Thermal ecology of Interior Alaska dragonflies (Odonata: Anisoptera)

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Summary

1. We examined the thermal ecology of Interior Alaska dragonflies (Odonata: Anisoptera). The relationships between mass and passive cooling rate, wing loading, minimum flight temperature (MFT) and thermoregulating ability were examined. These properties were also compared between the behavioural classes: perchers and fliers. All factors with the addition of seasonal and daily flight activity were related to generalized thermal strategies.

2. Passive cooling rate decreased while wing loading and MFT increased with mass.

3. While all species were able to elevate thoracic temperature, larger species were better able to maintain a constant temperature.

4. Both the smallest and largest species of dragonflies were capable of activity at ambient temperatures of approximately 14 C by employing different thermal strategies: low MFT and physiological heat production, respectively.

5. For small species active in cool conditions low MFT may be favoured even if accompanied by poor thermoregulating ability. By contrast, thermoregulation and specialization for high-temperature performance may be favoured in both small and large species during the warmer summer flight season.

6. The smallest and largest dragonflies in Interior Alaska have the shortest and longest daily activity periods, respectively. However this pattern does not hold for the intermediate-sized dragonflies. Thermal strategy displays no clear relationship to daily activity pattern.

Key-words: Minimum flight temperature, thermoregulation, thermoregulatory performance index

Introduction

For many insects the ability to both elevate and regulate body temperature is positively correlated with the intensity and duration of activities that directly influence fitness (Heinrich 1977, 1981; Singer 1987; Convey 1989; Ybarrondo & Heinrich 1996). The ability of insects to thermoregulate has been widely reported (Heath & Adams 1969; Heinrich 1974; see May 1976 and Heinrich 1981 for reviews). However, there is no definitive suite of variables that allow researchers to specify *a priori* whether an insect is likely to be a thermoregulator. Rather, what is found is a continuum of abilities, ranging from weak to strong thermoregulation (May 1976; Bishop & Armbruster 1999). In addition, the circumstances under which thermoregulation will be most selectively favoured are not well defined.

To initiate flight or raise body temperature, insects can increase the temperature of flight muscles by one of three means: (1) passive exogenous warming (Corbet 1963, 1999; May 1976; Vogt & Heinrich 1983; Dreisig 1990), (2) behavioural repositioning to maximize exogenous heat input (May 1976, 1978; Vogt & Heinrich 1983; Heinrich 1993), or (3) endogenous physiological warming (May 1976, 1978, 1991; Vogt & Heinrich 1983; Heinrich 1993). Species incapable of endogenous heat production may benefit from having lower thoracic minimum flight temperatures (MFT) to expand their activity periods. By contrast, species capable of endogenous heat production may be able to reach high MFTs even when ambient temperatures are low. In addition, species in both behavioural categories may need to dissipate excess heat, especially at high ambient temperature.

Heinrich (1977) suggested that the thermal properties of flight muscle enzymes may result in a pattern where insects adapted to fly at low thoracic temperatures are unable to operate at high thoracic temperatures and vice versa (see also Huey & Kingsolver 1989, 1993). Thus two distinct strategies for maximizing adult activity and fitness may exist: one that enables activity at low thoracic temperature and one that operates

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through thermoregulation and optimal performance at high thoracic temperatures. These strategies may also change over the adult lifetime of a dragonfly (Marden 1995; Marden *et al.* 1996; Marden, Fitzhugh & Wolf 1998).

The purpose of the present study is to examine the thermal strategies used by mature adult dragonflies (Odonata: Anisoptera) in Interior Alaska. Adult dragonflies are good subjects for this research because of their wide range of mass (May 1976; Grabow & Ruppell 1995) and conspicuous behaviours (Corbet 1963, 1999; May 1976, 1978, 1991; Heinrich & Casey 1978). Dragonfly species are often qualitatively classified as 'perchers' and 'fliers' based on their predominate behaviour at ponds (Corbet 1963, 1999; Silsby 2001). Perchers make short sallies from horizontal perches to defend territory, search for mates and hunt, while fliers are nearly continuously in flight as they conduct these daily activities. These distinctions, although not absolute (Singer 1987), are correlated with mass (May 1976; Heinrich & Casey 1978; Vogt & Heinrich 1983; Grabow & Ruppell 1995) which, in turn, is associated with thermoregulatory ability (Corbet 1963, 1999; May 1976, 1978, 1991; Heinrich & Casey 1978) and physiological heat production through wing-whirring. Smaller dragonflies tend to be ectothermic perchers typically employing behavioural thermoregulation by postural adjustment or the cessation of flight and do not appear to have the ability to either wing-whir or shunt heat from the thorax to abdomen (Heinrich & Casey 1978; Heinrich 1981). Larger species tend to be periodic endothermic fliers that employ a combination of behavioural and physiological thermoregulation (Corbet 1963, 1999; May 1976, 1978, 1991; Heinrich 1981, 1993; Vogt & Heinrich 1983) and may either increase or decrease the flow of haemolymph between the thorax (flight muscles) and abdomen to dissipate excess heat or warm thoracic temperature to minimum flight temperature, respectively (May 1976; Heinrich & Casey 1978; Kammer 1981).

