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TERRITORIAL BEHAVIOUR IN *PSEUDAGRION HAGENI TROPICANUM* PINHEY (ZYGOPTERA: COENAGRIONIDAE)

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Observations were carried out at a stream in the Western Transvaal, Republic of South Africa. 68 males were given unique colour combinations which enabled recognition without recapture. The positions of males were recorded at each visit. Some males occupied the same territory for up to 39 days. They occupied their territories throughout the day excluding conspecific males, but allowed oviposition within the territory by conspecific pairs in tandem. Non-territorial males attempted to displace territorial males. Detailed analyses of territoriality were carried out by noting the type, duration and temporal distribution of 285 flights by 5 adult males. Territorial males spent between 2.7% and 19.8% of their territorial occupation in flight (mean 5.5%). Flight activities consisted of patrolling (18.9% of all flights, 46.7% of total flight time and 4.0 flights/h), shifting flights (40%, 15.1% and 8.4 flights/h), investigatory flights towards movement (34.1%, 27.6% and 3.1 flights/h) and feeding flights (7.0%, 10.6% and 1.5 flights/h). The mean durations of patrolling, shifting, investigatory and feeding flights were 23.0, 3.5, 8.6 and 14.2 s respectively. The flight season was from mid-August 1984 to mid-May 1985.

INTRODUCTION

The relationships between the presence of males at breeding sites, territoriality and reproductive behaviour are readily studied in Zygoptera, which are relatively easily observed. Territorial behaviour studies include Coenagrionidae (BICK & BICK, 1982; MOORE, 1983) and Calopterygidae (JOHNSON, 1962; PAJUNEN, 1966; WAAGE, 1973; HIGASHI & UEDA, 1982; NOMAKUCHI et al., 1984). Detailed studies of the flight activities of libellulid males at their territorial sites have been carried out by PARR (1980, 1983). As far as the present author is aware there have been no comparable studies of territoriality in the genus *Pseudagrion*.

The main aim of this paper is to interpret information obtained on the localization and range of behaviour of individual males of *Pseudagrion hageni tropicanum* Pinhey. The nominotypical race, *P. h. hageni* Karsch is a Cape endemic, but subspecies *tropicanum* ranges from Natal and Transvaal to East and West equatorial Africa (PINHEY, 1964, 1984). It is found in forest, woodland or bush adjacent to streams and rivers.

METHODS

P. hageni allows a close approacn and direct observation was the method of study. A suitable study area was chosen. From April 1984 to May 1985 68 males, all post-teneral, were captured and marked with a unique combination of coloured spots of enamel paint on the wings and/or abdomen. Released individuals returned to the capture area within 4-20 minutes and their subsequent behaviour did differ from unmarked males. On all visits the total number of males in the area was counted and as many males as possible were caught and marked, and their positions of capture noted. Resightings were noted, as well as times of arrival and departure. Estimates of lengths of territorial occupation and male longevity were obtained from resighting data of marked individuals. Whenever possible, behaviour of females and non-territorial males was recorded. Individual males were observed for long periods in order to record detailed behaviour within their defended territories. Observations commenced early in the mornings before the arrival of *P. hageni* and continued throughout the day until the insects had left the area. This was supplemented by part-day visits until the end of May 1985. Detailed analyses of behaviour were made by noting the types, duration, outcome and temporal distribution of 285 flights by 5 adult territorial males during 13 hours and 34 minutes of observation. A stop-watch was used to time the observed activities.

HABITAT AND ODONATA FAUNA

The study area was along a small perennial stream on the farm Bergwind at the foot of the Magaliesberg mountains in the Western Transvaal, South Africa. The stream originates just above the study area and is clear and unpolluted. It is narrow but widens at intervals into small pools with still water at the sides fringed by vegetation. The pools contain water plants and natural debris. The study area is partly shady throughout the day. In addition to *P. hageni*, 13 other Odonata species were regularly seen in the study area. The most common were *Trithemis a. arteriosa* (Burm.) and *Orthetrum julia falsum* Longf. which established territories within the study area. There were also smaller numbers of *Trithemis furva* Karsch, *T. kirbyi ardens* Gerst., *T. stictica* (Burm.), *Crocothemis sanguinolenta* (Burm.), *Orthetrum t. trinacria* (Sel.), *O. c. chrysostigma* (Burm.), *Palpopleura lucia* (Dru.), *Anax speratus* Hag. and *A. imperator mauricianus* Ramb. Other Zygoptera present were *Lestes plagiatus* (Burm.) and *Ellattoneura glauca* (Sel.).

