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DO *CORDULEGASTER* MALES DEFEND TERRITORIES? A PRELIMINARY INVESTIGATION OF MATING STRATEGIES IN *CORDULEGASTER BOLTONI* (DONOVAN) (ANISOPTERA: CORDULEGASTERIDAE)

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The behaviour of *C. boltoni* was observed and the presence of individually marked males was recorded continuously at a rivulet in the Fichtelgebirge, south-eastern Germany. The males spend a considerable amount of their time patrolling up and down along rivulets. They are aggressive towards each other, but do not restrict their flight range and do not delimit territories. Females only rarely visit rivulets for mating and ovipositing, without obvious site preference. — The intraspecific aggression effects a spacing-out of the males and possibly a regulation of male density at the mating place (or rendezvous site). This behaviour of being aggressive towards competitors but not delimiting territories may be an optimal mating strategy for *Cordulegaster* males in their specific ecological situation.

INTRODUCTION

In male dragonflies territorial behaviour has been described in a wide range of species of various families (cf. CORBET, 1962, 1980). Almost nothing is known, however, about the Cordulegasteridae. Their behaviour could be of considerable interest in understanding the evolution of aggressive and territorial behaviour in anisopteran dragonflies (KAISER, 1974b), since many primitive traits are present in this family.

The interest in the behaviour of dragonfly males has further increased by general considerations about mating systems (cf. PARKER, 1978). Dragonflies provide an example of competition for females at distinct mating

places. Due to the wide range of mating strategies realized in dragonflies (CORBET, 1980; KAISER, 1976, 1982a) their behaviour may be especially favourable for testing theoretical considerations. One question which has to be answered for *Cordulegaster* is: How do *Cordulegaster* males partition their mating places and thereby their mating chances?

In the present paper some observations on *Cordulegaster boltoni* are presented. Despite their preliminary nature, I hope they prove worthy of discussion in view of the almost complete lack of knowledge concerning *Cordulegaster* behaviour.

METHODS

STUDY SITES

A study on a relatively dense population of *Cordulegaster boltoni*, using marking techniques, was carried out in 1978 at the Zinnbach rivulet (560 m above sea level) near Rehau and Hof (Fichtelgebirge; 50°15'N, 12°09'E) in south-east Germany. A section of 330 m length (Fig. 1) was observed continuously from July 27th to August 1st and on August 6th. The Zinnbach is still an almost unpolluted upland rivulet of 1 to 2 m width with sparse submerged vegetation and ample sandy banks. It flows through forests and mainly through meadows (with accompanying trees and bushes). In the study section trees and bushes were spaced out, while upstream and downstream the Zinnbach was completely overgrown by trees. During the study *Cordulegaster* apparently preferred this more open section.

Some casual observations on the behaviour of *Cordulegaster boltoni* and *C. bidentatus* were made from 1964 to 1970 at several small rivulets near Freiburg (Schwarzwald; 48°00'N, 7°45'E) in south-west Germany.

MARKING AND OBSERVATION TECHNIQUE

All dragonflies were marked individually with coloured wing bands by catching and then painting them with modified nail lacquer (KAISER, 1974a, 1982b). Marked individuals were identifiable individually at a distance of up to more than 10 m according to circumstances and flight position. The study section was kept under constant observation by walking up and down. All marked dragonflies were recorded in prepared outline maps of the study section.

Unfortunately, the whole section of 330 m length could not be overviewed at the same time, so the records are not complete. I saw no means of avoiding this shortcoming. I suppose the records to comprise at least ninety percent of dragonfly activity inside the study area (cf. also p. 145). A further complication arises since the dragonflies, although preferring the study section, occasionally flew up and downstream where they could not readily be followed.

The flight paths of individual dragonflies were followed for longer distances along the study section. I occasionally visited the adjacent sections of the rivulet, especially when following individual dragonflies.

