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Energy Intake and Expenditure in *Andrena Ilerda* and *Andrena leaena* (Hymenoptera: Andrenidae)

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Energy relationships of *Andrena ilerda* and *A. leaena* (Hymenoptera: Andrenidae) were studied in relation to various rapeseed and mustard species (*Brassica campestris* var toria, *B. juncea*, *B. napus* and *B. carinata*). Laboratory measurements of physiological energetics were compared with field observations on time budget-energy intake to infer daily energy budget balance. The energy balance varied from one day to another and from crop to crop but in general, the foraging profitability for both the species of bees was in the order: *B. napus* > *B. carinata* ≥ *B. juncea* > *B. campestris* var toria. *B. napus* appears to be competitively superior as a forage crop.

Key Words: Energy, *Andrena ilerda*, *A. leaena*, Rapeseed and mustard, Pollination

Introduction

Rapeseed and mustard are by far the most important oilseed crops of India. They are grown in an area of 4.4 million hectares (Yadav, 1987). Adequate cross-pollination is vital for any significant increase in seed production (Mohammad 1935, Bisht et al. 1983, Sihag 1986). Over 100 species of insects have been reported to visit these crops (Mohammad 1935, Kapil et al. 1971). Of these, *Andrena ilerda* and *A. leaena* are the most important and efficient pollinators of rapeseed and mustard crops (Mohammad 1935, Kapil et al. 1971, Abrol 1985, Sihag 1986). Besides physical and biological factors such as color, shape and odour (Faegri & Vander Pijl 1979), energy requirements of bees and the energy rewards offered by the flowers determine to a large extent whether or not a given bee species can be a dependable flower visitor (Heinrich & Raven 1972, Heinrich 1975, 1983, Abrol 1985, 1986, 1987, 1989, Abrol et al. 1988). The mutualistic interactions between bees and their forage depend upon the energy balance resulting from the energy requirement-reward system (Abrol 1985, 1986). Though information is available on foraging rates, energy intake and foraging costs of various pollinators (e.g. Wolf & Hainsworth 1971) there has been little attempt to obtain an overall picture of all these factors affecting foraging energetics. In most pollinator species it is difficult to measure with precision their foraging efficiencies under natural conditions, due to problems associated with discerning their daily activities and determining energy expenditure specific to each type of activity. Many studies of foraging economics have focussed on birds particularly nectarivores (Stiles 1971, Wolf & Hainsworth 1971, Gill & Wolf 1975) as they are usually easy to observe and their activities are readily classifiable into discrete categories (e.g. flight, rest and torpor, and because their energy intake is rather easily quantified. Solitary bees because of their individual nesting habits, share many biological

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properties with birds and provide an alternative system for this type of investigation. They can be easily watched and categories of behaviour discerned and timed. This paper reports on the energy balance of two soil nesting bees, *Andrena ilerda* and *A. leaena* and concentrations on the apparent relationship between the energy intake from the environment and the time-energy budgeting pattern of these bees.

Material and Methods

The energetic relationships of *Andrena ilerda* and *A. leaena* were studied in relation to their foraging upon *Brassica napus, B. carinata, B. juncea* and *B. campestris* var toria. To determine differential attractability and energy balances the studies were conducted under the following sub-headings.

Sampling of bee populations

The relative abundance of bees was assessed, using the methodology of Abrol (1985), at Oilseed Farm of Haryana Agricultural University, Hisar, India (28°N and 76°E). Five plots each measuring $1m^2$ were selected and the number of bees visiting each plot were counted for 30 seconds.

Determination of energetic reward/flower/day

Inflorescences were bagged with nylon mesh to exclude all the nectarivorous insects. The nectar from the flowers was sampled with the help of microcapillary pipettes at an interval of 2 hrs throughout the day. The volume of nectar obtained was measured with the help of 5λ pipettes and its sugar concentration determined with a hand refractometer (Toshniwal, Model, 1093). Caloric reward/flower/day was calculated following Heinrich (1975) assuming that 1 mg of sugar, irrespective of the type, yields 16.74 joules of energy (1 cal = 4.186 joules).

