

## Near–Far Search: An Evolutionarily Stable Foraging Strategy

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This study addresses the momentary rules of nectar foraging behavior on carpet-type, small inflorescences. It has been suggested that patchiness in the distribution of nectar can give an advantage to “near–far” type of foraging strategies; that is, to foragers which search “near” (in the neighborhood of the last visited flower) as long as the nectar yield is high enough and go “far” otherwise. To explore the evolutionary stability of near–far search, various foraging strategies were compared, according to two, slightly different optimality criteria: the number of flowers emptied during a fixed length bout and the number of flowers visited until total extraction of the entire inflorescence. With long bouts (in the case of a single forager) or a substantial probability of revisits to the same inflorescence (in the case of multiple foragers), a near–far foraging strategy is an ESS. Furthermore, prior patchiness in the nectar distribution is not a necessary condition for the evolutionary stability of near–far search. It turns out that during near–far foraging some patchiness is created by the foraging process itself, which the near–far forager can exploit later on.

### Introduction

After deciding in which area and on which plant species to forage for nectar, a nectar forager has still to decide on its “movement rules”. Generally, these can be classified into three levels: movements between individual plants, movements between flower patches of the same plant and movements between individual flowers within the same patch. In a forager’s reality, decisions at each level have to be made without having complete, real-time information about the quality of the various resource patches. This quality distribution can vary both in space and time, as a result not only of the plant activity but also of the foraging activity itself (Pleasants & Zimmerman, 1979, 1983; Zimmerman, 1981; Zimmerman & Cook, 1985; Possingham, 1989; Waser & Mitchel, 1990; Selten & Shmida, 1991; Cohen & Shmida, 1993).

However, as was first pointed out by Oaten (1977), the rewards can provide a forager with information about its environment. Thus, the nectar collected by the forager, which primarily serves as an energy supply, can also provide it with some information as to the quality and the distribution of this resource, and consequently affect its subsequent movements.

Among flower foraging bees, the actual movements are the result of two basic components, the distance of the flight and the direction of the flight. Pyke (1978: 88–89) reports that “the more time a bumblebee spends at a flower on an inflorescence, the more likely it is to fly to another flower on that inflorescence”. Since the amount of nectar obtained from a flower is positively correlated with the time spent at that flower, Pyke’s observations suggest that “the likelihood of a bumblebee flying from one flower to another on the same inflorescence increases with the amount of nectar obtained at the first flower”. Waddington (1980) has shown that while honeybees usually make very short flights between consecutively visited flowers, the distance increases as a function of

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the number of non-rewarding visits which immediately preceded the flight. Thus, if a poor, non-rewarding patch is encountered, inter-floral flights tend to be relatively longer (see also Heinrich, 1979; Best & Bierzychudek, 1982; Thomas *et al.*, 1982; Zimmerman, 1982a; Zimmerman & Cook, 1985; Galen & Plowright, 1985). Moreover, these studies demonstrate that in rich, highly rewarding patches, the foragers veer more frequently as they move, and with more acute angles than they do on less rewarding patches. After one or few non-rewarding visits, the turning angle is quite obtuse, and the bees often move straight ahead. More tortuous search paths, following higher prey density, have also been reported for birds (Smith, 1974; Gill & Wolf, 1977; Zach & Falls, 1977). As a result, the foragers engage in an "area restricted searching" (Tinbergen *et al.*, 1967). Selten & Shmida (1991) have termed the resulting movement rule as a "near-far" search: as long as the recent reward is high enough, a bee adopting the near-far strategy tends to stay and look for the next flower in the neighborhood of the last visited flower, whereas a low reward induces her to search further away. As demonstrated by recent field studies (Kadmon *et al.*, 1991; Kadmon & Shmida, 1992), such a behavior is displayed by solitary bees foraging on *Anchusa strigosa* flowers.

