CURRENT TOPICS IN DRAGONFLY BIOLOGY
Vol. 4

Including a discussion focusing on
interference among larvae

Transcript of discussion recorded during plenary session
of the 10th International Symposium of Odonatology at
Johnson City, Tennessee on 10 August 1989

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

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INCLUDING A DISCUSSION FOCUSING ON
INTERFERENCE AMONG LARVAE

Edited by
Philip S. Corbet

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1990

C O N T E N T S

PREFACE

At the 7th, 8th and 9th International Symposia of Odonatology the programme included a plenary session devoted to topics of current interest to odonatologists. Each session was recorded and transcribed, and subsequently published as a Supplement in the Societas Internationalis Odonatologica (S.I.O.) Rapid Communications series as Nos 2, 6 and 8. At the 10th International Symposium of Odonatology in Johnson City, Tennessee in August 1989 a similar plenary session was held and, thanks to the efforts of the Symposium Secretary, Professor D. M. JOHNSON, and of a member of the Symposium Organising Committee, Dr A. V. PROVONSHA, we were again able to record the whole session in a way that made transcription feasible.

In editing the transcript, I have made minor changes, or corrections, needed to improve readability and comprehensibility. The discussion lasted about an hour and a half. During the first half hour (Part One) several topics were briefly addressed; the rest of the session (Part Two) was spent discussing interference among larvae, this being a topic of special interest to odonatologists at the host institution, East Tennessee State University. As before, to put the discussion in context, I have compiled a short bibliography and a list of contributors and their addresses. Also included are indexes to contributors and dragonfly taxa. Citations to entries in the bibliography are indicated in the text by numbers in parentheses.

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

> CUYLER, R.D. 1990. In *Current topics in dragonfly biology*, P.S. CORBET (ed.), p. 6. *Soc. int. odonatol. rapid Comm. (Suppl.)* 00: viii + 28 pp.

It is a pleasure to thank Mrs Jillian SUTHERLAND for producing the final typescript and the University of Dundee and the Symposium Organising Committee for financial help towards the cost of my participation in the Symposium. My warm thanks are again due to Professor Bastiaan KIAUTA for helping to expedite publication.

The original tape of the discussion has been deposited in the archives of S.I.O. The transcript of side 2 begins on page 11.

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DISCUSSION

Preamble

CORBET: I should like to welcome you to the fifth of our plenary seminars. These have been a feature of S.I.O. International Symposia since the one held at Chur, Switzerland in 1981. These seminars, or discussion sessions, offer a good opportunity for us to exchange information and views on various topics in odonatology, especially those topics which may be elucidated by the exposure of chance or anecdotal observations, because such observations are unlikely ever to be published or shared with a large group of odonatologists; also, of course, there is the value of interaction among ourselves during these discussion sessions which is beneficial as long as it does not lead to cannibalism!

I should like to thank Dan Johnson, Secretary of the Organising Committee, and members of the Committee for having asked me to chair such a session at this Symposium and also those who submitted suggestions for topics to be discussed in it.

I propose that we allot the time this afternoon as follows: in Part One, which will last for about half an hour, we might focus on several, brief, diverse topics in succession to see if the pooling of information that we have may help to generate ideas or questions and identify future investigations; in Part Two, which could last for about an hour, we might examine in detail aspects of larval ecology. Such a format in Part Two would repeat a move that was made at Madurai, India during the 9th S.I.O. Symposium in 1988. At Madurai we devoted much of the seminar to discussing priorities for research in India and in particular the ways in which we could elucidate the movements of *Pantala flavescens*. There are obvious advantages in adopting this approach and so this is what I propose to do today.

Part One: diverse topics

Adult fitness and size

CORBET: The first topic that I wish to raise is female fitness. Is adult female fitness correlated with size? I wonder, Tony, if you could lead us into this subject?

WATSON: I only want to make a brief point which I made to Philip earlier and that is whether there is any relationship between female size in a given species (specifically, of course, in a species in which female size is variable and especially, perhaps, in which size changes with season) and fecundity or the size and properties of eggs? It seemed to me that these were issues that could bear on the rather gloomy stories that we were hearing about the fate of larvae and eggs, or eggs laid and larvae hatched late in the season.

CORBET: I might interpolate here that the correlation between adult female size and fecundity has been well established in certain other groups of aquatic insects, particularly mosquitoes (1).

Could I ask you, Dave, whether you have anything to add to this question?

THOMPSON: I have two brief comments. One is concerned with clutch size, and the other with egg size. Both comments refer to coenagrionid damselflies.

In one-day clutches of *Coenagrion puella*, clutch size is negatively correlated with body size (54) (this is a counterintuitive finding); for two-day clutches there is no correlation between clutch-size and body size; but in instances in which the inter-clutch interval is greater than two days you find the conventional relationship in which clutch size increases with body size (2).

Coming to the second point - egg size - we found no relationship in *C. puella* between egg size and body size. I would say that there was a great deal of variation in egg size. For *Pyrrhosoma nymphula* all we have been able to find is the conventional relationship that clutch size increases with body size, but for egg size we have found that smaller individuals produce larger eggs (51).

CORBET: I wonder, Ola, if you have anything to add to this from your studies? Did you, for instance, measure adult female size in *Enallagma hageni*?

FINCKE: I did measure female size (50). I found no correlation between female size and total number of eggs laid but this was probably because most of the females did not live long enough to lay their entire clutch of eggs; so I really have nothing to add to Dave's comments. I think his studies are much better than mine in that respect.

WAAGE: I would add to the question by asking whether or not female size relates to survivorship as well as to clutch size, and I would suggest looking at Koenig and Albano's paper on *Libellula (Plathemis) lydia* (3) where I think they have looked at correlates of body size and longevity, because longevity seems to be one of the major contributors to reproductive success. It might be worth checking that; Ola or Dave may know of other papers in which that is true. There have been quite a few studies of this topic.

CORBET: Dave, please would you comment if you have anything to say in the light of Ola's or Jonathan's remarks?

THOMPSON: Female size and longevity seem to be highly correlated in the two coenagrionid species that I have worked with (54).

