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Thermoregulation in Endothermic Insects

Body temperature is closely attuned to activity and energy supplies.

Bernd Heinrich

In insects, as in other animals, body temperature is one parameter affecting the rate of energy expenditure, the rate at which food can be located and harvested, and the facility with which predators can be avoided. A "poikilothermic" caterpillar (1, 2) may be restricted for weeks to one plant where it ingests large quantities of leaf tissue. The small percentage of nutrients extracted from the large bulk of this foodstuff (3) is channeled primarily into body tissues. A "heterothermic" (4) moth, on the other hand, is often highly mobile while feeding from scattered flowers. It utilizes high-energy fuels (5) which permit intense metabolic rates that cause endothermy (heat production at rates sufficient to increase body temperature).

Endothermy, as such, has long been known to exist in insects (6). In 1837, 6 years after thermocouples were first

used to measure the body temperature of insects (7), Newport (8) reported that sphinx moths and bumblebees may elevate their thoracic temperature above ambient temperature by muscular activity. Preflight warm-up was described by Dotterweich in 1928 (9), and in 1965 Heath and Adams (10) reported that the sphinx moth *Celerio lineata* stabilizes its thoracic temperature during flight over a range of ambient temperatures. It has only recently been demonstrated that some insects regulate their body temperature by physiological means. The regulation of body temperature by behavioral means such as basking, on the other hand, is a well-established phenomenon. It has been described in the desert locust *Schistocerca gregaria* (11), in butterflies (12), beetles (13, 14), cicadas (15, 16), and arctic flies (17).

Various aspects of thermoregulation

in insects have been reviewed (18, 19), but at the time these articles were written, little was known about the mechanisms involved. I will here examine recent developments and comparative aspects of insect physiology relating to thermoregulation in the contexts of energetics and ecology.

Muscle Activity and Endothermy

In insects, essentially all endothermic increases of body temperature above ambient temperature are the result of heat produced by the active flight muscles. These muscles are, metabolically, the most active tissues known (20, 21). The mechanical efficiency of the flight mechanism of both insects and birds is approximately 10 to 20 percent (22); more than 80 percent of the energy expended during flight is necessarily degraded to heat. Flight activity and endothermy are thus invariably linked, at least in the larger insects (20, 23), and endothermy in flight is in large part an obligatory phenomenon.

Body temperature during flight and stridulation. A high muscle temperature is not only a consequence of muscle activity. It is also a prerequisite for flight. In order to lift a load in free flight, or to fly at a certain speed, the insect must exert a specific force per wingbeat and maintain a minimum wingbeat frequency. This requires that the contractions of the upstroke and downstroke muscle be sufficiently rapid

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and brief that they do not significantly overlap and contract against each other during the wing stroke. This requirement is fulfilled when the temperature of the muscles is sufficiently high (24–27). Alternatively, there is little overlap in the contractions of the antagonistic muscles when the wingbeat frequency, and concomitantly the rate of muscle shortening, is low. Different relative wing sizes and power requirements determine the wingbeat frequency sufficient for flight.

The muscle temperature required for activity, and generated by it, varies widely. Small flies have rapid heat loss and little buildup of body heat during flight (28). On the basis of metabolic rates and rates of convection heat loss, the thoracic temperature cannot be more than 1°C above ambient in small flies such as midges and fruit flies (29–35). The wingbeat frequency and flight speed of the flies varies nearly directly with ambient thermal conditions (34, 36, 37), also suggesting that thoracic temperature varies with ambient temperature during flight. However, flight is possible at relatively low ambient (and presumably low thoracic) temperatures in some of them; midges may fly at 6°C (38). The flies can be air-

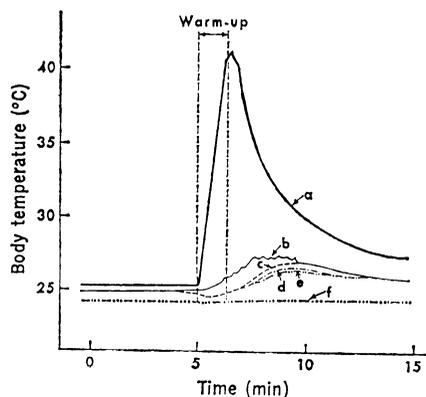


Fig. 1. Thoracic temperature (a) and abdominal temperatures [(b) ventral anterior, (c) ventral posterior, (d) dorsal posterior, and (e) dorsal anterior], and ambient temperature (f) during warm-up and subsequent cool-down of a *Bombus vosnesenskii* queen (total body weight, 0.63 g; thorax, 0.23 g). Each of the five body temperatures was recorded at 13-second intervals from 46-gauge copper-constantan thermocouples with a Honeywell multichannel potentiometric recorder. During warm-up the temperature of the thorax increased 15.5°C in 1.3 minutes. Abdominal temperature increased during cool-down of thoracic temperature. The slight drop in abdominal temperature at the initiation of warm-up is probably due to evaporative cooling during the rapid abdominal respiratory movements (41).

borne at only a fraction of their maximum wingbeat frequency.

The flight muscles of some of the larger insects, on the other hand, must be near or above 40°C before sufficient wingbeat frequency and lift can be generated to support the animals in free flight (25, 39). Some of these insects, including moths and bumblebees, are covered with a dense layer of pile that may halve the rate of convective heat loss (35). The combination of high metabolic rate, relatively large body size, and insulation results in the retention of sufficient heat to cause the passive elevation of thoracic temperature during free flight, to the extent of more than 20°C above ambient temperature (39). Thus, at ambient temperatures above 25°C, such insects would overheat, and further flight would be prevented unless active mechanisms of cooling came into play. However, the insulation also helps to maintain a sufficiently high thoracic temperature to allow flight at low ambient temperatures (40). For example, bumblebees (large queens) may fly with a thoracic temperature of 36°C at an ambient temperature of 3°C (41).

