ENDOTHERMY AND TEMPERATURE REGULATION IN BEES: A CRITIQUE OF 'GRAB AND STAB' MEASUREMENT OF BODY TEMPERATURE

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Summary

'Grab and stab' methods have become standard in the measurement of insect body temperatures. The gradient of the best-fit regression of body temperature on ambient temperature is often used as a measure of the thermoregulatory ability of a species. The temperatures recorded are commonly accepted as slight underestimates of actual values prior to capture due to passive cooling between capture and insertion of the thermocouple. Here we present laboratory experiments involving tethered flight which show that bees often warm up on cessation of flight, and that errors due to warm-up over the time interval typically associated with 'grab and stab' sampling may be significant. More importantly, the errors due to warm-up in two species are shown to change with ambient temperature, thus affecting the form of the relationship between ambient and body temperatures. We compare laboratory and field data to illustrate the way in which warm-up errors may exaggerate apparent thermoregulatory ability, and we urge greater caution in the interpretation of 'grab and stab' data.

Introduction

'Grab and stab' measurement of insect body temperatures, using a thermocouple usually mounted inside a hypodermic needle, has become a standard field technique. The insect whose body temperature is to be measured is typically captured in a net and held using insulating gloves or forceps (e.g. Heinrich, 1979; Louw & Nicolson, 1983; Cooper *et al.* 1985; Heinrich & Buchmann, 1986; Dyer & Seeley, 1987), or restrained against an insulating material such as styrofoam (e.g. Chappell, 1982, 1984; Baird, 1986; Stone *et al.* 1988). The thermocouple is then inserted into the thorax or other body tagma, and the maximum temperature recorded. The assumption has always been that as soon as the insect is captured it starts to lose heat. As Baird (1986) stated in his work on the bee *Xylocopa virginica*, 'individuals in the net either became agitated or calm, presumably cooling passively'. Some workers have tested the accuracy of the technique by

examining the cooling characteristics of either freshly dead, heated insects or tethered insects over the period between capture of the insect and insertion of the thermocouple (e.g. Heinrich, 1979, 1986; Rawlins, 1980; May & Casey, 1983). The conclusions in all cases are (a) that body temperature measurements are underestimates, and (b) that errors are of the order of 1°C and, once acknowledged, can be disregarded.

Because of these assumptions, the aim of all workers has been to minimize the time between the capture of the insect and insertion of the thermocouple. The values obtained are then taken as accurate indications of what the body temperature was during the activity immediately preceding capture, generally flight. Readings obtained more than a certain time after capture are discarded as inaccurate. Maximum tolerated handling times vary between studies, and often depend directly on how easily the insect can be restrained, in the net or otherwise, in a suitable position for insertion of the thermocouple. Tolerated handling times vary from 3s (Cooper et al. 1985; Heinrich, 1986; Morgan & Heinrich, 1987) to 10–12 s in cases where several tagmata are to be sampled (e.g. Baird, 1986), with the average tolerable handling time around 5–7s (e.g. Chappell, 1982; Louw & Nicolson, 1983). This method is often but not always (e.g. Rawlins, 1980) fatal to the insect.

One method of calculating the errors in 'grab and stab' measurements is to 'grab and stab' an insect whose body temperature is being measured continuously. However, we do not know of any ideal study that involves both continuous measurement of body temperatures during and after flight and 'grab and stab' measurement after restraint in a net. Insects captured in a net should probably not be regarded as flying (since their wing movement is generally restricted) but as physiologically prepared for flight and escape at the earliest possible opportunity. Furthermore, it is known that attacking honeybees elevate their body temperatures above usual levels for flight (Heinrich, 1979), and it seems reasonable to suspect that other endothermic bees may continue to de so when agitated within the confines of a net.

Body temperatures thus obtained are plotted against the ambient temperatures at the time and site of capture to obtain a regression of thoracic (T_{th}) or abdominal (T_{ab}) temperature on ambient temperature (T_a). For an animal that regulates its body temperature, the gradient of the best-fit regression for the data over the range of T_a in which regulation occurs must be less than 1: the lower the gradient, the better the level of thermoregulatory ability. Discovery of data showing this relationship is considered 'prima facie evidence for regulation' of body temperature (May & Casey, 1983). Although authors often correctly state that such a relationship is only an indicator of thermoregulatory ability (e.g. Morgan & Heinrich, 1987), it has been tempting to regard a gradient of less than 1 for the regression of T_{th} on T_a as sufficient evidence of thermoregulatory ability, even when the range of T_a over which the data were obtained has been very narrow (e.g. May & Casey, 1983, for Eulaema cingulata, where N is small and the T_a range only 22–26°C). It has been assumed not only that the errors in the 'grab and stab'

technique are small, but also that they are constant as a function of T_a and therefore do not affect the form of the T_{th}/T_a relationship.