BEHAVIOUR

FEEDING FLIGHT

In feeding flight the dragonflies fly to and fro, often loosely orientated along forest roads or along the edges of forest clearings or brushwood. The flight height is considerably variable, mostly around 1 m, but may be much higher over bushes. The flight paths resemble those described for *Aeshna cyanea* (KAISER, 1974a, Fig. 4); in most cases they appear to be rather random, but sometimes they follow a fixed pattern for a short while. During feeding flight insects are grasped with the legs in the manner usual for dragonflies. There are apparently no differences between males and females. I have observed *Cordulegaster* in feeding flight in the immediate vicinity of rivulets as well as at least several hundred metres away from the nearest rivulet. *Cordulegaster* fly with considerable less agility than aeshnids and are easy to catch even in feeding flight once they have approached close enough to the net.

PATROL FLIGHT

Mature males spend up to several hours every day flying up and down along rivulets in patrol flight. Their flight is rather straight, steady and moderately fast and does not feature hovering; the flight height is mostly 10 to 30 cm, but may vary. Sometimes the males fly in a rather jerky manner. On the whole their manoeuvring ability is rather inferior in comparison to other dragonflies. Nevertheless, they fly throughout the day, although frequently pausing and settling (cf. Figs 2 and 3).

The flight paths recorded from several males flying at the Zinnbach are depicted in Figure 1. The males have a tendency to fly in one direction of the rivulet for quite a long distance (up to several hundred metres) before turning and flying the same way back. Despite this general tendency they turn around now and then and cover a shorter length of a few metres one or several times prior to continuing their flight. Changing direction is obviously encouraged by landmark features such as a bush overhanging the water surface. Now and then I observed males flying to and fro over such a stretch demarcated by vegetation; this lasted for no more than a few minutes before the dragonfly moved on. This behaviour gives the impression that the dragonfly patrols a territory; nonetheless, for the males, no individually fixed areas could be identified.

Two patrolling males start fighting as soon as they catch sight of each other. The distance over which the dragonflies detect each other varies considerably and ranges mostly between one and three metres. The fights are not vigorous compared with other dragonflies. Often the combatants

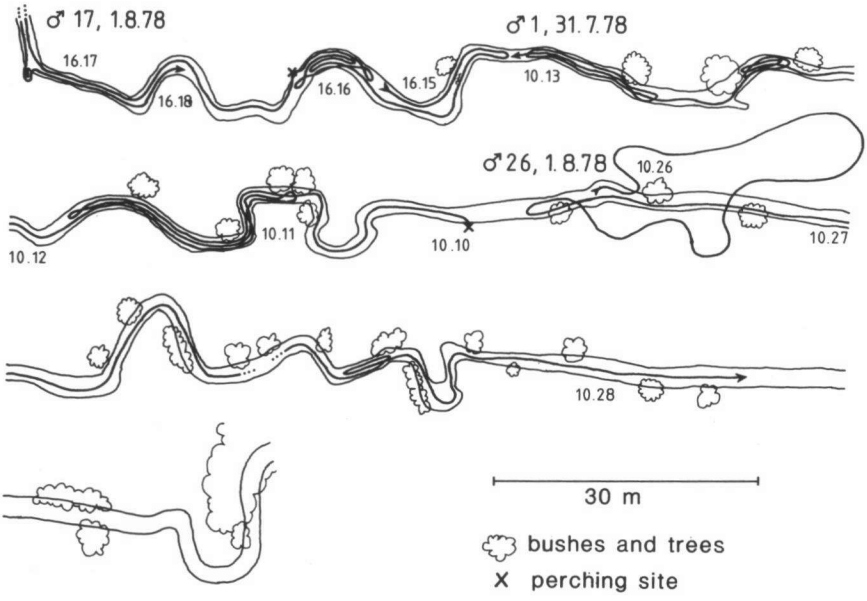

Fig. 1. The study section of the Zinnbach with examples of flight patterns recorded from 3 different *Cordulegaster* males. The number of the individual and the time as the path develops are given. Crosses indicate perching sites. The rivulet flows from the bottom right to the upper left. On the left side of the rivulet (bottom side in the picture) are meadows with grass, on the right tall grass and herbs with brushland at some distance.

