, but adults live about the same time I think. One advantage may be that the spring species which are mostly well synchronised are exposed to predation from birds and if the emergence takes place on only a few days birds from far away cannot learn by searching for them because at that time the birds have young to be fed. In the case of summer species, birds only have to find food for themselves so that feeding - and that means searching for freshly emerged dragonflies - is less intense in the summer than in the spring.

CORBET: I am thinking of the work that Orians[76] has done on the food of the Yellow-headed Blackbird. If I remember rightly (perhaps you can confirm this Dennis) most of the food of the Yellow-headed Blackbird in marshes comprised species like *Enallagma* which are summer species and have an extended emergence period, which would be consistent with the point you are making. So the birds would have ample time to learn where this source of food was each season.

SCHMIDT: I can only remember the sparrows at Bonn feeding on *Erythromma viridulum*.

CORBET: I can remember blackbirds, the European Blackbird, taking a very heavy toll of emerging *Anax imperator* which has a very synchronised emergence, or did in that habitat, but this was very largely because they were a few cold days which slowed everything up and also made it difficult for the adult dragonflies to fly from the emergence site early in the morning[77].

ROBERTSON: I think a point should be noted with respect to synchronous emergence. If you look at one species, fine: it has a synchronous emergence in one spot and the predators can't get hold of it. But if you look at all the species that emerge at the pond you may get a whole lot of synchronous ones like this and then whoever's the predator is set up, just sitting there waiting for everything to come out. So, if you look at the whole spectrum of what's coming out of the pond, I'm not so sure that synchrony will really help an individual species that much.

CORBET: Only if it's the first one.

ROBERTSON: Even then I'm not too sure: birds live more than one year.

PILON: We had one experience this summer at a station with one of the species I mentioned. There were starlings all over the place; and at home for three years now I have been observing swallows: they're feeding their chicks essentially with young *Sympetrum* - the only thing that they're bringing back to the nest. I was sitting just below watching them! They are specialisers.

CORBET: People in Winnipeg have recently been encouraged to build nesting boxes for Purple Martins in their back gardens. I think the encouragement has come principally from the makers of these nesting boxes and people have been told that if they do this they will be rid of mosquitoes in the garden, but someone told me when I was there last week that most of the food brought back by the Purple Martins was dragonflies!

PAULSON: Just to add again to Eberhard's hypothesis, which I think is a very good one; even though birds learn that predator-satiation is a very real concept in that the larger the number that can emerge at once, the smaller the probability that an individual dragonfly will be taken by a predator, so synchrony, if it indeed occurred right at the time of maximum bird young in the nest (which would be very easy to test), could be a very good hypothesis indeed, I think.

CORBET: Whether the birds had learned about it or not?

PAULSON: Right. Simply because they're aren't enough of them.

TENNESSEN: Might it not be possible that synchronised early spring species are rather short-lived? I'm thinking of mayflies in which, for example, *Hexagenia* in our area emerges synchronously and they only live for one or two days and it's important for an individual to emerge with the group in order to find a mate. I was wondering if this might not have some significance in dragonflies too. Maybe the summer species with a long emergence period are more long lived.

CORBET: It was suggested[75]at one time, on the basis of a very few records, that spring species live for a shorter time in the adult stage than do summer species. But as more precise information on the length of life has accumulated I don't think that idea has held up. Someone may wish to correct me.

PARR: I don't think there's any difference in the length of life of *Pyrrhosoma* compared with that of *Ischnura elegans*. And on this general topic I think you have to be very careful about the possible significance of any kind of mass emergence and predation for these insects. Seeing large numbers, apparently large numbers, of *Gomphus (vulgatissimus)* being taken on the banks of the River Thames last year, you could quite easily jump to the conclusion that they were a bad influence on the whole population of *Gomphus*. But of course it might have been a good one. We just don't know, do we? We have no idea and we can't really say what proportion of the population are being taken - not without a lot of work.

