Energy Intake Efficiency as a Determinant of Foraging Decisions in Honeybees *Apis dorsata* and *A. florea*

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Abstract

Foraging behaviour of two honeybee species *Apis dorsata* and *A. florea* was studied in relation to energy production rates of *Brassica campestis var toria*, *Coriandrum sativum*, and *Foeniculum vulgare*. Energy produced ranged from a minimum of 0.0176 ± 0.01 joules per flower per day (*C. sativum*) to a maximum of 0.4275 ± 0.14 joules per flower per day (*B. campestis var toria*). *A. dorsata* preferred *B. campestis var toria* compared to other two crops. As the *A. dorsata* could harvest more energy compared to *A. florea* which mostly relied upon low rewarding *C. sativum*, and *F. vulgare*. The foraging population of both the bee species also exhibited the same pattern. Evidently, such preferences seem to be associated with the foraging profitability of the pollinators.

Key words: Energy rewards, *Apis dorsata*, *Apis florea*, Foraging rates, Benefits, Foraging behavior

INTRODUCTION

Physical attributes of flowers such as colour, shape and odour are well known features that attract pollinators (Faegri and Vander Pijl, 1966; Srinivasan, 1994). One source of variation in foraging cues between different plants is the nectar, which may provide variety of stimuli. It provides nourishment for animals ranging from mites to man (Colwell, 1973). Flower visitors and host plant relationship depends upon the energy demands and the quantity of food it can harvest from flowers, thus resulting in mutal adaptations between the two (Churchill and Christenson, 1970; Hainsworth and Wolf, 1972; Heinrich and Raven, 1972; Hickman, 1974; Hocking, 1953; Stiles, 1975). Nectar is the potential energy reward provided by the flowers to their visitors. It has been found to be very significant parameter that decisively shapes the behaviour of pollinators in relation to their energy demands (Abrol,

1986, 1992; Heinrich & Raven, 1972; Heinrich, 1975a).

Pollinator - plant interaction has co-evolved as reciprocal selective factors shaping the behaviour, physiology and ecology of each other. In the course of evolution, there has been a competition between the plants for pollinators and between the pollinators for plants (Heinrich and Raven, 1972). The "energetics" approach has been a major focus of behavioural ecologists for studying foraging behaviour of insect visitors of flowering plants (Krebs and McCleery, 1983; Schaffer *et al.*, 1979; Schmid-Hempel, 1984; Southwick and Pimental, 1981; Abrol, 1989, 2005, 2007). Heinrich and Raven (1972) emphasized the role of energetics in flower foraging and in the evolution of bee flower relationship.

The food rewards from a plant species is the quantity of food that can be collected per unit time. This quantity is a function of the distance between flowers and the speed with which food rewards can be gathered from them.

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Acquisition of energy rewards comes only with the costs. Time and energy are spent during all foraging activities. The rate at which flowers can be manipulated can make the difference between profit and loss. Flowers have different structure that require different pattern to be learned through trial and error for acquiring food. All this information is used to choose between flowers of different species and to make foraging decision. Optimal foraging theory (Schoener, 1971; Pyke *et al*., 1977; Krebs, 1978) hypothesizes animals will forage in ways that maximized some measure of foraging efficiency. The "currency" (Schoener, 1971) that is usually thought to be maximized is net rate of energy intake although other possibilities exist (Pyke *et al*., 1977).

The purpose of this paper is to focus on an understanding and predicting of some aspects of foraging behaviour of two honey bee species, *Apis florea* Fab. and *A. dorsata* Fab., based on energetics of foraging. Honey bees are the ideal subjects for testing optimal foraging theory as they can be easily observed working on flowers. Their energy intake could be quantified by rate of their flower visitation as they exclusively feed on sugar nectars which are source of energy for all life activities. Their activities could be easily discerned into different categories and the energy budget of individual foraging honey bees can be calculated by determining the proportion of time spent in various activities and then measuring the energetic cost of each activity by rate of oxygen consumption per unit time in each activity.

Natural selection is expected to favour efficient foraging patterns and this expectation forms the basis of a large body of optimal foraging theory. Because it is difficult to measure fitness directly, optimal foraging models are generally solved for the behavior that will maximize the animal's net rate of energy intake. The net rate of energy intake is defined as the energy gained while foraging minus the energy spent on foraging, divided by time spent in foraging. The logic is that an animal that maximizes its net rate of energy intake can spend the least time foraging and can gain the maximum surplus of energy to devote to survival and reproduction. Based on these ideas, the studies were conducted and the results obtained are presented in this paper.

