Evol Ecol (2009) 23:245–259
DOI 10.1007/s10682-007-9220-6

ORIGINAL PAPER

Consequences of food distribution for optimal searching behavior: an evolutionary model

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Received: 23 May 2007 / Accepted: 4 October 2007 / Published online: 17 October 2007

Abstract Resource distribution can vary greatly in space and time. Consequently, animals should adjust their searching tactics to such spatio–temporal patterns in accordance with their innate capabilities, or alternatively, they should use a genetically fixed searching tactic that has been evolved in response to the specific pattern of the food they experience. Using a simulation model and a genetic algorithm, we show how optimal searching tactics change as a function of food spatial pattern. Searching tactics for hidden prey can be approximated using the following three components: (1) Extensive search mode (ESM), the type of movement before encountering a food item; (2) Intensive search mode (ISM), the type of movement after encountering a food item; and (3) ISM duration. Both ESM and ISM are characterized by movement tortuosity. We show that searching behavior adaptively changes as a function of food pattern. When food is distributed in a regular pattern, ISM is more directional than ESM, but under a clumped food pattern, ISM is much more tortuous than ESM. It may suggest that animals with larger spectra of searching tactics should experience greater variance or seasonal changes in their food pattern than animals with narrow spectra of searching tactics. Increased forager attack radius diminishes the differences between ESM and ISM, and thus the use of these three components to model searching in animals with higher attack radii is not appropriate. Increased handling time, which is a surrogate of reducing habitat profitability results in longer patch residency time as expected by optimal foraging theory. To conclude, we suggest that using such a combined approach of simulation models and genetic algorithms may improve our understanding of how extrinsic and intrinsic factors interact to influence searching behavior.

Keywords Area-restricted search · Attack radius · Foraging · Handling time · Genetic algorithm · Searching tactic

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Introduction

Foraging is an essential part of an organism's ability to survive and reproduce. Many animals cannot sense their food from a long distance. Thus, searching optimally for food patches or items with limited information is an important component of foraging behavior (Bouskila and Blumstein 1992). This may require the forager to adjust its searching tactic to information gathered while foraging, e.g., Bayesian foraging (Iwasa and Higashi 1981). Such a process is very common in nature, for instance, a microorganism searching for high concentrations of glucose (Keller and Segel 1971), a worm searching for high densities of microorganisms (Hills et al 2004), or a badger searching for worms below the ground (Mellgren and Roper 1986). Searching tactics are diverse and are influenced by internal characteristics of the animal, such as hunger level (e.g., Bond 1980; Ferran and Dixon 1993; Grünbaum 1998) or circadian rhythm (Nakamuta 1987), and by external characteristics, such as the natural distribution of food items or patches. Maximizing fitness requires optimizing the searching tactics according to the spatial distribution of food patches and to the temporal variation in food abundance. In other words, the best tactic for searching in a clumped pattern of food may be totally different from that used when searching in a regular pattern. Therefore, animals should adaptively adjust their searching behavior according to the degree of environmental heterogeneity they experience.

The optimal searching tactic of a forager exploiting resources distributed in patches has been studied both theoretically (e.g., Benhamou 1992; Grünbaum 1998) and empirically (e.g., Carter and Dixon 1984; Nakamuta 1985; Nolet and Mooij 2002). Searching tactics in this case usually consist of three components: (a) the type of movement before encountering the first food item, which may indicate the presence of other food items in its vicinity, i.e., a food patch; (b) the type of movement after encountering a food item; and (c) the duration of this second movement pattern, or the time before returning to the original movement pattern (in a clumped pattern this is analogous to patch residency time). This classification is useful only when patches do not have distinct detectable borders or when searching for hidden food items. Therefore, when a forager lacks information about patch location, it may use the encounter with a food item as a signal to shift its movement pattern.

