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SHORT COMMUNICATIONS

TERRITORIAL BEHAVIOUR IN *PSEUDAGRION KERSTENI* (GERSTAEKER) (ZYGOPTERA: COENAGRIONIDAE)

I. MESKIN

202 South Rand Clinical Centre, 2nd Street, La Rochelle, Johannesburg-2197, Republic of South Africa

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Observations were carried out at a stream in the Western Transvaal, Republic of South Africa. 104 ♂ were given unique colour combinations which enabled recognition without recapture. The positions of males were recorded at each visit. Males established new territories each day but occasionally occupied the same territory for 2 or 3 days. Conspecific males were excluded from the territories but tandem pairs were allowed to oviposit. Detailed analyses of territorial behaviour were carried out by noting the type, duration, outcome and temporal distribution of 165 flights by 2 adult ♂. Males spent between 12.1% and 14.3% of their territorial occupation in flight (mean 13.3%). Flight activities consisted of patrolling (44.8% of all flights, 58.2% of total flight time and 23.3 flights/h), shifting flights (24.9%, 8.6% and 14.3 flights/h), and investigatory flights towards movements (30.3%, 33.3% and 15.4 flights/h). The mean durations of patrolling, shifting and investigatory flights were 12.2, 2.9 and 18.2 s respectively. The flight season was from mid-September 1989 to mid-June 1990.

INTRODUCTION

This paper continues the descriptions of territorial behaviour in the genus *Pseudagrion* Selys, first reported for *P. hageni tropicanum* Pinhey (MESKIN, 1986) and *P. citricola* Barnard. *P. i. inconspicuum* Ris and *P. salisburyense* Ris (MESKIN, 1989). The species discussed, *P. kersteni* (Gerstaeker), is generally abundant from the Cape to equatorial Africa and is to be found adjacent to pools, lakes, streams or rivers but is absent in swamps or thick forest (PINHEY, 1984).

The aim of this paper is not only to interpret information obtained on the localization and range of behaviour of individual males of *P. kersteni* but also to relate some aspects of this to previous studies of the other species of *Pseudagrion* so far studied.

METHODS

As with the other *Pseudagrion* species studied so far *P. kersteni* allows a close approach, and direct observation in the field was the method of study adopted. A suitable study area was delineated. The detailed study methods have been described (MESKIN, 1986, 1989). From August 1989 to August 1990 and also during October 1991 a total of 104 post-teneral males were captured and marked. Monthly two-day visits were made for the duration of the study and data accumulated on population numbers, localization and distribution. Detailed analyses of behaviour were obtained by noting the types, duration, outcome and temporal distribution of 165 flights by 2 territorial males during 3 hours and 27 minutes of observation. All observations were undertaken on warm sunny days with minimal cloud cover.

HABITAT AND ODONATA FAUNA

The study area has been fully described (MESKIN, 1986). It was situated on a section of a small unpolluted perennial stream at the foot of the Magaliesberg mountains in the Western Transvaal, South Africa. The stream is narrow but at intervals it forms small pools of two types, one of which consists of still quiet water, while the other contains swiftly flowing water in at least part of the pool. All the pools are fringed by natural vegetation and contain natural debris. The habitat is partly shaded throughout the day. The odonate fauna in the present study was similar with the exception that *P. kersteni* occurred in larger numbers during the flight season 1989/1990. This is attributed to habitat change when increased rainfall during 1989/1990 provided areas more suitable to *P. kersteni*'s specific habitat requirements. Of special interest is the presence of a sympatric and synchronous population of the closely-related *P. hageni tropicanum* Pinhey.

TERRITORIAL BEHAVIOUR

P. kersteni males occupy specific areas which are defended against conspecific males. Within the territory are a number of favoured perching sites in a small radius from which the male undertakes flights and to which he returns. The perches are often at one end of the territory and only occasionally centrally situated.

