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TEMPERATURE DEPENDENCE OF FLIGHT ACTIVITY OF ODONATA BY PONDS *

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The relationship between the onset and the level of odon. flight activity and ambient temperature (T_a) was investigated at mating sites mainly in northern Germany, but also in southern France. Several spp. were able to fly at lower T_a at the mating site in September than in June and July. The level of flight activity depended on T_a. In summer, *Ischnura elegans* (Zygoptera) and *Orthetrum cancellatum* (Anisoptera), could fly at the lowest T_a and exhibited special warming-up strategies. Southern spp. started activity at the mating site at higher T_a than did northern spp.

INTRODUCTION

Temperature adaptations of insects play a major role in their life history (HEATH & ADAMS, 1969) and are subject to physical and physiological forces: as poikilotherms, insects have to achieve a suitable operating temperature through heat gain, but on the other hand they must not overheat (HEATH, 1971; EDNEY, 1971; SHELLY, 1982). Here body size, body colour, behaviour, endogenous heat production, and temperature regulation are important (MAY, 1991; HEINRICH, 1993; SCHMITZ, 1994). Many authors assume the existence of an upper and a lower temperature threshold and therefore a temperature optimum for activity of each insect species (WILLIAMS, 1940; TAYLOR, 1963). Insects living at high latitudes have to start activity at low temperature in order to increase the time available to feed and reproduce.

Much information exists about the activity of odonates, insects that can often be observed flying or mating on sunny cloudless days (PEZALLA, 1979; FINCKE,

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* Dedicated to Peter MILLER, remembering his inspiring discussions, very helpful comments and innovative ideas.

1982; BANKS & THOMPSON, 1985). MAY (1976b, 1977, 1991) published data on the activity of Odonata, comparing body temperature (T_b) with ambient temperature (T_a).

LUTZ & PITTMAN (1970) investigated the temperature thresholds of some Odonata in North Carolina. But there is no information about the minimum T_a at which flight began of the first species (*Argia violacea* and *Epicordulia princeps*), because they were already flying at 20°C, below which there were no observations of T_a. For one species of Zygoptera (*Enallagma geminatum*) these authors give the lower threshold of T_a for the beginning of activity as 20-22°C, whereas all other species started their activity at 24-28°C. STERNBERG (1990) warmed up cooled Anisoptera in the laboratory until they started to fly. Only few field data exist for the beginning of flight activity of Odonata at low temperatures (ROWE & WINTERBOURN, 1981; VOGT & HEINRICH, 1983). In this paper this need is net by comparing results from odonates flying in northern Germany with those flying in southern France. Additional aims of this investigation were to find out if the preferred temperature is different in summer and autumn and how flight activity can be influenced through behavioural thermoregulation.

MATERIAL AND METHODS

This investigation was carried out in northern Germany between the following dates: 5-17 May, 8 June-25 July and 6-19 September 1993. The study area „Im Klei" (Tab.I) is situated 7 km NE of Braunschweig, and encompassed 12 ponds with diameters ranging from a few metres to 80 m.

The data were obtained using two different methods: a transect method and an intensive "continuous" observation.

For the first method, the species, sex and behaviour of all odonates was recorded along a transect 220 m long. The following categories were distinguished: sitting; being chased; flying; copula and ovipositing. The transect method was carried out at the beginning of each day and was than repeated usually every hour. – The "continuous" observation was conducted each day at just one pond following the first transect. The beginning of flight activity and the level of activity at the mating site were recorded. The level of activity was related to ambient temperature, which was divided into intervals of 2 °C.

Table I

Investigation areas, geography, climate, investigation periods and methods

Locality	Geogr. position N	E	Annual average temp. (°C) / rainfall (mm)	Investigation period (1993)	Method
Im Klei, N Germany	52°15',	10°35'	8 / 654	5 - 17 May 8 June - 25 July 6 May - 19 Sep.	continuous observation, transect method
Crau, S France	43°34',	4°50'	14,5 / 543	23 May - 3 June 23 Sep. - 1 Oct.	continuous observation

Furthermore, the following abiotic factors were measured and recorded every ten minutes:

Ambient temperature (T_a) in the sun was measured in the flight space of the odonates 1 m above the ground; the electrode of the thermometer (Greisinger, GTH 1160) was held in the direction of the sun without any shade. Additionally, every ten minutes relative radiation was measured on a dark surface which was exposed to the sun but protected from the wind. Later, as the data were analysed it became obvious that this relative radiation fluctuated so much that it was not useful for statistical analysis.

