

Efficient harvesting of renewing resources

Kazuharu Ohashi and James D. Thomson

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

Many foraging animals return to feeding sites to harvest replenishing resources, but little is known about efficient tactics for doing this. Can animals with adequate cognitive abilities increase their efficiency by modifying their behavior according to memories of past experience at particular sites? We developed a simulation model of animals harvesting renewable resources from isolated patches in undefended, competitive situations. We compared four foraging tactics: (1) moving stochastically without using any information from past experiences (random searching); (2) moving stochastically, but going longer distances after encountering lower reward (area-restricted searching); (3) repeatedly moving along a fixed route (complete traplining); and (4) traplining, but sampling and shifting to neighboring rewarding patches after encountering low reward (sample-and-shift traplining). Following Possingham, we tracked both the resources actually harvested by a focal forager (i.e., rewards) and the standing crops of resources that accumulated at patches. Complete traplining always produces less variation in elapsed time between visits than random searching or area-restricted searching, which has three benefits: increasing the reward crop harvested, if resource renews nonlinearly; reducing resource standing crop in patches; and reducing variation in reward crop per patch. Moreover, the systematic revisitation schedule produced by complete traplining makes it more competitive, regardless of resource renewal schedule or competitor frequency. By responding to their past experiences, using sample-and-shift traplining, foragers benefit only when many patches are left unvisited in the habitat. Otherwise, the exploratory component of sample-and-shift traplining, which increases the movement distance and the variation in elapsed time between visits, makes it more costly than complete traplining. Thus, traplining will usually be beneficial, but foragers should switch between “impatient” (sample-and-shift traplining) and “tenacious” (complete traplining) traplining, according to temporal changes in surrounding situations. *Key words:* information use, Possingham, renewable resource, sample and shift, simulation model, trapline. [*Behav Ecol* 16:592–605 (2005)]

In nature, many animals need to collect foods from renewable resource patches scattered in space. Thus, patterns of movement among these patches are considered a key factor in their fitness. A well-known example of a patchily distributed renewable resource is nectar or pollen for floral visitors (Carthew and Goldingay, 1997; Dreisig, 1985; Gass and Garrison, 1999; Gilbert, 1980; Gill, 1988; Janson et al., 1981; Kadmon, 1992; Kamil, 1978; Lemke, 1984; Paton and Carpenter, 1984; Racey and Swift, 1985; Tiebout, 1993; Williams and Thomson, 1998). Many other types of foods, including extrafloral nectar (Dreisig, 2000; Schilman and Rocas, 2003), seeds (Cody, 1971), insects washed onto the river banks (Davies and Houston, 1981), exudate from trees (Schulke, 2003), fruits (Janson, 1998), foliage (Watts, 1998), and prey organisms involved in many predator-prey or parasitoid-host interactions (reviewed by Briggs and Hoopes, 2004), will also fall into this category.

Previous studies of how foragers should move among resource patches have often made two assumptions. First, returns to the same patch have been considered disadvantageous because, owing to depletion of the resource, it yields little or no reward (reviewed by Williams and Thomson, 1998; but see also studies on nectarivorous birds and mammals above). Second, animals have been assumed to forage without knowledge of patch locations and quality (resource renewal rate, competitor density, and the time elapsed since last visit, etc.), as if they are “searching” in novel habitats (e.g., Higgins

and Strauss, 2004). Based on these assumptions, previous studies have tended to focus on simple movement rules between successively visited patches that function to reduce revisitations, such as choices of “movement distance” and “turning angle” (Cartar and Real, 1997; Cresswell, 2000; Kipp, 1987; Pyke, 1978, 1981; Schmid-Hempel, 1986; Waddington, 1979; Zimmerman, 1979, 1981, 1982). With replenishing resources, these assumptions are valid at small spatial scales, such as movements between flowers on a plant or inflorescence, but not at larger scales. Revisitation at long intervals, approximating the replenishment schedules of the patches, can be efficient (Gill, 1988; Janson, 1998; Kadmon, 1992; Possingham, 1989; Stout and Goulson, 2002; Watts, 1998). Also, individual animals often confine their foraging within relatively small areas or territories for days or weeks (Comba, 1999; Davies and Houston, 1981; Gill and Wolf, 1975; Heinrich, 1976; Linhart, 1973; Manning, 1956; Paton and Carpenter, 1984; Thomson, 1996; Thomson et al., 1982). Such foragers may have opportunities to remember patch locations and quality and to use such memories to improve their performance. Analysis of such situations must consider such factors as the timing of returns to the same patches, the schedule of resource replenishment, and the possible usefulness of information gained from past experience at particular patches.

The efficiency of harvesting renewable resources will be influenced by two aspects of the timing of returns: the mean and the variance of elapsed time between visits on each patch. As the mean elapsed time between visits on each patch increases, a forager will encounter a larger reward crop at each visit (Bell, 1990; Cody, 1971; Davies and Houston, 1981; Williams and Thomson, 1998). Furthermore, Possingham’s (1989) simple analytical model showed that a reduction of variation in elapsed time between visits (“systematic foraging”) will bring three advantages to a forager. First, the mean resource standing crop encountered by random visitors will be

Address correspondence to K. Ohashi, who is now at Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba Science City, Ibaraki 305-8572, Japan. E-mail: kohashi@mail.ies.life.tsukuba.ac.jp.

Received 6 June 2004; revised 8 January 2005; accepted 17 January 2005.

lower, which will deter interlopers (“defense by exploitation”; Paton and Carpenter, 1984). Second, the mean reward crop encountered by the focal forager will be higher when resource renews in a nonlinear, decelerating way. Third, the variance of the reward crop encountered by the focal forager will be lower, which will be beneficial when risk-averse foraging is favored. Possingham also suggested two patterns of spatial use that could possibly reduce the variation in elapsed time between visits: “area-restricted searching” (ARS) and “traplining.” ARS is a well-known behavior of foragers that move longer distances after they encounter less reward, which has been reported for a variety of animals (reviewed by Motro and Shmida, 1995). Traplining or trapline foraging is repeated visitation to a series of resource points or patches in a predictable order, which has been reported for bumblebees (Comba, 1999; Heinrich, 1976; Manning, 1956; Thomson, 1996; Thomson et al., 1982, 1987), euglossine bees (Ackerman et al., 1982; Dressler, 1982; Janzen, 1971), butterflies (Gilbert, 1980), hummingbirds (Garrison and Gass, 1999; Gill, 1988; Tiebout, 1991), wagtails (Davies and Houston, 1981), bats (Lemke, 1984; Racey and Swift, 1985), and primates (Garber, 1988; Janson, 1998; Janson et al., 1981; Watts, 1998). Despite Possingham’s foundational analysis, however, there has been little further evaluation of the relative performance of the patterns of spatial use, especially in the competitive situations that prevail in nature.

The reward crop encountered by a forager at a patch will also depend on the intensity of competition and the resource renewal rates on the patch, as well as the elapsed time since its last visit to the patch. If foragers can respond to past experience at each patch, therefore, their foraging success may be improved. In the case of renewable resources, animals should respond to reward experience in a “win-stay, lose-shift” manner: stay or return to rewarding patches, but shift from or avoid less-rewarding patches. Foragers can move in a win-stay, lose-shift manner simply by responding to the reward encountered at the last one or few patches as in ARS. But if foragers can retain longer memories of previous reward experiences at particular patches and respond in a win-stay, lose-shift manner when they return to those patches, they might enjoy even higher foraging success. Many previous authors have inferred that trapliners can learn patch locations (Manning, 1956; Thomson, 1996) and also that they can respond to reward experience at particular patches (Cartar, 2004; Garrison and Gass, 1999; Gill, 1988; Thomson, 1988; Thomson et al., 1982). It is still unclear, however, how and whether such behavioral responses to past reward experience (hereafter, “information use”) can improve foraging success.

Therefore, we aimed to identify the benefits and costs of traplining versus less-structured searching behavior for foraging animals harvesting renewable resources from a series of undefended, isolated patches. Because the situations we wished to examine, such as competition among foragers moving in different nonrandom patterns, are analytically intractable, we used computer simulations instead of a more formal analysis. We assumed that foragers adopt one of four foraging tactics: (1) random searching (RS), (2) ARS, (3) complete traplining (CT), and (4) searching and shifting traplining. An animal may adopt these alternative patterns in a conditional way (reviewed by Bell, 1990; Helfman, 1990). However, here we aimed to characterize the primary consequences of each tactic (movement pattern or foraging path) rather than to simulate complex strategies that real animals might use. We addressed how and whether the foraging effectiveness of each tactic changes with variation in the resource renewal schedules, the spatial distribution of resources, the intensity of competition, and the tactics adopted by competitors.

THE MODEL

General

We consider one or more foragers harvesting food from N_p isolated patches that are randomly scattered in a two-dimensional space. Each position of foragers and patches was given as a pair of exact X and Y coordinates that vary from 0 to h . The spatial distribution of patches was generated by a Monte Carlo procedure, in which a pair of X and Y coordinates was chosen randomly for each patch (Figure 1). Throughout this paper, we use the term “resource” to denote food in patches and the term “reward” to denote food that is harvested by foragers. Resource renews within each patch according to one of two renewal schedules, an infinite linear increase or a linear increase toward a maximum value beyond which the standing crop of resource in a patch does not increase. Hereafter, we refer to these as linear and nonlinear renewal, respectively. In both cases, a forager arriving at a patch consumes all the accumulated resource. This assumption is frequently adequate for nectarivores visiting individual flowers (Kamil, 1978; Wolf et al., 1976), although in other cases, foragers may leave residual resource behind. Depletion to a fixed level can be easily introduced into the model, and it will not affect the results as long as the resource level left behind is constant. For simplicity, we assume that the depletion process is effectively instantaneous compared with the time scale of renewal, that is, the time spent at a resource patch is invariably zero. Thus, the standing crop of resource in a patch (R) is determined by the resource renewal rate (r), elapsed time since last visit (t_p), and the maximum resource abundance per patch (R_m):

$$\begin{aligned} R &= rt_p && \text{for } t_p \leq R_m/r, \\ R &= R_m && \text{for } t_p > R_m/r. \end{aligned} \quad (1)$$

When resource renewal is linear, R_m is set as infinite.

Foragers are nonterritorial; they compete with one another only by consuming resource. The exception occurs when two or more foragers arrive at a patch at exactly the same time; in this case, all foragers leave without consuming any resource. We assume that there is no time lost in any decision making, so all foraging time involves movements between patches. The movement speed is constant, and a forager moves one unit of distance per unit of time. Therefore, we measure distance and time with a single unit, t . By definition, all foraging movements are made between two distinct patches, that is, a forager never immediately returns to the patch it just left. In our model, each forager starts from any one of the N_p patches in the habitat and continues to travel among patches according to one of the four foraging tactics described below. The foraging stops when the cumulative travel time reaches a fixed value (T). We refer to T as “maximum foraging time.”

