

Time and energy budgets of alfalfa pollinating bees *Megachile nana* Bingh and *Megachile flavipes* Spinola (Hymenoptera: Megachilidae)

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MS received 29 July 1985; revised 11 April 1986

Abstract. Laboratory measurements of physiological energetics were coupled with the field observations on time budget/energy intake of *Megachile nana* and *Megachile flavipes* to estimate the daily energy budget. The energy budget varied from one day to another, and crop to crop. In general, the foraging profitability/attractibility was in the following order for both the species: *Parkinsonia aculeata* > *Medicago sativa* > *Trifolium alexandrinum*. The studies revealed the competitive superiority of *Parkinsonia aculeata* over *Medicago sativa* and *Trifolium alexandrinum*.

Keywords. Energy budget; alfalfa; *Megachile nana*; *Megachile flavipes*; pollination.

1. Introduction

A major challenge facing an animal is the adaptive allocation of time and energy among its various daily activities associated with the self maintenance and reproduction. For ecological studies concerned with the optimization of time and energy budgets the division of efforts among various activities must be known. This necessitates first construction of time budgets and then conversion to appropriate energetic costs. The time and energy budgets of the organisms are quite variable, presumably in relation to varied ecological conditions and physiological costs. Since physiological processes such as metabolic costs, clearly are under short term control of the physical environment. The temporal constraints on control of the distribution of time and energy into various activities are not equally obvious. Most studies of time/energy budgeting have focussed on birds, especially nectarivores (Stiles 1971; Wolf and Hainsworth 1971; Gill and Wolf 1975) because (i) they are usually easy to observe, (ii) their activities are classifiable into discrete categories (e.g. flight, rest and torpor) and (iii) their energy intake is rather easily quantified. Because of their individual nesting habit the solitary bees share many of the similar properties, and provide an excellent workable system for this type of investigation. They can be easily monitored, and categories of behaviour discerned and timed. This paper reports on the time-energy budgets of two alfalfa pollinating bees *Megachile nana* Bingh and *M. flavipes* Spinola, and concentrates on the apparent relationship between the energy intake from the environment and the time/energy budgeting pattern of these bees.

2. Materials and methods

The time-energy budgets of *M. flavipes* and *M. nana* were studied in relation to *P. aculeata*, *M. sativa* and *T. alexandrinum*. To determine differential attractibility and energy budget balance, the following studies were conducted.

2.1 *Sampling of bee population*

The relative abundance of bees was assessed by the method suggested by Linsley *et al* (1952) with some modifications to suit the present investigations. For this purpose, 5 plots each measuring 1 m² were selected and bees were counted for 30 s from each side of the plot.

2.2 *Determination of caloric reward/flower/day*

Inflorescences were bagged with the nylon mesh to exclude all the nectarivores. The nectar from the flowers was sampled with the help of microcapillary pipettes at an interval of 2 h throughout the day. The volume of nectar obtained was measured with the help of 5 λ pipettes and its sugar concentration determined with a hand refractometer. Caloric reward/flower/day was calculated following Heinrich (1975) that 1 mg of sugar irrespective of the type yields 16.74 joules of energy.

2.3 *Rate of foraging/nectar extraction*

The time spent by a bee gathering nectar was recorded using a chronometer with an accuracy of 0.01 s. The number of flowers visited by an individual and time taken to do so was recorded by following their movements as long as possible. Accordingly the number of flowers visited per minute was calculated.

2.4 *Determination of time budgets*

The time budgets of the marked bees were obtained by watching their activities right from commencement to cessation at the experimental nesting sites of the Department of Zoology. All activities were timed with a stop-watch to the nearest of 0.5 s. For data analysis the timed observations were divided into 3 discrete categories.

2.4a *Flying or foraging*: This was the total time the bees spent for collecting nectar, pollen, mud and leaves etc.

2.4b *Activity*: This included the time spent in nest after returning from foraging trips. During this period, the bee remained active and unloaded the pollen mass.

2.4c *Resting*: This period was taken when the activity of the bees ceased and did not come out.

