FAST, TEMPERATURE-CONTROLLED COLOUR CHANGES IN *CHLOROCYPHA STRAELENI* FRASER (ZYGOPTERA: CHLOROCYPHIDAE)

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Abstract – The dorsal surface of the abdomen of male *C. straeleni* is bright red at temperatures above 30-35°C, but it turns grey-black in 25-40 min when cooled to 25°C. On return to > 35°C the bright red colour may return in < 10 min. The abdomens of territorially active males observed at a forest stream in Uganda were always found to be bright red. Similarly the abdomen of *Platycypha caligata* turns from blue to grey-blue when cooled. In both species darkening is due to the distal migration of black pigment granules within the epithelial cells. At high temperatures the granules become clumped proximally near the basement membrane. Darkened males may be less readily detected by predators or rival males.

Introduction

Colour changes in response to temperature changes are well known in some Zygoptera and in two genera of Anisoptera (O'FARRELL, 1964; MAY, 1976; VERON, 1974; CORBET, 1980). In these, cooling promotes a darkening of blue sclerites whereas warming causes them to return to a bright blue colour. Darkening is a slow process in some species, taking up to 9 h in *Austrolestes annulosus* (VERON, 1976) but it is faster in some coenagrionids. Colour changes have been shown to be due to the migration of black pigment granules which in the dark form move distally to lie just under the cuticle (VERON et al., 1974; cf. FILSHIE et al., 1975). Such changes are usually most striking in males and they may allow cool, inactive insects to be cryptic whereas warm in-

sects are brightly coloured. It has also been suggested that the darker colouring of cool insects enhances the rate of warm-up by absorbing radiation (cf. VERON, 1974).

Among dragonflies and damselflies, such physiological colour change has been reported previously only in blue species, and a similar change is known in a grasshopper, *Kosciuscola tristis* (FILSHIE et al., 1975). The bright red abdomen of *Chlorocypha straeleni* is shown here to be capable of comparable colour changes, becoming dark grey at below about 25°C, the response depending on the migration of dark pigment granules.

Material and methods

Observations were made on *Chlorocypha straeleni* Fraser at small streams in the Budongo Forest in western Uganda (MILLER, 1993) between 5 and 17 September, 1992. The dorsal surface of the abdomen of active males of *C. straeleni* is bright red, the thorax is black and green, and the face is light blue. Brief observations have also been made on *Platycypha caligata* at Hunter's Lodge in Kenya (MILLER & MILLER, 1992), in which the dorsal surface of the male's abdomen is normally bright blue.

Initial experiments were carried out by placing 3 to 5 live damselflies separately in small glass tubes (11 x 50 mm), which were then either kept in the shade or exposed to light. In further experiments, tubes each containing one damselfly were floated in beakers of water at known temperatures under uniform illumination and the abdominal colour was noted at 5-min intervals. The effects of light and temperature could in this way be separated. Control and experimental insects were photographed together.

Red-phase and dark-phase damselflies were preserved in 80% alcohol or in 5% formaldehyde, and microscopical examination of their epithelia was subsequently carried out using reflected and transmitted light.

Observations on live damselflies

When active male *C. straeleni* were captured at a stream and kept in a tube in the shade, the initially bright red abdomen turned grey-black after about 45 min. On exposure to sunlight they again became bright red in 5-10 min. In beakers of water at 25°C, males started to darken after 10 min and the change to grey-black was complete in 25-40 min. Some darkening was apparent at 30°C. When they were then kept at 40°C they began to turn red after 3-4 min and were fully red after 10-14 min. Light itself appeared to have no effect on the colouration. – Darkening usually commenced in segments 5-7 spreading out from a central region on each side, and segments 3 and 4 together with the more posterior segments then followed. Segments 3 and 4 initially preserved a medial bright red zone, about 250 μm wide, while in all fully darkened segments a thin red medial strip, about 50 μm wide, persisted. Segments 2 and 8-9 usually did not darken completely and they were slower to respond, while segment 10 showed little or no darkening. Neither the thorax nor the blue face showed any colour change. – All active males which were observed perching in the sun at the water's edge had bright red abdomens. Quiescent males perched in the shade have not been observed.