When food is clumped there should be a distinction between movement patterns between and within patches. Animals in this case identify the patch location by encountering a food item. Therefore, such an event is also associated with switching between movement patterns. Before finding a food item the movement pattern should be characterized by relatively straight lines and fast movement intended to minimize the time needed to move from one patch to another (hereafter 'extensive search mode' or ESM). However, the movement pattern after finding a food item should be characterized by a more tortuous and careful movement in order to increase the likelihood of encountering additional food items in the vicinity of the first, and in order to gain maximum benefit from the patch before leaving it (hereafter 'intensive search mode' or ISM) (Bond 1980; Ferran and Dixon 1993). Similar searching tactics have been documented in a variety of species (Bond 1980; Bell 1985; Nakamuta 1985; Motro and Shmida 1995; Baum and Grant 2001; Nolet and Mooij 2002), using various methods to quantify the movement tortuosity (fractal dimensions, Dicke and Burrough 1988; correlated random walk models, Kareiva and Shigesada 1983; and others, Benhamou 2004). Benhamou (1992) used a simulation model to illustrate that when food is clumped, a structured searching tactic combined of three components (i.e., ESM, ISM and duration of ISM) is more successful than employing a searching method with a constant pattern of movement. Moreover, he showed that either the ESM's directionality or the ISM's tortuosity are influenced by the degree of patchiness (patch density and inter-patch distance). Here we use a single framework to expand the previous knowledge on searching in clumped distribution by examining also other spatial patterns (i.e., regular and random). In addition, we test for the effect of the interplay between two important foraging traits, handling time and attack radius, on searching behavior. By doing so, we minimize the need for making a priori assumptions on how different extrinsic and intrinsic factors interact to influence searching behavior.

A searching tactic consisting of the same combinations of ESM and ISM may not be effective across different food patterns. A directional ESM and a tortuous ISM, which characterize searching in a clumped pattern, may fail while searching in random and especially regular food patterns. The optimal searching tactic for a regular pattern of food has rarely been studied, probably because food in nature is usually clumped. However, some species do experience a regular food pattern, e.g., a grasshopper searching for shrubs in a desert landscape, where small bushes are distributed evenly. In this case, there is a negative auto-correlation in space between the locations of food items, and the immediate optimal response to finding a food item is to move in a straight line. Thus, the directional ESM-tortuous ISM shift will not be useful (as suggested by Krakauer and Rodriguez-Girones 1995). Similarly, in a random food pattern, searching behavior composed of ESM, ISM and ISM duration is not necessary, and it is probably better to use a fixed movement pattern (as described in Zollner and Lima 1999). The tortuosity of such a pattern is affected by the overall density—the more abundant the food, the more tortuous the movement.

We used a genetic algorithm (hereafter, GA) approach of optimization to study the optimal searching tactics of a forager experiencing different food patterns in a spatially-explicit environment. We systematically changed the food density inside the patches, the patch area, and the number of patches, and quantified the emerging adaptive components of the forager's searching tactic (i.e., ESM, ISM and ISM duration). In addition, we varied the attack radius or perceptual scale of the foragers to enable them to detect food items from a greater distance (this can also be thought of as affecting information state), and the handling time after consuming a food item, and studied the effect on searching tactics. Different attack radii can lead to different optimized traits; it has been demonstrated that the attack radius can influence various considerations made by the forager (Viswanathan et al 1999; Broom and Ruxton 2005). In addition, handling time has also been considered as a major component of searching and foraging behavior, and the relative time devoted to handling may vary with prey size and foraging mode (Griffiths 1980).