In *Calopteryx cornelia* (HIGASHI & UEDA, 1982) and in four *Pseudagrion* species studied (MESKIN, 1986, 1989) there may be four levels of response by territorial males to movement within their territories, viz., (1) approach-without--aggressiveness; (2) approach-chase; (3) approach-threat-chase; and (4) approach--threat-fighting (including circle flight). In *P. kersteni* the first level occurred in response to any flying object moving into the territorial space. It included responses to Anisoptera and large wasps. The entry of a conspecific male into the visual area of a territorial male elicited the second response. Similar-sized zygopterans entering the territory (either *P. hageni tropicanum* or *Ellatoneura glauca*) elicited either the first or second level of response. The third level of behaviour occurred when a conspecific intruder, on being approached, turned and faced the territorial male and threat behaviour ensued. This consisted mostly of a brief face-to-face confrontation, after which the intruder fled with bent posterior section

of abdomen followed by the resident male for a short distance. Occasionally, a more prolonged face-to-face confrontation ensued combined with side-to--side movements of both males and always with the antagonists facing each other. This always resulted in the intruder fleeing. No up-and-down or circular movements or fighting was noted, i.e., no extensions into level four. The whitish-blue pruinose facial colouration and whitish-blue and black thoraxes of the males were presented to opponents during all confrontations.

Territories were vigorously defended against conspecific males but tandem pairs, apart from an initial brief investigatory flight, were not interfered with and oviposition took place within occupied territories as well as elsewhere.

The establishment of territories led to the spacing out of males along the stream. An indication of male density was obtained on 20 October 1989 when 9 territorial males were found at regular intervals in the study area. As the length of stream was 27 m this gives a density of one male per 3 m of stream. During October 1991 (9-11) a density of one male per 3.2 m of stream was obtained when 11 males were found along 35 m of stream.

TERRITORY DEFENDED

The territorial area was determined by the range of distance beyond which the male did not respond to intruders. This was about 50 cm and thus a territory was about 1 m in diameter. The stream is narrow, from 1-2 m wide, and territories were always situated above visibly flowing water and the male perched on emergent or overhanging vegetation at levels of 3-45 cm above water level. Adjacent still pools were not utilized and were occupied by territorial male *P. hageni tropicanum* (MESKIN, 1986). Within the territories are oviposition sites consisting of partially submerged twigs and water plants.

TERRITORIAL ATTACHMENT

Territorial males occupied their territories throughout the day occasionally leaving for brief periods. Territories were abandoned when the area was in shadow.

Of 9 territorial males marked on 21-III-1990 (Tab. I) 4 were not present where marked 4 days later; 2 were found in their original territories and 1 in a new territory 17 days later; 1 in a new territory 4 days later and back in the original territory after 17 days; and 1 in the same territory after 4 and 17 days.

Of 12 males marked on 9-X-1991 6 occupied territories for a single day only; 1 occupied a new territory on each of 3 successive days; 1 occupied a new territory the following day and was back at the original territory on the third day and on a new territory 5 days later; 3 stayed in the same territory for 2 successive days; 1 stayed in the same territory for 2 successive days and was there 5 days

Table I

Territorial occupation by *P. kersteni* males during March-April, 1990 and October, 1991. – [OT: original territory where first marked; – NT: first new territory; – NNT: second new territory; – A: not present in any of the previously identified territories]

Male No.	Dates of territory occupation and identification	Duration of continuous territorial occupation (days)
1,2,3,4	21-III (OT); – 25-III (A)	
5	21-III (OT); – 7-IV (OT)	
6	21-III (OT); – 25-III (NT); – 7-IV (OT)	
7	21-III (OT); – 7-IV (NT)	
8	21-III (OT); – 7-IV (OT)	
9	21-III (OT); – 25-III (OT); – 7-IV (OT)	
10	9-X (OT); – 10-X (A); – 11-X (A); – 16-X (A)	1
11	9-X (OT); – 10-X (NT); – 11-X (NNT); – 16-X (NT)	1, 1, 1
12	9-X (OT); – 10-X (A); – 11-X (NT); – 16-X (A)	1
13	9-X (OT); – 10-X (NT); – 11-X (NT); – 16-X (NNT)	1, 2
14	9-X (OT); – 10-X (A); – 11-X (A); – 16-X (A)	1
16	9-X (OT); – 10-X (NT); – 11-X (A); – 16-X (A)	1, 1
17	9-X (OT); – 10-X (A); – 11-X (A); – 16-X (A)	1
18	9-X (OT); – 10-X (A); – 11-X (NT); – 16-X (A)	1, 1
19	9-X (OT); – 10-X (OT); – 11-X (A); – 16-X (A)	2
20	10-X (OT); – 11-X (OT); – 16-X (A)	2
21	10-X (OT); – 11-X (OT); – 16-X (OT)	3

later.