In addition to these differences between large and small insects, the muscle temperature required by some of the larger insects varies also between (i) different muscles that are used for different activities and (ii) between different species. The following examples illustrate some of the variation in Orthopterans. The twitch duration of the relatively "slow" dorsal longitudinal hindwing depressor muscle in the locust *Schistocerca gregaria* is 50 milliseconds at 25°C, but only 35 msec at 35°C (26). In another Orthopteran, the male katydid *Euconocephalus nasutus*, the twitch duration of the first tergocoxal forewing muscle (wing elevator) is about two times faster than that of *S. gregaria* at any given temperature. The males also use the muscle during stridulation (when the right and left forewings are rubbed together at about 160 hertz). In females of *E. nasutus*, on the other hand, where this muscle is used only during flight (wingbeat frequency is 16 to 20 hertz, as in *S. gregaria*) the contraction time is nearly the same as that of *S. gregaria* (26, 27, 42). The muscles must have a temperature of at least 35°C (in the males) before they can contract at 150 hertz; at 25°C these muscles contract in a smooth tetanus

when activated at the same frequencies. It is therefore not surprising that the katydids *E. nasutus* (and *Neoconocephalus robustus*) initiate stridulation only when thoracic temperature exceeds 33°C, and that during stridulation they maintain their thoracic temperatures 5° to 15°C above ambient temperature (43).

Heat production by warm-up (shivering). When an insect comes to rest in shade, its body temperature often becomes practically equal to ambient temperature within minutes. Since a relatively high thoracic temperature is a prerequisite for flight in the larger insects, they would remain permanently grounded if they were incapable of increasing the temperature of their musculature prior to flight.

Heat production by the flight muscles and the elevation of thoracic temperature (Fig. 1) prior to flight (or stridulation in some Orthoptera) has been observed in insects of various orders, including Lepidoptera (6, 9, 44, 45), Hymenoptera (46, 47), Coleoptera (40), and Orthoptera (43, 48). Activation of the power muscles for flight without externally visible wing motion, resulting in apparent shivering, is also observed in Diptera (49), but only modest increases of thoracic temperature have been observed in flies (34). Many species of insects from

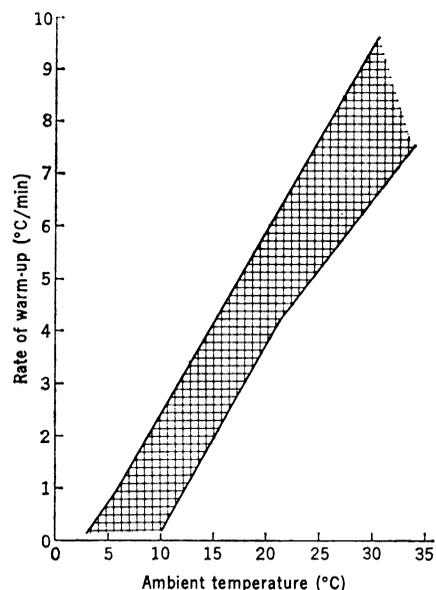


Fig. 2. Rate of increase in thoracic temperature during preflight warm-up in large (0.5 to 4.0 g) moths in relation to ambient temperature. The crosshatched area includes the mean values for *Manduca sexta* (52), *Hyles euphorbia* (60), *Deilephila elphenor* (60), and *Hyalophora cecropia* (61).

the above orders are incapable of warm-up, and the mechanism has presumably evolved independently on numerous occasions.

Warm-up (shivering) involves numerous patterns of activation of the flight muscles (50). During warm-up in "synchronous" flyers (those with a fixed phase relationship between nervous impulses to the power muscles of flight and the resulting muscle contractions), the upstroke and downstroke flight muscles are activated nearly at the same time (43, 45, 51) rather than alternately as in flight. During shivering, the antagonistic flight muscles thus contract primarily against each other, and the muscle contractions are usually accompanied by wing vibrations of small amplitude rather than by wingbeats (45, 52). In most of the "asynchronous" flyers (many wingbeats per single activation of the indirect muscles) there is a lack of wing vibrations during warm-up, primarily because of a mechanical uncoupling of the muscles from the wings (53), rather than because of synchrony of activation of antagonistic muscles. In addition, it is probable that in asynchronous flyers the muscles are nearly in tetany during warm-up at action potential frequencies of more than 15 hertz (54, 55), particularly when thoracic temperature is low.

In a variety of Lepidoptera the rates of wing vibration are directly correlated with muscle temperature (52, 56-58). As thoracic temperature increases throughout warm-up (Fig. 2), so does the rate of wing vibration and, concomitantly, the rate of heat production (52). However, the rate of wing vibration is set by the central nervous system, and the increase in rate of wing vibration is thus presumably not due to a temperature effect on the muscles, as such. Flight is initiated when the metabolic rate is near that observed in free flight (Fig. 3).

Although the results cited above indicate that more heat is produced per unit time at higher muscle temperatures, it had previously been concluded that the muscles produce more heat during warm-up at low temperatures than at high in order to actively "compensate" for heat loss and to warm up at the same rate (58, 59). This view has been questioned, and the different results, which are probably due to different experimental methods having been used, have been discussed (60, 61). Although the rate of warm-up is

much more rapid at high than at low ambient temperatures, the increase of thoracic temperature during any one warm-up is usually relatively linear rather than exponential because as thoracic temperature increases both the heat production and the heat loss increase at the same time. The results fit the model that heat production is directly related to thoracic temperature (52).

Thermoregulation by Intermittent Activity

Intermittent flight, intermittent warm-up activity, or a combination of the two, are means of thermoregulation via endothermy. However, during flight, heat production is necessarily continuous, while during shivering it may be continuous, intermittent, or may occur at different rates, particularly when thoracic temperature is being stabilized (Fig. 4). The different options for heat production during shivering and flight necessarily affect thermoregulation. Although the "flight" muscles of insects are well known to be multifunctional (43, 62), they appear to be used for only one function

at a time. They cannot be used for shivering and flight simultaneously. Therefore, an insect such as a hovering sphinx moth that remains in continuous flight does not have the same options for regulating its thoracic temperature as a bee that lands on flowers at frequent intervals.

