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TERRITORIALITY AND MOVEMENT PATTERN IN A POPULATION OF *CALOPTERYX CORNELIA* (SELYS) (ZYGOPTERA: CALOPTERYGIDAE)

K. HIGASHI[1]* and T. UEDA[2]

[1]Department of Biology, Faculty of Liberal Arts, Saga University, Saga, 840, Japan

[2]Department of Biology, Faculty of Science, Kyoto University, Kyoto, 606, Japan

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The relationship between maturation stage and movement pattern was studied in a *C. cornelia* population on the Muromi River, Fukuoka, Japan. Adult males intruding into another male's territory were expelled aggressively by the resident, but they usually remained within a range of 50-60 m along the stream. On the other hand, tenerals of both sexes appearing in an adult male's territory were not expelled, and they usually remained at the periphery of a territory. However, they were likely to move upstream during the study period. As the population density at the stream increased, mature males established their territories between the existing territories of other males.

INTRODUCTION

Aspects of the behaviour of the genus *Calopteryx* have been studied extensively by many investigators in Europe (BUCHHOLTZ, 1951, 1955; ZAHNER, 1960; PAJUNEN, 1966b, KLÖTZLI, 1971; HEYMER, 1973) and America (JOHNSON, 1962b; WAAGE, 1973, 1979). Of this genus three species, *C. atrata, C. virgo japonica* and *C. cornelia*, inhabit Japan. Ecological and behavioral studies on these species have been reported by YAMAMOTO (1955), ASAHINA & EDA (1956), HIGASHI (1973) and AIDA (1974).

* This investigation was performed while the author was in the Department of Biology, Faculty of Science, Kyushu University.

Several studies have reported the influence of territorial behaviour on dispersal in other species of dragonflies (e.g. JOHNSON,,1962a; MOORE, 1964; PAJUNEN, 1966a; HIGASHI, 1969; KAISER, 1974a, 1974b, 1974c; CAMPANELLA, 1975). For example, HIGASHI (1969), in his study of *Crocothemis servilia*, showed that the movement of individuals among pools is mainly caused by territorial behaviour. Also, studies of dispersal of calopterygid species have been reported by BUCHHOLTZ (1955), ZAHNER (1960), JOHNSON (1962b), WAAGE (1972) and KLÖTZLI (1971). WAAGE (1972), in his study of *C. maculata*, and KLÖTZLI (1971), for *C. virgo*, have both reported on the degree of movement and its effect on the estimation of mean longevity of the damselflies.

In this paper, the attention was focussed on the relationship between the stage of maturation and the movement pattern caused by territorial behaviour.

STUDY AREA AND METHODS

This study was carried out at the confluence of the main and tributary streams of the Muromi River located about 12 km from the mouth of the river. This river flows through the western part of Fukuoka City. The study area is shown in Figure 1.

We divided the streamlets into ten habitat sections of 5 m length each. The perch sites of the damselflies were identified by marking stones in the stream with fast-drying ink ("Magic Ink").

The damselflies were marked individually on the wing by fast-drying white lacquer. When a damselfly was captured for marking it was classified as teneral or mature according to the degree of hardness of wing and body, and the coloration of abdomen and abdominal pruinescence. The behaviour of damselflies did not appear to be affected by marking them on the wings.

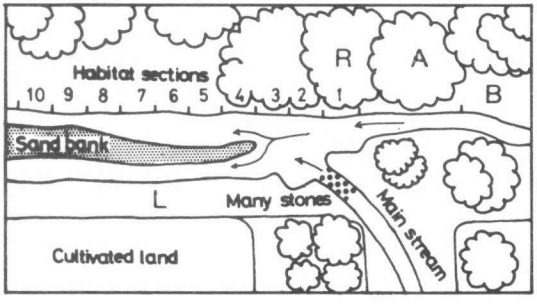

Fig. 1. A map showing the study area. A, B, L and R1-R10 indicate the habitat sections. Arrow and flower-shape indicate water current and trees, respectively.

Along the Muromi River four species of calopterygid damselflies were recorded: *Mnais pruinosa, C. cornelia, C. atrata* and *C. virgo japonica.*

This study was carried out from June 7 to 13, 1975. Censuses were made at one-hour intervals from 10.00 to 17.00 on June 8 and 9, and individual numbers and the habitat sections in which they were found were recorded. Observations of territorial and reproductive behaviour of the damselflies were conducted for four hours per day during the study period.

RESULTS

TERRITORIAL BEHAVIOUR

The territorial and reproductive behaviour of *C. cornelia* was briefly described by HIGASHI (1973). A more detailed description of the territorial behaviour is presented here.