Cloud cover was recorded as percentage cover. Average velocity and maximum wind speed were measured with an electronic anemometer (Windy, Navis electronics, Ferropilot) in ms^{-1} 1 m above the ground. Additionally, wind was measured (e.g. in wind protected areas) where dragonflies were flying.

In southern France (Tab.I) the observations were carried out by means of "continuous" observation during 23 May-3 June and from 23 September-1 October 1993 at a gravel pit 50 m long and 40 m wide.

EXPERIMENTS ON THE CHOICE OF PERCHING SITES BY *ORTHETRUM CANCELLATUM*. – With the help of wooden plates (30 × 30 cm) the warming-up behaviour was investigated. Ten plates were painted with different dull colours. Always two plates were given a white, grey, green and black surface. Two plates remained unpainted and thus had a light sand colour. In each case, 2 × 5 plates of different colour were placed close together 10 m away from the largest pond in the meadow, adjacent to this pond to the East. The temperature on the surface was measured. Temperature and whether or not an individual was sitting on a plate were recorded every half an hour. If a dragonfly was present it was chased away after registration and the succession of the plates changed. In this way any influence of the spatial arrangement of the plates on the results of the experiment was excluded.

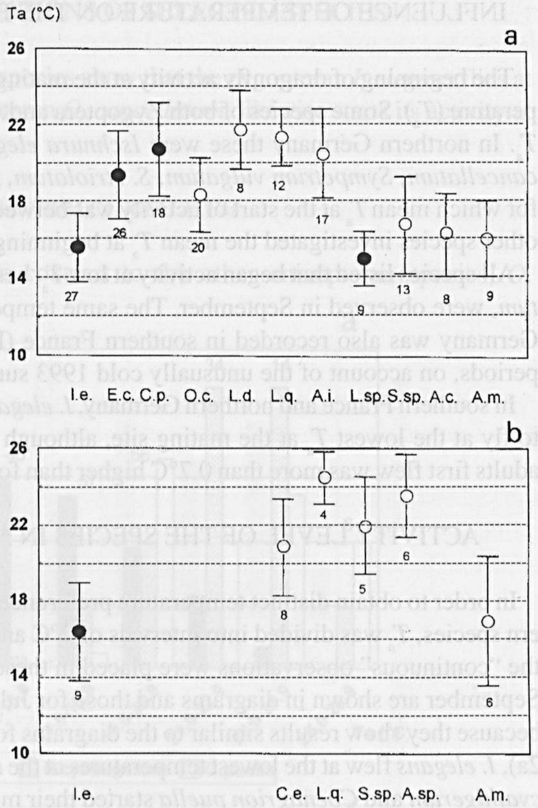

Fig. 1. Means ± SD of ambient temperature (T_a) at the beginning of dragonfly flight activity at the mating site: (a) In northern Germany; – (b) in the Crau in southern France. ●: Zygoptera, ○: Anisoptera. – The numbers show sample sizes. I.e. = *Ischnura elegans*, – E.c. = *Enallagma cyathigerum*, – C.p. = *Coenagrion puella*, – L.s. = *Lestes sponsa*, O.c. = *Orthetrum cancellatum*, – L.d. = *Libellula depressa*, – L.q. = *L. quadrimaculata*, – C.e. = *Crocothemis erythraea*, – S.sp. = *Sympetrum vulgatum* and *S. striolatum*, – A.i. = *Anax imperator*, – A.sp. = *A. imperator* and *A. parthenope*, – A.c. = *Aeshna cyanea*, – A.m. = *A. mixta*.