In this paper, we examine the thermal ecology of 10 Interior Alaska dragonfly species. We analyse the relationships between mass, behavioural class, passive cooling rate, wing loading, minimum flight temperatures and thermoregulating ability. We relate these findings to daily and seasonal patterns of thermal inputs and dragonfly activity. The goals of this study were three-fold. We sought to: (1) examine the adult thermal ecology of the complete dragonfly fauna of our region, (2) relate thermal strategies to daily activity patterns and (3) address whether the commonly applied behavioural classes of 'perchers' and 'fliers' were representative of distinct thermal strategies. We predicted that: (1) our northern taxa would be strongly constrained by ambient environmental conditions, (2) thermoregulating ability would be positively related to the daily time available for activity and (3) fliers would be better thermoregulators and thus achieve longer daily activity periods while percher activity would be more strongly constrained by ambient environmental conditions.

Materials and methods

The dragonfly (Anisoptera) community near Fairbanks, Alaska (64 48′ N; 147 42′ W) consists of 10 species in five genera (Table 1). Three of these genera contain perchers and the other two contain fliers (T. Sformo & P. Doak, personal observation; see also Paulson 1999). *Libellula quadrimaculata* is classified as a percher but exhibits aspects of both behavioural patterns (D. R. Paulson, personal communication).

In this study, we consider species individually (unless otherwise noted) in all cases except for the three *Leucorrhinia* spp., which we could not identify to species in the field.

Mean fresh total body mass for adults varies nine-fold among species from the lightest *Sympetrum internum* (0·09 g) to the most massive *Aeshna eremita* (0·86 g) (Table 1), and mass significantly differs among taxa with the exception of the species pairs *Aeshna interrupta* and *A. palmata* and *Sympetrum danae* and *S. internum* (Table 1). Mean thoracic mass varies eight-fold among the taxa and displays a similar pattern to that of total body mass (Table 1).

All field work was conducted at three ponds near Fairbanks, Alaska: a fishless pond approximately 1364 m long with a maximum width of 40·5 m covering up to 30 000 m^2, a second fishless pond approximately 1019·5 m^2 and a third pond which is part of a large wetland area and had only one measurable shore approximately 30 m in length (for details see Sformo 2003). With the exception of *Sympetrum internum*, all taxa were present at all ponds. *S. internum* was primarily observed in a grassy area beside the first fishless pond.

MORPHOMETRIC CHARACTERS

We captured mature, adult specimens in the field and transported them alive in partially sealed, labelled plastic bags in a cooler with moistened towels to prevent desiccation. Total body mass was usually measured within 5 h and was strongly correlated with mass measured in the field (correlation, $r = 0.94$, unpublished data); thoracic and abdominal mass, total body length, forewing and hindwing length were measured within 24 h.

PASSIVE COOLING RATE

To measure cooling rate, a 33 gauge copper–constantan mini-hypodermic thermocouple probe with a diameter of 0·2 mm (Omega model HYP-0, Omega Engineering Inc., 1 Omega Dr. Stanford, Conn. 06907) was implanted into the centre of the thorax of a freshly killed individual. This technique ensured that the probe was inserted to a depth at least 10 times the wire diameter. The entire dragonfly was mounted 4 cm above a Styrofoam block. The mounted dragonfly was heated with a 250-W infrared heat lamp until thoracic temperature (T_{th})

Table 1. Predominant behaviour at ponds, mass and thermoregulatory data for dragonfly species of Interior Alaska arranged from least to most massive. Morphometric data were collected in 2000–2001

Taxon	Behaviour	Mean body mass (g)† (SE) N	Mean thoracic mass (g)† (SE) N	Thermoregulatory Performance Index (SE) N
Sympetrum internum	Percher	0·09[a] (0·002) 55	0·04[a] (0·003) 13	0·96* (0·14) 13
Sympetrum danae	Percher	0·10[a] (0·001) 139	0·05[a] (0·007) 20	0·98* (0·09) 82
Leucorrhinia hudsonica, *L. borealis,* *L. proxima*	Percher	0·21[b] (0·005) 106	0·09[a] (0·005) 35	0·40 (0·05) 73
Cordulia shurtleffii	Flier	0·27[c] (0·004) 46	0·11[b] (0·003) 19	0·46 (0·09) 55
Libellula quadrimaculata	Percher	0·40[d] (0·006) 85	0·19[c] (0·004) 31	0·47 (0·05) 44
Aeshna palmata	Flier	0·64[e] (0·004) 149	0·25[d] (0·003) 63	0·1** (0·08) 30
Aeshna interrupta	Flier	0·65[e] (0·004) 106	0·27[e] (0·004) 38	0·06** (0·03) 58
Aeshna eremita	Flier	0·86[f] (0·009) 47	0·36[f] (0·005) 25	0·17** (0·08) 36

†Different superscript letters indicate a significant difference in means (Tukey-Kramer).
*TPI does not significantly differ from a value of 1 – thermoconformer.
**TPI does not significantly differ from a value of 0 – thermoregulator.

was 22 C above ambient. The lamp was then turned off and thoracic temperature was recorded every 5 s as the individual cooled. Operative environmental temperature (T_e: the temperature of a dead, mounted dragonfly of the same species, placed in still air approximately 1 m from the heating source) was recorded approximately every 5 s as the freshly killed individual cooled. Cooling rate was determined for each species and showed approximately exponential decay. The difference between the T_{th} and T_e of each individual was calculated and then log-transformed to obtain a linear relationship with time. The slope of the log-linearized relationship is the passive cooling rate K (C/min C).

