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Endothermic heat production in three species of Nymphalidae (Lepidoptera)

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Summary

Endothermic heat production is often described as an uncommon mechanism in butterflies, although shivering has been reported in a number of species. Here, we detail initial observations of endothermic heat production by three Nymphalidae species (subfamily Nymphalinae) ; the Painted Lady, *Cynthia cardui* (L.) ; Peacock, *Inachis io* (L.) and Red Admiral, *Vanessa atalanta* (L.). Closed wing shivering occurred over the whole experimental ambient temperature range of 14.5-23°C. All species and individuals tested showed inreased thoracic temperatures while shivering. The maximum excess temperatures and the rates of warming recorded for the three species were T_{ex} = 16.5°C at 3°C min^{-1} for *C. cardui* (T_a = 19°C) ; T_{ex} = 18°C at 4°C min^{-1} for *I. io* (T_a = 16°C) and T_{ex} = 13°C at 4.3°C min^{-1} for *V. atalanta* (T_a = 17°C). We suggest that endothermic heat production may contribute to the widespread distribution and generalist habitat associations of these long lived butterflies. We also suggest that the role of endothermic heat production in butterflies needs further examination.

Résumé

La production de chaleur endothermique est souvent considérée comme un mécanisme peu commun chez les papillons, bien que le «frissonnement» ait été signalé chez plusieurs espèces. Ici, nous détaillons des observations préliminaires sur la production de chaleur endothermique chez trois espèces de Nymphalidae (sous-famille Nymphalinae). Le «frissonnement» ailes fermées s'est produit à toutes les températures expérimentales de 14,5 à 23°C. Toutes les espèces et tous les individus testés ont présenté une température thoracique élevée pendant le «frissonnement». Les températures maximales en excès et les taux de chauffage observés pour les trois espèces ont été T_{ex} = 16,5°C à 3°C min^{-1} pour *C. cardui* (T_a = 19°C) ; T_{ex} = 18°C à 4°C min^{-1} pour *I. io* (T_a = 16°C) et T_{ex} = 13°C à 4,3°C min^{-1} pour *V. atalanta* (T_a = 17°C).

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Nous suggérons que la production de chaleur endothermique pourrait contribuer à la grande extension de la répartition géographique et aux associations à habitat généraliste de ces papillons qui ont une grande longévité. De surcroît, nous estimons que des études supplémentaires sur le rôle de la production de la chaleur endothermique chez les papillons mériteraient d'être entreprises.

Introduction

Flight is essential for most Lepidoptera. In the majority of temperate species of butterfly the required thoracic temperature (T_{th}) for flight is above that of ambient air temperature (T_a). A number of studies of the temperatures required for sustained voluntary flight indicate that species with moderate to fast wing beat frequencies require T_{th} of 28-40° C, with vigorous flight restricted to the range of 33-38° C (Kingsolver, 1985). For species with slow, gliding flight, which do not require the same power and frequency of muscle contraction, flight may be initiated at lower thoracic temperatures ; for example 10° C for overwintering monarch butterflies, *Danaus plexippus* L. (Nymphalidae) (Chaplin & Wells, 1982) and 17-18° C for *Parnassius phoebus* F. (Papilionidae) (Guppy, 1986).

There are two possible options for heat gain during pre-flight warm-up ; physiological (generating internal metabolic heat) or behavioural (choice of microhabitats, orientation and posture relative to the sun) (Heinrich, 1981). For butterflies, the most common method of raising body temperature is to use some form of basking. Endothermic heat production is often described as an uncommon mechanism in butterflies (Kingsolver 1985 ; Shreeve 1992 ; Heinrich, 1993), although shivering has been reported in a number of species, including Papilionidae, Hesperiidae and Nymphalidae (Findlay, Young & Findlay, 1983 ; Dennis, 1993).