Methods

We created a spatially-explicit individual-based simulation model, using MATLAB (v.6.5). We used a grid-based arena, similar to that used in previous studies of searching behavior (e.g., Benhamou 1992; Nolet and Mooij 2002). Simulated animals started in a random position, searched in a 100 × 100 arena and could move one square during each time step in one of the eight possible directions. Animals searched for food items distributed differently, when every food item occupied one square and was not renewable. Each simulation was run for 1000 time steps. Animals were characterized by three relevant "traits": (1) ESM directionality, which we define here as the movement before an encounter with a food item; (2) ISM directionality, which is defined here as the movement after an encounter with a food item (and may be either more directional or tortuous than the ESM); and (3) ISM duration, which is the number of time steps the searching animal uses

Table 1 Probabilities of different angles taken on a step, relative to the angle taken on the previous step. Initial movement patterns are more directional; later ones (until no. 20) become more tortuous. Moves 21–25 are negatively auto-correlated movement patterns, i.e., there is less chance of moving forward. ESM and ISM for the simulated animals were initially randomly chosen from this table. Note that the summation of each row is 100%, because values in columns third to fifth should be considered twice

	Probability of angle relative to previous move				
No.	0° (%)	±45° (%)	±90° (%)	±135° (%)	180° (%)
1	100	—	—	—	—
2	97	1.5	—	—	—
3	95	2.5	—	—	—
4	90	3	2	—	—
5	85	5	2.5	—	—
6	80	7	3	—	—
7	75	9	3.5	—	—
8	70	10	5	—	—
9	65	12	5.5	—	—
10	60	14	6	—	—
11	55	15	7.5	—	—
12	50	16	9	—	—
13	45	18	9.5	—	—
14	40	20	10	—	—
15	35	20	12.5	—	—
16	30	20	15	—	—
17	25	20	16.5	1	—
18	20	20	18	2	—
19	15	15	15	10	5
20	12.5	12.5	12.5	12.5	12.5
21	10	10	14	14	14
22	5	10	15	15	15
23	—	7.5	17	17	17
24	—	5	15	20	20
25	—	—	20	20	20

ISM, after an encounter with a food item. The directionality level (i.e., the probability to keep moving in the same direction) was encoded according to Table 1, from strict directional movement (100% probability of moving forwards, 1st row) through equal probabilities to move to each of the eight possible directions (similar to random walk, 20th row), to a negatively auto-correlated movement (higher probability to move backwards than forwards, rows 21st–25th). Each simulation began with an animal searching using ESM. The shift to ISM is triggered by finding a food item and lasts for the time steps specified in the ISM duration. Each time a new food item is encountered ISM duration is reset. We used a "torus model" to cope with the problem of foragers exiting the arena edges. According to this method, an individual exiting the arena edge immediately appears from the opposite side (e.g., Zollner and Lima 1999; Nolet and Mooij 2002).

A GA (Goldberg 1989; Mitchell and Taylor 1999) is a powerful optimization tool and is suitable for investigating how searching tactics are influenced by environmental heterogeneity because it allows an adaptive emergence of the components of searching tactics (i.e., ESM, ISM and ISM duration). Optimization through GA is inspired by the process of natural selection. However, GA does not represent a real evolutionary process and is merely a technique to search for optimal solutions among various possibilities. While using a GA, an initial population of individuals\chromosomes, characterized by different traits\genes, goes through stages analogous to the process of natural selection. The basic GA includes three steps (Mitchell and Taylor 1999): (1) An initial population is randomly created; (2) A fitness function gives a "score" for each individual; and (3) A set of genetic operators is applied to the old population to create a new one, and the process is repeated.

Our initial population included 50 haploid individuals\chromosomes with randomly selected traits\genes for ESM directionality, ISM directionality and ISM duration. The optimization was operated on these traits. The "fitness function" scored each genotype according to its food capturing performance in the grid-based model described earlier. Each food item captured during the first 1000 time steps scored one point. The population in the next generation was created in proportion to the scores achieved, reflecting that successful genotypes had better chances to continue to the next generation. Twenty percent of the population size was devoted to the products of mutations and recombination (10% to each). Mutations were induced in the following way: A random trait was chosen and its value was changed either with ±1 for ESM and ISM or ±5 for ISM duration. Recombination was done between two parents at a random point (one parent donated two traits while the other parent donated only one). ESM and ISM values were limited between 1 and 25 (Table 1), and ISM duration was limited between 0 and 100 time steps. The simulation lasted for 30 generations, after which a relatively stable population was obtained. Average values for the three optimized traits (ESM, ISM and ISM duration) were documented for each population, and this process of optimization was repeated for 100 times to create a sufficient sample size.