The scope of the present work is to compare the reward expected from adopting the near-far strategy with that expected from several alternative search strategies. Since the activity of other foragers changes the resource distribution both in space and time, the optimal solution for a single forager can be different from that obtained in a multi-forager situation. Thus, we will examine the conditions under which the near-far search is an evolutionarily stable strategy (ESS—Maynard Smith & Price, 1973). This will be done for a "carpet" type of small inflorescences, i.e. small groups of flowers, arranged in patterns that do not induce any directionality (such as that induced, for example, by a vertical inflorescence) on the pollinator's movement.

The alternative strategies that will be considered, as well as the near-far strategy, are all simple in the sense that they require only a single-level memory, i.e. a "memory window" (Cowie, 1977) of length one. In other words, decisions are made on the basis of the reward obtained only at the last visited flower. Indeed, most of the observed departure rules suggest the possibility of a single-level memory (Harder & Real, 1987; Pleasants, 1989; Real *et al.*, 1990; Cresswell, 1990; Cuthill *et al.*, 1990; Kacelnik & Todd, 1992; Kadmon & Shmida, 1992). Waddington's (1980) experiments, on the other hand, indicate that

bumblebees may adjust their flight distances according to the information gathered from several recent visits.

### The Various Movement Strategies

We consider a group of  $N$  flowers, and define the following movement strategies:

(1) *Random Search*. The next flower to be visited can be any of the  $N - 1$  flowers in the group (excluding the last visited one, which is avoided on the immediately following step), chosen at random (with uniform probability). It should be noted that Random Search should not be confused with random foraging with respect to direction, exhibited by pollen-collecting bumblebees (e.g. Zimmerman, 1982b), which results in Near Search, defined next.

(2) *Near Search*. The next flower to be visited is always the nearest neighbor (or any of the nearest neighbors, in case of more than one) of the previously visited flower. Near Search has been observed in pollen-collecting bumblebees (Hodges & Miller, 1981; Zimmerman, 1982b; Haynes & Mesler, 1984).

(3) *Far Search*. The next flower to be visited is never a nearest neighbor, but a randomly chosen, other flower in the group.

(4) *Near-Random Search*. This strategy is a combination of Near and Random Search. The bee moves to a nearest neighbor as long as she is rewarded by the previous flower, but switches to Random Search after visiting a non-rewarding flower. Near Search is restored after visiting a rewarding flower.

(5) *Near-Far Search*. This strategy is a combination of Near and Far Search. The bee moves to a nearest neighbor as long as she is being rewarded by the previous flower, but switches to Far Search after visiting a non-rewarding flower. Near Search is restored after visiting a rewarding flower.

### Foraging in a Large, Patchy Environment

The apparent advantage of near-far foraging in patchy areas is demonstrated in this section, where the efficiency of Near-Far and Random Search are compared.

Consider an area with  $N$  flowers, and foraging bouts of a fixed length  $M$  (i.e.  $M$  flowers are visited in each bout). Before foraging starts, a proportion  $q$  ( $0 < q < 1$ ) of the flowers are full (with the same amount of nectar, for computational simplicity), whereas  $1 - q$  of the flowers are empty. In visiting a full flower, the forager draws out all the nectar and the flower becomes empty. (Compare, however, with Zimmerman, 1983.) The flowers are considered to be

anonymous and emptied flowers are not marked. Thus, only by visiting a flower, the forager can find out whether it is full or empty (e.g. Cresswell, 1990). We also assume that the duration of a foraging bout is short, so that nectar is not renewed during a single bout.

In determining which foraging strategy, Near-Far or Random Search, is more successful, we compare the expected number of full flowers encountered in a single bout (that is, the expected number of flowers that the forager empties during a bout) for the two strategies.

For Random Search, the expected number of emptied flowers can be obtained analytically (see Appendix A) and is given by

$$\mu = q \left\{ 1 + (N-1) \left[ 1 - \left( 1 - \frac{1}{N-1} \right)^{M-1} \right] \right\}. \quad (1)$$

For Near-Far Search, the expected number was estimated by computer simulations. Thus, we considered a  $40 \times 40$  flower torus (a doughnut shaped surface), with an initial proportion  $q = 1/2$  of full flowers. The area was divided into alternating full and empty patches. Three levels of patchiness were considered: a pattern with four ( $20 \times 20$  flower each) large patches, a pattern with 16 ( $10 \times 10$  flower each) medium size patches, and a pattern with 64 ( $5 \times 5$  flower each) small patches. For each pattern, four different bout lengths were considered: 20, 50, 100 and 200 visits.