encircle and brush against one another before each continues his patrol flight. Occasionally I have observed more vigorous fights lasting up to 10 seconds, the males charging each other repeatedly. From time to time one male reacts to a fight by leaving the immediate vicinity of the rivulet, flying over meadows or along bushes; and eventually he may settle. *Cordulegaster* males are also attacked by males of other large dragonfly species, e.g. *Aeshna* and *Somatochlora*. In these species fights are much more fierce and if approached vigorously *Cordulegaster* males give way to them.

Cordulegaster males often settle during patrol flight on plants overhanging the water surface or in the vicinity of the rivulet (ROBERT, 1959; MÜNCHBERG, 1964). They do not move the head in watching passing insects as do gomphids and libellulids. They react to slight disturbances by flying up and continuing the patrol flight or approaching other dragonflies if provoked.

The patrol flight in its typical form is clearly distinct from the feeding flight in being strictly orientated over the water surface; the flight height is

kept constant, males fight each other, and feeding does not occur. Patrol flight is frequently performed less intensely and there are gradual transitions from patrol flight to feeding flight.

BATHING

On one occasion I observed a male which struck the water surface four times consecutively before flying up and cleaning the wings by bending the abdomen upwards and clapping the wings together. Then he stretched the abdomen again thereby wiping the upper wing surface (for the same cleaning movement in *Aeshna* cf. KAISER, 1974a, Fig. 17). The male then disappeared in the nearby brushland.

MATING

As soon as a patrolling male catches sight of another flying dragonfly he approaches it. If it is a male both will start fighting. If it is a female she will fly away from him as he approaches, sometimes very swiftly. He tries to keep up with her and to seize her from above with his legs, then to bend his abdomen forwards and to fasten his abdominal claspers to her head. The pair then leaves the rivulet and disappears somewhere in the vegetation. There is no evident courting behaviour but males try eagerly to catch every female. During the study I observed about one mating per day. As mating occurred rather rarely and pairs left the waterside I cannot present more detailed information about mating.

OVIPOSITION

Cordulegaster females have a prominent ovipositor and the behaviour of inserting eggs in a sandy substrate while flying has often been described (e.g. CORBET, 1962; ROBERT, 1959; VÖLKER, 1955, 1970). I observed *Cordulegaster* females flying along rivulets probing here and there by hovering in one spot, the body axis held vertically, and then dipping the lower part of the abdomen rhythmically into the water. During this probing the females also try spots which are apparently unsuitable because after a few dips they will fly on and try some other site.

Having found a suitable place, usually a bank of sand or fine gravel covered by a few centimetres of water, the female starts continuously hovering and dipping into the sand with 1 to 2 dips per second. Now and then the female hovers without dipping, turning on the spot, before continuing or moving to another place. The female usually stays at one site for some minutes, but I have observed one female remaining at one locality for longer than a quarter of an hour. Oviposition places are not very uniform, differing

in the depth of the water (few millimetres to five centimetres), colour and structure of the substrate (bright sand or gravel to dark ground interfused with mud), and in the surroundings (forest with tall trees and lacking undergrowth to open meadows). I have too few observations to be able to indicate preferences. MÜNCHBERG (1964) reports that females also lay eggs in deep water; I have no information as to whether females dipping the abdomen into the water without contacting the bottom actually release eggs or just probe.

PRESENCE AT THE MATING PLACE

DAILY VISITS

Most marked males visited the study area daily. Of the 28 males marked from July 29th to July 31st, 18 males were recorded again, 15 of these on several days (Tab. I). This indicates that the males have a tendency to keep to a certain section of the rivulet for a longer period.

