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ASPECTS OF TERRITORIAL BEHAVIOUR IN THREE SPECIES OF *PSEUDAGRION* SELYS (ZYGOPTERA: COENAGRIONIDAE)

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Observations were carried out at a stream in the southern Transvaal, Republic of South Africa, on 3 sympatric spp. Males were given unique colour combinations which enabled their recognition without recapture. *P. citricola* and *P. i. inconspicuum* males established territories which they occupied throughout the day and from which they exluded conspecific males, and within which they allowed oviposition by other species. New territories were established each day. Detailed analyses of territorial behaviour were carried out by noting the types and outcome of 84 flights by 3 ♂ *P. citricola* and 149 flights by 2 ♂ *P. i. inconspicuum* during 285 min of observation. Flight activities consisted of patrolling (11.9% and 4.7% of all flights respectively), shifting (26.2% and 14.1%), investigatory (45.2% and 81.2%) and feeding flights (16.7% in *P. citricola* only). Observations of the behaviour of 23 ♂ *P. salisburyense* showed that it was non-territorial. The flight season of *P. salisburyense* was from early Oct. 1986 to mid-May 1987, and *P. citricola* and *P. i. inconspicuum* from early Nov. 1986 to mid-May 1987.

INTRODUCTION

This paper continues the descriptions of territorial behaviour in the genus *Pseudagrion* Selys reported first for *Pseudagrion hageni tropicanum* Pinhey (MESKIN, 1986). Three species occurring sympatrically and synchronously on a stream in the southern Transvaal were studied to elucidate the relationship between the presence and localisation of males at the breeding sites, their ranges of behaviour and occurrence and degree of territoriality. A long-term aim is to acquire information for comparative behavioural studies in as many species within this genus as possible.

The three species discussed are *Pseudagrion citricola* Barnard, an endemic species of pools and streams in the Cape, Natal and Transvaal; *P. i. inconspicuum*

Ris, an inhabitant of streams, rivers or pools hitherto recorded only from the S.W. Cape, Angola and further North, but plentiful in the study area; and *P. salisburyense* Ris, which inhabits reedy or grassy pools, streams or river margins and is common in South and Eastern Africa (PINHEY, 1984).

METHODS

All three species are sluggish, allowing close approach, thus facilitating direct observation which was the principal method used in this study. Records were accumulated from June 1986 to May 1987. At the first visit a length of 10 metres along the bank of the chosen stream was marked off with numbered pegs at 1-metre intervals. As many males as possible were captured, marked with a unique combination of colours using enamel paint and their positions noted. Marking them in this way did not appear to affect their subsequent behaviour. At each subsequent visit, all mature males present within the study area were counted and the position of any previously marked individual was noted. Any unmarked individuals were captured, marked and released, and their positions noted.

Detailed and continuous observations of some marked individuals were undertaken. Detailed analyses of behaviour of these individuals were made by noting the types, duration and outcome of 233 flights by 3 males of *P. citricola* and 2 males of *P. i. inconspicuum* during 285 minutes of observation. 23 *P. salisburyense* males were closely observed for varying lengths of time.

At least one visit a month for one year was undertaken to determine the flight seasons and relative numbers of each species. Observations were made of reproductive activity.

HABITAT AND ODONATA FAUNA

The study area was on a stream located on the farm Rietfontein, approximately 35 km South of Johannesburg, South Africa (S26° 30′ E28° 10′). The stream arises from a spring and is fairly clear and unpolluted. It is fringed by grasses and contains emergent water plants and debris including sticks and other temporary perching places. The debris is at the sides of the stream where the flow is sluggish; in the centre of the stream the flow is swift. The width of the stream is 2 to 3 metres and the maximum depth 60 cm. It is subject to intermittent spates after heavy rains. The study area was exposed to the sun for most of the day but shaded in late afternoon.

In addition to the three species of *Pseudagrion* the following Odonata were noted; large numbers of *Elattoneura glauca* (Sel.), *Enallagma glaucum* (Burm.), *Aeshna minuscula* McLachlan, *Trithemis furva* Karsch and *Orthetrum c. caffrum* (Burm.).

TERRITORIAL BEHAVIOUR

The behaviour of males of all three species was classified according to the degree of aggressive responses to intruders. As with *Calopteryx cornelia* (HIGASHI & UEDA, 1982) there can be four levels of response, viz., (1) approach - without - aggressiveness; - (2) approach - chase; - (3) approach - threat - chase; and - (4) approach - threat - fighting (including circle flight).