TERRITORIAL BEHAVIOUR

P. hageni males occupy small areas which are defended against all other conspecific males. Once established in such a territory, the male returns to it on successive days over a period of many weeks, spending most of the sunlight hours there. More or less centrally within the territory there is a settling base consisting of several favoured perches 10-40 cm above water level. The perches consist of

bare sticks or water plants and from these the male undertakes various types of flights and returns immediately afterwards. The behaviour of territorial males can be classified into 3 levels (compare with *Calopteryx cornelia;* HIGASHI & UEDA, 1982). The first level, approach without aggressiveness, occurs when any moving object enters the territorial space and the male flies towards the object and after investigation returns to perch. The next level, approach-and-chase, occurs in response to either a conspecific male or a similar sized male of another Zygoptera species entering the territory. The resident male flies directly at the intruder, which immediately retreats, and is followed for a short distance by the resident, who then returns to perch. Larger species, such as *Lestes plagiatus* or *Orthetrum julia,* were approached and then ignored. The third level of behaviour, approach-threat-chase, occurs when a conspecific intruder turns and faces the approaching territorial male and threat behaviour results. This consists of a face-to face encounter and lasts from 6-36 seconds. The males, with their bright orange faces and post-ocular spots and green-striped thoraxes fly from side-to--side in semi-circles always facing each other and with jerky up-and-down movements. There is sometimes an extension of this threat display into one or more circular flights, first one and then the other retreating, but always face-to-face. This lasts much longer, up to 67 seconds being recorded. There is no physical fighting. After the threat behaviour phase the intruder is pursued until out of the territory.

P. hageni females oviposit underwater with a male in tandem. Such pairs often entered a territory and oviposited very close to the resident male, who, beyond an initial investigatory and possibly short following flight only, ignored them.

TERRITORY DEFENDED

The territorial area was determined by the range of distance beyond which the territorial male did not respond to intruders. This was about 50 centimetres for *P. hageni,* where a typical territory is about 1 m from one side to the other and 1 m from the water's edge. Territories are found at the side of the stream in small bays where the current is slow. Within the territory are oviposition sites consisting of partially submerged twigs or water plants, which also provide perches.

TERRITORIAL ATTACHMENT

Males arrived shortly after direct sunlight had reached their territories and when temperatures had risen above 10° C, e.g., on April 16th 1984 sunlight reached the territory of male no. 19 at 8.50 and he arrived at 8.55 when the temperature was 11° C. Males occupied their territories throughout the day except for occasional forays into the surrounding vegetation. These occurred on only 5 occasions during 13½ hours of observation, and varied from 2-10 minutes

Table I
Territorial occupation by *Pseudagrion hageni* males during 1984

Male No.	Dates of territorial occupation	Minimum territorial occupation (days)
1	Apr. 7, 8, 10, 19 20, 23	
	May 9	33
6	Sept. 9, 16, 27, 28	20
9	Sept. 27, 28, 29	
	Oct. 14, 15	19
13	Oct. 14, 17, 24	
	Nov. 3, 4	22
47	March 6, 13	8
52	March 6, 13, 20	
	Apr. 13	39
54	March 6, 13	8

in duration. Males remained in their territories for a while after sunlight had gone, e.g., male No. 19 left the territory at 16.38 h, whereas sunlight had disappeared at 16.19 h. In poor weather conditions, such as rain and cold, the population did not appear at the territorial sites. Males occupied territories for considerable periods of time (Tab. I). Males No. 1 and No. 52 were seen in the same territories each time visits were made, thus occupying them for 33 and 39 consecutive days respectively. These are minimum periods as the insects were still in possession of their territories when last observed and were not likely to have been marked on their first day of occupation.