The most studied example of thermoregulation by shivering, where intermittent muscle activity is possible, is that of honeybees and bumblebees. Over some ranges of ambient temperature the metabolic expenditure of individual grounded honeybees is inversely related to ambient temperature (63, 64), as in vertebrate homeotherms (4). [The honeybees generate heat for thermoregulation several days after emergence (63).] Thermoregulation by endothermy in grounded bees involves their activating the indirect flight muscles as in preflight warm-up, rather than using them to drive the wings. Shivering can be intermittent, or it can occur at a wide range of activation frequencies and thus produce variable rates of heat production (47). Stationary bumblebees may maintain their body temperature near 36° to 38°C for hours or days at ambient temperatures as low as 2°C (65, 66). The metabolic

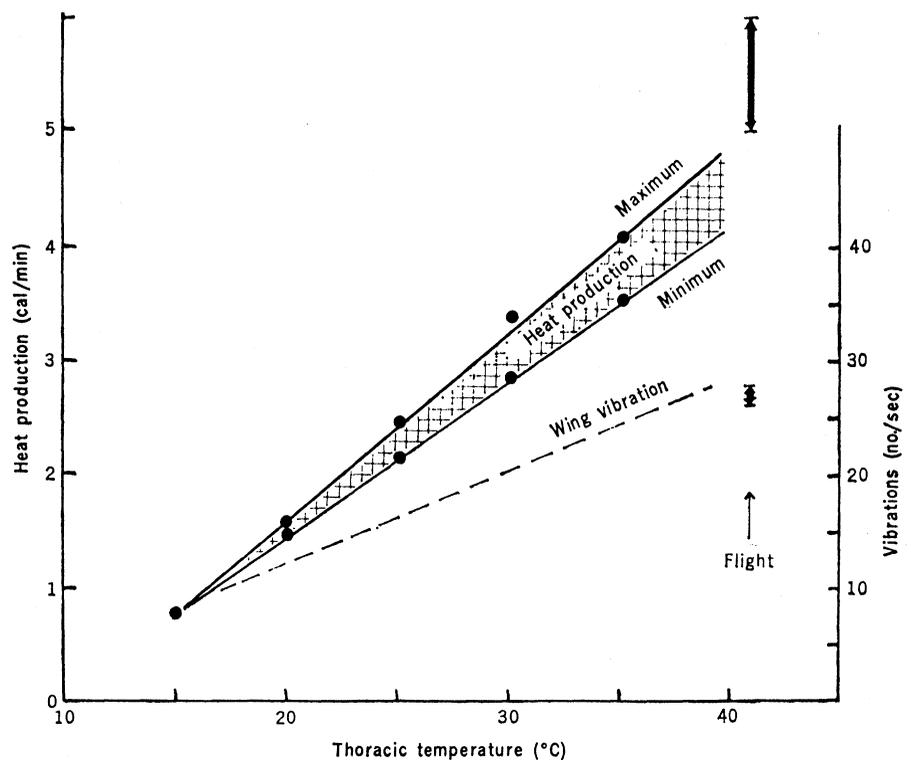


Fig. 3. Rates of wing vibration and calculated rates of heat production during preflight warm-up in the sphinx moth *Manduca sexta* in relation to thoracic temperature (either at the beginning or during the course of warm-up) [adapted from Heinrich and Bartholomew (52)]. Arrows at 41°C indicate average wingbeat frequency and rate of heat production of a 1.5-g moth during free flight (40).

rate during this (near maximum) muscular activity for heat production is, at 180 milliliters of oxygen per gram of thorax per hour, nearly the same as that in flight (41, 66). The maintenance of an elevated thoracic temperature is always accompanied by high frequencies of action potentials to the flight muscles (67), and the bees' metabolic rate is directly related to the action potential frequency (54, 67). Increases of thoracic temperature in the absence of action potentials have not been observed.

It has been proposed, on the basis of studies of the activities of enzymes in bumblebees (68) and malignantly hyperthermic pigs (69), that these animals may engage in nonshivering thermogenesis by a recycling of fructose 6-phosphate resulting in the utilization of adenosine triphosphate. However, muscle activity and heat production were not examined in the bee studies, and in the "inactive" bees the flight muscles might have had a low temperature, as in torpid bees (70).

Although heat for thermoregulation is probably not produced intermittently in insects such as sphinx moths and some dragonflies during continuous flight in the field, data superficially indicating that intermittent heat production does occur can be produced in

the laboratory. The insects can be forced to become intermittently active for short durations by confining them in a small space or by restraining them by a tether such as thermocouple leads. Tethered moths usually fly to the end of their tether (unless supported by it after loss of tarsal contact), stop activity when they can go no further, and immediately begin to cool to ambient temperature. A moth may go through several heating and cooling cycles before appearing to give up all attempts to fly away. If the moths are attempting to attain a specific thoracic temperature in order to initiate flight, but are prevented from engaging in flight, they would have an overall lower energy expenditure than during flight over a given period of time. Furthermore, they would shiver less frequently at the high than at the low ambient temperatures and the metabolic expenditure over a given period of time would vary accordingly, thus yielding data that are laboratory artifacts superficially resembling the classic thermoregulatory behavior of endothermic vertebrates.

In contrast to sphinx moths which hover, bees fly intermittently while foraging in the field. They can thus produce heat by shivering during the intervals that they are perched on

flowers. The durations of flight and perching are brief; bumblebees may visit 20 to 30 different flowers per minute. In bumblebees, heat may be produced specifically for thermoregulation by muscular activity during the intervals that they are perched on the flowers (71, 72), but at ambient temperatures higher than 24°C (in shade) the difference between the thoracic and the ambient temperatures is primarily the result of flight metabolism; little additional heat is produced at these temperatures for thermoregulation during the stops at flowers. It is thus obvious that in terms of overall energy expenditure, it is less economical for bees to forage at low than at high ambient temperatures. At ambient temperature near 0°C, however, the large temperature gradient between the body and ambient air causes the convective heat loss during flight to be so rapid that even bumblebees are unable to remain in continuous free flight. Under such conditions they regulate thoracic temperature by stopping flight, engaging in warm-up until thoracic temperature is elevated, and then resuming flight (41).

Thermoregulation during Flight

As previously noted, the heat produced as a by-product of flight metabolism necessarily elevates thoracic temperature during continuous flight, and if the heat production and heat loss from the insect during flight are passive phenomena then the difference between thoracic and ambient temperatures, whether large or small, should be constant at all ambient temperatures for any individual. The maintenance of a specific thoracic temperature during continuous flight at a given ambient temperature therefore does not imply temperature regulation, but the maintenance of the same thoracic temperature over a range of ambient temperatures does. The regulation of thoracic temperature in flying sphinx moths is now well documented, but certain aspects of the mechanism, or mechanisms, whereby thoracic temperature is stabilized are not.

