ADAPTATION OF *AESHNA CAERULEA* (STRÖM)
TO THE SEVERE CLIMATE OF ITS ENVIRONMENT
(ANISOPTERA: AESHNIDAE)

K. STERNBERG

Staatliches Museum für Naturkunde, Rosenstein 1,
D-70191 Stuttgart, Germany

Because the actual range of *A. caerulea* is restricted to the high latitudes of northern Europe and the higher mountains of central Europe, the species is seen as a typical glacial relict, which needs a cool subarctic climate. However, the thermal demands of the larvae are very complex. Young larvae are thermophilic and need more or less constant temperatures of about 20°C, while older larvae generally tolerate the lower temperatures but prefer higher values for moulting and digestion. Due to the brown colour of the water, the dark (peaty) bottom ground and/or the shallowness, typical breeding sites of *A. caerulea,* are warm habitats even in cold climates, so that quick larval growth is ensured. In contrast to the aquatic microhabitat, the environment of adults is cool, severe and appears uncomfortable for dragonflies. However, the unusual basking behaviour and physiological specializations, especially the physiological colour change in males, make the species well adapted to such microclimatic conditions. Adult preference for lower temperatures thus restricts the distribution of *A. caerulea* to the cooler climates of the high North and subalpine and alpine zones.

INTRODUCTION

In the Preboreal, about 10 000 - 9 000 years ago, when the European postglacial climate was still cool-continental, *A. caerulea* probably was distributed in most central European lowlands (cf. STERNBERG, in press). With increasing temperature, *A. caerulea* retreated to high latitudes and altitudes of the high mountains in the early Atlanticum. Probably during the high Atlanticum, about 6 000 years ago, its distribution became disjunct, and it is now restricted to the high North between 56 and 70°40' N (Norway, near Hammerfest) (VALLE, 1931) and the high mountains of south central Europe between 1 000 m and 2 700 m, typical for a boreo--alpine or boreo-mountainous distribution type. Figures 1 and 2 show the moun-

Fig. 1. Breeding site of *A. caerulea* at a bog at a height of about 1270 m (Feldberg region, southern Black Forest, Germany). Photo by the author, 1986.

tainous breeding sites.

In both sub-areas the climate is very cool, with long and severe winters and short and cool summers. This seems to be quite unsuitable for dragonflies, because they are normally 'children of the sun' and prefer warmer climates and higher temperatures. Therefore it has to be asked, which adaptations allow *A. caerulea* to survive under such conditions. Adaptations have to be searched for in both the larval (incl. embryonic) and the adult stage (cf. also STERNBERG, 1993a).

Because of its former (supposed) and actual range *A. caerulea* is often seen as a glacial relict, representing the subarctic fauna in central Europe. Its preference for low temperatures is seen as the main reason for its occurrence in the far North and at high altitudes in mountains. This opinion seems to be supported by the fact, that (1) at its lower distribution limits in central Europe, where temperatures normally are thought to be too high for *A. caerulea*, it shows a strong affinity with *Sphagnum* bogs whose microclimate generally is seen to be cold-continental, and (2) that this affinity becomes weaker with increasing altitude.

MATERIAL AND METHODS

Eggs were collected in a bog in the southern Black Forest (Baden-Württemberg, FRG) and reared under natural photoperiod.

In experiment 1 eggs of one clutch (from one female only) were divided into three groups. During prediapausal and postdiapausal embryonic development, eggs of group 1 were kept at 16°C, those of group 2 at 21°C and of group 3 at 26°C. During diapause (November - March) all eggs were kept at constant 4°C. After hatching, larvae of each of these 3 groups were divided into 3 subgroups: larvae of group 1a were kept at 16°C, those of group 1b at 21°C and of group 1c at 26°C. The same was applied to larvae of group 2a-c and 3a-c. So there were 9 groups of larvae, with different temperature combinations during embryonic and larval development (Fig. 3).

In experiment 2 eggs were kept as above, but the rearing temperature of freshly hatched larvae oscillated between 16°C (during night) and 21 or 26°C (during day).