MATERIALS AND METHODS

Study site

The study was conducted in the experimental field of Sher-e-Kashmir university of agricultural sciences and technology located at a distance of 13 km from Jammu city (32° 33' and 33 07° Northern Latitude, 74° 27' and 77° 21' East longitude and 81° East of Greenwich, 348 amsl). The climate of the area is typically subtropical.

Sampling procedures

Observations were made on two honey bee species *A. florea* and *A. dorsata* visiting flowers of *Brassica campestis var toria, Coriandrum sativum*, and *Foeniculum vulgare* during the months of February-March. The data were recorded on alternate days during the experimental period. For this purpose, 5 plots of one m^2 were selected randomly and the number of bees of each species visiting the flowers on marked plots were recorded in the beginning of each hour from 0900 to 1700 h for 5 minutes from each side of the plots by visual counting method. The mean of these 5 observations constituted a reading for each observation period. The floral attractability of the two honey bee species was evaluated on the basis of density of bees visiting each crop in a unit time (Abrol 1992). Observations were restricted to nectar collecting individuals only.

Table 1. Nectar productivity and energy reward per flower in three plant species

Plant species	Nectar volume (μl)	Nectar sugar conc. (%)	Total sugar (mg)	Energy (joules)
Brassica campestris	0.225±0.04	45.40±0.34	0.1021±0.02	0.4275±0.14
Coriandrum sativum,	0.009±0.01	47.7±1.04	0.0042±0.021	0.0176±0.01
Foeniculum vulgare	0.0143±0.03	49.5±0.24	0.0070±0.02	0.0293±0.12
CD at 5%	0.42	6.24	0.034	1.20

Table 2. Rate of flower visitation by two honey bee species collecting nectar from three plant species

Plant species	Number of flower visitation per miniute	
	Apis florea	*A. dorsata*
Brassica campestris	7.07 ± 1.00	13.20 ± 0.07
Coriandrum sativum	16.50 ± 0.33	10.73 ± 0.39
Foeniculum vulgare	19.13 ± 0.39	14.03 ± 0.040

Table 3. Tongue length and body weight of two honeybee species

Bee species	Tongue length (mm)	Body weight (mg)
Apis florea	3.31	22.6
A. dorsata	6.45	123.0

Sampling of nectar and calculation of energy per flower

Nectar was measured at 2 hourly intervals between 0900 and 1700 h with 5λ microcapillary pipettes. Nectar sugar concentration was estimated with pocket refractometer (Erma, Japan make).

The amount of sugar and energy content per flower per day was calculated using the formula.

Amount of sugar per

Flower per day (mg) =

$$\frac{\text{Nectar volume (μl) x Nectar sugar concentration (\%)}}{100}$$

Energy per flower per day (joules) = Amount of sugar per flower per day (mg) x 16.74 where, 16.74 is the joule of energy obtained from one 1 mg of sugar irrespective of the type of sugar (Heinrich, 1975a). The energy intake was determined by the rate of flower visitation of each bee species. The rate of flower visitation per minute was calculated by recording the time spent by a bee gathering nectar. Time was recorded by a chronometer with an accuracy of 0.1 sec. The energy harvest per minute was calculated using the formula: r x e, where r = rate of flower visitation and e = energy per flower.

Statistical analysis

The recorded data were analyzed following Sokal and Rholf (1981). The data were analyzed to compare the differences in behavior of two species in terms of attractibilty to different floral sources, flower visitation rates and tongue length, differences in nectar characteristics such as nectar volume, nectar concentration, nectar sugars and energy per flower in different plant species. Analysis of Variance (ANOVA) technique was performed using SPSS 16.0 version in order to compare the differences and draw quantified conclusions.