Comparable changes have been seen in *P. caligata* whose abdomen turns from bright blue to grey on cooling to below 25°C, returning to a bright blue on warming to >30°C. In this species segments 2-4 have a medial black band and red lateral regions, and the colour change is confined to two relatively small blue islands either side of the midline. As in *C. straeleni*, segments 5-8 darken before the remainder.

Observations on preserved damselflies

Males preserved in 80% alcohol retain their colour in the state in which they were killed. The cuticle of the abdominal sternites is densely black. In contrast the tergite cuticle is transparent and the coloration is due to pigments contained within the epithelial cells below. In *C. straeleni* these are filled with a red pigment which in the light microscope does not appear to be granular. The cells also contain clumps of black granules located proximally near the basement membrane in a red-phase abdomen. The granules move distally and may also become more dispersed in the dark phase, sometimes leaving a more or less clear central region in each cell. – Viewing the internal surface of a red-phase tergite with reflected light revealed a thick sprinkling of black granular clumps each lying centrally in the proximal

part of an epithelial cell. The clumps were about 10-13 μm across, the cells being 15-20 μm in diameter. Under high-power magnification the clumps could be seen to be composed of granules about 1 μm in diameter. Most of the granules were clumped centrally but a few lay dispersed towards the cell margins. The inside of a tergite in the dark phase, viewed with reflected light, showed a yellow-pink surface with few black granular clumps, whereas an external view through the transparent cuticle showed that most cells appeared black with the granules usually more dispersed.

In a dark-phase tergite it is possible to peal off the basement membrane to which the proximal ends of the cells adhere and thus to reveal more clearly the distribution of granules in the distal, more peripheral, regions of the cells. In such tergites the distal migration and dispersal of the granules appear to displace and obscure the red pigment. In some cells the granules were seen to be clumped mainly in the central region, but in others they were evenly dispersed throughout the cytoplasm. In the former case each clump of granules could be seen to be surrounded by a thin red zone, giving an over-all chestnut--brown colour to the segment.

In those parts which are unaffected by temperature and remain red in an otherwise darkened abdomen, such as the mid-line regions or the 10th tergite, the granules remain proximally positioned. Thus when they were viewed from within by reflected light, patches of dark granules could be seen in these regions.

When cells were squashed and then viewed under high power the granules were found to remain clustered apparently held together by a cytoskeletal network, perhaps of microtubules as described by FILSHIE et al. (1975).

Discussion

Conclusions about cellular mechanisms based on the examination of poorly fixed material can at best be tentative. However the detection of granules situated proximally in red-phase and distally in dark-phase abdomens strongly suggests that the mechanism of colour change is similar to that described in some blue odonates (VERON et al., 1974) and in the blue grasshopper *Kosciuscola* (FILSHIE et al., 1975). This is made all the more likely by the observation that blue as well as red chlorocyphids show similar temperature-dependent colour changes. Colour changes have not previously been described in red odonate species, or in the Chlorocyphidae. Moreover in other species they occur at lower temperatures than in chlorocyphids.

One implication of the darkening at temperatures below 25°C is that bright red males perched on territorial sites in the sun maintain abdominal temperatures above this level. Such a temperature in the thorax would facilitate instant take-off in pursuit of rivals or females (cf. MAY, 1991). No colour change was noted in the thorax or head, nor was any colour change seen in the dark coloured females whose epithelia lack black granules. The likely function of colour change is to reduce the visibility of inactive males perched in the shade, rather than to enhance the rate of warm-up when exposed to the sun. By this means inactive males may be able to avoid detection both by other males and by predators.

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