CORBET: Well, it seems to me from what has been said already, and recognising the inevitable paucity of data on the subject, that female size probably is positively correlated with fitness in a broad sense but I note particularly that probably very few people have measured inter-clutch interval and broken out egg size or fertility on that basis. Perhaps this is something that we should give more attention to in future. Are there other comments on this topic please, recognising that we shall have to move along fairly quickly?

ANHOLT: I have got some pretty good data on measuring lifetime reproductive success in female *Enallagma boreale*. My measures of lifetime reproductive success, however, go from the time of emergence until death, and they involve marked individuals. What is most relevant here has to do with survival from emergence to reproductive maturity. There are two parts to the data. The first is that probability of survival for females is independent of size. The second is that when females eclose the abdomen is essentially just an empty bag and so, as far as I can tell, most eggs are produced from resources that are gathered during the prereproductive phase of the adult, and mass gain between emergence and reproductive maturity is independent of adult size. Following that, the number of clutches in females that do survive to reproductive maturity also seems to be independent of size; so, at least in *Enallagma boreale*, female reproductive success seems to be independent of size at emergence.

CORBET: In this connection I might mention briefly that, if you have data on survival during the maturation period which are comparable with those for survival after the maturation period (that is during the reproductive period) they will be of considerable comparative value because such data are often omitted. I have in mind particularly some elegant work done by Uéda and Iwasaki in Japan on *Lestes temporalis* (4). This showed a survival of virtually one hundred per cent during the maturation period; then, as soon as reproductive activity began, survivorship declined daily according to the normal pattern. Brad, do you wish to add anything?

ANHOLT: I envy Uéda his data because my estimate for survival, based on marking, is somewhere around six per cent and, depending on the year, sometimes as low as three per cent; so it is clearly highly variable and these examples are probably two extremes.

CORBET: It is worth noting that *Lestes temporalis* may have been a special case because adults were aestivating in woodland.

WAAGE: I want to caution against a fixation on size, as opposed to weight or contents. I think that one thing that is becoming apparent is that, at the transition from the larval to the adult stage, the absolute size (the fixed size of the box that contains the dragonfly or damselfly) may be a consequence of the larval stage but it is not evident that the contents or the distribution of the contents of the organism is determined at that point (i.e. emergence) although it may be during the maturation period. So I think we need to be careful not just to measure length or some similar dimension because the body weights of these individuals and the contents change drastically during their lifetime. So I am asking that people pay a little more attention to the contents as well as the external size.

Emergence date and latitude

CORBET: May I move to the next topic? It came out, almost by chance, during discussions with Jill Silsby and Ken Tennessen at this Symposium, that certain species that have a wide latitudinal distribution in North America may be emerging at the northern end of that distribution earlier than they do at the southern end. Many years ago, E. M. Walker revealed this possibility in, I think it was, *Leucorrhinia* in Canada: it appeared that the far northern populations of *Leucorrhinia* at least compensated for the latitudinal difference that separated them from populations in southern Ontario so that the northern populations may indeed have emerged earlier (5, 6). This raises the question of what mechanism might be in operation here and where (if these observations are repeatable, which we do not yet know) this would lead in terms of future research. I was talking about this yesterday with Ken Tennessen. I wonder, Ken, whether you could mention any examples that show an earlier emergence at the northern end of a species' distribution than at the southern end?

TENNESSEN: *Aeshna umbrosa*, which is widely distributed across the United States, occurs as far south as central Alabama and, although I do not have good data on when the species emerges in the south, when you are on the streams where it does occur you don't see it until probably September. I think that it flies much earlier than that in the north: I remember seeing it in New York in early August.

CORBET: Rob Cannings do you have anything to add in the light of your experience of dragonflies in the Yukon?

CANNINGS: I think that we do have that kind of information, Philip, but unfortunately it is not in my head. I think that I could certainly dig up a number of examples. *Coenagrion resolutum* might be one example. Also some species of *Aeshna* - *Aeshna sitchensis* or *septentrionalis* - but I can't give you enough useful information off the top of my head.

CORBET: Would be it be fairly easy to assemble a brief summary of such information?

CANNINGS: Yes, I think so; I could do that as soon as I get back.

CORBET: Before you sit down may I ask if it is your recollection that this is indeed so?

CANNINGS: I think so, yes; I am not sure how significant it would be, but I think there are a number of examples in several different families that I could probably give you that would suggest this trend.

CORBET: Thank you. Before we leave this topic I should like to mention its obvious relationship to gradients of latitude. I know that Mike Samways is particularly interested in this because of his situation in Natal. Do you have any information yet, Mike, that would indicate a compensatory effect at higher altitude for the beginning of emergence of different species in your area?

SAMWAYS: Philip, our work is still very preliminary (7), but it is already clear that, over the three-thousand metre altitudinal gradient in southern Africa, the season at high elevations is simply shorter: dragonflies emerge later and end the flying season earlier than they do at lower elevations.

CORBET: That would conform with Peter Morin's observation mentioned during his paper this morning (8) that one of the effects of latitude in North America is to condense the whole flying season of an assemblage of species.

FLINT: I have noticed the same phenomenon in caddisflies, and I once formulated for my own information a programme of what was going on. I immediately separated spring-emerging species from fall-emerging species because they work in opposite directions. In other words, spring-emerging species emerge earlier in the south than in the north; and the reverse is true: the fall-emerging species emerge much earlier in the north and later in the south. And the equivalent of going higher in elevation is to go father north. So you can add that into your formula. I sort of tested that. I was worried about what was going on with *Neophylax*, a caddisfly that emerges basically in the fall. I was at Highlands in North Carolina just a little ways away and they weren't far enough along in their life-cycle; so I decided to go up higher in the mountains and there I found them ready for emergence. So when you are thinking about these things bear in mind that spring-emerging species and fall-emerging species practically overlap far to the north.

CORBET: That provides a very interesting matrix against which we can compare our observations on dragonflies. (Rob, presumably you are writing this down?) I was thinking that it would be particularly interesting to have these Trichoptera data in mind, and perhaps also to make a third category which would be relevant to dragonflies: that is what we call 'summer species'. Have these observations been published, Oliver?

FLINT: No.