INFLUENCE OF TEMPERATURE ON THE BEGINNING OF ACTIVITY

The beginning of dragonfly activity at the mating site depended on ambient temperature (T_a). Some species of both Zygoptera and Anisoptera became active at low T_a. In northern Germany these were *Ischnura elegans*, *Lestes sponsa*, *Orthetrum cancellatum*, *Sympetrum vulgatum*, *S. striolatum*, *Aeshna cyanea* and *A. mixta*, for which mean T_a at the start of activity was between 15.1-18.4°C (Fig.1a). For the other species investigated the mean T_a at beginning of activity was 19.4-21.8°C.

All species listed that began activity at low T_a, besides *I. elegans* and *O. cancellatum*, were observed in September. The same temperature range found in northern Germany was also recorded in southern France (Fig. 1b) during the observation periods, on account of the unusually cold 1993 summer in the South.

In southern France and northern Germany, *I. elegans* was the species which started to fly at the lowest T_a at the mating site, although the mean T_a at which southern adults first flew was more than 0.7°C higher than for the northern ones (see below).

ACTIVITY LEVEL OF THE SPECIES IN NORTHERN GERMANY

In order to obtain distinct temperature preferences for flight activity of the northern species, T_a was divided into intervals of 2°C and the recorded activity levels of the "continuous" observations were placed in these classes. The data for June and September are shown in diagrams and those for July are only described in the text, because they show results similar to the diagrams for June. Among Zygoptera (Fig. 2a), *I. elegans* flew at the lowest temperatures at the mating site, whereas *Enallagma cyathigerum* and *Coenagrion puella* started their main activity when *I. elegans* had already reduced its activity. Among Anisoptera, *O. cancellatum* (Fig. 2b) started activity at the lowest temperature; in July it flew in the T_a class between 13.0--14.9°C. In contrast, *Libellula quadrimaculata* and *Anax imperator* appeared later in the day at the pond, i.e. at higher temperatures.

The flight temperature adaptations of *I. elegans* and *O. cancellatum* differed from those of other species observed. In contrast to all the other investigated species, *I. elegans* flew at the lowest T_a (13.0-14.9°C). *O. cancellatum* appeared at the mating site and flew between 13.0 and 16.9°C.

In autumn, all investigated species, apart from *E. cyathigerum* and the *Sympetrum* species, started to fly at the mating site at a T_a between 10.8 and 12.9°C (Figs 3a,b). The behaviour of the *Sympetrum* species was distinctive, in that they did not fly at a T_a lower than 13.0-14.9°C. With increasing temperature, a strong increase in the number of individuals and in flight activity was observed. In the figures, the numbers above the bars show the frequencies of temperature ranges. Higher temperatures were measured less often. If the number of flights were to be corrected mathematically (the activity of the rarer temperature cases would be multiplicated to reach the same frequency), there would be more flights at higher temperatures.

SPECIAL ADAPTATIONS OF SELECTED SPECIES

All comparisons between the species show that the zygopteran *I. elegans* flies at the lowest T_a and that the anisopteran *O. cancellatum*, likewise starts its activity at low T_a.