CANNINGS: We have made some observations on several species of *Lestes* in saline ponds[30]. Synchrony of emergence in *Lestes disjunctus*, *L. congener* etc. seems to be more prevalent in ponds where these species are sympatric. In other words, where you have the species living together, they tend to isolate themselves temporally; presumably this reduces competition between the species. *Lestes congener* is able to survive high salinities; and in the same lake series where it's found in lakes that have salinities over 10,000 micromoles where *disjunctus* and *dryas* cannot survive, it emerges completely asynchronously through a much longer period than it takes to emerge in ponds nearby where the other species occur with it. This is a very simple observation but it seems to me perhaps that the synchrony in this case is an adaptation that separates the flying seasons of the species in that area.

CORBET: It's difficult to see how it could be implemented, isn't it - how the response to this situation could be translated into synchronous emergence?

CANNINGS: It just seems so much of a coincidence that exactly the same thing happened in a group of chironomids that I was studying: exactly the same situation happened in exactly the same lakes, where asynchrony in emergence was noticed in the species that lived allopatrically from its close relatives.

DEACON: I was wondering if synchronous emergence could not just be an artefact of an adaptation to a temperate environment. Is there any incidence of synchronous emergence in the tropics? Because the same conditions would hold for the tropics; if this is an adaptation for inundation, then we should have examples of synchronous emergence in the tropics as well.

CORBET: Yes. There are quite a number of examples of synchronous emergence that I know of among aquatic insects. They don't include dragonflies, but chironomids, chaoborids, and particularly mayflies, can show synchronous emergence of great precision in a habitat in the tropics which hardly changes at all right through the year, like a very large tropical lake on the equator[78]. But living alongside them are many more species that don't have a synchronous emergence and I'm left without any kind of hypothesis to handle this.

PAULSON: In Costa Rica where I lived for over a year and monitored odonate populations, there were a number of species of odonates that had total flight seasons no longer than some of our highly synchronised dragonflies up here. It was in the beginning of the rainy season that they appeared. Like many tropical dragonflies, they are not as abundant as some temperate forms, but they appeared, flourished and disappeared within a month and a half.

CORBET: Do you know anything about their life history? What happened during the rest of the year?

PAULSON: I have no idea what the larvae are doing. They're stream species, all of them, in tropical forest streams.

PARR: I think by inference we could include Chutter's example in which he analysed the life history of *Pseudagrion salisburyense*[79]. This would fall into the category of a synchronised emergence. He found it had five generations in a year. The site is not exactly in the tropics, but it's sub-tropical and from his graphs the members of the population had to be pretty well synchronised; they couldn't be spread out over a big interval of time. Certainly not much more than a month at the most.

JOHNSON: There has been no discussion yet of the potential among the larvae for deriving some benefit either from synchronous or asynchronous oviposition, and the hatching which presumably follows, or from the potential for larval interactions to result in synchrony. I don't know that it happens - I'm just getting a grasp of larval interactions - but the potential for the larger members of a population to consume the smaller members will certainly cause contraction in the total number of instars that exists as you go through time, and there would be a real disadvantage associated with being a late-emerging individual if your offspring were going to be eaten by the early-emerging individuals. If that turns out to be an important interaction within species then I could see a potential explanation for synchrony. Eberhard probably disagrees!

SCHMIDT: No. I have in mind to mention Ulf Norling's point (in this Symposium): that the strategy for overwintering may result in synchronisation.

PRITCHARD: I was just going to comment on behalf of Curtis Nimz in relation to Dan's last statement, because this is exactly the subject of Curtis' Ph.D. work. So if you can wait for a couple of years we'll have all the answers!

PAULSON: Just to add to what I said about the tropical stream odonates that were highly synchronised, I'd already forgotten my work in Florida. In southern Florida there are several species of pond-breeding anisopterans that are highly synchronised and have a very strict one-year life-cycle, staying in the same instar for a considerable time, emerging over a short period and being present for about two months[2]; and so again low temperatures clearly aren't something that are synchronising this population from either an ultimate or a proximate point of view. So something interesting is going on there that's independent of adaptations to high latitudes.

LEGGOTT: Is there any pattern possibly between the overall abundance in terms of population size and synchronous *versus* asynchronous breeding? In other words may it be advantageous for populations which are smaller, for species which exist in low densities or in isolated small habitats, to be synchronised in their breeding unlike those in which the population size is large ...? I don't know if there is such a correlation, or whether anyone's looked at this.