The attachment to a place is not perfect. A substantial number of the marked males did not reappear. Some males might have been scared away

Table I

Date of marking and daily records of marked males of *Cordulegaster* in the study area in 1978

Date of marking	No. of ♂	Date with daily record				
		29-VII	30-VII	31-VII	1-VIII	6-VIII
27-VII	1		+	+	+	+
29-VII	3		+	+	+	
	4	+	+	+	+	
	6			+		
	9		+	+	+	+
	14		+	+	+	+
	15	+		+		
	16		+	+	+	
	17			+	+	+
	19	+	+	+	+	+
30-VII	20			+	+	
	21		+			
	22				+	+
	24		+			
	25			+	+	+
	26			+	+	
	27				+	+
	28			+	+	
31-VII	31			+	+	

by being caught and painted; and, consistent with this view, the majority of the marked males did not reappear on the same day. However, most males visited the study area for a while and did not reappear later on: obviously there is a constant change of individuals in a local population (cf. Tab. II). On August 6th, only 6 males of the 36 previously marked (July 27th to August 1st) were observed; as this date is rather late in the flying season and as the weather was not as fine as on the former days this result could be partly due to a loss of males or to some males not being active at the rivulet during this particular day. The males newly marked each day, however, clearly indicate that there is a constant low rate of immigration of males who probably visited other parts of this or other rivulets on previous days (cf. also KIAUTA, 1964).

Among the 4 marked females, I encountered one again during the short observation period. Females apparently visit rivulets much less frequently than males and not necessarily every day but only after a pause of several days.

VISITS DURING THE COURSE OF A DAY

The recorded presence of individual males in the study section of 330 m length during two days is depicted in Figures 2 and 3. There are two restraints to the completeness of the data as already discussed: the study area could not be completely checked for dragonflies at any one moment, and the dragonflies also visited adjacent sections of the Zinnbach. Thus a male reported at one moment was definitely present, but a male not reported at a certain instant might have been at another location of the rivulet. However, it is rather improbable that a male not reported for five or ten minutes actually had been inside the study area as I kept almost constantly moving up and down and I should have seen it after a few minutes had it been on the wing.

The pattern of presence of the individual males indicates that males may be active at the water throughout a warm day (e.g. male No. 14 in Fig. 2, and male No. 26 in Fig. 3) and will stay there at least for several hours (e.g. male No. 1 in Figs 2 and 3). A close look reveals that the highest density of males is reached during the late morning until noon. In the afternoon the number of males is markedly lower despite high temperatures. This pattern is repeated in the number of fights during the day (Fig. 3).

The males are not constantly active in patrolling but settle quite often for lapses of time of less than a minute to a quarter of an hour (e.g. male No. 26). Males which settled in the vegetation were hard to detect; many of the gaps in the records are probably due to the males having settled.