In this paper we investigate changes in body temperatures at the end of tethered flight in several bee species, and compare detailed laboratory and field data for three species. We show that 'grab and stab' errors may not in fact lead to underestimates of body temperature, but to overestimates; and that these errors can be important in conclusions concerning thermoregulatory ability.

Materials and methods

Field measurements of body temperature were made using a copper–constantan thermocouple mounted inside a fine hypodermic needle (diameter 0·6 mm). Values were obtained for both thoracic and abdominal temperatures, the order in which the two parts were sampled being switched for alternate bees. Both measurements were completed within 6 s through the net while the bee was held using the pressure of the net against a small block of styrofoam. Measurements were always carried out in shade, and T_a was measured immediately afterwards using the dried thermocouple as close as possible to the site of capture. In general, captured bees struggled and buzzed audibly, both these phenomena ceasing as soon as the thermocouple was inserted.

For measurement of body temperatures during tethered flight, bees (always females unless specified otherwise) were first narcotized using carbon dioxide, and placed in a styrofoam clamp on a cooled stage. A small hole was made in the dorsum of the thorax with an entomological pin. A thermocouple consisting of 40 gauge copper wire inside steel syringe tubing with an external diameter of 0·25 mm was inserted <1 mm into the aperture, and sealed in place using adhesive (Copydex, Unibond-Copydex Ltd, UK). Once the adhesive had dried, the bees were released from the stage and allowed to warm to room temperature, which for the interspecific comparisons was always 21·5–22·5°C. Experiments were all carried out in still air. Bees were given a piece of styrofoam to hold in their feet. The bee was tethered only by the thermocouple, and thus did not support its own weight. The importance of this experimental limitation is considered in the Discussion. Warm-up was initiated voluntarily, or induced by gentle tapping of the abdomen with fine forceps. Flight was also initiated voluntarily, the bee releasing the styrofoam, and prolonged when necessary by continued tapping. When body temperature during tethered flight had stabilized, the styrofoam was reintroduced to the bee's feet and flight and wing movement ceased. Thoracic temperatures were recorded continuously using a Portec P.I.8013 digital thermocouple meter and Linseis chart recorder. All bees were released with no apparent harmful effects.

The temperature at which the bee dropped the styrofoam and initiated tethered flight is referred to as the voluntary flight temperature (VFT), and the stable temperature resulting after continuous flight at a given ambient temperature the stable flight temperature (SFT).

Creightonella frontalis (Fabricius) (Megachilidae) and *Amegilla sapiens* (Cockerell) (Anthophoridae) were investigated in August and September 1987 at the Christensen Research Institute, Madang, Papua New Guinea. *Anthophora plumipes* (Pallas) (Anthophoridae) and *Bombus terrestris* (L.) (Apidae) were studied between March and July 1988 at the Zoology Department, Oxford University, and *Colletes cunicularis* (L.) (Colletidae) at the Bee Research Unit, University College, Cardiff in April 1988.