Metabolic rate. It has been maintained on numerous occasions that the mechanism of temperature regulation in flying moths involves the regulation of the rate of heat production (58, 73-75). However, in none of these studies have the metabolic rates of animals in actual continuous flight been

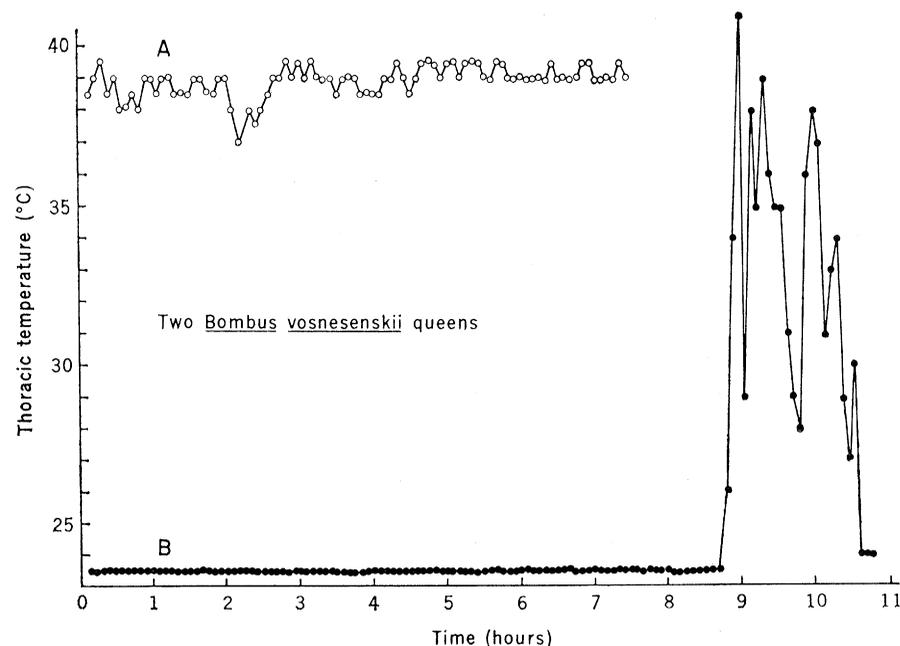


Fig. 4. Thoracic temperatures of captive bumblebee queens. (A) A *Bombus vosnesenskii* which had initiated nest building and which maintained a high thoracic temperature continuously at night (7 p.m. to 3 a.m.) while remaining relatively stationary. (B) The thoracic temperature of an overwintered *B. vosnesenskii* (from 1 a.m. to 12 p.m.) which had not yet initiated nest building. Her thoracic temperature remained near ambient temperature at night. Temperatures were recorded at least once per minute and are here plotted at 5-minute intervals. Ambient temperature was 23° to 25°C [adapted from Heinrich (41, 65)].

utilized. The measurements of the metabolic rates during "flight" and "continuous activity" refer to insects grounded in microrespirometers scarcely large enough to allow them to spread their wings. These data of "flight" metabolism (59, 73) have been used to construct models of thermoregulation of flying moths, even though the observed respiratory rates at the higher ambient temperatures are close to those observed during torpor (76). The most parsimonious interpretation of the data is that, given the methods described, the moths were not as active as they would have been in continuous free flight, and that they were able to thermoregulate in the same way as grounded bees.

Low values for metabolism and body temperature can be expected if the insect is allowed to stop flight or is supported so that it can skip wingbeats during the period of measurement. Furthermore, metabolic rate, heat production, and body temperature also depend on flight effort. During flight on a roundabout flight mill, or during fixed flight on a tether, the insect does not necessarily support its full weight. This has a large effect on the physiology of thermoregulation. While the sphinx moth *Manduca sexta* is mechanically supported during flight on a flight mill, where lift is not controlled, thoracic temperature and metabolic rate vary either passively with ambient temperature or with whatever flight effort the moth happens to "choose" (40). The respiratory rate can be less than half that in free flight. Similarly, locusts have a metabolic rate as low as 15 ml of oxygen per gram of body weight per hour during tethered flight at low wing loading, but the metabolic rate doubles with a doubling of lift (31, 32). The metabolic rate of bumblebees also approximately halves during fixed flight in comparison to free and unsupported flight (41, 67). In these insects, the thoracic temperature declines during supported flight but only at the low air temperatures (40, 67). The high metabolic rates of insects in continuous free flight in large jars (40, 41, 60, 77) are close to those computed from the observed fuel consumption of bees in flight in the field (78). Data on the metabolic rates of insects at different flight speeds are lacking, and data on the metabolism of continuous flight therefore appear to be a better approximation of flight metabolism upon which to base models of thermoregulation than data from grounded animals.

Throughout the range of ambient temperature where thoracic temperature is stabilized during free flight (Fig. 5), the respiratory rate of sphinx moths of at least four species remains, at 40 to 70 ml of oxygen per gram of body weight per hour, independent of ambient temperature (40, 60). As in bumblebees (41), the metabolic rate probably varies with the load the insect carries. Since the insects accumulate negligible oxygen debt during flight (79), it can be concluded from these observations that the sphinx moths do not regulate their work output during continuous flight for the purpose of temperature regulation. The heat production is necessarily high at all ambient temperatures, if the animals remain in continuous flight.

The possibility that some insects regulate their rate of heat production for thermoregulation when they are in continuous flight cannot yet be excluded, however. It is possible, for example, that some insects that have large wings (such as butterflies or dragon-

flies) and glide or have intermittent wingbeats, thermoregulate by flying with a lower wingbeat frequency at high ambient temperatures in order to avoid overheating (80). It may also be possible for the insects to reduce the activation frequency of the flight muscles to avoid overheating if the load that is carried is light. However, these possibilities are not supported by direct evidence.