In another laboratory experiment (experiment 3) larvae of different instars were reared in a trough

of 0.7 × 0.06 × 0.04 m (l × b × h); one end was cooled by ice and the other heated up to 30°C with an aquarium heater. The sides and the bottom of the trough were isolated with styropor®. The larvae were allowed to select a position within a temperature gradient between 0 and 30°C.

Behaviour of adults were observed at several waters in the Black Forest and the Swiss Alps (Flumserberg region, canton St Gallen; Berner Mittelland, canton Bern) during 1979-1995.

ADAPTATIONS OF PREADULT STAGES

Remembering the cold climate in the region where *A. caerulea* lives, it is surprising that rearing experiments under different temperature conditions suggest that larvae of *A. caerulea* are thermo-philic during the first few weeks after hatching. Larvae could survive this period only if water temperature was about
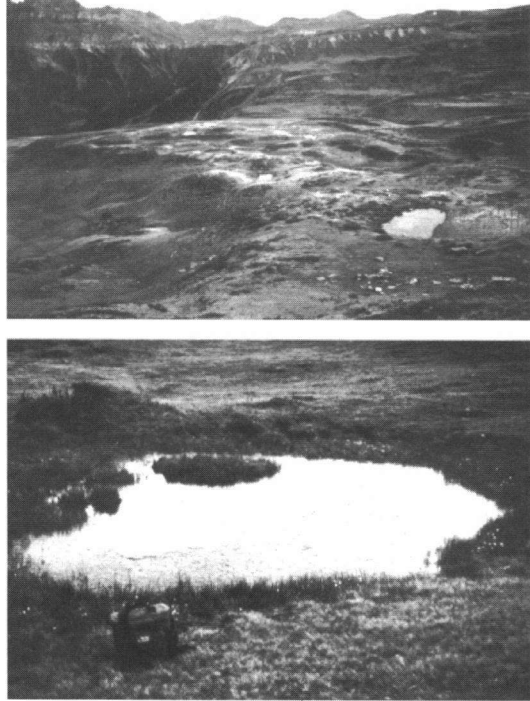

Fig. 2. Alpine groundmoraine-landscape (Flumserberg region, eastern Swiss Alps) (above) with small moraine lakes (below) as typical alpine biotopes of *A. caerulea*. Photo by the author, 1987.
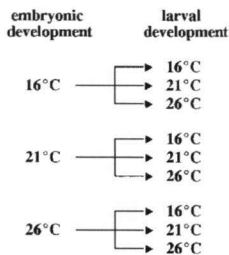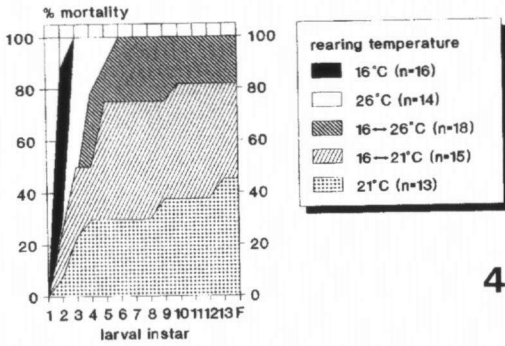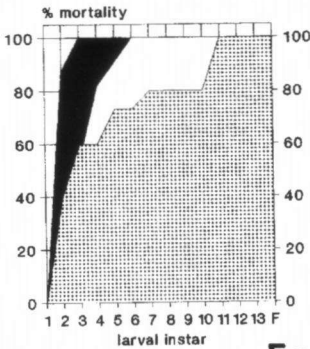
constant at 21°C (experiment 1), or the temperature between day and night oscillated only between 16 and 21°C (experiment 2). At constant temperatures of 16 and 26°C all larvae died during instar 1 and 2; also when the temperature oscillated daily between 16 and 26°C no larvae survived the first weeks after hatching (Fig. 4). These and some other experiments suggest that young larvae need more or less constant temperatures of about 20°C.