Results

After establishment of a stable flight temperature, cessation of flight led to three different types of body temperature response in the bee species examined; (a) passive cooling (Fig. 1B), (b) a brief rise in temperature followed by passive cooling (Fig. 1A,C,D), and (c) rapid prolonged temperature increase due to endothermic activity (Fig. 2).
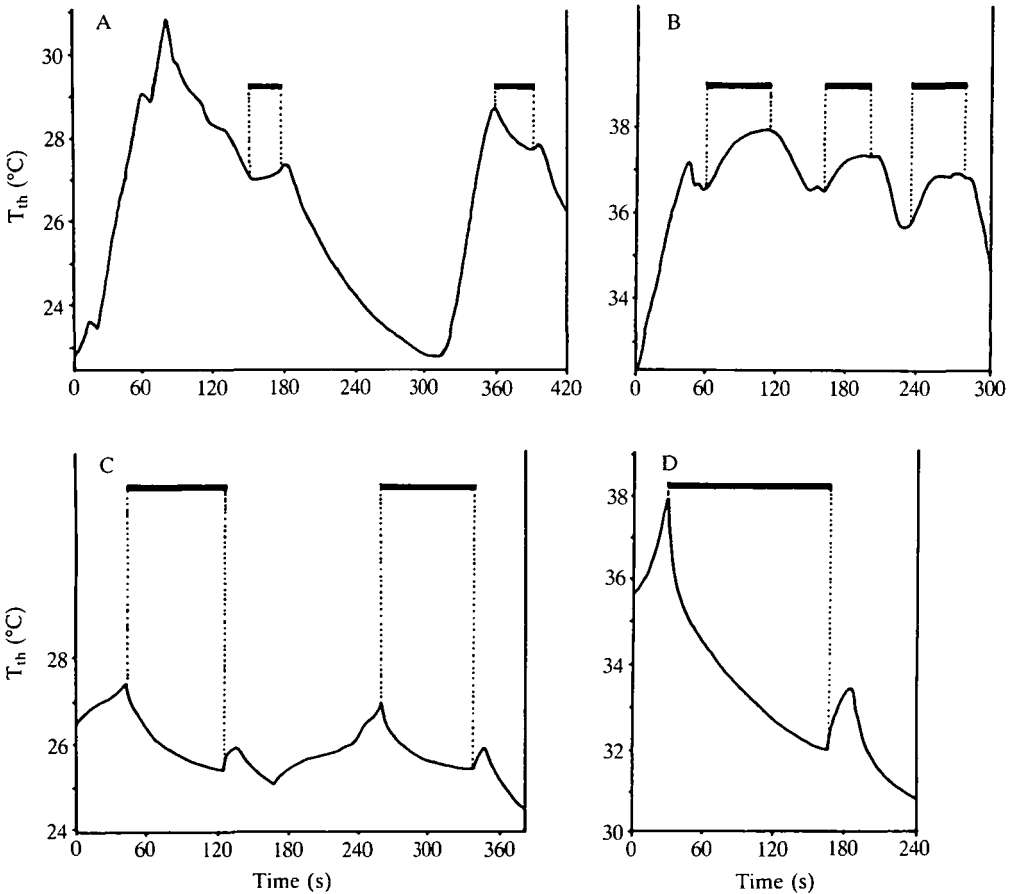

Fig. 1. Typical changes in body temperature at the end of tethered flight at $T_a = 22\,°C$ in four bees. Flight is indicated by solid bars. (A) *Colletes cunicularis*. (B) *Anthophora plumipes*. (C) Male *Creightonella frontalis*. (D) *Creightonella frontalis*.
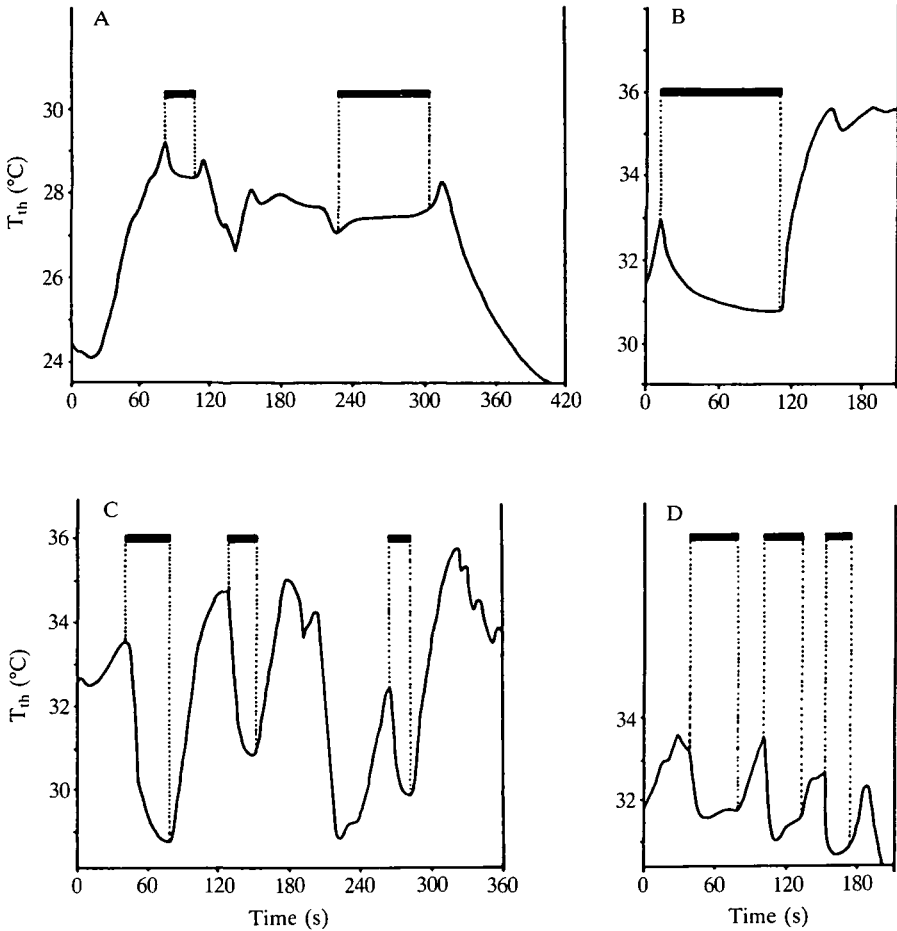
Fig. 2. Four cases of post-flight warm-up. (A) *Colletes cunicularis*. (B) *Creightonella frontalis*. (C) *Anthophora plumipes* at 10°C. (D) *A. plumipes* at 22°C.