ORTHETRUM CANCELLATUM

WARMING-UP STRATEGY. – In contrast to the other anisopteran species, *O.*

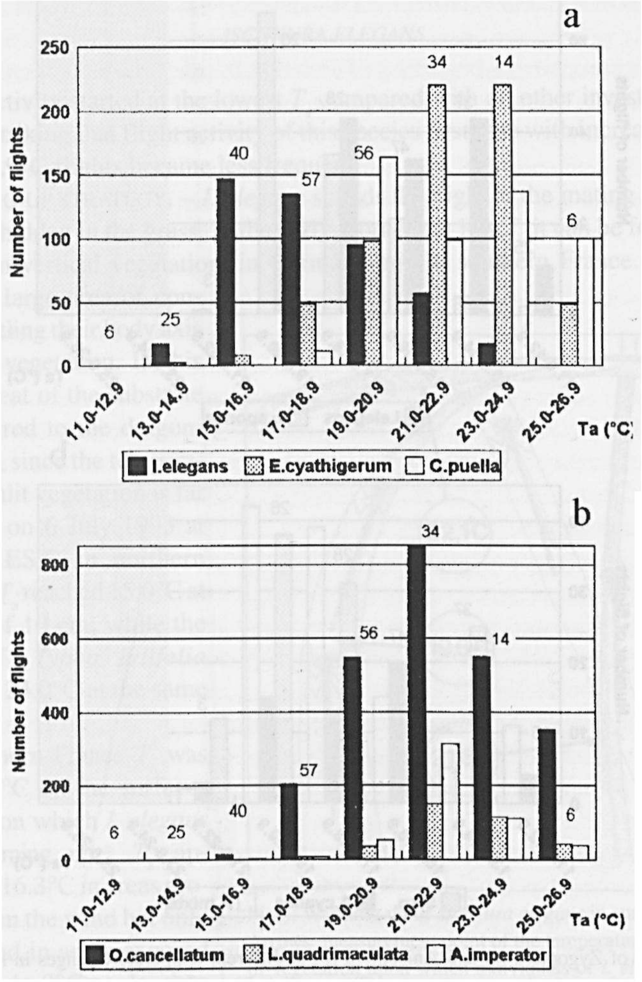

Fig. 2. Flights of Zygoptera (a) and Anisoptera (b) at different temperature ranges in northern Germany, in June. – Ambient temperature (T_a) was divided into intervals of 2°C (ordinate) and correlated with the number of flights (abscissa). Frequencies of temperature ranges placed above bars.

cancellatum did not come directly to the mating site, but first landed on warm, dry grassy spots in the meadow next to the largest pond. The surface temperature of these dry grass patches exceeded T_a, measured at the same time, up to 30°C. Adults were found on cool days, often in the early morning, sitting on these warm patches from which they shuttled back and forth to the pond. On cool mornings the dragonflies landed more often, and after a smaller number of flights, on the warm dry patches from which they had taken off. This could also be observed on days at low

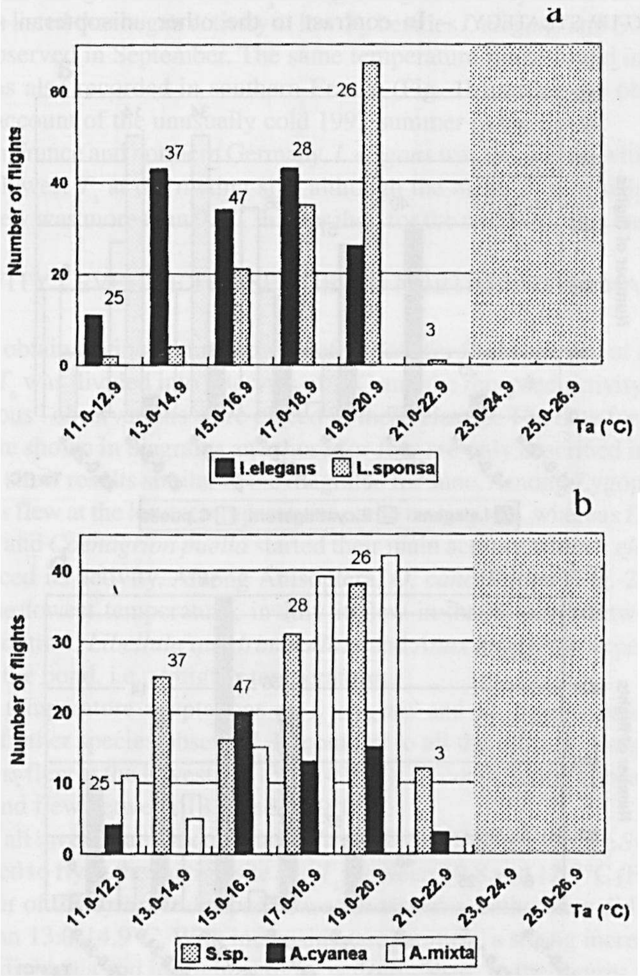

Fig. 3. Flights of Zygoptera (a) and Anisoptera (b) at different temperature ranges in northern Germany, in September. – Ambient temperature (T_a) was divied into intervals of 2°C (ordinate) and correlated with the number of flights (abscissa). Frequencies of temperature ranges placed above bars. The grey areas indicate temperature intervals which occurred only in summer, its inclusion facilitates a comparison with Fig. 2.

T_a, when the sun disappeared behind clouds. Some individuals would rest on the insolated side of a mound at the largest pond. Here, surface temperatures exceeded T_a by about 10°C.