We tested increasing densities of food items in regular and random patterns (20, 50, 100 and 200 food items), while keeping all other factors constant (e.g., arena size of 100×100 squares). All additional tests were conducted in clumped patterns of food. We tested increasing densities of food items (20, 50, 100 and 200 food items), the effect of an increase in the number of patches (3, 5, 7 and 9 patches) and an increase in each patch area (8×8, 16×16, 24×24 and 30×30 squares for each patch), while keeping the overall food density constant. These two treatments result in a decrease in patch density. While changing a single factor (i.e., either the total number of food items, the number of patches or the patch area) the two other factors were held constant (100 food items and 5 patches of 16×16 squares each). In the clumped pattern, the patch centers were fixed, but the food item locations around the centers were randomly chosen in each repetition, with a maximal possible distance from the patch center. When choosing the centers our purpose was to maximize inter-patch distances so that two adjacent patches will not merge into one larger patch, and to keep the distance to nearest neighbor patch center similar for all patches, as possible. Two (or more) food items were not allowed to occupy the same square.

We extended the model by adding two additional characteristics to the simulated searching animals. First, we let the animals have attack radii of different sizes. During the initial trials, the attack radius was zero, and the forager could only detect a food item if both occupied the same position. We later let the forager encounter and attack food items located at greater distances: one additional square in each direction (nine squares including the animal position), two additional squares (25 squares), and three additional squares (49 squares). A forager could consume only one food on a time step; therefore, if more than one food item was encountered, only one item is randomly selected. Next, we added a handling period following prey capture during which the forager could neither move nor search for food. We compared between the optimized traits of foragers having different handling times (5, 10 and 20 time steps). Note that while the forager handles the prey, ISM counter is still running, i.e., ISM search phase also includes the total time that the forager spends handling prey items. This is because the response of the forager to prey encounter usually lasts only for a limited period, depending on a neurological trigger (e.g., in *C. elegans* ISM is triggered by a dopamine release after encountering bacteria; Hills et al 2004). When a long handling time is involved, the neurological trigger should be stronger, resulting in a longer ISM phase, which will include both handling and tortuous search time. Finally, we combined these two new characteristics in order to test for possible interactions: Handling time was held long (10 time steps) and attack radius was gradually increased and vice versa, attack radius was held large (two additional squares) and handling time was gradually elongated.

Results

We plotted the change in the three properties of movement on graphs relative to the parameter changed (food density, number of patches, handling time, etc). Table 2