Estimating the expected number of emptied flowers was done by drawing samples of 1000 simulated Near-Far bouts (for each of these 12 combinations) and calculating the mean number of flowers emptied per bout. These estimates, accompanied by the corresponding estimates of their standard errors, are presented in Table 1, together with the expectations for Random Search, which were calculated using eqn (1).

The results (all are statistically significant) indicate the following.

(i) In a patchy environment, Near-Far is more advantageous than Random Search.

(ii) The larger the size of the patches, the greater the advantage.

### A Single Forager on a Small, Full Inflorescence

We turn now to small inflorescences and consider the case of a single forager, performing a single foraging bout. Before foraging starts, all the flowers are full.

In determining which of the above-mentioned foraging strategies is more successful, we use two slightly different criteria.

#### (I) FORAGING BOUTS OF A FIXED LENGTH

We assume that during a foraging bout, a forager visits the same number ( $M$ ) of flowers. We then compare the expected number of full flowers encountered in a single bout (that is, the expected number of flowers that the forager empties) for the various foraging strategies.

For Random Search, the expected number of emptied flowers is given by eqn (1) (with  $q = 1$ ). For the other strategies, the expected number was estimated using computer simulations.

Three different sets of simulations were considered, one set with a 19-flower plane inflorescence, another set with a 19-flower globular inflorescence and a third set with a 37-flower plane inflorescence. All these are carpet-type inflorescences.

Each inner flower of the 19-flower plane inflorescence (see Fig. 1) has exactly six near-neighbors, while half of the peripheral flowers have three and half have four.

The flowers of globular inflorescence are the vertices of a regular dodecahedron, which is a polyhedron having 12 faces and 20 vertices. (For comparison with plane inflorescence, we used one vertex for a ‘‘stem’’.) Thus, 16 flowers have three near-neighbors, while each of the three flowers surrounding the stem has only two.

The 37-flower plane inflorescence is a 19-flower one with an additional outer whorl.

TABLE 1  
*Expected number of flowers emptied during bouts of a fixed length M in a patchy, 40 × 40 flower environment*

Foraging strategy	Number of flowers emptied during a bout of length $M$			
	$M = 20$	$M = 50$	$M = 100$	$M = 200$
Random	9.947	24.636	48.513	94.085
Near-Far				
four patches	13.344 ± 0.077	33.041 ± 0.116	65.008 ± 0.161	125.877 ± 0.219
16 patches	12.827 ± 0.072	31.597 ± 0.116	62.535 ± 0.160	120.775 ± 0.230
64 patches	11.849 ± 0.071	29.117 ± 0.110	57.204 ± 0.158	111.389 ± 0.212

Expectations for Random Search were obtained using eqn (1). For Near-Far, estimates (mean ± SE) were obtained by computer simulations (1000 simulated bouts for each case).

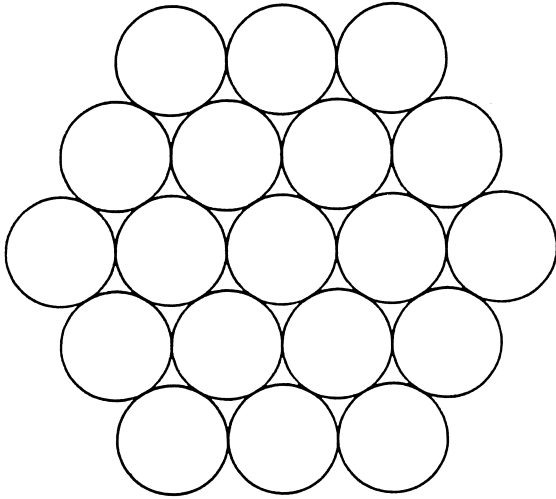


FIG. 1. A 19-flower plane inflorescence.

