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Effects of flight behaviour on body temperature and kinematics during inter-male mate competition in the solitary desert bee *Centris pallida*

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Abstract. Body temperatures and kinematics are measured for male *Centris pallida* bees engaged in a variety of flight behaviours (hovering, patrolling, pursuit) at a nest aggregation site in the Sonoran Desert. The aim of the study is to test for evidence of thermoregulatory variation in convective heat loss and metabolic heat production and to assess the mechanisms of acceleration and forward flight in field conditions. Patrolling males have slightly (1–3 °C) cooler body temperatures than hoverers, despite similar wingbeat frequencies and larger body masses, suggesting that convective heat loss is likely to be greater during patrolling flight than during hovering. Comparisons of thorax and head temperature as a function of air temperature (T_a) indicate that *C. pallida* males are thermoregulating the head by increasing heat transfer from the thorax to the head at cool T_a . During patrolling flight and hovering, wingbeat frequency significantly decreases as T_a increases, indicating that variation in metabolic heat production contributes to thermal stability during these behaviours, as has been previously demonstrated for this species during flight in a metabolic chamber. However, wingbeat frequency during brief (1–2 s) pursuits is significantly higher than during other flight behaviours and independent of T_a . Unlike most other hovering insects, *C. pallida* males hover with extremely inclined stroke plane angles and nearly horizontal body angles, suggesting that its ability to vary flight speed depends on changes in wingbeat frequency and other kinematic mechanisms that are not yet described.

Key words. Bees, *Centris pallida*, flight, kinematics, thermoregulation.

Introduction

During flight, many species of bees regulate thoracic muscles at temperatures exceeding 40 °C and achieve rates of metabolism and mechanical power production approaching 800 and 120 W kg⁻¹ body mass, respectively, and thus represent the extreme of aerobic locomotor capacity in animals. The patterns and mechanisms of thermoregulation and force production in these powerful flyers are becoming increasingly well-understood (see Dudley, 2000; Harrison & Roberts, 2000; Harrison & Fewell, 2002; Roberts *et al.*, 2004), yet the applica-

tion of this understanding to flight behaviour in natural settings remains a significant challenge. Laboratory and field studies of bumblebees (*Bombus*) and carpenter bees (*Xylocopa*) show that these groups prevent overheating of the flight muscles during flight at high air temperatures (T_a) by increasing circulatory heat transfer from the thorax to the abdomen (Baird, 1986; Heinrich & Buchmann, 1986), whereas honey bees (*Apis mellifera*) greatly increase evaporation during flight at high T_a . Some species such as *Apis mellifera*, the desert solitary bee *Centris pallida* Fox, and certain euglossines thermoregulate during hovering flight in the laboratory by decreasing metabolism (and concomitant heat production) at high T_a (Harrison *et al.*, 1996; Roberts *et al.*, 1998; Roberts & Harrison, 1999; R. Dudley, personal communication). Correlated with this response in these species is a decrease in wingbeat frequency (f) at high T_a . To date, there are few data available to confirm this pattern of thermoregulation during natural

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flight behaviours, with no available direct measurements of flight metabolism in the field. Field observations of the inverse f vs. T_a relationship have been reported only for hovering *C. pallida* (Roberts & Harrison, 1998), patrolling *Centris caespinae* males (Spangler & Buchmann, 1991) and foraging *Bombus* spp. (Unwin & Corbet, 1984).

Variation in f and metabolism is a somewhat unexpected means of thermoregulation in flight because previous work indicates that bees have limited ability to vary these parameters, even under apparently demanding circumstances such as forward flight and loading. For example, *Bombus* in laboratory flight do not vary metabolism, stroke amplitude (Φ), f and power production between airspeeds between 0 and 4.5 m s^{-1} (Dudley & Ellington, 1990a,b; Ellington *et al.*, 1990) but, as in many insects, generate forward thrust by decreasing the body angle (χ) and increasing the stroke plane angle (β) relative to horizon (definitions as in Ellington, 1984), a postural shift that increases the horizontal force vector generated by the wings and propels the insect forward (Dudley & Ellington, 1990a). Similarly, metabolism increases only slightly and f is unaffected due to nectar and pollen loading of up to 40% of body mass in *A. mellifera* (Feuerbacher *et al.*, 2003), whereas orchid bees generate excess power for hovering in heliox (21% O_2 /79% He), which is approximately one-third as dense as sea-level air, by increasing stroke amplitude but not f (Dudley, 1995).