CORBET: Well I'm not sure whether it would be justified to take the example from Back Lake that Ken gave us (in this Symposium), but if it is then there are very good data there for looking at this question and as I recall there wasn't any correlation between abundance and synchrony. Am I right, Ken?

DEACON: Yes.

CORBET: Incidentally, in the study I undertook in Lake Victoria in Africa I was looking at this very point in a number of aquatic insect groups and I couldn't find any correlation between synchronous emergence and abundance although I firmly expected to when I began.

CANNINGS: In the example I just mentioned of *Lestes* in this saline lake series[30], where in the more saline lake *Lestes congener* emerged asynchronously, the population was much larger in that case. Exactly the same thing was true with the chironomid species that we looked at there. Along the same line and with regard to what Dan Johnson mentioned, it seems to me that in *Lestes*, where the larval development is very rapid - it is completed in only two or three months - and where you have two or three congeneric species developing in the same pond, if there is competition, it might result in a more synchronous development of each individual species, separating them to reduce competition. And this might be one means by which the three species could emerge synchronously at different times of the summer. Whereas in a lake where *Lestes congener* lives by itself there is little competition from any other dragonflies and the emergence is very, very asynchronous. It's just an idea that I have.

GARRISON: In relation to the question that was posed earlier about the correlation between small populations and synchrony, at least with *Ischnura gemina*, an alternate strategy occurs where you have populations which are quite small and have an effective breeding size of less than a hundred and yet the species adopts the strategy of having a very long life span and multiple-matings, thus ensuring widespread variability; essentially this produces a panmictic population where all the matings can be unique. So it doesn't have to happen that way.

PAULSON: I guess it hasn't been mentioned that several people have presented evidence that they thought was at least suggestive of avoidance of competition in larvae by synchrony being effected at different times and in different instars. Two such people are Art Benke, who worked in the southeast on libellulids and corduliids[80], and Janet Kime, who studied aeshnids in the northwest[81]. It'll surely prove to be a different reason for every species probably.

Cohort-splitting and diapause in larval populations

CORBET: Could we look now at the question of cohort-splitting which came up today? Does anyone have anything to add to this question? I would think it's of great importance to a larval population if cohort-splitting takes place. Possibilities that were mentioned were that the thermal environment of the egg might dictate which of several growth types the hatching larva might embark upon. There is also the possibility that, depending on when a larva hatched from the egg, it might or might not 'catch the bus', so to speak, during the seasonal progression of photoperiod. It might be just too late and be put into long-day diapause and thus see its more precocious contemporaries zooming off on another growth curve and being held up itself for another year. These are two ways in which we thought the cohort-splitting might occur. I am talking about a discontinuity here, not simply a range of variable growth rates: a splitting that would result in a major difference in times of emergence of possibly up to one year. Does anyone have anything to contribute to this question, which seems to me of great importance in our understanding of larval population?

JOHNSON: I don't have data on this yet but, listening to Ulf Norling's talk this morning, it really intrigued me that what I was interpreting yesterday as fairly subtle effects on the weight of individual larvae not affecting their survival could very well turn into fairly dramatic effects in terms of their development time if it happened at the right time of year and at the right position relative to this critical size. It's certainly something I'm going to look for. I don't know whether I'll find it or not. In my lake I have not looked in enough detail at individual species and populations really to say whether there is some fraction of the cohort that is being split or not, but I have the motivation to do that now. I'll go back home and look and see what I can find.

PILON: In our rearing of the five species of Zygoptera that we have, we notice that the small larvae (smaller than the group) that are in the middle of their life-cycle, let's say in the 3rd, 4th, 5th and 6th instars, pick up extra instars and then they will not only catch the others up but become bigger than the ones who are developing normally. It seems to be linked to the condition to which eggs are submitted at the very geginning. But we still need further research on that. I am not willing to hypothesise too much.

CORBET: The impression I get from having read Schaller's work[82,83] and your contributions, Jean-Guy[84,85], is that we're still not in a position to be sure that the thermal environment of the egg determines the rate of growth afterwards. Would you agree with that?