For each set, five different bout lengths were considered ( $M = 10, 15, 20, 25$  and  $30$  for the 19-flower sets, and  $M = 20, 30, 40, 50$  and  $60$  for the 37-flower set). Field observations indicate that these are quite typical bout lengths for solitary bees (e.g. Schreiber, 1993).

For both 19-flower sets, estimates of the expected number of flowers, emptied during a bout, were

obtained for each of the four strategies (i.e. Near, Far, Near–Random and Near–Far Search), whereas for the 37-flower set, estimates were obtained only for the Near–Far strategy. Thus, in the 19-flower sets, all five search strategies are compared, whereas only Random and Near–Far Search are compared in the 37-flower set.

Estimating the expected number of emptied flowers was done by drawing samples of 1000 simulated bouts (for each of these 45 combinations), and calculating the mean number of flowers emptied per bout. These estimates, accompanied by the corresponding estimates of their standard errors, are presented in Table 2, together with the expectations for Random Search, which were calculated using eqn (1).

The results (all are statistically significant) can be summarized as follows:

(i) Near Search was the strategy that consistently (i.e. for every bout length and inflorescence shape) displayed the worst performance. This is not surprising, since staying in the neighborhood increases the probability of recurrent visits to the same flowers. For the bout lengths considered, Near Search performed better on the plane, than on the globular inflorescence.

TABLE 2

*Expected number of flowers emptied during bouts of a fixed length  $M$  and expected number of visits (rightmost column) required to empty the entire inflorescence*

(a) *Plane inflorescence (19 flowers)*

Foraging strategy	Number of flowers emptied in a fixed-length bout					Length of exhaustive bout
	$M = 10$	$M = 15$	$M = 20$	$M = 25$	$M = 30$	
Random	8.239	10.914	12.924	14.434	15.569	63.912
Near	$6.653 \pm 0.044$	$8.896 \pm 0.055$	$10.431 \pm 0.066$	$11.686 \pm 0.067$	$12.830 \pm 0.069$	$104.825 \pm 1.412$
Far	$8.129 \pm 0.033$	$10.743 \pm 0.040$	$12.790 \pm 0.044$	$14.256 \pm 0.045$	$15.432 \pm 0.044$	$66.263 \pm 0.748$
Near–Random	$7.797 \pm 0.028$	$10.581 \pm 0.038$	$12.814 \pm 0.041$	$14.434 \pm 0.043$	$15.652 \pm 0.042$	$62.508 \pm 0.678$
Near–Far	$7.915 \pm 0.026$	$10.843 \pm 0.034$	$13.089 \pm 0.040$	$14.700 \pm 0.042$	$15.908 \pm 0.040$	$62.347 \pm 0.687$

(b) *Globular inflorescence (19 flowers)*

Foraging strategy	Number of flowers emptied in a fixed-length bout					Length of exhaustive bout
	$M = 10$	$M = 15$	$M = 20$	$M = 25$	$M = 30$	
Random	8.239	10.914	12.924	14.434	15.569	63.912
Near	$6.350 \pm 0.046$	$8.289 \pm 0.058$	$9.989 \pm 0.067$	$11.352 \pm 0.072$	$12.569 \pm 0.071$	$99.435 \pm 1.335$
Far	$8.190 \pm 0.032$	$10.764 \pm 0.039$	$12.895 \pm 0.043$	$14.307 \pm 0.042$	$15.462 \pm 0.041$	$65.301 \pm 0.695$
Near–Random	$7.655 \pm 0.029$	$10.575 \pm 0.038$	$12.791 \pm 0.042$	$14.449 \pm 0.044$	$15.701 \pm 0.043$	$61.322 \pm 0.677$
Near–Far	$7.771 \pm 0.027$	$10.723 \pm 0.037$	$13.016 \pm 0.041$	$14.715 \pm 0.043$	$15.970 \pm 0.041$	$59.592 \pm 0.652$