Foraging tactics

With the following computer algorithms, we generated four spatial-use patterns that we term (1) RS, (2) ARS, (3) CT, and (4) sample-and-shift traplining (SST). Descriptions of the baseline parameter values for the model and the model variables are given in the Appendices.

It is worth emphasizing that each tactic’s algorithm is just an arbitrary tool to generate a movement pattern that characterizes each tactic. We focused on how fundamentally different patterns of movement (foraging paths and reward history) affected the foraging success of the forager rather than on the “realism” of the algorithms that generated those patterns. Irrespective of the cognitive processes that animals actually

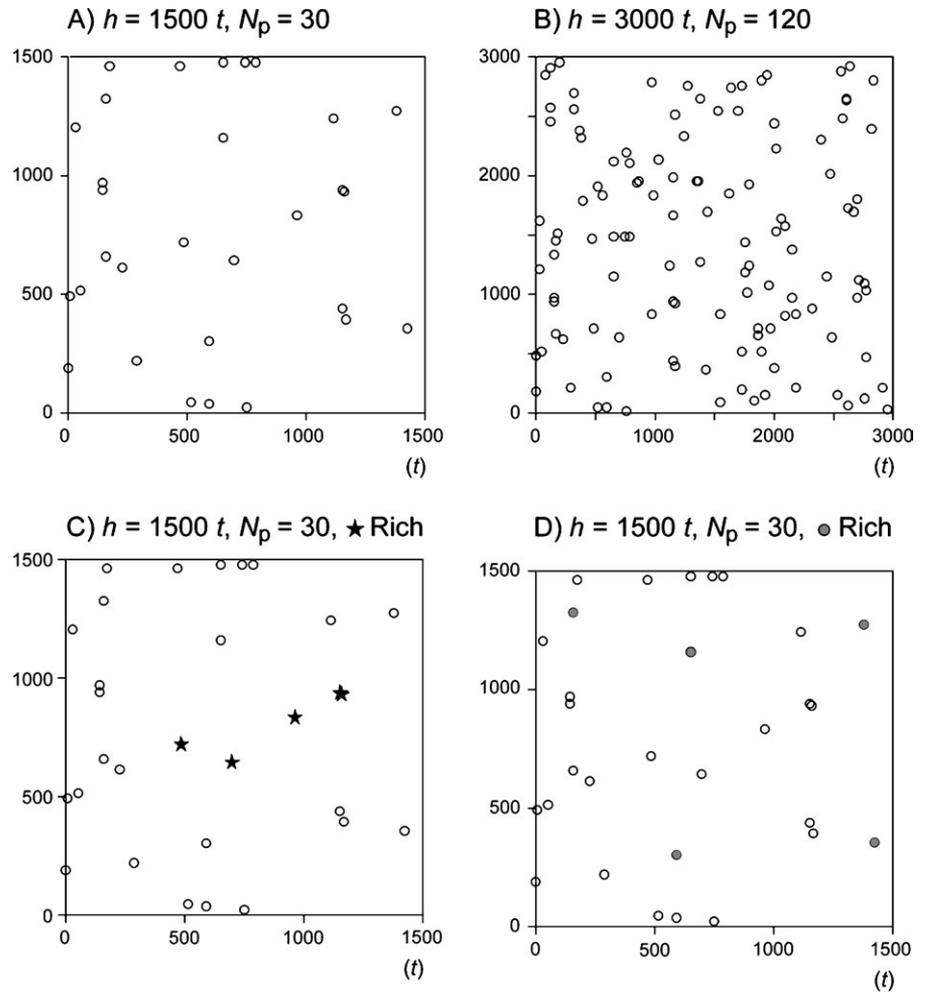


Figure 1

Distributions of resource patches. (A) Small habitat, (B) large habitat, (C) small habitat where five rich patches were spatially “aggregated,” and (D) small habitat where five rich patches were spatially “scattered.” Each symbol represents one patch. Small habitat (A, C, and D) is extracted from the southwest corner area ($1500 \times 1500t^2$) of the large habitat (B) which is generated by choosing random pairs of X and Y coordinates repeatedly.

use, for example, any kind of algorithm that produces traplining behavior should give similar results.

Random searching

Truly random movement (i.e., selecting the next destination by a random draw from the set of all patches) is not a realistic behavior. Based on observations in pollination systems (e.g., Zimmerman, 1979), therefore, we preferred to model a probabilistic search tactic (Higgins and Strauss, 2004) that makes shorter interpatch moves more common than longer moves. We define eight distance ranges, D_1 – D_8 , each of which has an upper and a lower limit of distance ($0 < D_1 \leq l_1$, $l_1 < D_2 \leq l_2$, ..., $l_7 < D_8 \leq l_8$). One of the eight distance ranges is chosen at a probability P_1 – P_8 , respectively ($P_1 > P_2 > P_3 > P_4 > P_5 > P_6 > P_7 > P_8$). The next visit is made to a randomly chosen patch within the chosen range. Thus, the probability of choosing a patch declines with its distance from the current patch, but the choice of a patch is random within the range. When there is no relevant patch within the range, the forager enlarges the distance range by $20t$; for example, D_2 is enlarged to $D_2(l_1 - 10 < D_2 \leq l_2 + 10)$. The same procedure is repeated until the area includes at least one patch. We assign distance ranges and probabilities to enable fair comparisons among tactics.

Area-restricted searching

We created a variant of RS in which case where a forager conditionally moves longer distances after it encounters less-rewarding patches. For simplicity, we specify a single

threshold crop encountered (C_i) for choosing between two search modes, “near” and “far.” We restricted our analysis to situations where the maximum resource level per patch (R_{m}) is rarely reached when there are two or more foragers (so the reward level is effectively depressed by competition). In such situations, the average reward crop will be inversely proportional to the number of foragers in the habitat, which should also affect the decision making of foragers. Hence, we assumed that animals adopt an operational threshold crop, C_i/N_f . Let the reward crop encountered and the number of foragers in the habitat be C_e and N_f , respectively. When $C_e > C_i/N_f$, one of the two distance ranges ($D_{1,2}$) is chosen at a probability $P_1/(P_1 + P_2)$ and $P_2/(P_1 + P_2)$, respectively. When $C_e \leq C_i/N_f$, one of the other three distance ranges (D_{3-8}) is chosen at a probability P_3/P_{far} , P_4/P_{far} , P_5/P_{far} , P_6/P_{far} , P_7/P_{far} , and P_8/P_{far} , respectively, where P_{far} is $P_3 + P_4 + P_5 + P_6 + P_7 + P_8$. In both cases, the next visit is made on a randomly chosen patch within the range. When there is no available patch within the range, the forager enlarges the distance range, as in RS.

Complete traplining

The algorithm for this tactic consists of two phases: (A) establishment of the trapline in the first circuit and (B) consolidation in subsequent circuits. In phase A, the forager moves preferentially between close patches, but its moves are further influenced by an additional “force” that repels the forager from recently visited patches but draws it back to

patches visited long ago. This “magnetic force” exerted on a forager at the patch p is determined as:

$$M_p(t_f) = a(t_f - b), \quad (2)$$

where t_f is elapsed time since last visit made by the focal forager. Parameters a and b are both positive constants. For patches that the forager had never visited before, $M_p(t_f)$ is given as 0. Immediately after the forager visited the patch ($t_f = 0$), $M_p(t_f)$ is lowest and negative (a repulsive force). Then $M_p(t_f)$ increases linearly with increasing t_f at a constant rate a . After t_f exceeds b , $M_p(t_f)$ changes to a positive value (a gravitational force). Next, a score (S) is calculated for each of the $(N_p - 1)$ patches in the habitat:

$$S = M_p(t_f) + 1/d + E, \quad (3)$$

where d is the distance from the current patch and E is a random number generated from a normal distribution, with mean μ and variance δ . Then the forager visits a patch with the highest score. The error term E introduces some stochasticity and avoids producing identical trapline sequences. By repeating such a choice procedure, the forager moves between close patches that it had never visited before. As time goes on, the forager is increasingly drawn back to the patches it had visited during its earliest stage, as their scores (S) increase. Finally, the forager returns to the starting patch or one of these early patches, which ends its circuit. Thus, the formation of a circuit occurs purely through following the algorithm of phase A. Once a circuit is completed, the sequence is “memorized” by the forager as its trapline. For the rest of the maximum foraging time (phase B), a CT forager just repeats this trapline. Throughout phase B, each patch is visited once by the forager in one circulation. The total length of an entire trapline (travel distance or time before a forager returns to the same patch) is positively correlated with the parameter b in Equation 2 (in contrast, the parameter a has no effect on traplines). Hereafter, we define the parameter b as the “repulsion period.”

Sample-and-shift traplining

Trapliners may modify their traplines in a win-stay, lose-shift manner in response to the reward experience at each patch in the latest circuit. We model this tactic by modifying phase B in CT. To keep the algorithm simple, we introduce a single threshold encountered crop (C_a) that determines whether or not a forager samples another patch in the next circuit; similarly, we introduce a second threshold encountered crop (C_b) that determines whether or not the forager incorporates the sampled patch as a new member of the trapline. When the forager encounters a less-rewarding patch in its trapline, that is, the reward crop (C_e) is C_a/N_f or smaller, it samples another patch in the next circuit instead of revisiting the patch, according to the same rules adopted in RS. If the sampled patch is rewarding ($C_e > C_b/N_f$), the forager drops the former patch from the trapline and employs the sampled patch for the following circuits; if the sampled patch is less rewarding ($C_e \leq C_b/N_f$), the forager returns to the former patch in the next circuit. Note that the forager determines whether it employs the sampled patch or not purely depending on the reward crop it encountered at the last visit. Even if a patch had been dropped from the trapline in the past, the same patch may be employed later again if the forager finds it rewarding by sampling.

Currencies

Because the maximum foraging time (T) is usually reached while the forager is traveling between patches, the total time

spent from the start to the last patch visited, which is equivalent to the total distance moved, is usually slightly smaller than T and varies among runs and foragers. Therefore, we calculate foraging success as (total reward crop collected during a foraging trip)/(total time spent from the start to the last patch visited). This index, rate of reward intake, represents long-term foraging success of individual foragers and is an appropriate currency in cases where animals are expected to maximize their long-term rate of energy intake. The rate of reward intake is influenced by two factors: (1) the time elapsed since the last visit (by any forager) at each patch visited and (2) the total distance moved. When resources are replenished linearly, the elapsed time since the last visit will be directly related to the reward crop collected. When resource renewal saturates at a time scale similar to the average interarrival time, an increase in elapsed time often does not increase reward crop in a linear way, but a decrease in elapsed time frequently reduces reward crop in a linear way. Therefore, reward crop will be smaller if the elapsed time between visits to a patch is more variable, even if the average is the same. In this situation, the rate of reward intake would be increased by reducing variation in elapsed time between visits. To evaluate this effect, therefore, we compare linear and nonlinear resource renewal conditions. We also use another currency of foraging performance, that is, the coefficient of variance (CV) of reward crop per patch, to evaluate the profitability of each tactic for risk-averse foragers that maximize short-term foraging success (Real and Caraco, 1986).

