Effect of experience on foraging behavior towards artificial nectar guide in the cabbage butterfly, *Pieris rapae crucivora* (Lepidoptera: Pieridae)

Ikuo Kandori* and Naota Ohsaki

Laboratory of Entomology, Faculty of Agriculture, Kyoto University, Kyoto 606–8502, Japan

(Received 11 March 1997; Accepted 22 September 1997)

Abstract

We examined the effects of nectar guides of artificial flowers on the feeding behavior of naive and experienced butterflies, *Pieris rapae crucivora* Boisduval. A colored spot on artificial flowers triggered the responses of naive butterflies to probe around the spot on the flower, which contributed to their finding the source of nectar. This means that the spot acted as a nectar guide. Butterflies correlated nectar guides with the nectar source and improved their foraging efficiency by experience. Such improvement was not observed on flowers without a guide, which suggested that the nectar guide should play an important role in the improvement of foraging efficiency in *P. rapae* butterflies. Furthermore, butterflies foraged more consistently on flowers with a guide than those without guide after three days of conditioning for either flower type. If this foraging manner is widespread among other insect pollinators, visit consistency based on insect learning might have been a selective force for the nectar guide in natural entomophilous flowers.

Key words: Associative learning, innate response, foraging on flowers

INTRODUCTION

The majority of entomophilous flowers have so-called “nectar guides” or “floral guides” (e.g., Scora, 1964; Tanaka, 1982; Penny, 1983; Lunau and Maier, 1995). The guides are colored differently from the other parts of the flower (e.g., Daumer, 1958; Tanaka, 1982; Penny, 1983), and lead insect pollinators to the nectary of the flower.

Foraging behavior towards a nectar guide has been studied in terms of innate reaction to the guide. For example, inexperienced honey bees extended their proboscis on passing across a borderline between the peripheral corolla and central nectar guide (Daumer, 1958). Naive bumble bees showed antennal contact at the guide area on the flower (Lunau, 1990). However, these studies are focused mainly on bees (Daumer, 1958; Lunau, 1990, 1991, 1992), and a few on the hoverfly (Lunau, 1988) and the hawkmoth (Knoll, 1922, 1924). Whether or not butterflies show an innate feeding response to the guide has not been examined as yet.

Meanwhile, many flower-visiting insects, such

as honey bees (e.g., Menzel, 1985; Schmid-Hempel et al., 1985; Dukas, 1987; Gould, 1987a, b, 1988), bumble bees (e.g., Heinrich, 1976, 1979; Laverty, 1980; Waser, 1986; Dukas and Real, 1991, 1993a, b), butterflies (e.g., Swihart and Swihart, 1970; Lewis, 1986, 1989; Goulson and Cory, 1993; Weiss, 1995; Kandori and Ohsaki, 1996) and the hawkmoth (Kelber, 1996), are known to learn some flower traits during foraging for flowers (see review and a book, Papaj and Prokopy, 1989; Papaj and Lewis, 1993). For example, butterflies can shorten “discovery time” from landing to finding the source of nectar on the flower (Lewis, 1986) and bumblebees can shorten “handling time” from entering to leaving the flower by trial and error (Laverty and Plowright, 1988). However, the clues in the flower that are learned to increase handling efficiency have not been demonstrated nor has an investigation on the relationships between nectar guide and learning in flower-visiting insects been done.

In this study we examine the innate and learned feeding response of the white cabbage butterfly, *Pieris rapae crucivora*, to artificial

*To whom correspondence should be addressed at: Fax: 075-753-6474, E-mail: kandori@kais.kyoto-u.ac.jp

flowers with or without nectar guides. The findings reveal that nectar guides contribute to the improvement of foraging efficiency by triggering innate proboscis extension and by promoting associative learning. To our knowledge, this is the first direct demonstration of learning with regard to the nectar guide in insects. The results also suggest that insect learning and visit consistency might have been a selective force for the nectar guides in natural entomophilous flowers.

MATERIALS AND METHODS

This study was conducted in outdoor cages ($1.8 \times 1.8 \times 1.8$ m) in a field on the campus of Kyoto University, Kyoto, Japan. *P. rapae* butterflies were obtained from either eggs, larvae or pupae collected in crop fields around Kyoto University. The larvae were placed on fresh leaves of *Brassica oleracea* L. (cabbage) in 450 ml plastic cups. Approximately 20 larvae were reared in each cup in the laboratory under natural temperature (about 15–25°C) and day length (about 12L 12D). Immediately after emergence, the butterflies were numbered on the hind wings with an oil-soluble marker, and introduced into outdoor cages regardless of sex. There were some weeds on the ground inside the cage. However, there were no flowering plants in or adjacent to the cage during the experiments. The butterflies were kept without food for one or two days before the experiments and consequently none of them were allowed to experience feeding prior to the experiments. Some pairs mated before the experiment.

