Odonatologica 17(3): 205-212 *September 1, 1988*

DENSITY-DEPENDENT BEHAVIOUR IN *AESHNA CYANEA* (MÜLLER) MALES AT THE MATING PLACE (ANISOPTERA: AESHNIDAE)

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Received September 11, 1987 / Revised and Accepted April 27, 1988

Marking experiments showed that under high male density conditions the behaviour of *A. cyanea* males is strongly territorial; when male density is low, long-range patrol flights without territorial attachment are observed. It is suggested that this variable behaviour is an adaptation to fluctuations in male density which maximizes mating chance.

INTRODUCTION

In anisopteran dragonflies a variety of mating systems occur (CORBET, 1980). Male strategies reported for different species range from aggressive behaviour without site attachment (e.g. SCHMIDT, 1964; KAISER, 1974; CANNINGS, 1982) to strong localization with exclusive occupancy of space (e.g. JACOBS, 1955; HEYMER, 1969). Besides interspecific differences in the spacing behaviour, there also are great intraspecific differences (e.g. UBUKATA, 1975; HILTON, 1983; PARR, 1983; SHERMAN, 1983). Numerous models have been developed to explain the spatial distribution of individuals at the mating place (e.g. PARKER, 1970, 1974; WALTZ, 1982; POETHKE & KAISER, 1985, 1987; COURTNEY & ANDERSON, 1986; UBUKATA, 1986) and there is strong evidence that (at least in the flyer-type dragonflies) strong site attachment and territoriality are adaptations to high male density at the mating place. With the help of computer simulations which allow a quantification of mating frequencies for male densities and for males of different behaviour it has been shown (POETHKE & KAISER, 1987) that the patrol flight behaviour of *Aeshna cyanea* males can be understood as an adaptation to the low male densities at the mating place typical of this species: while strong localization and the establishment of territories will maximize the mating chances in high-density situations it pays to search the whole mating place (pond) if the number of competitors present at the pond is small. Bearing this in mind, it was of particular interest to study the behaviour of *A. cyanea* males when male density at the mating place was high. How would the males of this species — typically known as patrollers without pronounced site attachment — behave in situations when site attachment and territoriality are more efficient mating strategies than far-range patrolling?

In the following I will present some observations that show that even males of this species may show strong localization if male density at the mating place is high. Under these circumstances males will limit their patrol flight to small sectors of the shoreline and defend these "territories" against competitors. The observations show that both types of behaviour (long-range patrol flight as well as strong localisation at small sectors of the shoreline) may be interpreted as density-dependent unfoldings of the same strategy (MAYNARD SMITH, 1982).

STUDY SITE AND METHODS

Observations were carried out at a small, partly overgrown pond near Botzelaer, a small village near Aachen at the border of Germany, the Netherlands and Belgium. The pond is situated amidst large pastures and is supplied by a well.

In July and August 1984, I individually marked 158 males of *A. cyanea* with coloured wing-bands (for a detailed description of the marking method see KAISER, 1974). To register the spatial distribution of the males along the shoreline and the flight paths of individual males the shoreline was subdivided into 10 sectors (Fig. 1). I chose sectors so that they were separated by natural landmarks. This method of subdivision results in areas of differing size but it facilitates the clear determination of the dragonflies' actual localisation. On the other hand, it reduces the number of changes of shoreline-section that had to be registered because dragonfly males often used these landmarks as turning points during their search flight. For a total of 64 visits of marked males I registered the localisation of the males every two seconds. Usually only one male at a time could be observed, but with the help of a second observer it was possible in some cases to observe two males at a time.

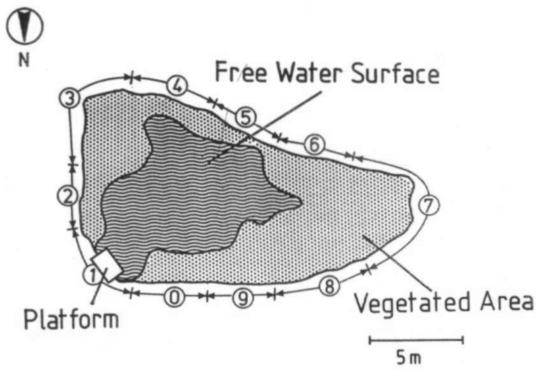

Fig. 1. Situation at the pond. The shoreline is subdivided into ten sectors. The sectors are bordered by natural landmarks and differ in size.

RESULTS

Males of *A. cyanea* pay several short visits every day to their mating places at small ponds (for a detailed description of mating behaviour in this species see KAISER, 1974, 1976). At the water, males patrol the whole shoreline searching for females. Patrolling males often interrupt their flight, hovering on the spot, and they frequently change the direction of their flight (KAISER, 1976). When searching males encounter a conspecific, they immediately fly towards it. If it is a female, they try to seize her and copulate, if it is another male, both males will start fighting (KAISER, 1974).