Table 2 Summary of results in different treatments

#	Pattern	Treatment	ESM	ISM	ISM duration
1	Regular	Increasing food density (Fig. 1a–b)	Asymptotic increase in tortuosity ($\chi^2 = 18.1$)	Asymptotic decrease in tortuosity ($\chi^2 = 20.22$)	Decrease in time steps ($\chi^2 = 19.8$)
2	Random	Increasing food density (Fig. 1c–d)	Increase in tortuosity ($\chi^2 = 12.27$)	Decrease in tortuosity ($\chi^2 = 41.31$)	No clear pattern of change ($\chi^2 = 4.89$)
3	Clumped	Increasing food density (Fig. 2a–b)	Decrease in tortuosity ($\chi^2 = 32.73$)	Increase in tortuosity ($\chi^2 = 21.98$)	Decrease in time steps[a] ($\chi^2 = 49.26$)
4	Clumped	Increasing number of patches (Fig. 2c–d)	Increase in tortuosity ($\chi^2 = 33.54$)	Decrease in tortuosity ($\chi^2 = 116.02$)	Asymptotic decrease in time steps ($\chi^2 = 24.31$)
5	Clumped	Increasing patch area (Fig. 2e–f)	Increase in tortuosity ($\chi^2 = 21.34$)	Decrease in tortuosity ($\chi^2 = 227.03$)	Decrease in time steps[a] ($\chi^2 = 8.62$)
6	Clumped	Increasing attack radius (Fig. 3a–b)	Almost no change ($\chi^2 = 11.02$)	Decrease in tortuosity ($\chi^2 = 265.95$)	Decrease followed by increase in time steps ($\chi^2 = 33.9$)
7	Clumped	Increasing handling time (Fig. 3c–d)	Almost no change ($\chi^2 = 4.9$)	Almost no change ($\chi^2 = 6.5$)	Increase in time steps ($\chi^2 = 38.59$)
8	Clumped	Increasing attack radius[b] (Fig. 4a–b)	Slight decrease in tortuosity ($\chi^2 = 20.6$)	Decrease in tortuosity ($\chi^2 = 97.61$)	Decrease in time steps ($\chi^2 = 69.11$)
9	Clumped	Increasing handling time[c] (Fig. 4c–d)	Almost no change ($\chi^2 = 4.36$)	Asymptotic increase in tortuosity ($\chi^2 = 54.28$)	Slight decrease in time steps ($\chi^2 = 5.33$)

[a] The decrease follows a slight increase in time steps (Fig. 2b, f)

[b] while keeping handling time constant and long

[c] while keeping attack radius constant and high

summarizes the results of all treatments. Grimm and Railsback (2005) suggested using a simple straightforward statistical analysis, such as one-way ANOVA, when analyzing simulation results. We followed their suggestion and used a similar test for non-parametric data, the Kruskal–Wallis test (Table 2). P values were not reported because they depend on the arbitrarily sample sizes defined in our simulations (i.e., P values automatically shrink when more simulations are performed).

Regular pattern

Across treatments, ESM was much more tortuous than ISM (Fig. 1a), and therefore we concluded that a behavioral switch occurred after locating a food item. Increased food density brought about an increase in the tortuosity of the ESM phase of searching and a decrease in the tortuosity of the ISM phase (Fig. 1a). ISM duration decreased with increasing food density (Fig. 1b).