2.5 *Metabolic measurements*

The metabolic expenditures specific to each type of activity (i.e. rest, flight and activity) and temperature were obtained from the regression equations (table 1). The oxygen consumption determinations were made in rest, flight and activity following

Table 1. Respiration rate regressions (temperature vs oxygen consumption).

| Species | State of activity | Regression equation | N | Syx |
|--------------------|-------------------|-----------------------|----|-------------|
| <i>M. nana</i> | Flight | $Y = -31.74 + 2.556x$ | 33 | ± 1.980 |
| | Activity | $-1.214 + 0.06692x$ | 35 | ± 0.039 |
| | Resting | $-0.421 + 0.03616x$ | 32 | ± 0.091 |
| <i>M. flavipes</i> | Flight | $-49.13 + 2.916x$ | 33 | ± 3.410 |
| | Activity | $-0.5280 + 0.03116x$ | 38 | ± 0.029 |
| | Resting | $-0.5638 + 0.0296x$ | 33 | ± 0.004 |

Abrol (1986) at temperatures 20°, 25°, 30°, 35° and 40°C within which foraging occurs, using constant volume Warburg respirometers. The specific procedure followed in each case is detailed below:

2.5a Determination of oxygen consumption during flight: Experiments were conducted during day time in complete darkness so that even in day time if bees are exposed to flickering flashes of light, they get stimulated and initiate flight. Flickering flashes were maintained by connecting 100 watt lamp with the circuit of rotating drum of kymographic apparatus which automatically gave 640 flickering flashes/minute.

2.5b Determination of oxygen consumption during active state: Bees were collected at peak activity hours from the field. The lag period between collection and measurement of oxygen consumption approximately never exceeded more than one hour.

2.5c Determination of oxygen consumption during resting state: Bees are diurnal and their activity remains suspended during night which constitutes their resting period. The respiratory measurements were made during the night time and bees used were collected from the field in the evening and kept in darkness prior to the start of the experiment. The bees were introduced into the Warburg flasks with blunt forceps under red light to which bees are insensitive (i.e. blind). The observations from the respiroscope were recorded using spot light so that the bees may not get disturbed.

The rate of oxygen consumption was calculated on unit weight basis. The oxygen consumption values were converted to energy values by considering that 1 ml of oxygen consumption is equivalent to 20.93 joules of energy expenditure irrespective of the substrate utilized (Heinrich 1975).

2.6 Evaluation of time-energy budget balance

The data were computed following Pyke (1979) with some modifications to suit the present investigations. To compute the time-energy budget balance following variables were defined

T = Total available time for various activities (i.e. 24 h).

T_f = Total foraging time/day.

T_a = Total active time/day.

T_r = Total resting time/day.

C_f = Rate of energy expenditure while foraging (joule/day).

C_a = Rate of energy expenditure while active (joule/day).

C_r = Rate of energy expenditure while resting (joule/day).

Thus it follows that

$$T = T_f + T_a + T_r \quad (1)$$

and

$$C = C_f \times T_f + C_a \times T_a + C_r \times T_r \quad (2)$$

Where C = total energetic cost (joule/day).

Gross energetic gain of the bees is given by

$$G = \mu r T_f. \quad (3)$$

Where r = the rate at which a bee visits flowers for nectar while foraging.

μ = Standing crop of nectar (average energy/flower/day).

T_f = Total foraging time.

Thus by subtracting (2) from (3) we get

$$E = \mu r T_f - C_f T_f + C_a T_a + C_r T_r. \quad (4)$$

Where E = net energy balance (joule/day).

3. Results

The data in table 2 show the time-energy budgeting pattern of *M. nana*. It was found that *M. nana* on an average spent 184 min in foraging (nectar pollen etc.), 194·40 min

Table 2. Time-energy budget of *M. nana*/day.

| Date of observation | Proportion of time spent (min) | | | Average temperature (°C) | |
|---------------------|--------------------------------|-------------|--------------|--------------------------|-------|
| | Foraging (Tf) | Active (Ta) | Resting (Tr) | Day | Night |
| April 1984 | | | | | |
| 15 | 163 | 217 | 1060·00 | 30·30 | 21·60 |
| 17 | 181 | 205 | 1054·00 | 31·00 | 22·00 |
| 24 | 202 | 222 | 1016·00 | 31·20 | 22·30 |
| 26 | 180 | 183 | 1077·00 | 33·50 | 21·50 |
| 28 | 194 | 170 | 1076·00 | 33·00 | 21·40 |
| Average | 184 | 199·40 | 1056·40 | 31·80 | 21·76 |

Energy budget of *M. nana*/day (average weight of bee = 27·17 mg, n = 90).