PILON: Yes, I would agree with you.

CORBET: On the question of additional instars, I think several people have had the experience that if a larva is subjected to conditions that induce a long-day diapause, such that temperature is high but growth rate is suppressed (as Ulf was describing for us today) it may moult but hardly grow at all. Now in this case its total number of instars might be quite high but this would not be associated with a corresponding increase in size.

PILON: We didn't observe that, that's for sure.

CORBET: You have observed that Ken, haven't you, in *Leucorrhinia intacta?*

PILON: We've been working with *Enallagma.*

CORBET: Yes certainly. It needn't necessarily apply to many species. But you've seen that in the summer haven't you Ken?

DEACON: I've seen that in *Xanthocnemis* and in *Austrolestes* in New Zealand[86], both Zygoptera.

(Side 3 begins.)

LUTZ: Yes. In raising *Tetragoneuria* some years ago, just raising them from the egg to adulthood, we found supernumerary moults, just based on the constant conditions, around about instars 8, 9 and 10.

CORBET: Were these in larvae which appeared to have their growth delayed, do you remember?

LUTZ: I don't really remember, Phil. Some of these nymphs we were simply raising to try to get some idea about the number of instars, and I don't remember the conditions under which they added supernumerary moults. But it's very clear that they did - you'd see it; you'd know it.

CORBET: In my laboratory we've recently found that when *Pyrrhosoma nymphula*, a western European species, was in a long-day diapause in summer in the penultimate instar it would moult twice in this instar, hardly growing at all, and finish up as a slightly larger larva (for its instar) at the end of it.

LUTZ: I would add that we also saw some consolidation of instars. An animal would appear to be in instar 9 and then would moult and would clearly have skipped instar 10 and be in instar 11 - at least the small end of that instar's range. Very clearly it just consolidated.

CORBET: A very large increase in size? I think that's pretty unusual.

PICKUP: I've noticed also in *Coenagrion puella* that the effect of a diapause on the percentage head-width increase between one moult and another is very unpredictable.

CORBET: The effect of diapause?

PICKUP: Yes. When an animal goes into diapause I've found that you can sometimes get a very small increase, and sometimes a very large increase. It's very unpredictable.

CORBET: When does diapause occur in *Coenagrion puella* please?

PICKUP: In virtually all of instars 8 to 11 but not in the final instar.

CORBET: And how do you detect it? I mean how do you know that this or that larva is in diapause?

PICKUP: By measuring the feeding rate. The feeding rate of a larva about to enter diapause typically starts off at the rate that is normal for that instar. And then after a period of say ten days (it's very variable but usually occurs when the larva is well into the instar) the feeding rate drops to the tick-over level and then it can continue very slowly. And then when the animal actually does moult the feeding rate is usually lifted up just a little bit before it actually moults. So it suggests that the animal is diapausing towards the end of its instar. But it's not totally predictable.

Diagnosis of diapause in larvae

CORBET: This question has brought us to the next topic I was going to raise and that is: How does one recognise when a larva is in diapause? Do we have any criteria we can use? We have a larva in the hand and we want to know whether it is in diapause or not. Jonathan has told us that one way might be to check on its feeding rate, if we already have a base-line for comparison. Are there any other criteria that exist which allow us to tell whether a larva is in diapause or not?

PILON: Based on our rearings, it's impossible to say if it's in diapause or not. Except that it's taking a longer time. That's all.

CORBET: But the feeding rate doesn't seem to change?

PILON: Yes, it's changing; it's going down.

DEACON: Continuing on with the feeding rate: Jonathan do you have an idea of what sort of reduction you did obtain with the feeding rate?

PICKUP: It varies according to temperature: 12 to about 20% of the maximum level.

DEACON: I did some preliminary studies on this when I was working on *Xanthocnemis* in New Zealand, and I found that the feeding rate of the diapausing individuals was reduced by half compared with the normal rate. So there is a noticeable, reduction in the feeding rate.

CORBET: Ulf, could you tell us if you've noticed that the feeding rate drops in larvae that are in diapause - say in the long-day diapause?

NORLING: I have never looked at feeding rate.

