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COLOUR CHANGE AND MATURATION IN *BRACHYTHEMIS LEUCOSTICTA* (BURMEISTER) (ANISOPTERA: *LIBELLULIDAE*)

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The relationships between colour phases, sexual maturity and age were studied, using capture-recapture, dissections and direct observations. All young individuals were found to have greenish-yellow background body colour, which darkened to brown in females and to black in males. All males had a blackish wing banding which darkened with age, although many females (about 63%) lacked it. When present, the wing band in females in brownish and in some individuals darkens with age. Full sexual maturity was recognised by the presence of spermatophores in the penis (males), or by the presence of sperm in the reproductive system (females). In males sexual maturity coincided with the development of the completely black body and heaviest wing banding. In females, sexual maturity was closely correlated with brown body colour, but no clear association could be detected between intensity of female wing banding and sexual maturity or age. The mean age of males at the onset of sexual maturity was about 11 days.

INTRODUCTION

Brachythemis leucosticta (Burm.) is a common libellulid in many parts of tropical, subtropical and Mediterranean Africa (PINHEY, 1961). It is mainly associated with large bodies of water, such as lakes and larger rivers, but it may appear at any water including small temporary pools, and it is also frequently seen at considerable distances from water. *B. leucosticta* is frequently the numerically dominant anisopteran both at, and away from water in suitable habitats. Because of this it probably plays an important role in the ecology of these habitats. CORBET (1959) has shown that *B. leucosticta* is an important constituent of the food of young crocodiles, *Crocodilus niloticus*, in Uganda.

In several respects *B. leucosticta* is a rather atypical libellulid. For example, flight activity may be observed at any time from first light to after nightfall and it is suspected that it does fly to some extent after dark, especially during the warmest months of the year. It frequently shows a strongly gregarious habit both at water and away from it; and individuals or swarms of both sexes of various ages exhibit a persistent tendency to follow moving objects such as man and cattle.

It is clearly desirable to be able to recognize the associations between colour, degree of sexual maturity and age for the purposes of many ecological and behavioural studies (e.g. LORD, 1961). It is with these matters that this paper is primarily concerned.

In this work the capture-recapture method was used extensively as it is considered that free flying individuals are more likely to reveal the natural colour changes with time, than individuals which are kept in captivity. Furthermore, attempts to keep individuals of *B. leucosticta* alive in captivity met with very little success, the insects usually dying within a day or two.

The work was carried out between September, 1971 and July, 1973 at Samaru Lake which is on the northern edge of the Institute for Agricultural Research campus of Ahmadu Bello University, Zaria, Nigeria. Zaria lies within the Guinea Savana zone of West Africa. Samaru Lake, also known as Bomo Lake, was constructed from a marshy flood plain (fadama) by damming a small intermittent stream. The lake has an area of about 21.9 hectares when full, and was constructed for irrigation purposes.

B. leucosticta is very similar superficially to *Parazyxomma flavicans* (Martin) and may easily be confused with it. The two species may, however, be readily separated in the hand through differences in venation. In *B. leucosticta* the triangle and sub-triangle are each single celled, whereas *P. flavicans* has the triangle two celled and the sub-triangle three celled. Also, in *B. leucosticta* about four Rspl cells are doubled, whereas in *P. flavicans* the Rspl cells form a single row. We are indebted to R.M. Gambles (pers. comm.) for pointing out these differences to one of us (M.J.P.) before the work commenced. *P. flavicans* was found beside University Farm Lake, about 2.1 km north west of Samaru Lake, in June, 1971, and its presence at Samaru Lake was assumed. It was, however, only found in September, 1972, at Samaru Lake by which time most of the field work had been completed.

METHOD

Marking technique

The individuals of *B. leucosticta*, caught in an insect net, were marked on the wings using a coded system of dots, similar to that suggested by PARR, GASKELL & GEORGE (1968), so that each insect received a unique number. The

four wings were held vertical to the body when marking was done, spots of paint being applied to the underneath of the wings using a slender grass stem. As it was desirable to recapture the marked individuals as frequently as possible from day to day in order to note body and wing colour changes, conspicuously pigmented enamel paint was preferable to dull colours. After a trial period it was decided that white was much more conspicuous than other colours under the conditions prevailing at the time, and it was, therefore, used throughout the study.

Grading of wing and body pigmentation

A wide range of pigmentation can usually be observed within a colony of *B. leucosticta*. Males have been observed either with a greenish-yellow or brown background colour with a blackish pattern to their thorax and abdomen, or to be predominantly black. Males always seem to have a band of greyish, brownish of blackish pigment between the nodus and pterostigma of all the wings. It is noticeable that the darkest wing pigment is associated with the darkest body coloration.

In the female, the greenish-yellow ground colour to the body may either occur in conjunction with a brown wing band, or it may be associated with absence of pigment on the wing. A brown ground body colour may also be associated with either an absence or presence of a brown wing band. The female, also, invariably possesses a dark pattern of brown or blackish on the body, but this varies considerably in its intensity.