WING LOADING

To determine wing area and wing loading for each species, we clipped fore- and hindwings at the base of the four main veins distal to the wing joint. The wings, a ruler and a 1-cm^2 piece of paper were colour-photo scanned at 150 dots per inch. Using NIH Image software (Scion Image™, Scion Image, 82 Worman's Mill court, Suite H, Frederick, Margland 21701), we standardized length and area and traced wing perimeter. Wing loading was determined as a ratio of fresh mass (g) to wing area (cm^2).

MINIMUM FLIGHT TEMPERATURE

During May to mid-September in 2000 and/or 2001,

we measured minimum flight temperature (MFT); measurements were taken in the lab, at the Institute of Arctic Biology Greenhouse, or at the nearby study ponds.

To estimate MFTs, we recorded the lowest temperature at which a species maintained level flight (as per May 1976, 1978, 1998). For field measurements, we located roosting individuals unable to fly during cool mornings. Once we determined that individuals could not fly, we heated them in our hands, released them and then recaptured them after a horizontal flight of a few metres (following methods of Heath & Adams 1969; May 1976; Polcyn 1994). Upon recapture, we recorded T_{th} with a thermocouple (diameter approximately 0·4–0·2 mm) thrust into the thorax (see Materials and methods: Passive Cooling Rate). This standard method will yield estimates of MFT that are slightly higher than actual MFT. On the occasions that we recorded the T_{th} of an individual unable to fly, we found that T_{th} approximated ambient temperature (T_a). Once individuals were sighted at ponds, however, field MFT recording was stopped. Since it is not always possible to locate roosting individuals of all species in the field, we brought specimens of some species into the laboratory and cooled them in a refrigerator. To estimate MFT, we warmed specimens and tossed them into the air. Once they were able to maintain horizontal flight by flying to a mesh net a few metres away, we recorded T_{th} as above.

THERMOREGULATION

To measure thermoregulating ability, we netted active, sexually mature dragonflies at each study site between 05.00 and 24.00 h Alaska Daylight Time (ADT) throughout a species' flight season. No species of dragonfly were found to roost overnight at ponds. Perchers were considered active when they were present at a pond and used the perch to defend territory, watch for females or hunt for prey. Fliers were always netted while on the wing. We recorded T_{th} of individual dragonflies within 7 s of capture using a thermocouple (Physiotemp BAT 12, Physiotemp Instruments, Cliftor, NJ, USA) equipped with a 29-gauge copper–constantan (Cu-Cn) probe. The lead was thrust into the thorax ventrally and posterior to the last pair of legs (see Materials and methods: Passive Cooling Rate). Immediately after recording live-specimen temperature, we recorded temperature of a dragonfly model with a continuously inserted but otherwise identical thermocouple. The model was a freshly killed specimen in the same species or genus (for the *Leucorrhinia* spp., which are so morphologically similar that they cannot be easily distinguished in the field), and usually the same species, placed in an unshaded location and at equilibrium temperature with the environment, given the model's particular thermal properties of size, shape and colour (Bakken 1976, 1980, 1992; Crawford, Spotila & Standora 1983; Hertz, Huey & Stevenson 1993; Forrester *et al*. 1998). The model's thoracic temperature was used as an estimate of T_e. After recording live and model temperature, we used the same thermocouple to measure T_a, and we measured incident solar radiation with a Li-Cor photometer placed on a foam pad at ground level and free from any obstruction.

For each species, the Thermoregulatory Performance Index (TPI) was computed as the slope of the least squares regression of T_{th} against T_e (Bishop & Armbruster 1999). To determine if species thermoregulate, we compared TPI with a theoretical isothermal line (slope = 1), as well as a line with slope = 0 that represents perfect thermoregulation.

The thoracic temperature that we measured for perchers during perching activity may be somewhat inflated. It is difficult to net individuals without eliciting take-off and hovering. To minimize these effects, we did not record thoracic temperatures of individuals that hovered for more than 2 s before capture. It is unlikely that this error is great enough to affect TPI indices since the temperature is consistently raised only 1–2 C (T. Sformo & P. Doak, personal observation) regardless of T_{th}, resulting in a slightly elevated but parallel slope of the regression line of T_{th} against T_e.

PHENOLOGY AND ACTIVITY PATTERNS

In 2001, we examined adult phenology and surveyed hourly activity whenever we were in the field collecting thermoregulation data. From 7 June to 15 September 2001, we surveyed study ponds on 26 days for a total of 220 hourly surveys over the season. At least once each month, we examined activity continuously from 06.00 to 24.00 h to determine times of first and last daily activity. For each species we defined the maximum number of hours available for daily activity as the time between the earliest and latest observed flight.

To quantify activity, we set up 12 8-m^2 quadrats at each of the three study ponds. The quadrats were 2 m wide and extended 2 m over the pond and 2 m on shore. Each hour, we surveyed activity by counting and categorizing individuals (genus and/or species) that either perched in or flew through the quadrats. Each quadrat was surveyed for 30 s at a time. Taxon-specific dragonfly activity for a given time period was calculated as the mean number per quadrat averaged over all 12 quadrats.