CORBET: I can confirm that in *Pyrrhosoma nymphula* it does drop, though I haven't got quantitative evidence for this. But every day we record whether larvae fed *ad libitum* need more food or not and the ones that are in diapause hardly ever need more food. They don't ear nearly as much as the others.

LUTZ: If we are going to define diapause in terms of a reduction in food consumption, how then does it differ from quiescence or hibernation or another form of relative inactivity? I suggest that diapause cannot be so easily defined, at least in the beasts I work with[87].

CORBET: In answer to your first question: I think some people would say that a distinction between diapause (or whatever else we want to call this kind of delayed development) and quiescence is that the delayed development characteristic of diapause will occur even though the physical conditions for growth are permissive, whereas quiescence is a *direct* response to conditions that are unsuitable for further development. This can be checked by returning the animals to permissive conditions and finding that the quiescence stops. I think that would be a useful distinction between 'diapause' (or whatever it is) and 'quiescence'. But I think that probably most people would not want to regard diapause as necessarily a similar phenomenon in every insect that shows it, and they are probably rather dissatisfied with the one term being used very widely. Are there any comments on the use of the term 'diapause' or on what this concept means to us in the Odonata? We have diapause in the adult as well of course - in the form of aestivation as found in *Sympecma, Aciagrion* and *Indolestes*[64], probably in some of the tropical *Lestes*[64], and in *Bradinopyga*[88].

DEACON: In trying to identify characteristics of larvae in diapause we have identified feeding rate. Another obvious characteristic is that of prolonged development in this stage where a particular instar takes much longer under the same conditions than in another individual that is held at these same conditions but collected at another time of year. So that you have this individual which is in diapause and which may show a rate of development two or three times less than that found in a normally developing individual. Aside from the feeding and the duration or the rate of development, I have been interested in metabolic rate; but I've never come across a satisfactory means of measuring respiration to see if there is a difference between diapause and non-diapause individuals. I found that in some experiments that I did there was no difference between the two groups, but I attributed that to the type of respirometer that I was using. The diapause individuals and the non-diapause individuals seemed to be reacting in the same way to the unusual condition of being shaken around in the respirometer; so they both achieved the same rate of respiration. Maybe somebody has some other criteria to suggest besides the feeding rate and the duration.

PAULSON: I've worked with larvae and had some of them die because they were in insufficient water, and I wonder if you could measure respiratory rate indirectly by the volume of water needed by a larva to survive. Obviously you would be sacrificing a certain number of them but I wonder if you could look at a LD50 for water volume or something like that and get a really good idea of their respiratory rate.

DEACON: I suspect there are means of measuring the respiration rate but I haven't had the facilities to do this. There is the closed-bottle technique but you are going to run into the problem of perturbation: when you handle the larvae they are going to remain excited for a certain amount of time. If you are using the closed-bottle technique this is going to affect the results as well. But there may be a settling-down period as far as respiration is concerned. I believe there have been some experiments in which the metabolic rate of an aestivating desert snail could be increased an hundredfold simply by tapping the snail. This made it suddenly 'come back to life again'. So if you are handling the dragonfly larvae, you may produce the same sort of unusual response.

CORBET: We are getting rather near the end of our time now: we're scheduled to stop at 10 o'clock. I've got two more topics which we may not want to spend many minutes on but which I'd like to include since we do have a bit of time, and I hope I'll leave a few extra minutes in case anyone would like to suggest anything else.

Maiden flight of Pantala flavescens

CORBET: First I'd like to ask whether anyone has witnessed the maiden flight - the first adult flight after emergence - of *Pantala flavescens*. There are two observations that come close to doing this, one is from Japan[89] and the other is from central Florida[90]. In both cases the newly emerged adults flew away from water but were seen during the next few days feeding in swarms fairly close to the emergence site. Now of course it wasn't known that they were exactly the same adults but this was a reasonable inference I think. Then after a few days - two or three days - they all disappeared suddenly, not to return. That's the only information that I know of for this very widespread tropical dragonfly which migrates with the rain fronts in the Inter-Tropical Convergence Zone. I much regret this, because I suspect that observing the maiden flight may tell us something important about the way this species starts a migration. I wonder if anyone has seen anything which might bear on this question?