Rate of foraging/nectar extraction

The time spent by a bee gathering nectar was recorded using a chronometer with an accuracy of 0.01 sec. The number of flowers visited by an individual land time taken to do so was recorded by following their movements as long as possible. Based on this data, the number of flowers visited/minute was calculated.

Determination of time budgets

For this purpose, several active nests of *A. ilerda* and *A. leaena* in the soil were selected and their bees marked for individual recognition following Abrol (1985). For this purpose the bees were kept in a petridish and pressed slightly under a wire gauze mesh to make them stationary and marked with the nail polish on their thorax through wire gauze mesh with a fine camel hair brush. Different colours were used for different bees. Bees whose antennae, eyes and wings were spoiled with nail polish were discarded to avoid error. The diurnal time budgets of the marked bees were obtained by watching their activities from the time bees left until they returned to their nests. All activities were timed with a stopwatch to the nearest of 0.5 sec. For data analysis the timed observations were divided into discrete categories.

(a) *Flying or foraging:* This was the total time the bees spent collecting nectar and pollen.

(b) *Activity:* This included the time spent in the nest after returning from the foraging trips.

(a) *Resting:* This was the period when the field activity of the bees ceased and did not come out.

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 (figure 1). The oxygen consumption determinations were made at rest, during flight and activity following Abrol (1986) at temperatures of 20°, 25°, 30°, 35° and 40°C (the period within which foraging occurs), using contant volume Warburg respirometers. The specific procedure followed in each case is detailed below:

Determination of oxygen consumption during flights: 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/minutes.

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.

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).

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 the following variables were defined:

T = Total available time for various activities (i.e. 24 hrs)
Tf = Total foraging time/day
Ta = Total active time/day
Tr = Total resting time/day
Cf = Rate of energy expenditure while foraging (joules/day)
Time-energy budget of bees