Thus, males mostly occupied their territories for 1 day only and established new territories each day. The new territories were sometimes at the same site as the previous day but more often close by. Data from field observations suggested that successive territories were established within 10-15 m of each other.

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 11.34-12.56 hours on 20 October 1989 and 11.30-12.35 on 25 October 1989; male No. 5 from 11.32-12.32 on 21 March 1990. The combined data from both males appear in Table III.

Territorial flight components were recognised and have been described (MESKIN, 1986). The results for *P. kersteni* are discussed below.

(1) PATROL FLIGHTS. – These flights from perches within the territory out over water were complicated and included much searching behaviour during which the emergent and bank vegetation were carefully inspected. Some short and simple flights were made. The flight path varied from more or

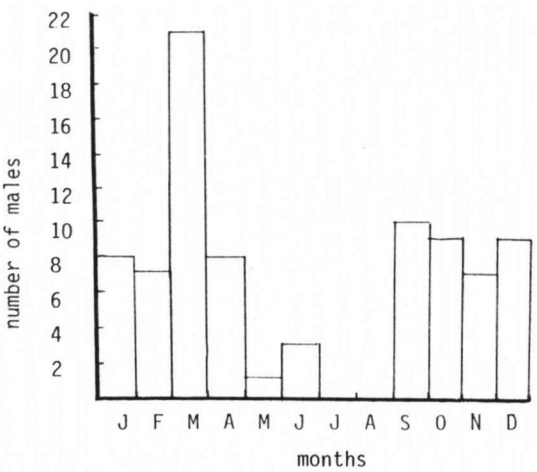

Fig. 1. Average numbers of *Pseudagrion kersteni* males present per day for each month in study area (August 1989 - August 1990).

less circular or elliptical to more complex, and the distance travelled from 1-4 m. The duration varied from 5-39 s, with a mean of 12.2 s. Almost half (44.8%) of the total number of flights undertaken during territorial occupation were patrol flights and occupied more than half (58.2%) of the total flying time. An average of 23.3 patrol flights per hour was made.

(2) SHIFTING FLIGHTS. – These flights, made when shifting from one perch to another, were of short duration (1-7 s, mean 2.9 s), were about a quarter of the total number of flights (24.9%) and occupied 8.6% of the flying time. An average of 14.3 flights per hour was made.

(3) FLIGHTS TOWARD. – These included purely investigatory flights and return to perch if the intruder was not conspecific, as well as initially investigatory flights followed by aggressive behaviour if the intruder was a *P. kersteni* male. The duration of purely investigatory flights was from 2-10 s with a mean of 5.1 s whereas that of aggressive flights was longer (3-38 s, mean 13.1 s). Only 3 encounters with females were observed. On each of these occasions the females fled immediately on being approached by the males and were pursued for short distances but were not caught.

Feeding flights were not observed in territorial males, but they were seen feeding in the company of both females and immature males during the evening.

From the tables it can be seen that *P. kersteni* territorial males spend 86.7% of territorial occupation at rest. They remain quite still on their perches from where flights are begun and ended. Occasionally, abdominal bobbing movements and facial and abdominal cleaning with the legs were noticed. The average number of flights undertaken was 35 per hour. These can be divided into two broad types, i.e., those that are initiated by movements within the range of vision (flights toward) and those which are spontaneous and appear to be intrinsic behaviour patterns. The latter included both patrol and shifting flights and made up 69.7% of all flights and occupied 66.8% of the total flying time with 37.6 flights/h. The number of flights towards movement was low by comparison

