ON REVERSIBLE, TEMPERATURE-DEPENDENT COLOUR CHANGE IN MALES OF THE DRAGONFLY *AESHNA CAERULEA* (STRÖM, 1783) (ANISOPTERA: AESHNIDAE)

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Males of *A. caerulea* show a reversible colour change, controlled only by temperature. The Tyndall-blue of the abdominal spots and eyes changes to greyish purple with decreasing temperature (< 16° C), the reverse colour change occurs with increasing temperature (> 10° C). The colour change is possibly controlled by the same mechanisms as recorded in *Austrolestes annulosus* and *Diphlebia nymphoides*, although in *A. caerulea* it seems to be more rapid. Colour change and the special perching behaviour, as temperature-regulating mechanisms in *A. caerulea* males, and their adaptive value, are discussed.

INTRODUCTION

Colour change in Odonata is well known. Irreversible colour change occurs in larvae after moulting in adaptation to the brightness of their environment and in adults during the development of mature colouration following metamorphosis. This colouration is correlated with the maturation of gonads. It is generally known that the colour of some libellulid females, which normally is different from that of males, can change to male colour in very old age by disturbance of hormones (JURZITZA, 1978). This can also be observed in some aeshnids and coenagrionids. These colour changes are all irreversible and normally proceed slowly with a duration of some days. This is called "morphological" colour change, since it is only caused by metabolism (producing and reducing of pigments).

Less well known are the reversible colour changes in odonates, caused by pigment granules wandering in chromatocytes in the cuticle. This so-called

"physiological" colour change was first discovered by O'FARRELL (1963, 1964) in some Australian Zygoptera, and was subsequently reported also in some American damselflies (MAY, 1976a). In most of these species colour change is probably primarily a function of temperature, though in some cases it is governed by the intensity of incident light (cf. O'FARRELL, 1968), or possibly by psychological factors (stress), e.g. in *Argia apicalis* (BICK & BICK, 1965).

Up to now *Anax imperator* was the only European dragonfly known to have reversible temperature controlled colour change (JURZITZA, 1967).

MATERIAL AND METHODS

Adults of *Aeshna caerulea* were observed and collected in a Sphagnum bog in the Southern Black Forest (Baden-Württemberg, FRG). *Aeshna juncea, A. subarctica* (from different bogs in the Southern Black Forest), *A. cyanea, A. mixta* (from lakes near Freiburg, Baden-Württemberg) and a male of *A. affinis* (captured at a lake 6 km W Freiburg) were sampled for comparison.

To induce colour change (darkening) the collected individuals (2 to 3 males and females of all species, except *A. affinis*) were exposed to low temperature (4° C) in a refrigerator for 1-2 hrs. To test the influence of light on colour change during cooling the dragonflies were kept in darkness or they were illuminated through a pane of glass of the inner door of the refrigerator (to keep off heat) by a 60 Watt lamp which was positioned at a distance of 40 cm from the tested individuals. For the reverse colour change experiments the dragonflies were exposed to several temperatures (10°, 12°, 15°, 18°, 25° C [± 1° C]) in dark and illuminated constant-temperature rooms for 1 to 2 hours. The distance between the 60 Watt lamp or the UV-lamp, and the tested individuals was 40 cm.

In those experiments where the dragonflies were kept in dark the colour of the tested individuals was checked by a short illumination by a torch (0.3 Watt) with 5-minute intervals. In the other experiments the insects were watched continuously. The temperature was measured in the immediate vicinity of the tested animals.

In order to examine the effect of the blue colour in UV-illumination the fully coloured (blue)males of *A. caerulea* were put under a UV-lamp.

FIELD OBSERVATIONS

In August 1982 abnormal behaviour in a male of *Aeshna caerulea* was observed: The male remained on a pine trunk, a few centimetres above the ground for more than one hour after sunset, it did not fly into the top of a tree at the edge of the bog to spend the night in the usual overnight area. With temperature decreasing from 18 to 12° C, a slow darkening of the blue abdominal spots was noticed. Within about 30 to 45 minutes the blue spots turned brownish, then greyish purple and became very similar to the colour of the lichenous bark on which the male was sitting (Figs 1-3). As a result, the shape of the dragonfly's body became more and more blurred, an effect that was strengthened by the decreasing daylight.