TERRITORIAL FLIGHT ACTIVITIES

To obtain data on territorial flight activities, detailed observations were made on individual established territorial males (cf. Tab. II). Male No. 1 was observed from 12.00-13.30 h and 15.30-16.40 h on 7 April 1984, and from 11.04-12.07 h on 8 April; male No. 22 from 10.01-11.42 h and from 12.06-13.47 h on 22 April 1984; male No 8 from 12.20-13.29 h on 9 May 1984; male No. 13 from 8.51-9.51 h and 11.20-12.10 h on 15 October 1984, and from 8.18-9.18 h and 11.40-12.10 h and 12.51-13.21 h on 16 October, and 13.05-13.35 h on 17 October; male No. 36 from 12.18-13.18 h on 4 November 1984. The combined data from all 5 males appear in Table III. The following territorial flight components were recognised:

(1) Patrol flights — These were flights from perches within the territory out over water and back again, or flights within the territory over the emergent vegetation and the immediate bank vegetation and back to perch. Patrol flights were spontaneous as far as could be determined and almost always of a circular nature, or more complex. The distance travelled was from 1.5-4.0 m and the mean duration 23 seconds (Tab. III). Sometimes an intruder

Table II
Territorial flight activities of some *Pseudagrion hageni* males

Activities measured	Type of flight					
	Patrol	Shifting	Investigatory	Aggressive	Feeding	*Total*
			Individual No. 1 (7-8 April, 1984; 223 min)			
No. of flights	10	15	10	3	2	*40*
Total duration of flight (s)	163	74	45	67	14	*363*
Min. & max. duration of flight (s)	6/40	3/7	3/9	17/30	7	
Mean duration of flight (s)	16.3	4.9	4.5	22.3	7	
No. of flights/h	2.7	4.0	2.7	0.8	0.5	*10.7*
% of all flights	25.0	37.5	25.0	7.5	5.0	
% of total flight time	44.9	20.4	12.4	18.5	3.9	
% of territorial occupation in flight	1.2	0.6	0.3	0.5	0.1	*2.7*
% of territorial occupation at rest						*97.3*
			Individual No. 22 (22 April, 1984; 202 min)			
No. of flights	10	46	22	0	12	*90*
Total duration of flight (s)	198	132	84	0	106	*500*
Min. & max. duration of flight (s)	10/34	2/7	3/10	0	5/15	
Mean duration of flight (s)	19.8	2.9	3.8	0	8.8	
No. of flights/h	3.0	13.7	6.5	0	3.6	*26.8*
% of all flights	11.1	51.1	24.4	0	13.3	
% of total flight time	39.6	26.4	16.8	0	21.2	
% of territorial occupation in flight	1.6	1.1	0.7	0	0.1	*3.5*
% of territorial occupation at rest						*96.5*

Activities measured	Type of flight					
	Patrol	Shifting	Investigatory	Aggressive	Feeding	*Total*
			Individual No. 8 (9 May, 1984; 69 min)			
No. of flights	12	15	7	1	5	*40*
Total duration of flight (s)	582	48	24	9	152	*815*
Min. & max. duration of flight (s)	10/150	2/4	2/7	9	30/40	
Mean duration of flight (s)	48.5	3.2	3.4	9	30.4	
No. of flights/h	10.4	13.0	6.0	0.9	4.3	*34.6*
% of all flights	30.0	37.5	17.5	2.5	12.5	
% of total flight time	71.4	5.9	2.9	1.1	18.7	
% of territorial occupation in flight	14.1	1.2	0.6	0.2	3.7	*19.8*
% of territorial occupation at rest						*80.2*
			Individual No. 13 (15-17 October, 1984; 260 min)			
No. of flights	20	20	11	25	1	*77*
Total duration of flight (s)	275	92	45	300	11	*723*
Min. & max. duration of flight (s)	6/30	3/6	3/8	10/36	11	
Mean duration of flight (s)	13.8	4.6	4.1	12.0	11.0	
No. of flights/h	4.6	4.6	2.5	5.8	0.2	*17.8*
% of all flights	26.0	26.0	14.3	32.5	1.3	
% of total flight time	38.0	12.7	6.2	41.5	1.5	
% of territorial occupation in flight	1.8	0.9	0.3	1.9	0.1	*5.0*
% of territorial occupation at rest						*95.0*