Table II

Territorial flight activities of some *P. kersteni* males

Activities measured	Type of flight				
	Patrol	Shifting	Investigatory	Aggressive	Total
	Individual No. 1 (20-25 October 1989; 147 min)				
No. of flights	48	16	14	22	100
Total duration of flight(s)	708	47	74	245	1074
Min. & max. duration of flight(s)	5/39	1/7	3/10	3/38	
Mean duration of flight(s)	14.8	2.9	5.3	11.1	
No. of flights/h	19.6	6.5	5.7	9.0	40.8
% of all flights	48	16	14	22	
% of total flight time	65.9	4.4	6.9	22.8	
% of territorial occupation in flight	8.0	0.5	0.8	2.8	12.1
% of territorial occupation at rest					87.9
	Individual No. 5 (21 March 1990; 60 min.)				
No. of flights	27	22	5	11	65
Total duration of flight(s)	258	65	25	164	512
Min & max. duration of flight(s)	5/23	1/6	2/10	4/22	
Mean duration of flight(s)	9.6	3.0	5.0	15.0	
No. of flights/h	27	22	5	11	65
% of all flights	41.5	33.8	7.7	16.9	
% of total flight time	50.4	12.7	4.9	32.0	
% of territorial occupation in flight	7.2	1.8	0.7	4.6	14.3
% of territorial occupation at rest					85.7

comprising 30.3% of all flights and occupying 33.3% of the time spent in flight with 15.4 flights/h.

On 20 October 1989 male No. 1 made a total of 21 patrol flights during 82 min of observation. During the first 40 min, 15 flights, with an average duration of 17.9 s per flight, were made and only 6 during the last 42 min (average duration 16.3 s per flight). This may indicate a change in intrinsic behaviour patterns controlling patrol flights, and its relationship with exogenous factors, especially temperature (CORBET, 1962), needs to be considered.

FLIGHT SEASON AND POPULATION NUMBERS

An indication of the flight season was obtained by counting the number of males present in the study area on each bi-monthly two-day visit from August 1989 to September 1990 and averaging out to the number of males present per day for each month (Fig. 1). Counts were only made on fair weather days. The flight season was from mid-September 1989 until mid-June 1990. Numbers were constant from September 1989 until April 1990 and then declined, with a few males persisting until June 1990. Population numbers peaked in March with more than twice the average numbers of males present.

Table III

Summary of territorial flight activities of 2 *P. kersteni* males recorded in Table II – [Accumulated data for observation time of 207 min]

Activities measured	Type of flight				
	Patrol	Shifting	Investigatory	Aggressive	Total
No. of flights	75	38	19	33	165
Total duration of flight(s)	966	112	99	409	1586
Min & max. duration of flight(s)	5/39	1/7	2/10	3/38	
Mean duration of flight(s)	12.2	2.9	5.1	13.1	
No. of flights/h	23.3	14.3	5.4	10.0	53
% of all flights	44.8	24.9	10.8	19.5	
% of all flight time	58.2	8.6	5.9	27.4	
% of territorial occupation in flight	7.6	1.2	0.8	3.7	13.3
% of territorial occupation at rest					86.7

DISCUSSION

P. kersteni and *P. hageni tropicanum* occurred sympatrically and synchronously in the study area and both exhibited territorial behaviour (MESKIN, 1986). Competition is minimised, firstly, by spatial resource partitioning and, secondly, by the distinctive colours of the males, enabling them to recognise and interact with males of their own species, and thereby reduce unnecessary interaction with those of other species (CORBET, 1962). However, tandem pairs of both species oviposited freely within the occupied territorial areas of the males of either species, as well as elsewhere. Thus, territorial males did not appear to be defending specific oviposition sites. A consequence of territorial behaviour was the spreading out of males along the length of the stream. The specific territorial microhabitats are likely to be more attractive to females and a single male defending such an area is more likely to copulate. Females of both species oviposited synchronously and in the same places and it appears that larval competitive interactions would be severe under such conditions. It is evident that the study of female reproductive behaviour, and especially choice of habitat and oviposition sites, needs to be undertaken and related to male reproductive behaviour. Larval interactions in these interesting species provide a further unexplored area of investigation.

P. kersteni appears to occupy an intermediate position when its range and intensity of territorial behaviour is compared to that of the other four species of *Pseudagrion* so far studied (MESKIN, 1986, 1989). *P. salisburyense* is non-territorial and shows little aggressive behaviour, whereas *P. hageni tropicanum* males occupy the same territories for up to 39 consecutive days and are the most aggressive of the species studied so far. *P. citricola*, *P. i. inconspicuum* and *P. kersteni* males establish new territories each day and are aggressive, but less to than *P. hageni tropicanum*. Future studies will be aimed at quantifying and

qualifying these and other parameters of behaviour to try and provide meaningful comparisons between as many species of *Pseudagrion* as possible.

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