Two types of artificial flowers were used in the experiments (Fig. 1), which we termed

Fig. 1. Illustration of two types of artificial flowers with (a) and without (b) nectar guides (obliquely striped). Both types of flower have a hole in the center from which butterflies can take sucrose solution.

Fig. 2. Spectral reflection of three artificial flower colors used in the experiments. 1, yellow; 2, red; and 3, blue.

“flowers with nectar guides” and “flowers without nectar guides.” Both types of flowers consisted of colored paper of 5 cm in diameter with a hole of 0.5 cm in diameter at the center. Flowers with nectar guides had an additional paper disc, 1 cm in diameter, of a different color around the hole. In some experiments, an Eppendorf tube (1.5 ml) containing 20% sucrose solution was attached under the hole so that butterflies could suck nectar from it. Blue, red, and yellow papers were used as the flower colors. The spectral reflectances of the colored paper, which were recorded with a diode array spectrometer (uv-240, Shimadzu) using BaSO₄ as the white standard (assumed reflectance 100%), are shown in Fig. 2. Many insects cannot recognize

Fig. 3. Arrangement of four artificial flowers.

the color red. However, *Pieris brassicae* has a photoreceptor sensitive to red (Lunau and Maier, 1995), and *P. napi* prefers red and blue equally (Goulson and Cory, 1993). Even if *P. rapae* could not perceive red as the flower color, the experiments only required that the insects be able to distinguish each of the three colors.

Preference for flower color and type in naive butterflies. In the first experiment, we examined the preference of butterflies for flower color and type in naive butterflies, using four artificial flowers of two colors and two types: blue flowers, red flowers, blue flowers with red guide (termed blue-with-red flowers), and red flowers with blue guide (termed red-with-blue flowers). The four flowers were arranged on the apices of a regular square, forming a patch of 30 cm in diameter (Fig. 3). Each flower was supported by a wire from the center of the square. The patch was set 60 cm above the ground on a plastic stick in the center of each outdoor cage, where 10–15 naive butterflies had been kept without food for 1 or 2 days after emergence.

The first landing on and the proboscis extension thereafter to a particular flower was taken to indicate a preference for the flower. The individuals were removed from the cage soon after the first landing and proboscis extension to minimize behavioral interference among individuals on the flower. When two individuals landed on the same flower at almost the same time, the latter landing was not counted because it might have been elicited by the former landing, though such cases were rarely observed. The position of flowers were switched after every visit by revolving the patch by 90°, so that the potential effect of flower position on the preference would be canceled. The experiment was conducted for 1 h around noon in October of 1995. The weather was sunny during the experiment. The maximum temperatures in the cage were 23–28°C.

Foraging behavior of naive butterflies and its modification by experience. In the second experiment, we examined the behavioral response of naive butterflies to the two flower types: blue flowers and blue-with-red flowers as flowers without and with a guide, respectively. We focused on two variables of behavior during foraging on flowers. One was frequency of “unsuc-

cessful attempts” in which butterflies failed to find the source of nectar on the flower and flew away. Another was “discovery time” that butterflies spent after landing on the flower before finding the nectar source for each “successful attempt” in which they found the source of nectar.

Before the experiment, naive butterflies had been kept without food for two days after emergence. In the experiment, either two blue flowers or two blue-with-red flowers were set 60 cm above the ground in the outdoor cage for each butterfly. Each flower was constructed an apparatus (Fig. 4), which allowed butterflies to suck nectar for only 5 s per each successful attempt to increase their feeding chances. Each butterfly was examined until its foraging intervals became longer than 10 min or it completed 20 “successful attempts.” Two different flower types were tested simultaneously on sunny days in October and November of 1995. The maximum temperatures were 23–30°C.

Flower choice by experienced butterflies. In the third experiment, we examined whether the butterflies were persistent in foraging for a certain flower type. Initially, naive butterflies were kept in the outdoor cages in which either blue flowers or blue-with-red flowers were provided as nectar sources. After three days of experience

Fig. 4. Apparatus to observe butterflies' foraging behavior: (a) flower disc; (b) Eppendorf tube containing 20% sucrose solution; (c) weight to keep balance; (d) and (e) wire supports. When the weight is lifted slightly by a finger (right arrow), the Eppendorf tube goes down (left arrow) and butterflies can no longer suck nectar. In this way, they were allowed to suck for 5 s per each successful foraging.

with those flowers, the experienced butterflies were then provided with four flowers of two kinds, without nectar.

