

## Behavioural energetics of some insects

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**Abstract.** Foraging behaviour of insects includes the following energy-requiring processes: (i) location and (ii) gathering. Some insects do incur additional energy cost on transporting and storing food. Energy cost of foraging ranges from 2 to 5 % of the energy gained in bees and wasps. Initiation of flight, in large and insulated insects obligatorily requires 'warming-up' of muscle temperature and maintenance of endothermy by over 20°C above the ambient. Overheating is avoided by pumping the cooler abdominal blood into the hot thorax. Pollinating insects include (i) hovering high-energy foragers, which expend more energy and visit more flowers per unit time and (ii) walking low-energy foragers, which expend less energy and visit few flowers per unit time. Decreasing of "wing loading" is another strategy adopted by saturniids, which do not feed as adults. Most bees forage, when flowers are just blooming, and when they have maximum nectar reward to offer. From the model study on energy cost of oviposition, it has been shown that *Sceliphron violaceum* makes greater and greater effort to complete the process of food provisioning and sealing the larval nest, when it has invested more and more energy on foraging and provisioning spiders to the larviposited young ones.

**Keywords.** Behavioural energetics; foraging behaviour; *Sceliphron violaceum*; high-energy foragers; walking low-energy foragers.

### 1. Introduction

A survey on pertinent literature reveals that there is a large number of publications concerning energetics (Waldbauer 1968; Scriber and Slansky 1981; Muthukrishnan and Pandian 1983) and behaviour (Saunders 1976) of insects. However, only a few publications are available on behavioural energetics of insects. Hence, it is chosen to highlight in this paper only the following aspects: (i) Energy cost of foraging and (ii) Energy cost of oviposition in selected insects.

### 2. Energy cost of food acquisition

In all insects acquisition of food involves a series of behavioural responses; while these responses are related, and perhaps inter-dependent, they are separate processes each under the control of a set of physical and chemical co-ordination. The processes are (i) energy cost of maintaining food supply (*e.g.* ants which maintain aphid population); (ii) energy cost of locating food supply, (iii) energy cost of gathering or catching food, (iv) energy cost of processing of food (*e.g.* conversion of nectar into honey), (v) energy cost of eating food and (vi) energy cost of transporting and storing food (*e.g.* bees) (see Lawton 1973). Of these, processes related to the energy costs of locating and gathering food are important; some insects such as bees and wasps do invest energy on transporting and storing food. Interestingly, much work has been done on the energy cost of transporting and storing food by bees and wasps (Heinrich 1979).

### 2.1 *Endothermy and initiation of flight*

Mechanical efficiency of the flight mechanism of insects is approximately 10–20% (Weis-Fogh 1972). More than 80% of the energy expended during flight is necessarily degraded into heat. Curiously those insects, which are large and insulated, retain 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 required to initiate flight varies over the relatively narrow range of 40–45°C (Kammer and Heinrich 1978). For instance, when the sphinx moth *Manduca sexta* vibrates its wings at the rate of 40 times/sec, and produces about 1 J/min of energy, its thorax is heated to 38°C, and the moth is ready for a take-off (Heinrich and Barthelone 1971). Flight activity and endothermy are thus invariably linked in several insects, and endothermy in flight is a large part an obligatory phenomenon (Heinrich 1974). Temperate insects such as *Bombus* sp. invest quite a lot of energy (2.18 kJ/g thorax/hr) to elevate the thoracic temperature to about 40°C from the ambient temperature of 3–16°C, tropical insects such as *Schistocerca* sp. may require far less energy to elevate its thoracic temperature to over 35°C from the ambient temperature of 20–25°C. Information on the energy cost of endothermy and initiation of flight for tropical insects is almost totally wanting and a comparative study of this aspect for tropical and temperate insects will be rewarding.

### 2.2 *Thermoregulation during flight*

Most insects are small and uninsulated, so that over-heating of the flight musculature is not a general problem. However, build-up of heat is rapid in the flight muscle of some of the large, uninsulated insects. In these insects, the over-heating is avoided by transferring the hot blood from the thorax to the abdomen, when the abdominal heart (dorsal vessel) beats rapidly and pumps the cool blood through the heated thorax. For instance, the thoracic temperature of *Manduca sexta* never exceeds 40°C, and the excess heat is passed into the cool abdomen (26°C), by adjusting the rate of heart beat. More than pre-flight heating and endothermy, cooling and thermoregulation during flight should pose a major problem to the tropical insects. However, no publication is available on this subject for tropical insects.