(c) *Plane inflorescence (37 flowers)*

Foraging strategy	Number of flowers emptied in a fixed-length bout					Length of exhaustive bout
	$M = 20$	$M = 30$	$M = 40$	$M = 50$	$M = 60$	
Random	15.921	21.096	25.001	27.947	30.169	161.660
Near–Far	$15.254 \pm 0.041$	$20.780 \pm 0.052$	$25.072 \pm 0.060$	$28.293 \pm 0.063$	$30.512 \pm 0.059$	$146.757 \pm 1.398$

Expectations for Random Search were obtained using eqns (1) and (2). For the other search strategies, estimates (mean  $\pm$  SE) were obtained by computer simulations (1000 simulated bouts for each case).

- (ii) Random performed better than Far Search.
- (iii) Near-Far performed better than Near-Random.

Hence it is interesting to compare the Random and the Near-Far strategies.

(iv) In all three sets, Random was found to be the best performing strategy for short bouts, but Near-Far turned to be the best strategy for longer bouts. (For long enough bouts, Near-Random also did better than Random Search.)

It seems that while performing a Near-Far (or a Near-Random) search, the forager itself creates some patchiness (recall that we have started with a uniform, full-flower inflorescence), which it exploits later on during the bout. Indeed, if we compare the near-neighbor similarity with respect to nectar occurrence, we find that on an inflorescence which has been foraged by a Near-Far forager, near-neighbors tend to be more similar (i.e. both full or both empty), than on an inflorescence visited by a Random forager. This comparison was done by simulating Near-Far and Random foraging bouts on a 19-flower plane inflorescence. After a fixed number (i.e. 5, 10 and 15) of flowers had been emptied, all 42 pairs of near-neighbors were examined. To each pair, either a +1 or a -1 was assigned, according to whether or not both neighbors were similar, and the mean of these 42 numbers was calculated, to give the value of the “near-neighbor similarity index” for that bout. For each of the six combinations, a sample of 2000 bouts was drawn. Table 3 presents the sample means (accompanied by the estimated standard errors) of the similarity index for the different combinations. The results clearly demonstrate a much larger similarity index under Near-Far than under Random Search, especially during the early stages of the bout. (Note that for both strategies, the similarity index is larger at the early stages of the bout, when most of the flowers are still full, and at the late stages of the bout, when most of them are already empty. This, however, should not preclude the use of this index for contrasting the two strategies.)

TABLE 3

*The near-neighbor similarity index (see text) after S flowers have been emptied from a 19-flower plane inflorescence*

Foraging strategy	Near-neighbor similarity index		
	S = 5	S = 10	S = 15
Random	0.1797 ± 0.0027	-0.0497 ± 0.0031	0.3004 ± 0.0025
Near-Far	0.3410 ± 0.0032	0.1082 ± 0.0036	0.3547 ± 0.0027

Estimates (±SE) were obtained by computer simulations (2000 simulated bouts in each case).

## (II) EXHAUSTING THE ENTIRE INFLORESCENCE

Another criterion by which the relative success of the various foraging strategies can be determined is the number of visits required for emptying the entire inflorescence. While in reality, a forager does not linger so much on the same inflorescence, the expected number of visits until complete exhaustion can nevertheless measure the efficiency of the search strategy.

For the Random Search strategy, the expected length of an exhaustive bout can be obtained analytically (see Appendix B), and is given by

$$\mu = 1 + (N - 1) \sum_{t=1}^{N-1} t^{-1}. \quad (2)$$

For the other strategies, the expected length was estimated by simulations. The estimates, accompanied by the corresponding estimates of their standard errors, are presented in the right-most column of Table 2, together with the expectations for Random Search, which were calculated using eqn (2).

The results clearly indicate that Near Search requires the longest bout in order to empty the entire inflorescence. Far Search is much faster, and Random is even more so. Near-Far is slightly faster than Near-Random, and both are faster than Random Search. Thus, according to this criterion, Near-Far is the most efficient of all five foraging strategies.