Two experiments were conducted on different days. In the first experiment, the blue flower-experienced butterflies were provided with blue and yellow flowers, while the blue-with-red flower-experienced ones were provided with blue-with-red and yellow flowers. In the second experiment, the blue flower-experienced butterflies were provided with blue and yellow flowers, while the blue-with-red flower-experienced ones were provided with blue-with-red and yellow-with-red flowers. We selected yellow as an alternative because it was also favored as a nectar source by naive butterflies in our preliminary experiment (not shown), though yellow was still more favored than blue. Only the first landing on and proboscis extension thereafter to a certain flower was referred to as a choice for that flower for each butterfly, because the following landings might have been affected by the first landing. The experiments were conducted in October, 1995. The maximum temperatures during the experiments were 23–30°C. Natural day length was around 11.5L 12.5D.

RESULTS

Preference for flower color and type by naive butterflies

Naive butterflies preferred blue and blue-with-red flowers to red and red-with-blue flowers (Table 1). This suggests that naive *P. rapae* butterflies preferred blue to red as a flower color and that they preferred the two flower types equally: flowers with and without nectar guide.

Foraging behavior of naive butterflies and its modification by experience

In the second experiment, foraging behavior of naive butterflies on the two flower types were compared. Before the first “successful attempt,” the frequency of “unsuccessful attempts” to blue flowers was 0.91 ± 0.31 (mean $\pm$ S.E.), while that to blue-with-red flowers was 0.60 ± 0.17 (mean $\pm$ S.E.) (Table 2). The difference between the two was not significant (Mann-Whitney *U* test; $p=0.469$). The frequency of

Table 1. Preference of flower color and type by naive butterflies

Color and type ^a	Landings ^b	1-Group χ^2 test
Blue	21	
Red	1	
Blue with red	15	
Red with blue	2	
Color		$\chi^2=27.923$, $p=0.0001$
Type		$\chi^2=0.641$, $p=0.423$

^aTwo types of artificial flowers: flowers without guide (blue, red) and flowers with guide (blue with red, red with blue) were tested.

^bFirst landings by 39 butterflies were counted.

“unsuccessful attempts” did not decrease with successive attempts to blue flowers (regression: $y=0.014x+0.654$, $r^2=0.002$, $n=670$, $p=0.225$), while it decreased significantly with successive attempts to blue-with-red flowers (regression: $y=-0.016x+0.361$, $r^2=0.022$, $n=732$, $p<0.001$) (Fig. 5). Kendall’s rank correlation, selecting only individuals that completed 20 successful attempts, shows the same results ($\tau=-0.015$, $n=400$, $p=0.650$ vs. $\tau=-0.134$, $n=480$, $p<0.001$).

In the first successful attempt, discovery time was longer, though not significantly, on blue flowers than on blue-with-red ones (5.92 ± 1.11 vs. 3.51 ± 0.62 mean $\pm$ S.E.(s); Mann-Whitney *U* test; $p=0.067$) (Table 3). Discovery time did not shortened with continuous attempts to blue flowers (regression: $y=-0.033x+7.239$, $r^2=0.001$, $n=670$, $p=0.530$), while it shortened significantly to blue-with-red flowers (regression: $y=-0.084x+3.576$, $r^2=0.012$, $n=732$, $p=0.003$) (Fig. 6). Kendall’s rank correlation, selecting only individuals that completed 20 successful attempts, shows the same results ($\tau=0.036$, $n=400$, $p=0.288$ vs. $\tau=-0.087$,

Table 2. Frequencies of unsuccessful attempts before the first successful attempts to either blue or blue-with-red flowers by naive butterflies

Flower type	<i>N</i>	Mean	S.E.
Blue	45	0.91	0.31
Blue-with-red	47	0.60	0.17

Mann-Whitney *U* test; $p=0.469$.

Data are from Fig. 5.

Fig. 5. Frequencies of unsuccessful attempts (mean $\pm$ S.E.) by naive butterflies which are shown for each two successive successful attempts. ●, butterflies visiting blue flowers (flowers without guides); ○, butterflies visiting blue-with-red flowers (flowers with guides). Numerals indicate sample sizes. Regression lines are also included in the figure.

