

Effects of recent experience on foraging decisions by bumble bees

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Received: 27 May 1992 / Accepted: 27 January 1993

Abstract. The temporal and spatial scales employed by foraging bees in sampling their environment and making foraging decisions should depend both on the limits of bumble bee memory and on the spatial and temporal pattern of rewards in the habitat. We analyzed data from previous experiments to determine how recent foraging experience by bumble bees affects their flight distances to subsequent flowers. A single visit to a flower was sufficient to affect the flight distance to the next flower. However, longer sequences of two or three visits had an additional effect on the subsequent flight distance of individual foragers. This suggests that bumble bees can integrate information from at least three flowers for making a subsequent foraging decision. The existence of memory for floral characteristics at least at this scale may have significance for floral selection in natural environments.

Key words: Information processing – Decision rules – Foraging – Flight distance – Bumble bees

The standing crop of nectar varies considerably among flowers within a species as a result of variation in the rate of nectar production and the movement patterns of foraging nectarivores (Heinrich 1979; Pleasants and Zimmerman 1979; Tauber and Barnes 1979; Zimmerman 1981, 1983; Southwick and Southwick 1983; Real and Rathcke 1988; Cresswell 1990; Waser and Mitchell 1990). High variances in nectar production and standing crop may require foragers to base their floral choice decisions on large samples of flowers, because the information from only a few flowers is likely to be very imprecise.

The temporal and spatial scales employed by foraging bees in sampling their environment and making foraging decisions are crucial for understanding the consequent

patterns of reward distribution and pollen flow (Levin 1978; Waser and Mitchell 1990). However, it is not clear what sample size bees use in their characterization of the floral environment. The appropriate sample size depends both on the limits of memory storage and retrieval, and on the spatial and temporal pattern of rewards in the habitat. Surprisingly, Cresswell (1990) suggested that bumble bees (*Bombus bimaculatus*) visiting wild bergamot (*Monarda fistulosa*) base their foraging decisions on a single flower. He found that the nectar volume in only the last flower visited affected decisions to leave an inflorescence. Basing foraging movements and decisions on a single visit seems unlikely, unless bees have (1) severe computational constraints on memory that limit their ability to incorporate information from previous visits, or (2) the foraging environment is highly autocorrelated (in space and/or time), so that bees do not need to integrate information over several samples (Gibson 1966; Real 1991, 1992).

To see if bumble bees integrate information from more than a single flower, we analyzed data from our previous experiments on the effect of nectar variance on learning by bumble bees (*B. bimaculatus*) (Dukas and Real 1993). More specifically, we determined how recent foraging experience affects flight distances to subsequent flowers.

Materials and methods

The methods used in the experiments are described in Dukas and Real 1993. Details relevant to this study are briefly described below. Experiments were conducted in a 120 × 120 × 18 cm wood enclosure containing 100 flowers of *Abelia floribunda*. The flowers were placed in randomly chosen coordinates on a 48 × 48 position grid. In each experiment, there were equal numbers of two randomly distributed floral types differing in color. One floral type was rewarding, and the other floral type was non-rewarding. We conducted two sessions for each experiment; in the first session, one floral color was rewarding, while in the second session, it was non-rewarding. All flowers of the non-rewarding type contained 5 µl of water. We modified the nectar distribution in flowers of the rewarding type among experi-

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ments to generate four nectar variances: 0, 1, 2, and 4 μl^2 . In general, to increase nectar variance, we decreased the fraction of rewarding flowers that provided a nectar reward while we increased the volume in those that were rewarding. The remaining flowers of the rewarding type contained 5 μl of water in each. Bees rejected and left water filled flowers immediately after probing. We held the mean nectar volume in the rewarding floral type constant at 1 μl per flower.

Wild caught naive worker bumble bees (*B. bimaculatus*) were placed individually in plastic cages and deprived of food for three hours. An experimental session consisted of 6–7 trials. During each trial, we allowed a single bee to forage on 30 flowers and recorded the identification number of each flower visited. We then refilled the flowers and introduced another bee. Experiments were terminated when bees visited more than 85% of the flowers of the rewarding floral type.

Flight distance to the next flower

The integration of information across floral visits may best be revealed by assessing any change in flight distance as a function of the historical sequence of the reward status of previously visited flowers. For example, if the distance flown from a rewarding flower is greater when that flower is preceded by a non-rewarding flower (versus the distance when preceded by a rewarding flower), then information is clearly integrated over more than the last flower visited.

For each bee in each experiment, we first compared the mean flight distance after visiting a single (a) nectar-filled flower of the rewarding type, (b) water-filled flower of the rewarding type, and (c) flower of the non-rewarding type. Second, we compared the mean flight distance after visits to a sequence of (a) 1, 2, or 3 nectar-filled flowers of the rewarding type, (b) 1, 2, or 3 waterfilled flowers of the rewarding type, and (c) 1, 2, or 3 flowers of the non-rewarding type. Sample sizes for longer sequences were too small for analysis. Flight distances were measured as the linear distances separating successively visited flowers. We compared flight distances using a split-plot analysis of variance to assess effects of variance and trial number.