Where cessation of flight was followed by passive cooling, were the tethered bee to be sampled using 'grab and stab' the errors would be typically approximately 0·5°C after 5 s and 0·9–1·3°C after 10 s (Table 1). This is true whether the bee flying at a T_a of 22°C has a high SFT, such as *A. plumipes*, or a lower SFT, such as male *C. frontalis*, and irrespective of whether the bee has a high mass, such as female *Creightonella*, or a lower mass, such as female *Colletes cunicularis*. Although small bees, with their higher surface area to volume ratio, should lose heat more rapidly than larger bees for a given temperature excess, larger bees typically have a higher SFT excess above T_a than small bees (e.g. 8·1°C for *C. frontalis*, 4·4°C for *Amegilla sapiens*). The greater the temperature excess, the more rapid the cooling will be. In the time involved in 'grab and stab' sampling, these two counteracting effects on rates of temperature change seem to balance each other out. In fact, cooling errors do not change significantly with changing T_a

Table 1. *Summary of data for body mass, stable flight temperature and end of flight changes in body temperature*

Species	Mean body mass (mg)	T_a (°C)	SFT (°C)	Mean temperature change over 5 and 10 s (°C)					
				Prolonged warm-up		Brief temperature rise		Cooling	
				5 s	10 s	5 s	10 s	5 s	10 s
Anthophora plumipes	185 ± 3 (N = 15)	22	35·1 ± 0·3 (N = 52)	0·65 ± 0·1	1·1 ± 0·25	0·2 ± 0·1	−0·1 ± 0·1	−0·6 ± 0·05	−1·33 ± 0·1
Anthophora plumipes	185 ± 3 (N = 4)	10	29·4 ± 1·0 (N = 9)	1·55 ± 0·05	2·4 ± 0·2				
Bombus terrestris	295 ± 35 (N = 8)	22	33·3 ± 0·3 (N = 20)	0·9 ± 0·1	1·65 ± 0·1	0·0 ± 0·1	−0·4 ± 0·1	−0·6 ± 0·1	−1·05 ± 0·15
Colletes cunicularis	112 ± 4 (N = 7)	22	28·6 ± 0·3 (N = 56)	0·66 ± 0·05	1·65 ± 0·05	0·13 ± 0·05	−0·3 ± 0·1	−0·3 ± 0·05	−1·0 ± 0·1
Creightonella frontalis female	305 ± 13 (N = 10)	22	30·1 ± 0·3 (N = 22)	1·4 ± 0·1	2·05 ± 0·1	0·65 ± 0·2	0·4 ± 0·2	−0·4 ± 0·1	−0·9 ± 0·2
Creightonella frontalis male	113 ± 7 (N = 6)	22	25·3 ± 0·3 (N = 15)						
Amegilla sapiens	117 ± 4 (N = 10)	22	26·4 ± 0·5 (N = 24)	1·2 ± 0·1	1·65 ± 0·15	0·43 ± 0·05	0·15 ± 0·1	−0·5 ± 0·1	−1·05 ± 0·15

Errors are ± 1 s.E.

SFT, stable flight temperature; T_a, ambient temperature.

for either *A. sapiens* or *C. frontalis*. Our estimates of these errors agree well with published estimates and, if cooling were the general case for insects netted in the field, the errors could probably be ignored as small and systematic.