Wing loading in relation to body temperature. Since the muscle temperature in flight is a consequence of the power output, and since a certain temperature must be attained for a given power output, it is necessary to examine the circumstances under which power output is varied in order to distinguish between the possibly active mechanisms and the "passive" mechanisms of heat generation. The minimum metabolic expenditure that is required for an insect to remain airborne depends, in part, on body weight. One of the parameters which gives an indication of the work output required from the thoracic

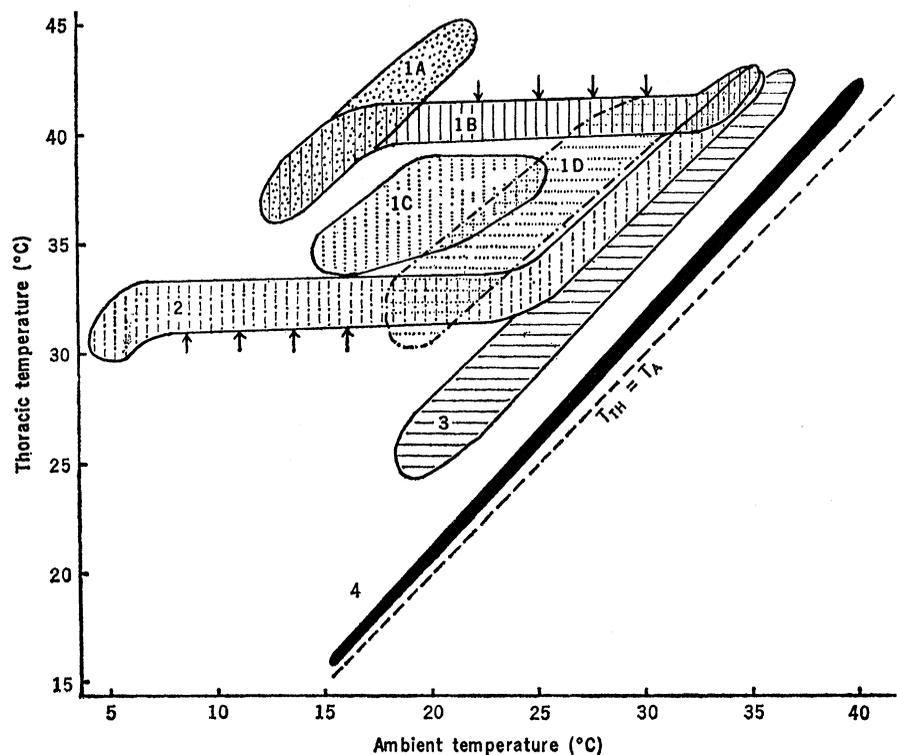


Fig. 5. Diagrammatic representation of thoracic temperatures (T_{TH}) of insects in flight (or foraging, or both) in relation to ambient temperature. 1. The sphinx moth *Manduca sexta* [A, free flight with ligated dorsal vessel; B, free flight, unaltered (adapted from Heinrich (39)); C, flight on a tether [adapted from McCrea and Heath (58)]; and D, flight on roundabout flight mill [adapted from Heinrich (40)]. 2. Bumblebees, *Bombus vagans*, while foraging (intermittent flight) from flowers in the field [adapted from Heinrich (71, 72)]. 3. The butterfly *Danaus plexippus* [adapted from Kammer (57)] and the desert locust *Schistocerca gregaria* [adapted from Weis-Fogh (32)] during tethered flight. 4. Blowflies during tethered flight [in part based on data from Yurkiewicz and Smyth (28) and Rowley and Graham (37)]. Arrows pointing up indicate thoracic temperature near minimum for flight; arrows pointing down indicate thoracic temperature near upper zone for "comfort." Abdominal temperatures (T_A) in most cases vary directly with ambient temperatures.

muscles during flight is the ratio of wing area to body weight—that is, the wing loading. This varies widely between different species and between different individuals in any one species. Thoracic temperature and wing loading are positively correlated in different species of sphinx moths (Fig. 6), in various taxa of other moths (81), and perhaps in individuals of the same species (40, 56).

Wing loading probably affects power output during flight and inferences about the power output during the wing stroke can be made from electrophysiological data on the number of motor units recruited and the extent to which they are activated. For example, saturniid moths, and butterflies, which fly with a low wingbeat frequency, activate their indirect flight muscles with bursts of impulses per wingbeat during flight, and the number of impulses per burst is correlated with wingbeat frequency and stroke amplitude, both of which are variable (45, 82). Double rather than single firing per muscle contraction results in a greater force of

contraction (83) and greater metabolic rate (32, 33). Moths such as *Hyalophora cecropia* probably modulate power output during free flight, since the animals range widely in weight whereas their wing size is relatively constant.

There remains the question of whether the temperature of the muscles is regulated to fit the work output in these moths, or whether thoracic temperature varies passively with increased work output and concomitant heat production. Both alternatives are probably correct, muscle temperature probably being related in part to whether or not thoracic temperature is regulated. Sphinx moths retain more heat in the thorax during flight at low than at high ambient temperatures (84, 85) and perhaps also under higher wing loading than low (40). The resulting higher thoracic temperature permits a higher metabolic rate (Fig. 3), which may be necessary in order for the heavier animals (those having fed or carrying eggs) to fly with speed and agility. The alternative hypothesis (that higher thoracic temperature is only a direct consequence of

higher metabolic rate and greater heat production) is applicable in these moths at the low air temperatures where the rate of passive heat loss is still sufficient to prevent overheating. In large moths during tethered flight (at low metabolic rates), and in the smaller un-insulated insects with necessarily more rapid rates of heat loss, the thoracic temperature is a passive function of the rates of metabolism and convective cooling over a much greater range of ambient temperatures than during free flight of large insects with high metabolic rates (Fig. 5).

Large wings allow insects to fly with a low wingbeat frequency (86) and allows some butterflies to initiate flight without prior endothermic warm-up (87) and to continue flight by gliding (88, 89); the energy expenditure of locomotion is thus reduced in such insects. It is of interest that the saturniids, and some sphinx moths that do not feed as adults, often have large wings relative to their total body weight, and thick insulating layers of scales. Reduced wing loading by an increase in wing size may have been selected during evolution because it allowed a reduction in energy expenditure for a given distance of flight when it was not economically advantageous, in terms of energy expenditure, to harvest nectar while hovering.

Although bumblebees do not regulate thoracic temperature during stationary fixed flight, the large queens do so during free flight, even at ambient temperatures near 2°C. The seemingly passive thoracic temperature during stationary flight, and the variable thoracic temperature under a variety of wing loadings during free flight in moths and bees, suggest that the thermostat dual "set point" model (19, 58, 73, 74) for thermoregulation in insects is either not applicable during flight, or the model is applicable only over a wide range of thoracic temperature.

Thermoregulation and exteroceptors. It is well known that insects adjust their flight effort (and consequently their rate of heat production) in relation to sensory input from exteroceptors (90, 91). The compound eyes, mechanoreceptors from Johnston's organ, and facial hairs provide sensory input for reflex mechanisms (92) which are used to maintain specific flight speeds.