Because individual person's reactions to colour are so subjective it was decided to match the colours exhibited by *B. leucosticta* with Standard Colour Samples (S.C.S.) in KORNERUP & WANSCHER (1967).

The greenish-yellow and brown ground colour and the black body colour of the male match with S.C.S. 2B6/2C5; 3C5 and 20H2 respectively. The female greenish-yellow and brown colours match 2B5/2B6 and 3C5 respectively.

The wing pigment of both sexes has been graded arbitrarily, depending on the intensity of the pigment present, again by reference to Standard Colour Samples. Five and seven grades were allocated for males and females respectively (Fig. 1 and Tab. I). It should be noted that the grades do not correspond in the two sexes, and that the area of the wing covered by pigment varies considerably between stages and also between individuals which are referable to the same stage on the basis of the degree of pigmentation. It will be noticed that the differences between grades 0 and 1 in males is considerable. No intermediates between 0 and 1 have been seen in the field, and it was presumed that this was because the pigmentation initially develops very rapidly. This has since been confirmed in the laboratory by noting the quick appearance of pigment in teneral males. Stage 1 is reached about six hours after emergence.

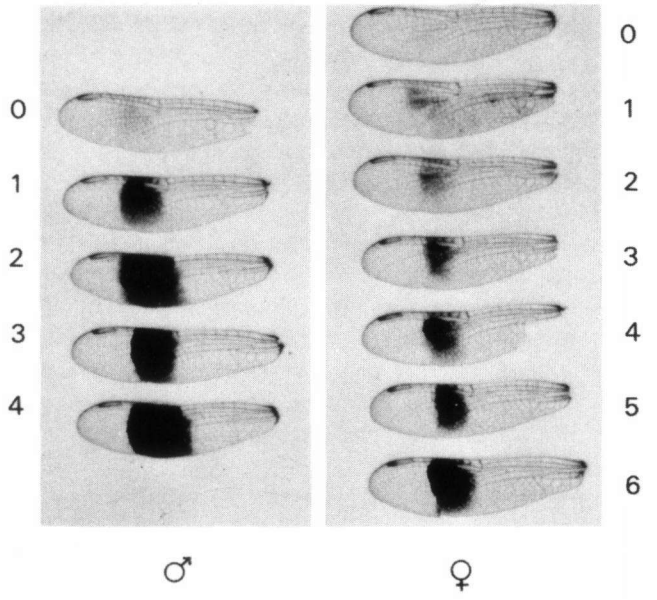

Fig. 1. Grades of wing pigmentation in *Brachythemis leucosticta* (Burm.). (Cf. also Table I).

Table I

Grading of wing pigmentation in *Brachythemis leucosticta* by reference to Standard Colour Samples (S.C.S.)

Males		Females	
Grade of pigmentation	S.C.S.	Grade of pigmentation	S.C.S.
0	Clear → 4A2 → 5A2	0	Clear
1	5E5	1	5B3
2	5F8	2	5B3
3	5F5	3	5C6
4	6F2	4	5D5
		5	5E6
		6	5E6 → 5F6

Dissections

Sexually mature individuals were recognized by examination of the reproductive organs of both sexes. The various stages in the sexual maturation process of males were identified by testis preparations, and the mature state by finding

spermatophores in the penis. On the assumption that mating occurs very soon after the completion of the maturation process, full sexual maturity in females was recognized by the presence of sperm in the spermathecae, common duct and the chamber associated with the common duct from the spermathecae.

RESULTS

Colour changes determined by capture-recapture

One hundred and five males and 150 females contributed to the capture-recapture data. Thirty-six percent of the males were recaptured at least once, whereas only 24 percent of the females were ever seen again. Analysis of the capture-recapture data indicated that the different colour forms and degrees of pigmentation may be related to age, sexual maturity and individual variation.

The greenish-yellow (2B5/2B6/2C5) ground colour recorded for many individuals is clearly characteristic of young *B. leucosticta*. This gradually darkens to, and remains at brown (3C5) in females, but in males the brown continues to darken until it is indistinguishable from the black pattern (20H2).

All males, apparently, develop the characteristic dark wing band, but only 53/145 (37 percent) of females bore any wing pigmentation. The low recapture rate of females resulted in the collection of very little information relating to the speed of colour change. One female individual was caught and marked on 29 September, 1971, when it was greenish-yellow and had no pigment on the wings. This insect was recaptured 24 days later with the body brown and the wings with stage 6 pigmentation. This at least indicates that ageing in the female may be associated with a change to brown body colour and that a heavy wing band may develop after the wings have previously been hyaline. However, from the meagre information on females, it is suspected that female wing pigmentation, if it develops at all, does so relatively quickly, irrespective of the final degree of pigmentation. Out of 145 females scored for wing and body colour, 119 were mature (stage II body colour) and 26 immature. The percentage of the individuals with pigmented wings which were mature was 75.5 (40/53) and the percentage of individuals with hyaline wings which were mature was 85.9 (79/92): these figures do not seem to support the possibility that the development of wing pigmentation is strongly associated with ageing. In males, the changes in the degree of wing pigmentation are highly correlated with darkening of the body ground colour, so that stages 0 - IV in body darkening each correspond almost exactly temporally with the appearance of the equivalent stages 0 - 4 of wing colour. In males the body changes with age from greenish-yellow, through brown to the black of the mature insect. The mean time taken to fully develop the black body colour, stage IV, and the stage 4 wing pigmentation was about 11 days, although one precocious individual did so in about six days (Tab. II).