Proportion of energy expenditures (joule/min/bee)

| Foraging (Cf) | Active (Ca) | Resting (Cr) |
|---------------|-------------|--------------|
| 0·4692 | 0·0086 | 0·0034 |

Energy expenditure/bee/day $C = C_f \times T_f + C_a \times T_a + C_r \times T_r$

$= 0·4692 \times 184·00 + 0·0086 \times 199·40 + 0·0034 \times 1056·40 = 91·63$ joule.

Thus $C = 91·63$ joule/bee/day

Note: (i) Calculation based on combined time budget figure.

(ii) Calculation based for each category of the time budget at the temperatures indicated.

in nesting/active state and 1056.40 min in resting/day. The energy expenditures at the temperatures 31.8°C (foraging and activity) and 21.76°C (resting) as determined from the rate of oxygen consumption was found to be 91.63 joule/bee/day. However, *M. flavipes* under similar conditions spent 216.00 min in foraging, 233.60 min in activity/nesting and 990.40 min in resting. The energy expenditure was found to be 146.38 joule/bee/day (table 3).

The data on the energy rewards offered by their host plants and the time spent in extracting these rewards for both the species are presented in table 4. In general, *P. aculeata* produced 2.90 ± 0.45 joule/flower/day, *M. sativa* 1.20 ± 0.12 joule/flower/day while *T. alexandrium* produced 0.393 ± 0.057 joule/flower/day. The

Table 3. Time-energy budget of *M. flavipes*/day.

| Date of observation | Proportion of time spent (min) | | | Average temperature (°C) | |
|---------------------|--------------------------------|-------------|--------------|--------------------------|-------|
| | Foraging (Tf) | Active (Ta) | Resting (Tr) | Day | Night |
| April 1984 | | | | | |
| 15 | 188.00 | 247.00 | 1005 | 30.30 | 21.60 |
| 17 | 198.00 | 218.00 | 1024 | 31.00 | 22.00 |
| 24 | 222.00 | 249.00 | 969 | 31.20 | 22.30 |
| 26 | 243.00 | 214.00 | 982 | 33.50 | 21.50 |
| 28 | 229.00 | 239.00 | 972 | 33.00 | 21.40 |
| Average | 216.00 | 233.60 | 990.4 | 31.80 | 21.76 |

Energy budget of *M. flavipes*/day (average weight of bee = 43.72 mg, n = 90).

Proportion of energy expenditure (joule/min/bee)

| Foraging (Cf) | Active (Ca) | Resting (Cr) |
|---------------|-------------|--------------|
| 0.6647 | 0.00704 | 0.00118 |

Energy expenditure/bee/day $C = Cf \times Tf + Ca \times Ta + Cr \times Tr$
 $= 0.6647 \times 216.00 + 0.00704 \times 233.60 + 0.00118 \times 990.40 = 146.38$ joule.

Thus $C = 146.38$ joule/bee/day.

Note: (i) Calculation based on combined time budget figure.

(ii) Calculation based for each category of the time budget at the temperatures indicated.

Table 4. Energy reward/flower/day and number of flowers visited/min by *M. flavipes* and *M. nana*.

| Species | Joule/flower/day ^a | Flowers visited/min ^b | |
|-----------------------|--|-------------------------------------|------------------------------------|
| | | <i>M. flavipes</i> | <i>M. nana</i> |
| <i>M. sativa</i> L. | 1.20 ± 0.128 (1.028 - 1.411) | 12.55 ± 1.83 (10.52 - 15.20) | 8.55 ± 2.91 (6.52 - 11.30) |
| <i>P. aculeata</i> | 2.90 ± 0.459 (2.140 - 3.328) | 9.07 ± 2.74 (6.92 - 12.32) | 5.40 ± 0.89 (3.45 - 6.80) |
| <i>T. alexandrium</i> | 0.393 ± 0.057 (0.3110 - 0.4759) | 16.89 ± 2.35 (14.81 - 19.87) | 12.42 ± 3.09 (8.45 - 15.41) |