RESULTS

The data presented in table 1 revealed that three plant species differed significantly in production of nectar, concentration of nectar, amount of total sugar produced and the energy content of flowers. *B. campestis var toria*, on an average produced 0.225 ± 0.04μl of nectar per flower per day as compared to *C. sativum*, and *F. vulgare* which produced very less volume of nectar 0.009 ± 0.01 and 0.0143 ± 0.03μl per flower per day, respectively. However, flowers of *C. sativum*, and *F. vulgare* on the other hand produced nectar of very high sugar concentration 47.7 ± 1.04 and 49.5 ± 0.24 as compared to *B. campestris var toria* (45.40 ± 0.34). Since volume of nectar produced in *B. campestris var toria* was much higher as higher as compared to *C. sativum*, and *F. vulgare*, correspondingly total amount of sugar and energy produced per flower were also high.

The data presented in table 2 revealed that *Apis florea* Fab. had higher foraging rates on *C. sativum*, and *F. vulgare* flowers as compared to *B. campestris var toria* and could make more energetic gains despite the later plant producing more nectar and energy per flower. Evidently, availability of flowers and energy harvest per unit of time seems to make the differences in foraging preferences of the bees (Table 3). The data showed that *A. florea* was more attracted to *C. sativum* and *F. vulgare* providing less

Table 4. Rate of energy intake for two honey bee species collecting nectar from two plant species

Bee species/parameter	Plant species		
	Brassica campestris	*Coriandrum sativum*	*Foeniculum vulgare*
A. florea			
Rate of flower visitation per minute while foraging (r)	7.07 ± 1.00	16.50 ± 0.33	19.13 ± 0.39
Average energy per flower (c) joules	0.4275 ± 0.14	0.0176 ± 0.01	0.0293 ± 0.12
Average energy obtained per minute (r x c) joules	3.022	0.2904	0.560
A. dorsata			
Rate of flower visitation per minute while foraging (r)	13.20 ± 0.07	10.73 ± 0.39	14.03 ± 0.040
Average energy per flower (c) joules	0.4275 ± 0.14	0.0176 ± 0.01	0.0293 ± 0.12
Average energy obtained per minute (r x c) joules	5.643	0.188	0.4110

Table 5. Population density of bees on three plant species

Observation hour (h)	Population of bee/m^2					
	B. campestris		*C. sativum*		*F. vulgare*	
	A.d	A.f	A.d	A.f	A.d	A.f
0900	4.6 ± 0.36	0.8 ± 0.06	1.6 ± 0.11	8.2 ± 1.12	2.3 ± 0.24	16.07 ± 1.46
1100	6.4 ± 0.54	1.8 ± 0.14	2.4 ± 0.28	10.4 ± 1.24	3.3 ± 0.54	6.00 ± 0.67
1300	6.2 ± 0.68	3.4 ± 0.52	3.0 ± 0.32	8.6 ± 0.92	3.75 ± 0.38	6.3 ± 0.53
1500	2.8 ± 0.23	1.2 ± 0.21	1.6 ± 0.12	4.8 ± 0.58	1.85 ± 0.32	3.4 ± 0.34
1700	1.2 ± 0.13	0.0	0.8 ± 0.21	3.8 ± 0.63	0.95 ± 0.10	2.55 ± 0.42
Total	21.2 ± 1.36	6.4 ± 0.57	9.4 ± 0.83	35.8 ± 2.84	2.3 ± 0.24	16.07 ± 1.46

Where, Ad=*A. dorsata*, Af=*A. florea*; Values are mean $\pm$ S.D of 80 observations.

caloric rewards, than to *B. compestris* flowers having high caloric rewards. The differential foraging resulted from the fact that bees could easily harvest more energy per unit time from the simple flowers of *C. sativum* and *F. vulgare* than *B. compestris*, the flowers of which are more complex, making the visitor's approach much more complex. *A. dorsata* foraged on *B. campestris* more abundantly than did *A. florea*. Evidently, the pollinators with high energy requirements may not forage at the flowers which provide insufficient caloric rewards, With its small size and body weight, *A. florea* is better adapted to extract maximum rewards from plants with small flowers like *C. sativum* and *F. vulgare* (Table 3, 4). Population density of bees on these three plant species also differed significantly (Table 5). Flowers of *C. sativum*, and *F. vulgare* on an average attracted more number of *A. florea* during different hours of the day as compared to *B. campestris var toria* where *A. dorsata* was most predominant. The differences in foraging populations of both *A. florea* and *A. dorsata* among three plant species were highly significant (p<0.05).