Causes of damage to cerci of adult aeshnids

CORBET: The other question is: How do the cerci of male and female aeshnids get damaged, as they so frequently do? The cerci of females very often get damaged but so also do the cerci of males sometimes. It's been suggested that the cerci of female aeshnids may get damaged during copulation.

PAULSON: I'd just like to ask the further question of how the cerci function in female aeshnids. Does anybody have any ideas on that? Usually when you see them ovipositing the cerci are held at a fairly substantial angle, often even an acute angle, directed back toward the abdomen; so it's not as if they're probing down the branch or in a tactile way. They seem to be kept very much out of the way when females are ovipositing and I think that's a fascinating thing. As Philip said, not only are they very often damaged but in many aeshnids that have long cerci it's a common experience to find that these are virtually always broken off after they've been around for a while. There is obviously an abscission zone because they are usually broken off at the same place. So it's as if they are meant to be broken off - as if they may even have a signal function.

CORBET: Sid, you used this character for age-determination[91], didn't you, at one time? Did you have any thoughts on this question at the time?

DUNKLE: I have speculated, just as Dennis mentioned, that intact cerci might represent an important feature in the appearance of an immature female - for example in *Coryphaeschna ingens*, where the long streaming cerci have a very distinctive appearance. But then I had no information as to whether young females in *C. ingens* mate as frequently as do old females.

CORBET: This is very interesting. What comes to my mind are independent observations by Lieftinck[92] on *Oligoaeschna* and Lindley[93] on the libellulid *Zygonychidium*. In both cases these observers commented on the conspicuous nature of the long cerci in adults flying overhead. They remarked that it is easy to pick out these particular adults (among mixed-species groups) because they have long cerci. And I think Lindley also added that perhaps other *Zygonychidium* are recognising each other by this feature. If these cerci tended to get broken at the first copulation then this would offer a way of recognising unmated females. We might mention here also the intriguing dimorphism in the length of cerci in *Boyeria irene* which was noted by Wenger[94] many years ago. One feels that this ought to give us a clue to the function of cerci.

MAY: Is there any actual information as to when these cerci are broken, if indeed they are? Has it been observed that they are broken during copulation?

CORBET: I know of no such observation.

MAY: Maybe they act as the tails of hairstreaks do to fish. At least in the case of aeshnids, many of the females oviposit with the end of the abdomen beneath the water. Maybe it is at least conceivable that very long cerci divert any potential attacker from the vital parts of the abdomen.

CORBET: Perhaps we can derive a clue from the fact that, although the cerci are very often found to be broken in females of many aeshnid genera, most females with mating marks in certain genera have *intact* cerci: *Basiaeschna, Anax, Epiaeschna* are examples[91]. So one cannot generalise in the aeshnids.

Would anyone like to raise any more points in our closing minutes? In that case I thank you very much for your participation.

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 superscript designations in the text.