Endothermic heat production by butterflies is described as energetically expensive and inefficient because the generally narrow body and poor insulation leads to rapid heat loss (Kingsolver, 1985). Where it has been recorded in the butterflies *Danaus plexippus* (Kammer, 1970) and *Papilio polyxenes* (Rawlins, 1980) this mechanism of shivering only raises thoracic temperatures 4° C above ambient at the most , with a maximal recorded heating rate of 1.3° C min^{-1}. In two species of Nymphalidae greater excess temperatures have been found ; 18° C in *Vanessa atalanta* (Krogh & Zeuthen, 1941) and 8-11° C in *Nymphalis antiopa* (Douglas, 1986). In contrast, endothermic heat production is well documented in many species of moth, chiefly Sphingidae and

Saturniidae, which may elevate body temperature to at least 20°C above ambient by prolonged shivering (Heinrich & Bartholomew, 1971 ; Bartholomew & Casey, 1973).

Here, we detail initial observations of endothermic heat production by three Nymphalidae species (subfamily Nymphalinae) ; the Painted Lady, *Cynthia cardui* (L.) ; Peacock, *Inachis io* (L.) and Red Admiral, *Vanessa atalanta* (L.). The data presented here, taken with that of previously published work on Nymphalinae species (*V. atalanta*, Krogh & Zeuthen, 1941 and *N. antiopa*, Douglas, 1986) indicate that in some butterfly species pre-flight warm-up using endothermic heat production may be both rapid and produce a large excess temperature over ambient.

Materials and methods

Specimens of *C. cardui* ($N = 8$), *I. io* ($N = 6$) and *V. atalanta* ($N = 2$) were caught in an Oxfordshire garden between 10 August and 15 September 1994, or were from captive stock reared from eggs of wild females caught during the same period. Prior to measurements of endothermic heat production, individuals were kept for a maximum of 21 days, in a 50 cm × 50 cm × 60 cm flight cage, with free access to fresh cut flowers and honey-water. Trials took place in an unheated room over the temperature range 14.5-23°C, under conditions of low illumination (<5 watts m^{-2}). Butterflies were immobilised by placing them in a jar with ethyl acetate. As soon as they stopped moving vigorously (approximately 10-15 seconds) they were removed from the jar and restrained on a setting board, with the wings held open by paper strips. Immobilising specimens by placing them in a killing jar for a few seconds is a method recommended by Friedrich (1986) for hand pairing nymphalid butterflies. This technique was found to be preferable to cooling or to no immobilisation as it facilitated thermistor implantation with minimal damage. A 0.4 mm diameter micro thermistor probe (Skye Instruments : SKTS 200U/M, time constant <1.0 sec) was shallowly inserted under the dorsal thoracic cuticle and held in position by water soluble glue (Gloy^{TM}). The butterfly was released from the setting board when the glue had dried (approximately ten minutes). The leads from the thermistor probe consisted of a 1 m long, 0.13 mm diameter wire, leading to a lightweight screened cable connected to a data logger (Skye Instruments : SDL 2960). This arrangement allowed the butterfly free wing movement when settled, together with limited flight at the end of the tether. Butterflies treated in this way lived for up to ten days after the implant was removed, behaving in an apparently normal fashion (e.g. flying and feeding), suggesting that minimal internal damage was caused by the experimental procedure.

Temperatures were recorded at 30 second intervals. This time period was used in preference to shorter periods for ease of comparison with other studies presenting data on this time scale (e.g. Kammer 1970). In addition to butterfly thoracic temperature, simultaneous data were recorded from a bare thermistor probe (control probe) placed adjacent to the butterfly, and an integral temperature sensor with radiation shield to record ambient air temperature. For the first three trials two further controls were used ; freshly dead butterflies of the same species as the test specimen, one with wings set closed, the other with wings open (basking posture), with thermistors implanted in the same way as for the test specimen. As thoracic temperatures of these butterflies showed no difference from that of the control probe, they were not included in subsequent trials. Ambient and control probe temperatures never differed by more than 1° C.