^aMean \pm SD of 200 observations. ^bMean \pm SD of 35 observations.

rate of extraction of caloric rewards also varied from crop to crop and species to species. *M. flavipes* on an average visited 9.07 ± 2.74 flowers of *P. aculeata*, 12.55 ± 1.83 flowers of *M. sativa* and 16.89 ± 2.35 flowers of *T. alexandrium*/min while this rate was found to be 5.40 ± 0.89 , 8.55 ± 2.91 and 12.42 ± 3.09 , respectively for *M. nana*.

The energy budget resulting from the energy intake and expenditure is presented in table 5. The results highlighted that *P. aculeata* was most profitable as the bees could ensure a greater reward than the other two crops. The foraging profitability was in the following order: *P. aculeata* > *M. sativa* > *T. alexandrium*. The attractability of the bees, as evidenced by their foraging population on these crops, also exhibited the same pattern (table 6). The studies revealed that in competition for pollinators *P. aculeata* had an edge over *M. sativa*, while the latter was preferred than *T. alexandrium*. It is thus clearly evident that in competition with *P. aculeata* the other two crops are at disadvantage.

4. Discussion

Energy requirement of the bees and caloric rewards offered by the flowers determine whether or not an animal can be a dependable flower visitor (Heinrich and Raven 1972; Heinrich 1975). Rewarding system developed by flowers enable bees to make distinction between them and closely related species or ecotypes. This has resulted in

Table 5. Energy intake, expenditure and budget balance.

| Bee species | Plant species | Energetic gain (joule) | Energetic cost (joule) | Energy balance (joule) |
|--------------------|-----------------------|------------------------|------------------------|------------------------|
| <i>M. nana</i> | <i>P. aculeata</i> | 2843.63 | 91.63 | 2752.00 |
| | <i>M. sativa</i> | 1630.02 | 91.63 | 1538.39 |
| | <i>T. alexandrium</i> | 716.97 | 91.63 | 625.34 |
| <i>M. flavipes</i> | <i>P. aculeata</i> | 1442.20 | 146.38 | 1295.82 |
| | <i>M. sativa</i> | 945.99 | 146.38 | 799.61 |
| | <i>T. alexandrium</i> | 449.11 | 146.38 | 302.73 |

Note: Since solitary bees collected both nectar and pollen in a foraging trip therefore, to minimize error foraging time was halved for calculation of energy intake.

Table 6. Comparative abundance of bees.

| Bee species | Hour of observation | Abundance of bees (5 m ²) | | |
|--------------------|---------------------|---------------------------------------|-------------------------------|------------------------------------|
| | | <i>P. aculeata</i> ^a | <i>M. sativa</i> ^a | <i>T. alexandrium</i> ^a |
| <i>M. flavipes</i> | 10:00 | 35.30 ± 5.15 | 23.50 ± 3.80 | 7.50 ± 2.15 |
| | 20:00 | 44.40 ± 4.80 | 20.10 ± 2.79 | 13.80 ± 2.19 |
| | 14:00 | 30.80 ± 4.79 | 15.70 ± 1.85 | 10.40 ± 1.79 |
| | 16:00 | 12.70 ± 2.70 | 5.20 ± 3.15 | — |
| <i>M. nana</i> | 10:00 | 27.30 ± 3.90 | 12.90 ± 2.59 | 5.30 ± 1.30 |
| | 12:00 | 35.80 ± 4.10 | 15.20 ± 3.11 | 10.20 ± 1.97 |
| | 14:00 | 38.10 ± 3.75 | 13.20 ± 2.17 | 11.40 ± 1.87 |
| | 16:00 | 8.30 ± 1.80 | 5.80 ± 1.70 | 1.33 ± 0.40 |

—indicates no bee activity. ^aMean ± SD of 5 observations.