If the insect were losing altitude or decreasing its flight speed (as it would at low thoracic temperature), then it would be informed of such by visual

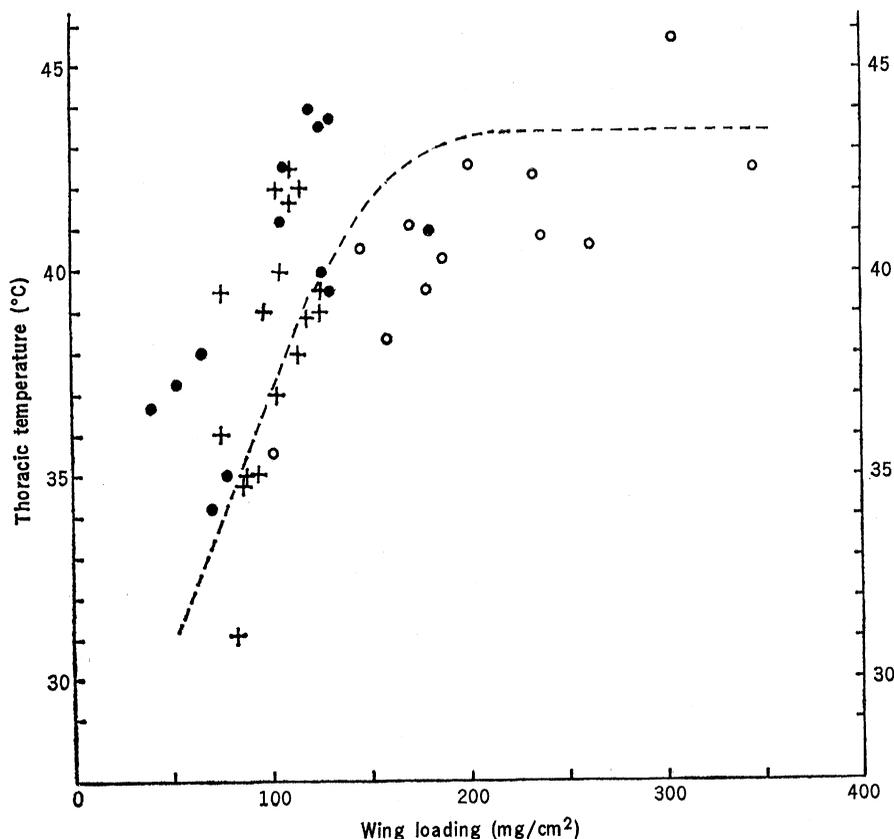


Fig. 6. Thoracic temperatures of sphinx moths from 25 species during free flight in relation to weight-relative wing area. Symbols: +, *Deilephila nerii*, ambient temperature 22° to 23°C [from Dorsett (56)]; ●, each point represents an average for a different species, ambient temperature 7° and 17°C [from Bartholomew and Heinrich (81)]; ○, each point represents an average for a different species, ambient temperature 19° to 21°C [adapted from Heinrich and Casey (60)]. Curve was gauged by eye.

and other sensory input. Increasing its flight effort to maintain a certain flight performance would automatically maintain the flight muscles above some minimum temperature. At least in honeybees, the activation frequency of the indirect flight muscles is varied as a consequence of visual input from exteroceptors (91). Perhaps the differences in metabolic rate (and thoracic temperature) between insects during free and supported flight is related to such factors. However, the scope for such regulation would be small during free flight requiring nearly maximal effort.

Regulation of power output (with accompanying changes in heat production) is achieved in synchronous flyers such as locusts and moths by varying the number of motor units recruited (from a total of five in the largest flight muscles), and by activating them multiply rather than singly to achieve a stronger muscle contraction during changes of lift and during turning maneuvers (83, 93). To my knowledge there are no data to indicate that the insects react similarly neurophysiologically or behaviorally (by modifying flight speed) to modify their muscle temperature during flight (94). In asynchronous flyers such as bees, the flight effort is, as in synchronous flyers, also regulated by the action potential frequency to the fibrillar flight muscles (54, 67, 92). A change in the tension of the thoracic box brought about by nonfibrillar muscles [the axillary lever in bees or the pleurosternal muscles in flies (49, 90)] may secondarily affect power outputs and presumably the rate of heat production by changes of load on the fibrillar muscles. This also remains to be investigated.

Regulation of heat loss. Most insects are small and uninsulated so that overheating of the flight musculature is not a general problem. However, buildup of heat is rapid in the flight muscles of some of the large insects. Overheating in some of these, such as the desert cicada (15) which feeds only when it is stationary, is prevented by flight cessation. In contrast, some of the larger (0.5 to 6.0 g) well-insulated sphinx moths feed while hovering. They produce 4 to 6 calories of heat per gram of body weight per minute in the thorax and at air temperatures higher than 20°C the passive rate of heat loss from the thorax may not be sufficient to keep the temperature of the flight musculature less than 40°C (39, 40). Some of the heat resulting from the

intense muscular activity in the thorax then becomes a waste product if the moths are prevented from landing. This heat is transferred (Fig. 7) by way of the blood from the thorax to the abdomen when the abdominal heart (dorsal vessel) beats rapidly and pumps cool blood through the hot thorax (84). (When the sphinx moth is at rest, the heart may also beat rapidly, but at times it may be silent or pulsations may be from the thorax to the abdomen rather than the other way around.) During flight at low ambient temperatures (39, 85) or during preflight warm-up (52), the heart appears to fibrillate weakly but rapidly, rather than pulsate, and boluses of fluid are no longer observed to travel from the cool abdomen into the thorax. The moth appears to restrict the flow of blood between thorax and abdomen at these times of rapid low amplitude heart movement, thus restricting the flow of heat between these parts of the body. A high thoracic temperature (greater than 43°C) no longer accelerates its pulsation rate when the ventral nerve cord is transected (84). The heart activity in the abdomen of these moths thus seems to be modified by signals from the head or thorax. It has recently been concluded that heart activity in the saturniid moth *Hyalophora cecropia* is regulated by way of the thoracic ganglia which is also sensitive to the temperature of the thorax (95).