RESULTS

Noncompetitive situations

To clarify the basic characteristics of each foraging tactic, we first show cases where there is no competitor in the same habitat. For RS and ARS runs, the values for parameters l_{1-8} and P_{1-8} were determined from the distribution of movement distances in CT (see Appendices) so that movement distance does not differ between RS and CT.

Figure 2 shows typical dynamics of the reward crops encountered at successive patches by a forager. When resource renewal is linear, a RS forager frequently encounters patches with little or no reward but occasionally hits “jackpot” patches with large reward crop. The low rewards come about because a RS forager frequently revisits patches that it has recently visited; the jackpot patches are those that, by chance, have not recently been visited. The rate of reward intake in RS largely depends on the number of jackpot patches hit. This large variation in elapsed time between visits causes a drastic decrease in the rate of reward intake when resource renewal is nonlinear (Figure 2; Table 1). The ARS tactic reduces the frequency of short-interval revisitations while increasing the frequency of hitting a jackpot, compared with RS (Figure 2). Therefore, when resource renewal is linear, an ARS forager enjoys a higher rate of reward intake than any other forager, despite its increased movement distance (Table 1). When resource renewal is nonlinear, however, the rate of reward intake in ARS decreases drastically because the CV in elapsed time between visits is larger than one (Figure 2; Table 1). The average rate of reward intake does not vary significantly with the threshold reward crop (C_t) (Kendall’s tau = 0.18, $p = .38$, $n = 15$; each average is calculated from 100 foraging trips).

In noncompetitive CT and SST, the reward crop encountered at each patch is constant after a trapline is established. The rate of reward intake increases with the repulsion period (b) because no patch is revisited before all the other patches in the trapline are visited. The mean number of patches

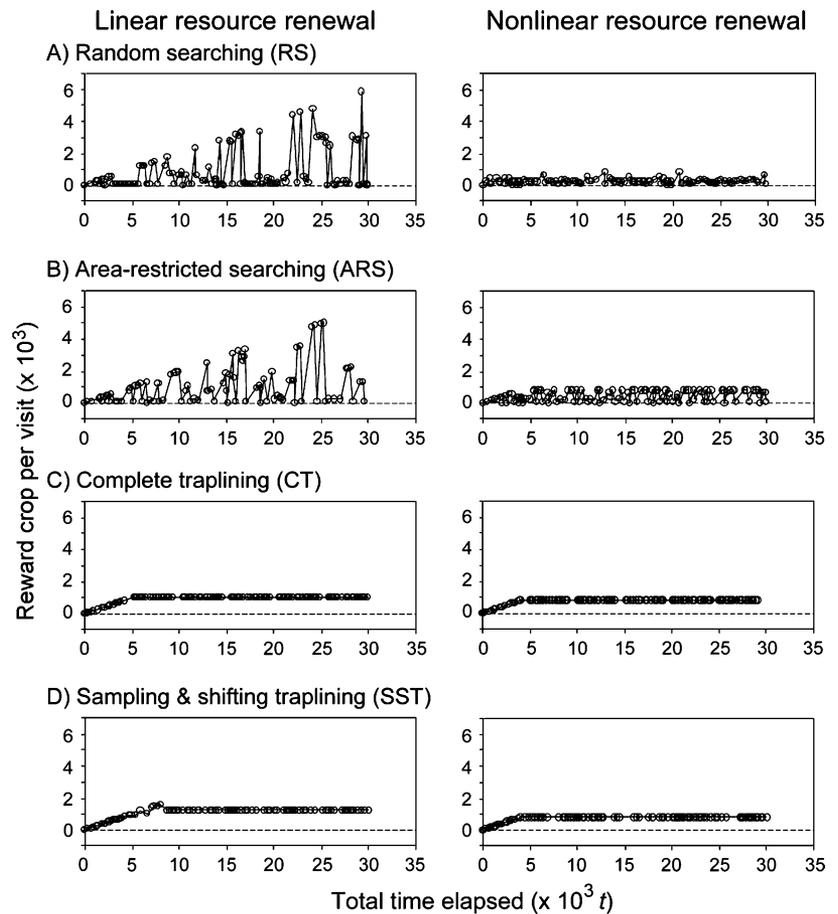


Figure 2
Rewards obtained at each visit in noncompetitive situations. Linear and nonlinear resource renewals are considered. Note that the jackpots are encountered by RS and ARS foragers but not by CT or SST.

included in a trapline is 19.3 (SD = 2.05, $n = 100$ foraging trips) when the repulsion period $b = 4000t$, which does not differ between CT and SST. In the case of Figure 2, the rate of reward intake does not differ among RS, CT, and SST as long as resource renewal is linear (Table 1). However, when resource renewal is nonlinear, CT and SST yield a higher rate of reward intake than RS and ARS (Table 1). This is

because the systematically scheduled revisitation minimizes variation in elapsed time between visits and, in turn, reduces the time that a patch spends not renewing. Moreover, the rate of reward intake in SST is slightly smaller than in CT for two reasons: first, variation in elapsed time between visits is larger in SST than in CT; second, the mean movement distance between patches is longer in SST than in CT.

Table 1
Foraging performance in noncompetitive situations

Tactic	Rate of reward intake	Average reward crop encountered	Average movement distance (t)	Average CV of elapsed time between visits	Average CV or reward crop per patch
(A) Linear					
RS	3.50 ± 0.50	907.2 ± 145.7	261.9 ± 21.0	1.36 ± 0.14	1.36 ± 0.14
ARS	3.82 ± 0.43	1076.9 ± 118.6	284.7 ± 12.8	1.16 ± 0.10	1.16 ± 0.10
CT	3.55 ± 0.38	928.0 ± 53.4	267.1 ± 34.7	0.29 ± 0.022	0.29 ± 0.022
SST	3.52 ± 0.36	1255.5 ± 104.9	364.9 ± 45.0	0.42 ± 0.050	0.42 ± 0.051
(B) Nonlinear ($R_m = 800$)					
RS	1.55 ± 0.12	404.2 ± 43.7	263.0 ± 20.3	1.37 ± 0.15	0.79 ± 0.0074
ARS	1.73 ± 0.11	489.0 ± 22.4	285.2 ± 12.2	1.13 ± 0.10	0.65 ± 0.027
CT	2.87 ± 0.42	731.3 ± 74.0	262.9 ± 38.5	0.28 ± 0.024	0.25 ± 0.018
SST	2.15 ± 0.24	711.0 ± 9.96	338.1 ± 36.9	0.54 ± 0.033	0.29 ± 0.021
(C) Nonlinear ($R_m = 500$)					
RS	1.13 ± 0.069	290.0 ± 24.2	260.0 ± 18.7	1.37 ± 0.14	0.67 ± 0.063
ARS	1.21 ± 0.064	343.4 ± 10.5	286.9 ± 12.4	1.17 ± 0.11	0.55 ± 0.020
CT	1.77 ± 0.25	469.8 ± 4.40	273.6 ± 38.6	0.29 ± 0.022	0.21 ± 0.018
SST	1.38 ± 0.14	461.7 ± 5.48	341.6 ± 35.2	0.54 ± 0.039	0.24 ± 0.019

Values are mean \pm SD, calculated from 100 iterations of each condition.

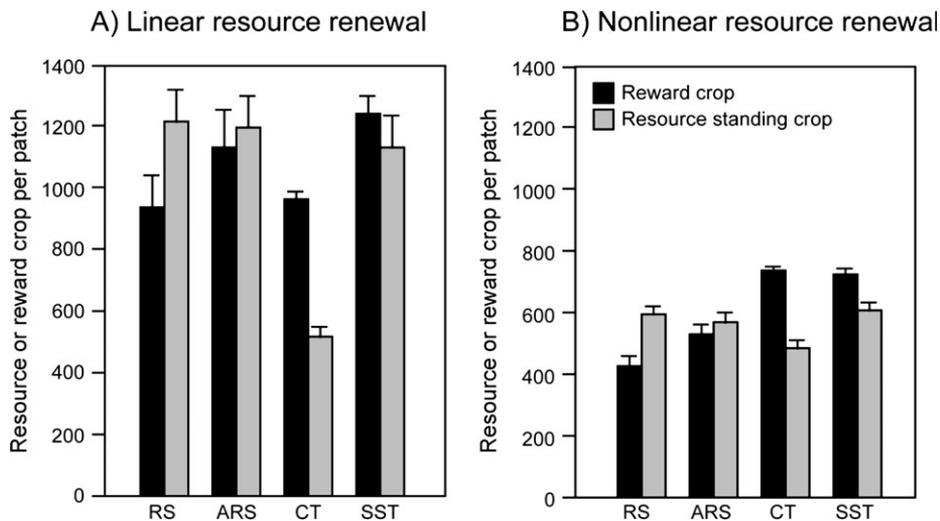


Figure 3
Effects of foraging tactics on spatial distribution of resource standing crop. Boxes and bars are mean \pm SD, calculated from one foraging trip in which patch number in a trapline is 19.

Variation in elapsed time between visits also affects two other aspects of foraging, the variation in reward crop per patch and the spatiotemporal distribution of resource standing crop among patches. The former determines how much better the foraging tactic is for risk-averse foragers (see *Currencies*), and the latter determines how effectively the tactic could decrease reward for intruders that randomly sample resources from patches. The mean CV of reward crop per patch is always ranked as RS > ARS > SST > CT, regardless of resource renewal schedules (Table 1). The difference between trapliners (CT and SST) and nontrapliners (RS and ARS) is larger than those between CT and SST or RS and ARS, as expected from variation in elapsed time between visits. Figure 3 compares the mean and SD of reward crop encountered by foragers with those of resource standing crop when we sampled patches 100 times randomly in space and time. When resource renewal is linear, the mean resource standing crop in traplined patches in CT is reduced by almost one-half of the mean reward crop. This is because the amount of resource gained by randomly sampling patches at any time is always less than or equal to the constant reward crop encountered by the CT forager. In SST, the mean resource standing crop at visited patches is much higher than in CT, although it is still lower than the mean reward crop. This is because some patches are visited by the SST forager only at the beginning of a foraging bout. These patches accumulate a large amount of resource as the bout progresses. Thus, single CT foragers (and SST foragers with established traplines) could discourage any possible intruders from staying in their foraging areas by depressing the mean resource standing crop. In contrast, no single nontrapliner (RS or ARS) could decrease the mean resource standing crop below the reward crop it encounters itself. Trends are similar when resource renewal is nonlinear, although the difference between reward crop and resource standing crop is smaller.