Results

When butterflies were released from the setting board, the typical pattern of behaviour was to settle with wings closed. Shivering occurred either spontaneously or in response to mild disturbance (e.g. gently flicking the wings). Butterflies shivered while standing still with wings closed, shivering being manifested by high frequency, low amplitude vibrations of the wings. Shivering occurred over the whole experimental ambient temperature range of 14.5-23° C. All species and individuals tested showed increased thoracic temperatures while shivering (Tab. 1). After a few minutes (mean = 4.8 mins, S.E. = 0.28, N = 28 shivering bouts) they usually attempted to fly (flying vigorously for a few seconds at the end of the tether), after which they would settle again with their wings closed.

At the lower ambient temperature range (14.5 ± 6° C) the mean thoracic temperature when flight was attempted by *C. cardui* was 24.4 ± 1.1° C (N = 6). For *I. io*, at T_a of 15-16° C, the mean thoracic temperature for attempted flight was 30.7 ± 2.3° C (N = 3). At the upper ambient temperature range, mean thoracic temperatures at flight initiation were higher for *C. cardui* (mean = 31.1° C, at T_a of 19-20° C, N = 2) but not for *I. io* (mean = 30.0° C, at T_a of 20-23° C, N = 3). Mean thoracic temperature at flight initiation for *V. atalanta* was 29° C at T_a of 17-17.5° C (N = 2). After attempted flight, individuals usually returned to a posture of standing with closed wings as they cooled. This pattern

Table 1

Thoracic temperatures (° C) achieved by shivering in the painted lady (*C. cardui*), peacock (*I. io*) and red admiral (*V. atalanta*).
Data are presented for means for each individual at specific temperatures, and for population means (pooled data across limited temperature ranges)

Cynthia cardui					*Inachis io*					*Vanessa atalanta*				
Individual	n	T_a	T_{ex}	rate	Individual	n	T_a	T_{ex}	rate	Individual	n	T_a	T_{ex}	rate
A	1	14.5	11.5	1.3	A	2	15.0	11.2	1.7	A	1	17.0	13.0	4.3
B	2	15.0	11.0	1.7	B	2	15.0	17.0	3.4	B	1	17.5	10.5	3.5
C	2	15.0	9.2	2.0	C	1	16.0	18.0	4.0					
D	2	15.0	7.7	1.7	D	3	20.0	10.0	3.0					
E	2	15.5	4.5	0.8	E	3	20.0	10.0	3.0					
F	1	16.0	11.5	2.3	F	1	23.0	7.0	1.5					
G	3	19.0	15.2	3.0										
H	1	20.0	8.0	1.3										
T_a			T_{ex}	rate	T_a			T_{ex}	rate	T_a			T_{ex}	rate
14.5-16.0		**mean**	9.2	1.6	15-16		**mean**	15.4	3.3	17-17.5		**mean**	11.7	3.9
(N = 6)		**sd**	2.8	0.5	(N = 3)		**sd**	3.7	1.2	(N = 2)		**max**	13.0	4.3
		max	11.5	2.3			**max**	18.0	4.0					
19-20		**mean**	11.6	2.1	20-23		**mean**	9.0	2.5					
(N = 2)		**max**	15.2	3.0	(N = 3)		**sd**	1.7	0.9					
							max	10.0	3.0					

T_{ex} = excess thoracic temperature (thoracic minus ambient) ; T_a = ambient air temperature ; rate = warm-up rate, °C min^{-1} ; n = number of shivering bouts ; N = number of individuals was often repeated with subsequent bouts of shivering followed by an attempt at flight. Fig. 1 illustrates increased thoracic temperatures achieved by shivering, for a peacock and painted lady butterfly tested simultaneously. Fig. 2 shows a similar pattern for a red admiral.