I suppose that the marked males not recovered had emigrated from the

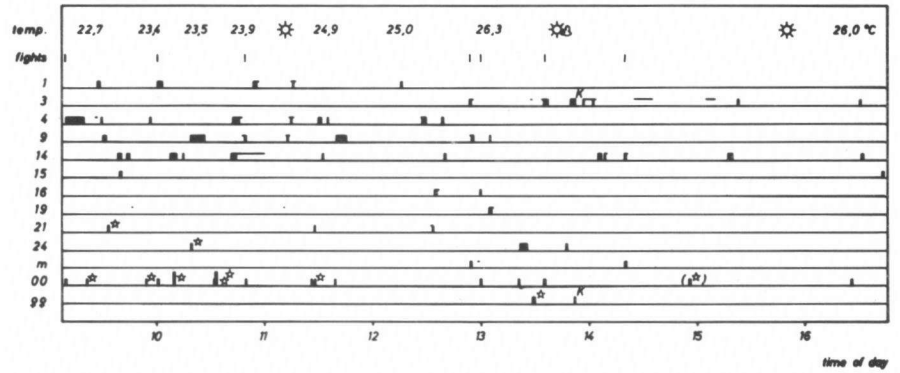

Fig. 2. Recorded presence of all *Cordulegaster* individuals in the study area at the Zinnbach on July 30th, 1978. On this day a large proportion of all males was newly marked (cf. Tab. II). Each line represents one individual male with its number (cf. Tab. I). The line m indicates males which were marked but could not be identified. In the line oo all males not yet marked have been included together. In the line ♀♀ all females observed are presented. A broad mark represents the dragonfly patrolling along the rivulet, a thin mark indicates the dragonfly settled. The qualifications with respect to the completeness of the records are discussed in the text. In the top row are indicated air temperature and cloudiness; in the second row each observed fight between two males is represented by a dash. An asterisk (*) indicates that a not yet marked dragonfly has been caught and marked individually. A *K* indicates a copulation or copulation attempt (at least tandem position). The 00 male marked last on this day was caught outside the study area and is therefore enclosed in brackets. The time of day is given as MEZ.

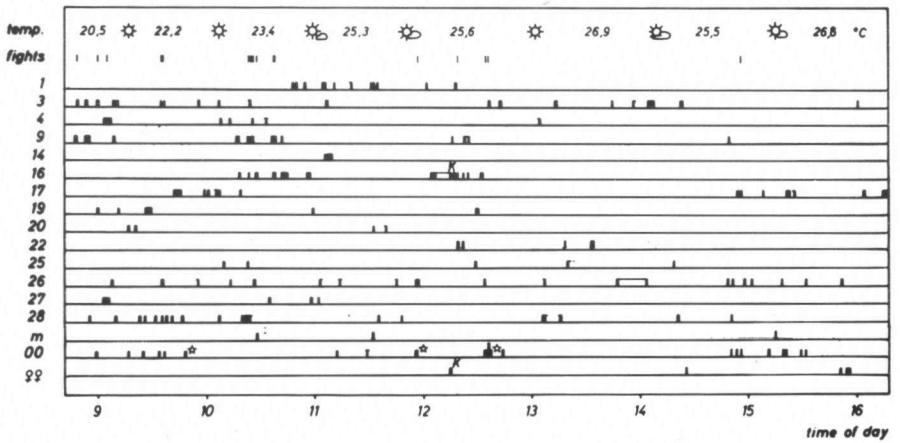

Fig. 3. Recorded presence of all *Cordulegaster* individuals in the study area at the Zinnbach on August 1st, 1978. Explanation of symbols in Fig. 2.

study area. Obviously the *Cordulegaster* males have a tendency to remain at the same section of a rivulet on successive days but occasionally they move to other places. MÜNCHBERG (1964) draws the same conclusion from his observations on marked *Cordulegaster* males. One male (No. 19), which I caught nearly 1 km upwards from the study section and released in the study section after marking it, was recorded in the study section on the following days. This suggests that the males tend to remain where they are.

On a few occasions I followed individual males for distances up to about 800 m along the rivulet. The full range of the rivulet covered by one male during a day could not be assessed; at the Zinnbach it may well be a stretch of several kilometres in length; the males obviously concentrated on certain sections such as the study area.

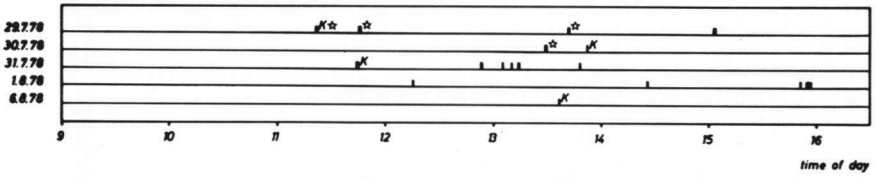

Fig. 4. Continuously recorded presence of *Cordulegaster* females at the Zinnbach study area on all five days. Each line represents one day, all females recorded on this day are represented with broad lines. An asterisk (*) indicates a female being caught and marked, a *K* indicates a female being grasped by a male and attempted copulation (at least tandem position).