In our model, trapliners do not minimize total movement distance to visit all the patches in their traplines. In other words, they do not solve the so-called traveling salesman problem (e.g., Cramer and Gallistel, 1997). However, our results suggest two possible advantages of reducing route distance. First, short routes may reduce net movement cost when resource renewal is nonlinear because the cost of increased distance cannot be fully counterbalanced by the increase in reward crop. For example, the rate of reward intake of a trapline with 18 patches decreases with its route distance when $R_m = 800$ (Kendall's tau = -0.96 , $p < .0001$, $n = 22$ foraging trips). When resource renewal is linear,

however, the cost of increased distance is fully counterbalanced by the increase in reward crop encountered at each patch (Kendall's tau = -0.18 , $p = .27$, $n = 22$ foraging trips where each trapline includes 18 patches). Second, short routes may decrease the mean *resource standing crop* (i.e., mean *reward crop* for intruders) when resource renewal is linear. For example, the mean resource standing crop at traplined patches increases with route distance of a trapline with 18 patches (Kendall's tau = 0.48 , $p = .0025$, $n = 22$ foraging trips). When resource renewal is nonlinear, however, this advantage will decrease because the reward crop encountered approaches the resource standing crop.

1 Versus 1 competition between different tactics

We simulated competition between two foragers, using the same parameter combinations as in Table 1. As summarized in Figure 4, a RS forager is highly vulnerable to competition from any type of forager because its foraging success largely depends on jackpot patches that are vulnerable to being taken by a competitor. Using ARS decreases this vulnerability to competition, but the improvement is not large enough to surpass trapliners. Changes in the threshold reward crop (C_i ; 100–1600) do not alter the qualitative results. Of the four tactics, CT yields the highest foraging performance, especially when resource renewal is nonlinear. Surprisingly, the information-using SST tactic is actually worse than CT, both in the rate of reward intake and in the CV of reward crop per patch. This is because SST foragers move between more distant patches (e.g., SST versus CT competition: mean interpatch distance \pm SD = $384.9 \pm 49.8t$, $n = 100$ foraging trips; see also Table 1) and more variation in elapsed time between visits in competition. SST use does decrease the number of shared patches at which two circuits overlap (number of shared patches in SST versus CT: on the first circuit mean \pm SD = 12.2 ± 3.7 , on the last circuit mean \pm SD = 8.30 ± 3.0 , $n = 100$ foraging trips). These costs of information use are most obvious in SST versus CT competition; the reduction of shared patches benefits both the CT forager and the SST forager, but the SST forager incurs all of the costs of increased movement and variation in elapsed time.

Competition among CT and other tactics with different frequencies

Having demonstrated the superiority of CT in 1 versus 1 competitions, we then introduced variation in the number of

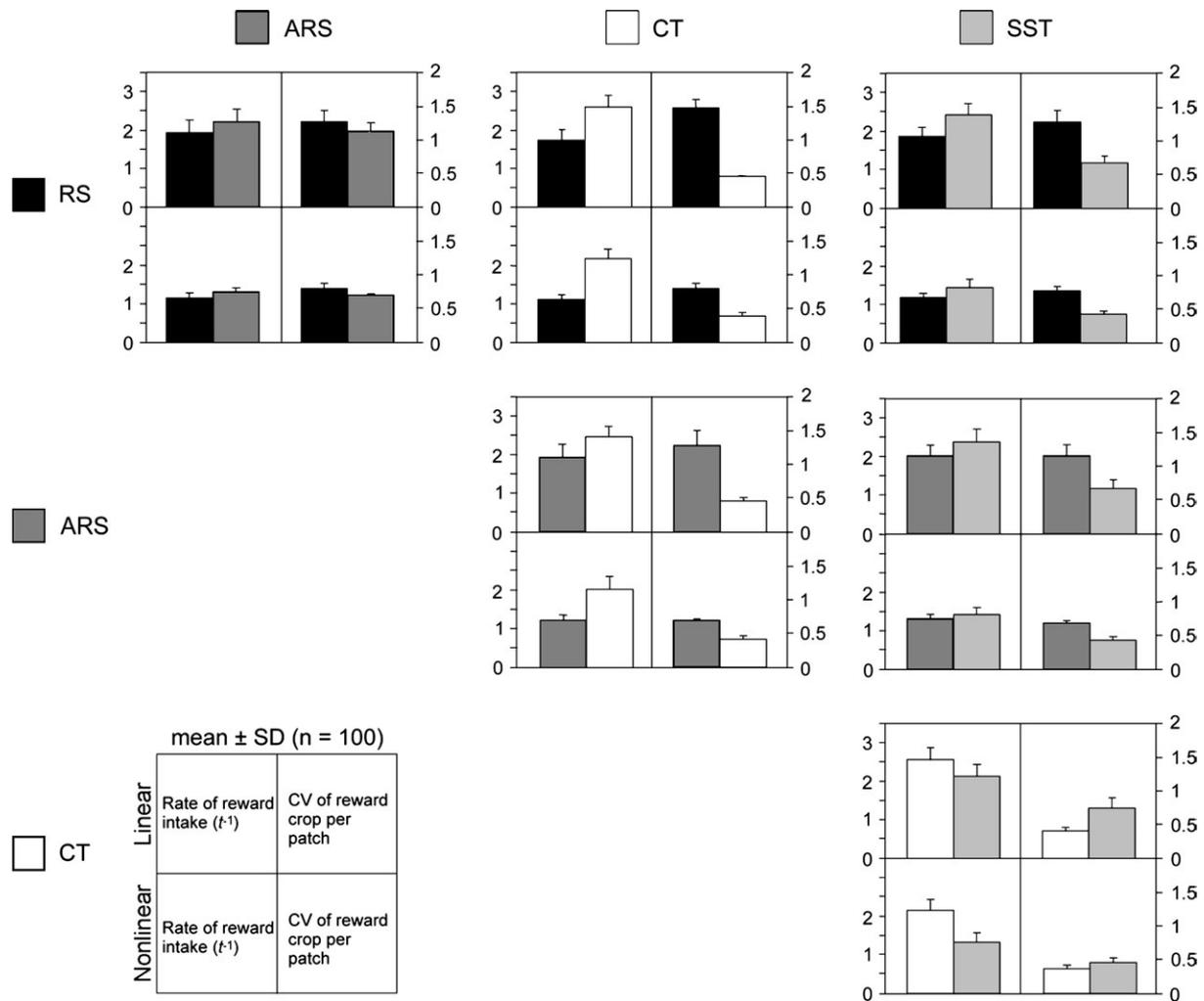


Figure 4
Foraging performance in 1 versus 1 competition between different foraging tactics. Boxes and bars are mean \pm SD, calculated from 100 iterations of each competition.

competitors to see if the advantages of CT still hold. Figure 5A shows cases where a CT forager is added into a habitat in which all the others adopt another tactic. When RS foragers dominate a habitat, a CT forager obtains a higher rate of reward intake and a lower CV of reward crop per patch. Differences between the two tactics become smaller at higher RS densities, but they still exist even when there are 10 RS foragers. The trend in ARS versus RS and SST versus RS are parallel to CT versus RS, although SST yields higher performance than ARS.

Figure 5B shows cases where a non-CT forager is added into a habitat in which all the others adopt CT. None of the three types of forager can either obtain a higher reward intake or a lower CV of reward crop per patch than CT foragers; the foraging performances of non-CT foragers rank as SST > ARS > RS. Differences between the two tactics become smaller at higher CT densities.

Because these comparisons pit one tactic against another, they are reminiscent of attempts to specify an evolutionarily stable strategy (ESS) (Maynard Smith, 1982). We should stress, however, that our intention here is not to find an ESS. Our model describes competition at an ecological scale, that is, competition in one habitat where an individual adopts one fixed tactic of foraging. If a tactic is less efficient in a particular situation, it does not mean that it would be expected to vanish

from an animal's repertoire. Losers or potential losers may change their tactics depending on competitive situations, their foraging experience, age, and physical conditions ("mode switching"; Bell, 1990; Helfman, 1990). Alternatively, they could move to other habitats, in which case, the intensity of competition would decrease. Optimal or ESSs for real animals will be a complex of these behavioral options, including decisions about switching between different tactics or habitats ("conditional strategy"; Dominey, 1984); such an analysis is beyond the scope of this paper. Our concern is to understand mechanistically how the foraging success of a trawler is influenced by the number of competitors and the tactics they adopt.

Competition among foragers with the same tactic

Even though CT is the most effective tactic in competition with the others, ARS- or SST-dominated habitats might yield a higher foraging performance than a CT-dominated habitat by avoiding excess competition among individuals, that is, "resource partitioning." To examine this possibility, we compared cases where various numbers of foragers in the habitat adopt the same tactic (Figure 6). When resource renewal is linear, all of the four tactics yield similar rates of reward intake, except that two or three SST foragers yield the highest