DATA ANALYSIS

We examined the relationships of passive cooling rate, wing loading, MFT and TPI to total body mass. We used Felsenstein's (1985) method of phylogenetically independent contrasts, as implemented by PDTREE (Garland *et al*. 1993) to account for phylogenetic non-independence of these traits when compared across taxa. All traits were ln-transformed for analyses. We used the phylogeny: (((((Sd, Si), Leu) Lq), Cs), (Ae, Ap, Ai)) (Bechly 1998). The three *Aeshna* species were included as a polytomy, and we subtracted one degree of freedom to compensate for this. We computed separate statistics with all branch lengths set to 1 and with branch lengths computed with Pagel's arbitrary method (Pagel 1992).

We also examined whether passive cooling rate, wing loading, MFT and TPI differed between behavioural groups (perchers *vs* fliers). We employed phylogenetically corrected ANCOVAs with mass included as a covariate (PDSINGLE) and simulated 1000 random data sets used a bootstrap method to determine significance at $\alpha = 0.05$ (PDSIMUL, PDANOVA; Garland *et al*. 1993). As with the phylogenetically independent contrasts models were run both with branch lengths of 1 and as determined with Pagal's arbitrary (Pagel 1992).

We used linear mixed models to examine the factors impacting activity levels for the different genera. We examined the effects of date, time of day, ambient temperature, solar radiation and all two-way interactions. Ambient temperature and solar radiation were calculated as the mean of measurements taken just prior to and immediately after each hourly survey; both their linear and quadratic effects were examined in the models. Study pond was included as a random effect. Non-significant interactions were dropped from models. Model assumptions were met without the need for any transformations of the data. The reported results are for the reduced models.
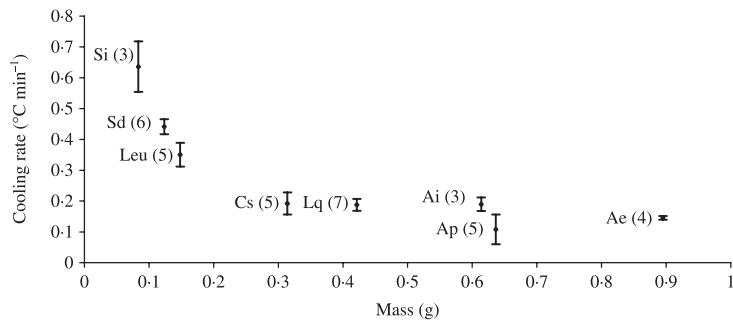
Fig. 1. Mean passive cooling (± SE) as a function of total body mass. Sample sizes are given in parentheses. Different letters above bars indicate significant differences in means (*P* < 0·05; Tukey–Kramer). Abbreviations are as follows: Ae = *Aeshna eremita*, Ai = *A. interrupta*, Ap = *A. palmate*, Cs = *Cordulia shurtleffii*, Lq = *Libellula quadrimaculata*, Leu = *Leucorrhinia* spp., Sd = *Sympetrum danae*, Si = *S. internum*.
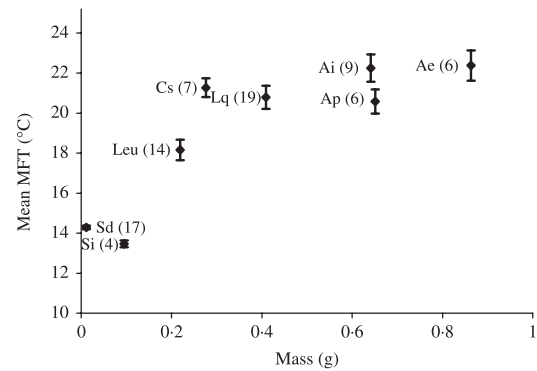

Fig. 3. Mean minimum flight temperature (± SE) as a function of mean body mass. Abbreviations and notations as in Fig. 1.
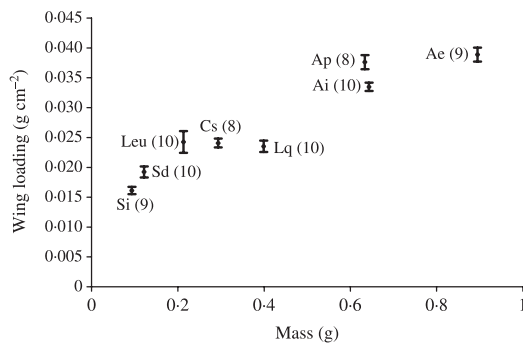

Fig. 2. Mean wing loading (± SE) as a function of mean body mass. Abbreviations and notations as in Fig. 1.

Results

Phylogenetically independent contrasts revealed significant relationships between all the examined variables and mass. Cooling rate decreased (Fig. 1) while wing loading increased with increasing mass (Fig. 2, Table 2). Small taxa had lower MFT (Fig. 3) while larger taxa were better thermoregulators (lower TPI) (Fig. 4), as demonstrated by their positive and negative relationships with mass (Table 2).

PERCHERS *vs* FLIERS

Percher and flier behavioural groups did not significantly differ in cooling rate ($F_{1,4}$ = 1·58, *P* > 0·05), wing load-

ing ($F_{1,4}$ = 1·63, *P* > 0·05), or TPI ($F_{1,4}$ = 0·50, *P* > 0·05) as determined by phylogenetically corrected ANCOVAs with ln-mass included as a covariate. However, perchers did have significantly lower MFT when compared with fliers ($F_{1,4}$ = 24·56, *P* < 0·01).