The darkening of the abdomen began at the 4th to 7th segments, progressing slowly in posterior direction. The first two or three segments were the last to darken. The colour change began in the centre of each spot and moved slowly to
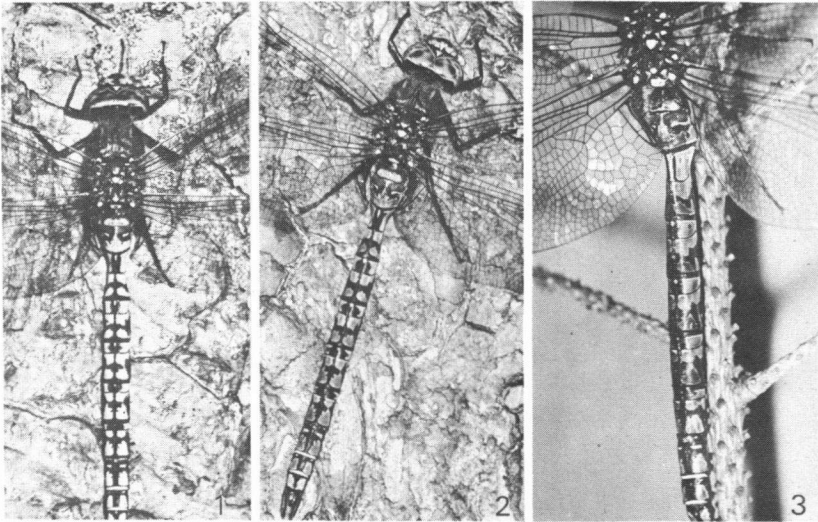
Figs 1—3. *Aeshna caerulea,* male: (1) In bright blue phase; — (2) The same individual, in dark phase, eyes still blue (note the remaining blue margins in the darkened spots); — (3) The darkened abdomen in close-up.

the edge. Sometimes a thin blue line remained along the margins. Finally, about 70 minutes after the first signs of colour change, at a temperature of 10° C, the blue of the eyes changed to a brownish grey.

No further observations were made that evening, but the next morning the male still sat at the same place and the abdomen was still in the dark phase. After sunrise, when temperature reached about 12-14° C, change from the dark to the bright blue phase began in all segments more or less simultaneously and was completed in about 50 minutes.

Three hours after sunrise (11.00 h), even though the temperature reading in the immediate vicinity of the dragonfly was 23° C, the male did not move; it appears to have died during the night. This may explain its somewhat unusual behaviour the previous evening. The specimen was taken to the laboratory for further experiments.

At the same time, other *caerulea* males had been on wings for one to two hours. Half an hour after sunrise, one of these, with a darkened abdomen, was seen flying towards the centre of the bog, where it rested upon a dark peat ground for taking the sun.

LABORATORY EXPERIMENTS

Within 36 hours the dead male was exposed to alternating temperatures twice (4 and 25° C), and normal colour change was observed as described above. The well coloured (blue) insect was shock-frozen at -20° C. Under this condition the colour remained blue for at least 3 months, but 3 months later the blue was completely darkened.

Live individuals of both sexes of *A. caerulea, juncea, subarctica, cyanea, mixta* and a male of *A. affinis* were also exposed to alternating temperatures. None of these species, except the males of *caerulea,* showed any sign of colour change. The only factor influencing colour change in the *caerulea* males was temperature; light or darkness were without any effect (cf. Tab I).

Recordings on the temporal progress of colour change are given as follows:

Sept. 3: 22.35h Male with bright blue abdomen and eyes placed into refrigerator at temperature
                        of 4° C;
           22.45h blue of abdomen becomes pale; eyes bright blue;
           22.50h blue spots of the 6th to 7th abdominal segments become grey;
           23.00h most blue spots are darkened, only the first two segments are still blue; darkening
                        seems to move from the posterior end to the anterior;
           23.15h whole abdomen darkened, the first two segments still slightly blue;
           23.45h the colour of the abdomen perhaps a bit darker than before, some blueish borders
                        at lateral edges of spots;
            0.00h no further colour change in abdominal spots, eyes grey-brown.

Sept. 4   (Process of colouration in a male exposed to 25° C):
            0.25 h Beginning of experiment;
            0.28 h spots became slightly lighter;
            0.39 h male very vital, all abdominal spots middle-blue;
            1.00 h colouration nearly completed;
            1.07 h male very vital, colouration seems to be completed.

Further experiments showed that the darkening process always began at the 3rd to 7th abdominal segment at a temperature range of 14-16° C. Darkening of abdomen was completed in about 40-60 minutes and of eyes in about 70-80 minutes (at 4° C). Only a temperature below 12° C seems to induce colour change in eyes (for details cf. Tab. Ia).

Darkening of different abdominal spots seemed to begin at different temperatures, but this effect was very slight. The reverse colour change seemed to begin at 13-14° C (Table Ib) and was completed in about 30-45 minutes.

Females of *Aeshna caerulea* did not show any colour change. The blue colour illuminated in UV showed no reflection but absorbed strongly.