P. salisburyense exhibited both the first and second levels of response in reaction to movement within its supposed visual field. Thus, individuals of any species which appeared within 30 cm were approached, and sometimes pursued for a short distance, after which the male returned to perch. Males often shared

their perches with up to eight other male *P. salisburyense* and also with single males of the other two species of *Pseudagrion* as well as other Odonata. Males sharing a perch would only occasionally fly up at another perched male in an attempt to displace it. This was usually unsuccessful, the attempt being repulsed with a lifting of the wings in what appeared to be a threat display. Males returning from flights occasionally tried unsuccessfully to displace perched males. At no time was an individual chased from the area. In general, *P. salisburyense* males moved about freely with little intraspecific interference. Either of the other *Pseudagrion* species would sometimes chase *P. salisburyense* some distance but no threat behaviour was seen. It thus appears that *P. salisburyense* is non-territorial.

Male *P. i. inconspicuum* and *P. citricola* exhibited all four levels of aggressive responses. Individual males established territories from which conspecific males were excluded and to which the territory holder repeatedly returned. Heterospecific male intruders were approached sometimes with and sometimes without aggressiveness and a short chase ensued. If a conspecific male entered the supposed visual field of the territorial holder an aggressive episode occurred which involved both males facing each other during flight and exposing their brightly coloured faces (absent in *P. salisburyense*) while alternately flying towards each other and then retreating. There also occurred side-to-side confrontations often with circular flights. The flight movements were small in extent and rapid. All such encounters ended with the intruder sooner or later turning tail, being excluded from the territory and being pursued by the resident male for a distance which varied from a few centimetres to a metre or two. Both species behaved in the same way.

TERRITORY DEFENDED AND TERRITORIAL ATTACHMENT

The males of all three species perched on grass stems, on the banks of the stream or on debris and emergent vegetation a short distance above the surface of the water.

P. salisburyense males do not defend a territory but will defend the perch they occupy at the time should another male fly at them. Prolonged observations of a number of marked individuals showed that they moved up and down the stream and settled on one perch for a short time only. Typically they fly up at movement and return to a different perch. *P. salisburyense* males were not evenly distributed along the stream but tended to be concentrated in some areas, preferring perches over water (Tab. I).

Both *P. citricola* and *P. i. inconspicuum* defended territories, sometimes from a single centrally-situated perch, and sometimes from two or even three perches within the territory. The size of the territory defended was regarded as the distance beyond which the males did not respond to intruders. In both species this

Table I
Distribution of males of 3 *Pseudagrion* species along the stream on 28-I-1987, 1-II-1987 and 18-II-1987

Species	No. of males perched on bank vegetation	No. of males perched on debris over water	*Total*
citricola	1	14	15
i. inconspicuum	16	4	20
salisburyense	3	19	22

was about 30 cm and thus territories were approximately 60 cm in diameter. Almost all (14 out of 15) *P. citricola* territories were located around perches just above water level whereas those of *P. i. inconspicuum* were mostly (16 out of 20) found on the banks of the stream (Tab. I).

The duration of territorial attachment in *P. citricola* and *P. i. inconspicuum* did not exceed one day. The longest a *P. citricola* male was observed continuously on the same territory was 6 hours (*P. i. inconspicuum* 5 hr). No marked male was found to occupy the same territory on two successive days. The recovery of marked individuals of all species was very low. Only two *P. citricola* and three *P. salisburyense* were relocated in the study area after marking, one each the next day and the others 7 days later.

Little interspecific competition for perch sites was observed. Although some chasing of heterospecifics by males of all species was noted this was apparently insufficient to affect the presence of any individuals in the area. Interspecific conflicts were resolved in the following ways. Between *P. citricola* and *P. i. inconspicuum* there was virtual equivalence but between these two species and *P. salisburyense* it was always *P. salisburyense* that retreated and settled on a perch some distance away. This is probably a reflection of the higher level of aggressive behaviour noted in the territorial species. No interaction between any *Pseudagrion* species and other Odonata was noticed beyond initial investigatory flights.

An interesting observation of perch sharing was observed. One territorial male each of *P. citricola* and *P. i. inconspicuum* shared an emergent stick 20 cm in length with 6 male *P. salisburyense* for over two hours. Intruding *P. citricola* and *P. i. inconspicuum* males were chased out of the territories by their respective conspecific territory holders. All other *Pseudagrion* entering the area were only investigated. Other Odonata briefly sharing this popular venue were an *Orthetrum* and an *Enallagma* species. All individuals were always within two to ten cm of each other. Very little interspecific aggression was noted.