THE EXPERIMENT. – The plates were brought out into the meadow at the largest pond before *O. cancellatum* became active. If there were no disturbances within 50 m, males often settled on the plates when they appeared at the mating site, but only on the unpainted natural-wooden plates. When the dragonflies had settled, a careful and slow approach to within 5 m was possible. *O. cancellatum* was recorded 32 times on an unpainted, natural-wooden plate but never on a painted plate.

ISCHNURA ELEGANS

Flight activity started at the lowest T_a compared with all other investigated species. It is striking that flight activity of this species first rose with increasing T_a, but at 19.0-20.9°C flights became less frequent.

WARMING-UP STRATEGY. – *I. elegans* spends the night at the mating site or very close to it hidden in the grass. In the early morning at low T_a it can be found sitting inactive on vertical vegetation, in Germany and in southern France. The adults achieve a large area of contact by nestling their body axis along the vegetation. In this way the heat of the substrate is transferred to the dragonfly's body, since the temperature of sunlit vegetation is far above T_a: on 6 July 1993 at 09:20 (MESZ) in northern Germany T_a reached 15.6°C at a height of 10 cm, while the surface of *Typha latifolia* measured 24.0°C at the same height.

In southern France T_a was 19.6-22.1°C on the surfaces of plants on which *I. elegans* was warming up; T_a approached 16.3°C in areas protected from the wind but only 14.3°C and in areas exposed to the wind - 8°C cooler than the temperature on the surface of the vegetation (Fig. 4). Sev-

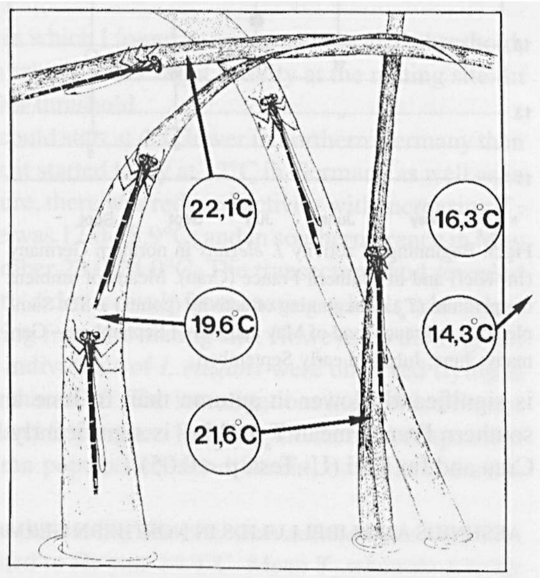

Fig.4. Warming up of *Ischnura elegans* in southern France. – Arrows: measurement point of the temperature on the surface of vegetation upon which individuals of *I. elegans* were sitting as figured. Circles: ambient temperature (T_a in °C). Upper right circle: T_a protected from the wind by vegetation; – lower right circle: T_a in an area exposed to wind.

eral individuals would fight vigorously for these warming-up places. At the gravel pit in southern France, *I. elegans* became active on windy days in sheltered regions, after having warmed up on dry parts of vegetation. I observed individuals of creeping from the shaded side of vegetation to the sunlit one. Still unable to fly they could already move their legs. With increasing T_a, they changed their sitting posture: they no longer nestled the body axis against the vegetation but took up a typical zygopteran posture, with only the legs touching the substrate. When T_a reached about 14.0°C, the damselflies started to fly.

I. ELEGANS IN NORTHERN GERMANY AND IN SOUTHERN FRANCE

In order to compare the beginning of activity of *I. elegans* in the North, Im Klei, and in the South, mean air temperature at the beginning of activity at the mating site is shown (Fig. 5). In southern France, it starts flight activity at higher T_a, especially in May. This comparison between southern France and northern Germany is possible because in early summer as as well in autumn cool temperatures occurred in southern France, which corresponded to those in northern Germany, meaning that a beginning of activity of *I. elegans* at low T_a would have been possible, theoretically, in both investigation areas.