JOHNSON: I have two comments. First, I am pretty sure that Scott Wissinger has recently published some relevant data in this respect (9). I have read so many of those papers lately that I cannot remember which says what, but that I think that Scott has some data that would be relevant. My second comment is that, when we are talking about the emergence period, we ought to be sensitive to the need to know whether we are dealing with univoltine or semivoltine populations, or parts of cohorts, as Tom and I pointed out in our paper this morning (10). I would think that a univoltine part of a cohort, or population, might not be able to accomplish such early emergence because it would be struggling to complete development in one year, whereas those semivoltine guys that are spending a whole summer just in diapause could easily come out as early (the next spring) as they wished, and the northern populations would have a tendency to be more semivoltine.

VOGT: Just a brief comment regarding *Aeshna umbrosa* that Ken Tennessen was speaking about earlier: I have observed adult males on the wing in northern Wisconsin - I believe that it was on 22 July this year. It was a memorable date because I happened to be collecting *Somatochlora hineana* at the same time. That's all I have to say regarding *Aeshna umbrosa*.

CORBET: Now that we have that hard observation from close to the northern part of the range of *A. umbrosa*, can I ask you, Sid, if you can tell us something about the flight season of *umbrosa* at the southern limit of its range in North America?

DUNKLE: Well we don't have any species of *Aeshna* in Florida (11); so I haven't researched the flight seasons of *Aeshna*. But, looking at the flight seasons of various North American Anisoptera, I wasn't aware that any did what you have described. It seems that, where adequate data are available, in no case that I know of does a species emerge earlier in the north than it does in the south. So I'll be real surprised if we find any such examples. But I think that, if we do, it will be due to what Dan Johnson has just described: that is, species having a semivoltine life-cycle in the northern part of their range.

CUYLER: A comment about *Aeshna umbrosa*. Its normal flying season seems to be from early September to some time around the middle of November, but one year I took one mature specimen in early July. That was on just one occasion. It has been taken as late as 3 December in central North Carolina. Now, with regard to spring species, it is well known that *Libellula (Ladona) deplanata* is the only libelluline in North America that is a spring species. Well things can go wrong, because I took a mature male one year around the middle of November! That was during an unusually warm autumn.

CORBET: Duncan, may I confirm something? When you mentioned your observation of *Aeshna umbrosa* in July, this was in North Carolina, right?

CUYLER: That's right.

DONNELLY: A few observations. I lived for seven years in Texas, although most of my life has been spent in New York, and I did have an opportunity to contrast such things as flight times in the south and the north. One thing has to be made clear from the start: it is sometimes very difficult to establish the (earliest) emergence date. There are really three dates that are available to us. First, the date at which we can observe emergence in the laboratory in freshly caught, final-instar larvae. This is not a very meaningful date. Second, the date on which we are lucky enough to see emergence in the field - and 'luck' is the operative word here; and third, the date on which one starts to see dragonflies on territory, which may be much, much later. In the case of *Gomphus (Stylurus)*, for instance, a month, or at least the larger part of a month, may elapse, between the second and third dates but I have observed in many cases (in *Progomphus obscurus* for instance) that I can actually go to the south and collect them as what would seem to be not overly old individuals much later in the year than I can find them in New Jersey. Now that's observation number one. This does give the impression that many things seem to be later in the south. But another observation has always puzzled me. We have at least two damselfly species which can serve as examples. The first is *Lestes disjunctus australis* which occurs from Texas up to New York; and the second is *Hetaerina titia*, sometimes called *tricolor*, which occurs from Texas up to about Maryland. Let's start with *titia*. In the north you find adults in October. In Texas you find them in April and May and then also in November. Now for *Lestes disjunctus australis*. If you find them in the north they fly in the spring and the sub-species *disjunctus* in the late fall. So they seem to be temporally separated. If you go to Texas you will find *disjunctus australis* flying both very early in the spring, in March and April, and then again in November. I am not certain that there isn't some overwintering (of the adults); I don't know whether these species are semivoltine; in other words I don't understand the total life-history. Certainly there are some examples of two distinct flying seasons for some species in the south.

CORBET: Well I think that at the very least this provides some interesting points of departure for future work in phenology which could be helped very greatly by observations of flying dates in county lists and so on. Are there any more comments on this topic?

WAAGE: I caution that flying dates may not tell you as much as more detailed larval studies and I really want to emphasise what Dan said. There is a fairly large literature on life-history in relation to latitude - dealing with crickets, frogs and other animals - which shows the same sort of thing that you are talking about: individuals that spend an extra year as juveniles may get an extra early start in spring. Also, anecdotal material is very misleading. I could give you a nice anecdotal example of detailed population records of emergence in *Calopteryx maculata* and *Calopteryx aequabile* at least two, maybe three, weeks earlier in northern Michigan than in Rhode Island but that is solely a consequence of Rhode Island being coastal. As far as the climate is concerned, spring comes later in Rhode Island than it does in northern Michigan; so one really has to look out for simple correlations with latitude and the dates of first sightings. I think that detailed larval studies and population studies are necessary to sort this out.

CORBET: On that particular subject I would put in a personal plea for those who work on larvae to try wherever possible to separate off the category of final (i.e. F-0) instar from the penultimate (i.e. F-1) instar, and within the final instar to distinguish larvae that do and do not show signs of metamorphosis (12-16). To do this can be immensely valuable when trying to interpret the significance of larval populations in relation to emergence.

Phenology of Anax junius

Well one more topic for the last two minutes. I will condense this because Rudy Raff, Scott Wissinger and Hal White, who are principals in this affair, are not here. On two occasions during the last 20 years, workers at a latitude of about 40° N in Scotia, Pennsylvania (17) and in Purdue, Indiana (9), who have been collecting exuviae (cast larval skins) of the final larval instar after emergence, have collected exuviae of *Anax junius* either at the end of March or during the first two weeks of April. I find myself completely baffled by this and so does Hal White to whom I have talked at some length about his and Rudy Raff's finding at Ten Acre Pond in Pennsylvania in March 1963 (17). I was hoping that Scott Wissinger would be here and that we could explore this phenomenon further. However, if anyone sees this as something that does not require explanation because it is so obvious, I should be glad if they could speak up. The point is that water and air temperatures in late March and early April in Indiana and Pennsylvania are such that no self-respecting anisopteran would even have started metomorphosis, let alone have emerged.