The male's territory is at the side of the stream where the current is relatively slow. In the territory, there are oviposition sites consisting of submerged dead branches and logs, roots of reeds (*Phragmites communis*) and other immersed vegetation. The male perches on stones or logs near the oviposition sites. A territorial male usually perches at one site and occasionally patrols his territory. He does not use other stones as perch sites except when he is guarding an ovipositing female.

A territorial male quickly approaches any other male intruding into his territory and, after pursuing the intruder from his territory for a distance of up to 10 m, returns immediately to the perch site. The level of aggressive response to intruding mature males is closely related to the distance between the resident's perch site and the point of encounter. When this distance, for example, is about 5 m the territorial male approaches the intruding male and makes a short pursuit and/or returns without pursuing him. When the distance is more than 5 m, the territorial male sometimes does not respond to another male perched on the stones near his territory. The territorial area can be

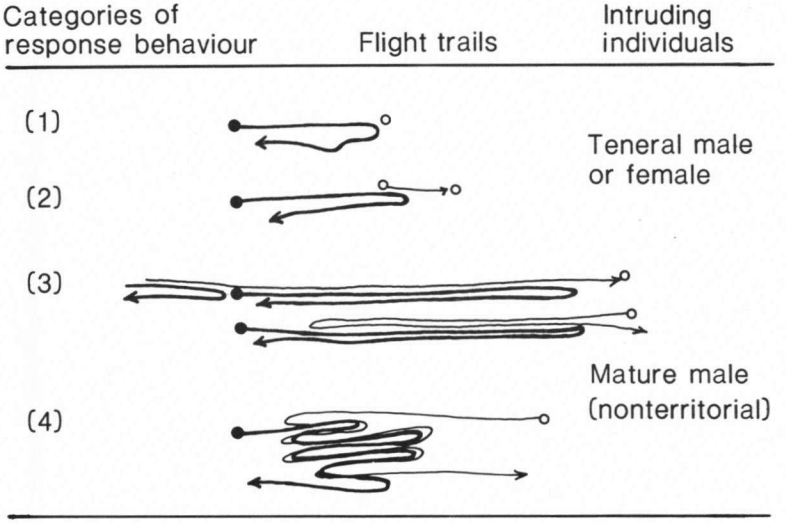

Fig. 2. Schematic illustration of flight trails. Black circle and thick arrows indicate the territorial male. For explanation of categories of response behaviour see text.

Table I
Response behaviour of territorial male toward intruding individuals

Intruding individuals	No response	Response category (1)	(2)	(3)	(4)	Courtship	Total
Mature male	2	1	0	16	2	0	21
Teneral male	4	3	6	3	0	0	16
Mature female	1	6	0	0	0	6	13
Teneral female	3	6	2	0	0	0	11

The figures indicate the frequency of response behaviour. The frequency of response category [No. response, (1) + (2) & (3) + (4)] is significantly different between teneral and mature males (χ^2-test). For explanation of response category see text.

determined by the range of distance beyond which the territorial male does not respond to intruding males.

The behaviour of territorial males can be classified into four levels according to the degree of aggressive responses, viz. (1) Approach without aggressiveness; — (2) Approach-chase; — (3) Approach-threat-chase; and — (4) Approach-threat-fighting (including circle flight). The flight trails of territorial male and intruding damselflies for each level are shown schematically in Figure 2. The relationship between the observed frequency of these response levels by territorial males and the stage of maturation of intruding damselflies is shown in Table I. When the intruding male is a mature one, the territorial male's response was usually level (3) and (4). When a mature female appeared in the territory, the male quickly approached her, sometimes courted her, but did not display aggressive

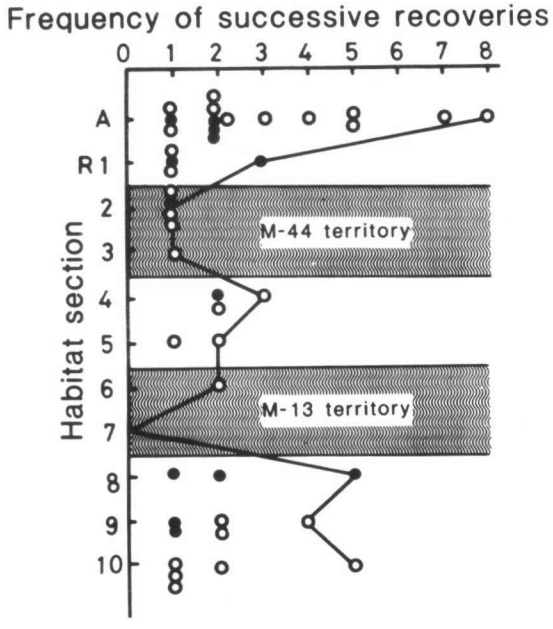

Fig. 3. Successive recoveries of teneral and mature males in each habitat section. Open and black circles indicate the teneral and mature males, respectively.