Table I

Combinations of the tested parameters, temperature (± 1° C) and light (distance lamp to tested individuals 40 cm), and the occurrence of colour change in males of *Aeshna caerulea* (+: striking response; 0: weak response; —: no response; ++: use of lamp; ——: no use of lamp)

(A) COLOUR CHANGE FROM BLUE TO DARK PHASE				
Temperature °C	Illumination		Darkening body	Darkening eyes
	60-W-lamp	UV-lamp		
25	++	——	—	—
25	——	++	—	—
25	——	——	—	—
18	++	——	—	—
18	——	++	—	—
18	——	——	—	—
15	++	——	0	—
15	——	++	0	—
15	——	——	0	—
12	++	——	+	—
12	——	++	+	—
12	——	——	+	—
10	++	——	+	+
10	——	++	+	+
10	——	——	+	+
4	++	——	+	+
4	——	++	+	+
4	——	——	+	+

(B) COLOUR CHANGE FROM DARK TO BLUE PHASE				
Temperature °C	Illumination		Blueing body	Blueing eyes
	60-W-lamp	UV-lamp		
4	++	——	—	—
4	——	++	—	—
4	——	——	—	—
10	++	——	—	—
10	——	++	—	—
10	——	——	—	—
12	++	——	—	0
12	——	++	—	0
12	——	——	—	0
15	++	——	+	+
15	——	++	+	+
15	——	——	+	+
18	++	——	+	+
18	——	++	+	+
18	——	——	+	+

DISCUSSION

Reversible, "physiological" colour change occurs only in a few insects. In addition to dragonflies, such colour changes have been reported in larvae of the culicid midge *Chaoborus (Corethra)* (GELEI, 1928; DUPONT-RAABE, 1949; GERSCH, 1956), in the phasmid *Carausius (Dixippus) morosus* (GIERSBERG, 1928; ATZLER, 1930; PRIEBATSCH, 1933; JANDA, 1936; KALMUS, 1938; DUPONT-RAABE, 1957; MOTHES, 1960), in the Australian alpine grass-hopper *Kosciuscola tristis* (KEY & DAY, 1954a, 1954b; FILSHINE et al., 1975), in the Hercules beetle, *Dynastes hercules* (HINTON & JARMAN, 1973) and in some chrysomelid beetles (MASON, 1929; SCHMIDT, 1941; ZUR STRASSEN, 1960; KOCH, 1982).

It is remarkable that in most (or all?) of the dragonflies and in *Kosciuscola* colour change takes place only in the blue parts of the integument and in blue eyes. In Odonata blue colours are usually due to microgranules in the sub-cuticular epidermis. During the blue phase the microgranules are underlain by a layer of dark pigment. The bright Tyndall-blue of many Aeshnidae and Coena-grionidae results from selective scattering of the short wave-lengths caused by microgranules and absorption of the remaining wave lengths due to the dark pig-ment layer (BECKER, 1941; BYERS, 1975).

The occurrence of different colours during the colour change is due to the reversible rearrangement of Tyndall-active microgranules and dark pigment particles in the epidermal chromatophores (O'FARRELL, 1964; VERON, 1974a; BYERS, 1975; FILSHIE et al., 1975). In the extreme dark phase the pigment particles move to the distal ends of epidermal cells and aggregate near the cuticle and cover the Tyndall-active granules. In the bright-phase the distribu-tion of granules is exactly reversed (O'FARRELL, 1964).

In *Austrolestes annulosus* the colour change from bright blue to extreme dark takes about 9 hours to completion and is centrally controlled by a "darkening factor" (perhaps a neurosecretory substance). The reverse change, which is much more rapid, is completely autonomous (VERON, 1976). Thus, the physiological control of *Austrolestes* chromatophores is similar to that of other arthropods, such as *Limulus* (BROWN & CUNNINGHAM, 1941) and decapod crustaceans (HANSTROM, 1935). The onset of darkening at the posterior end of the abdomen indicates that the darkening factor is produced primarily at this end and moves in the anterior direction (VERON, 1976). These observations in *A. annulosus* (VERON, 1975) and also in *Diphlebia nymphoides* (O'FARRELL, 1964, 1968) agree with those in the male of *Aeshna caerulea*, where anterior abdominal segments begin to darken a few minutes after the posterior segments. The colour change in *caerulea* males is much more rapid than in *Austrolestes* and *Diphlebia*, especially the darkening process of the abdomen which is completed in less than 60 minutes in *caerulea*, in about 540 minutes in *Austrolestes*

(VERON, 1976) and in about 180-480 minutes in *Diphlebia* (O'FARRELL, 1964).

Nothing can be said as to the regulation mechanism of colour change in *Aeshna caerulea,* since no further physiological experiments could be carried out. With reference to evidence described above, the physiological control in *caerulea* seems to be similar to that in *Austrolestes.* The unusual colour change of a decapitated male of *Anax imperator* (JURZITZA, 1967) perhaps is due to a different control system that may be peculiar to this species.