The maximum excess temperatures and the rates of warming recorded for the three species were T_{ex} = 16.5°C at 3°C min^{-1} for *C. cardui* (T_a = 19°C) ; T_{ex} = 18°C at 4°C min^{-1} for *I. io* (T_a = 16°C) and T_{ex} = 13°C at 4.3°C min^{-1} for *V. atalanta* (T_a = 17°C). When butterflies were quiescent (before shivering and after cooling down from a shivering bout), thoracic temperatures were not significantly different from that of the control probe ($t = 0.7$, $P = 0.49$, N = 24).

Discussion

The maximum excess temperatures and the rates of warming recorded were higher than those found for *P. polyxenes* (Rawlins, 1980) and *D. plexippus* (Kammer, 1970) which belong to a different family and subfamily (Papilionidae and Danainae respectively) from that of the species tested here. Our results are directly comparable with two earlier studies of members of the Nymphalidae, subfamily Nymphalinae ; *Vanessa atalanta* (Krogh and Zeuthen, 1941) and *Nymphalis antiopa* (Douglas, 1986) which may achieve a T_{ex} of 8-18°C by shivering. Thoracic temperatures recorded at flight initiation for the three Nymphalinae species we tested are similar to those found for voluntary flight initiation of other species of butterfly which do not engage in gliding flight (Kingsolver, 1985 ; Shreeve, 1992).

Our data, taken with that of Krogh & Zeuthen (1941) and Douglas (1986), representing four species of Nymphalidae, subfamily Nymphalinae, may indicate that there is a phylogenetic component to the shivering posture adopted and temperature excess achieved by these butterflies. Further investigation of the occurrence of endothermy in different butterfly taxa would help to clarify this. The ability to use endothermic means of heat production may be particularly advantageous to these generally long lived butterflies and contribute to their overall widespread distributions and generalist habitat associations.

Throughout their ranges both *I. io* and *V. atalanta* undergo winter diapause as adults. The ability to generate heat by shivering would enable overwintering adults to warm-up and move from (or within) cool, dark hibernation sites, when behavioural means of warming up are not an option. Douglas (1986) reports that *N. antiopa*, which also overwinters as an adult, raises its thoracic temperature by shivering