The females paid visits throughout the warm part of the day, after 11 a.m. (Fig. 4). In comparison to the males, female visits are rare events. Such visits are frequently terminated by a male seizing or chasing the female; in the latter case the female may withdraw briefly and revisit the rivulet at another place. The data available suggest that the females visit the rivulet somewhat later during the day than the males, but no definite conclusions can be drawn. Further, the data do not indicate that egg-laying females avoid being disturbed by males in that they only visit the water in the evening after the males have ceased to be active (females of *Aeshna juncea*, for example, show this behaviour; KAISER, 1976). The copulations were observed around midday. Thus it would appear that females visit the rivulet with roughly equal probability from late morning until afternoon, but the observed visits are too few to draw substantial conclusions.

TOTAL NUMBERS OF MALES PRESENT EACH DAY

The number of all males (marked and unmarked) visiting the study area every day was astonishingly constant despite the continuous exchange of individuals (Tab. II). On the four days from July 29th to August 1st the

Table II
Number of males daily visiting the study area

Date	29-VII	30-VII	31-VII	1-VIII	6-VIII
Already marked	0	8	13	15	8
Newly marked	17	9	4	3	7
Total	*17*	*17*	*17*	*18*	*15*

number was 17 or 18, on August 6th it was 15. This constant value is even more remarkable as the proportion of marked males changed notably and weather conditions varied to some extent (maximum air temperatures between 26°C and 27°C on the first 3 days, 28°C on August 1st, 21°C on August 6th, but varying degrees of cloudiness on the different days).

The time of day when as yet unmarked males appeared and were caught may be informative. Of the 17 males marked on July 29th, the first day of continuous observation, 14 were caught in the morning between 10.00 and 11.32, the other 3 after noon. On July 30th, of the 9 marked males 7 were caught between 9.22 and 10.33, one at 11.28, and only one in the afternoon (Fig. 2). On the following days all the new males were caught around noon. On August 6th the 7 new males were caught between 10.36 and 12.06. This might imply that males who return to an area already visited on the previous days visit this area earlier than males having so far visited other sections or rivulets. One might infer from this that those males arriving late in the day have been expelled from other sections.

Although the observation period was too short and more data are needed to draw definite conclusions, these preliminary results seem to indicate that there is some regulatory mechanism, limiting the number of *Cordulegaster* males at the mating place.

DISCUSSION

CORDULEGASTER MALES DO NOT DELIMIT TERRITORIES

The most widely used definition of a territory as "any defended area" is in this abridged form not a sufficiently sensitive tool to investigate territorial behaviour. To facilitate a more detailed discussion I shall regard territorial behaviour as being composed of two components:

(1) Site-dependent intraspecific aggression;

(2) Individual site attachment.

These criteria imply that each territory owner is dominant inside his own territory and subordinate outside, so that he may be driven out by neighbours

when trespassing into their territories. To arrive at a stable partitioning of the mating place each individual male should choose another site to defend to which it adheres for some time (KAISER, 1974a, 1982a).

If all males were equally aggressive towards each other over the whole mating place or if all individuals tried to defend the same site, the result would be a constant jumbling of fighting males, a situation which has actually been observed in *Onychogomphus* (KAISER, 1974b).

Territorial behaviour as defined above has the effect of dispersing the individuals more or less uniformly over the mating place thereby achieving a spatial partitioning of the mating place and thus the mating chances (cf. KAISER, 1974a, 1982a for a full discussion with references).

Cordulegaster males are undoubtedly aggressive towards each other, but they are aggressive with the same intensity along the whole rivulet and all patrol the whole rivulet thus not restricting their patrol flight to individually delimited areas. This means that in *Cordulegaster* males aggression does not vary site-dependently, nor do the males have individual site attachment. Thus — according to the definition given above — territorial behaviour cannot be ascribed to *Cordulegaster* males.

Obviously it is not helpful to argue that the whole rivulet is a "defended area". Many males fight inside this "area" without achieving delimitation of individually fixed areas. Certain stretches of the rivulet may be visited more often than others and therefore there may be preferred areas. However, as far as I have observed these preferences are not individual ones but rather all males show a preference for the same sections.