The assumption of an especially intense UV reflection of the Tyndall-blue granules could not be confirmed. The very bright blue suggests the possibility of an intraspecific communication based on strong UV reflection, as assumed to be the case in *Pachydiplax longipennis* (ROBEY, 1975) and *Argia fumipennis* (SILBERGLIED, 1979),or it may be that strong UV reflection at the blue spots protects the alpine *caerulea* from the intense UV in high altitudes (though this is not so in the high latitudes, where *A. caerulea* is very common, and which represent the main portion of its range).

KEY & DAY (1954a) suggest that thermo-regulation is the adaptive advantage of colour change in the alpine grasshopper *Kosciuscola tristis.* Measurements of internal temperatures in *Diphlebia nymphoides* (O'FARRELL, 1963) also lead to the assumption that colour change in this damselfly has a thermo-regulatory function: avoiding "overheating" in very hot situations in bright colour-phase (i.e. perching on sun-warmed rocks during the heat of the day), and shortening of the warm-up-phase and increasing the period of activity in cold mornings in dark-colour-phase (O'FARRELL, 1963, 1964, 1968). However, colour change in Australian Zygoptera is not peculiar to any taxon or ecological niche (O'FARRELL, 1964). In *Anax imperator* thermo-regulation, as conditioned by colour change, is of no importance, since the difference between bright and dark phase is too small (JURZITZA, 1967).

VERON (1974b) showed in *Austrolestes annulosus* that the temperature difference between individuals in the dark phase and those in the blue phase, was not more than 0.23° C. He also stated that already the orientation to sun during basking and flight leads to a clear gain in thoracic temperature. Colour change by itself, therefore, is probably not (very) important for thermo-regulation in *A. caerulea.* The peculiar basking behaviour of this species (which is very uncommon in European aeshnids and which is very similar to that in libellulids) could be seen as a more effective thermo-regulatory mechanism, enabling the boreo-alpine *A. caerulea* to inhabit the high altitudes and high latitudes. *A. caerulea* basks for extremely long periods of time (sometimes more than 30 minutes) on a more or less horizontal, sun-warmed substrate, very often dark peat of dried pools, where the males take shelter from the cold wind and where temperatures sometimes exceed 35° C.

VERON (1974b, p. 464) concluded "that dark-phase colouration is in some

way necessary for insects to reorient themselves to sun when in flight, and that receptors other than compound eyes or ocelli are used in orientation". The epidermal thermoreceptors which possibly work more effectively in the dark-phase than in blue-phase colouration could also help the males of *A. caerulea* to find the warmest or optimal basking places in their habitats or right positions during basking, especially in cool mornings and during cool days. This, and the rather fast colouration and decolouration (in comparison to the Australian damselflies) as a tentative adaptation to the quickly changing weather in their habitats, could make the males most sensitive to critical temperatures and could enable them to perform the normal activities even at low temperatures. At temperatures above the critical point, the blue colour of the abdomen may be used in intraspecific recognition, as has been recorded from other odonates (JOHNSON, 1962; BICK & BICK, 1985).

O'FARRELL (1964) stated that it is difficult to understand why other dragon-flies of the same (extreme) habitat have no colour change and do not have the same heliothermic behaviour as *A caerulea*. Too little is known of the biology of the other species and other mechanisms of thermo-regulation, such as heat control by modifying abdominal haemolymph circulation in the large persistently flying Aeshnidae (MAY, 1976b). A special behaviour could regulate body tempe-rature and could avoid overheating, e.g. by adopting temperature dependent postures and wing positions. Flying behaviour can be of thermo-regulatory value: for example, *Aeshna cyanea* tends to fly in shaded areas during hot periods, while some other aeshnids and corduliids settle in shade when tempera-ture rises above 35-37° C (WALKER, 1912; own observations). Other tentative thermo-regulatory mechanisms and strategies were recorded by HANKIN (1921), DIGBY (1955), CORBET (1962), MILLER, (1962) and MAY (1975, 1976b).

It is remarkable that species often associated with *A. caerulea,* e.g. *Somato-chlora alpestris, S. arctica* and *Aeshna subarctica,* are permanently dark coloured. As excellent flyers they are all of great mobility and possibly regulate body temperature by orientation to sun during flight, as VERON (1974b) pointed out in *Austrolestes annulosus.* But this (active) temperature regulatory mechanism may be less economic than the (passive) heliothermic basking behaviour of *A. caerulea,* which would favour the latter in extreme cold climates.

In addition to this, colour change may be of some other adaptive value: the greyish purple of the dark-phase colouration could be seen as camouflage, pro-tecting the male from predation in the cool weather periods, the conspicuous light blue may be used in intraspecific communication.

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