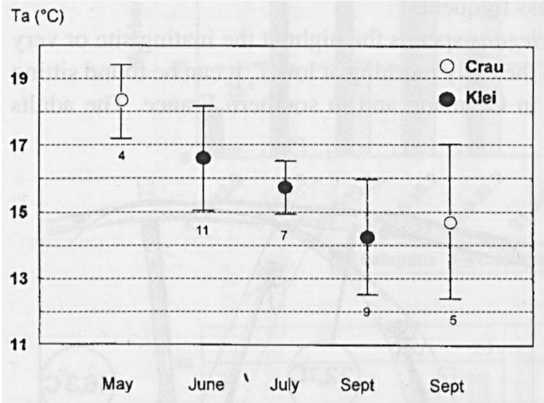

Fig.5. Beginning of activity *I. elegans* in northern Germany (Im Klei) and in southern France (Crau). Means of ambient temperature (T_a) of beginning of activity (points) ± SD. Sample sizes in France: end of May and end of September; – Germany: June, July and early September.

Mean T_a at the beginning of activity of *I. elegans* at Im Klei is significantly lower in autumn than in June and July (U- Test, $p < 0.05$). In southern France mean T_a in May is significantly higher than in September in the Crau and Im Klei (U- Test, $p < 0.05$).

AESHNIDS AND LIBELLULIDS IN NORTHERN GERMANY AND IN SOUTHERN FRANCE

Mean T_a when *Anax imperator* began to fly at the mating site in northern Germany was 20.6°C which is about about 3°C lower than for the same species and *A. parthenope* in the South (U- test, $p < 0.05$). Similar differences also become clear in the comparison of the *Sympetrum* species in September. In the South they start activity at a T_a of almost 22°C, which is more than 5°C above the value for the northern population (U- test, $p < 0.02$).

On the other hand, the comparison between *Aeshna mixta* in the North and in the South shows only small differences. The mean T_a for flight beginning in southern France, at 16.9°C, is only 0.8°C above the northern German T_a (U- test, $p > 0.5$).

DISCUSSION

The zygopteran, *I. elegans*, begins flight at the lowest T_a and the anisopteran *O. cancellatum* also starts to fly in cool weather. What enables them to do so? There are several factors which influence thermal adaptations and heat gain in insects, as there are thresholds for flight, body colour and size, energy saving flight and behavioural thermoregulation (HEINRICH, 1993). Temperature thresholds for activity are not necessarily fixed but can be changed during the life of an individual by acclimatization (BUFFINGTON, 1969; MEATS, 1973). But thermal adaptations can affect odonates' phases of activity and may influence their global distribution. These influences will be discussed in comparison with other orders of insects.

THRESHOLDS FOR FLIGHT

I. elegans was the only species in which I found an upper and lower T_a threshold, implying a temperature optimum which limits flight activity at the mating site. In all other cases I found only a lower threshold.

In summer, flight of *I. elegans* could start at 4°C lower in northern Germany than in southern France. In September, it started to fly at 12°C in Germany as well as in France. Above a certain temperature, there was reduced activity with increasing T_a. In northern Germany this T_a range was 17.0-18.9°C; and in southern France in May it was 27.0-28.9°C, and in September 23.0-24.9°C. The transect method revealed that, in Germany, reduced activity did not result from mating wheels which had settled, but from adults disappearing from the mating site. However in the very hot July of 1994 in southern France, individuals of *I. elegans* were observed flying at the same gravel pit at a T_a of more than 30°C. The investigations in southern France in 1993 were carried out in May and September. Possibly the thermal adaptations of the spring, summer, and autumn populations are different, or flight occurs in very hot summers at high T_a.

The lower threshold for flight at the mating site of *O. cancellatum* was very low, too, the minimum T_a when it started to fly was 14.9°C. Mean T_a when its activity began is below those of all other investigated species in June and July, except *I. elegans*.

Probably there exist seasonal adaptations in flight activity. The north German autumn is characterized by cool nights and the air warms up only slowly during the day. The odonates flying in autumn have been able to adapt to this cold weather in order to reproduce successfully. They fly at T_a in which the investigated species in the summer - apart from *I. elegans* - did not show any activity. Odonates flying in summer can forgo flight activity at the mating site on cool days. At low T_a, flight entails a high energy cost (K. Hoffmann, pers. comm.) which need not be expended in summer because days with favourable climatic conditions will probably follow.