## Recurrent Bouts and the Evolutionary Stability of Near-Far Search

In this section we consider the possibility of recurrent foraging bouts to the same inflorescence. These are assumed to be frequent enough, so that no significant amounts of nectar are produced in the interval between successive bouts. (The conclusions of the preceding section, which dealt with the case of a single forager, obviously apply also to cases of recurrent, but infrequent bouts, that is cases where the inter-arrival time is long enough, enabling the complete replenishment of nectar.)

We wish to show that Near-Far Search can be an evolutionarily stable foraging strategy also in situations involving multiple bouts to the same small inflorescence. Thus, we assume that Near-Far is the prevalent strategy in the population, and compare the payoff of a mutant (adopting any of the other foraging strategies) to the payoff of a wild-type individual (adopting the Near-Far strategy).

This was demonstrated using a 19-flower plane inflorescence (see Fig. 1). First we considered the expected number of flowers emptied during a bout on a fresh, as yet unvisited inflorescence, by foragers

using the various foraging strategies. For the Random Search strategy, the expected number was obtained using eqn (1). For the other strategies (i.e. Near, Far, Near–Random and Near–Far), the expected number was estimated by computer simulations. The results are given in Table 4 (the “first bout” column). Next we considered the expected number of flowers emptied (by each of the strategies) during a second bout on an already visited inflorescence. The first visit to that inflorescence was assumed to be done by the common, Near–Far forager. The simulation results are given in Table 4 (the “second bout” column). Two different sets, each assuming a different bout length (i.e.  $M = 15$  and  $M = 20$ ) were considered.

For the 15-visit bout length, Random Search turned out to be the most successful (and Near–Far the second best) during the first bout, but Near–Far was the most successful (and Random Search the second best) during the second bout.

For the 20-visit bout length, Near–Far turned out to be the most successful of all strategies during both the first and the second bouts.

Thus, if the probability for a bout to be the second on an inflorescence is large enough, Near–Far is the most advantageous strategy; that is, in a population adopting the Near–Far strategy, an individual having any of the other foraging strategies has a selective disadvantage.

What value should this probability have for Near–Far Search to be evolutionarily stable? Consider  $N$ -flower inflorescences, and let  $\pi_k$

( $k = 1, 2, 3, \dots$ ) be the probability for a bout to be the  $k$ -th on an inflorescence. (Clearly,  $\pi_k \geq \pi_{k+1}$  for all  $k$ .) Suppose that Near–Far is the prevalent strategy in the population, and let  $W_k$  and  $M_k$  be the expected number of flowers emptied during the  $k$ th bout by a wild-type and a mutant forager, respectively. A sufficient condition for Near–Far to be resistant to such mutants is that  $A\pi_1 + B\pi_2 > 1$ , where  $A = (N - M_1 - W_2)/(N - W_1 - W_2)$  and  $B = (N - W_1 - M_2)/(N - W_1 - W_2)$  (see Appendix C). For a Random Search mutant, a somewhat more refined condition can be obtained, with  $A = [W_1(N - M_1) - M_1W_2]/[M_1(N - W_1 - W_2)]$  and  $B = W_2(N - M_1)/[M_1(N - W_1 - W_2)]$ . Thus, for the case presented in Table 4(b), a sufficient condition for Near–Far to be an ESS is that  $1.1755\pi_1 + 1.0489\pi_2 \geq 1$  and  $1.1793\pi_1 + 1.0216\pi_2 \geq 1$ . Note that this is only a *sufficient* condition for the evolutionary stability of Near–Far Search. Generally, this strategy is expected to be evolutionarily stable under wider conditions.

## Discussion

Many studies, theoretical as well as empirical, point out that patchiness in the distribution of nectar plays an important role in the foraging behavior of pollinators. While it has been suggested that patchiness confers an advantage to near–far type of foraging strategies, no theoretical work has yet demonstrated the possibility that near–far can be evolutionarily stable. The present work, which mostly considers movements within a small, carpet-type group of flowers, outlines conditions for the evolutionary stability of near–far.

