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Foraging Behaviour of Bees as Influenced by Quality and Quantity of Rewards from Flowers

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Abstract Foraging behaviour of four honeybee species (*Apis mellifera A. cerana, A. dorsata* and *A. florea*) was studied in relation to energy production rates of *Prunus persica* and a simultaneously blooming weed, *Lepidagathus incurva*. Energy produced ranged from a minimum of 0.642±0.01 joules (*L. incurva*)/flower/day to a maximum of 1.49±0.14 joules/day (*P. persica*). The weed having higher nectar sugar concentration and high flowering density attracted more number of bees as compared to peach. The foraging rates of bees were much higher on the weed and they could harvest more energy per unit time from the weed flowers. Evidently, food acquisition efficiency and quality of food determines the foraging decision of bees.

Key words Honeybees, Energetics, Foraging behaviour, Flower choice, Profitability, Pollination

Introduction

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). In recent years, 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). 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. 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 makes 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 decisions. MacArthur and Pianka (1966) developed a theoretical and empirical construct, the optimal foraging theory (OFT), which lead to a better understanding of foraging behavior. Emlen (1966) demonstrated the need for a model where food item selection of animals could be understood as an evolutionary construct which maximizes the net energy gained per unit feeding time. Optimal foraging theory (Schoener 1971, Pyke et al. 1977, Krebs 1978., Waddington and Holden,. 1979., Waddington,. 1982) hypothesizes animals will forage in ways that maximized some measure of foraging efficiency. The "currency" (Schoener 1971) usually thought to be maximized is net rate of energy intake although other possibilities exist (Pyke et at. 1977). Natural selection is expected to favor efficient foraging patterns and this expectation forms the basis of a large body of optimal foraging theory. Honey bees are the ideal subjects for testing such theories as they can be easily observed working on flowers. The purpose of this paper is to focus on understanding and predicting some aspects of foraging behaviour in four honey bee species, *A. mellifera, A. cerana, Apis florea* Fab. and *A. dorsata* Fab., based on energetics of foraging.

Materials and Methods

Observations were made on four honey bee species, *A. mellifera, A. cerana, A. florea* and *A. dorsata* visiting flowers of *Prunus persica* (peach) and a weed (*Lepidogathus incurva*). The data were recorded on

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the alternate days during the experimental period. For this purpose, five branches of uniform size from trees of same age were randomly selected and number of insect pollinators of each species were recorded by visual counting method at the beginning of each hour. And 1000 flowers for five minutes were counted from 0900-1700 h on all the days of observation. The mean of these observations was constituted of reading for each hour. In case of weed (*L. incurva*) five 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 at the each side of the plots by visual counting method. The mean of these 5 observations was constituted of a reading for each observation period. The floral attractability of the four 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. Nectar was measured at 2 hourly intervals between 0900 and 1700 h with 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.

$$\text{Amount of sugar per Flower per day (mg)} = \frac{\text{Nectar volume } (\mu l) \times \text{Nectar sugar concentration } (\%)}{100}$$

Energy per flower per day (joules) = Amount of sugar per flower per day (mg)×16.74

16.74 is the joule of energy obtained from 1 mg of sugar irrespective of the type of sugar (Heinrich, 1975; 1 mg=4 cal=4×4.186 joules=16.74 joules). The energy intake was determined by the rate of flowers visitation of each bee species. The time spent by a bee gathering nectar was recorded using a chronometer with an accuracy of 0.1 sec. The rate of flowers visitation per minute was calculated. The energy harvest per minute was calculated using the formula: r×e, where r=rate of flower visitation and e=energy per flower. The recorded data were analyzed following Sokal and Rholf (1981).

Results

The data presented in table 1 revealed that two plant species differed significantly in production of nectar, concentration of nectar, amount of total sugar produced and the energy content of flowers. *Prunus persica* on an an average produced 0.28±0.04 μl of nectar per flower per day as compared to *Lepidogathus incurva* which produced very less volume of nectar 0.08±0.01 μl per flower per day. However, flowers of *Lepidogathus incurva* on the other hand produced nectar of very high sugar concentration (48.00±1.04) as compared to *P. persica* (32.00±0.34). Total amount of sugar and energy per flower in terms of volume of nectar produced were higher than *P. Persica*.

Population density of bees on these two plant species also differed significantly (Table 2). Flowers of *L. incurva* on an average attracted more number

Table 1. Nectar productivity and energy reward per flower in two plant species (N=20)

Plant species	Nectar volume (μl)	Nectar sugar conc. (%)	Total sugar (mg)	Energy (joules)
Prunus persica	0.28±0.04	32.00±0.34	0.0896±0.02	1.49±0.14
Lepidogathus incurva	0.08±0.01	48.00±1.04	0.0384±0.021	0.642±0.01
CD at 5%	0.42	6.24	0.034	1.20