TEMPORAL SEQUENCE OF MALES AT THE MATING PLACE

In *Aeshna cyanea* (KAISER, 1974a) and *A. juncea* (KAISER, 1976) the males pay several short visits per day to the pond serving as mating place. The males constantly relieve each other at the pond. Intraspecific aggressive encounters thereby influence the duration of the visits and the temporal sequence of the males at the mating place. In these species intraspecific aggression functions so as to regulate the temporal partitioning of the mating place ("temporial" behaviour; KAISER, 1974a). In checking for temporal sequencing in *Cordulegaster* males I conclude — as far as the records allow — that they stay at or immediately near the mating place for at least several hours if not for the whole warm part of the day. All males are present at about the same time. Most males arrive in the morning, and those arriving later in the day may well have already patrolled at other places. Thus in *Cordulegaster* males there seems to be no (or at least no clear) sequencing of the presence at the mating place.

INTRASPECIFIC AGGRESSION AND MATING CHANCES OF INDIVIDUAL MALES

In concluding that intraspecific aggression of *Cordulegaster* males is neither effective in spatial nor in temporal partitioning of the mating place we have to ask: what function has intraspecific aggression in *Cordulegaster* males; and what effect has aggression on the mating chances of the individual males?

In assuming that each male behaves so as to maximize its mating chances I conclude that a male will search at those places and during those times where and when it is most likely to encounter a responsive female. In order to estimate a male's chances of encountering a female we must be familiar with the females' behaviour of visiting the rivulet. As already discussed, it is reasonable to conclude from the few data of the present study that *Cordulegaster* females arrive at a suitable rivulet throughout the warm part of the day and probe for oviposition sites at every place with about equal probability. So the chances of meeting a female are about the same throughout most of the day and at all places of a uniform rivulet.

As females make only a few visits, meeting a female will be a rather rare event for a male. So from a *Cordulegaster* male's point of view he should patrol the rivulet as extensively as possible for as long as possible.

In maximizing his own chances a male should try to minimize competition from other males also patrolling the same region of the rivulet; he can avoid or lower competition in one of two ways: (1) By expelling other males; (2) By retreating himself and moving to another place with fewer competitors.

The alternative employed should depend on the resulting success. I would expect that at a low competitor density — which means infrequent encounters with other males — any one male should try to expel opponents, while at a high density with consequent frequent encounters a male should prefer to retreat. This supposed "playing a mixed strategy" will be discussed elsewhere.

Chasing a competitor away may have different effects. If the competitor flies a considerable distance away he may change to another rivulet (KIAUTA, 1964) or to another distant region of the same rivulet, thereby very probably avoiding further contact with his opponent; or he may just move such a distance that he is out of the present action radius of his opponent but patrolling essentially the same region of the rivulet. Nevertheless, in all cases fighting results in a spacing-out of the patrolling males.

If a male delimited a territory which he could overview totally and from which he could exclude every other male he would necessarily restrict his encounter expectancies to a very short stretch of the rivulet and would therefore have a very low chance of meeting a female. Obviously in *Cordulegaster* cruising around and tolerating a certain amount of competition may result in

higher mating chances than delimiting territories.

These rather speculative considerations assign to the aggressive behaviour of *Cordulegaster* males the function of reducing competition for females. It also appears clear that this strategy of partitioning mating chances between *Cordulegaster* males is quite different from the territorial or "temporial" behaviour observed in other dragonfly species. Considering the ecological situation of *Cordulegaster* inhabiting long stretches of rivulets with a very low density it is plausible that the behaviour of *Cordulegaster* males is different from that of other dragonflies living in different ecological situations. The behaviour of species living in similar conditions to *Cordulegaster* could be expected to resemble that of *Cordulegaster*. Thus the behaviour of *Cordulegaster* may provide a piece for assembling a general theory and understanding of the complex variety of mating systems in dragonflies.

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