Larval viability depends not only on the microclimate during larval development, but is also influenced to some extent by the temperature during embryonic development. This could be seen in larvae kept at different rearing temperatures during embryonic and larval development (experiment 1). In this experiment most larvae survived at a temperature of 21°C during embryonic and larval devel-

Fig. 3. Temperatures in an experiment in which eggs and larvae were kept under different conditions (for results see Fig. 5).
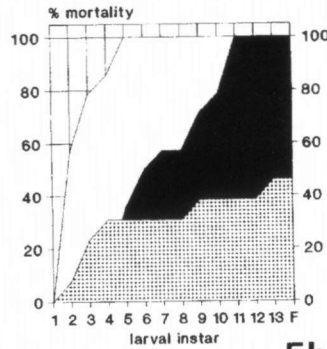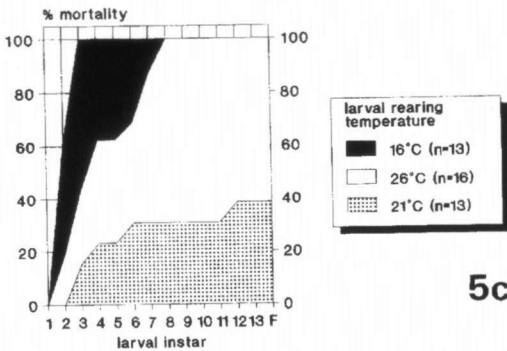
Figs 4-5. Cumulative mortality rates of *A. caerulea* larvae: (4) reared at constant temperatures of 16, 21 and 26°C, and at temperatures oscillating daily between 16 and 20°C (16<>20°C) and 16 and 26°C (16<>26°C) (after STERNBERG, 1990); – (5) reared at different temperatures during embryonic and larval development (cf. Fig. 3). Temperature during prediapausal and postdiapausal embryonic development was 16°C (above), 21°C (middle) and 26°C (below); F = final instar (after STERNBERG, 1990).

opment. All larvae kept at 16°C or 26°C died before instar 11, but when the temperature during the egg stage was 21°C, larvae survived conspicuously longer (P<0.001; chi--squared) at 16°C than when the embryonic temperature was 16 or 26°C (Fig. 5).

Larvae are most sensitive to the microclimate (and other environmental conditions) during instar 1-6, especially during instar 1-2. During this period larval mortality was highest (Fig. 6). Larvae older than instar 6 are comparatively insensitive and most tolerant to many environmental influences.

Fig. 6. Mortality rates of larvae (n = 110) during some thermal experiments.

In experiment 3 larvae changed their positions within the temperature gradient irregularly and could be seen nearly everywhere in the groove. But all larvae of each instar group spent most time within a certain temperature range. This was about 20°C in the youngest group (Fig. 7), which was the optimal temperature value for larval development (see above). But shortly before and after moulting and during digestion they preferred temperatures > 20°C. Older larvae preferred other temperatures. The temperature preference changed with progressing season, so experiments carried out at different times in a year led to distinct preferences. One result is shown in Figure 7. Larvae of other species, e.g. *Aeshna juncea*, *A. subarctica elisabethae*, *A. cyanea*, which all coexist with *A. caerulea*, preferred other temperatures.

These experiments suggest that larvae of *A. caerulea* have many different temperature demands, which change with age, physiological condition of larva, and season. Field observations confirm these results.