Table II

Change of body and wing colour with age in male *B. leucosticta*

Wing		Body		
Grade of pigmentation	S.C.S.	Grade of pigmentation	S.C.S.	Mean age in days of 33 individuals
0	Clear → 4A2 → 5A2	0	2B6	–
1	5E5	I	2B6	0.5
2	5F8	II	2C5	1.0
3	5F5	III	3C5	4.0
4	6F2	IV	20H2	11.0

Determination of maturation by dissection

Males: Forty-two individuals in different stages of wing and body coloration were examined for the presence or absence of spermatophores by dissection of the penis. From Table III it is quite clear that in the male sexual maturity is attained when stage 4 and body stage IV are reached. All younger stages when dissected had no spermatozoa in the penis, and were, therefore, assumed to be effectively immature although the testes were often well developed.

Females: Sexual maturity in female *B. leucosticta* was recognized by finding spermatophores in the spermathecae and associated parts of the reproductive system. Table IV shows that in females, the degree of wing pigmentation cannot be used to determine ageing and the onset of sexual maturity; more useful in this sex is body colour. Young females have been observed in September and October with wing pigmentation up to stage 4, with the body still greenish-yellow. When they were dissected they either had no recognizable ovary, or the ovaries were just developing, or the ovaries and spermathecae had developed but no spermatophore was found in the reproductive system. We assume that these latter individuals had not mated as they were not fully sexually mature. The brown colour of the female body which matches S.C.S. 3C5 has been used to determine sexual maturity externally. In 16 out of 19 cases of individuals with

Table III

Presence or absence of spermatophores in the dissected penis of *B. leucosticta*

Grade of wing pigmentation	Numbers dissected	Numbers having spermatophores in penis
1	7	0
2	6	0
3	9	0
4	20	20
Totals	*42*	*20*

Table IV

The presence or absence of spermatophores in the dissected spermathecae of *B. leucosticta*

Grade of pigmentation	Numbers dissected	Numbers having spermatophores in the spermathecae
Wing stages 0 - 4 Body stage I	13	0
Wing stage 0 Body stage II	19	16*
Wing stage 1 - 6 Body stage II	14	14
Totals	*46*	*30*

*Not including three which were mating when caught, but which lacked sperm in the spermathecae.

stage 0 and body stage II (brown), spermatozoa were found inside the spermathecae. It is significant that the three cases which had no sperm in the spermathecae were caught when mating. It is evident from this that they were possibly mating for the first time. All the other 14 individuals dissected which had pigment on the wing and had brown body colour contained spermatophores.

DISCUSSION

Although the combination of evidence from capture-recapture data and dissections has yielded useful information for male maturation rates, it has failed to establish the time taken by females to mature sexually. No males below wing stage 4 and body stage IV have ever been observed at water, or have ever been observed mating at water or elsewhere. This adds to the already conclusive evidence that it is the black body and wing band of the male that denotes the sexually mature state. Females with no pigment on the wing but with brown bodies have been seen to mate, thus providing supporting evidence that it is the brown body colour that is useful in determination of sexual maturity in the female, not the presence of pigment on the wings. It seems that in female *B. leucosticta*, three situations may be proposed regarding the development of wing pigmentation:

(1) Some individuals may develop dark pigment on the wings very quickly at the teneral stage;
(2) Some individuals develop varying degrees of pigmentation at different rates during the post-teneral stages;
(3) Some individuals do not develop wing pigment at all.

However, more evidence is needed before the relationships between female wing banding, age, sexual maturity and individual variation are properly under-

stood. With respect to males, our data for the Zaria area of Nigeria indicate that the description (PINHEY, 1961) of *B. leucosticta* which says that "In teneral and young but sexually mature males the dark band is absent or shows only as a trace. . ." cannot hold.

We feel that there is a general need for a more accurate and careful use of the terms 'mature' and 'sexually mature' in odonatological literature. Whenever either term is employed it should be accompanied by a statement or a definition making clear the author's meaning. Very often the term 'mature' simply only means post-teneral and absolutely no evidence is available to indicate the real state of maturity of the insect in question. Simple dissections of newly caught individuals should usually enable this point to be quickly clarified. Species which have a long imaginal life and which do not show sexual behaviour until many months have passed may, perhaps, present difficulties in their classification as immature or mature. For example, males of the libellulid *Crocothemis divisa* exist throughout the six months long dry season in northern Nigeria in a dull greyish colour phase, and only assume the bright red colour associated with sexual activity at the start of the rains. However, even in such species, an examination of the genitalia should allow a rational conclusion to be reached regarding the state of sexual maturity.

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