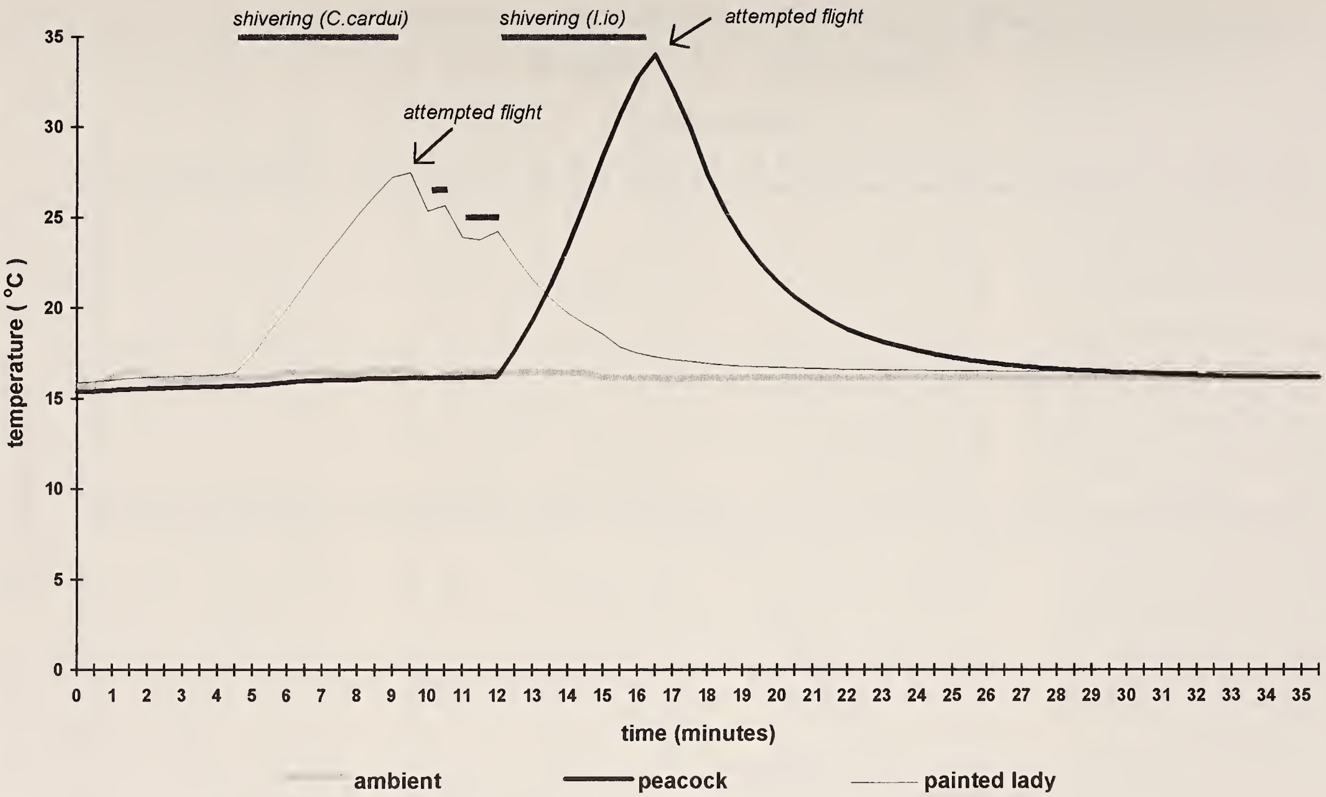

Fig. 1. Thoracic temperatures during shivering in the Painted lady, *C. cardui* and Peacock, *I. io*.