MAY: I would just like to add another simple observation on the last topic regarding *Anax*. Although I did not observe emergence, I did observe very, very early adult flight at a small pond in Illinois at about the same latitude, and it was striking that the flight of *Anax* appeared to be perfectly normal patrolling, rendezvous, site-type flight; the individuals appeared to be fresh but mature and it was striking that they were very active at this one site and that no other dragonflies were active elsewhere in the vicinity. This was in the first week of April.

CORBET: I think that we can now say with confidence from the growing number of observations that these would be mature individuals brought up by air currents from the south (18).

Part Two
Interference among larvae

CORBET: I'd like now to move to Part Two and look at the general problem of larval interference - both intraspecific and interspecific. By this I mean larvae interfering with each other in a way that may lead to mortality or a reduction in fitness in the larvae involved.

First, the subject of interference mortality. I wonder if someone would be willing to start discussion on whether or not larvae that interfere with each other and show ritualistic, agonistic behaviour towards members of their own species of the same instar can be regarded as territorial. Ola, you had something to say about this this morning. Would you be willing to say what your feeling is about the literature that you have read on this subject so far?

FINCKE: I would just stress that the use of the word 'territorial' can be problematic and that if you use it with regard to larvae it is necessary to explain what you mean because, from what I have read, and from what I have observed in *Megaloprepus caerulatus* (19), I personally would not call it territoriality because the behaviour or aggressiveness does not necessarily change when the larva moves out of the space that it has just defended. In other words, it may move to another area and be as aggressive there as it was earlier so that, as I said this morning, I would agree with Rob Baker in that I think that larvae are exhibiting a dominance hierarchy based on size, rather than a defence of a particular area; and this differs from what most of us I think consider territoriality to consist of in adult odonates, in which the degree of aggression decreases as the individual moves away from its territory.

CORBET: You have mentioned the criterion of differing intensities of 'aggression' or 'defence' depending on the proximity to the focus of activity. Do you also attach importance to the residence time of a larva on a particular perch or do you regard that as unimportant?

Clearly, it has to be more than a minute or two, but do you think it is important to include in the definition of territory how long a larva defends a particular perch?

FINCKE: I think that in his study (20) Rowe found that they defended a particular perch for many, many days. I guess that what he didn't show was that if you removed that larva and placed it in another situation its behaviour would change there, and I doubt that it would. I mean that I think it would remain dominant in another area as well. Yes, so certainly the length of time is important. I do not want to say necessarily that we should not use the term 'territoriality' in larvae: I remember going through the definitions of territoriality in Paris with respect to adults and there was a lot of confusion in the literature because people used the term in many different ways without really explaining what they meant; so I would simply make a plea that if we use the term we be very careful and always describe what we mean by it.

CORBET: Thank you. Well that certainly suggests further experiments for increasing the rigour of the use of the term 'territoriality' where it is applied to dragonfly larvae. Would anyone else like to contribute to this part of the debate?

MAY: I would like to ask Ola, or anyone else who would like to answer: what is the basis for insisting on that particular criterion that you suggested? I do not want to put words into your mouth, but is it in the back of your mind that if it is to be called 'territoriality' there should be some spatially fixed resource of benefit that is being defended? It that really the crux?

FINCKE: Well, if it is to be analogous with territoriality as we seem to use it in adult odonates or as it is used in vertebrate literature, yes: it is usually a specific space. Otherwise, it seems to me, you are just defending some personal space and that personal space moves with you as you move around.

WAAGE: Perhaps what Ola was saying, or what I would say, is that the word 'territoriality' is meaningless because it has such a long history of definitions starting with a defended area which could be the personal space around an individual, a specific site with which something is associated - food, a resource, and so on. As the definition of territoriality has changed in the ecological and behavioural literature over the years, it has acquired two other definitions. One of them is that that space is a resource for which there is a cost of defending it and for which the individual obtains a benefit from defending it. The definition of territoriality in the recent theoretical literature (21) has become an economic one - that of a resource being defended at a particular cost and for which a particular benefit accrues from defending it. The second dimension is that the way to identify a territorial individual defending a particular resource, or space, as Ola says is to move that individual out of it and see if it does as well outside the territory as within it. So I think that there are two dimensions involved here. One is that the word itself is meaningless; there has to be a description of what you mean associated with it. And second, that the use of the word 'territoriality' in the modern literature is moving much more towards a cost-benefit analysis, and doing that cost-benefit analysis forces you into a description and a quantification of exactly what you mean. That is probably the way one ought to proceed.

PILON: During the course of my rearing work (22), I observed two facts, coming from an accident, if you like. I was rearing individual larvae in petri dishes and sometimes one larva would escape and enter the dish occupied by another larva. What I observed is that, if both larvae were about the same size, they both shared the space of the petri dish; so it seems that the food is the only restriction. If one of the two larvae was smaller, it would be eaten.

CORBET: Do you remember the species that were involved?

PILON: It happens with the five species of *Enallagma* (23) that we reared and also with *Ischnura verticalis* (24).

JOHNSON: In response to Jon's statement about what resource is being defended, it might be useful to ask how many of us think that the resource being defended is a feeding site (Macan's "fishing site" (25)) and how many think that it is a refuge from predation, which I think is Richard Rowe's conclusion (26). In both cases the resource is associated with the perch: if you move the beast to another perch, you wouldn't expect the behaviour to change and yet the resource, in some sense, exists. I have found that this makes it rather difficult to decide what is territoriality and what is just aggression.

CORBET: This is a very interesting dichotomy, and I suppose we mustn't eliminate the possibility that sometimes larvae may be doing both: there may be selective pressures on them from both of these directions. Would anyone like to speak in favour of the view that the perch defended by some dragonfly larvae is primarily a feeding site?

BAKER: Would you repeat the question?

CORBET: Would you like to support the contention that the perch a larva is defending is being defended primarily because it is a feeding site?