$n=480$, $p=0.004$).

The above results suggest that the nectar guide triggered the responses of naive butterflies to probe around it on the flower and that butterflies correlated nectar guides with the nectar

Table 3. Discovery times (s) in the first successful attempts by naive butterflies on either blue or blue-with-red flowers

Type	N	Mean	S.E.
Blue	45	5.92	1.11
Blue-with-red	47	3.51	0.62

Mann-Whitney U test; $p=0.067$.

Data are from Fig. 6.

Table 4. Artificial flower choice by butterflies who experienced a certain flower type for three days

Butterflies' experience	Flower types	
	Blue	Yellow
Blue flower ^a	8	26
Blue-with-red flower ^b	20	1

2-group χ^2 test: $\chi^2=26.71$, $p<0.0001$.

Only the first landing by each butterfly was counted.

^aChoice between blue and yellow flowers by blue-flower experienced butterflies.

^bChoice between blue-with-red and yellow flowers by blue-with-red flower experienced butterflies.

source by experience.

Flower choice by experienced butterflies

After three days of experience, the blue-with-red flower-experienced butterflies were more likely to choose the experienced flowers than the blue flower-experienced ones (Tables 4, 5). This suggests that butterflies foraged more persistently on flowers with a guide where they could easily find the nectar source than those without guides.

Table 5. Artificial flower choice by butterflies who experienced a certain flower type for three days

Butterflies' experience	Flower types	
	Blue	Yellow
Blue flower ^a	14	20
Blue-with-red flower ^b	19	7

2-group χ^2 test: $\chi^2=6.06$, $p=0.014$.

Only the first landing by each butterfly was counted.

^aChoice between blue and yellow flowers by blue-flower experienced butterflies.

^bChoice between blue-with-red and yellow-with-red flowers by blue-with-red flower experienced butterflies.

Fig. 6. Discovery times (mean $\pm$ S.E.) of naive butterflies: the time from landing on the flower to finding the source of nectar, for each successful attempt. ●, butterflies visiting blue flowers (flowers without guides); ○, butterflies visiting blue-with-red flowers (flowers with guides). Numerals indicate sample sizes. Regression lines are also included in the figure.

DISCUSSION

This study revealed that efficient foraging by *P. rapae crucivora* is achieved by two steps: innate responses and the following associative learning to nectar guides. That is, a contrasting colored spot on the flower, acting as nectar guide, triggers innate proboscis extension which contributed to their finding the nectar source, and butterflies associate the guide and the nectar source more closely by subsequent learning. Such foraging mechanisms may have an adaptive advantage. Natural flowers with nectar guides generally provide nectar near the guide. This general floral conformation must be recognized innately rather than by learning, which is costly in time. However, the arrangement of the guide and the source of nectar differs between flower species. Therefore, specific adaptation to a certain flower species must be achieved by learning (see also Stephens, 1993). This study revealed that the nectar guide also promotes associative learning between the nectar guide and the source of nectar (Figs. 5, 6).

It is not certain, however, that *P. rapae* is likely to perceive red as a flower color like two other pierids (see Lunau and Maier, 1995; Goulson and Cory, 1993). The guide color used in this

study was red that was less preferred to blue (Table 1). Nevertheless, the butterflies recognized the red spots on the blue flowers as a nectar guide. This suggests that the butterflies can recognize a nectar guide simply when its color is different from the flower or corolla color, even if the former is not attractive compared to the latter. In nature, however, flowers with a nectar guide often offer a more attractive guide color than corolla color, and the color type leads insect pollinators like honeybees (Daumer, 1958) and bumblebees (Lunau, 1990) to the nectar source. In this study, we did not test all the possible color combinations in the experiment using flowers with a guide. If we use a more attractive guide color like blue-with-yellow flower, the innate response and the following learning may be enhanced. However, naive butterflies prefer blue-with-yellow to blue flowers (unpublished data) so that it is impossible to conduct a choice experiment to compare the learning effect in the third experiment (Tables 4, 5). If we use a more conspicuous corolla color like yellow-with-red and yellow flowers during the experience period (Tables 4, 5), it is doubtful whether we could detect the learning effect because yellow was most favored by naive butterflies.

The majority of natural entomophilous flowers possess nectar guides (e.g., Scora, 1964; Tanaka, 1982; Penny, 1983; Lunau and Maier, 1995), which lead insect pollinators to the nectar source (e.g., Daumer, 1958; Lunau, 1990, 1991, 1992). This study revealed that *P. rapae* butterflies come to forage more consistently on artificial flowers with guides where they could easily find the source of nectar than ones without guides. If this foraging manner is widespread among other insect pollinators, they will selectively forage for natural flowers with a guide, which will increase the rate of seed sets. That is, visit consistency based on insect learning might have been a selective force for the nectar guide in natural entomophilous flowers.