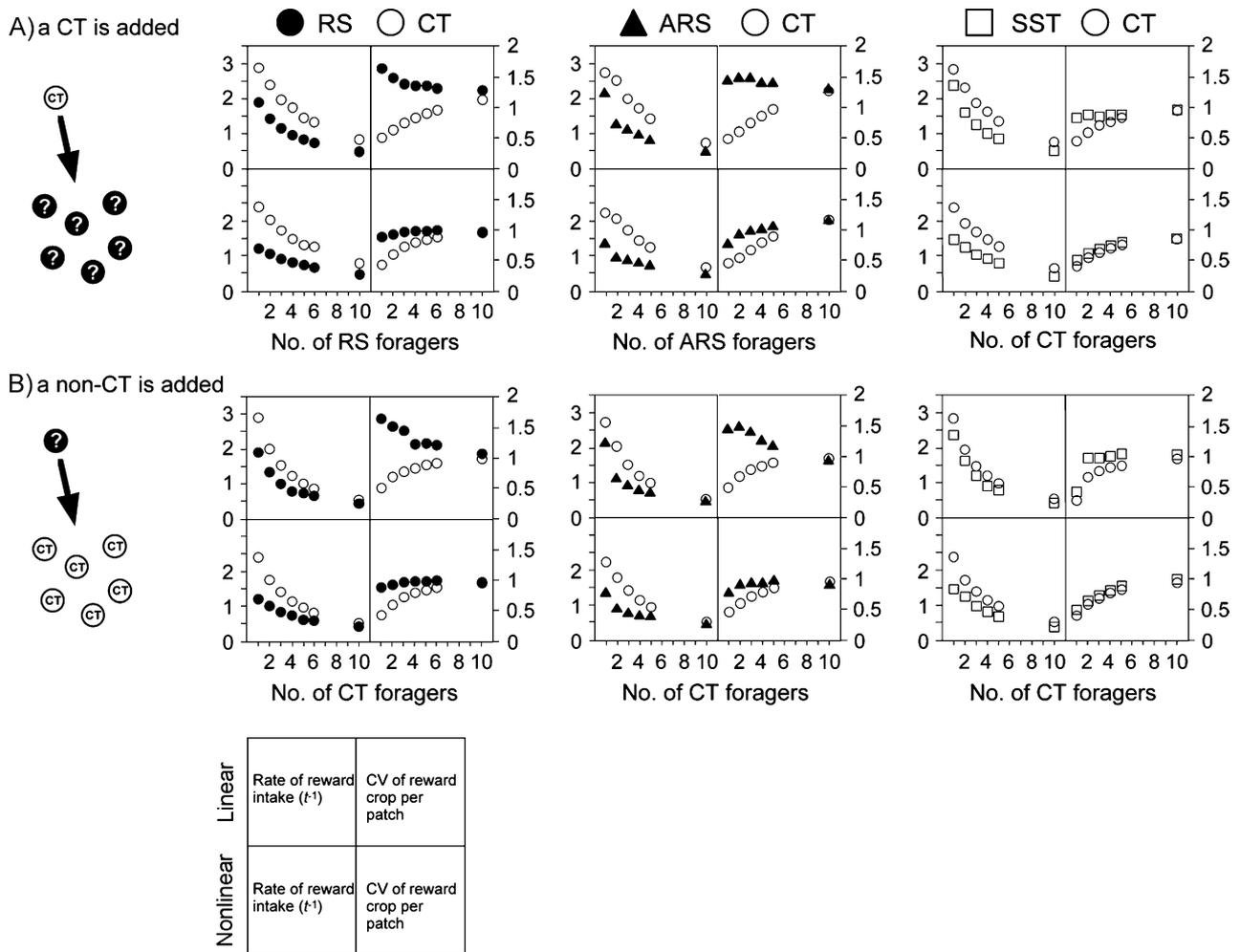


Figure 5 Foraging performance of CT and others under various competitor frequencies. (A) A CT forager is added into the habitat dominated by another tactic. (B) A non-CT forager is added into the habitat dominated by CT. Each symbol represents the mean, calculated from 100 iterations of each competition. Error bars are omitted because they are too small to draw.

rate of reward intake. When resource renewal is nonlinear, trappliners (CT and SST) gain higher rates of reward intake than nontrappliners (RS and ARS). Information use in ARS and SST, however, does not increase the rate of reward intake compared with RS or CT. As competitor density increases, the rate of reward intake decreases monotonically, and all tactics perform similarly poorly. On the other hand, trappliners achieve a lower CV of reward crop per patch than nontrappliners, irrespective of competitor densities or resource renewal schedules.

Here, we also show how the repulsion period (b) affects the foraging performance of CT in competition. When two or more CT foragers are competing, they often produce partly similar trapplines because of their tendency to move between close patches. Figure 7 shows an example where two CT foragers are competing. As the repulsion period increases, the number of shared patches at which two or more circuits overlap also increases due to an increase in trappline length. As more patches are shared, the mean reward crop per patch decreases (linear renewal: Kendall's tau = -0.18 , $n = 200$ individual foraging trips, $p = .0002$; nonlinear renewal $R_m = 800$: Kendall's tau = -0.12 , $n = 200$ individual foraging trips, $p = .012$), and the CV of reward crop per patch increases (linear renewal: Kendall's tau = 0.26 , $p < .0001$, $n = 200$

individual foraging trips; nonlinear renewal with $R_m = 800$: Kendall's tau = 0.22 , $p < .0001$, $n = 200$ individual foraging trips). Because of these overlap effects, the rate of reward intake of these foragers initially increases but then saturates (when resource renewal is linear) or decreases (when resource renewal is nonlinear) with increases in the repulsion period.

Competition in a larger habitat

As we have seen, CT is the most robust tactic in various competitive situations. Nevertheless, here we suggest a situation where a temporary adoption of SST could be more advantageous than a continuous adoption of CT. Recall that SST yields the highest rate of reward intake when there are only two or three foragers and resource renewal is linear (Figure 6A). This might happen because CT foragers cannot reduce the overlaps among trapplines even if there are more patches left unvisited, but SST foragers can move into such "competitor-free" patches by modifying their trapplines. To test this hypothesis, we examined changes in foraging performance through time when a SST forager is added into a large habitat ($N_p = 120$) in which all the others adopt CT. As shown in Figure 8A, information use in SST decreases more shared

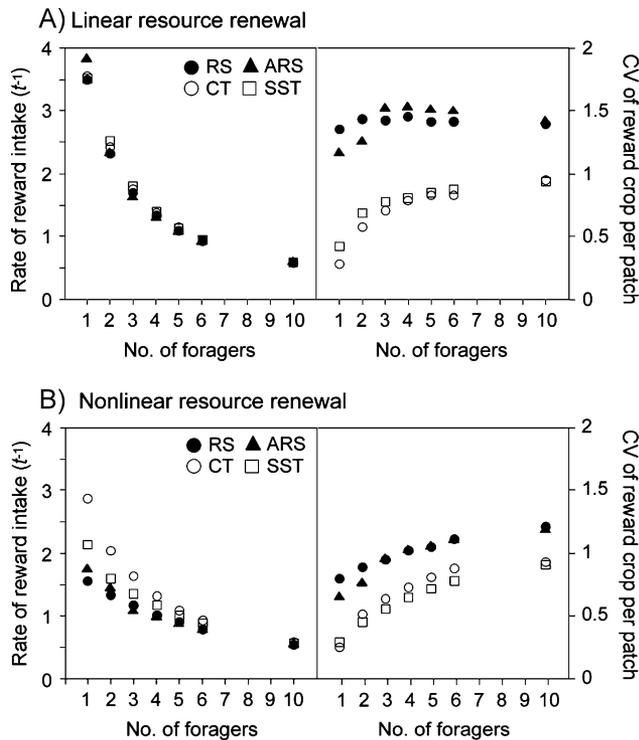


Figure 6
Foraging performance when a habitat is dominated by the same tactic. Each symbol represents the mean, calculated from 100 iterations of each competition. Error bars are omitted because they are too small to draw.

patches for a SST forager than for CT foragers. In spite of increased movement costs in SST, this shift to less-competitive patches makes a SST forager superior to CT foragers in terms of the rate of reward intake during the latter half of the foraging period (Figure 8B). On the other hand, the CV of reward crop per patch in SST is still higher than in CT during the latter half of foraging time. These results suggest that sampling and shifting could become advantageous, but only temporarily, when many patches are left unvisited in the habitat.

Effects of resource heterogeneity in space

In all the above simulations, we assumed that patches in a habitat are homogeneous in resource renewal rate. When resource renewal rate varies among patches, however, foraging performance of each tactic and its competitive ability might be changed. First, information-use foragers (ARS and SST) might be better at discovering and concentrating on rewarding patches, so that they could surpass CT competitors in the same habitat. Second, average foraging performance may be higher in an ARS- or SST-dominated habitat than in a CT-dominated habitat, because of the resource partitioning among individuals. To examine these possibilities, we ran simulations with five “rich” patches with higher resource renewal rates ($r = .6t^{-1}$) and 25 “poor” patches with lower resource renewal rate ($r = .12t^{-1}$). Note that the average resource renewal rate per patch in the habitat is not changed from the homogeneous condition ($r = .2t^{-1}$). Two types of spatial distribution of rich patches were examined (Figure 1C): (1) spatially aggregated within the habitat and (2) spatially scattered within the habitat.

Patterns in the rate of reward intake are almost identical to those in homogeneous conditions when two different tactics

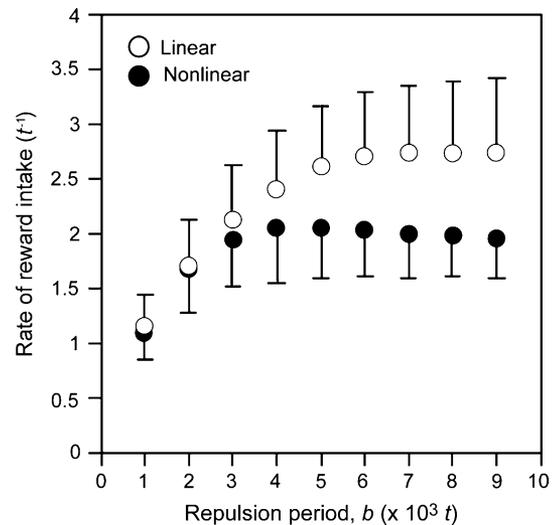


Figure 7
Relationship between repulsion period, b , and rate of reward intake (mean + or - SD) when two complete trapliners are competing. The declines in reward intake with repulsion period are due to increasing overlap between larger traplines.

compete. The CV of reward crop per patch also follows qualitatively similar patterns to, but is larger than, those in homogeneous conditions. In other words, CT remains the most efficient tactic in various competitive situations even when patches vary in resource renewal rate. Results are not shown here because they are almost identical to Figures 4 and 5.

Figure 9 shows the relationships between foraging performance and the competitor density in cases where all foragers in a habitat adopt the same tactic, which is comparable to Figure 6A. To see the maximum effects of spatial heterogeneity of patch quality, here we show only cases where resource renewal is linear. When rich patches are spatially aggregated and competitor densities are very low, both ARS and SST increase their rates of reward intake compared with those in homogeneous conditions, and SST foragers enjoy the highest rate. RS and CT foragers, on the other hand, yield similar rates with those in homogeneous conditions. These results arise because only ARS and SST foragers increase their relative visitation rate to rich patches, calculated as $100 \times (\text{number of visits to focal patch}) / (\text{sum of number of visits to all patches in the habitat})$ (Table 2). On the other hand, qualitative patterns of the CVs of reward crop per patch are similar to, but larger than, those in homogeneous conditions.

When rich patches are spatially scattered, only SST foragers increase the rate of reward intake, while all the others decrease it compared with homogeneous conditions. These results are consistent with the pattern that only SST foragers increase their relative visitation rate to rich patches, while the others do not (Table 2). In spite of these changes in the rate of reward intake, qualitative patterns of the CVs of reward crop per patch are similar to, but larger than, those in homogeneous conditions.

