Odonatologica 25(3): 307-311 *September 1, 1996*

PRE-FLIGHT WARMING UP OF MATURING *AESHNA MIXTA* LATREILLE (ANISOPTERA: AESHNIDAE)

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Received January 9, 1996 / Revised and Accepted February 15, 1996

It is shown that maturing *A. mixta* can use shivering as a pre-flight warming up strategy, which gives the insects the capacity to switch between pure ectothermy and a combination of ectothermy and endothermy. So far this has been evidenced in mature odonates only. Since this strategy opens the way to eocrepuscular flight in immatures, this may be a cue in explaining the role of twilight zone flight. For the first time the relationship between ambient temperature (T_a) and shivering on the duration of the pre-flight period was investigated under natural conditions. The duration of shivering was negatively, but just not significantly, correlated with the ambient temperature. The duration of shivering and T_a did not effect the duration of the pre-flight period. Shivering intensity, however, significantly reduced the time prior to take-off. The observations suggest that abdominal shivering may represent part of an endothermic strategy.

INTRODUCTION

In dragonflies, as in other flying insects, the thoracic temperature (T_h) has to reach a certain level before flight is possible (MAY, 1976; VOGT & HEINRICH, 1983). Large aeshnids do not take off before they reach a T_h of at least 30°C (VOGT & HEINRICH, 1983). According to CORBET (1962, 1980) Aeshnidae are 'fliers': species that fly continuously during their active phase. All 'fliers' are able to actively increase their thoracic temperature endothermically by shivering (HEINRICH & CASEY, 1978; VOGT & HEINRICH, 1983; HEINRICH, 1993 but see POLCYN, 1994).

Within the genus *Aeshna*, shivering preceding take-off has been observed in adults of *A. grandis* and *A. cyanea* (or *A. mixta*, the author could not discriminate between these two species) (POND, 1973). BROWNETT (1992), on the contrary, reported that maturing individuals of *A. mixta* prepared for flight by basking, with the wings motionless. He never observed wing-whirring prior to take-off. This possibly indicates an ontogenetic switch in thermoregulatory behaviour as was already found in other dragonflies (WATANABE, 1991; MARDEN, 1995).

Because shivering increases T_h, it is expected that this also reduces the duration of the pre-flight period. To our knowledge, this prediction has never been tested. Since the rate of T_h increase is positively related to the ambient temperature (T_a) (VOGT & HEINRICH, 1983), we also expected a negative relation between the duration of shivering and T_a.

The objective of this study was to test whether (1) maturing *A. mixta* also use shivering as a warming-up strategy ; (2) the duration of shivering is negatively correlated with T_a and (3) shivering decreases the duration of the pre-flight period.

MATERIAL AND METHODS

Maturing *A. mixta* were netted in tree-lined lanes and woodland edges near Antwerp (Belgium) on 7 sunny and windless days in September 1993. Immediately after capture each individual was placed in a light-proof container where it was stored at approximately 4°C for 30 minutes. Then it was positioned on a small stick (50 cm) perpendicular to the sun. We measured the pre-flight period (time between release and take-off), the duration of wing-whirring, the ambient temperature (in the sun at a height of 50 cm), and noted the body parts used for shivering (forwings, hindwings or abdomen).

The effects of shivering duration, the shivering intensity and T_a on the duration of the pre-flight period were analyzed using a backward multiple regression procedure with normally distributed errors and the identity link using the statistical package GLIM (CRAWLEY, 1993). Shivering intensity was defined as a factor with four levels: no movements, only abdominal shivering, whirring with two wings and whirring with four wings. To test for different effects of the levels of shivering intensity we used the contrast procedure (CRAWLEY, 1993).

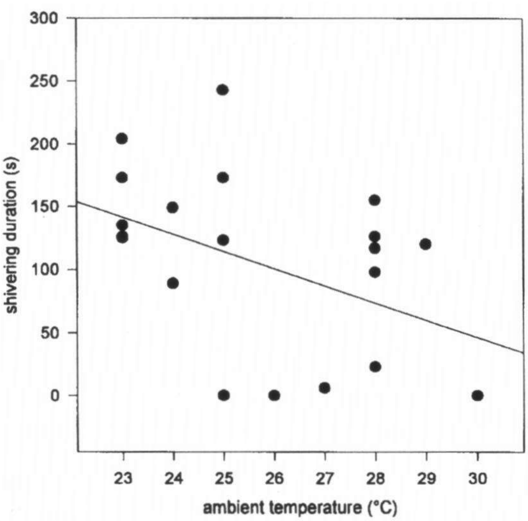

Fig. 1. Duration of the shivering period in function of the ambient temperature (T_a).

RESULTS

Of the tested 27 animals, 8 did not shiver after being placed on the stick. Four of these had whirred with their wings during their stay in the container and were excluded in the analysis. The pre-flight period lasted on average 200±180 s (range 0-871 s). Only a minority (0.15) of immatures did not use any shivering. Two animals shivered only with two wings, while one animal only used the abdomen. Wing whirring was not always continuous but ranged from 9% to 100% of the pre-flight period (87±73 s).