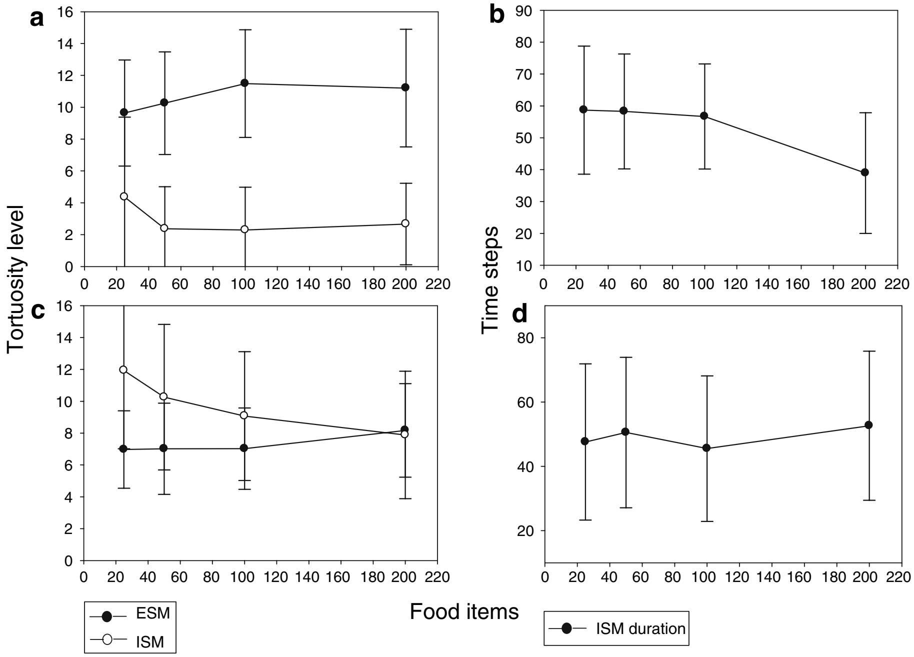

Fig. 1 Searching tactic components in regular (**a**, **b**) and random (**c**, **d**) patterns of food (means of 100 replications of the GA ± 1 SD; $n = 100$), when the overall food density is increased (20, 50, 100 and 200 food items). Simulations were run for 1000 time steps, arena size was 100 × 100 squares, handling time and attack radius were minimal (i.e., zero), and the three traits (ESM, ISM and ISM duration) were obtained using a GA. In regular pattern, ISM was less tortuous than ESM. Increased overall food density resulted in (**a**) an increase in ESM tortuosity; a decrease in ISM tortuosity; and (**b**) a decrease in ISM duration. Searching tactic components in random pattern of food differed between low and high food densities. Increased food density resulted in (**c**) an increase in ESM tortuosity and a decrease in ISM tortuosity. (**d**) There was no clear pattern of change in the ISM duration

Random pattern

Increased food density brought about an increase in ESM tortuosity in an increasing rate (Fig. 1c). ISM tortuosity decreased with food density in a decreasing rate (Fig. 1c), until there was no difference between ESM and ISM at a density of 200 food items. There was no clear pattern of change in the duration of ISM (Fig. 1d).

Clumped pattern

ESM and ISM directionality differed in the clumped pattern across treatments, when ISM was much more tortuous than ESM (Fig. 2a). Increasing overall food density reduced ESM tortuosity in a decreasing rate. It had an opposite effect on ISM while increasing its tortuosity (Fig. 2a). ISM duration was usually negatively correlated with food density (Fig. 2b). Either raising the number of patches or increasing the area of patches (resulting both in a decrease in each patch density) increased the ESM tortuosity, decreased the ISM tortuosity (Fig. 2c, e) and decreased the ISM duration (Fig. 2d, f).

Attack radius

Increasing the attack radius resulted in a slight change in ESM tortuosity (a decrease followed by an increase in tortuosity). However, ISM became less tortuous as the attack radius increased in a decreasing rate, until it matched ESM at the maximum attack radius tested (Fig. 3a). ISM duration first decreased with an increase in the attack radius, but afterwards increased slightly (Fig. 3b).

Handling time

Handling time did not affect either ESM or ISM directionality (Fig. 3c). However, ISM duration increased with increased handling time (Fig. 3d).

Interaction between attack radius and handling time

To test for possible interaction between attack radius and handling time, we varied one of these variables while keeping the other constant and compared the results to those described in “Attack radius” and “Handling time” above. The effect of increasing attack radius on searching tactic components (decrease in ISM tortuosity, minor changes in ESM) was consistent between high and low levels of handling time (compare Fig. 4a, b with Fig. 3a, b). In contrast, the effect of increased handling time on searching tactic components was not consistent between high and low levels of attack radius. When attack radius was high, increased handling time had a positive effect on ISM tortuosity and a slight negative effect on ISM duration. At minimal attack radius, no effect could be detected on the ISM tortuosity and there was an opposite effect on ISM duration (compare Fig. 4c, d with Fig. 3c, d).