It turns out that prior patchiness is not a necessary condition for the evolutionary stability of near–far search. This strategy can be advantageous even if nectar is uniformly spread, and no patchiness exists previous to the foragers visit. Evidently, during near–far foraging, some patchiness in the nectar distribution is created by the foraging process itself. If foraging bouts are long enough (in case of a single forager), or if there is a substantial probability of being the second visitor on an inflorescence (in case of multiple foragers), the near–far foragers can exploit that patchiness later on. This can overcompensate the near–far forager for its disadvantage during the earlier part of the foraging process, when most of this patchiness is created.

The evolutionarily stable foraging strategy, which is determined by the fitness considerations of the foragers, obviously exerts a selective pressure on the nectar producing plants. In addition to its possible

TABLE 4

*Expected number of flowers emptied during first bouts and during second bouts (which follow a first bout by a Near–Far forager)*

(a) *Bouts of length 15*

Foraging strategy	First bout (mean $\pm$ SE)	Second bout (mean $\pm$ SE)
Random	10.9138	4.6617 $\pm$ 0.0092
Near	8.8408 $\pm$ 0.0250	3.6418 $\pm$ 0.0216
Far	10.7598 $\pm$ 0.0182	4.6322 $\pm$ 0.0191
Near–Random	10.6002 $\pm$ 0.0171	4.8146 $\pm$ 0.0194
Near–Far	10.8844 $\pm$ 0.0159	4.9106 $\pm$ 0.0197

(b) *Bouts of length 20*

Foraging strategy	First bout (mean $\pm$ SE)	Second bout (mean $\pm$ SE)
Random	12.9239	4.0075 $\pm$ 0.0125
Near	10.3686 $\pm$ 0.0287	3.1408 $\pm$ 0.0205
Far	12.7972 $\pm$ 0.0197	4.0322 $\pm$ 0.0189
Near–Random	12.7904 $\pm$ 0.0190	4.0806 $\pm$ 0.0192
Near–Far	13.1084 $\pm$ 0.0184	4.1190 $\pm$ 0.0196

The expected number for Random Search (first bout) was obtained using eqn (1). For all other cases, estimates (mean  $\pm$  SE) were obtained by computer simulations (5000 simulated bouts in each case).

influence on the nectar production process, the foraging strategy can affect the evolution of other plant characteristics, such as the size and the geometry of the inflorescence. These, in turn, will have an effect on the foraging strategies. This co-evolutionary process, a consequent of the mutual dependence of plants and pollinators, may be responsible to the development of vertical, spiral and other directionality-enhancing inflorescences, such as the unilateral inflorescences of *Heliotropium* spp. (Boraginaceae), *Gladiolus italicus* (Iridaceae) and *Platanthera holmboei* (Orchidaceae), where the probability of repeated visits to the same flower during a nectar foraging bout can be considerably reduced (to the mutual advantage of both the plant and the pollinators).

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## APPENDIX A

### Expected Number of Flowers Emptied During a Bout Using the Random Search Strategy

Consider an inflorescence with  $N$  full flowers, and a Random Search foraging bout of length  $M$ .

Let  $X_k$  ( $k = 1, 2, \dots, M$ ) be 0 or 1, according to whether the  $k$ -th visited flower was empty or full. Let  $p_k = \text{Prob}(X_k = 1)$ . Thus, the number of flowers emptied during the bout is  $\sum_{k=1}^M X_k$ , and its expectation  $\mu$  is  $\sum_{k=1}^M p_k$ .