In summary, information use in heterogeneous conditions could increase the rate of reward intake at a habitat level, by adjusting the relative visitation rates to patches according to their resource renewal rates. SST foragers can always concentrate on rich patches irrespective of spatial distributions of those patches, but ARS foragers can do it only when rich patches are spatially aggregated. This advantage, however, dissipates when competitor density is high or when multiple tactics compete in the same habitat. CT is still the most

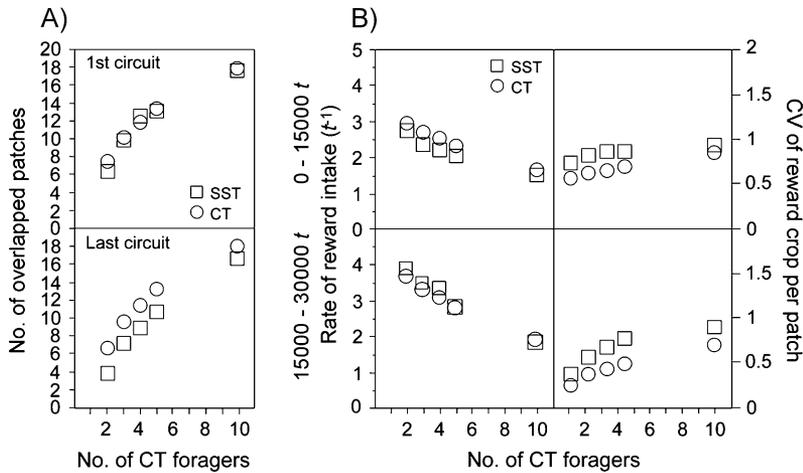


Figure 8
Changes in foraging performance through time when a SST forager and one or more CT foragers are competing in a large habitat. (A) Change in the number of shared patches among the first and the last circuits. (B) Changes in the rate of reward intake and the CV of reward crop per patch. The first row is the former half of foraging time (0–15,000t), and the second row is the latter half of foraging time (15,000–30,000t).

efficient tactic in those conditions, unless any large competitor-free space exists in the habitat.

DISCUSSION

Advantages of traplining behavior

The advantages of traplining depend on the intensity of competition. In noncompetitive situations, systematic revisitation in CT offers three essential benefits: (1) an increase in the rate of reward intake when resource renews in a decelerating (or saturating) way, (2) a decrease in the variation

in reward crop per patch, which will increase the short-term rate of reward intake for a risk-averse forager, and (3) a decrease of the mean resource standing crop per patch, which will discourage intruders from foraging on these patches (defense by exploitation). All these advantages are identical with those for systematic foraging in the analytical model of Possingham (1989), and we will refer to them as “Possingham effects.”

In moderately competitive situations, a trapliner cannot reduce variation in elapsed time between visits on patches that are frequently visited by competitors. As a trapline often spreads widely in space, however, other patches in a trapline may not be shared by competitors. On these less-competitive patches, a trapliner can maintain low variability of elapsed time between visits and therefore benefits from Possingham effects. Moreover, low variability of elapsed time between visits increases the rate of reward intake even when resource renewal is linear because it reduces chances that patches are depleted by others after they accumulate a large amount of resource. For these reasons, complete trapliners are the most efficient competitors with the highest rate of reward intake and the lowest variability of reward crop per patch, regardless of resource renewal schedule or competitor frequency.

The only field study that directly sought to measure Possingham effects (Williams and Thomson, 1998) failed to find them. Although the bees that visited most heavily were able to maintain statistically significant regularity of return times, they were not able to arrive at times when the accumulated resource was greater than random because the situation was too competitive. The single *Penstemon strictus* plant observed by Williams and Thomson (1998) received bumblebee visits every few minutes. As we have shown, the differences in foraging performance among tactics become smaller as the competitor density increases. Although we believe that this is the case in Williams and Thomson (1998), it should also be noted that the authors could have missed existing advantages of traplining because they observed only one focal plant. As mentioned above, a trapliner might maintain systematic returns on less-competitive patches, even when it experiences large variability of elapsed time on a competitive patch. Ideally, future studies should compare foraging performance of competitors across all the patches they visit.

Our model also has some implications for the size and geometry of traplines. First, we found that the mean reward crop per patch is a concave-down function of the repulsion period (saturating when resource renewal is linear; hump-shaped when resource renewal is nonlinear) because larger

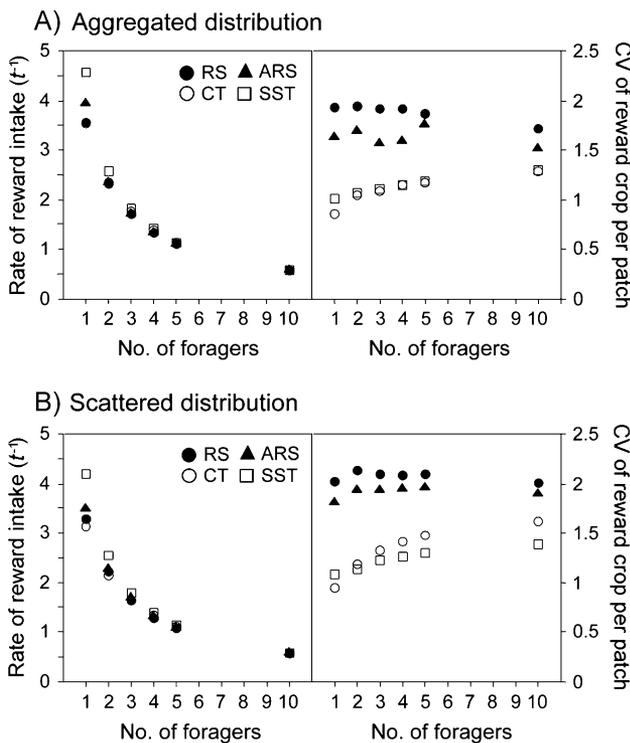


Figure 9
Foraging performance when a habitat is dominated by the same tactic. Each symbol represents the mean, calculated from 100 foraging trips. Five rich patches are (A) spatially aggregated and (B) spatially scattered (see Figure 1C). Error bars are omitted because they are too small to draw.

Table 2
Changes in visitation rate to patches with different resource renewal rates

Distribution of rich patches	Tactic and no. of competitors	Changes in relative visitation rate to rich patches ^a		<i>P</i>	Changes in relative visitation rate to poor patches ^b		<i>p</i>	
		0.2 (homo) →	0.6 (rich)		0.2 (homo) →	0.12 (poor)		
Aggregated	1 ARS	3.69 ± 0.40	4.68 ± 0.64	.043	3.26 ± 1.22	3.07 ± 1.10	.26	
	5 ARS	3.58 ± 0.87	5.40 ± 1.29	.043	3.29 ± 2.15	2.92 ± 1.64	.019	
	10 ARS	3.28 ± 0.77	5.02 ± 1.24	.043	3.35 ± 1.98	3.00 ± 1.47	.0045	
	1 SST	3.16 ± 0.14	4.65 ± 0.088	.043	3.37 ± 0.27	3.07 ± 0.21	.0017	
	5 SST	3.45 ± 0.11	4.32 ± 0.089	.043	3.31 ± 0.28	3.14 ± 0.24	<.0001	
	10 SST	3.49 ± 0.080	4.22 ± 0.12	.043	3.30 ± 0.29	3.16 ± 0.28	<.0001	
	1 RS	3.82 ± 0.41	3.95 ± 0.64	.22	3.24 ± 1.51	3.21 ± 1.37	.93	
	5 RS	3.67 ± 0.50	3.69 ± 0.60	.69	3.27 ± 1.31	3.26 ± 1.34	.90	
	10 RS	3.70 ± 0.43	3.62 ± 0.38	.043	3.26 ± 1.31	3.28 ± 1.33	.54	
	1 CT	3.56 ± 0.25	3.57 ± 0.25	.50	3.29 ± 0.97	3.29 ± 0.98	.99	
	5 CT	3.58 ± 0.33	3.65 ± 0.34	.043	3.28 ± 0.92	3.27 ± 0.89	.99	
	10 CT	3.64 ± 0.34	3.64 ± 0.31	.50	3.27 ± 0.92	3.27 ± 0.92	.76	
	Scattered	1 ARS	3.18 ± 0.79	3.26 ± 2.29	.89	3.36 ± 1.20	3.35 ± 1.76	.48
		5 ARS	3.31 ± 2.96	3.75 ± 0.38	.50	3.34 ± 1.81	3.25 ± 0.13	.60
		10 ARS	3.26 ± 2.91	3.30 ± 1.97	.50	3.35 ± 1.61	3.34 ± 1.49	.68
1 SST		3.42 ± 0.081	4.16 ± 0.48	.043	3.32 ± 0.29	3.17 ± 0.15	.042	
5 SST		3.10 ± 0.38	3.76 ± 0.38	.043	3.38 ± 0.21	3.25 ± 0.13	.0001	
10 SST		3.07 ± 0.42	3.68 ± 0.40	.043	3.39 ± 0.22	3.26 ± 0.17	<.0001	
1 RS		2.96 ± 1.55	2.84 ± 1.23	.69	3.41 ± 1.39	3.43 ± 1.18	.68	
5 RS		2.83 ± 1.29	2.87 ± 1.35	.89	3.43 ± 1.20	3.43 ± 1.21	.70	
10 RS		2.84 ± 1.29	2.94 ± 1.34	.043	3.43 ± 1.20	3.41 ± 1.28	.29	
1 CT		2.55 ± 0.99	2.62 ± 0.97	.69	3.49 ± 0.80	3.48 ± 0.67	.53	
5 CT		2.58 ± 0.89	2.53 ± 0.78	.35	3.49 ± 0.77	3.49 ± 0.76	.56	
10 CT		2.54 ± 0.79	2.51 ± 0.98	.69	3.49 ± 0.82	3.50 ± 0.82	.8	

^a Changes in relative visitation rate on rich patches before ($r = .2$) and after ($r = .6$) the introduction of heterogeneity of patch quality.

^b Changes in relative visitation rate of poor patches before ($r = .2$) and after ($r = .12$) the introduction of heterogeneity of patch quality.

Only linear resource renewal is considered. As regards distribution of rich patches, see Figure 1C,D.

Values are mean ± SD, calculated from 100 iterations of each condition.

Probabilities were calculated for testing changes in the visitation rate between homo and hetero situations, using Wilcoxon's signed-ranks tests.

Relative visitation rates to a certain patch in homo and hetero situations as a pair (5 pairs for rich patches, and 25 pairs for poor patches).

trapplines have more shared patches with one another as well as greater elapsed time per patch. Therefore, smaller traplines would become more advantageous as the number of competitors increases in a habitat, especially when resource renewal is nonlinear. Such an effect may partly explain the observed increase or decrease in the size of foraging areas of individual bumblebees from day to day (Makino and Sakai, 2004). Thomson et al. (1987) also reported that traplining bumblebees expanded or shifted their foraging areas after other bees were removed from the local habitat, which may support our idea that smaller foraging areas or traplines will be preferred in competitive situations. Second, we found that a reduction of circuitry of traplines decreases the mean resource standing crop in traplined patches when resource renewal is linear, while it increases the rate of reward intake when resource renewal is nonlinear. Thus, any ability to solve the "traveling salesman problem" (Cramer and Gallistel, 1997), even approximately, might benefit animals in terms of the increased rate of reward intake or the increased defense by exploitation. These hypotheses need to be empirically tested in future.