Fighting males usually give up their close attachment to the shoreline and often they leave the pond in the course of their fight. Whether a male will return to the pond after the fight depends on the time he has already spent at the mating place. The longer he has been at the water, the greater the probability he will leave the pond to his competitors. Thus, *A. cyanea* males take turns in the use of the mating place. POETHKE & KAISER (1985) have shown that the function of this time-sharing behaviour is to maximize mating opportunities. Contrary to the

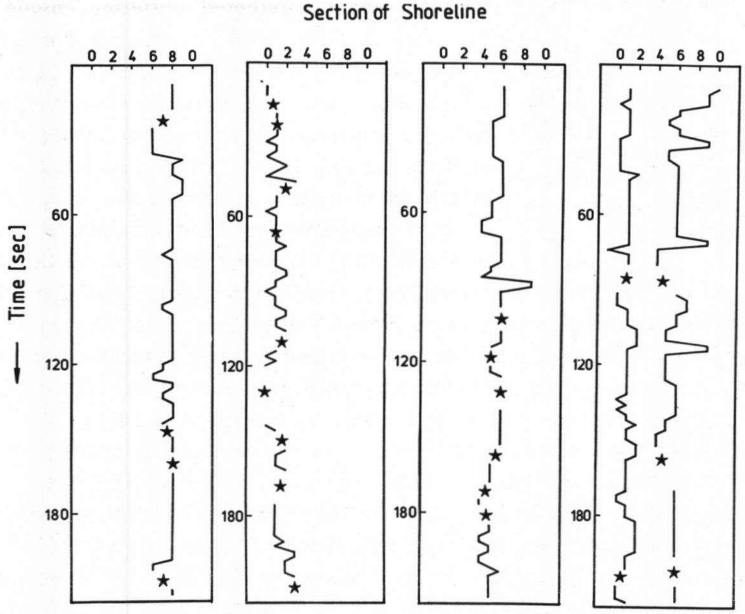

Fig. 2. Four typical records of flight paths of *Aeshna cyanea* males at the shoreline. The numbers refer to the sectors of the shoreline as shown in Fig. 1. Stars indicate intermale fights. The records were taken: (a) 22 August 1984, 10.56 am.; — (b) 23 August 1984, 9.09 am.; — (c) 28 August 1984, 2.15 pm.: — (d) 29 August 1984, 11.10 am.

spatial partitioning of the mating place as found in several damselflies (WAAGE, 1983; MOORE, 1983) and also in some libellulids (JACOBS, 1955; McVEY, 1981; HILTON, 1983), aeshnids have developed a system of temporal partitioning of the mating place.

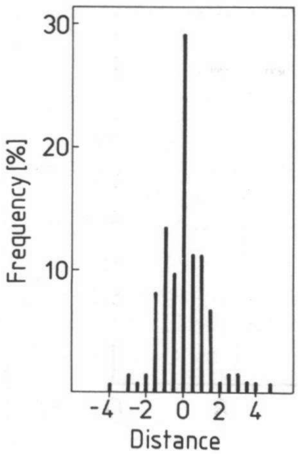

Fig. 3. Frequency distribution of the distance (in sectors according to Fig. 1) between the sector occupied by a male when the fight began and the sector occupied by the male immediately after the end of the fight.

During the whole observational period at the pond under study male densities were much higher than typical of *A. cyanea*. MOORE (1962) found densities of one per 100 m of shoreline to be typical of this species, while KAISER (1974) rarely found more than five males per 100 m shoreline during his extensive observations. During my observations I rarely found fewer than three males at the pond (≐ 6/100 m) and often eight or more (> 15/100 m). As Figure 2 shows, fights are rather frequent and males are strongly localized in this situation. In contrast to the long-range patrol flight behaviour reported by KAISER (1974, 1976) for this species, males spent their time at the mating place in relatively small sectors of the shoreline. These "territories" were mostly occupied during the whole visit and when localized males were attacked by intruders they returned to their sector after the fight. Sometimes males changed from one sector to another during their visit. Localized males attacked conspecifics as soon as they caught sight of them. This behaviour is not limited to the range of the territory. It also holds, if competitors are registered in a neighbouring sector (even attacks towards males flying on the other side of the pond were observed occassionally). Since male visits rarely last for more than 30 minutes, territories are occupied by different males in the course of a day. Territorial borders are variable according to environmental conditions, such as direction and intensity of sun and wind, temperature, etc.

It is evident that males recognize their territories: fighting males leave the shoreline and during a fight — which may take up to several minutes — the competitors often cross several sectors of the shoreline (which may result in a number of other males joining in the fight). However, males usually return to the same shoreline section they had occupied before the fight (Fig. 3). Though males may have to cross the water surface and some other sectors of the shoreline on their way back, they rarely take up their search flight in another sector than the one occupied before the fight. Other sectors are crossed in a fast flight. This behaviour is not limited to particular sections of the shoreline, but is valid for almost all sections (Fig. 4).