### 2.3 *Energy cost of foraging*

Measured and calculated energy cost of flying for insects vary over a large continuum. In general most values fall between 418 and 2090 J/g/hr. They represent 50 to 100 fold increases over the resting metabolic rate (Kammer and Heinrich 1978). Necessarily, an insect may forage by hovering at high energy cost for a shorter duration or by walking at low energy cost for a longer duration. Table 1 shows the foraging cost of some bees and wasps, for which information is available. The report by Southwick and Pimentel (1981) is by far the most complete one for the estimation of foraging energetics of insects. A colony consisting of 50000 bees (*Apis mellifera*) is estimated to collect 259 kg nectar worth 1590680 kJ and 24 kg pollen worth 339066 kJ annually by flying a cumulative distance of about 13 million km. At an energy cost of foraging as 13.8 J, i.e. 4.6 J/km

**Table 1.** Foraging costs in some insects.

Predator	Prey	Foraging cost (% acquired food energy)	Reference
<i>Bombus vagans</i>	Nectar	8.2	Heinrich (1972a, b)
<i>Apis mellifera</i>	Nectar and pollen	3.7	Southwick and Pimentel (1981)
<i>Delta conoideus</i>	Caterpillar	2.7*	Muthukrishnan and Senthamilselvan (1985)
<i>Trypoxylon rejector</i>	Spider	1.6*	Muthukrishnan and Senthamilselvan (1985)
<i>Sceliphron violaceum</i>	Spider	5.2*	Pandian and Marian (1985)

\*Considering energy cost of flight as equivalent to 418.6 J/g/hr, a value reported for the wasp *Vespa crabro* by Weis-Fogh (1967).

(Tucker 1970; Dade 1977; Schaffer *et al* 1979), a bee travels over 3 km to collect 370.7 kJ worth nectar and pollen, *i.e.* the energy cost of foraging is 3.7% (Southwick and Pimentel 1981). Similar calculation for the estimation of foraging cost of the bumble bee *Bombus vagans* shows that it spends about 8% of the food energy on acquiring it (Heinrich 1972a, b). Estimations on energy cost of foraging in walking and swimming insects are totally wanting.

Several species of wasps forage on caterpillars or spiders and transport them to the nest to provide food for their larvae. Flying a distance of about 68.4 km, *Trypoxylon rejector* (Sphecidae) predate and transports 190 spiders (7–22 mg each) worth 24.1 kJ in about 11 hr and 36 min for providing food for larvae developing in 9 cells in a nest. Covering a distance of 0.64 km in 4 trips *Delta conoideus* forages and transports 4 caterpillars (71–182 mg each) worth 4.2 kJ in about 2 hr and 57 min for provisioning one cell with a single larva (Muthukrishnan and Senthamilselvan 1985). Investing 1.04 kJ on flight for 2 hr and 30 min, *Sceliphron violaceum* transports spiders worth 13.32 kJ to provide food for its larva developing in an unused hole of electrical socket. Energy cost of foraging in these wasps amounts to 1.6, 2.7 and 5.2% whereas *T. rejector* and *D. conoideus* have to invest another fraction of their respective food energy on nest building activity, *S. violaceum* has avoided the investment of nest building by choosing unused holes.

#### 2.4 Metabolic strategies of flower foragers

In the extremes there are two basic metabolic strategies of harvesting food energy from flowers: (i) Hovering high-energy foragers, which expend more energy and visit more flowers per unit time and (ii) Walking low-energy foragers, which expend less energy and visit few flowers per unit time. Hovering flight places heavy energy demands on insects (836 J/g/hr; Weis-Fogh 1972). This mode of foraging increases the rate of intake of food energy. For example, hovering flies *Bombilius* spp visited 21 flowers of *Houstonia caerulea*/min; whereas *Syrphus* spp which do not hover at flowers, visited

only 5/min. Hovering moths *Hemaris* spp. visited 50 *Kalmia angustifolium* flowers/min, whereas non-hovering *Bombus* spp visited only 15/min. The food rewards of a composite inflorescence for example, are generally individually too small to be economically harvested by hovering. But they can be gathered by a butterfly or a bee that lands on the flowers and reduces its energy expenditure. Low-energy food sources can generally not be harvested by high-energy foragers, which can make much more rapid energy profits from high-energy food sources (Kammer and Heinrich 1978).

Large wings allow insects to fly with a low wing beat frequency and allow some insects to initiate flight without prior endothermic warming-up and to continue flight by gliding; the energy expenditure of locomotion is considerably reduced in such insects. Thus, the third strategy of reducing the energy cost of flying is to decrease 'wing loading' by increasing the wing area per unit body weight. Some saturniid moths and sphinx moths, which do not feed as adults, represent the extreme examples of this kind of strategy. Having relinquished energy intake, and having to rely only on the fixed energy reserves, they have minimized the energy cost of flying by decreasing the 'wing loading' as much as possible (Nachtigall 1966; Pringle 1974).

### 2.5 Blooming times

Flower density is another important factor that affects the energy cost of foraging. Although the flower density is ultimately determined by population density of the plants; it is altered by the time and duration of blooming. Synchronous blooming of the flowers of a species in a given plant population would minimize the temporal and energy costs of flying between plants (Heinrich and Raven 1972). Besides, flower density, (i) daily time of blooming, (ii) amount of energy reward provided, (iii) type of flower product (nectar or pollen or both), and (iv) structures affecting access nectar or pollen are some factors that may modify the energy cost of foraging. Thus, *Bombus* spp., which can forage at ambient temperatures of 5°C or less, forage at an energy cost two or three times greater than that at 26°C (Heinrich 1972a, b). Hence, flowers which are pollinated at low temperatures should either provide more energy rewards than those blooming at high temperatures (perhaps one reason for the low efficiency of honey production in tropical bees) or be denser so that they can be visited in rapid succession (Heinrich and Raven 1972).