Costs and benefits of information use in traplining behavior

Because complete trapliners never change their foraging routes, they might suffer from some disadvantages when their routes happen to include many undesirable patches. This is

likely to occur when many trapliners are competing because they tend to move between close patches and produce routes that resemble one another. In other words, complete trapliners cannot reduce the spatial heterogeneity in patch quality that is generated by overlaps of their foraging routes. Because of this inflexibility, a habitat dominated by complete trapliners yields the same rate of reward intake as a habitat dominated by nontrapliners. Similarly, complete trapliners cannot reduce the spatial heterogeneity in patch quality derived from variation in resource renewal rate among patches. Our simulations revealed that this inflexibility in heterogeneous conditions decreases the rate of reward intake for complete trapliners, unless patch quality is spatially aggregated.

These drawbacks of CT can be improved by using information in a win-stay, lose-shift manner. We demonstrated two examples of conditions where SST outperforms CT. First, in a larger habitat, the tendency for traplines to overlap can produce competitor-free space that is rarely visited. In this situation, a sample-and-shift trapliner can increase its reward intake by occupying this competitor-free space. Second, when resource renewal rate varies among patches, a habitat dominated by an intermediate number of sample-and-shift trapliners yields a higher rate of reward intake than habitats dominated by other types of foragers. Thus, information use helps trapliners to reduce spatial heterogeneity of resource availability in the habitat, which results in an increase in the

rate of reward intake under certain conditions. These results are consistent with findings in a field experiment with bumblebees where a trapliner that shifted its feeding location toward a “competitive vacuum” (created by removal of competitors) yielded a higher rate of food collection than the other bees (Thomson et al., 1987).

Our results also show, however, that the sample-and-shift process incurs two inevitable costs. It increases the movement distance between patches, and it reduces the Possingham effects for trapliners by increasing variability of elapsed time between visits. These costs show up in pairwise competition between CT and SST. When the SST forager shifts to reduce overlap, it bears the costs of making the adjustment, but the CT forager receives equal benefits. SST is also less advantageous than CT when the underlying spatial heterogeneity of patch quality is blurred due to intense competition or due to nonlinear resource renewal. In these situations, CT is always a more efficient tactic than SST because sampling and shifting does not increase reward crop per patch despite its large costs.

Our results suggest that trapliners should switch between “tenacious” CT and “impatient” SST, according to temporal changes in surrounding situations. For example, an impatient tactic will help a trapliner to find profitable areas when it exploits a novel food habitat. When trapliners encounter a persistent decrease in resource availability at patches due to competition or deterioration of patches, the impatient mode will also help them to move out from these patches. Animals in nature may actually adopt flexible mode switching of this sort. Traplining bumblebees normally maintained individual foraging areas or traplines for more than 10 days but extended or shifted foraging areas to adjacent plant patches in a few days when many flowers were bagged experimentally or withered (Comba, 1999). When resource availability drops suddenly or the costs of movement are larger than the benefits, in contrast, trapliners should stick or revert to a tenacious mode. Such considerations may partly explain the observations in traplining hummingbirds that resident birds responded to simulated intrusions of the feeders they were traplining by returning at short intervals for 1 or 2 h after the loss (Garrison and Gass, 1999; Gill, 1988).

Although switching between tenacious and impatient modes would occur most commonly in response to changes in resource availability in traplined patches, other factors might also influence the switch. For example, maintaining a certain level of sampling or low tenacity will help trapliners to monitor temporal increases in resource availability outside their routes. Flower visitors, for example, face new opportunities when new patches or species of plants come into bloom, or when competitors die or depart. In the particular case of bumblebees, forager mortality rates are high enough (approximately 4.5% per day; Rodd et al., 1980) that previously exploited traplines will open up frequently. In fact, traplining bumblebees occasionally sample peripheral patches irrespective of reward they encounter and shift or expand their traplines to those patches if they prove rewarding (Comba, 1999; Manning, 1956; Thomson et al., 1982, 1987). We would expect such bees to be less tenacious than longer-lived animals such as hummingbirds. And also, resident hummingbirds are expected to be more tenacious than migrants. Further empirical data will be needed to test these hypotheses.

A key assumption of our model, which causes large costs in SST, is that animals spend no time extracting resource from a patch. In some real systems (e.g., bees on *Penstemon* plants; Williams and Thomson, 1998), resource extraction time may actually exceed interpatch travel time. Intuitively, such situations would seem to favor SST over CT because the relative importance of movement cost is smaller, but more modeling should be done.

Foraging without traplines

We found that nontrapliners (searchers) can obtain a higher rate of reward intake than trapliners in habitats where the competitor density is quite low and resource in patches renews endlessly. However, nontrapliners cannot benefit from any Possingham effects because the coefficient of variation of elapsed time between visits is larger than one, even when they use information to reduce short-term revisitations (ARS). This result does not support Possingham’s (1989) expectation that ARS is a mechanism of systematic foraging that will decrease the coefficient of variation of elapsed time between visits to below one. Moreover, the mean reward crop per patch of area-restricted searchers decreases rapidly when there are competitors because patches are more likely to be depleted by others before they accumulate larger amount of resource.

When resource renewal rate is variable with positive spatial autocorrelation, area-restricted searchers increase their visits to more rewarding patches. This adjustment makes the mean rate of reward intake in an ARS-dominated habitat higher than those in CT- or RS-dominated habitats (but lower than a SST-dominated habitat). When rewarding patches are not spatially aggregated, area-restricted searchers cannot concentrate on rewarding patches, so the above advantage dissipates. In addition, area-restricted searchers are vulnerable to competition from trapliners even when patch quality varies. Thus, ARS is less effective than SST when patches vary. Many foraging animals are known to exhibit ARS behavior when they are foraging on nonrenewable resource patches at small temporal scales (reviewed by Motro and Shmida, 1995). Our results show, however, that traplining is a better tactic at larger temporal scales.

Conclusions

Possingham (1989) was the first to point out the possible advantages of visiting renewable resource patches in a systematic pattern. He suggested that traplining and ARS were possible mechanisms of producing this systematic pattern. In this paper, we confirmed that traplining can produce the systematic pattern, but ARS does not. Moreover, we found that trapliners can maintain this systematic pattern even when other animals are foraging independently in the same habitat, which makes trapliners the most efficient competitors, regardless of resource renewal schedule or competitor frequency. To our knowledge, this is the first time that functional significance of periodical returns in traplining has been explicitly demonstrated under competitive situations.

We also found that adding a component of information use, that is, sampling and shifting, to traplining entails large costs in terms of increased movement distance and variability of elapsed time between visits. These costs often exceed the increase in reward crop per patch and tend to decrease the foraging performance of trapliners. We suggest that information use in traplining should be used only for temporary adjustments to changing resource availability in traplined patches or for occasional sampling to monitor changes in the surrounding environment. Future studies on traplining behavior should pay more attention to such mode switching between tenacious and impatient tactics in relation to changing resource environment and also accumulate more data to characterize traplining behavior itself (e.g., ontogeny, persistence, and geometry).

Finally, our results may also have some implications for the coevolution of plants and pollinators. The spatial-use patterns of pollinators will influence pollen dispersal among plants and, in turn, plant fitness. Our results suggest that plants could influence the foraging patterns of pollinators by

altering the replenishment schedules of floral rewards. Relevant aspects of reward amounts and energetic values vary among flowers, plants, populations, and plant species (nectar: Boose, 1997; Castellanos et al., 2002; Cruden et al., 1983; Delph and Lively, 1992; Dreisig, 1995; Harder and Cruzan, 1990; Johnson et al., 2003; Nepi et al., 2003; Smithson and Gigord, 2003; pollen: Harder, 1990; Robertson et al., 1999). Moreover, real plants can adjust resource renewal schedules not only through nectar and pollen presentation schedules within flowers but also by the scheduling of flower openings within plants. With these levels of adjustment, effectively unlimited "linear" schedules may not be far-fetched. More empirical and theoretical studies are needed to understand whether such variations in resource renewal of plants can be profitably viewed as strategies for manipulating pollinators (Ohashi and Yahara, 2001; Zimmerman, 1988).

Peter Abrams offered us a PC for running long-term simulations. Useful discussion has been contributed by many colleagues, especially: James Burns, Ralph Cartar, Hiroyuki Matsuda, and Tetsukazu Yahara. Ralph Cartar, Chris Higgins, and an anonymous reviewer made useful comments on the manuscript. This research was partly supported by a fellowship of the Japan Society for the Promotion of Science for Research Abroad to K.O. and Natural Sciences and Engineering Research Council grants to J.D.T.

APPENDIX A

TABLE A1

Baseline parameter values (when not stated)

Parameter	Description	Value
H	Length of one side of foursquare habitat	$1500t$
N_p	Number of patches	30
R	Resource renewal rate	0.2
R_m	Maximum resource abundance per patch	Infinite (linear renewal) 800 (nonlinear renewal)
T	Maximum foraging time per trip	$30,000t$
l_1	Upper limit of D_1 (RS and ARS)	$150t$
l_2	Upper limit of D_2 (RS and ARS)	$300t$
l_3	Upper limit of D_3 (RS and ARS)	$450t$
l_4	Upper limit of D_4 (RS and ARS)	$600t$
l_5	Upper limit of D_5 (RS and ARS)	$750t$
l_6	Upper limit of D_6 (RS and ARS)	$900t$
l_7	Upper limit of D_7 (RS and ARS)	$1050t$
l_8	Upper limit of D_8 (RS and ARS)	$1200t$
P_1	Probability that D_1 is chosen (RS and ARS)	0.450
P_2	Probability that D_2 is chosen (RS and ARS)	0.260
P_3	Probability that D_3 is chosen (RS and ARS)	0.189
P_4	Probability that D_4 is chosen (RS and ARS)	0.047
P_5	Probability that D_5 is chosen (RS and ARS)	0.023
P_6	Probability that D_6 is chosen (RS and ARS)	0.015
P_7	Probability that D_7 is chosen (RS and ARS)	0.009
P_8	Probability that D_8 is chosen (RS and ARS)	0.007
A	Rate of increase in magnetic force (CT and SST)	10
B	Elapsed time at which magnetic force changes from repulsive to "gravitational" (CT and SST)	$4000t$

μ	Mean of error term in score function of patch (CT and SST)	0
δ	Variation of error term in score function of patch (CT and SST)	0.0005
C_t	Threshold crop at the current patch for choosing distance to the next patch (ARS)	300
C_a	Threshold crop at the current patch for sampling (SST)	1000
C_b	Threshold crop at the sampled patch for shifting (SST)	1000