The high thermal demands of *A. caerulea* larvae seem to disagree with the climatic conditions in the high North and the upper mountains in its distribution area. However, high abundances of *A. caerulea* larvae (exuviae) only can be found in waters which are conspicuously warmer than those breeding sites where fewer larvae (exuviae) were found (Tab. I).
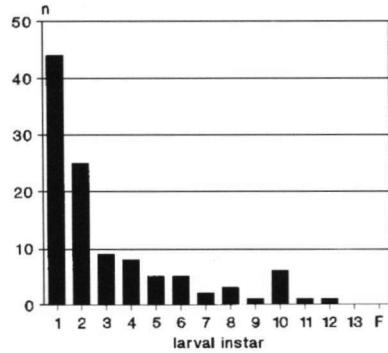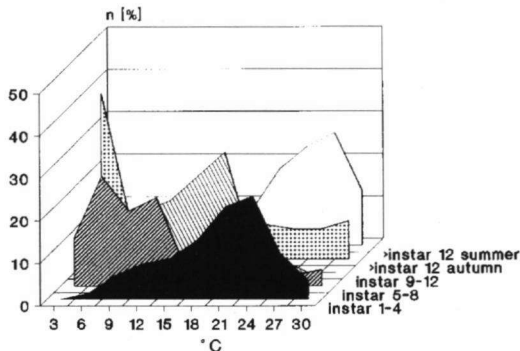

Fig. 7. Distribution of larvae in a temperature selecting experiment (experiment 3).

Table I

Mean temperatures (in °C) during 24 h in larval habitats and non-breeding places of *A. caerulea* in the Black Forest and the Swiss Alps

Type of habitat	Black Forest (20-VIII-1984) 1275 m NN	Swiss Alps (11-VIII-1987) 1800-2000 m NN
breeding	19,5	18,2
	17,6	17,1
	18,4	16,7
	19,1	15,8
	16,3	17,8
non-breeding	12,4	10,8
	11,2	13,2
	11,8	11,8
	9,5	12,2
	10,2	11,7
	11,7	-

Compared with waters where few or no *A. caerulea* larvae live, the temperature in the breeding sites of *A. caerulea* rises more rapidly and to higher values due to solar radiation, because (1) their depths are only 10 - 20 cm, (2) they are often overgrown, (3) the colour of their water is more or less brown due to dissolved humic acids and (4) the substrate often consists of dark peat. Additionally, during the day, larvae prefer the dense mosses (*Sphagnum, Drepanocladus*), which reach the water surface and whose dark colour additionally warms up the water. On cold nights only the upper water layers (surface) become cool and the deeper layers remain warm; this lead to a significant inverse temperature stratification (Fig. 8) (cf. STERNBERG, 1993b, 1994). Further, temperature fluctuations in the upper water layers are high, and, compared with the environmental temperature outside the water, the temperature of deeper water layers remains at a high and nearly constant level within the same pond, even during the night and also during short periods of bad weather (STERNBERG, 1994).
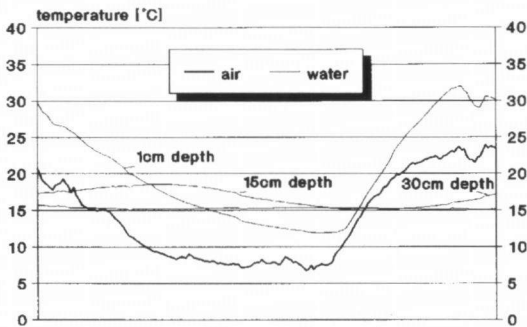

Fig. 8. Temperature in the air and at different depths of a bog pond. Notice the inverse temperature stratification during the night (after STERNBERG, 1994).

These together lead to a very suitable microclimatic regime in the larval habitats of *A. caerulea*. In respect of the absolute (mean) temperature and daily temperature amplitude, the temperature mosaic within one pond is very remarkable. Different thermal regimes can be found even within a few centimetres. Larvae in the field (Black Forest, Alps) make use of this different temperature mosaic, entering deeper water during a cool night and spending most time near the warm surface during a sunny day. These observations confirm the temperature selecting experiments (see above).

ADAPTATIONS OF ADULTS

In contrast to larvae, adult *A. caerulea* are well prepared for a cool raw climate due to ethological, morphological and physiological adaptations.

ETHOLOGICAL ADAPTATIONS

In contrast to other aeshnids, the flight of *A. caerulea* is not very persistent: adult *A. caerulea* often rest on sun-warmed substrates, such as dark (peaty) ground, stones or tree trunks.