This study examines the effects of T_a and flight behaviour on body temperature and f for male *C. pallida* during mating flights at a nest aggregation site in the Sonoran Desert where, in late spring, hundreds or even thousands of *C. pallida* males aggregate and aggressively compete for the opportunity to mate with newly emerged virgin females (Alcock, 1976; Alcock *et al.*, 1977). At these aggregations, a size-dependent behavioural hierarchy exists among males where larger individuals search for emerging females via patrolling flights a few centimetres above the ground, whereas smaller males hover stationary in defence of small (approximately 1 m^3) territories along the peripheries of the nest aggregation site (Alcock *et al.*, 1977; Alcock, 1995). Hoverers, but not patrollers, frequently engage in brief (2–3 s) pursuits among intra-specific males (Alcock, 1976). Although most desert bees restrict their activity to cooler daytime periods (Willmer & Stone, 1997), *C. pallida* males begin their mating flight activity at approximately 07.00 h and cease their patrolling flights at approximately 11.00 h, whereas hovering persists later into the afternoon (Alcock, 1976). During this period, T_a can increase by as much as 20°C , whereas the thorax temperature (T_{th}) of hovering males is maintained at $45 \pm 2^\circ\text{C}$ (Chappell, 1984; Roberts *et al.*, 1998). This system allows a unique opportunity to analyse thermoregulation and kinematics of bees in natural forward and hovering flight.

Materials and methods

Body segment temperature, air temperature and body mass

Flying *C. pallida* males were studied at a large (100 m^2) nest aggregation site near Apache Junction, Arizona, and body

temperature measurements were made during April 1996. The thorax, head and abdomen temperatures (T_{th} , T_{h} and T_{ab} , respectively) of hoverers were originally presented by Roberts *et al.* (1998). Body segment temperatures were measured for bees captured during flight in full sunlight. After a bee was netted, it was quickly restrained by gently flattening the net on a piece of low density foam. Within 10 s, body segment temperatures were measured with a Physitemp MT 29/1B microprobe thermocouple (diameter = 0.33 mm, time constant = 0.025 s) connected to a Physitemp BAT-12 thermometer. Shade T_a at the site of capture and filming was also measured with the microprobe thermocouple. Bees were then placed in small vials, frozen over dry ice, returned to the laboratory and weighed to the nearest 0.1 mg on a Mettler AE240 analytical balance.

Measurements of T_{th} , T_{h} and T_{ab} during flight were used to test whether *C. pallida* males were thermoregulating flight muscles by increasing heat transfer from the thorax to the head or abdomen at high T_a . Variation in heat transfer between the thorax and head or abdomen was analysed according to a model detailed by Baird (1986), May (1991) and Stavenga *et al.* (1993). Variation in the heat transfer between the thorax and head or abdomen was inferred from the ratio of the head or abdominal temperature excess ($T_{\text{h}} - T_a$ or $T_{\text{ab}} - T_a$, respectively) to the thoracic temperature excess ($T_{\text{th}} - T_a$). If the assumptions of the model are met (Stavenga *et al.*, 1993) and heat transfer from the thorax to the head does not vary with T_a , then the head temperature excess ratio (R_{h}), where:

$$R_{\text{h}} = (T_{\text{h}} - T_a) / (T_{\text{th}} - T_a), \quad (1)$$

should be independent of T_a . Similarly, if the assumptions of the model are met and heat transfer from the thorax to the abdomen does not vary with T_a , then the abdominal temperature excess ratio (R_{ab}), where:

$$R_{\text{ab}} = (T_{\text{ab}} - T_a) / (T_{\text{th}} - T_a), \quad (2)$$

should be independent of T_a . However, if heat transfer from the thorax to the head or abdomen is increased at high T_a , as would be expected if the head or abdomen were being used as a 'thermal window' to dissipate excess heat generated in the thorax, then R_{h} or R_{ab} should increase with T_a . Conversely, if heat transfer from the thorax to the head or abdomen is increased at low T_a (as would be expected if T_{h} or T_{ab} were being regulated at a value above T_a), then R_{h} or R_{ab} should decrease with T_a .