The mechanism of thermoregulation

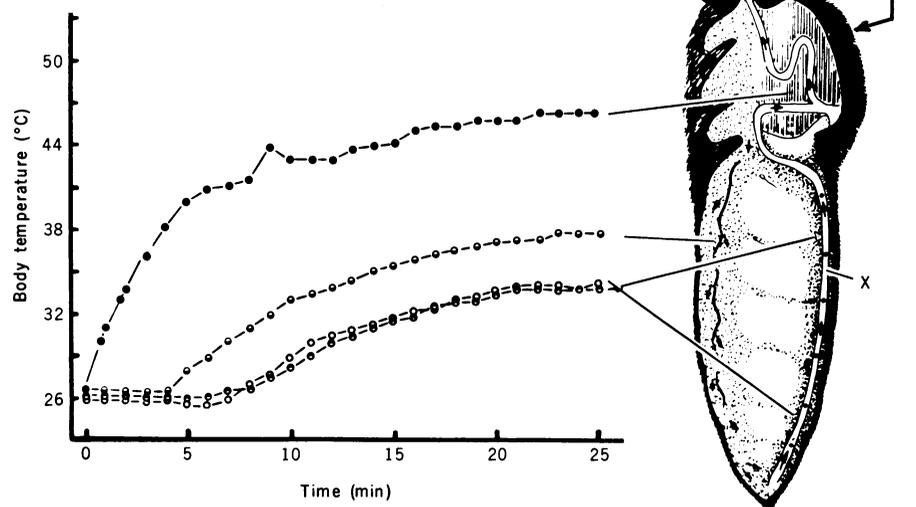


Fig. 7. Body temperatures of a restrained sphinx moth *Manduca sexta* during 25 minutes of heat application to the thorax. Lines on the sagittal view of the body connect the positions of the implanted thermocouples to the temperatures that were recorded there. As thoracic temperature approached and exceeded 40°C, the frequency and amplitude of the beating of the dorsal vessel (X) increased while abdominal temperature began to increase concomitantly. Arrows indicate the direction of blood flow. The moth was later killed with ether and heated with a similar input of heat. In the dead moth thoracic temperature increased to 53°C while the temperature of the abdomen increased 2°C above ambient, rather than 10°C [adapted from Heinrich (84)].

(thereby increasing heat flow out of the thorax) if the flow into and out of the thorax alternated in pulses rather than flowing in both directions at the same time. Restriction of the flow of blood from abdomen to thorax to discrete pulses, so that the flow is not continuous, should have a similar effect. The mechanics of this fluid flow are unknown.

Heat transfer to the abdomen has also been observed in bumblebees during the incubation of their brood (Fig. 8). During brood incubation the abdomen is brought into contact with the brood cluster, and heat flows into it by conduction (98) rather than being dissipated to the environment by convection, as in flying sphinx moths. However, the bees have the option of producing or not producing heat while incubating.

Regulation of the direction of air flow through the tracheal system may also have an effect on heat transfer, but the small specific heat of air would make it an inefficient medium of heat transfer. However, if the movement of air is combined with the evaporation and condensation of water, then its movement could be of much larger sig-

nificance. For example, heat in the thorax would be used to produce water vapor (in unsaturated air), and this heat would be released in the cooler abdomen as the vapor condenses there. These possibilities have not been examined.

Most insects do not cool themselves by active evaporative mechanisms (99). The availability of cooling through avoidance reactions and forced convection, and the need for water retention, may select against such a mechanism. However, the blood-sucking tsetse fly *Glossina morsitans* of equatorial Africa can feed while in sunshine on the hot hide of a mammal. While taking blood the insect temporarily has an abundance of liquid. At high ambient temperatures it opens its spiracles. This allows water to evaporate, and the body temperature may decline as much as 1.6°C (100).

Avoidance reactions, such as shade-seeking (101, 102), are part of the repertoire of behavioral thermoregulation whereby, perhaps at random, a suitable temperature is encountered (103). Forced convection appears to be a variation of escape behavior to effect cooling. For example, the butterfly *Precis villida* which is killed by over-

heating if forced to remain stationary in sunshine on the ground under some conditions, initiates flight frequency, and, by convective cooling, maintains its thoracic temperature at less than 42°C even at midday near the equator where it remains in the sunshine (87). Structural features may also prevent overheating in sunshine. Some butterflies (87) and a cicada (102) appear to use the wings to shade the body, and the subelytral space of some beetles shields the abdomen from solar radiation (104). The long legs of certain ants and beetles living on sand exposed to direct sunlight act as stilts to remove the bodies of these animals from the high temperatures of the substrate, while light pigmentation of the elytra reduces heat input from above (13, 105).

Energy Supplies and Endothermy

Like some of the small birds, bats, and rodents that enter torpor when food supplies are scarce or when temperatures are low (4), insects also adjust their activity and endothermy in relation to energy supplies and in relation to the energy costs of thermoregulation. The maintenance of a high body temperature when an animal does not need to be physically active is energetically costly, particularly in small animals. However, small body size permits rapid heating as well as rapid cooling (4). A small insect can warm up and initiate activity in several minutes or less, and it can remain hidden while it is in torpor. A large and conspicuous vertebrate animal, on the other hand, needs several hours to go through a heating and cooling cycle (52), and the ability to reduce body temperature when activity was not of immediate necessity would give such an animal fewer advantages. In the insects, heterothermy is the rule rather than the exception, and the periods of endothermy and activity are usually confined to short durations and to specific times (106).

Activity, endothermy, and flight range (107) are also related to the availability of energy supplies during foraging. This is illustrated when one considers that a moth weighing 2 g, for example (with a respiratory rate of 50 ml of oxygen per gram of body weight per hour), must take in on the average at least 2 milligrams of sugar per minute in order to break even, energetically, while foraging. It is apparent that foraging for nectar can only be energetically profitable if many flowers with relatively