THERMOREGULATION

All species were able to elevate their thoracic temperature above operative temperature, but the degree of thermoregulatory ability varied. Both *Sympetrum* species were unable to maintain a steady T_{th} across T_e; their thermoregulatory performance indices did not differ significantly from the isothermal line (Table 1, Fig. 4). By contrast, TPI for the other percher taxa, *Leucorrhinia* spp. and *Libellula quadrimaculata*, indicated moderate thermoregulatory abilities (Table 1, Fig. 4).

The smallest flier, *Cordulia shurtleffii*, had an intermediate TPI that was similar to that of the larger percher species; thus, it has a moderate ability to thermoregulate. By contrast, TPIs of the three aeshnid species did not significantly differ from zero, indicating that they are good thermoregulators (Table 1, Fig. 4).

PHENOLOGY AND ACTIVITY PATTERNS

In 2000–2001, adult dragonfly activity in Interior Alaska began in late May–early June and continued

Table 2. Results of phylogenetically independent contrasts examining relationships with mass. Mass and each response variable were ln-transformed, and all branch lengths were set to 1

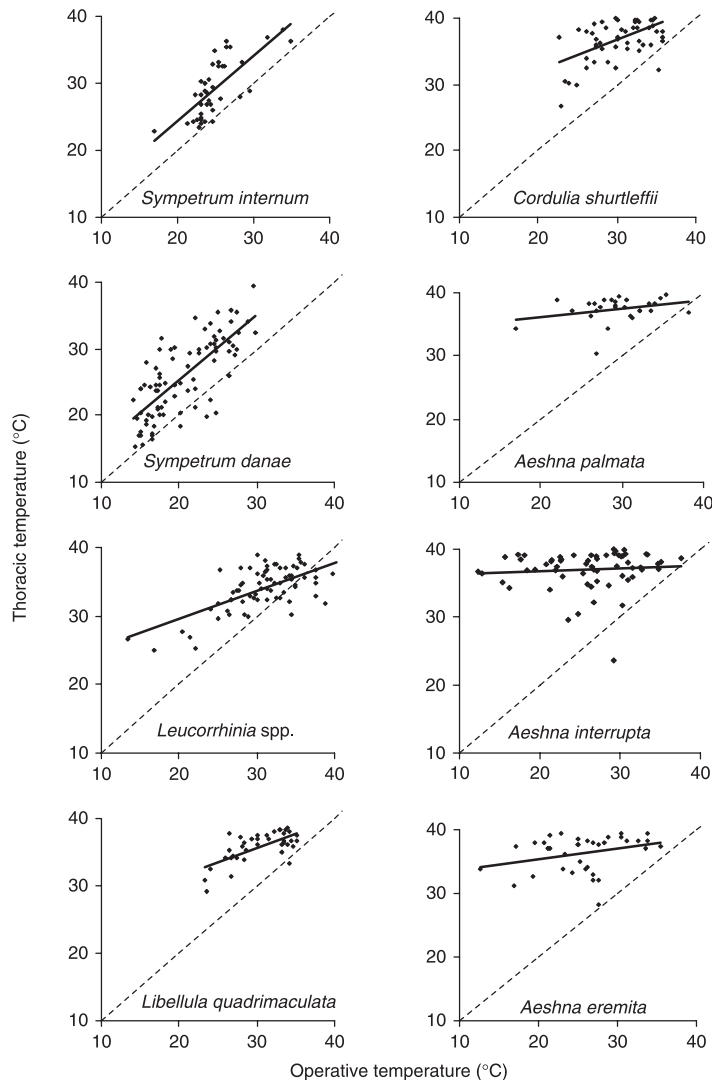| Response	Y intercept (± SE)	Slope (± SE)	r^2	$F_{1,6}$	P
Cooling	−2·219 (0·0214)	−0·618 (0·019)	0·65	10·93	0·016
Wing load	−3·26 (0·09)	0·34 (0·09)	0·72	15·61	0·007
MFT	3·24 (0·08)	0·28 (0·08)	0·67	12·08	0·0132
TPI	−2·11 (0·53)	−0·70 (0·49)	0·25	2·04	0·203

Fig. 4. The relationship between T_{th} and T_e for each species. The least squares linear regression (solid) and isothermal lines (dotted) are shown.

Fig. 5. Phenology of adult dragonflies near Fairbanks, Alaska in 2001. Activity is the mean number of individuals found in 12 8-m² quadrats during each hourly survey period divided by the number of survey periods per day. See Fig. 1 for abbreviations.

through mid-September; this matches the general pattern reported by Paulson (1999). Unless otherwise noted, activity results are from 2001. The highest species richness was observed from early June through mid-July. Within 4 days of observing first adult activity, both perchers and fliers were active and up to five species co-occurred at ponds on a majority of days during the period 9 June to 21 July 2001 (Fig. 5).

The activity of *Libellua quadrimaculata* and *Cordulia shurtleffii* reduced by late June to early July 2001, while *Leucorrhinia* spp. continued until 21 July. The addition of aeshnids (*Aeshna eremita*, *A. palmata* and *A. interrupta*) in late June marked maximum species richness of eight co-occurring fliers and perchers.