Wingbeat frequency and flight posture

Near the geographical centre of the aggregation site, a boom-mounted video camera was vertically orientated such that patrollers and pursuers were filmed dorsally as they flew beneath the camera. Pursuits were defined as two bees flying over the board in tandem, with one immediately behind the other, whereas all other bees flying over the

board were defined as patrollers. The lens of the camera was 2 m above the ground, and a white piece of plywood (1 × 1.2 m) was placed on the ground directly below the video camera to serve as a blank background. Flying *C. pallida* males were easily observed on the video recordings as they flew over the white background. For measurements of f , an optical tachometer (Unwin & Ellington, 1979) was also directed at the plywood backdrop when the bees were being filmed, and the audio output of the optical tachometer was recorded onto the audio track of the videotape.

The extent to which repeated observations of individuals were made during filming of forward flying bees is not known because it was not possible to capture a given bee just after it had passed over the board. According to Alcock (1976), patrolling *C. pallida* males occupy broadly overlapping home ranges varying from 8–46 m², suggesting that repeated measures of individuals might occur with the present protocol. However, six patrollers marked on the dorsal thorax at the filming site were not observed again at the site over three consecutive mornings of filming. Furthermore, individual patrollers were routinely observed to span nearly the entire width of the nest emergence site in broad, sweeping flights, a few centimetres above the ground. Thus, measurements of f during patrolling and pursuits were considered to be independent observations for statistical analysis.

The f of hoverers during hovering and the acceleratory phases of pursuits were also determined from optical tachometer recordings. The strong site fidelity of territorial hoverers allowed numerous recordings for an individual, and therefore f was measured during hovering and the initiation of pursuit flights for nine hoverers to determine the extent to which individual bees could vary f . Video recordings were used to determine β and χ (see Introduction for definitions) for these bees during hovering flight. Video images of hovering bees were obtained with the video camera levelled horizontally and positioned laterally to the bee. Still frames were captured from these recordings and Scion Image software was used to determine β and χ (see Fig. 1 for representative image). Only those sequences providing lateral views of controlled, unaccelerated hovering flight were used in the determination of flight posture; ascending, descending or manoeuvring flight was ignored.

The optical tachometer recordings were digitized and visualized using the SpectraPLUS (Pioneer Hill Software, Poulsbo, Washington, D.C.) sound analysis program. Each recorded sequence contained 6–10 clearly distinguishable, uninterrupted wingbeats. For a given bee, f was determined to the nearest 2 Hz by dividing the number of clearly distinguishable, uninterrupted wingbeats in the sequence by the duration of the sequence (measured to the nearest 0.0001 s).

Results

Body temperatures and mass

For both hovering and patrolling bees, T_{th} , T_h and T_{ab} significantly increased with T_a (Table 1; Fig. 2). For T_{th} , T_h

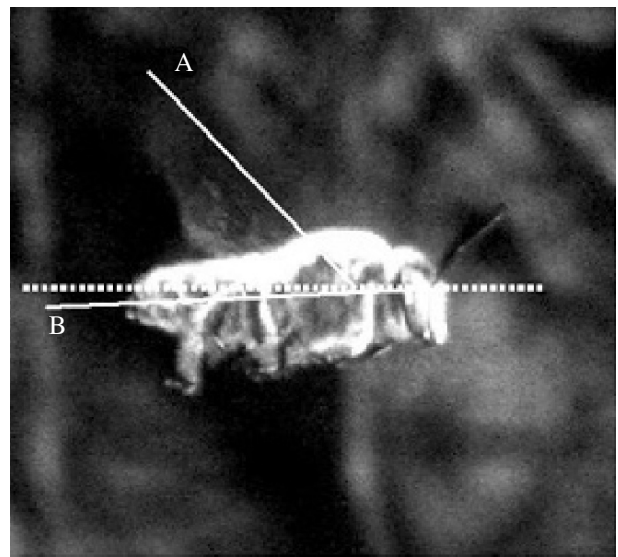


Fig. 1. A hovering *Centris pallida* male. Note extremely inclined stroke plane (A) and nearly horizontal body axis (B).