INFLUENCE OF BODY COLOUR ON HEAT GAIN

For heat gain by Odonata through solar radiation the surface colour of the body and the ability to absorb radiation through the cuticle are important. In odonates, colour change at different T_a is known (e.g. O'FARRELL, 1963; VERON, 1974; MAY, 1976a; STERNBERG, 1990; MILLER, 1993), but its function is not well understood.

HAMILTON (1973) described activity patterns in beetles, depending on whether they are black or white in colour. Heat gain in the dark-coloured insects should be greater than that in light-coloured ones (HENWOOD, 1975). The dorsal side of *I. elegans* is almost totally black. In *I. elegans* males, nearly 90% of the surface of the abdomen is black, wheras in *Enallagma cyathigerum* and *Coenagrion puella* males only about 40% is black. In the morning, individuals take advantage of the early sun (HENWOOD, 1975) to warm up. If *I. elegans* is able to transfer heat from the abdomen to the thorax, this may enable her to fly at lower T_a than all other Odonata I investigated.

ROLAND (1982) also found that darker individuals of *Colias nastes* and *C. meadii* (Lepidoptera: Pieridae) could be active under natural conditions at lower T_a than lighter-coloured ones. On the other hand, he speculated that darker individuals overheat on hot days and are thus forced to move into shaded areas. This may also apply to *I. elegans*. With increasing T_a between 17.0 and 18.9°C in northern Germany, this damselfly reduced its activity and disappeared at yet higher T_a. Disappearance from the mating site may have been due to the small amount of shading vegetation at the intensively observed pond, which had only been dug out in 1991.

The body colour of male *O. cancellatum* shows dark and light areas. The head, thorax and tip of the abdomen are dark brown, while the rest of the body has a light-blue pruinosity. Heat absorption in this species probably occurs particularly in the area of the head and thorax, which can provide the flight muscles with the necessary warmth. This is an advantage for *O. cancellatum* since in libellulids heat gain through wing shivering is very rare, and they depend mainly on an increase in muscle temperature through T_a and radiation before they can start to fly.

ENERGY-SAVING FLIGHT

In flight, heat loss in small zygopterans is probably high, compelling them to warm up anew from time to time. No information could be found about heat gain of the flight muscles in Zygoptera during flight. In flight, zygopterans beat their fore- and hindwings alternately, which results in a regular and energy-saving flight. Anisopterans can fly in this way, too, but the change to a parallel and phase-shifted wingbeat during acceleration is also known to occur (RÜPPELL, 1989). This type of flight and the long distances usually covered cost more energy, which could be the reason why they have to reach higher temperatures before starting to fly (HEINRICH, 1993). Butterflies with a lower wingbeat frequency can fly with lower T_b than the species with higher wingbeat frequencies (GUPPY, 1986). This seems to apply also to dragonflies, since in all seasons and areas the Zygoptera, which have lower wingbeat frequencies than the Anisoptera (RÜPPELL, 1989), began to fly at lower T_a than the latter.

THERMOREGULATION THROUGH PERCH CHOICE

The odonate species most successful in broadening their activity period by becoming active at low temperatures did so by means of behavioural adaptations rather than by obvious physiological adaptations. In insects, warming up through wing shivering before flight is known, for example, in butterflies (KAMMER, 1970). In dragonflies the ability to warm up by wing shivering is largely confined to the more "primitive" species, such as the aeshnids. In Zygoptera and the libellulids, the possibility of T_b increasing by wing shivering and heat transfer from the thorax to the abdomen is virtually lacking (MAY, 1976a; 1991). "Perchers" (CORBET, 1962) achieve an increase in T_b primarily through perch choice and through orientating their body axis to the sun. Besides Odonata (MAY, 1976b), other insects such as grasshoppers (WALOFF, 1963; CHAPELL, 1983), cicadas (HEINRICH, 1993) and butterflies (KEVAN & SHORTHOUSE, 1970; RUTOWSKI et al., 1994) bask in the sun in order to increase T_b.