1. JURZITZA, G., 1974. *Odonatologica* 3: 221-230.

2. PAULSON, D.R., 1966. *The dragonflies (Odonata:Anisoptera) of southern Florida.* Ph.D. thesis, Univ. Miami, Florida.

3. GODLEY, J.S., 1980. *Ecol. Monogr.* 50: 411-436.

4. PARR, M.J., 1977. *Odonatologica* 6: 271-276.

5. HASSAN, A.T., 1981. *Zool. J. Linn. Soc.* 72: 289-296.

6. SCHMIDT, E., 1977. *Verh. des Sechsten Internat. Symp. über Entomofaunistik in Mitteleuropa 1975, The Hague:* 27-42.

7. POOSCH, H., 1973. *Natur und Naturschutz Mecklenburg* 11: 5-14.

8. SONEHARA, I., 1980. Personal communication.

9. GARDNER, A.E., 1950. *Ent. Gaz., Lond.* 1: 128-138.

10. DUMONT, H.J., 1971. *Bull. Ann. Soc. R. Belg. Ent.* 107: 211-235.

11. DREYER, W., 1978. *Odonatologica* 7: 309-322.

12. WAAGE, J.K., 1978. *Odonatologica* 7: 77-88.

13. WILLIAMS, F.X., 1936. *Proc. Hawaii. ent. Soc.* 9: 273-349.

14. MACHADO, A.B.M., 1977. *Abstr. 4 Internat. Symp. Odonatology, Gainesville, Florida:* 11.

15. SHERK, T., 1981. Personal communication.

16. MEINERTZHAGEN, I.A., R. MENZEL & G. KAHLE, 1983. *J. comp. Physiol.* (A) 151: 295-310.

17. CORBET, P.S., 1983. Odonata in phytotelmata. In *Phytotelmata: terrestrial plants as hosts for aquatic insect communities,* J.H. FRANK & L.P. LOUNIBOS (eds), pp. 29-54. Plexus, Marlton, New Jersey. (Table 3 on p. 39.)

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

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

20. MACHADO, A.B.M. & A. MARTINEZ, 1982. *Odonatologica* 11: 15-22.

21. DEMARMELS, J.DE, 1982. *Bol. Ent. Venezolana* N.S. 2: 94-101; and *in litt.*

22. CALVERT, P.P., 1911. *Ent. News* 22: 402-411.

23. WESTFALL, M.J., 1964. *Quart. J. Florida Acad. Sci.* 27: 67-85.

24. LAESSLE, A.M., 1961. *Ecology* 42: 499-517.

25. PINHEY, E., 1966. *Arnoldia (Rhodesia)* 2(33): 1-24.

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

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

28. STEINER, H., 1948. *Zool. Jb. Jena (Syst.)* 78: 65-96.

29. SCHMIDT, E., 1964. *Faunistische Mitteilungen aus NordDeutschland* 2: 197-203.

30. CANNINGS, R.A., S.G. CANNINGS & R.J. CANNINGS, 1980. *Odonatologica* 9: 19-28.

31. KELTS, L.J., 1977. *Ecology of two tidal marsh insects* Trichocorixa verticalis *(Hemiptera) and* Erythrodiplax berenice *(Odonata), in New Hampshire.* Ph.D. thesis, Univ. New Hampshire.

32. BUXTON, P.A., 1923. *Animal life in deserts.* Arnold, London.

33. LIEFTINCK, M.A., 1976. *Cah. ORSTOM Sér. Hydrobiol.* 10: 165-200.

34. WATSON, J.A.L., 1982. *J. Aust. ent. Soc.* 21: 309-311.

35. WINSTANLEY, W.J., 1982. *In litt.*

36. DUMONT, H.J., 1982. *Palaeoecology of Africa* 14: 1-24.

37. ROBERT, P.-A., 1958. *Les libellules (odonates).* Delachaux & Niestlé, Neuchâtel.

38. WATSON, J.A.L., 1981. Odonata (dragonflies and damselflies). In *Ecological biogeography of Australia,* A. KEAST (ed.) pp. 1141-1167. Junk, The Hague.

39. CANNINGS, R.A., 1982. *Odonatologica* 11: 219-223.

40. WILLEY, R.L. & H.O. EILER, 1972. *Am. Midl. Nat.* 87: 215-221.

41. DUNSON, W.A., 1980. *Physiol. Zool.* 53: 445-452.

42. TINKHAM, E.R., 1949. *Ent. News* 60: 15-17.

43. LIEN, J.C. & K. MATSUKI, 1979. *Nature and Insects* 14: 57-60.

44. ASAHINA, S., 1957. *Shin-Konchu* 13(8): 49-55.

45. EDA, S., 1964. *Tombo* 7: 13-16.

46. TROTTIER, R., 1973. *Can. Ent.* 105: 975-984.

47. ARAI, Y., 1983. *Gekkan-Mushi* 1983 (143): 17-22. (OA 4091.)

48. ASAHINA, S., 1981. *Tombo* 24: 43.

49. ZAIKA, V.V., 1977. *Zool. Zh.* 56: 848-854. (OA 1825.)

50. PORTMANN, A., 1921. *Die Odonaten der Umgebung von Basel.* Inaug. Dissertation, Basel, Lorrach.

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

52. ARTHINGTON, A.H. & J.A.L. WATSON, 1982. *Aust. J. Mar. Freshwater Res.* 33: 77-88.

53. WATSON, J.A.L., A.H. ARTHINGTON & D.L. CONRICK, 1982. *Aust. J. Mar. Freshwater Res.* 33: 517-528.

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

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

56. ROBACK, S.S., 1974. Insects (Arthropoda: Insecta). In *Pollution ecology of freshwater invertebrates,* C.W. HART & S.L.H. Fuller (eds), pp. 313-376. Academic Press, New York.