A common observation on cessation of tethered flight, particularly in certain species, was a brief rise in temperature of variable magnitude followed by passive cooling. Typical examples of these phenomena are shown in Fig. 1A,C,D. These rises in temperature are rapid enough to give a noticeable error in 'grab and stab' measurements within the usual 5 s handling time, but in all cases the magnitude of the error would be small. In female *C. frontalis*, for example, thoracic temperatures had risen $0.65 \pm 0.2\,^{\circ}\mathrm{C}$ above SFT after 5 s and had fallen to $0.4 \pm 0.2\,^{\circ}\mathrm{C}$ above SFT after 10 s. For both of the species with the highest SFT excesses (*A. plumipes* and *B. terrestris*, Table 1), these brief rises in temperature were rare and of negligible size, expressed more in terms of a delay in cooling of a few seconds. Errors were often smaller after 10 s than after 5 s, but in all cases were smaller than errors due to cooling, and again. can probably be ignored. The probable origin of this phenomenon is considered in the Discussion.

However, some bees of all species showed immediate rapid warm-up on cessation of tethered flight, generally leading to further flight. Here the errors involved are larger. Warm-up after flight is identifiable by a sustained increase in T_{th} with time whose gradient compares well with prolonged periods of warm-up preceding flight. They may be brief (*Colletes cunicularis*, Fig. 2A) or sustained (*Creightonella frontalis*, Fig. 2B). *C. frontalis* females showing warm-up achieved, on average, $1.4\,^{\circ}\mathrm{C}$ above SFT after 5 s and $2.1\,^{\circ}\mathrm{C}$ after 10 s (Table 1) at an ambient temperature of $22\,^{\circ}\mathrm{C}$. *Bombus terrestris* warmed up, on average, by $0.9\,^{\circ}\mathrm{C}$ after 5 s and by $1.6\,^{\circ}\mathrm{C}$ after 10 s at the same air temperature.

The magnitude of predicted 'grab and stab' errors due to warm-up ('warming error') is a function of ambient temperature in at least two of the species investigated. Thus, at $22\,^{\circ}\mathrm{C}$ *A. plumipes* raised T_{th} by $0.6\,^{\circ}\mathrm{C}$ after 5 s and $1.1\,^{\circ}\mathrm{C}$ after 10 s, whereas at an ambient temperature of $10\,^{\circ}\mathrm{C}$ these values became 1.5 and $2.2\,^{\circ}\mathrm{C}$, respectively. Fig. 3 shows the significant negative correlation between the magnitude of warming errors and T_a for *C. frontalis*.