and T_{ab} vs. T_a regressions, patrollers had significantly greater slopes and significantly lower intercepts than hoverers (Table 1; Fig. 2). Head temperature excess ratios (R_h) significantly decreased as T_a increased in both hoverers and patrollers (Fig. 3), and the slopes and intercepts of these regression lines were not significantly different [analysis of covariance (ANCOVA); slope: $F_{1,66} = 0.47$, $P = 0.50$; intercept: $F_{1,66} = 0.85$, $P = 0.36$]. Abdominal temperature excess ratios (R_{ab}) were not significantly affected by T_a in hoverers ($r^2 = 0.11$) or patrollers ($r^2 = 0.05$). The body masses (mean \pm SE) of patrollers (175.1 ± 8.4 mg) were significantly larger (t -test, d.f. = 66, $P < 0.001$) than those of hoverers (122.2 ± 3.7 mg).

Table 1. Regressions and ANCOVA for body temperatures vs. T_a for hovering and patrolling *Centris pallida* males.

	Hoverers ($n = 30$)	Patrollers ($n = 40$)	ANCOVA ($F_{1,66}$, P)
T_{th}			
Slope	0.149	0.248	4.11, 0.047
Intercept	41.34	37.32	8.57, 0.005
r^2	0.37	0.68	
P	< 0.001	< 0.001	
T_h			
Slope	0.219	0.388	4.22, 0.044
Intercept	34.31	28.05	7.32, 0.009
r^2	0.24	0.70	
P	0.005	< 0.001	
T_{ab}			
Slope	0.447	0.657	4.20, 0.045
Intercept	22.90	15.68	6.24, 0.015
r^2	0.41	0.84	
P	< 0.001	< 0.001	

T_{th} , Thorax temperature; T_h , head temperature; T_{ab} , abdomen temperature.

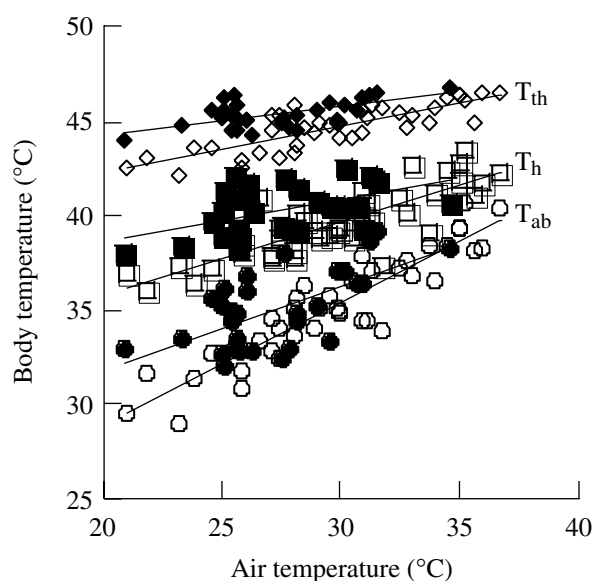


Fig. 2. Body temperature vs. abdomen temperature for patrolling and hovering *Centris pallida* males. See Table 1 for regression and ANCOVA analyses. Open symbols = patrollers; closed symbols = hoverers; diamonds = thorax temperature (T_{th}); squares = head temperature (T_h); circles = abdomen temperature (T_a).