Like libellulids, adults of *A. caerulea* are typical perchers. They bask on horizontal or more or less vertical substrates, press their body close to the ground and lower their wings so that the wing tips touch the substrate. This behaviour is quite unusual in aeshnids. Due to the direct contact of their bodies, *A. caerulea* can take up the warmth of the substrate. Additionally, the lowered wings work as a glasshouse: depending on the colour of the substrate, the temperature under the wings can be up to 7°C warmer than above them (STERNBERG, 1990). Thus the air under the wings acts as an external air sac which prevents heat loss from the thorax. This works most effectively in strong wind: if the basking site is exposed to wind, the right or left wing tips are directed to the wind. This maximizes the wing area

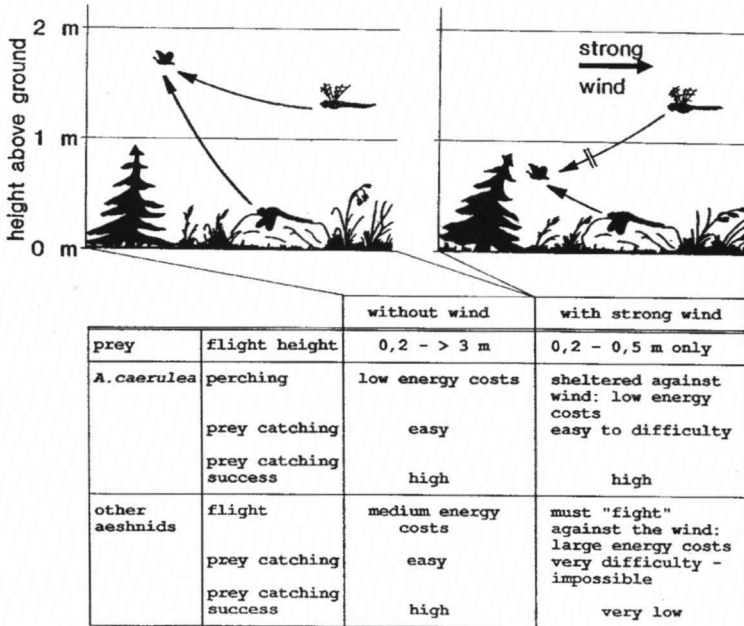|		without wind	with strong wind
prey	flight height	0,2 -> 3 m	0,2 - 0,5 m only
A.caerulea	perching	low energy costs	sheltered against wind: low energy costs
	prey catching	easy	easy to difficulty
	prey catching success	high	high
other aeshnids	flight	medium energy costs	must "fight" against the wind: large energy costs very difficulty - impossible
	prey catching	easy	
	prey catching success	high	very low

Fig. 9. Prey catching in *A. caerulea* (perching on a stone) and in flying aeshnids under non-windy and windy conditions.

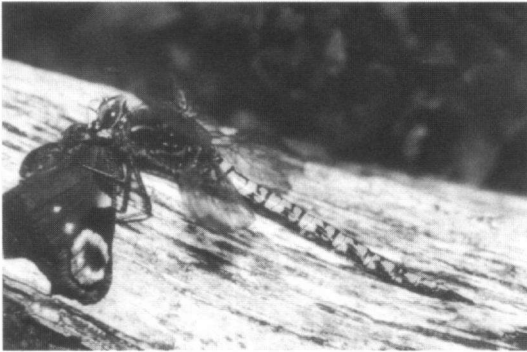Fig. 10. Male *A. caerulea* preying on *Inachis io* on a stormy day. Photo by the author, Sept. 1994.

exposed to the wind; the wings are pressed on to the substrate and the enclosed air is protected optimally. Due to this specialized basking behaviour, *A. caerulea* needs only very little energy for warming up and for maintaining suitable body temperature, in contrast to continuously flying dragonflies (fliers).