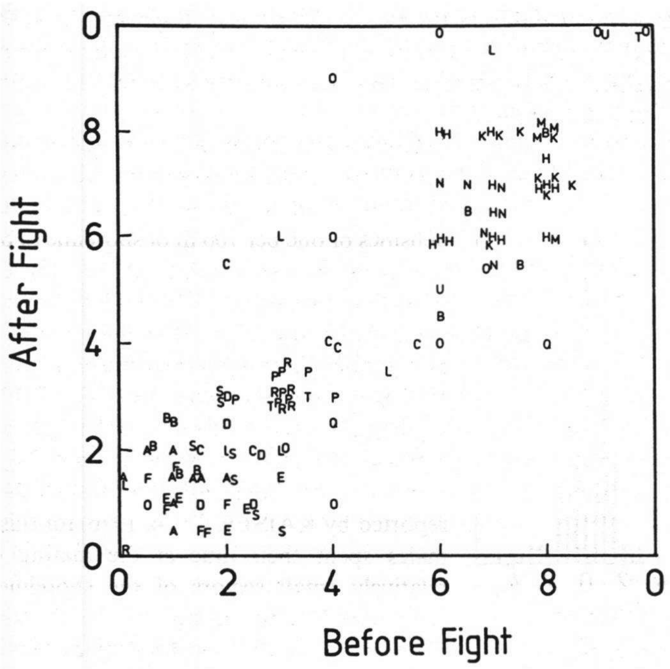

Fig. 4. Relation of the sector of the shoreline that is occupied after the end of a fight with a conspecific male to the sector that was occupied before the fight (diiferent letters refer to different individuals).

DISCUSSION

Adult *A. cyanea* males may obviously adjust their behaviour to the actual male density at the mating place. In high density situations they are strongly localized and search a small part of the shoreline only; if male density is low they show their typical long-range patrol flight along the whole perimeter of the pond. Similar observations exist for a number of other anisopteran species. UBUKATA (1975, 1986) observed that males of *Cordulia aenea* get more and more site attached when the frequency of inter-male encounters rises with increasing male density. A similar change of behaviour has been reported by HILTON (1983) for *Libellula julia* and by PARR (1983) for *Nesciothemis nigeriensis*. Also for *Cordulegaster boltoni* a new study (Kaiser, unpubl.) has shown that the typical long-range patrol flight behaviour of this species (KAISER, 1982) is limited to low-density situations. During observations at a dried-up rivulet in Spain, which was frequented by an unusually high number of males, *Cordulegaster* males were very site-attached and males often defended small territories (cf. also KIAUTA, 1964).

Since adult dragonflies are unable to identify conspecifics in the distance, we may ask how they manage to adjust their behaviour to the actual male density at the mating place. UBUKATA (1986) reported that *Cordulia aenea* males may recognize conspecifics at a distance of approximately one metre. *A. cyanea* males will react to large dragonfly-sized flying objects that are up to approximately five metres away. However, none of the anisopteran species have the visual prerequisites that allow a continuous monitoring of male density at the mating place.

Our answer to this question was inspired by an observation that is reported by DAVIES & HOUSTON (1984, p. 148) in a paper on territory economics. They observed the mating behaviour of *Libellula quadrimaculata* and found that the territorial system of this species is maintained through all individuals following the same simple movement rule: "fly until you meet a neighbour, then turn round and fly back again". This rule is very similar to the behaviour of *Cordulia aenea* as it is reported by UBUKATA (1986), but it is much too simple to describe the behaviour of *A. cyanea* males at the mating place. The patrol flight of *A. cyanea* males is characterized by frequent changes in the direction of flight (KAISER, 1976) and usually a change in direction is not caused by a conspecific male. Anyhow from what we know so far about the behaviour of *A. cyanea* males we may derive a movement rule that is quite similar to that of *Libellula quadrimaculata* and *Cordulia aenea:* At the mating place the males fly to and fro in a random way. Since conspicuous landmarks (e.g. rocks, bushes, poles) are favourite turning points on their flight path, the shoreline may be described as a number of sectors that are separated by such landmarks. Usually the males will frequently change from one sector to the next during their search for females. If we assume that the readiness of a male to cross the border between two sectors is greater the longer the male has been undisturbed by conspecifics, the resulting male behaviour will concur with our observations (high male density) as well as with that of KAISER (1974) (low male density). When male density is high, intermale encounters will be frequent and consequently males will be very reluctant to leave their sector of the shoreline. In this situation an observer will see that the shoreline is divided into a number of territories and that individual males are very site–attached. When male density is low, males will rarely fight and consequently they will frequently change from one sector of the shoreline to the next. In this situation an observer will find the typical non-territorial patrol flight behaviour as has been reported by KAISER (1974) for this species.

Males will optimally respond to male density at the mating place by following the simple strategy: (a) After fights with conspecifics go back to the sector of the shoreline you occupied before the fight; — (b) Be more reluctant to leave the sector if fights are frequent. We have shown that males follow the first part of this rule and further effort will be invested to test if they also follow the second. From what we know so far, there is strong evidence that for *A. cyanea* males the categories "territorial" or "non-territorial" are not adequate for the characterization of their mating behaviour. More detailed observations are needed and in several cases they may show that two populations (or even two species) which in the first place seemed to differ in their mating strategy, follow the same strategy which may find different expression under different ecological conditions.

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