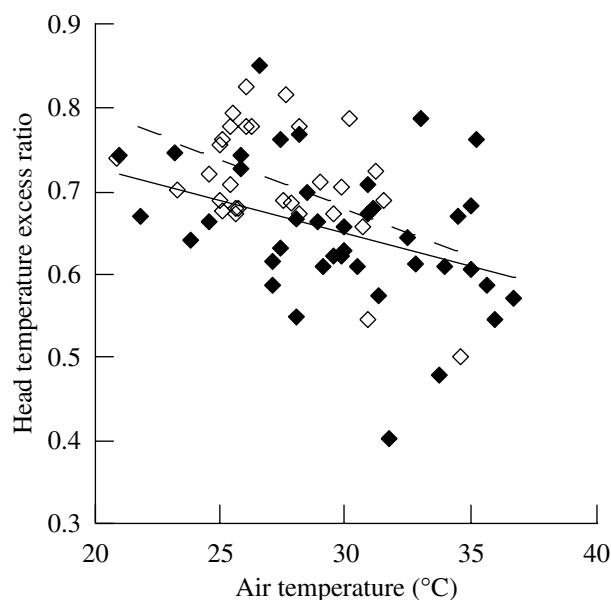


Fig. 3. Head temperature excess ratios $[(T_h - T_a)/(T_{th} - T_a)]$ for patrolling (closed symbols, solid line) and hovering (open symbols, dashed line) *Centris pallida* males. Linear regressions: Patroller $R_h = (-0.008 \cdot T_a) + 0.89$, $r^2 = 0.14$, $F_{1,38} = 6.16$, $P = 0.02$. Hoverer $R_h = (-0.012 \cdot T_a) + 1.04$, $r^2 = 0.23$, $F_{1,28} = 8.48$, $P = 0.01$ (data from Roberts *et al.*, 1998). Slopes and regressions not significantly different (see text for ANCOVA results). T_h , Head temperature; T_a , abdomen temperature.

Flight kinematics

During patrolling flight, f significantly decreased with increasing T_a (Fig. 4), as has been previously reported for hovering *C. pallida* males (Roberts & Harrison, 1998; Fig. 4). The slopes and intercepts of f vs. T_a regressions were not significantly different between hovering and patrolling bees (ANCOVA; slope: $F_{1,134} = 0.001$, $P = 0.99$; intercept: $F_{1,134} = 0.335$, $P = 0.56$). When pooled across all T_a [which did not significantly differ (t -test, d.f. = 95, $P = 0.95$) among observed patrollers ($27.4 \pm 0.4^\circ\text{C}$) and pursuers ($27.4 \pm 0.8^\circ\text{C}$)], f during pursuits (228.8 ± 2.0 Hz) was significantly greater than during patrolling flight (204.3 ± 2.3 Hz; t -test, d.f. = 95, $P < 0.001$). By contrast with hovering and patrolling, f during pursuits over the nest aggregation site was not significantly correlated with T_a ($r^2 = 0.02$; Fig. 4).

For each of the nine observed territorial hoverers, the average f during the initial acceleratory phases of pursuit flights was significantly greater than during hovering (Fig. 5; paired t -test, d.f. = 10, $P < 0.001$). Hovering *C. pallida* males maintained an extremely inclined stroke plane ($41.0 \pm 1.9^\circ$; Fig. 1) and held their bodies nearly parallel to the horizon ($4.1 \pm 0.7^\circ$; Fig. 1).

Discussion

Centris pallida, particularly hovering males, maintain perhaps the highest and most stable T_{th} among flying insects

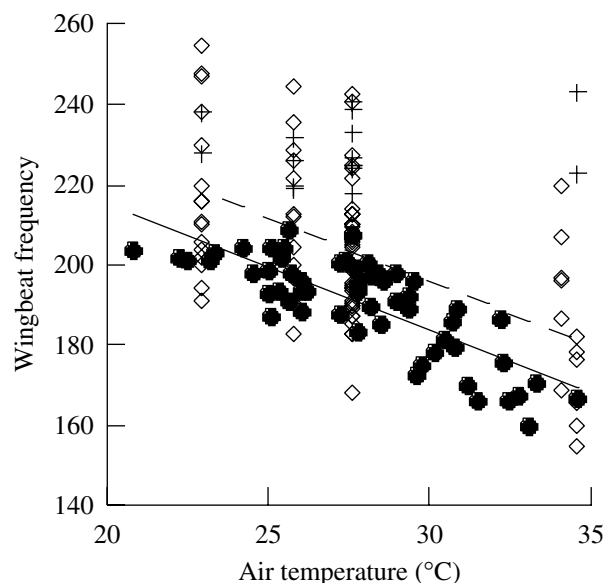


Fig. 4. Wingbeat frequency vs. abdomen temperature (T_a) for male *Centris pallida* bees during hovering (circles), patrolling (diamonds) and intermale pursuits (crosses). Linear regressions: Hovering $f = (-3.166 \cdot T_a) + 278.85$, $r^2 = 0.62$, $F_{1,55} = 91.4$, $P < 0.001$ (data from Roberts & Harrison, 1998). Patrolling $f = (-3.178 \cdot T_a) + 291.35$, $r^2 = 0.28$, $F_{1,79} = 31.4$, $P < 0.001$.