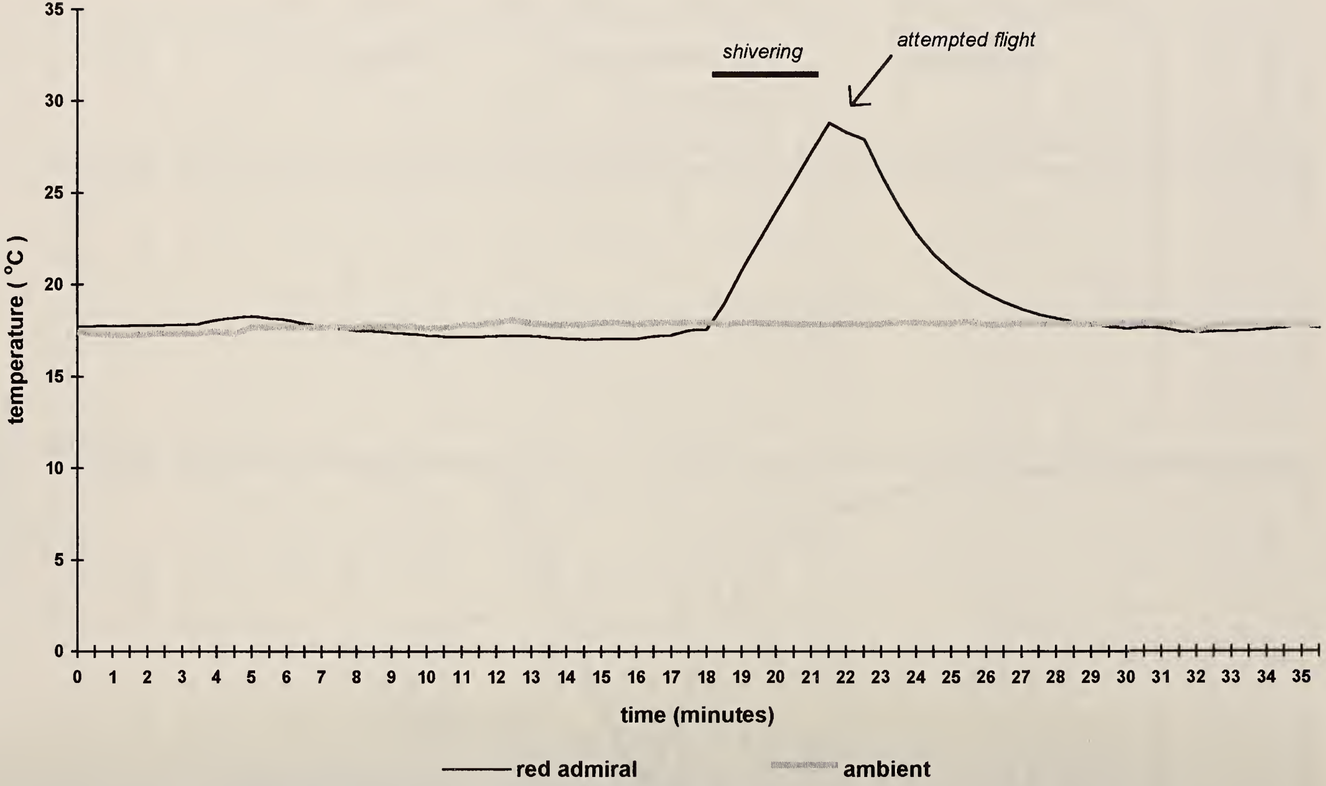

Fig. 2. Thoracic temperatures during shivering in the Red Admiral, *V. atalanta.*

to enable it to move from tight, dark hibernation roosts to open sunlit areas where it can bask. A similar function for shivering has been suggested for the black swallowtail, *P. polyxenes*, which uses endothermic heat production as a subsidiary warm-up mechanism under conditions of low solar radiation and ambient temperature. Under these circumstances shivering probably generates enough heat to allow minimal activity for activities such as changing habitat or regaining a roosting site if dislodged (Rawlins & Lederhouse, 1978). Shivering, followed by flight, has been observed in an overwintering *I. io* when dislodged from its roost (C. Maier pers. obs.).

Prior to entering diapause and immediately afterwards overwintering adult butterflies spend considerable time feeding to accumulate and replace stored energy reserves respectively (Pullin, 1986). In autumn and early spring ambient temperatures may be low and solar radiation of low intensity. At these times of the year these energy sources may also be extremely variable, both within and between days. In such marginal circumstances the ability to employ endothermy may allow individuals to maximise the time they can spend feeding.

Cynthia cardui does not enter winter diapause and is probably not a permanent resident within Europe, its main permanent centres being in North Africa, Arabia and Asia (Emmet & Heath, 1989). *Vanessa atalanta* is also a temporary resident in northern latitudes with permanent centres within southern Europe. Both are strongly opportunistic and engage in extensive migration. Endothermic heat production may facilitate this strategy, allowing summer survival in extreme northern areas including locations within the Arctic Circle. It may also account for observations (Emmet & Heath, 1989) of active adults of both species during warm winter days in December and January within the British Isles.

All three species are fairly brightly coloured on their dorsal wing surface but the underside is cryptic against usual resting backgrounds. All can adopt an open winged (dorsal) basking posture, but basking in conditions of low solar radiation, when body temperature is too low for efficient flight, may make individuals vulnerable to potential predator attack. Several studies suggest that butterflies are most at risk from predation in marginal temperature and weather conditions when effective thermoregulation and active flight are difficult (Rawlins & Lederhouse, 1978 ; Bowers, Brown & Wheye, 1985 ; Kingsolver, 1987). The ability to raise thoracic temperature endothermically, with closed wings, may in certain circumstances enable flight temperature to be achieved without compromising the protection afforded by the cryptic pattern of the hind wings.

We suggest that the role of endothermic heat production in butterflies needs further examination, in respect of actual temperatures achieved and in relation to the energetic cost of this warming method. We further suggest that for nymphalid species there is a case for further research into how periodic endothermy may contribute to adult overwintering success and what role it might play in migratory strategies.

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