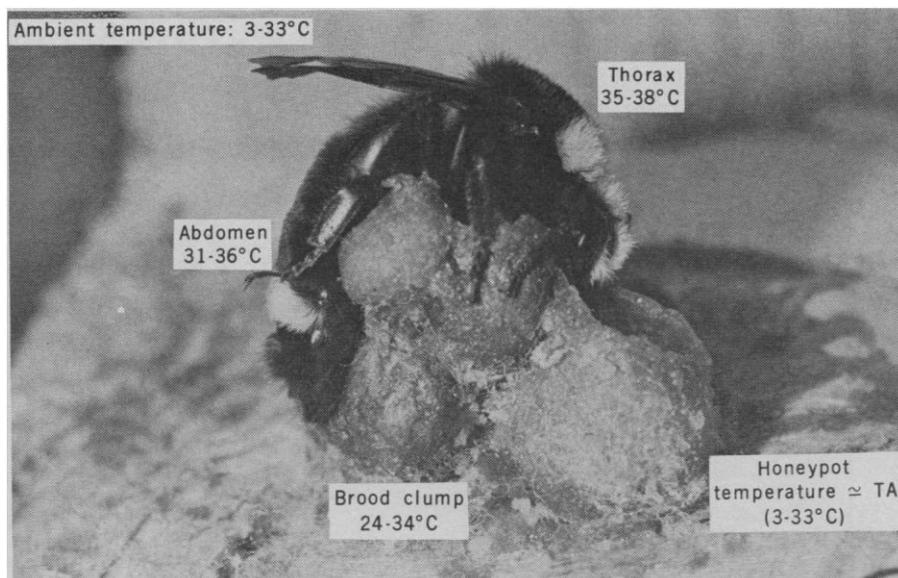


Fig. 8. A *Bombus vosnesenskii* queen incubating her initial brood clump. The bee presses her thorax and abdomen onto the brood clump and faces her honey pot. The honey pot is filled during the daytime, and its contents are consumed in several hours, or a day, depending on ambient temperature (66). In captivity, with an ample supply of sugar syrup, bees may incubate nearly uninterruptedly for several weeks or more (41, 65). The incubation response is initiated by a scent that may be a pheromone deposited by the bee herself (111). There is a thick insulating pile on the thorax and the top of the abdomen, thin insulation on the ventral side of the abdomen, and a narrow petiole between the thorax and the abdomen. This brood clump contained pupae and a second batch of freshly deposited eggs (in bulge below the right tibia). It was maintained at 24° to 34°C at ambient temperatures ranging from 31° to 36°C. The honey pot is not incubated and remains near ambient temperature. The heat is produced in the thorax and flows into the brood clump primarily by way of the abdomen (98), which provides the closest contact.

high-energy food rewards can be visited in a short time (108).

Some of the relationships between energy supplies, energetics of foraging, and thermoregulation have been examined in bumblebees, which derive essentially all of their energy supplies from nectar. Since many outcrossing plants may be under selective pressure to minimize the food rewards of their flowers to increase the frequency of fertilization and cross-pollination (109), the bees foraging from these flowers should, in turn, be under selective pressure to increase their foraging profits. This should select for adaptations that help to maintain a positive energy balance when food supplies are low and that maximize the speed of foraging when nectar supplies are ample. Body temperature is a large factor in both conditions; it can be altered to fit the foraging "strategy" on specific sources of food (72).

Bumblebees must have a thoracic temperature of at least 29° to 30°C before they are capable of maintaining themselves in free flight (71). The metabolic rate associated with the maintenance of a thoracic temperature 25°C above ambient temperature is, as flight, not feasible on a continuous basis in the field unless the bees have access to high-energy fuel. Many situations preclude the large metabolic expenditure of foraging and endothermy (72).

When the flowers from which the bees are foraging are dispersed in space, the bees fly from one flower to the next in rapid succession, and they must therefore continuously maintain their thoracic temperature above 30°C. The bees have the option of either producing heat, presumably at different rates (67, 110), or of ceasing heat production for intervals of seconds or milliseconds when perched on flowers. The willingness to expend energy for thermoregulation is related to the available food supplies in the field (72) as well as in the nest (65). When ample food is available, the energy investment for foraging and thermoregulation is relatively great, and the maintenance of a high thoracic temperature allows the bees to forage rapidly at low ambient temperatures where many other nectar-foraging insects cannot be active. The thermoregulatory virtuosity of bumblebees, which are restricted primarily to the temperate and arctic regions, allows these insects to supply their annual colonies with food that must often be collected from a great variety of flowers under a wide range of weather conditions.

Summary

On the basis of body weight, most flying insects have higher rates of metabolism, and hence heat production, than other animals. However, rapid rates of cooling because of small body size in most cases precludes appreciable endothermy. The body temperature of small flies in flight is probably close to ambient temperature, and that of flying butterflies and locusts is 5° to 10°C above ambient temperature. Many moths and bumblebees are insulated with scales and hair, and their metabolism during flight can cause the temperature of the flight muscles to increase 20° to 30°C above ambient temperature.

Curiously, those insects which (because of size, insulation) retain the most heat in the thorax during flight, also require the highest muscle temperature in order to maintain sufficient power output to continue flight. The minimum muscle temperature for flight varies widely between different species, while the maximum temperature varies over the relatively narrow range of 40° to 45°C. As a consequence, those insects that necessarily generate high muscle temperatures during flight must maintain their thoracic temperature within a relatively narrow range during flight. Active heat loss from the thorax to the abdomen prevents overheating of the flight motor and allows some large moths to be active over a wide range of ambient temperatures. Bumblebees similarly transfer heat from the flight musculature into the abdomen while incubating their brood by abdominal contact.

Many of the larger insects would remain grounded if they did not actively increase the temperature of their flight muscles prior to flight. Male tettigoniid grasshoppers elevate their thoracic temperature prior to singing. In addition, some of the social Hymenoptera activate the "flight" muscles specifically to produce heat not only prior to flight but also during nest temperature regulation. During this "shivering" the "flight" muscles are often activated in patterns different from those during flight. The muscles contract primarily against each other rather than on the wings. However, the rate of heat production during shivering and flight is primarily a function of the action potential frequency rather than of the patterns of activation.

Thermoregulation is a key factor in the energetics of foraging of some of

the flower-visiting insects. The higher their muscle temperature the more flowers they can visit per unit time. When food supplies are ample, bees may invest relatively large amounts of energy for thermoregulation. While shivering to maintain high body temperatures during the short intervals they are perched on flowers (as well as while in the nest), bumblebees often expend energy at rates similar to the rates of energy expenditure in flight. Unlike vertebrates, which usually regulate their body temperature at specific set points, the body temperature of insects is labile. It often appears to be maintained near the lower temperature at which the muscles are able to perform the function at hand. The insects' thermal adaptations may not differ as much from those of vertebrates as previously supposed when size, anatomy, and energy requirements are taken into account.

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