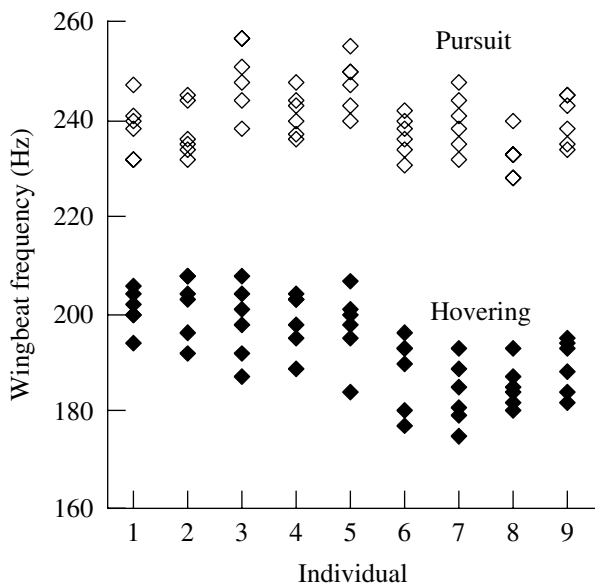


Fig. 5. Wingbeat frequency (f) during hovering flight and the initiation of pursuits for nine territorial *Centris pallida* males. For each bee, $n=6$ at each flight behaviour. Bees were measured at abdomen temperature (T_a) from 22.5 to 29.4°C, and presented in increasing order of T_a . Mean hovering f , but not mean pursuit f , significantly decreased with increasing T_a . Least square regression: Hovering $f = (-2.644 T_a) + 262.34$, $r^2 = 0.78$, $F_{1,7} = 30.58$, $P = 0.001$.

(Chappell, 1984; Roberts *et al.*, 1998; for comparative data, see Heinrich, 1993; Roberts & Harrison, 1998). Hoverers exhibit slightly better thermal stability than patrollers because their $T_{th} \cdot T_a$ slope (0.15) is significantly less than that of hoverers (0.25). *Centris pallida* patrollers have lower body segment temperatures than hoverers, despite similar f and larger body masses, suggesting that patrollers lose more heat via convection than hoverers and that the maintenance of stable, elevated body temperatures, particularly during flight at low T_a , is more difficult during patrolling than during hovering.

Independence of R_h and R_{ab} with T_a indicates that patrolling and hovering *C. pallida* males do not thermoregulate flight muscles by using the head or abdomen as thermal windows at high T_a via circulatory heat-shunting from the thorax to these regions. By contrast, R_h is negatively correlated with T_a in both hoverers and patrollers, indicating that *C. pallida* males thermoregulate the head (at the expense of T_{th} regulation) by increasing heat transfer from the thorax to the head during flight at low T_a . Thermoregulation of the head may serve to increase the visual and olfactory acuity needed to detect and discriminate among conspecific males and virgin females. Evaporative heat loss is an important mechanism used by *A. mellifera* to prevent overheating during flight at high T_a (Roberts & Harrison, 1999), but it appears unlikely to be so in patrolling *C. pallida* because evaporative loss from hovering *C. pallida* males increases only slightly as T_a increases from 25 to 35°C

(Roberts *et al.*, 1998). However, evaporative heat loss may be greater during patrolling flight due to a decrease in boundary layer thickness resulting from greater airspeeds over the body.

The inverse relationship between f and T_a for hoverers and patrollers suggests that the regulation of T_{th} by *C. pallida* in the field is accomplished to some degree by variation in metabolic heat production. This hypothetical pattern of thermoregulation is supported by inverse metabolism vs. T_a relationships demonstrated for *C. pallida* (Roberts *et al.*, 1998) and *A. mellifera* (Harrison *et al.*, 1996; Roberts & Harrison, 1999). Although no study to date has directly measured metabolism as a function of body temperature or T_a during forward flight in insects, there is some indirect evidence that variation in metabolic heat production may contribute to thermal stability during forward flight in a wide variety of endothermic insects. May (1995) estimated that the metabolic heat production of the dragonfly *Anax junius* during crepuscular feeding flights decreases from 397 to 296 mW g⁻¹ as T_a rises from 21 to 26.5°C, based on wind-tunnel cooling curves, the specific heat of dragonfly tissue and observed flight velocities. Furthermore, a significant negative relationship between f and T_a has been reported for patrolling *C. caesalpiniae* males (Spangler & Buchmann, 1991) and the dragonflies *A. junius* and *Epiptera cynosura* during forward flight (May, 1995).