a mutualistic development of a co-evolutionary process and have evolved co-partnership between the two (Leppik 1977). The interdependence of pollinating bees with flowers depend much upon their energy requirement and the balance sheet they share with flowers (Heinrich and Raven 1972). The pollinators with high energy requirements may not forage at the flowers, which provide low caloric rewards (Heinrich 1983). *P. aculeata* provided the maximum caloric reward/flower/day followed by *M. sativa* and *T. alexandrium*. The former crop/plant attracted the bees in large numbers followed by the latter two crops. This differential attractability was probably due to the caloric rewards. *M. sativa* was intermediate in attracting foraging population and had an competitive edge over *T. alexandrium*. The bees visited *M. sativa* during early hours of the day, thereafter the foraging population shifted to *T. alexandrium*. This was probably due to the depletion of nectar in *M. sativa* which compelled the foraging population to visit even low rewarding flowers of *T. alexandrium*. Similar results were obtained by Heinrich (1975) who reported that the bees may visit low rewarding flowers, when the nearby resources are depleted or become sparse. Jain and Kapil (1980) reported that *P. aculeata* had an edge over *M. sativa* in attracting foraging population of these bees. They reasoned that presence of maltose component in nectar of *P. aculeata* (not present in *M. sativa* and *T. alexandrium*) was the main cause of attracting large number of bees. The present investigations however do not support their contention, since according to Rowley (1976), there is no biochemical pathway for the synthesis of maltose in nectar yielding plants, wherever it is present, arises as a bacterial/fungal contaminant and/or due to the glucophilic enzymes introduced by the insects. Therefore, to assign the attractability to this foreign element seems to be inappropriate. In the present investigations, besides the physical factors the attraction of bees was attributed to the caloric rewards offered by the flowers and foraging profitability resulting there from. This view is also supported by their comparative abundance on these crops under similar conditions (table 6).

The above studies examine some of the features of the economical crop plants competing for pollinators, however, future research is needed on related aspects like (i) factors effecting yield of nectar in *M. sativa*, (ii) genetic manipulations and selection of varieties with attractive petals, (iii) to study the pests and parasites of bees, and (iv) to increase their population through management practices. These studies if carefully undertaken are likely to generate better understanding for utilization of these bees as perspective pollinators.

Acknowledgements

The author wishes to thank Dr R P Kapil, for providing necessary facilities and Indian Council of Agricultural Research, New Delhi for financial assistance in the form of a Fellowship.

References

- Abrol D P 1986 Metabolic expenditures of *Megachile nana* Bingh and *M. flavipes* Spinola (Hymenoptera: Megachilidae) as determined by rate of oxygen consumption; *J. Anim. Morphol. Physiol.* 33 (in press)
- Gill F B and Wolf L L 1975 Economics of feeding territoriality in the golden winged Sunbird; *Ecology* 56 333-345

- Heinrich B 1975 Energetics of pollination; *Annu. Rev. Ecol. Syst.* **6** 137–171
- Heinrich B 1983 Insect foraging energetics; in *Handbook of Experimental Pollination Biology* (ed) C E Jones and R J Little (New York: Scientific and Academic Press) p 187
- Heinrich B and Raven P H 1972 Energetics and pollination; *Science* **176** 597–602
- Jain K L and Kapil R P 1980 Foraging rhythm of Megachilid bees in relation to the flowering of *Medicago sativa* L. and *Parkinsonia aculeata* L.; *Indian Bee J.* **42** 35–38
- Leppik E E 1977 *Floral evolution in relation to pollination ecology* (New Delhi: Today and Tomorrow's printers and publishers) 104–108
- Linsley E G, Macswain J W and Ray F S 1952 Outlines for ecological life histories of solitary and semisocial bees; *Ecology* **33** 558–567
- Pyke G H 1979 The economics of territory size and time budget in the golden winged Sunbird; *Am. Nat.* **114** 131–145
- Rowley F A 1976 The sugars of some Philippine nectars; *J. Apic. Res.* **15** 19–22
- Stiles F G 1971 Time, energy and territoriality of the Anna humming bird (*Calypste anna*); *Science* **173** 818–821
- Wolf L L and Hainsworth F R 1971 Time and energy budgets of territorial humming bird; *Ecology* **52** 980–988