Activities measured	Type of flight					
	Patrol	Shifting	Investigatory	Aggressive	Feeding	*Total*
	Individual No. 36 (4 November, 1984; 60 min)					
No. of flights	2	18	10	8	0	*38*
Total duration of flight (s)	25	56	62	98	0	*241*
Min. & max. duration of flight (s)	12/13	2/6	3/9	6/33	0	
Mean duration of flight (s)	12.5	3.1	6.2	12.3	0	
No. of flights/h	2.0	18.0	10.0	8.0	0	*38.0*
% of all flights	5.3	47.4	26.3	21.1	0	
% of total flight time	10.4	23.2	25.7	40.7	0	
% of territorial occupation in flight	0.7	1.6	1.7	2.7	0	*6.7*
% of territorial occupation at rest						*93.3*

would be encountered during a patrol flight and aggression would ensue, however, this flight was classed as a patrol flight if it commenced spontaneously. Occasionally abdominal water dipping was seen during a patrol flight.

(2) Shifting flights — The purpose of these flights seems to be to shift from one perch within the territory to another. They occurred apparently spontaneously and were of short duration (mean duration 3.5 s; cf. Tab. III).

(3) Flights toward — These were flights towards an object and were always initiated by movement within the territory. Such flights were initially investigatory, followed by return to perch, or followed by sexual behaviour or followed by aggression, display and chase of a conspecific male intruder. The duration of purely investigatory flights varied, but was short, with a mean of 4.3 seconds. Aggressive flights were of comparatively long duration, with a mean of 12.8 seconds (Tab. III).

(4) Feeding flights — Occurred when the male investigated movement from his territorial perch, or during a patrol flight, when prey (often small Diptera) was encountered and taken to a perch and eaten. Such feeding episodes were comparatively infrequent, varying from 0.2-4.3 per hour (Tab. II).

(5) Avoidance flights — These were caused by disturbance from the observer

Table III
Summary of territorial flight activities of the 5 *Pseudagrion hageni* males recorded in Table II. (Accumulated data for observation time of 814 min)

Activities measured	Type of flight					
	Patrol	Shifting	Investigatory	Aggressive	Feeding	*Total*
No. of flights	54	114	60	37	20	*285*
Total duration of flight (s)	1243	402	260	474	283	*2662*
Min. & max duration of flight (s)	6/150	2/7	2/10	6/36	5/40	
Mean duration of flight (s)	23.0	3.5	4.3	12.8	14.2	
No. of flights/h	4.0	8.4	0.4	2.7	1.5	*17.0*
% of all flights	18.9	40.0	21.1	13.0	7.0	
% of total flight time	46.7	15.1	9.8	17.8	10.6	
% of territorial occupation of flight	2.6	0.8	0.5	1.0	0.6	*5.5*
% of territorial occupation at rest						*94.5*

or large wasps, were infrequent, and have not been included in the data.

From the tables it can be seen than *P. hageni* territorial males spend 94.5% of the time within their territories at rest. Apart from occasional abdominal bobbing movements and cleaning of abdomen and face with the legs, they remain quite still on their perches, from where flights are begun and ended. The number of flights undertaken ranged widely between individuals, from 10.7-38.0 flights per hour, with a mean of 23.1.

Flights from perches can be divided into two types, i.e., those that are initiated by movement within the range of vision, and those which are spontaneous and appear to be intrinsic behaviour patterns. The latter include both patrol and shifting flights. Patrol flights were of the longest duration (23 s), but only 4 per hour were made. About half of the total flying time (46.7%) was taken up by patrol flights. Shifting flights were quite frequent (8.4 flights/h), but of short duration (mean 3.5 s).