When SFT is plotted as a function of T_a for female *C. frontalis*, the gradient of the best-fit regression is 0.83 ($N = 45$, $r = 0.92$, $P < 0.0001$) (closed symbols on Fig. 4). If the errors due to warm-up after 5 or 10 s from Fig. 3 are added to the real SFT values, the result must be a line whose gradient is less than 0.83, giving a false indication of greater thermoregulatory abilities. To illustrate this point, T_{th} after 10 s as a function of T_a for all female *C. frontalis* tested is shown as a dashed line in Fig. 4. Although only 53 % of female flights were followed by warm-up, the net population effect on the relationship between T_{th} and T_a due to increased warm-up errors at low T_a is a reduction in the gradient from 0.83 to 0.74 ($N = 45$, $r = 0.85$, $P < 0.0001$), or an apparent increase in 'thermoregulatory ability'. The gradient of the best-fit regression for T_{th} after 5 s is 0.76 ($N = 45$, $r = 0.86$, $P < 0.0001$), and most of the apparent increase in 'thermoregulatory ability' for this species thus occurs within the accepted handling time. Were all individuals to
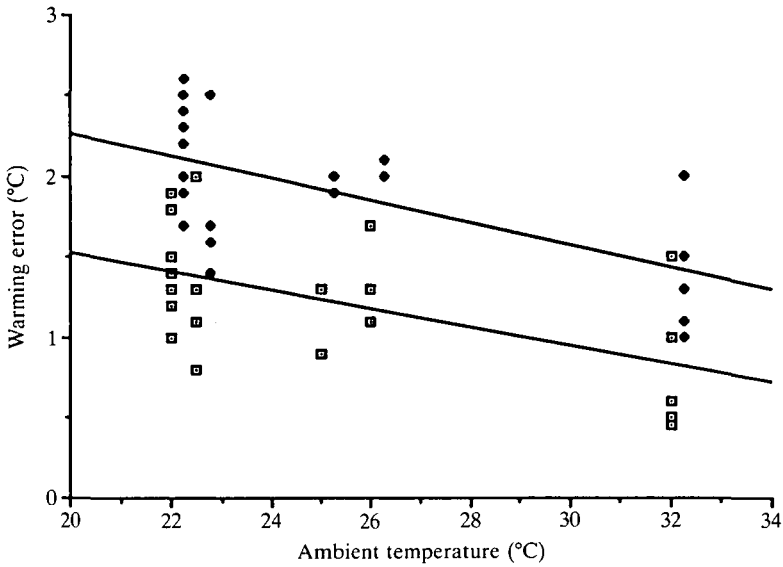
Fig. 3. The relationship between warming errors after 5 s (☐) and 10 s (◆) and ambient temperature for females *Creightonella frontalis* showing post-flight warm-up. Best-fit regressions: after 5 s $y = 2 \cdot 7 - 0 \cdot 06x$, $r = 0 \cdot 56$, $P < 0 \cdot 01$; after 10 s $y = 3 \cdot 6 - 0 \cdot 07x$, $r = 0 \cdot 62$, $P < 0 \cdot 01$.
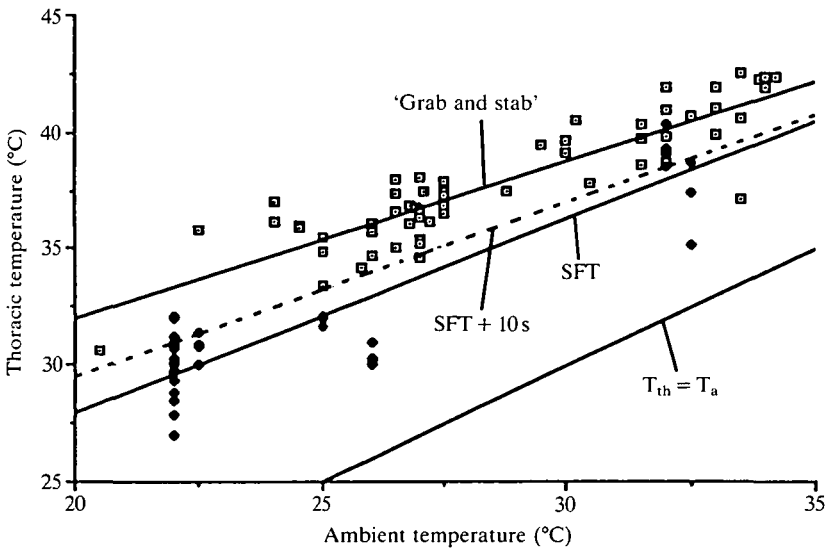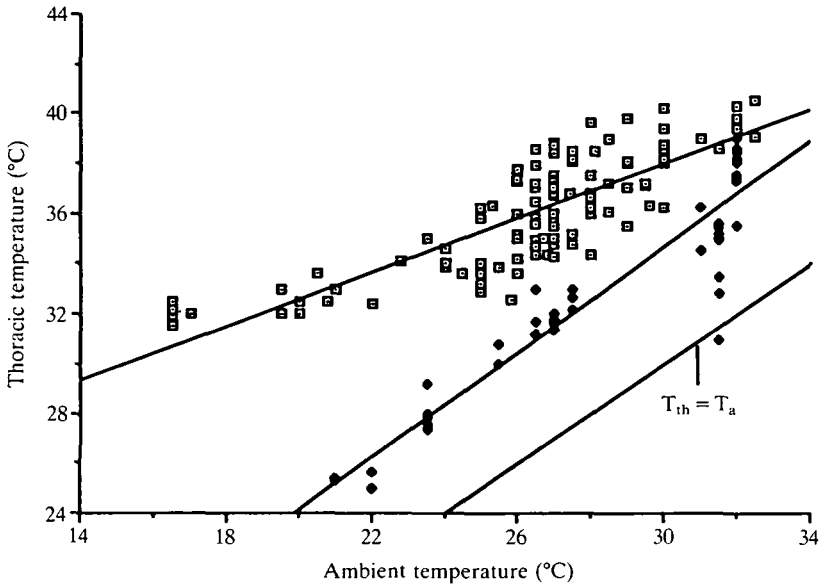

Fig. 4. Thoracic temperatures (T_{th}) measured using 'grab and stab' (☐) and stable flight temperature (SFT) (◆) as functions of ambient temperature (T_a) for female *Creightonella frontalis*. The dashed line indicates temperatures 10 s after cessation of tethered flight (individual points not shown). Best-fit regressions: 'grab and stab' data $y = 18 \cdot 5 + 0 \cdot 68x$, $r = 0 \cdot 88$, $P < 0 \cdot 001$; SFT data $y = 11 \cdot 3 + 0 \cdot 83x$, $r = 0 \cdot 92$, $P < 0 \cdot 001$.