During the period 22 July to 4 August 2001, only the three *Aeshna* species were observed. The perchers in the genus *Sympetrum* (*Sympetrum danae* and *S. internum*) appeared on 6 August, alongside *Aeshna* fliers, and both genera continued activity to 15 September 2001, when we ended our observations (Fig. 5).
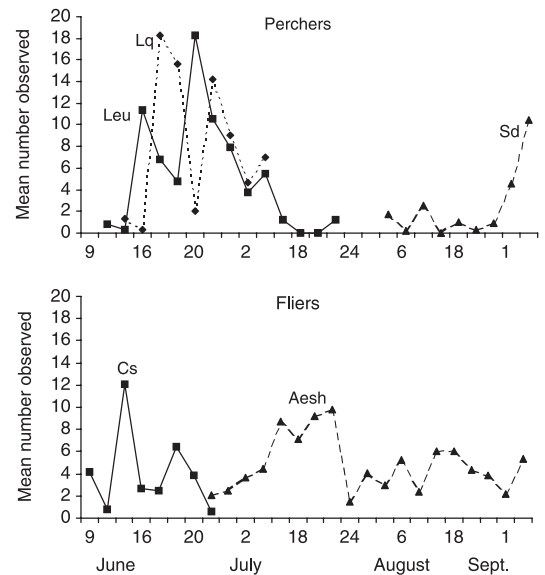
We do not have survey data for *Sympetrum internum* because they were seldom present at ponds in either year. They appeared to spend most of their time in fields where they forage, copulate and oviposit on moist soil or at small ephemeral ponds.

All perchers showed a pattern of increasing daily activity with increasing T_a (Table 3), and all showed a significant quadratic response to time of day (Table 3, Fig. 6). *S. danae* displayed a significant negative response to Solar Radiation (SR), as well as a number of significant interactions (Table 3, Fig. 6).

The activity of the smallest flier species, *Cordulia shurtleffii*, significantly decreased with T_a; the linear and quadratic effects of time of day were also significant (Table 3, Fig. 6).

The *Aeshna* spp. displayed a strikingly different pattern to all other taxa. They were active from early morning (08.00 hours) to late evening (24.00 hours) (Fig. 6), and displayed no significant relationships between activity and any of the tested variables (Table 3).

Discussion

In many insects, elevated and regulated thoracic temperature is positively correlated with the intensity and duration of activities, such as prey capture, predator avoidance and reproduction, that directly influence fitness (Heinrich 1977; Convey 1989; Marden 1989, 1995; May 1995; Marden *et al.* 1998). Both low and high thoracic temperatures can result in reduced or halted activity. Excess heat loads can be managed by increasing heat loss or by reducing metabolic or environmental heat inputs. Polcyn (1994) suggested that at

Table 3. Results of linear mixed model analysis of dragonfly activity

Taxon	Source	Estimate	SE	df	F	P
Sympetrum danae	Time	−2·450	3·144	1, 52	0·61	NS
	T_a	6·9790	1·975	1, 52	12·48	0·0009
	Sr	−0·084	0·029	1, 52	8·31	0·0057
	Time^2	0·3426	0·147	1, 52	5·43	0·0237
	Time × T_a	−0·5082	0·125	1, 52	16·37	< 0·0001
	Time × Sr	0·0113	0·002	1, 52	18·7	< 0·0001
	T_a × Sr	−0·0028	0·001	1, 52	4·63	0·036
Leucorrhinia spp.	Time	−5·2562	1·468	1, 120	12·82	0·0005
	T_a	1·1543	0·236	1, 120	23·88	< 0·0001
	Sr	0·0066	0·004	1, 120	2·72	NS
	Time^2	0·1635	0·047	1, 120	11·87	0·0008
Cordulia shurtleffii	Time	6·6614	1·290	1, 91	26·67	< 0·0001
	T_a	−0·5901	0·183	1, 91	10·35	0·0018
	Sr	−0·0049	0·003	1, 91	1·75	NS
	Time^2	−0·2115	0·042	1, 91	24·57	< 0·0001
Libellula quadrimaculata	Time	−5·415	2·119	1, 86	6·53	0·0124
	T_a	1·8473	0·302	1, 86	37·13	0·0001
	Sr	0·0024	0·006	1, 86	0·14	NS
	Time^2	0·1553	0·070	1, 86	4·9	0·0295
Aeshna spp.	Time	0·1238	0·1089	1, 149	1·29	NS
	T_a	0·1258	0·1252	1, 149	1·01	NS
	Sr	0·0017	0·002	1, 149	0·51	NS

high T_a some species may increase flight speed and thus convective cooling, but this behaviour would also result in increased metabolic heat generation. Heinrich & Casey (1978) found that some species actually decrease flight time at high T_a. May (1995) reported that as T_a increased, the dragonfly *Anax junius* reduced wing-beat frequency, which probably resulted in reduced metabolic heat production and a decreased heat load. Among the Interior Alaska dragonfly species only *Cordulia shurtleffii* displayed a negative relationship between activity and T_a (Table 3), suggesting that the other species either did not experience conditions leading to excess heat load or were able to remain active through behavioural or physiological compensating mechanisms.

On the other hand, Interior Alaska dragonfly activity is clearly limited by low ambient temperatures (Figs 3 and 4) with monthly mean minimum temperatures in Fairbanks (2·2, 8·3, 9·9 and 7·3 C for May to August; Western Regional Climate Center, www.wrcc.dri.edu) well below MFTs for all species. Low-temperature activity can be achieved in two ways: a low thoracic MFT or the ability to warm the thorax to a higher MFT even when ambient temperatures are low. Once warmed to MFT, flier species may benefit from endothermic heat produced as a by-product of flight. By contrast, the short sallies of perchers are less likely to produce enough heat to maintain elevated thoracic temperatures between sallies.