The number of aggressive intraspecific interactions varied from 0.6 flights/hour in April and May 1984 to 6.9 flights/hour in October and November 1984.

This is probably a reflection of a seasonally changing pattern of activity related to a decreased population density in autumn (April and May) as compared to spring and summer (October and November) (Tab. II). This was also seen in the percentages of flight times amongst the various males, e.g., in autumn the percentage of total flight time spent in patrol flights was 44.9, 39.6 and 71.4 in Nos 1, 22 and 8 respectively, and in spring/summer it was 38.0 and 10.4 in Nos 13 and 36. More time was spent in investigatory flights (flights toward) when the population density was high, e.g., 47.7% and 66.4% of the total flying time in Nos 13 and 36 during October and November as compared to 30.9%, 17.8% and 4.0% in Nos 1, 22, and 8 respectively during April and May.

FLIGHT SEASON AND POPULATION NUMBERS

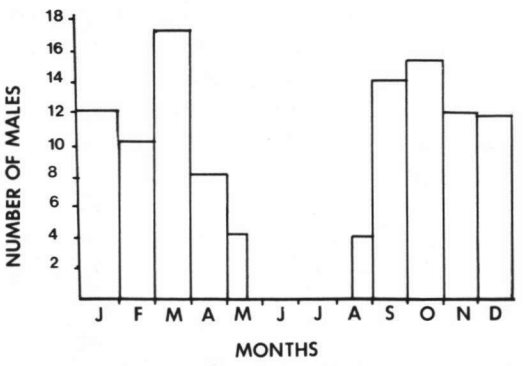

Fig. 1. Average numbers of *Pseudagrion hageni* males present per day for each month in study area (August 1984--July 1985).

A rough indication of the flight season was obtained by counting the number of males present within the study area for 2 days per week every 2 weeks from August 1984 to June 1985 and averaging out to the numbers of males present per day for each month (Fig. 1). Counts were only made on fair weather days. The flight season commenced from mid-August 1984 until mid-May 1985. Numbers were fairly constant from mid-September until the end of March and then decreased until no *P. hageni* were found at the end of May 1985.

NON-TERRITORIAL MALES

Fully mature males were seen in areas outside the territories. They entered territories from time to time and were repulsed by the resident males. A prolonged assault by a non-resident male was observed from 14-16th October 1984. Two males were marked on the 14th October. No. 13 was a territorial holder and No. 15 was mostly observed perched on the periphery of the territory. Careful observation showed the latter not to be occupying a territory. From time to time No. 15 made incursions into No. 13's territory and was repeatedly repulsed. During an absence of No. 13, No. 15 took possession of the territory, chasing

intruders and returning to perch. After 23 minutes No. 13 returned and immediately drove No. 15 out. For 3 days No. 15 made repeated unsuccessful incursions into the territory, often with prolonged aggressive interactions with No. 13. On a return visit on the 18th November 1984, No. 15 had become the territory holder and No. 13 had gone.

DISCUSSION

Feeding flights occurred within the territory (1.5 flights/h), but it was not clear whether prey was accidentally come across or how important this is in the nutrition of the territorial male. Active searching for prey was seen in the late afternoons, after territories were abandoned, and the insects carefully searched the surrounding vegetation.

P. hageni males occupy territories over long periods of time and energy is spent excluding intruding males. However, conspecific pairs in tandem oviposit in the territory without interference. What then are the males defending? Suitable areas for oviposition are patchily distributed on the stream. Within these areas, visibility from perches is good and intruders can be easily detected and driven out and approaching females detected. It is suggested that these areas are likely to attract more females, and a single male defending such an area is thus more likely to copulate. However, non-territorial males were also successful in mating and the question arises as to their role and whether there are possibly alternative mating strategies in *P. hageni.*

It is hoped that this study of *P. hageni* territorial behaviour reveals what may be an interesting area of comparative research in the genus *Pseudagrion,* which is so well represented in Southern Africa. It is particularly necessary to study reproductive behaviour and relate this to the territorial behaviour reported here.

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