Clearly,  $p_1 = p_2 = 1$ . For  $k \geq 2$ ,  $p_{k+1}$  equals  $p_k$  if the  $k$ -th flower was empty, and equals  $p_k - 1/(N-1)$  if the  $k$ -th flower was full. Thus,

$$p_{k+1} = p_k(1 - p_k) + [p_k - 1/(N-1)]p_k = p_k[1 - 1/(N-1)].$$

Hence,

$$p_k = [1 - 1/(N-1)]^{k-2} \quad (k = 2, 3, \dots, M),$$

and

$$\begin{aligned} \mu &= \sum_{k=1}^M p_k = 1 + \sum_{k=2}^M [1 - 1/(N-1)]^{k-2} \\ &= 1 + (N-1) \left[ 1 - \left( 1 - \frac{1}{N-1} \right)^{M-1} \right]. \end{aligned}$$

If originally not all the flowers are full, then this expression should be multiplied by the initial proportion of full flowers.

## APPENDIX B

### Expected Length of an Exhaustive Bout using the Random Search Strategy

Consider an inflorescence with  $N$  full flowers and a Random Search foraging bout, which goes on until all flowers have been emptied.

We call a visit successful, if it is to a full flower. Let  $X_k$  ( $k = 1, 2, \dots, N$ ) be the number of failures between the  $k-1$  and the  $k$ th success. Hence  $X_1 = 0$ . For  $k \geq 2$ ,  $X_k$  equals 0 with probability  $(N-k+1)/(N-1)$ , whereas with probability  $(k-2)/(N-1)$ ,  $X_k - 1$  has a geometric distribution, with expectation  $(k-2)/(N-k+1)$ . Thus the expectation of  $X_k$  is  $(k-2)/(N-k+1)$ . The total number of visits required to empty the entire inflorescence is  $N + \sum_{k=1}^N X_k$ , and its expectation is

$$\begin{aligned} \mu &= N + \sum_{k=2}^N [(k-2)/(N-k+1)] \\ &= 1 + (N-1) \sum_{t=1}^{N-1} t^{-1}. \end{aligned}$$

## APPENDIX C

### A Sufficient Condition for the Evolutionary Stability of Near-Far Search (Multiple Bouts)

Consider  $N$ -flower inflorescences, and let  $X$  be the number of bouts per inflorescence. Let  $p_m = \text{Prob}(X = m)$  ( $m = 0, 1, 2, \dots$ ), and  $E(X)$  the expectation of  $X$ . Thus, the probability that a bout is the  $k$ -th visitor to an inflorescence is

$$\pi_k = \left[ 1 - \sum_{m=1}^{k-1} p_m \right] / E(X). \quad k = 1, 2, 3, \dots$$

Suppose that Near-Far is the prevalent strategy in the population, and let  $W_k$  and  $M_k$  be the expected number of flowers emptied during the  $k$ th bout by a wild-type and a mutant forager, respectively. Near-Far is resistant to such mutants if

$$\sum_{k=1}^{\infty} W_k \pi_k > \sum_{k=1}^{\infty} M_k \pi_k.$$

Since  $M_k \leq N - \sum_{m=1}^{k-1} W_m$ , it follows that

$$\begin{aligned} \sum_{k=1}^{\infty} M_k \pi_k &\leq M_1 \pi_1 + M_2 \pi_2 \\ &\quad + (N - W_1 - W_2)(1 - \pi_1 - \pi_2). \end{aligned}$$

Also,

$$\sum_{k=1}^{\infty} W_k \pi_k \geq W_1 \pi_1 + W_2 \pi_2.$$

Hence, a sufficient condition for Near-Far to be resistant to these mutants is

$$W_1 \pi_1 + W_2 \pi_2 > M_1 \pi_1 + M_2 \pi_2 + (N - W_1 - W_2)(1 - \pi_1 - \pi_2),$$

or  $A\pi_1 + B\pi_2 > 1$ , where  $A = (N - M_1 - W_2)/(N - W_1 - W_2)$  and  $B = (N - M_2)/(N - W_1 - W_2)$ .

For a Random Search mutant,

$$M_k = M_1 \left( N - \sum_{m=1}^{k-1} W_m \right) / N.$$

Hence,  $A = [W_1(N - M_1) - M_1 W_2] / [M_1(N - W_1 - W_2)]$  and  $B = W_2(N - M_1) / [M_1(N - W_1 - W_2)]$ .