APPENDIX B

TABLE B1

Model variables

Variable	Description
R	Resource standing crop
t_p	Elapsed time since last visit at a patch
D_{1-6} or D'_{1-6}	Distance ranges from which the next patch is chosen (RS and ARS)
P_{far}	Sum of P_3 to P_8
t_f	Elapsed time since last visit made by a particular forager (CT and SST)
$M(t_f)$	Magnetic force function between a forager and a patch (CT and SST)
S	Score function of patch (CT and SST)
d	Distance from the current patch in score function of patch (CT and SST)
E	Error term in score function of patch (CT and SST)
C_c	Reward encountered crop (ARS and SST)
N_f	Number of foragers (ARS and SST)

REFERENCES

- Ackerman JD, Mesler MR, Lu KL, Montalvo AM, 1982. Food-foraging behavior of male *Euglossini* (Hymenoptera, Apidae)—vagabonds or trapliners. *Biotropica* 14:241–248.
- Bell W, 1990. Searching behavior patterns in insects. *Annu Rev Entomol* 35:447–467.
- Boose DL, 1997. Source of variation in floral nectar production rate in *Epilobium canum* (Onagraceae): implications for natural selection. *Oecologia* 110:493–500.
- Briggs CJ, Hoopes MF, 2004. Stabilizing effects in spatial parasitoid-host and predator-prey models: a review. *Theor Popul Biol* 65:299–315.
- Cartar RV, 2004. Resource-tracking by bumble bees: responses to plant-level differences in quality. *Ecology* 85:2764–2771.
- Cartar RV, Real LA, 1997. Habitat structure and animal movement: the behaviour of bumble bees in uniform and random spatial resource distributions. *Oecologia* 112:430–434.
- Carthew SM, Goldingay RL, 1997. Non-flying mammals as pollinators. *Trends Ecol Evol* 12:104–108.
- Castellanos MC, Wilson P, Thomson JD, 2002. Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). *Am J Bot* 89:111–118.
- Cody ML, 1971. Finch flocks in the Mohave desert. *Theor Popul Biol* 2:142–148.
- Comba L, 1999. Patch use by bumblebees (Hymenoptera Apidae): temperature, wind, flower density and traplining. *Ethol Ecol Evol* 11:243–264.
- Cramer AE, Gallistel CR, 1997. Vervet monkeys as travelling salesmen. *Nature* 387:464–464.
- Cresswell JE, 2000. A comparison of bumblebees' movements in uniform and aggregated distributions of their forage plant. *Ecol Entomol* 25:19–25.
- Cruden RW, Hermann-Parker SM, Peterson S, 1983. Patterns of nectar production and plant-pollinator coevolution. In: *Biology of nectar production* (Elias TS, Bentley BA, eds). New York: Columbia University Press; 81–125.

- Davies NB, Houston AI, 1981. Owners and satellites—the economics of territory defense in the pied wagtail, *Motacilla alba*. *J Anim Ecol* 50:157–180.
- Delph LF, Lively CM, 1992. Pollinator visitation, floral display, and nectar production of the sexual morphs of a gynodioecious shrub. *Oikos* 63:161–170.
- Dominey WJ, 1984. Alternative mating tactics and evolutionarily stable strategies. *Am Zool* 24:385–396.
- Dreisig H, 1985. Movement patterns of a clear-wing hawkmoth, *Hemaris fuciformis*, foraging at red catchfly, *Viscaria vulgaris*. *Oecologia* 67:360–366.
- Dreisig H, 1995. Ideal free distributions of nectar foraging bumblebees. *Oikos* 72:161–172.
- Dreisig H, 2000. Defense by exploitation in the Florida carpenter ant, *Camponotus floridanus*, at an extrafloral nectar resource. *Behav Ecol Sociobiol* 47:274–279.
- Dressler RL, 1982. Biology of the orchid bees (Euglossini). *Annu Rev Ecol Syst* 13:373–394.
- Garber PA, 1988. Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica* 20:100–106.
- Garrison JSE, Gass CL, 1999. Response of a traplining hummingbird to changes in nectar availability. *Behav Ecol* 10:714–725.
- Gass CL, Garrison JSE, 1999. Energy regulation by traplining hummingbirds. *Funct Ecol* 13:483–492.
- Gilbert LE, 1980. Ecological consequences of a coevolved mutualism between butterflies and plants. In: *Coevolution of animals and plants* (Gilbert LE, Raven PH, eds). Austin: University of Texas Press; 210–231.
- Gill FB, 1988. Trapline foraging by hermit hummingbirds—competition for an undefended, renewable resource. *Ecology* 69:1933–1942.
- Gill FB, Wolf LL, 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333–345.
- Harder LD, 1990. Pollen removal by bumble bees and its implications for pollen dispersal. *Ecology* 71:1110–1125.
- Harder LD, Cruzan MB, 1990. An evaluation of the physiological and evolutionary influences of inflorescence size and flower depth on nectar production. *Funct Ecol* 4:559–572.
- Heinrich B, 1976. The foraging specializations of individual bumblebees. *Ecol Monogr* 46:105–128.
- Helfman GS, 1990. Mode selection and mode switching in foraging animals. *Adv Stud Behav* 19:249–298.
- Higgins CL, Strauss RE, 2004. Discrimination and classification of foraging paths produced by search-tactic models. *Behav Ecol* 15:248–254.
- Janson CH, 1998. Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Anim Behav* 55:1229–1243.
- Janson CH, Terborgh J, Emmons LH, 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* 13:1–6.
- Janzen DH, 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171:203–205.
- Johnson SD, Peter CI, Nilsson LA, Agren J, 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84:2919–2927.
- Kadmon R, 1992. Dynamics of forager arrivals and nectar renewal in flowers of *Anchusa stigosia*. *Oecologia* 92:552–555.
- Kamil AC, 1978. Systematic foraging by a nectar-feeding bird, Amakihi (*Loxops virens*). *J Comp Physiol Psychol* 92:388–396.
- Kipp LR, 1987. The flight directionality of honeybees foraging on real and artificial inflorescences. *Can J Zool* 65:587–593.
- Lemke TO, 1984. Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. *Ecology* 65:538–548.
- Linhart YB, 1973. Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. *Am Nat* 107:511–523.
- Makino TT, Sakai S, 2004. Findings on spatial foraging patterns of bumblebees (*Bombus ignitus*) from a bee-tracking experiment in a net cage. *Behav Ecol Sociobiol* 56:155–163.
- Manning A, 1956. Some aspects of the foraging behaviour of bumblebees. *Behaviour* 9:164–201.
- Maynard Smith J, 1982. *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Mouto U, Shmida A, 1995. Near-far search: an evolutionarily stable foraging strategy. *J Theor Biol* 173:15–22.
- Nepi M, Pacini E, Nencini C, Collavoli E, Franchi GG, 2003. Variability of nectar production and composition in *Linaria vulgaris* (L.) Mill. (Scrophulariaceae). *Plant Syst Evol* 238:109–118.
- Ohashi K, Yahara T, 2001. Behavioral responses of pollinators to variation in floral display size and their influences on the evolution of floral traits. In: *Cognitive ecology of pollination* (Chittka L, Thomson JD, eds). New York: Cambridge University Press; 274–296.
- Paton DC, Carpenter FL, 1984. Peripheral foraging by territorial rufous hummingbirds—defense by exploitation. *Ecology* 65:1808–1819.
- Possingham HP, 1989. The distribution and abundance of resources encountered by a forager. *Am Nat* 133:42–60.
- Pyke GH, 1978. Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor Popul Biol* 13:72–98.
- Pyke GH, 1981. Optimal foraging in hummingbirds: rule of movement between inflorescences. *Anim Behav* 29:889–896.
- Racey PA, Swift SM, 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera, Vespertilionidae) during pregnancy and lactation. 1. Foraging behavior. *J Anim Ecol* 54:205–215.
- Real L, Caraco T, 1986. Risk and foraging in stochastic environments. *Annu Rev Ecol Syst* 17:371–390.
- Robertson AW, Mountjoy C, Faulkner BE, Roberts MV, Macnair MR, 1999. Bumble bee selection of *Mimulus guttatus* flowers: the effects of pollen quality and reward depletion. *Ecology* 80:2594–2606.
- Rodd FH, Plowright RC, Owen RE, 1980. Mortality rates of adult bumble bee workers (Hymenoptera: Apidae). *Can J Zool* 58:1718–1721.
- Schilman PE, Roces F, 2003. Assessment of nectar flow rate and memory for patch quality in the ant *Camponotus rufipes*. *Anim Behav* 66:687–693.
- Schmid-Hempel P, 1986. The influence of reward sequence on flight directionality in bees. *Anim Behav* 34:831–837.
- Schulke O, 2003. To breed or not to breed—food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur (*Phaner furcifer*). *Behav Ecol Sociobiol* 55:11–21.
- Smithson A, Gigord LDB, 2003. The evolution of empty flowers revisited. *Am Nat* 161:537–552.
- Stout JC, Goulson D, 2002. The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. *Behav Ecol Sociobiol* 52:239–246.
- Thomson JD, 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*. *Evol Ecol* 2:65–76.
- Thomson JD, 1996. Trapline foraging by bumblebees: I. persistence of flight-path geometry. *Behav Ecol* 7:158–164.
- Thomson JD, Maddison WP, Plowright RC, 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54:326–336.
- Thomson JD, Peterson SC, Harder LD, 1987. Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency. *Oecologia* 71:295–300.
- Tiebout HM, 1993. Mechanisms of competition in tropical hummingbirds—metabolic costs for losers and winners. *Ecology* 74:405–418.
- Tiebout HM III, 1991. Daytime energy management by tropical hummingbirds—responses to foraging constraint. *Ecology* 72:839–851.
- Waddington KD, 1979. Flight patterns of three species of sweat bees (Halictidae) foraging at *Convolvulus arvensis*. *J Kans Entomol Soc* 52:751–758.
- Watts DP, 1998. Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 2. Reuse of foraging areas in relation to resource abundance, quality, and depletion. *Int J Primatol* 19:681–702.
- Williams NM, Thomson JD, 1998. Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. *Behav Ecol* 9:612–621.
- Wolf LL, Stiles FG, Hainsworth FR, 1976. Ecological organization of a tropical, highland hummingbird community. *J Anim Ecol* 43:349–379.
- Zimmerman M, 1979. Optimal foraging: a case for random movement. *Oecologia* 43:261–267.
- Zimmerman M, 1981. Optimal foraging, plant density and the marginal value theorem. *Oecologia* 49:148–153.
- Zimmerman M, 1982. Optimal foraging: random movement by pollen collecting bumblebees. *Oecologia* 53:394–398.
- Zimmerman M, 1988. Nectar production, flowering phenology, and strategies for pollination. In: *Plant reproductive ecology* (Lovett Doust J, Lovett Doust L, eds). New York: Oxford University Press; 157–178.