Table 2. Population density of bees on two plant species

Observation hour (h)	*Prunus persica*					*Lepidogathus incurva*				
	A.m	A.c	A.d	A.f	Mean	A.m	A.c	A.d	A.f	Mean
0900	1.60±0.21	2.2±0.09	4.6±0.36	0.8±0.06	2.3±0.24	2.5±0.22	5.2±0.12	8.2±1.12	1.6±0.11	16.07±1.46
1100	3.0±0.11	2.0±0.17	6.4±0.54	1.8±0.14	3.3±0.54	3.6±0.26	7.6±0.82	10.4±1.24	2.4±0.28	6.00±0.67
1300	2.6±0.24	2.8±0.32	6.2±0.68	3.4±0.52	3.75±0.38	5.4±0.73	8.2±1.02	8.6±0.92	3.0±0.32	6.3±0.53
1500	1.8±0.12	1.6±0.22	2.8±0.23	1.2±0.21	1.85±0.32	4.2±0.56	3.0v0.38	4.8±0.58	1.6±0.12	3.4±0.34
1700	1.2±0.14	1.4±0.13	1.2±0.13	0.0	0.95±0.10	3.0±0.23	2.6±0.21	3.8±0.63	0.8±0.21	2.55±0.42
Total	10.2±0.84	10.0±0.67	21.2±1.36	6.4±0.57		18.7±1.58	26.6±2.12	35.8±2.84	9.4±0.83	

Where, Am=*Apis mellifera*, Ac=*A. cerana*, Ad=*A. dorsata*, Af=*A. florea*; Values are mean±S.D of 80 observations of insects during different hours of the day as compared to *P. persica*. The data (Table 3) further revealed that weed had a very high flowering density (51.0±2.2 million flowers/ha.) as compared to that of fruit trees (17.6±1.81 million flowers/ha) and the weed also attracted large number of pollinating insects (23.0± 1.64 million/ha.) as compared to the fruit trees (3.8± 0.61 million/ha.). The differences for flowering density and foraging populations between the weed and the fruit trees were highly significant ($p<0.05$). The data presented in table 4 revealed that all the four species of honeybees, *A. mellifera, A. cerana, Apis florea* Fab. and *A. dorsata* Fab had higher foraging rates on *Lepidogathus incurva* flowers as compared to *Prunus persica* and they 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.

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 served as appropriate currency to assess the behaviour patterns. The study revealed that flowers of *P. persica* were highly rewarding followed by *L. incurva* ($P<0.01$; t-test; $n=40$) (Table 1). Therefore on the basis of amounts of energy produced, it was expected that flowers of *P. persica* should be highly attractive to foraging insects compared the other synchronously flowering and low-reward plant species. However, foraging attractability of *A. mellifera, A. cerana, Apis florea* Fab. and *A. dorsata* Fab.as determined by their population density on these plants (Table 2) showed a different pattern and did not support the above hypothesis. Flowers

Table 3. Population dynamics of bees in relation to flowers on two plant species

Date of observation	*Flowers/ha (million)*		*Bees/ha (million)*	
Feb. 2002	*L. incurva*	*P. persica*	*L. incurva*	*P. persica*
13	40.00	10.00	20.00	4.00
15	45.00	25.00	24.00	3.00
17	48.00	28.00	23.00	5.00
20	55.00	39.00	25.00	4.00
26	56.00	17.00	24.00	6.00
28	58.00	12.00	22.00	3.00
March, 2002				
4	60.00	0.80	22.00	2.00

Note: Number of flowers and bees/m2 were counted on weed and number of flowers and bees per ha calculated, accordingly.

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

Bee species/parameter	Plant species	
	Prunus persica	*Lepidogathus incurv*
Apis mellifera		
Rate of flower visitation per minute while foraging(r)	3.39±0.021	24.82±2.10
Average energy per flower(e) joules	1.49±0.11	0.64±0.06
Average energy obtained per minute(r×e) joules	5.05	15.88
A. cerana		
Rate of flower visitation per minute while foraging(r)	3.06±0.12	23.06±1.86
Average energy per flower(e) joules	1.49±0.11	0.64±0.06
Average energy obtained per minute(r×e) joules	4.55	14.75
A. florea		
Rate of flower visitation per minute while foraging(r)	1.82±0.26	4.76±0.28
Average energy per flower(e) joules	1.49±0.11	0.64±0.06
Average energy obtained per minute(r×e) joules	2.71	3.04
A. dorsata		
Rate of flower visitation per minute while foraging(r)	3.60±0.47	18.60±1.20
Average energy per flower(e) joules	1.49±0.11	0.64±0.06
Average energy obtained per minute(r×e) joules	5.36	11.90

of *Lepidogathus incurva* providing far less energy per flower per day but more in density than those of *P. persica* were more attractive and significantly more bees visited them (Table 2, 3). The contention that flowers providing less amounts of energy are relatively unattractive to foraging insects results in their switching over to high-reward flowers is also subject to follow behaviour patterns of foraging insects. The selective preference of foraging honey bees seemed to be related to their foraging rates and quality of rewards being available from *L. incurva* flowers (Table 3). The rates of the harvest can make large differences in energy returns (Pyke 1980; Pyke, 1982). Though the flowers of *L. incurva* produced less energy than that of *P. persica* but the bees could make more energy profit from them per unit time, due to the high density of flowers and higher foraging rates on them (Table 3, 4). 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. Beginning with Emlen (1966) and MacArthur and Pianka (1966) several authors have sought to predict the foraging behavior of animals by means of mathematical models. These models are very similar, in that they all assume that the fitness of a foraging animal is a function of the efficiency of foraging measured in terms of some "currency" (Schoener, 1971) -usually energy- and that natural selection has resulted in animals that forage so as to maximize this fitness. 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.

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