behaviour. Territorial males responded less agressively (level 1, 2 and 3) to teneral males. The few responses of territorial males toward teneral females were levels (1) and (2). These observations predict that nonterritorial and teneral males would not remain within the territory of a mature male. To confirm this prediction, census were performed in the study area at one-hour intervals from 10.00 to 17.00 on June 9, and the individuals of *C. cornelia* recovered in each habitat section were recorded. The successive appearance of teneral and nonterritorial males in each habitat section is shown in Figure 3.

It can be seen from Figure 3 that nonterritorial and teneral males were not recovered more than twice in succession within the habitat sections occupied by territorial males 44 and 13. In contrast, some of these males appeared repeatedly in habitat sections occupied by nonterritorial males. These results suggest that nonterritorial and teneral males avoid the territories where they are likely to be pursued by territorial males.

TERRITORIALITY AND MOVEMENT OF MALES

In order to show whether or not *C. cornelia* has a tendency to remain in a

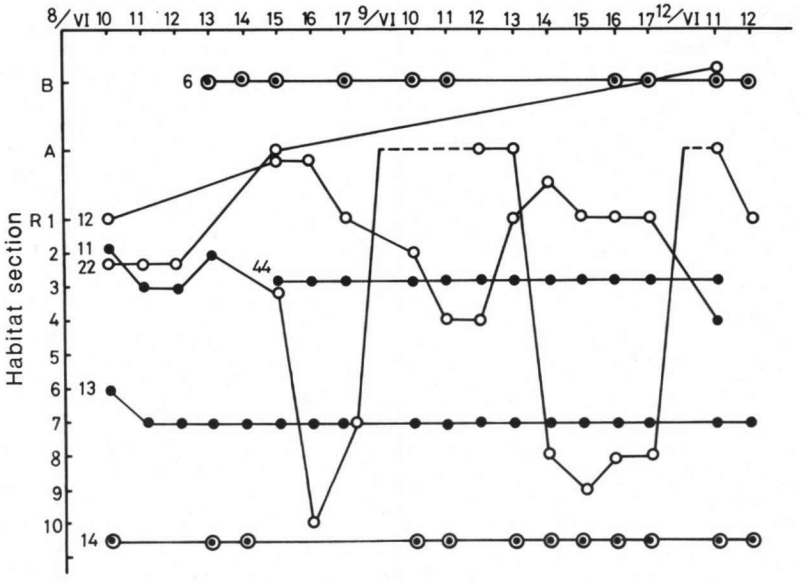

Fig. 4. Records of individuals recovered successively in each habitat section. The figures indicate individual numbers of mature males. Open and black circles indicate the territorial and nonterritorial males, respectively. Males numbered 6 and 14 are the territorial males at the fringe of the study area.

given habitat section, the individual mature males recovered in each habitat section during census periods are shown in Figure 4.

Based on movement pattern, mature males can be classified into two types, viz. (1) territorial individuals that remained in the same habitat section on successive days, such as males 11, 44 and 13, and (2) nonterritorial individuals that were found in several habitat sections during the study period, such as males 12 and 22. The typical movement of nonterritorial males is illustrated by males 11 and 12 in Figure 4. For example, male 11 occupied a territory on June 7 and 8, but was expelled by another male on June 8. Male 11 was repeatedly pursued by two others and was chased about in an area ranging 50 - 60 m along the stream. However, he did not leave the study area for several days. The same phenomenon is also observed in the case of male 12 (Fig. 4). These observations suggest that the movements of nonterritorial males are directly linked to the pursuing behaviour of territorial males.

As the population size of *C. cornelia* in the study area increased gradually during the study period, the number of territories established in the area increased from two on June 8 to four on June 12. This involved male 12 establishing his territory between those of males 44 and 13, and male 34 (recently matured) establishing his territory in a previously unoccupied area (Fig. 5). Male 11, who had previously been displaced by male 44, re-established his territory on June 13 when male 44 was predated by *Sieboldius albardae*.