There are several possible interpretations about the results of the third experiment whereby the flowers with guides enhance visit consistency by insect learning. One possibility is that the flower-with-guide experienced butterflies had a larger number of conditioning events, i.e., the number of times a butterfly was

rewarded, even within the same experience period, and therefore learned the flower color better than the flower-without-guide experienced ones, which might be indicated by the second experiment (Fig. 5). Another possibility is that the flowers with a guide required shorter discovery time than the flowers without a guide, which might have resulted in the more effective establishment of learning to the flowers with a guide. Further experiments are needed to solve this problem.

In recent years, many studies on the relationship between pollinator learning and flower morphology have been published (e.g., Waser, 1983; Laverty and Plowright, 1988; Harder and Cruzan, 1990; Lewis, 1993). They claim that from a standpoint of evolution of flower complexity, complex flower structure, requiring much handling time, leads to pollinator's constancy by memory limitation. The results of our study are apparently inconsistent with these arguments because flowers with guides enhanced insect's constancy since nectar guides reduced discovery time or handling time. Perhaps, complex flowers require long handling time at the first visit, but well-conditioned insects get rewards with fairly short handling time which may not be so different from simple flowers. It appears reasonable to think that insects should prefer flowers with shorter handling time if reward per flower is the same. While both floral complexity and nectar guide are important factors affecting handling time, the two may be independently considered with regard to their effect on foraging efficiency. For example, the former might have evolved by selective force to increase morphological diversity among flower species (Waser, 1986), while the latter is a product of convergent evolution. The former is closely related to insect memory constraints so that it is hard to maximize the foraging efficiency, while the latter is not related to memory constraints, which enables optimal maximization.

ACKNOWLEDGEMENTS

We express sincere thanks to Drs. E. Kuno, T. Takafuji, and T. Nishida for their valuable advice. This work was partly supported by the Grand-in-Aid for Scientific Research on Priority Areas (number 319), Project "Symbiotic Biosphere: An Ecological Interaction Network Promoting the

Coexistence of Many Species" Numbers 03269209 and 04264210 from the Ministry of Education, Science, Sports and Culture of Japan.

REFERENCES

- Daumer, K. (1958) Blumenfarben, wie sie die bienen sehen. *Z. vergl. Physiol.* 41: 49–110.
- Dukas, R. (1987) Foraging behavior of three bee species in a natural mimicry system: Female flowers which mimic male flowers in *Ecballium elaterium* (Cucurbitaceae). *Oecologia* 74: 256–263.
- Dukas, R. and L. A. Real (1991) Learning foraging tasks by bees: A comparison between solitary and social species. *Anim. Behav.* 42: 269–276.
- Dukas, R. and L. A. Real (1993a) Effects of nectar variance on learning by bumble bees. *Anim. Behav.* 45: 37–41.
- Dukas, R. and L. A. Real (1993b) Learning constraints and floral choice behaviour in bumble bees. *Anim. Behav.* 46: 637–644.
- Gould, J. L. (1987a) Landmark learning by bees. *Anim. Behav.* 35: 26–34.
- Gould, J. L. (1987b) Honeybees store learned flower-landing behavior according to time of day. *Anim. Behav.* 35: 1579–1581.
- Gould, J. L. (1988) Resolution of pattern learning by honey bees. *J. Insect Behav.* 1: 225–233.
- Goulson, D. and J. S. Cory (1993) Flower constancy and learning in foraging preferences of the green-veined white butterfly *Pieris napi*. *Ecol. Entomol.* 18: 315–320.
- Harder, L. D. and M. B. Cruzan (1990) An evaluation of the physiological and evolutionary influences of inflorescence size and flower depth on nectar production. *Func. Ecol.* 4: 559–572.
- Heinrich, B. (1976) Foraging specializations of individual bumblebees. *Ecol. Mono.* 46: 105–128.
- Heinrich, B. (1979) "Majoring" and "minoring" by foraging bumble bees, *Bombus vagans*: An experimental analysis. *Ecology* 60: 245–255.
- Kandori, I. and N. Ohsaki (1996) The learning abilities of the white cabbage butterfly, *Pieris rapae*, foraging for flowers. *Res. Popul. Ecol.* 38(1): 111–117.
- Kelber, A. (1996) Colour learning in the hawkmoth *Macroglossum stellatarum*. *J. Exp. Biol.* 199: 1127–1131.
- Knoll, F. (1922) Der tierversuch im dienste der blutenokologie. *Ber. Dtsch. Bot. Ges.* 40: 30–40.
- Knoll, F. (1924) Blütenokologie und sinnesphysiologie der insekten. *Naturwissenschaften* 12: 988–993.
- Laverty, T. M. (1980) The flower-visiting behaviour of bumble bees: Floral complexity and learning. *Can. J. Zool.* 58: 1324–1334.
- Laverty, T. M. and R. C. Plowright (1988) Flower handling by bumblebees: A comparison of specialists and generalists. *Anim. Behav.* 36: 733–740.
- Lewis, A. C. (1986) Memory constraints and flower choice in *Pieris rapae*. *Science* 232: 863–865.
- Lewis, A. C. (1989) Flower visit consistency in *Pieris rapae*, the cabbage butterfly. *J. Anim. Ecol.* 58: 1–13.
- Lewis, A. C. (1993) Learning in the evolution of resources: Pollinators and flower morphology. In *Insect Learning: Ecological and Evolutionary Perspectives* (D. R. Papaj and A. C. Lewis eds.). Chapman & Hall, New York, pp. 219–242.
- Lunau, K. (1988) Innate and learned behaviour of flower-visiting hoverflies—flower-dummy experiments with *Eristalis pertinax* (Scopoli) (Diptera, Syrphidae). *Zool. Jb. Physiol.* 92: 487–499.