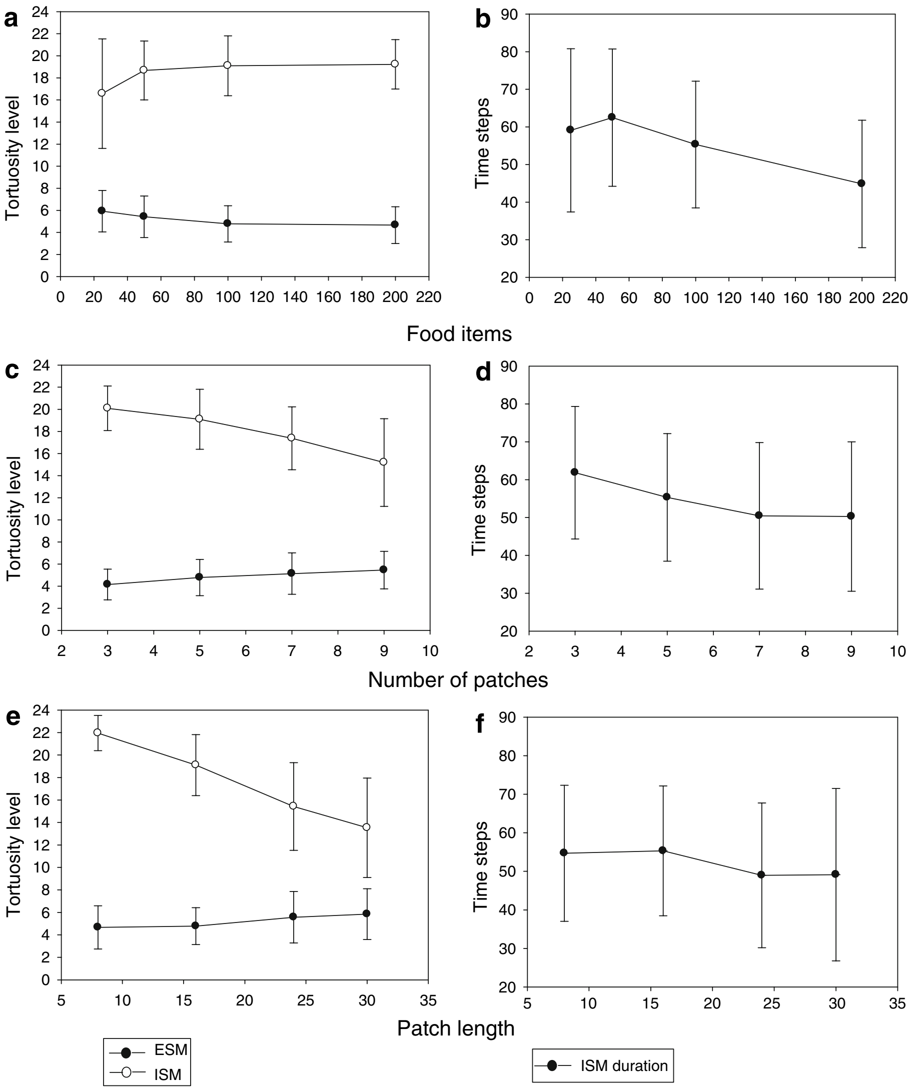

Fig. 2 Searching tactic components in clumped pattern of food (means of 100 replications of the GA ± 1 SD; $n = 100$), when increasing the overall food items (20, 50, 100 and 200 food items; **a**, **b**), when increasing the number of patches (3, 5, 7 and 9 patches; **c**, **d**) and when increasing the patch area (area of 8 × 8, 16 × 16, 24 × 24 and 30 × 30 squares). Simulations were run for 1000 time steps, arena size was 100 × 100 squares, handling time and attack radius were minimal (i.e., zero), and the three traits (ESM, ISM and ISM duration) were obtained using a GA. While increasing one of the three factors (either the total number of food items, patch number or patch area), the two other factors were held constant (100 food items, 5 patches and area of 16 × 16 for each patch). ISM was more tortuous than ESM. Increased overall food density resulted in (**a**) a decrease in ESM tortuosity; an increase in ISM tortuosity; and (**b**) a decrease in ISM duration. Decreasing each patch density by either increasing the number of patches while keeping the overall density constant or by increasing the patch area, resulted in (**c**, **e**) an increase in ESM tortuosity and a decrease in ISM tortuosity; and (**d**, **f**) a decrease in ISM duration