In our examination of Interior Alaska dragonflies, we found a broad range of MFTs, thermoregulating abilities and daily activity patterns. MFTs ranged from 14 to 22 C (Fig. 3). We found that all species could elevate T_{th} above T_e, but the ability to thermoregulate varied greatly across taxa (Fig. 4). The maximum

number of hours available for daily activity, as defined by the time between first and last observed flight, varied between species from 6 to 17 h (Fig. 6). Neither the ability to maintain constant body temperature across a range of ambient temperatures nor behavioural class was a good predictor of amount of time available for daily activity.

STRATEGIES FOR ACTIVITY AT LOW AMBIENT TEMPERATURES

Despite strikingly different abilities to elevate and maintain thoracic temperature, both the smallest and largest species of interior Alaska dragonflies can commence activity at ambient temperatures of approximately 14 C (Fig. 3). *Sympetrum danae* has a low MFT set point that allows activity when little behavioural thoracic warming is possible. Although they can elevate body temperature, they are unable to thermoregulate (Fig. 4). In accordance, the thermal niche of *Sympetrum* spp. is highly constrained by diurnal patterns in T_a and Sr and results in a maximum of only 5–7 h of time available for daily activity (Fig. 6). These species are further constrained by their obligate univoltine phenology that results in adult activity during the late summer and early autumn when conditions are cool (Fig. 5).

By contrast, MFT for the aeshnids is approximately 22 C (Fig. 3). However, by employing wing-whirring (T. Sformo & P. Doak, personal observation) to raise thoracic temperature they are also able to fly at ambient temperatures of 14 C. This may allow specialization of muscle enzymes for high-temperature performance (Heinrich 1977) while still enabling flight at low ambient
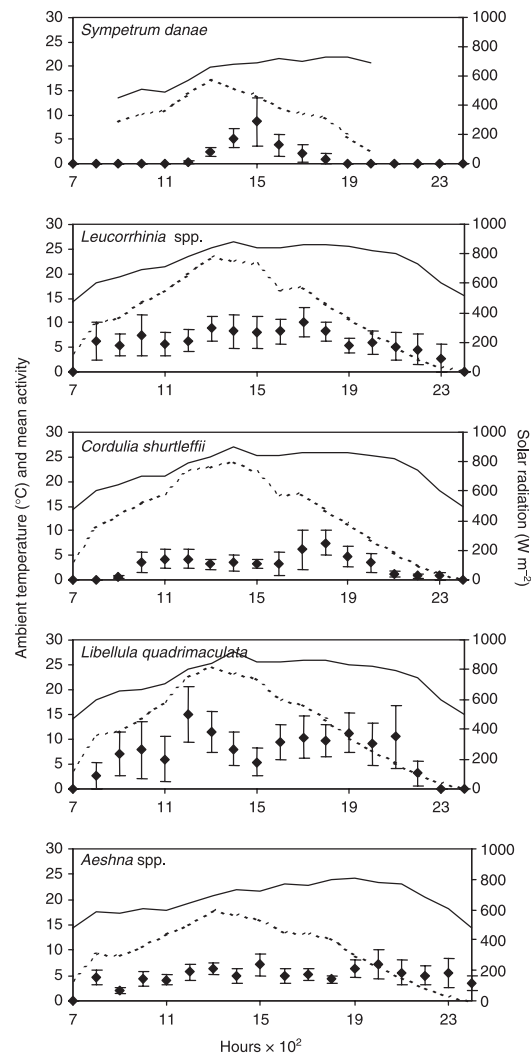
Fig. 6 Mean activity (± SE) by hour averaged over the flight season. Ambient temperature (solid line) and solar radiation (dotted line) are calculated as the hourly means for pre- and post-survey measurements and averaged over the flight season.

temperature. Their constant flight then continues to produce metabolic heat and high thermal resistance helps in the maintenance of thoracic temperature at low T_a. This strategy resulted in a maximum of 17 h a day suitable for flight.

BEHAVIOUR, THERMAL ECOLOGY AND DAILY ACTIVITY

Although dragonfly classification as either perchers or fliers is routinely linked to both behavioural and physiological thermoregulation strategies (Corbet 1963, 1999; May 1976, 1978, 1991; Heinrich & Casey 1978) we did not find these categories to be strong predictors of thermal strategies or the ambient conditions allowing activity. Of the thermal traits examined, only MFT differed significantly between perchers and fliers (Fig. 3). Additionally, the length of daily activity was not predicted by either behavioural category or mass (Fig. 6).

Although the smallest and largest dragonflies in Interior Alaska have the shortest and longest daily activity periods, respectively, this pattern does not hold for the intermediate-sized dragonflies. For instance, despite large differences in mass and thermal strategy, *Leucorrhinia* spp. achieve almost the same amount of daily activity as the largest Aeshinds. To reach this level of activity, *Leucorrhinia* spp. must overcome a high passive cooling rate (Fig. 1), but take advantage of a lower MFT. This allows them to remain active when perched without having to maintain an elevated T_{th}. Furthermore, their early summer phenology exposes them to relatively high T_a and Sr, resulting in approximately 16 h of daily activity.