There was a tendency for animals to shiver for a shorter time with increasing T_a (without two outliers, r=-0.42, $F_{1,18}$=4.1, p=0.058) (Fig. 1). Because of the rather low coefficient of determination R^2=0.17) the problem of collinearity (PHILIPPI, 1993) is small and both factors will be used in the analysis as independent factors.

The main effects T_a and the duration of shivering had no effect on the duration of the pre-flight period (Tab. I). Animals that shivered had a much shorter pre-flight period than animals that did not (R^2=0.64; Fig. 1; Tab. I). Shivering with the abdomen only was less successful in shortening the time to take-off than shivering with the wings. There was no significant difference in the duration of the pre-flight period of animals whirring with two or four wings (Fig. 2).

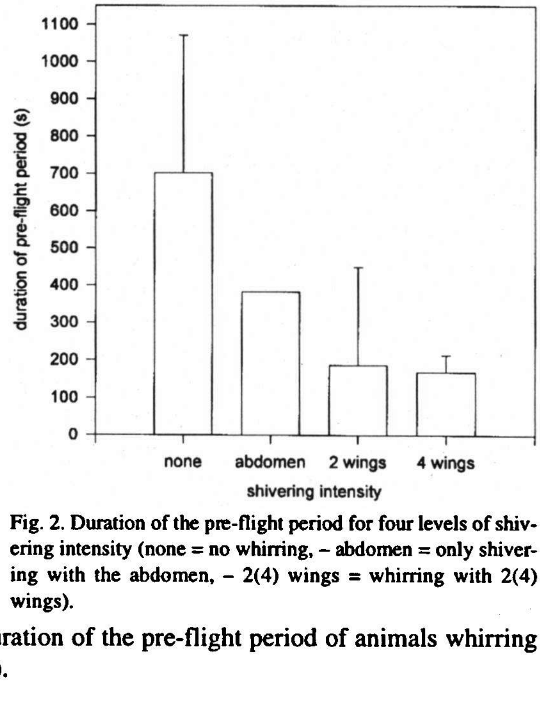

Fig. 2. Duration of the pre-flight period for four levels of shivering intensity (none = no whirring, – abdomen = only shivering with the abdomen, – 2(4) wings = whirring with 2(4) wings).

DISCUSSION

Our results show that maturing *A. mixta* are able to thermoregulate not only by basking (cf. BROWNETT, 1992) but also by metabolic heat production through shivering. So these animals can switch between a combination of ectothermy and endothermy and pure ectothermy (for a further discussion see MAY, 1978 and POLCYN, 1994). As predicted, shivering had a signifi-

Table I

Multiple regression analysis of the effects of shivering intensity, duration of shivering and T_a on the duration of the pre-flight period – [NS = not significant]

Main effect	df	F	p-value
Shivering intensity	3,17	5.24	0.0096
Duration of shivering	1,17	0.012	NS
T_a	1,17	0.0625	NS

cant shortening effect on the pre-flight period.

JÖDICKE (1993) considered the species as eocrepuscular (flying in the twilight period before sunrise and after sunset). Because he only studied animals at a pond, he probably only observed adults (CORBET, 1980). BROWNETT (1992) saw maturing individuals flying after sunset. Our results indicate that flight before sunrise is also physiologically possible in immatures (see e.g. CORBET, 1957). Information on its effective presence or absence in this stage would be an important cue in determining whether twilight zone flight plays a role in odonate reproduction (as suggested MAY, 1977, 1978; JÖDICKE, 1993, 1995) or whether it is merely a way of preventing overheating in fliers (MAY, 1987).

As expected, there was a negative, although not significant, correlation between T_a and the duration of shivering. On the other hand, our results suggest that the duration of the pre-flight period is unaffected by T_a. Perhaps the heat produced by shivering in these animals has a greater impact on their thermal balance than the environment. An alternative explanation is that the observed range of T_a's measured was too narrow and/or too high to detect a significant effect. The observed low levels of shivering intensity (only abdomen and two wings) can probably also be explained by the rather high observed T_a's.

Not all *A. mixta* whirred with both wing pairs, using the metabolic heat of both sets of flight muscles. POND (1973) also observed that an *A. grandis* used only the mesothoracic muscles to warm up. The positive effect of abdomen shivering was surprising. These movements were clearly distinguished from abdominal pumping because the entire abdomen shivered and movements were at a higher frequency than pumping movements. Because this shivering was done without any wing movements we exclude the possiblity that it is a reflection of low-amplitude flight-muscle shivering. This is the first report on the possible use of the abdomen during endothermic warming up (see HEINRICH, 1993). Further research is however needed to clearly demonstrate the thermogenic nature of this activity.

ACKNOWLEDGEMENTS

We thank HANS VAN DIJCK and an anonymous referee for valuable criticism. This study was partly supported by the Belgian National Fund for Scientific Research (RS is Research Assistant, LDB is Senior Research Assistant and EM is Research Associate).

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