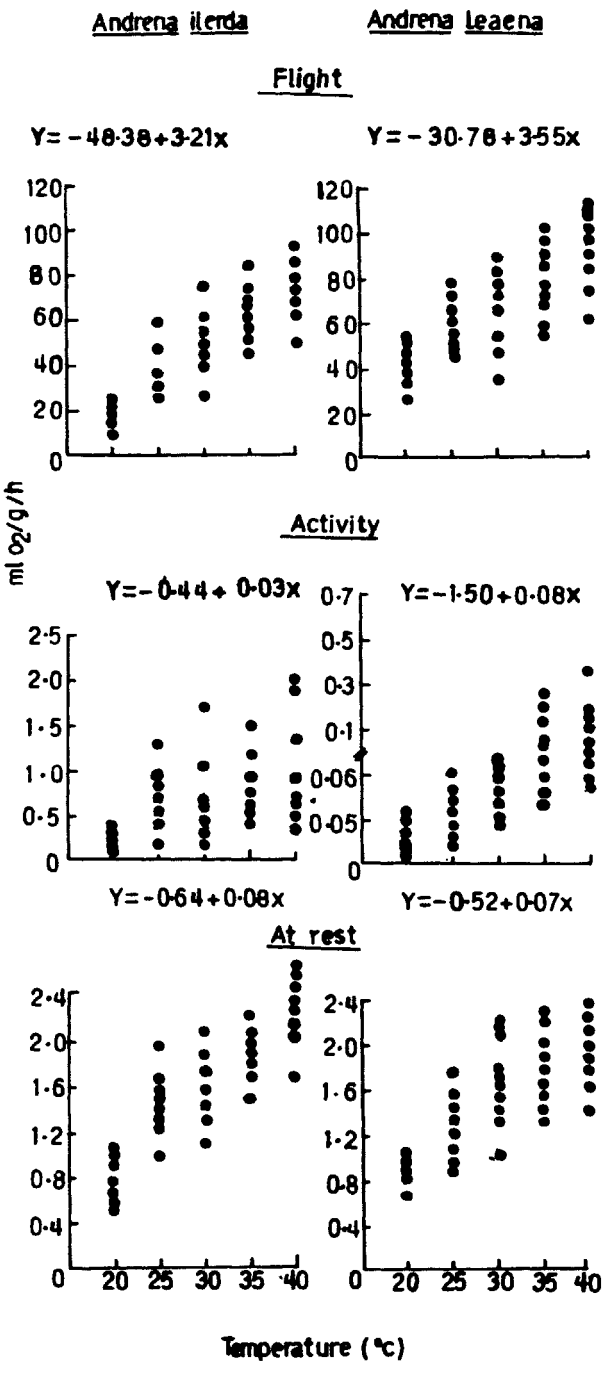

Figure 1 Oxygen consumption in relation to temperature and state of activity

Table 1 *Time energy budget of A. ilerda*

Date of observation	Proportion of time spent (min.)			Average temperature (°C)	
	Foraging (Tf)	Activity (Ta)	At rest (Tr)	Day	Night
November, 1983					
17	65.00	83.00	1292.00	18.60	12.60
25	73.00	104.00	1223.00	19.20	13.50
December, 1983					
6	54.00	43.00	1343.00	18.50	12.00
13	77.00	45.00	1318.00	19.50	13.50
23	111.00	52.00	1277.00	18.76	10.90
January, 1984					
3	122.00	36.00	1282.00	20.20	11.20
12	136.00	39.00	1265.00	19.40	13.50
22	89.00	26.00	1325.00	19.80	12.50
Average	90.87	53.50	1290.62	19.35	12.45

Energy budget of *A. ilerda*/day
(Average weight of bee = 65.40 ± 4.89 mg, n = 125)
Proportion of energy expenditure (joules/min/bee)

Foraging (Cf)	Active (Ca)	Resting (Cr)
1.015	0.0344	0.007183

Energy expenditure/bee/day C = Cf.Tf + Ca + Ta + Cr.Tr = 92.23 + 1.840 + 9.270 = 103.34 joules.
Thus C = 103.34 joules/bee/day.

Note: I. Calculation based on combined time budget data.
II. Calculation based for each Category of the time budget at the temperature indicated.

Ca = Rate of energy expenditure while active (joules/day).
Cr = Rate of energy expenditure while resting (joules/day)

Thus it follows that $T = Tf + Ta + Tr$. . . (1)
and $C = Cf \times Tf + Ca \times Ta + Cr \times Tr$ . . . (2)

where C = Total energetic cost (joules/day)

Gross energetic gain of the bees is given by

$G = \mu rTf$ . . . (3)

where r = The rate at which a bee visits flowers for nectar while foraging

μ = standard crop of nectar (average energy/flower)

Tf = Total foraging time (Since solitary bees collected both nectar and pollen in a foraging trip therefore, to minimize error foraging time was halved for calculation of energy intakes)

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

$E = \mu rTf - (Cf \times Tf + Ca \times Ta + Cr \times Tr)$

where E = Net energy balance (joules/day)

Table 2 *Time energy budget of **A. leaena***

Date of observation	Proportion of time spent (min.)			Average temperature (°C)	
	Foraging (Tf)	Activity (Ta)	At rest (Tr)	Day	Night
November, 1983					
17	55.00	84.00	1291.00	18.50	12.60
25	53.00	83.00	1304.00	19.20	13.50
December, 1983					
6	35.00	47.00	1358.00	18.50	12.00
13	68.00	101.00	1271.00	19.50	13.50
23	70.00	56.00	1314.00	19.76	10.90
January, 1984					
3	102.00	52.00	1286.00	20.20	11.20
12	100.00	42.00	1298.00	19.40	13.50
22	83.00	28.00	1329.00	19.80	12.50

Energy budget of *A. leaena*/day
(Average weight of bee = 43.80 ± 4.38, n = 110)
Proportion of energy expenditure (joules/min/bee)

Foraging (Cf)	Active (Ca)	Resting (Cr)
0.5810	0.2423	0.004972

Energy expenditure/bee/day $C = Cf.Tf + Ca.Ta + Cr.Tr = 0.5810 \times 70{,}75 + 0.2423 \times 62.87 + 0.004972 \times 1306.37 = 41.10 + 15.23 + 6.495 = 62.82$
Thus C = 62.82 joules/bee/day

Note: 1. Calculation based on combined time budget data.
2. Calculation based for each Category of the time budget at the temperature indicated.