- Lunau, K. (1990) Colour saturation triggers innate reactions to flowers signals: flower dummy experiments with bumblebees. *J. Comp. Physiol. A* 166: 827-834.
- Lunau, K. (1991) Innate flower recognition in bumblebees (*Bombus terrestris*, *B. lucorum*; Apidae): optical signals as landing reaction releasers. *Ethology* 88: 203-214.
- Lunau, K. (1992) A new interpretation of flower guide colouration: absorption of ultraviolet light enhance colour saturation. *Plant Syst. Evol.* 183: 51-65.
- Lunau, K. and E. J. Maier (1995) Innate color preferences of flower visitors. *J. Comp. Physiol. A* 177: 1-19.
- Menzel, R. (1985) Learning in honey bees in an ecological and behavioral context. In *Experimental Behavioral Ecology and Sociobiology* (B. Hölldobler and M. Lindauer eds.). Fischer Verlag, Stuttgart, pp. 55-74.
- Papaj, D. R. and A. C. Lewis (1993) *Insect Learning: Ecological and Evolutionary Perspectives*. Chapman & Hall, New York. 398 pp.
- Papaj, D. R. and R. J. Prokopy (1989) Ecological and evolutionary aspects of learning in phytophagous insects. *Annu. Rev. Entomol.* 34: 315-350.
- Penny, J. H. J. (1983) Nectar guide colour contrast: a possible relationship with pollination strategy. *New Phytol.* 95: 707-721.
- Schmid-Hempel, P., A. Kacelnik and A. J. Houston (1985) Honey bees maximize efficiency by not filling their crops. *Behav. Ecol. Sociobiol.* 17: 61.
- Scora, R. W. (1964) Dependency of pollination on patterns in *Monarda* (Labiateae). *Nature* 204: 1011-1012.
- Stephens, D. W. (1993) Learning and behavioral ecology: incomplete information and environmental predictability. In *Insect Learning: Ecological and Evolutionary Perspectives* (D. R. Papaj and A. C. Lewis eds.). Chapman & Hall, New York, pp. 195-218.
- Swihart, C. A. and S. L. Swihart (1970) Colour selection and learned feeding preferences in the butterfly, *Heliconius charitonius* Linn. *Anim. Behav.* 18: 60-64.
- Tanaka, H. (1982) Relationship between ultraviolet and visual spectral guidemarks of 93 species of flowers and the pollinators. *J. Jpn. Bot.* 57: 146-159.
- Waser, N. M. (1983) The adaptive nature of floral traits: Ideas and evidence. In *Pollination Biology* (L. Real ed.). Academic Press, Orlando, FL, pp. 241-285.
- Waser, N. M. (1986) Flower constancy: definition, cause and measurement. *Am. Nat.* 127: 593-603.
- Weiss, M. R. (1995) Associative colour learning in a nymphalid butterfly. *Ecol. Entomol.* 20: 298-301.