57. BALINSKY, B.I. & G.V. JAMES, 1960. *S. Afr. J. Sci.* 56: 101-104.

58. BALINSKY, B.I., 1967. *J. ent. Soc. S. Afr.* 29: 3-22.

59. PARR, M.J. & M. PARR, 1974. *Odonatologica* 3: 21-47.

60. GAMBLES, R.M., 1966. *Entomologist* 99: 161-173.

61. GEIJSKES, D.C. & J. van TOL, 1983. *De libellen van Nederland.* Koninklijke Nederlandse Natuurhistorische Vereniging, Hoogwoud.

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

63. TÜMPEL, R., 1899. *Die Geradflügler Mitteleuropas.* Perthes, Gotha.

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

65. BEEBE, M.B. & C.W. BEEBE, 1910. *Our search for a wilderness.* Constable, London.

66. YOUNG, A.M., 1980. *Biotropica* 12: 237-239.

67. RAYOR, L., 1983. *In litt.*

68. GEEST, W., 1905. *Z. wiss. InsektBiol.* 1: 254-256.

69. STORTENBEKER, C.W., 1967. *Agric. Res. Rep., Pudoc, Wageningen* No. 694: 1-118.

70. MAY, M.L., 1982. *Evolution* 36: 1051-1058.

71. McCAFFERTY, W.P., 1979. *Aquatic Insects* 1: 149-151.

72. HUTCHINSON, R., 1979. *Cordulia* 5: 13.

73. PRITCHARD, G., 1963. *Predation by dragonflies (Odonata; Anisoptera).* Ph.D. thesis, Univ. Alberta.

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

75. CORBET, P.S. & S.A. CORBET, 1958. *Nature, Lond.* 182: 194.

76. ORIANS, G.H., 1966. *Condor* 68: 321-337.

77. CORBET, P.S., 1957. *J. Anim. Ecol.* 26: 1-69.

78. CORBET, P.S., 1958. *Nature, Lond.* 182: 330-331.

79. CHUTTER, F.M., 1961. *Arch. Hydrobiol.* 57: 430-463.

80. BENKE, A.C., 1978. *J. Anim. Ecol.* 47: 335-350.

81. KIME, J., 1974. *Ecological relationships among three species of aeshnid dragonfly larvae (Odonata: Aeshnidae).* Ph.D. thesis, Univ. Washington.

82. SCHALLER, F., 1960. *Ann. Sci. nat. (Zool.)* 2: 751-868.

83. SCHALLER, F. & M. MOUZE, 1970. *Ann. Soc. ent. Fr.* (N.S.) 6: 339-346.

84. FONTAINE, R. & J.-G. PILON, 1979. *Ann. Soc. ent. Québec* 24: 85-105.

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

86. DEACON, K.J., 1979. *The seasonality of four Odonata species from mid Canterbury, South Island, New Zealand.* Ph.D. thesis, Univ. Canterbury.

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

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

89. KUWADA, K., 1973. *Tombo* 15: 10-12. (OA 421.)

90. BYERS, C.F., 1941. *Proc. Fla Acad. Sci.* 6: 14-25.

91. DUNKLE, S.W., 1979. *Odonatologica* 8: 123-127.

92. LIEFTINCK, M.A., 1968. *Tijdschr. Ent.* 111: 137-186.

93. LINDLEY, R.P., 1970. *Entomologist* 103: 77-83.

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

95. SHERMAN, K.J., 1983. The evolution of reproductive strategies in a dragonfly, *Pachydiplax longipennis*. Ph.D. thesis, Cornell Univ., Ithaca, New York.

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INDEX TO CITED AUTHORS

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INDEX TO ODONATA

Species are listed under the generic name only.