BAKER: No, I cannot defend that. I believe that often more than one thing is going on in regard to the localization that a larvae is exhibiting. I believe that a lot of odonate larvae stay near food. That is one sort of process. I also believe, and in this I agree with Ola, that larvae are aggressive everywhere they go and in all sorts of situations. The fact that you see an animal being aggressive where it is staying near food does not mean that it is defending that site. It is simply being aggressive, as it is everywhere. So I do not even agree with Dan's alternative - that it must be defending either a feeding site or an anti-predator area. I think that larvae are aggressive for a variety of reasons, possibly just to avoid predation by conspecifics.

CORBET: May I ask how you view the fact that larvae of some species appear not to be aggressive at all, even when clustered at high density (40), for example *Enallagma cyathigerum* in our experience (27), whereas others are?

BAKER: I am not aware of that data which I find a little surprising. The only thing I can say from work that I have done is that at extremely high densities animals simply seem to stop moving altogether, possibly as a way of avoiding aggressive interaction. So they simply stop moving and do not interact as much at very, very high densities. Whether or not those densities occur in the field I don't know.

CORBET: So one gets a qualitative change in behaviour at very high densities?

BAKER: I believe that is possible.

CORBET: And then of course the other alternative that we are considering (and it may be not an alternative but another possibility) is that larvae that defend sites are defending refuges from predators, particularly perhaps fish, but not necessarily only fish. Would anyone like to support this contention, which is the only major one left at the moment? Dan, would you like to speak to this possibility?

JOHNSON: No! I find it a little difficult to decide whether any resource is really being defended but, if it is, it seems to me that those are indeed the alternatives. My impression is that we are dealing with creatures that are, as Rob says, very aggressive whenever they run into each other and I just wanted to see if someone could say whether defence was taking place or whether their behaviour is simply offensive whenever they encounter each other.

(Side 2 begins.)

MAY: The observations that lead me to the same sort of dilemma that Dan identifies relate to adults at feeding areas (28,62). Here they sit on perches analogously to the larvae and interact aggressively. The problem that I see with Ola's operational definition (of changed aggressive behaviour if you move them) is that the only place that you can move them to and where they can behave normally at all is another perch, and it may be that simply the fact of having a perch is the resource (if that is a legitimate definition of a resource) that they are defending. The choice between this perch and that perch is unimportant and therefore they will defend each equally; but the choice between having a perch and not having a perch is very important to them. If they don't have a perch they just go away, or do their best to find one. So I see a problem with using your criterion to see whether or not a resource is being defended because some resources are funny that way.

CORBET: I foresaw difficulties in carrying out an experiment to investigate that because there is a resident's-advantage asymmetry, but presumably it would be valid to transpose two larvae to a third site where neither of them had any advantage from being a previous occupant and then examine their interaction.

WAAGE: I should like to make an observation. Notice that we have stopped using the word 'territoriality'. What emerged was two kinds of aggressive behaviour: one, aggressive behaviour related to the place where you are (and this is what we are talking about primarily when we speak of perch sites); and the other, aggressive behaviour related to a particular, valuable resource. Obviously there is an intergradation between the two. Mike, I think that what you are talking about is a situation in which it would be very difficult to say that this particular perch differs from that particular perch in the economic equation regarding the costs and benefits of defence; however you might be able to say with a particular territory site that this one is going to attract more females or that that one has more food. So it is not easy to make that distinction. In fact it lies on a continuum and if one wishes to demonstrate a distinction it is very difficult to get appropriate data. I don't think that using the word 'territoriality' will solve the problem. I think we should go for the really difficult data, realising that individuals are aggressive where they are, and that where they are is a particularly important place in which to be aggressive as opposed to somewhere else. I think that there is a continuum there that has to be dissected out by good detailed work.

CORBET: I don't think that we should overlook the fact either that certain genera of larvae tend to be thigmotactic, that is to say their resting position is grasping a stem tightly, and that this may be a very important basis in the mechanisms of their feeding behaviour; so to have a place on a stem to which they can attach tightly may be an advantage in itself for such larvae whereas, as we know, there are larvae with a different habitus that are not thigmotactic.

ANHOLT: I agree completely with Jon Waage. I am not sure that it is useful to label an individual species as being territorial or non-territorial, except perhaps that it might have some use in a more systematic sense in some situations. The same species in different places among lots of vertebrates may be or may not be territorial, depending on abundances and so forth and I think that one of the problems of using the labels will be in creating a typological view of what a species does in a given place. It is much more useful to be able to say: "What is the behaviour?" And, if it interests you: "What are the consequences of that behaviour?" One of the alternatives that I might offer is to address the question: "Why do the damned things like to sit on perches anyway?" I mean, they do it; and the data that say that they feed better on perches is equivocal and the data that say that they survive better on perches is also equivocal, and I think that those are the kind of data that we want to gather. One of the consequences of that behaviour when larvae interact with each other is that, when they become very abundant, they become more evenly spaced than you would otherwise expect which is sometimes used as evidence for territoriality but is really just evidence that they interact with each other. Possibilities exist that relate to the two questions. One is that, when they are spaced out more, the food is more evenly proportioned; and another is that, when they are all clumped together, they are more susceptible to predation. Neither of those possibilities, as far as I know, has been tested.

CORBET: I had the impression that there were good data supporting the conclusion that complexity of microhabitat, by which I mean the abundance or diversity of perches, was correlated with a lower predation by fish (29,61).

ANHOLT: Yes, there are some data like that but, although I cannot remember the references, I think that there are others that are not so supportive. The second part to that is that that may be true but why should you care if anyone else is around you? Even if they like to sit on perches and that protects them from vertebrate predation or even invertebrate predation, why should it matter whether another individual is anywhere near you if predation is the issue? I guess the hypothesis would be that predation risk is higher when larvae are close together but you can think of other hypotheses that suggest that maybe it should be less. So it is unclear to me.

CORBET: Is Peter Morin here? Do you have anything that you would like to add to this discussion Peter?

MORIN: I really don't have a lot to add other than to say that we basically don't know what happens under the water in most ponds. Most of the data come from laboratory studies which are a great abstraction from what happens in the real world. If someone can find a way of spending a lot of time down in a real pond looking at these things we might find out what it really means. But I don't known many odonatologists who use SCUBA gear to pursue their search. So that's about all I can add.