ASKEW (1982) described perching behaviour in *I. elegans, E. cyathigerum* and *C. puella* in Great Britain. He distinguished between "roosting" during the night and on cool days and "resting", which occurs in the intervals between flights. In *I. elegans* I observed warming-up on the vegetation where adults were sitting before the beginning of activity. In order to accelerate warming-up, the damselflies crawled from shaded spots to sunlit ones and pressed their whole body against the substrate (roosting), thus taking advantage of the heat of the warm vegetation. Shortly before take off, however, only the legs contacted substrate (resting). On cool days and early in the morning the insects sometimes assumed the roosting posture during intervals in flight activity.

BUCHHOLZ (1957) and KRÜNER (1977) described the perching behaviour in the "percher" *O. cancellatum*. Krüner (1977) found that males, at a T_a of up to 26°C, sat on stones of the embankment of the mating site, while at higher T_a they sat on *Juncus* or dry twigs near the water.

In northern Germany, males *O. cancellatum* perched on dry patches of grass.

The posture of the wings also contributes to heat absorption, since I observed that settled individuals directed their wings horizontally downwards, thus diminishing the space between their wings and the patch of grass. This causes the warm air to be held close to the thorax and reduces heat loss through convection, as TRACY et al. (1979) described in a gomphid and STERNBERG (1990) in a libellulid and in an aeshnid.

My experiment with coloured plates shows that *O. cancellatum* is apparently able to perceive dry, for perching selected patches of grass visually. KREBS & WILDERMUTH (1976) have suggested that in the past, the preferred *O. cancellatum* habitat were fertile flood plains, where it perched on dry banks of sand and gravel. Nowadays, it inhabits gravel pits which offer similar perch sites. Bare sand warms up only very slowly. On the other hand, it cools down slowly, too, in decreasing temperatures. Therefore, perching on sand can prolong activity when temperatures are falling (SHREEVE, 1990). In northern Germany, the dry grass patches represent a corresponding structure which could fit into the "optical pattern" of *O. cancellatum.* This is shown by my experiment: *O. cancellatum* preferred the unpainted wooden plate rather than the black, i.e. the warmer, one. Nevertheless, these warm grass patches contribute towards the T_b increase, therefore *O. cancellatum* can become active in summer at the lowest T_a in northern Germany.

CONSEQUENCES OF THERMAL ADAPTATIONS: DISTRIBUTION AND MATING SUCCESS

I. elegans is the most widespread European damselfly (DUMONT & DUMONT, 1969). Its ability to be active at low T_a could contribute to its abundance and wide range, by enabling it to exploit a niche that is not available to other species. Therefore the early beginning of activity at the pond and its disappearance at increasing T_a cannot be interpreted as an ecological separation to avoid competition. In *I.elegans* mating is not restricted to warm, sunny days (KRIEGER & KRIEGER-LOIBL, 1956). Copulation wheels and ovipositions can be observed even on days when no other species appear at the mating site. In northern Germany, copulations of *I. elegans* can be observed at T_a 2-3°C lower than those of *Enallagma cyathigerum* and *Coenagrion puella.* The lowest T_a at which a copulation wheel of *I. elegans* was found was 10.9°C in September. PARR (1969) speculated that summer temperature might be an important factor in limiting distribution of species northwards. The thermal adaptation of *I. elegans* could put it at an advantage when colonizing a wide range of habitats in different climatic regions.

Body colouration in the different *Orthetrum* species might be correlated with their distribution. The range of *O. cancellatum* extends to Great Britain and Scandinavia, to the E as far as Mongolia, and to the S to the northern coast of Africa (ASKEW, 1988), covering, thus, very different climatic areas. *O. coerulescens* is the only other congener, which also has a brown-coloured head and thorax, and extends similarly far North. The more southern species, e.g. *O. brunneum, O.*

nitidinerve, and *O. ramburi*, show a light-blue pruinosity all over the body. Apart from reducing radiation absorption, this pruinosity could protect against evaporation, an important advantage for males that are almost always active at the mating site when the weather is favourable.

To fly early in the morning at low temperatures is an advantage for the *O. cancellatum* males. They can spend more time at the mating site, hence increase their mating chances, since their females often appear at the mating site early in the morning and on cool days (HILFERT & RÜPPELL, 1997).

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