TERRITORIAL FLIGHT ACTIVITIES

Detailed observations were made on individual established territorial males of

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

Activities measured	Type of flight				
	Patrol	Shifting	Investigatory	Feeding	*Total*
		Individual No. 1 (28 Jan., 1987; 48 min)			
No. of flights	4	6	14	4	*28*
No. of flights/h	5	7.5	17.5	5	*35*
% of all flights	14.3	21.4	50	14.3	
		Individual No. 2 (28 Jan., 1987; 56 min)			
No. of flights	2	10	10	4	*26*
No. of flights/h	2.1	10.7	10.7	4.3	*27.8*
% of all flights	7.7	38.5	38.5	15.3	
		Individual No. 3 (18 Feb., 1987; 50 min)			
No. of flights	4	6	14	6	*30*
No. of flights/h	4.8	7.2	16.8	7.2	*36*
% of all flights	13.3	20	46.7	20	

Table III
Territorial flight activities of some *Pseudagrion i. inconspicuum* males

Activities measured	Type of flight				
	Patrol	Shifting	Investigatory	Feeding	*Total*
		Individual No. 4 (28 Feb., 1987; 71 min)			
No. of flights	4	11	73	0	*88*
No. of flights/h	3.4	9.3	61.7	0	*74.4*
% of all flights	4.5	12.5	83		
		Individual No. 5 (28 Feb., 1987; 60 min)			
No. of flights	3	10	48	0	*61*
No. of flights/h	3	10	48	0	*61*
% of all flights	4.9	16.4	78.7	0	

P. citricola and *P. i. inconspicuum* (Tabs II, III). Data from all males of each species are in Table IV.

The following territorial flight components were recognised:

(1) [PATROL FLIGHTS] — These were from perches within the territories out over water or over the surrounding grass and back again. The flights were spontaneous as far as could be determined, i.e., were not initiated by movement within the visual field of the male. The distances travelled in both species were 0.5-1.5 m and the flight path was more or less circular. The number of patrol flights per hour was similar in both pecies, i.e., 3.9 per hour in *P. citricola* and 3.2 per hour in *P. i. inconspicuum.*

(2) [SHIFTING FLIGHTS] — The purpose of these appears to be to change perches within the territory. They occurred spontaneously and lasted a few seconds only.

(3) [INVESTIGATORY FLIGHTS] — These were towards an object and were

always initiated by movement within the territory. Flights were initially investigatory in nature and were followed by an immediate return to perch, by aggressive behaviour and pursuit of a conspecific male intruder, or by sexual behaviour if a female appeared. The duration depended on the nature of the intrusion and varied from five to twenty seconds and occasionally longer. After such a flight the male returned to perch within his territory. A difference in the number of investigatory flights by the two species was noted. The three male *P. citricola* averaged 14.8 flights per hour whereas the two *P. i. inconspicuum* males averaged 55.4 flights per hour.

(4) [FEEDING FLIGHTS] — These occurred when the male investigated movement while perched in his territory or on a patrol flight when prey was encountered and taken to a perch and eaten there. Only *P. citricola* was seen feeding while occupying a territory and the feeding episodes were infrequent (5.5. per hour; Tab. IV). Prey resting on the surface of the water as well as flying prey were taken. At the end of the day all species left the water and feeding took place on the banks of the stream.

Table IV

Summary of territorial flight activities of the males of 2 *Pseudagrion* species recorded in Tables II and III

Activities measured	Type of flight				
	Patrol	Shifting	Investigatory	Feeding	*Total*
P. citricola (3 ♂; accumulated data for observation time of 154 min)					
No. of flights	10	22	38	14	*84*
No. of flights/h	3.9	8.6	14.8	5.5	*32.7*
% of all flights	11.9	26.2	45.2	16.7	
P. i. inconspicuum (2 ♂; accumulated data for observation time of 131 min)					
No. of flights	7	21	121	0	*149*
No. of flights/h	3.2	9.6	55.4	0	*68.2*
% of all flights	4.7	14.1	81.2	0	

From the Tables it can be seen that in both species the number of spontaneous flights (patrol and shifting) was about the same, i.e., 3.9 and 8.6 flights per hour in *P. citricola* and 3.2 and 9.6 in *P. i. inconspicuum*. Therefore, about 12.5 spontaneous flights per hour occurred in both species.

Other flights (investigatory and feeding) are related to movement of other individuals and therefore depend on population densities. Differences in the reactions of the two species to movement within their territories was noticed in the field (Tab. IV). *P. i. inconspicuum* reacted to any movement within its visual range, e.g., to flies and bees, as well as larger wasps and Anisoptera. *P. citricola* reacted to Zygoptera which were near to its own size, mostly ignoring smaller or larger objects.

Flights in both species were short, varying from one or two seconds for shifting flights to 20 sec for investigatory flights.

FLIGHT SEASON AND POPULATION NUMBERS

A rough indication of flight season and population numbers was obtained by counting the total number of males of each species present in the study area on at least two visits per month throughout the year, taking care to include only fair-weather days. The results were averaged out to the number of males present on any day for each month (Fig. 1).