CORBET: Perhaps they should arrange to have a visiting scholarship to the University of California, Riverside where Ernie Bay has an underwater viewing chamber where you don't even have to even get wet in order to look at the larvae (52). Is Phil Crowley here?

CROWLEY: Getting back to what Brad Anholt said, I think that the reason for this aggression between larvae has a lot to do with pre-emptive attack, in that where density of larvae is relatively high it is a good idea to move dangerous, other individuals out of the way, and that that is one of the main factors accounting for aggressive interactions that we see in these systems. I think that Jon Waage's point about economics is an important point of view, but one of the economic factors is the risk of cannibalism associated with the presence of other individuals. We do not often see cannibalism when we stage encounters between individuals that meet each other head-on but in fact if you are not keeping an eye on the other guy it is possible that he could come at you from a direction in which you are not able to defend yourself very well and that pre-emptive attacks are a way of avoiding that situation.

CORBET: One has in mind the paper that we heard this morning about the possible function of caudal lamellae in being a first port of call for an attacking predator (30). On the subject of comparing conclusions drawn from the laboratory and the field I wonder Rob Baker if you would be willing to comment on one of your 1987 papers (31) in which you found no evidence in the field for the laboratory finding that large, dominant larvae exclude conspecifics from profitable feeding sites? I think it would be helpful if you could share some of your thoughts with us on the reasons for undertaking that work and on the way in which you did it.

BAKER: I believe in that paper (31) I was trying to do something quite specific. There had been a suggestion, starting with Thomas Macan (25), that animals under field situations may actually be able to exclude conspecifics from profitable fishing sites (as he put it). There is a lot of evidence from simple laboratory studies that says that this occurs: animals do localise in patches of food and do exclude conspecifics, usually smaller conspecifics, from these areas. I was interested in that paper to know whether such a process could actually be detected; and whether it was occurring under field situations because we have virtually no data on that. In the laboratory, as I have mentioned, large animals are able to exclude smaller animals and tend to force them away, and I use the very simple argument that, if this sort of thing is occurring in the field and if it is occurring with any frequency, you might expect to find under field conditions smaller animals moving more frequently than large ones because the large ones have taken all the feeding areas and they have forced the smaller ones to move away; and, because they have been forced to move away, the smaller ones will swim more and they are going to end up dispersing; and if you use a kind of dispersal trap you might be able to find them more frequently. If I remember correctly, the basic message was that dispersal traps or artificial substrates constituted a perfect method of collecting all the size classes present in the pond. Conversely there is no evidence that small individuals are moving more frequently than large ones and I was forced to conclude then that there is very little evidence to suggest that large animals tend to force smaller animals away from feeding areas. That could of course be due to a variety of different reasons; I suspect that the most important one is the lack of statistical power in that paper but, on the other hand, I do not think that anyone has yet shown that fishing sites really do occur. It's a nice idea but so far we have no field evidence that good fishing areas actually occur under field conditions.

CORBET: Are there any further contributions to this topic? I am sure that a number of us have wondered how some of these studies of interactions and defences of perches apply to larvae with widely different habits (I am thinking now of the deep-burrowers like *Aphylla*, the shallow-burrowers like *Ictinogomphus* (32), the ones that are cryptic on the bottom like some libellulids and active surface-living larvae like *Anax* and *Lestes*). I wonder whether in your research group, Dan, when you have had occasion to look at several of these categories, you have given thought to the way in which some of the generalisations would have to be qualified by considering larvae in different categories?

JOHNSON: I'll have to confess that I wish that we had good information on that and I hope that some day we may acquire it, but at this point we have not really gathered much information on microhabitat differences. I am embarrassed to say that what shows up in a sweep-net is counted as being in the same place. The detailed behavioural observations have been made in Phil Crowley's laboratory in Kentucky but there there is the difficulty of creating discrete microhabitats and still being able to observe them and film then, which is the object of that work; so we don't really have good correlations between microhabitat use and behaviours and frequency of encounters and those sorts of things yet.

CORBET: What you say underlines the need for good aquariun studies with realistic simulation of different types of substrate and plant matrix, accompanied by good video observations. Phil, you mentioned this morning some of the video work that is going on in your laboratory. I wonder if you could contribute to the discussion by telling us the direction your work is taking at Kentucky at the moment? I am sure that it would be of general interest.

CROWLEY: I think that, relevant to what Dan was just talking about, the series of studies that we have done on *Tetragoneuria* to try to quantify their behaviour, under pieces of fibre-glass window screen to simulate something like leafy detritus, has suggested that the sort of thing that Rob Baker was mentioning - the fishing-site idea - while attractive, just doesn't seem to conform with what we observe in these aquaria. There is no reason to think, as far as I can tell, that in the real world and in the analogues that I have observed there are these discrete, fishing-site-like places or defensible parts of the bottom of an aquarium when we try to make it look like a littoral zone or like a detritus patch. We tend to discretise to be able to understand things but perhaps we are oversimplifying when we do that. I have done a series of experiments of that sort, trying to construct something that I could still watch and call a detritus-like habitat, and a series of other experiements in which I have been able to watch closely larvae moving around on sets of dowels. The upshot of those experiments is that I can interpret some of the behaviours, as densities are changed artificially, in terms of predator-avoidance where conspecifics are in fact the predators. So we can see them spread out more, move less and do other things that make them less vulnerable to each other. We have also done some experiments in aquaria in which large test tubes containing a dowel with coenagrionids marching around on it were put in aquaria that contained fish and we found shifts by the coenagrionids that were not exposed to the fish in any way other than visually, as if they were trying to avoid those potential predators. We have been able to make these observations, by the way, so that we could watch the process both in the light and under infra-red and, thanks to Truman Sherk, we are pretty sure that these larvae cannot see in infra-red (33, 34). We can watch them through the video camera projected into the next room and so can interpret behaviours both in the dark and in the light. We do see a response to other individuals that can be sensed tactilely in the dark under conditions we can observe using the video camera and we also see responses to both predators and conspecifics in the light in this kind of system. So I think it is one that certainly has much more potential than we have been able to exploit to tackle some of the problems that we have begun to discuss here this afternoon.