Fig. 5. Thoracic temperatures (T_{th}) measured using 'grab and stab' (▣) and stable flight temperature (SFT) (◆) as functions of ambient temperature (T_a) for *Amegilla sapiens*. Best-fit regressions: 'grab and stab' data y = 21·8+0·55x, r = 0·88, P < 0·001; SFT data y = 3+1·05x, r = 0·94, P < 0·001.

warm up after capture, and perhaps at a higher than usual rate owing to agitation within the confines of a net and/or the insulating properties of the net and the experimenter's gloved hand, these errors could only increase in magnitude. Field data for body temperatures in *Creightonella frontalis* females are also shown in Fig. 4 (open symbols). The gradient of the best-fit regression for the relationship between T_{th} and T_a is 0·68 ($N = 57$, $r = 0·88$, $P < 0·0001$). This is significantly lower ($F_{1,100} = 4·4$, $P < 0·05$; Sokal & Rohlf, 1981) than the gradient for the regression of SFT on T_a (0·83, above), but lies within the error margin that we would predict if most captured bees show endothermic behaviour during the period between capture and sampling (see the SFT + 10 s line in Fig. 4).

Field data for 'grab and stab' measurements of T_{th} in *Amegilla sapiens* are shown in Fig. 5 (open symbols). Again the gradient of the best-fit regression of T_{th} on T_a (0·55) is substantially less than 1 ($N = 100$, $r = 0·88$, $P < 0·0001$). However, a plot of SFT as a function of temperature has a gradient of 1 ($N = 47$, $r = 0·94$, $P < 0·0001$) (closed symbols, Fig. 5). Again the gradients of these two lines are significantly different ($F_{1,159} = 52·74$, $P < 0·001$). If we accept that SFT is a valid approximation to body temperatures during flight (see Discussion), then the accuracy of the 'grab and stab' data, particularly at low T_a, should perhaps be reassessed. It is our contention that warm-up by insects trapped in the net may well be a more serious source of error in thermoregulatory studies than has previously been appreciated.

Discussion

Recommendations for possible modifications of 'grab and stab' procedures clearly depend on which of the observed patterns of temperature change on cessation of flight actually occurs in the net in the field. Bees which are inactive as soon as they are captured, and do not struggle in the net, will cool passively, and should be sampled as quickly as possible. Bees which show a brief temperature rise before cooling passively show greater errors after 5 s than after 10 s, but in either case the errors are small. However, bees which go into warm-up on capture are likely to show greater errors, and in a previously unappreciated direction. In our experience, bees often do struggle energetically for the time interval between capture and sampling.

If errors in 'grab and stab' measurement of body temperatures do involve warming rather than cooling, some important assumptions about the technique must be revised. If cooling is more important, then it is true that smaller bees, with their higher surface area to volume ratios, will cool more rapidly than larger bees, other things being equal. This has led to the general assumption that errors involved in measuring body temperatures of large bees are smaller than those in small bees (e.g. May & Casey, 1983). The use of insulating gloves to hold the bee while the thermocouple is inserted will also reduce cooling by reducing the effective body area over which heat loss can occur.

However, if errors are generally due to warming these predictions are reversed. Owing to their lower surface area to volume ratios, larger bees will, other factors being equal, warm more over the sampling time interval than small bees (G. N. Stone & P. G. Willmer in preparation). Since gloves insulate the body against heat loss, their use will increase the magnitude of errors due to warming. These errors alone may generate more effective 'thermoregulation' in large bees than in small bees.

The relationship between the size of warming errors and ambient temperature is a predictable one where the bee does, in fact, have thermoregulatory ability. At its stable flight temperature, the bee's heat gain and heat loss are in equilibrium. Heat gain is due to muscular activity, and heat loss to two components; (a) passive cooling due to the SFT excess over T_a, and (b) forced convective cooling due to wing movement and, in the field, forward motion. Both passive and forced convective cooling increase with increasing SFT excess. At a given temperature excess, cooling due to forced convection will be greater than that due to passive cooling, the difference increasing with increasing speeds of air flow over the body (Chappell, 1982). In field situations during flight it must be reasonable to assume that, in maintaining a given SFT excess, most heat production is necessary to counter this forced convective heat loss. When wing movement ceases, as it is forced to do in a net, the bee's heat production will still be pitched to maintaining the SFT at that T_a. In the absence of forced convective cooling, and probably augmented by the agitated state of the bee in the net, this will lead either to a rapid rise in temperature of the brief type (Fig. 1A,C,D) or to prolonged warm-up (Fig. 2). The higher the SFT excess the bee was maintaining before capture, the