Table 3 *Energy reward/flower/day and number of flowers visited/minute by **A. ilerda** and **A. leaena***

Species	Joules/flower/day +	Flowers visited/minute	
		A. ilerda	*A. leaena*
Brassica campestris	1.454 ± 0.190	10.83 ± 1.59	9.02 ± 1.88
Var toria	(1.201-1.486)		
B. juncea	3.135 ± 0.480	14.75 ± 2.15	11.25 ± 2.23
	(2.887 − 3.286)		
B. napus	8.401 ± 0.551	13.25 ± 2.89	10.28 ± 1.97
	(7.911-8.999)		
B. carinata	7.421 ± 1.280	12.75 ± 2.01	9.87 ± 1.37
	(7.201 ± 8.442)		

Mean ± S.D. of 200 observations
Mean ± S.D. of 40 observations

Table 4 *Energy intake, expenditure and balance*

Bee species	Plant species	Energetic gain	Energetic cost (joules)	Energy balance (joules)
A. ileria	*B. campestris* var *toria*	715.45	103.34	602.11
	B. juncea	2100.97	103.34	1997.63
	B. napus	5057.51	103.34	4954.17
	B. carinata	4298.95	103.34	4195.61
A. leaena	*B. compestris* B. var *toria*	463.94	62.82	401.12
	B. juncea	1274.83	62.82	1184.81
	B. napus	3055.06	62.82	2992.24
	B. carinata	2585.80	62.82	2522.98

Results

The data presented in table 1 and 2 show the time-energy budget of *Andrena ilerda* and *A. leaena* respectively. The former species was found to spend more time and expand more energy in foraging than the latter. The energy reward offered by the plants and time spent in extracting these rewards for both the bee species is presented in table 3. The energy reward offered by the plant species was in the order: *B. napus* > *B. carinata* > *B. juncea* > *B. campestris* var toria. The rate of extraction of these rewards varied from one crop to another and species to species.

The theoretical energy balance resulting from energy intake and expenditure is presented in table 4. The results indicate that foraging on *B. napus* was most profitable as the bees could make higher energetic balance than the other three cross in bloom. The foraging profitability was in the order: *B. napus* > *B. carinata* > *B. juncea* > *B. campestris* var toria for both the bee species. The studies revealed that in competition for potential pollinators *B. napus* had an edge over *B. carinata*, while the latter was more preferred than *B. juncea* and *B. campestris* var toria. The attractability of the bees as evidenced by their foraging population on these crops also exhibited the same pattern (table 5). It thus appears in competition with *B. napus*, the other three crops are at a disadvantage in attracting pollinating andrenid bees.

Discussion

Pollinators differ in their energy requirements, from low energy groups such as ants and flies, to higher energy requiring endothermic group of mammals and birds (Heinrich 1983). Rewarding systems evolved by the flowering plants may favour discrimination by bees between them and closely related species or ecotypes. This has resulted in the mutualistic development of a co-evolutionary partnership between the two (Leppik 1977). The pollinators with high energy requirements may not forage at flowers which provide low caloric rewards (Heinrich 1975, 1983, Abrol 1985, 1986). The differential attractability of different *Brassica* spp. appears to be due to different caloric rewards. This view is supported by the comparative abundance of bees on these crops.

Table 5 *Population dynamics of* ***Andrena ilerda*** *and* ***A. leaena*** *on different rapeseed-mustard crops during different hours of the day*

Plant Species	Observation time (h)	Bee abundance/5m² (X ± S.D., n = 40) 10°°	12°°	14°°	16°°
			Andrena ilerda		
B. napus		15.80 ± 4.11	28.70 ± 6.20	30.50 ± 6.89	14.40 ± 3.16
B. carinata		6.72 ± 3.17	20.70 ± 6.20	27.95 ± 5.27	8.06 ± 3.27
B. juncea		4.50 ± 2.87	17.20 ± 5.11	20.30 ± 4.87	5.15 ± 2.11
B. campestris var *toria*		2.20 ± 1.89	8.60 ± 3.01	12.70 ± 3.87	3.40 ± 2.10
			A. leaena		
B. napus		13.20 ± 3.17	27.20 ± 4.15	25.40 ± 6.79	1.20 ± 0.85
B. carinata		9.50 ± 3.08	18.30 ± 5.10	14.80 ± 4.80	5.60 ± 1.87
B. juncea		5.40 ± 1.89	10.20 ± 2.80	7.30 ± 1.87	3.80 ± 0.97
B. compestris		1.20 ± 0.85	5.60 ± 1.87	5.40 ± 2.20	2.10 ± 1.01