CORBET: Thank you. Two areas of dragonfly behaviour which come to mind as you speak are the work by Kime (35) which showed that certain aeshnid larvae (and they are normally thigmotactic) preferred, though not by a very big difference, stems or rods of certain diameters which would indicate that, whatever the functional advantage of this might be, there may be preferences for perches of different kinds by larvae with different habits. Moving now to the subject of anti-predator behaviour (a subject of larval behaviour that has been very little studied, since the days of Abbott in the 1920s (36)), we may consider what some people call death-feigning - a catatonic response to the presence of a predator which some snakes also show. It has been recorded again more recently by Taketo (37) in the petalurid *Tanypteryx pryeri*. I wonder if anyone has any observations to contribute here on the subject of anti-predator behaviours, including those that might involve death-feigning?

JOHNSON: Let me speak for a couple of people who are not here. I know of nothing that has to do with death-feigning. Mark McPeek, who sent me some recent manuscripts on the subject, has told me that some species of *Enallagma* are quite good at avoiding fish predators through changes in their behaviour and at avoiding predation by *Anax* when fish are not present by escape behaviours (57); and Mark and one of my graduate students, Margarett Arrington, who is unfortunately not here this week, have both been focusing on a similar problem. We have species that live in the presence of fish and the absence of *Anax* and those that live in the presence of *Anax* and the absence of fish, and they seem to have evolved quite different behavioural repertoires, including different reactions to the presence of fish and the presence of *Anax* (38). So we have noticed that *Enallagma aspersum* that lives in our Ecology Pond (or that used to before fish invaded it a couple of years ago) is quite an active *Enallagma* compared with those that live in the lake. Mark has found similar pairs of species in Michigan and we were curious as to what the advantage of being active was. We were unable to demonstrate that it had any competitive advantage in better exploitation of resources or anything, but Mark's suggestion now is that the activity itself is a good way of avoiding *Anax*: that you are aware of that predator coming and that swimming from an *Anax* works, whereas trying to swim when a fish comes by is suicide; and Margarett's results and Mark's results corroborate each other quite well and some of this work has been done in conjunction with Catherine Blois and Phil Crowley (39) and with some behavioural observations in the system that Phil has described.

CORBET: Does this support the view, then, that the *Enallagma* larvae concerned are recognising the kind of predator that is close to them?

JOHNSON: Yes. They seem to be good at hiding from fish and escaping from *Anax*. That is the bottom line on Margarett's poster which she was not here to explain.

ROBINSON: We have run some additional experiments in our laboratory with *Enallagma civile*. In these experiments we had 16 larvae. From eight of them we removed the gills (caudal lamellae), and the other eight had a full complement of gills. We mixed them together and we observed cannibalism and gill removal much as I described earlier today for *Ischnura posita* (30). Then we repeated the same experiment using *Ranatra fusca*, the water scorpion - we put that in there - and we did the same experiment with *Anax junius*. *Ranatra* took the larvae of *Enallagma civile* regardless of their gill status, and the amount of gill removal was pretty close to what we found when we did not have *Ranatra* in there. Probably everyone is familiar with the fact the *Ranatra* is a sit-and-wait predator. When we put *Anax* in there, however, for those first two situations gill damage was about 20 to 25% (I am not sure of the numbers right now) for 24 hours. When we put *Anax* in there not a single one of the survivors had gill damage. So what this is suggesting, I think, is that *Anax* is more active as a hunter than *Ranatra* and that somehow the damselflies are modifying their behaviour so that they are not acting as they do when predators are absent; they are remaining much more quiescent. In fact, what happened was that *Anax* ate more of the gill-less organisms, but not for the reason we thought. From the work I described earlier today we had thought that gills would save a larva by allowing it to sacrifice its gills and then escape from the predator. In fact, since none of the survivors had missing gills, that must have been totally ineffective in this situation and we believe that probably two things are happening for the gill-less organisms in this case: they are moving the abdomen much as Melisa Moorman (53) described for autotomised individuals; so that they are a little more active and attracting the predators. And the other thing is that gill-less organisms are less likely to swim when faced with a predator, or when faced with a threat; so *Anax* can stalk them over the vegetation and swimming might be a very effective way of escaping from *Anax*, but if you don't have gills you don't swim as frequently.

CORBET: I recall at this point that the caudal lamellae, or gills if you like, of the Zygoptera, especially coenagrionids, are for the first few instars merely lanceolate projections at the posterior end of the abdomen but about halfway through larval development they start to become lamellate (41). I am wondering whether anyone has observed a change in the behaviour in regard to interacting with conspecifics between small Zygoptera larvae and large ones. Jean-Guy, you have done so much rearing work on different coenagrionids, I am wondering whether you have seen any differences that you might not have attached particular importance to until this moment.

PILON: No, I did not, because in our rearing we have a tooth-pick serving as a perch. The larva tends to cling to the perch, moving only to feed and after that coming back to the perch and not moving. So even if there is a change in the form of the lamellae between the earliest instar and the last instar, the larvae exhibited the same behaviour, under rearing conditions of course. I do not know what they are doing in the field.

DUNKLE: Another method of larval defence is stabbing with the anal spines in Anisoptera larvae (42). I observed a particularly interesting example of this when I was rearing *Triacanthagyna septima*. The larvae would typically rest head downwards on a stick at the surface of the water; if you poked at them with a pencil or some other object they would stab hard at it with those anal spines, squirt out the contents of the rectum and then run down the stick. And that was very effective: I could feel the power of the stab through the pencil and they create a cloud of bubbles at the surface of the water which would probably attract the attention of the predator; and then of course there was a sound associated with that. I thought that that would be extremely effective in avoiding certain predators.

WASSCHER: Here is an aspect of the larvae that is more functional than ethological: a few years ago I discovered that some larvae of species that occur in places where there are many fish have large dorsal spines whereas they had small dorsal spines in places that were acid and had no fish. In places that have many fish you can still find species with small dorsal spines but then they are mainly hidden, buried or hidden in some other way from fish predators. It seems likely that if the fish bite on the spines they may feel pricked by them and so they may spit out the prey, thus giving the larvae an extra opportunity to escape. It would be very interesting to see if there is much difference in larval behaviour between two species occupying the same habitat, one of which has large dorsal spines and the other of which has small dorsal spines.