greater the thermogenic output of the flight muscles, and the more rapid this post-flight warm-up will be. Thus, the greater the SFT excess, the greater the magnitude of the warming error. Hypothetical big bees which are genuinely good thermoregulators with a high SFT, for which errors due to cooling are assumed to be small, will thus show the highest errors due to warm-up. At 22 °C, *C. frontalis* females maintain an SFT excess of 8°C, whereas at a T_a of 32–32·5°C they maintain an SFT excess of 5°C. Warm-up within 5 s of cessation of flight is correspondingly greater at a T_a of 22 °C than at 32 °C. If, as is probable, power output during tethered flight is an underestimate of power output in free flight, the true forced convective cooling which the bee's thermogenic ability is normally countering will be greater, and the warm-up when this cooling is removed more rapid and of greater magnitude. Thus, our errors are almost certainly underestimates of the effect in the field.

The errors discussed here do not seriously challenge demonstrations of endothermy in many good regulators. Insects such as *Bombus vosnesenskii* (Heinrich, 1975) have such high temperature excesses at low T_a that even were the effects of potential post-flight warm-up errors taken into consideration a considerable 'genuine' temperature excess would remain. However, use of the gradient of the best-fit regression for the relationship between T_{th} and T_a as sufficient evidence of thermoregulation, particularly where the sampled range of T_a is small, should be discouraged. Some authors are at pains to use statistics only from large data sets with significant regressions (e.g. Morgan & Heinrich, 1987). As these authors state, 'Clearly the accuracy of this test depends on how well the data set represents the thermal relationships of the insect'. Nevertheless, in some cases, gradients from best-fit lines are used as indications of thermoregulation (e.g. May & Casey, 1983), when even the best fitted regressions are very poor approximations to the real data (the best-fit regressions to the data have non-significant values of *r*). Use of the gradient from such data sets is misleading.

A potential alternative and simple measure of body temperature in flight is the stable flight temperature used here. Manufacture of the necessary thermocouples, and their insertion without causing obvious stress to the animal, is relatively simple. In the field, temperatures can be dictated to a continuously running cassette recorder. In the laboratory, the same bee, given time to stabilize at different ambient temperatures, can give a whole series of SFT data. Thus it is possible to gain an indication of the thermoregulatory abilities in a species from a far smaller number of individuals, and without killing any of them. In field situations where the population of the study species is small, or where the natural range in T_a is limited, this technique has advantages. Although non-lethal techniques for measurement of body temperatures in the field have been developed (e.g. Willmer, 1986), these are subject to the same kinds of errors inherent in 'grab and stab', and open to other errors, such as variation in positioning of the thermocouple and lack of direct contact between thermocouple and flight musculature.

An obvious criticism of the use of SFT lies in the use of tethered flight as an

indicator of heat generated in true, free flight. It is our experience that once suspended flight is initiated, wingbeat frequencies measured using an optical tachometer (Unwin & Ellington, 1979) do not differ significantly from those measured in field conditions. For example, Unwin & Corbet (1984) report wingbeat frequencies in the field at an ambient temperature of 22 °C for foraging *Bombus pascuorum* of about 220 Hz. Tethered *B. pascuorum* showed a wingbeat frequency, measured with the same apparatus, of about 200 Hz. Flight power output depends not only on the frequency of wing movement, but also on its amplitude. Tethered flights were in all cases only accepted where the volume of sound produced approached levels in the field, and considerable draught was produced. An ideal apparatus would involve flight in a wind tunnel where both air flow and lift generated could be measured, as used by Esch (1976), but such sophisticated analysis is impracticable for most environmentally related studies of insect thermal biology. We suggest that a gradient of less than 1 for a regression of SFT on T_a may be a safer indicator of thermoregulatory ability. The assumption here is that the proportion of power used in free flight actually used in tethered flight is not itself a function of ambient temperature, and thus the error which no doubt exists does not affect the form of the relationship. This assumption remains to be tested.

We are not suggesting that 'grab and stab' be abandoned as a technique – it is and will probably remain the simplest and most accurate method of measuring body temperatures in the field. Nor are we recommending changes in technique – whether the bee cools or warms actively the best policy is to measure the bee's temperature as rapidly as possible, preferably without holding it. It will normally be clear to each field worker whether the captured insect is warming up in the net (audible buzzing and rapid abdominal pumping are good potential indicators of endothermic activity) and thus whether particular figures recorded for T_{th} are likely to be under- or overestimates. Thus what we advocate is a more thoughtful approach to the way 'grab and stab' data are interpreted.

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