Results

Bees flew shorter distances after visiting nectar-filled flowers of the rewarding type, compared with either water-filled flowers of the rewarding type, or flowers of the non-rewarding type. After visiting water-filled flowers of the rewarding type, bees flew slightly longer compared to their flights after visiting flowers of the non-rewarding type (Fig. 1, $F = 41.0$, d.f. = 2, 376, $P < 0.001$, Ryan-Einot-Gabriel-Welsch Multiple Range Test, $P < 0.05$). Nectar variance and trial number did not significantly affect flight distances ($F = 1.9$, d.f. = 2, 376, $P > 0.1$ for variance level; $F = 1.0$, d.f. = 4, 376, $P > 0.3$ for trial number).

Bees slightly decreased their mean flight distance after visiting longer sequences of nectar-filled flowers of the rewarding type (Fig. 1a, $F = 6.2$, d.f. = 1, 189, $P < 0.01$). On the other hand, they flew further after visiting longer sequences of water-filled flowers of the rewarding type (Fig. 1b, $F = 10.1$, d.f. = 1, 335, $P < 0.001$). However, there was no significant change in bees' flight distances after visiting longer sequences of flowers of the non-rewarding type (Fig. 1c, $F = 0.07$, d.f. = 1, 189, $P > 0.5$). Nectar variance and trial number did not significantly affect flight distances ($P > 0.1$ for all cases).

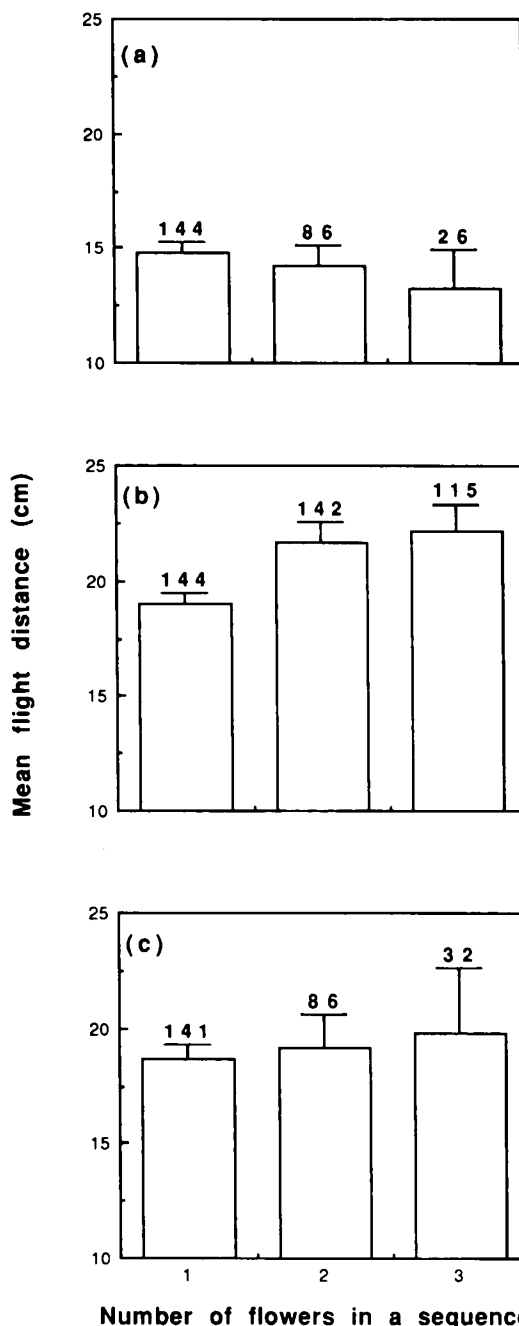


Fig. 1a–c. Mean (+ SE) flight distances of bumble bees ($n = 42$ bees) after visiting a sequence of (a) nectar-filled flowers of the rewarding type, (b) water-filled flowers of the rewarding type, or (c) flowers of the non-rewarding type. The number above the bars are the sample sizes of flight distances

Discussion

A single visit to a flower was sufficient to affect the flight distance to the next flower. However, longer sequences of two or three visits had an additional effect on the subsequent flight distance of bumble bees (Fig. 1). This suggests that bumble bees can integrate information from at least three flowers for making a subsequent foraging decision.

In our experiments, bees could not use the information from previously visited flowers to predict nectar availability in neighboring unvisited flowers because nectar was randomly distributed among flowers. Despite this random distribution of nectar, bees behaved as if they were foraging over a patchily distributed resource. They flew shorter distances after visiting (a) flowers with nectar compared to non-rewarding flowers, (b) longer sequences of nectar-filled flowers, and (c) shorter sequences of non-rewarding flowers. This suggests that bumble bees use a fixed decision rule which assumes a non-random distribution of nectar in flowers (Waser and Mitchell 1990; see also Waddington 1980). However, because we used bees with previous experience in the wild, it is possible that they had previously learned to respond to a patchy distribution of nectar and did not alter their behavior during the experiments. However, from our previous work we know that these experiments were carried out on a time-scale that should have enabled learning (Dukas and Real 1993).

Unfortunately, only a few sets of data are currently available that can be used to ascertain the degree of spatial and temporal autocorrelation in nectar rewards in natural environments (e.g. Real and Rathcke 1988; Waser and Mitchell 1990). More such data are needed if we are to provide an evolutionary account of information-processing in bees and generate a predictive theory of pollinator foraging in natural environments.

Acknowledgments. We thank J.R. Walters, S. Ellner L.D. Harder, E.D. Seaman and an anonymous referee for comments on the manuscript, E.D. Seaman for programming help, and C. Brownie for statistical advice. This study was supported in part by Sigma Xi grant to R.D. and NSF grants BNS 8719292 and BNS 8900292 to L.A.R.

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