In a strong wind, adults of *A. caerulea* normally bask on the ground, where the sub-strate is warmest and they can be sheltered against the wind. On the ground they are also in an optimal position for catching prey: on days with strong winds the air is nearly free of little insects, which are the preferred prey on sunny days, because most small insects remain hidden among the vegetation. Only a few are on the wing, and they fly very close to the ground vegetation. Normally those insects cannot be preyed upon by aeshnids because these dragonflies usually catch their prey by detecting and approaching from below. In strong winds the prey fly below the aeshnids, where they cannot be detected from above. But for perched *A. caerulea* searching from the ground, the prey flying close to the ground (and still above *A. caerulea*) are visible. So, even in a strong wind, the prey catching success may still be high in *A. caerulea* when it is low in other aeshnids (cf. Fig. 9).

It is remarkable that *A. caerulea* normally take litle notice of large Lepidoptera. However, on days with a strong wind the prey of *A. caerulea* consists only of Macrolepidoptera, which may be the only insects on the wing in such conditions. In the Black Forest the butterfly species preyed on often is *Boloria aquilonaris* (Nymphalidae) which is usually rare in this region but more common in the bogs where *A. caerulea* lives, but also *Inachis io* (Fig. 10), *Aglais urticae* (both Nymphalidae), *Erebia* spp. (Satyridae) and *Phytometra (Plusia) gamma* (Noctuidae). Furthermore, a strong wind requires much energy for continuously flying dragonflies, because they have to fly against the wind. Squally winds make a directed approach to prey flying at some heights above the ground almost impossible; but the effect of squalls decreases with height, so *A. caerulea* has the best chance of preying on insects close to the ground.

It was often observed that in such situations continuously flying dragonflies give up their efforts after some minutes and withdraw from the biotope, while *A. caerulea* still remain active. This basking behaviour also enables males of *A. caerulea* to watch for females passing through, so *A. caerulea* can also maintain its reproductive activity.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTIONS

Minimum flight temperature of thorax is positively correlated with body mass (cf. MAY, 1976). With a wing span of only about 80 mm, a body length of nearly 60 mm, and a body mass of ca 0.45 g (males) - 0.47 g (females), *A. caerulea* is one of the small European *Aeshna*-species, for which minimum flight temperature of thorax should be low and warm-up time short. But compared with *A. cyanea*, *A. juncea* and *A. mixta*, correlation between warm-up time and body mass is only significant in males but not in females. This probably is caused by the fact that warm-up rate is also influenced by body colours (cf. STERNBERG, 1996).
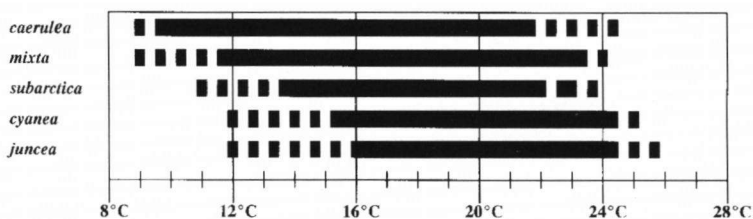

Fig. 11. Ambient temperature ranges at which males of some *Aeshna* species usually have been seen to be active in the field.

These results confirm the observation in the field: the nearly equally sized *A. caerulea* and *A. mixta* can both be seen to be active at lower ambient temperatures than the larger *A. subarctica elisabethae*, *A. cyanea* and *A. juncea*. But, on the other hand, the latter species have a higher upper temperature threshold than *A. caerulea* and *A. mixta* (Fig. 11). This is significant especially in *A. caerulea* which can be observed only sporadically at temperatures > 22°C. This leads to the conclusion that *A. caerulea* overheats at lower temperatures than in other *Aeshna*-species. If the ambient temperature is high, *A. caerulea* significantly prefer the brighter substrates for basking (e. g. sun-bleached wood, dry (grey) *Trichophorum cespitosum*), which does not heat up so much as dark substrates (e. g. peat). But this changed substrate preference obviously has only a little effect on overheating avoidance, because on hot days *A. caerulea* searches for more shaded places while other aeshnids are still active in the sun.