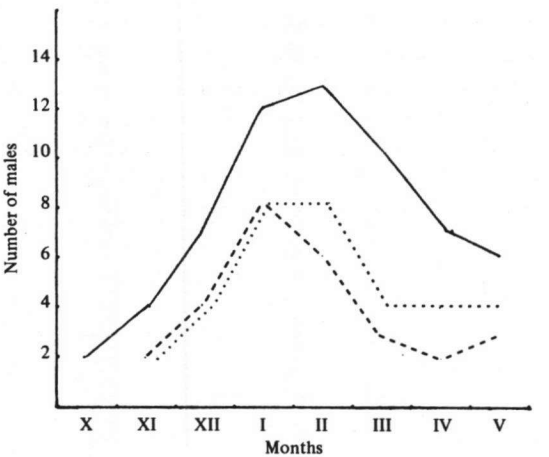

Fig. 1 Numbers of mature males of 3 *Pseudagrion* species present in the study area (June 1986 to May 1987: / = *P. salisburyense*; / = *P. citricola*; / = *P. i. inconspicuum*.

Population numbers of all three species were highest during midsummer. Their flight seasons were also very similar, *P. salisburyense* appearing first on 5 October 1986 and the two other species early in November 1986. By mid-May 1987 all three species were absent from the study area. Throughout the flight season *P. salisburyense* were seen in somewhat larger numbers than the two other species.

REPRODUCTIVE BEHAVIOUR

In all three species females approaching the stream were immediately seized and mating occurred on the bank vegetation. Oviposition was into living water plant stems, the pair in tandem descending below water level. Once the pair had attained tandem there was little interference by other males even if an occupied territory was entered and oviposition occurred within the territory. Females were often seen in the grass up to a few metres away and only approached the water to mate.

DISCUSSION

Among adult Odonata vision is considered to be the most highly developed

sense and plays an important role in most forms of behaviour (CORBET, 1962). Many species are known to rely on vision in male-to-male recognition (FRANTSEVICH & MOKRUSHOV, 1984). The distinctive colours of the males may perhaps be of adaptive value in enabling them to recognise males of their own species and thereby reduce unnecessary interaction with those of others (CORBET, 1962). In this study conspecific males appear to be distinguished largely by facial coloration, as in the territorial *Pseudagrion hageni tropicanum* (MESKIN, 1986). *P. citricola* has a yellow face and the mature territorial males of *P. i. inconspicuum* all exhibit a white pruinosity of the face which is clearly visible in the field. In other respects the species are very difficult to separate in the field. During aggressive confrontations the flights involved the males facing each other and displaying their colourful facial areas to their opponents. In contrast *P. salisburyense*, which is non-territorial, has no colourful areas and does not display. This seems to suggest that in territorial *Pseudagrion* species the facial colours are releasers for male-to-male aggression, thus supporting Corbet's suggestion.

Careful observation of *P. salisburyense* males showed little evidence of spontaneous flights, the individuals only reacting to movement within their supposed visual fields. In *P. citricola* and *P. i. inconspicuum* 38.1% and 18.8% respectively of flights were spontaneous, values which are similar to those for *P. hageni tropicanum* (MESKIN, 1986). Probably spontaneous flights are incorporated in the territorial behaviour of an established male and such vigilance helps to maintain a territory.

The implications of the different behavioural strategies employed by males of these three co-occurring species are important when one considers the coexistence of closely related species. Congeneric Odonata often resemble one another in life history, habitat preference and behaviour (MICHIELS & DHONDT, 1987; VAN NOORDWIJK, 1978). Resource partitioning is often based on spatial and/or temporal separation. The species in this study shared the same habitat and flight season, showed identical diurnal activity and mated and oviposited in the same places. Some differences in male behaviour were noted, *P. salisburyense* being non-territorial, whereas the other two maintained fixed territories. In the latter two there occurred differences such as separate site preferences for the establishment of territories. *P. i. inconspicuum* preferred to establish territories on the bank vegetation whereas *P. citricola* territories were mostly located over water and thus competition for sites was diminished. *P. citricola* is also more sedentary on its territory and feeds there whereas *P. i. inconspicuum* is much more active and does not feed while in possession of the territory. Such small differences however seem unlikely to account for their apparent coexistence. However there could be other factors, especially among larvae, which allow for this; or, because of the annual fluctuations of the environment, perhaps no equilibrium is ever reached, thus allowing a "continued transient coexistence" (VAN NOORDWIJK,

1978). There is much potential for investigation in this closely-related trio of *Pseudagrion* species.

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