While foraging in the early morning at an ambient temperature of 2°C from flowers of manzanita *Arctostaphylos otayensis*, *Bombus edwardsii* (0.1 g) has a thoracic temperature near 37°C. The energy cost of maintaining this thoracic temperature is 3.3 J/min. Each flower of *A. otayensis* provides nectar equivalent to 6.3 J in the early morning and the nectar reward dwindles to 1.3 J by noon. Thus, it is energetically advantageous for *B. edwardsii* to forage in the morning, when there is little competition for nectar, or the rate of nectar production is high (Heinrich and Raven 1972). Likewise, *Chilopsis* flowers provide the largest amount of nectar (2.4 ml/flower) in the early morning and as the result of foraging by *Bombus*, nectar volume declined to 0.3 ml/flower by 0930 hr. By taking into account the time required to suck up nectar and the energy cost of foraging at different times of the day, Witham (1977) calculated that in the early morning *Bombus* that took only the pool nectar was making a net foraging profit of 51 J/min, whereas that which went for both groove and pool nectars, could make a profit of only 41.4 J/min. In a country like India, where oil-seeds are in short supply, research work on pollination ecology of legumes deserves priority.

### 3. Energy cost of oviposition

For want of pertinent publication, the presentation on the energy cost of oviposition has been restricted to information collected by Pandian and Marian (1985) for *Sceliphron violaceum*. Male *S. violaceum* predated, stings, paralyzes spiders belonging to *Argiope pulchella*, *Cyrtophora cicabrosa* and *C. citricola* and deposits them into unused holes of electrical sockets. When the male has deposited spiders equivalent to  $68 \pm 9$  mg in about 35 min the female oviposits a single egg. Subsequently the male continues the process of spider deposition and seals the hole. From experimentations and observations lasting over 3 years, Pandian and Marian (1985) noted that the wasp deposits spiders equivalent to  $200 \pm 10$  mg. The male brings spiders weighing 3–60 mg/trip, and within 10–30 trips, he deposits 200 mg. Marian *et al* (1982) reported that spiders equivalent to 68 and 110 mg are the minimum requirements for the successful completion of larval and pupal stages respectively.

To test the ability of the wasp (i) to recognize its own prey, (ii) to add more prey and (iii) to keep in memory the quantity of prey provided at any stage, the process of spider deposition was interfered by Pandian and Marian (1985) by way of adding or removing

**Table 2.** Interference with the deposited spiders and response of the wasp *Sceliphron violaceum* (from Pandian and Marian 1985).

Deposited spider wt (mg)	Addition (+) or removal (-) of spider (mg)	Wasp response
Before oviposition		
18	+ 58 ± 14	All the wasps recognized and removed the added spiders; 60% wasps continued depositing spiders up to 200 mg but the others abandoned the hole
42	+ 19 ± 3	All the wasps recognized and removed the added spiders; 70% wasps continued depositing spiders up to 200 mg but the others abandoned the hole
After oviposition		
122	+ 83 ± 3	100% wasps recognized and removed the added spiders; 80% wasps closed the hole but the others abandoned the hole
112	+ 21 ± 3	100% Wasps recognized and removed the added spiders; 80% wasps sealed the hole; but the others abandoned the hole
106	+ 19, 63*	100% Wasps recognized and removed the added spiders but abandoned the hole
149	- 38 ± 3	50% Wasps added spiders up to 200 mg and sealed; the others, which have seen the interference, abandoned the hole
Nearing the sealing		
182	+ 74 ± 22	50% Wasps identified and removed the added spiders and sealed the hole; others abandoned the hole
193	+ 17 ± 4	100% Wasps removed the added spiders and sealed the hole
203	- 53 ± 6	Ignored and sealed the hole
201	- 201	Ignored and sealed the hole

\*These spiders were added accommodating them in between the originally deposited spiders.

spiders. Their intention was to study the response of the wasp (i) before oviposition, when spiders weighing less than 68 mg were deposited, (ii) after oviposition, when spiders weighing more than 110 mg were deposited and (iii) before the closure of the hole, when spiders weighing about 180–200 mg were deposited. From their observations presented in table 2, the following may be inferred: (i) an individual wasp is able to recognize its own prey from that of others, (ii) with increasing energy cost of spider deposition and hence food provisioning, a higher percentage of the wasps makes a greater effort to continue and to complete the process of spider deposition, and seal the hole, (iii) the wasp was capable of doing addition and its memory lasted at least for one day and (iv) the wasp was not capable of realising the removal of spiders from the hole. Briefly, greater the energy cost of providing food for its larva, greater is the effort by the wasp to successfully complete oviposition and provision of food for its larva. Energetics of oviposition behaviour is a woefully neglected area and requires immediate attention at least for those pests, which are being considered for biological control.

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