The bright yellow colour and reflective pattern of *B. napus* flowers may possibly be responsible for greater attraction of bees to these crops. Jones & Buchmann (1974) and earlier concluded that the yellow, highly reflective pattern of *Parkinsonia aculeata* flowers was one of the factors promoting attraction of bees. However, more research is needed on nectar yield, bee abundance and attraction of bees to flowers before economic practices such as genetic manipulations and selection of varieties with different petal colours can be recommended.

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References

Abrol D P 1985 Analysis of biophysical interactions in causing foraging behaviour of some bees—A study in bioenergetics. Ph.D. thesis, Haryana Agricultural University, Hisar, India: p. 286

——— 1986 Time and energy budgets of alfalfa pollinating bees *Megachile nana* Bingh and *Megachile flavipes* Spinola (Hymenopera: Megachilidae). *Proc. Indian Acad. Sci. (Anim. Sci.)* **95** 579-586

——— 1987 Influence of thermal and energetic constraints on the pollination activity of *Xylocopa pubescens* Spinola (Hymenoptera: Anthophoridae); *Environ. Ecol.* **5** 90-93

——— 1990 Energetics of nectar production in some apple cultivars as a predictor of floral choice by honeybees. *Tropical Ecology* **31** 116-122

———, Sihag R C and Kapil R P 1998 Physiological adaptations of subtropical bees in relation to energy intakes; *Res. Dev. Reporter* **5** 68-70

Bisht D S, Naim M and Mehrotra K N 1983 Studies on the role of honeybees in rapesed production; in *Proceedings of 2nd International Conference on Apiculture in Tropical climates*, K N Mehrotra (Ed.) Indian Agricultural Research Institute, New Delhi, pp. 491-496

Faegri K and Vander Pijl L 1979 *The Principles of Pollination Ecology*, 3rd edn. (New York: Pergamon Press)

Gill F B and Wolf L L 1975 Economics of feeding territorality in the golden winged Sunbird; *Ecology* **56** 333-345

Heinrich B 1975 Energetics of pollination; *Ann. Rev. Ecol. Syst.* **6** 137-171

——— 1983 Insect foraging energetics; in *Handbook of Experimental Pollination Biology* ed. C E Jones and R J Little (New York: Scientific and Academic Editions) 187 pp

——— and Raven P H 1972 Energetics and pollination ecology; *Science* **176** 597-602

Jones C E and Buchmann S L 1974 Ultrafloral-floral patterns as functions orientation cues in Hymenopterous system; *Anim. Behav.* **22** 481-485

Kapil R P, Kumar S and Atwal A S 1971 Insect pollinators of rapeseed and mustard; *Indian J. Ent.* **33** 61-66

Leppik E E 1977 *Floral Evolution in Relation to Pollination Ecology* 104-108 (New Delhi: Today and Tomorrow's Printers and Publishers)

Mohammad A 1935 Pollination studies in toria (*Brassica napus* L. Var dicholoma, Prain) and sarson (*Brassica campestris* L. Var sarson, Prain); *Indian J. Agric. Sci.* **5** 125-154

Pyke G H 1979 The economics of territory size and time budget in the golden winged Sumbird; *Am. Nat.* **114** 131-145

Sihag R C 1986 Insect pollination increases seed production in cruciferous and umbolliferous crops; *J. apic. Res.* **25** 121-126

Stiles F G 1971 Time, energy and territoriality of the humming bird (*Calypte 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

Yadav I S 1987 Rapeseed-mustard a potential crop for Haryana; *Indian Farming* **37** 18-20