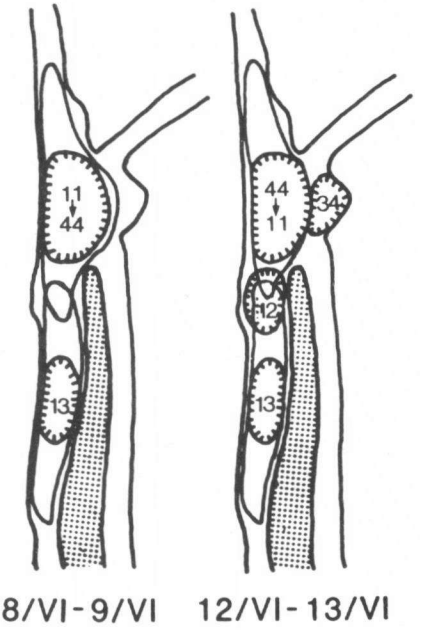

Fig. 5. Change in the number of territories established in the study area. The figures indicate the individual number of territorial males.

The movement of teneral males revealed that several individuals were repeatedly recovered in the same habitat sections, such as in area A and habitat sections R-8 and -10 where the territories are not established by mature males. The movements of teneral males were not as extreme as those of nonterritorial males 11 and 12. One reason for this phenomenon may be that teneral males were not aggressively pursued by territorial males (Tab. I).

THE MOVEMENT OF MATURE AND TENERAL FEMALES

As described previously, when a mature female appears in a territory, the territorial male quickly approaches her and occasionally courts in front of her if she perches. Although mature females were not pursued aggressively by territorial males, they were pursued from the territory during pair-forming behaviour of males such as courtship. When a female was not receptive to a male's courtship, she spread her wings widely, generally raised her abdomen dorsally and sometimes left the territory.

Although only a few teneral females were observed in the area, they were frequently recovered in the same habitat section. Territorial males exhibited little aggressive behaviour and no courtship behaviour toward them (Tab. I). For these reasons, teneral females were recovered in the same habitat sections and their movement was extremely limited.

Not only mature females but also both teneral males and females of *C. cornelia* spend most of the daytime at the stream.

DISCUSSION

The study area is about 12 km away from the mouth of Muromi River, and near the lower limit of the altitudinal distribution of *C. cornelia.* The study was carried out from 7 to 13 July, which covers the early stage of their flying season and the increasing stage of their population. The population estimation of *C. cornelia* was carried out by the mark-release method and calculations were made as by MANLY & PARR (1968). The estimates of population size on 8, 9 and 12 June were 53.1, 49.4 and 60.3, respectively.

Mature female dragonflies usually spend most of the daytime away from the water area, and appear at the water area for copulation (e.g. MOORE, 1952; JACOBS, 1955). Therefore, the number of females at the water area is usually smaller than that of males (e.g. PAJUNEN, 1966b; HIGASHI, 1976). However, during the study period, the sex ratio of *C. cornelia* was approximately 1:1 (31 males and 24 females marked; non-significant). Counts of the number of individuals at the stream at one- or two-hour intervals indicated that approximately the same number of both sexes of *C. cornelia* (average numbers of males and females were 11.3 and 17.0, respectively; $n = 11$), *C. atrata* ($\delta : \varphi = 5.3 : 6.7$; $n = 7$) and *C. virgo japonica* ($\delta : \varphi = 15.8 : 10.0$; $n = 4$) were observed in the water area during the daytime (HIGASHI, 1973, 1981). In contrast, the number of females of *M. pruinosa* on a mountain stream was lower than that of males ($\delta : \varphi = 39.2 : 4.5$; $n = 6$), because the females left the stream after ovipositing (HIGASHI, 1976).

JOHNSON (1966) has reported on the function and significance of the maiden flight of tenerals. OHGUSHI (1981) described that after emergence,

many species of aquatic insects move upstream (colonization cycles). Although handicapped by the short observation period, this study revealed that tenerals of *C. cornelia* also had a tendency to move upstream. Out of 43 initial captures, 75% of the individuals moved upstream, 7% moved downstream and 19% were recovered in the same habitat sections.

HIGASHI (1969), studying *Crocothemis servilia*, stated that the number of territories in a pool increases proportionately to the increase in number of individuals present in the pool. The results of *C. cornelia* shown in Figure 5 are identical with that of *C. servilia*. As population size in the area increased, some of the matures established their territory between occupied territories. In other words, the increase of territories causes the dispersion of oviposition sites in the stream, since the oviposition sites are restricted to a given area of the territory. These phenomena may incidentally be an important factor in decreasing density during the egg and larval stages, because the dispersion of oviposition sites spreads the eggs and larvae evenly in the stream.

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