DISCUSSION

The pollinators adopt behavioural patterns to maximize net foraging returns from flowers (Abrol, 1993; Waddington, 1982, 1985; Pyke, 1982). For honey bee collecting nectar, energy harvested served as appropriate currency to assess the behaviour patterns. The study revealed that flowers of *Brassica Campestris var toria* were highly rewarding followed by *Coriandrum sativum*, and *Foeniculum vulgare*. Therefore, on the basis of amounts of energy produced, it was expected that flowers of *Brassica Campestris var toria* should be highly attractive to foraging insects compared the other synchronously flowering and low-reward plant species. However, foraging attractability of *Apis florea* Fab. and *A. dorsata* Fab.as determined by their population density on these plants. showed a different pattern and did not support the above hypothesis. Flowers of *Coriandrum sativum*, and *Foeniculum vulgare* providing far less energy per flower per day than those of *Brassica campestris var toria* were more attractive to *A. florea* and significantly more bees

visited them. The contention that flowers providing less amounts of energy are relatively unattractive to foraging insects and results in their switching over to high-reward flowers is also subject to behaviour patterns of foraging insects. The selective preference of foraging *A. florea* seemed to be related to its body size and foraging rates and quality of rewards available from *Coriandrum sativum*, and *Foeniculum vulgare* flowers. The rates at which flowers can be harvested can make large differences in energy returns (Pyke, 1980; Pyke, 1982). Though the flowers of *Coriandrum sativum*, and *Foeniculum vulgare* produced less energy than that of *Brassica Campestis var toria* but the bees could make more energy profit from them per unit time, due to their floral compatibility and and higher foraging rates on them. *Apis dorsata* being larger in size preferred to forage on *Brsssica campestris* than on *Coriandrum sativum*, and *Foeniculum vulgare* which flower size and energy availabity was too small for the bees.

Foraging behaviour by *A. florea* and *A. dorsata*, which have been recorded as versatile pollinators of wide variety of field and fruit crops, varied in time and space. Abrol (1992) reported that bees with higher energy requirements do not forage on flowers providing low caloric rewards. The flowers of *F. vulgare, C. sativum, Daucus carota, Allium cepa, Trigonella foenumgraecum var. Kasuri* and *Mangifera indica* were not attractive to *A. dorsata* because the bees could make no profit from these crops; however, *A. florea* was observed in large numbers. The latter bee, with its smaller size and body weight, is morphologically better adapted to extract maximum caloric reward from the flowers. Because of relatively low energy requirements, *A. florea* was still able to maintain an energy balance and visited the crop in large numbers. *A. florea* visited flowers with low caloric rewards whereas *A. dorsata* preferred those with high rewards. Earlier, Sihag (1990) observed similar behaviour in *A. florea* and *A. dorsata* on *B. chinensis* and *Eruca sativa* wherein the flowers of *B. chinensis* were preferred. This behaviour was largely guided by their energy demands. Generally, the smaller flowers with little nectar are unattractive to large hovering animals such as humming birds and sphinx moths, which are probably not sufficient for their energetic demands. In general, the insect

pollinators are more sensitive to floral rewards and forage only on those flowers from which they can maximize net energy gains. In general, the size of the flower and caloric rewards in relation to size of visitor and energy requirements seems to be determinants for resource partitioning among the various bees and thus permitting co-existence under similar ecological conditions. The populations of certain species of pollinating bees were found to be a function of their body size as well as the size of the flowers, because the feeding pattern of many animals suffers as a function of their trophic structure (Heinrich, 1979a, b; Harder, 1985; Abrol and Kapil, 1991; Abrol, 2010, 2011).

The present study demonstrated that bee pollinators make foraging decisions depending upon the net foraging returns from flowers. The pollinators forage on flowers from which they can harvest more energy in a unit time notwithstanding the energy content in them, than on other flowers. Co-evolution has brought a close correlation between pollinator needs and floral energy expenditures (Heinrich, 1975b; Abrol, 1986, 1993). And if the floral reward is coupled with the foraging cost of the bees, only foraging on those species will be profitable whose energy reward exceeds the foraging cost of a pollinator. Probably, this is the reasons that *A. dorsata* preferred *Brassica compestris* var. *toria* over *F. vulgare, C. sativum*. On the other hand, *A. florea* did not exhibit a specialized foraging pattern and usually foraged on *F. vulgare* and *C. sativum*. The reason obviously seems to be the low foraging cost which may be compensated by the small quantity of nectar.

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