Avoiding overheating by searching for shaded places is probably a primitive form of a thermoregulatory behaviour. This fact may be of some significance for dragonfly phylogeny. Except for this behaviour, *A. caerulea* has no other means of avoiding overheating, such as the 'obelisk-position' of the gomphids and libellulids (cf. MAY, 1976). But from a sociobiological view, overheating avoidance by flying away is disadvantageous, because it lowers mating success due to a shortened presence at the breeding sites. This may be of some importance for males, because males, in contrast to females, are interested in a high copulation frequency. This may be the selection pressure for developing physiological reversible colour changes
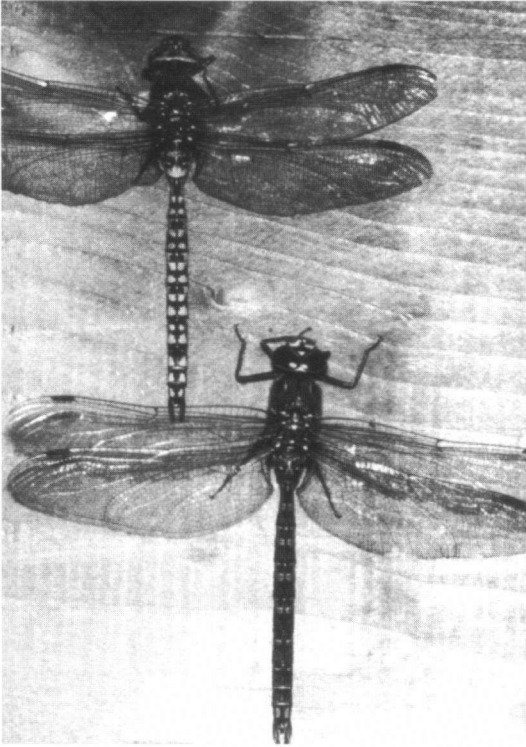
Fig. 12. The two colour phases in males of *A. caerulea*: above the male in the blue phase at higher temperatures and below in the dull phase at low temperatures. Photo by the author, 1989.

in the males of some anisopteran dragonflies (cf. STERNBERG, 1987, 1989), and may be the reason why no female of any European dragonfly species, so far known, has this ability.

Physiological colour change in *A. caerulea*, and probably also in other species, must be seen as a thermoregulatory mechanism. The ability to colour change presumably compensates to some extent for the absence of thermoregulatory behaviour in *A. caerulea* males. At temperatures below 12°C *A. caerulea* males are dull coloured (dark phase: 'functional melanism' (cf. STERN-BERG, 1996)), and above 12°C they are bright blue (blue phase) (Fig. 12). Due to higher radiation absorption males in the dark phase warm up very quickly and to higher values than blue coloured males; the temperature gain is up to 7°C under longwave-radiation (infra-red) (STERNBERG, 1996). This enables males to become active earlier in the morning and at lower temperatures than other dragonflies. In the blue phase, solar radiation of most wave-lengths is reflected, especially the longwave heat radiation (infra--red). Thus, the blue colour protects the male, at least to some extent, from overheating (cf. also O'FARREL, 1963 on *Diphlebia nymphoides*). Males can tolerate higher temperatures and can stay near the (hot) breeding sites for a longer time than females. So, due to this colour change males, on the one hand, can be active at low temperatures, and, on the other hand, are able to tolerate (relatively) high ambient temperatures, which both may benefit the copulation rate of males.

CONCLUSIONS

The actual distribution of *A. caerulea* is based on two facts:

(1) Because of its low upper temperature thresholds adults prefer the lower temperatures. This restricts the distribution to cooler climates, which can be found in the high North and in the subalpine and alpine zone. Thus, thermal demands of adult *Aeshna caerulea* are responsible for the pattern of its distribution area.

(2) Selection of warm aquatic habitats as breeding sites ensures a quick embryonic and larval development and, probably, this makes reproduction possible in these cold regions. The thermal demands during embryonic and larval development define the more local distribution.

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