By contrast, the small flier *Cordulia shurtleffii* has the second shortest daily activity period, despite being a moderate thermoregulator and sharing many thermal characteristics with the larger Aeshnids. These include continuous flight, ability to wing-whir and a high MFT. Yet *C. shurtleffii* has only approximately 11 h of daily activity time as compared with the 18 h seen for the Aeshnids (Fig. 6).

Despite differing behaviours, the most massive percher, *Libellula quadrimaculata*, and the least massive flier, *Cordulia shurtleffii*, are very similar in thermal ecology. While they do not significantly differ from the Aeshnids in their passive cooling rates or MFTs, they are significantly smaller and are not active at low ambient temperatures. We never observed *L. quadrimaculata* wing-whirring (T. Sformo & P. Doak, personal observation), an observation that corresponds with past research indicating that libellulid dragonflies are unable to physiologically warm themselves (Heinrich & Casey 1978; Heinrich 1993; Marden 1995). This delays the onset of flight until ambient conditions are adequate to passively heat flight muscles to MFT. Despite this constraint, *L. quadrimaculata* has the potential to be active for 15 h a day.

Cordulia shurtleffii experiences a similar delay in activity at low ambient temperatures despite its ability to wing-whir (T. Sformo & P. Doak, personal observation) and generate metabolic heat for warming. An inability to commence wing-whirring at low ambient temperatures or a voluntary takeoff temperature that substantially exceeds MFT could result in this pattern (Vogt & Heinrich 1983), although we did not examine these factors. High convective heat loss may limit the benefits of temperature elevation for small animals (Stone & Willmer 1989). Stone & Willmer (1989) and Stone (1994) have demonstrated that smaller and less endothermic bees reduce activity at high ambient temperatures. *C. shurtleffii* also appears to be further limited in time available for flight by constraints on activity at high ambient temperatures (Table 3). Thus, despite being a moderate thermoregulator, *C. shurtleffii* has the lowest daily activity after the small *Sympetrum* spp. (Fig. 6). Its thermal ecology resembles that of a percher more than the larger Aeshnid fliers.

FACTORS FAVOURING LOW MFT *vs* THERMOREGULATION

Heinrich (1977) noted that positive selection for performance at high temperature may be inversely correlated with low temperature performance, and Marden (1995) found some evidence for this trade-off in *Libellula pulchella*. Specialization at either extreme may preclude the other (Marden 1995; Marden *et al.* 1998) owing to deactivation and, eventually, denaturation of temperature-sensitive flight muscle enzymes (Heinrich 1977). Marden's (1995) research also lends support to the hypotheses that peak performance will be negatively correlated with thermal breadth (Huey & Kingsolver 1989) and highest in individuals able to function at high T_{th} (Bennett 1991). Species unable to elevate and maintain a constant T_{th} over a range of T_a may be forced to specialize for activity at either relatively low or high T_a with the cost of reduced performance at the other extreme.

Comparison of the two smallest genera, both perchers, may provide insight into the factors favouring low-*vs* high-temperature specialization. As noted, in our study region *Sympetrum* spp. cannot maintain a constant temperature with changing environmental conditions. However, in other regions, *Sympetrum* spp. of comparable size are capable of moderate thermoregulation by using postural adjustments (May 1976, 1998; Ishizawa 1994, 1998 as reported in May 1998). Interior Alaska *Leucorrhinia* spp. are about twice the mass of the *Sympetrum* spp.; they have a high passive cooling rate (Fig. 1), intermediate wing loading (Fig. 2) and an MFT intermediate between *Sympetrum* spp. and all other taxa (Fig. 3). Their moderate thermoregulating ability is similar to larger perchers and fliers (Fig. 4).

In the range of mass between *Sympetrum* spp. and *Leucorrhinia* spp. a range of thermal strategies may be possible with specialization largely governed by environmental conditions during each species' flight season. It is possible that *Sympetrum*'s small size and low thermal inertia combined with an inability to wing-whir and phenology that restricts it to activity in the late summer and early fall put it on an energy budget that necessitates activity at low ambient temperatures. The ability to maintain a positive energy budget under variable and often poor environmental conditions could easily outweigh the benefits of high-temperature performance. By contrast, *Leucorrhinia* spp. are active early in the season (Fig. 5) when temperatures are relatively high and there is less cloud cover (Wendler 1980). This difference in thermal regime could be enough to tip the trade-off between cool temperature activity and high-temperature performance. In a comparative study of bees, Stone & Willmer (1989) found thermal regime to be an important factor determining the relationship between body mass and both warm-up rate and T_{th} during flight.

Among Interior Alaska dragonflies both MFT and thermoregulating ability increase with increasing mass. Mass appears to have a stronger influence on thermal ecology than does behaviour. Both physiological heat production and low MFT can enable flight at low ambient temperatures. For small percher species active in cool conditions, a low MFT could conserve energy by allowing species to be active and ready to fly without maintaining an elevated T_{th} (but see May 1998). For these species, the ability to fly at low T_a may be necessary for maintenance of a positive energy budget given that their percher behaviour does not lead to the production of much endothermic heat as a by-product of flight. However, if peak performance is maximized by adaptation for activity at high thoracic temperatures, we would expect this strategy to be adopted whenever possible.

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