A hypothetical alternative thermoregulatory mechanism to varying metabolic heat production is to increase airspeed and resultant convective heat loss during flight at high T_a , assuming that increases in convection exceed any increases in metabolic heat production due to increased airspeed. Convective heat loss from dead bees suspended in wind tunnels increases exponentially with airspeed (Church, 1960; Chappell, 1982; Cooper *et al.*, 1985; Heinrich & Buchmann, 1986; Coelho, 1991), whereas rates of metabolism (Ellington *et al.*, 1990) and mechanical power output (Dudley & Ellington, 1990a) of *Bombus* flying in a wind tunnel do not vary across airspeeds of 0–4.5 m s⁻¹. As noted by Heinrich & Esch (1994), if these observations are generally applicable to bees in nature, then increasing forward airspeed at high T_a should increase convective heat loss without affecting metabolic heat production and enhance thermoregulation. This 'free-cooling' mechanism has been proposed as important for thermoregulation during forward flight in desert bees, including *C. pallida* and *Xylocopa* spp. (Heinrich, 1993, 1996; Heinrich & Esch, 1994). Furthermore, Heinrich & Buchmann (1986) report anecdotally that *Xylocopa varipuncta* in a temperature-controlled room fly faster at high T_a . Preliminary video analyses of *C. pallida* patrollers indicate independence of airspeed and T_a (Roberts, unpublished data), whereas the inverse relationship between patroller f and T_a suggests that the maintenance of higher airspeeds at higher T_a is unlikely. The effect of T_a on airspeed for endothermic flying bees awaits rigorous testing to assess the 'free-cooling' hypothesis.

Centris, similar to certain hoverflies (Syrphidae; Ellington, 1984; Ennos, 1989), are somewhat unusual among hovering insects in that they hover with an extremely inclined stroke

plane, β , and near horizontal body angle, χ . However, most insects hover with nearly horizontal β and inclined χ , and make the transition to forward flight and increased airspeed by increasing β and decreasing χ , with little change in f or stroke amplitude Φ (David, 1978; Azuma & Watanabe, 1988; Dudley & DeVries, 1990; Dudley & Ellington, 1990b; Wakeling & Ellington, 1997; Willmott & Ellington, 1997). This postural shift increases the horizontal force vector generated by the wings and propels the insect forward (Dudley & Ellington, 1990a). Inclined β hovering is believed to be an important feature enabling rapid airspeed changes and enhanced evasive or chasing capacities by facilitating the reorientation of the net aerodynamic force without substantive change of χ (Dudley, 2000). Analysis of the mechanisms by which inclined β hoverers change direction and speed in addition to increased f , such as modulation of angle of attack, await analysis via high-speed video.

The dramatic increase in f at the onset of pursuit likely reflects increased power requirements for achieving high rates of acceleration and airspeeds, as predicted by aerodynamic theory (Ellington, 1984, 1991). Dudley (1995) showed that increasing Φ , but not f , is the primary kinematic mechanism of increasing power during burst flights in hypodense gas mixtures for euglossine bees, whereas dragonflies and damselflies increase both Φ and f during acceleratory flight (Rüppell, 1989). Thus, it would not be surprising if *C. pallida* also increases Φ during pursuits.

Thermoregulation by pursuing *C. pallida* males apparently does not involve variation in metabolic heat production because n is independent of T_a during this behaviour. Although f during pursuits are 30–40 Hz higher than during hovering, very little change in T_{th} is expected during pursuits due because the factorial increase in metabolic rate predicted by the change in f (58%; Roberts *et al.*, 1998) is almost identical to the predicted factorial increase in thoracic conductance [53%; based on allometric conductance vs. airspeed curves for *A. mellifera* workers and drones in (Coelho, 1991)]. Even if conductance is unaffected by the rise in airspeed, the increase in T_{th} predicted by the rise in metabolic heat production over the course of a single pursuit (which lasts only 1–2 s on average) would be less than 0.5 °C, assuming a specific heat of 3.3 J g⁻¹ °C⁻¹ for insect muscle tissue (May, 1979).

Acknowledgements

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