FINCKE: With respect to ontogenetic changes in aggressiveness, I have noted that in larvae of *Megaloprepus caerulatus* I never got aggressive interactions in larvae less than about 7 mm long and in fact in nature, in the tree-holes, I found very small larvae often on the surface of floating leaves; in other words, when they get older they hide under the leaves and attach themselves to the wall of a tree-hole; but I often found several of the very small larvae on the upper surface of a leaf. I think that what they were doing was avoiding the areas occupied by the older larvae but the two size-groups did not interact and I never found (when I reared them together) thoracic holes or loss of lamellae until they were, maybe, 6 or 7 mm long (19).

CORBET: Rob Baker, I wonder whether at this point you would like to comment on papers by Susan Dixon and yourself in which you found that larval movement was depressed more when predators were present (43) and that this depression was more conspicuous in smaller larvae than in larger ones (44). Am I quoting you correctly?

BAKER: I am having trouble remembering all this stuff! I think that the point behind those papers was to see if we could approach anti-predator behaviour in dragonfly larvae from a cost-benefit point of view. We were trying to test Stein's ideas (55) on reactive *versus* fixed responses to predators. What we found was that relatively large larvae of *Ischnura verticalis* would stop some of their behaviours and not move very much when predators were directly present but that there was very little change in their movement compared with when predatory fish were not present. We also showed that when large larvae were not fed very well there was not much difference in their development compared to when they were fed very well. This was quite the opposite to what we found for relatively small larvae, say in about instar F-5. In the absence of fish F-5 larvae move a great deal: they crawl all over the place. However, when they are faced with a predatory fish, they stop moving almost entirely and there is a tremendous difference between fish and non-fish treatments for F-5. Also when you take F-5 larvae and give them relatively poor diets they fare much worse when they have a poor diet than when they have a lot of food. Our interpretation was that this basically fits Stein's ideas that if an animal is at a great deal of risk (as a large larva might be simply because it is more visible) it may evolve anti-predator behaviours in such a way that it is essentially shutting down its behaviour all the time; and it has evolved other ways of ensuring that it has enough food to continue its development. For smaller larvae, which may actually be at less risk, it may be preferable to continue moving until they have some evidence that a predator is there, possibly because they have to pay a greater cost in avoiding the predator. Our results basically seem to fit Stein's ideas (55).

JOHNSON: I should like to say that the last two comments from Ola and Rob seem to involve about the only observations I know of on larvae smaller than about F-3. Most of us concentrate on the large ones because it is easy to watch them and to video-tape them and yet I have a suspicion that a lot of the really interesting density-dependent phenomena of the sort that Brad was telling us about this morning (56,63) are probably concentrated in those even smaller, more vulnerable, less-good-at-surviving-starvation instars, about which we know very, very little.

I don't want to be the one to learn it, but someone should!

CORBET: Yes, a major reason why we know so little about smaller larvae, in addition to the ones that you have mentioned, is that most keys for the identification of larvae are based only on the characters of the final instar; and anyone who has studied the morphology of larvae will know very well that this is because it becomes increasingly difficult to identify larvae of many species the smaller they are. Before we close I should like to take up the remark by Marcel Wasscher about the relative development of the dorsal spines. I think, Marcel, you were referring mainly to dorsal spines, rather than lateral spines, on the abdomens of Anisoptera and to the possibility that this was correlated with exposure to fish predation. I would assume that a useful approach to this would be to look at the development of these spines on the same species in different types of habitat and an obvious candidate for this would be *Leucorrhinia* in certain species of which I think the spines are very poorly developed; moreover *Leucorrhinia* tends to be the example we always think of as a libellulid that is particularly vulnerable to fish predation (48,49).

WASSCHER: It is partly true for the European species, except for *albifrons* and *caudalis* which have very large spines and which live in mesotrophic waters with many fish; but with the other species of *Leucorrhinia* - *dubia* and *rubicunda* - it will be very good to study this question.

CORBET: It is interesting to note here that taxonomists have known about this dichotomy in *Leucorrhinia* for a considerable time (45,46) but I don't think that they suspected that it might have been correlated with exposure to fish predation.

ROBERTSON: Just a brief comment. Anyone who wants to work on this should be aware of the work by Madison workers on *Daphnia* and the facultative development of spines in response to the presence of the predator *Chaoborus* (58-60). I can't remember the name of the guy who did it.

JOHNSON: Stan Dodson.

MICHIELS: I would like to ask one specific question. In all the information I have from larval behaviour and ecology, which is a limited part of the whole literature available probably, I see no mention of difference in behaviour between male and female larvae. Can anyone give me information on this subject?

BAKER: This I do remember, because I did it about two weeks ago! I have just started some experiments designed to try to understand the apparent differences in sex ratio of odonate larvae at emergence. I believe that there is a general pattern for males to be underepresented at emergence (32). I simply wonder whether, as it seems that so many odonate larvae are killed by predators, there might possibly be a difference in the behaviour of male and female larvae which perhaps puts male larvae at greater risk? Now I have some very preliminary experiments using F-2 larvae of *Ischnura verticalis*, which can be easily sexed. I was quite surprised to find out that there is indeed more movement by male larvae: they tend to crawl more and to groom more. It is possible that this difference in behaviour of males puts them at greater risk. I don't know. What I would like to know is why males would want to forage more or move more than females. I have talked to Ola about this but we do not have any ideas; but these are very preliminary data.

CORBET: In closing this session, I would like to thank you all very much for your participation.

JOHNSON: Let me thank Philip.

Many of you know this; but for those of you who do not, and who might have something to contribute, let me say that I have more or less committed myself to preparing a review paper (47) on the subject of interference among larval odonates for *Trends in Ecology and Evolution*, a manuscript that I had hoped to have ready for criticism here, but I've been distracted! This session was in part suggested by me in the hope of bringing out a lot of the organisation for that paper; so any of you who have things in press that you know might be relevant to those considerations, and who haven't yet sent to me are asked to do so.

APPENDIX I

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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.

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APPENDIX II

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INDEX TO CITED AUTHORS

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

INDEX TO ODONATA

Species are listed under the generic name only.