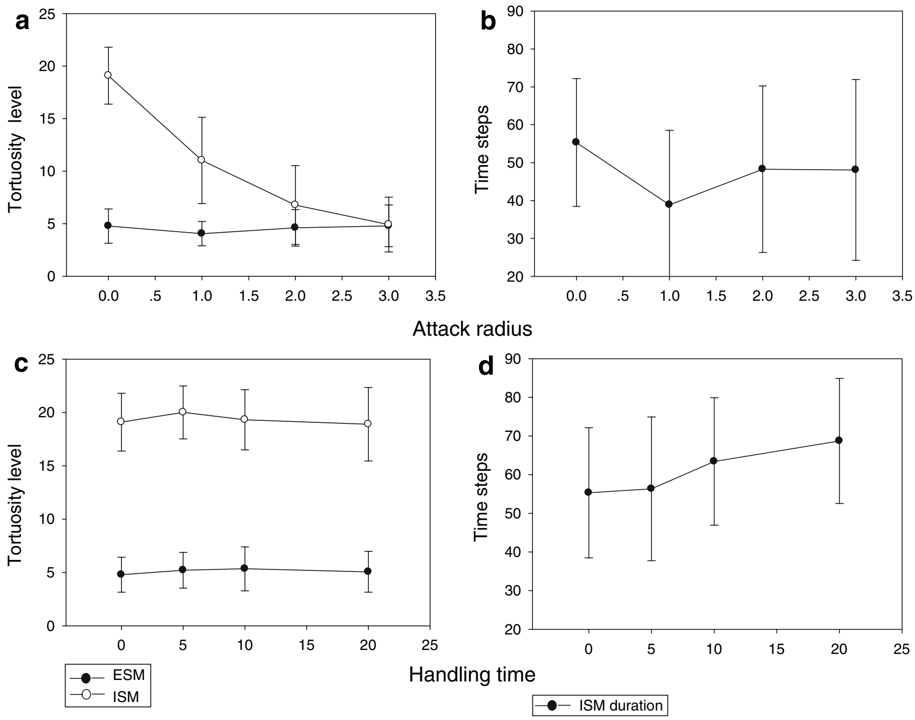

Fig. 3 Searching tactic components in clumped pattern (means of 100 replications of the GA ± 1 SD; $n = 100$) as a function of attack radius (0, 1, 2 and 3 additional squares of detection range in each direction) or handling time (0, 5, 10 and 20 time steps of handling). Simulations were run for 1000 time steps, arena size was 100 × 100 squares, there were 5 patches of 16 × 16 squares, and the three traits (ESM, ISM and ISM duration) were obtained using a GA. Note that when increasing attack radius, handling time was held zero, and vice versa. Increased attack radius resulted in (**a**) a decrease in ISM tortuosity; but (**b**) ISM duration showed a sharp decrease followed by an increase. Increased handling time resulted in (**c**) very minor changes in ESM and ISM tortuosity, and (**d**) a sharp increase in ISM duration

Discussion

Resource distribution may vary greatly in space or time on a seasonal or even daily basis (Ben-Natan et al 2004), and perception of the environment by organisms depends on their foraging scale (coarser versus finer scales; e.g., Ward and Saltz 1994). Consequently, organisms may experience the same environment differently (Ritchie 1998). It is thus difficult to imagine that a single optimal tactic would be successful across environments; rather, arriving at an optimal tactic requires adjusting searching tactic components adaptively to food spatial distribution. Furthermore, factors such as the rate of environmental change and the animal generation time are also expected to influence searching tactic components. For example, short-time behavioral adaptations and learning will be useful when the environmental change is fast relative to the animal's life span. Slower changes are better faced with genetic modifications between generations, while intermediate rates of change can be faced with phenotypic or developmental plasticity (Meyers and Bull 2002). Our evolutionary model shows that the emerging components of a searching tactic change adaptively as a function of the spatial arrangement of food. When food is

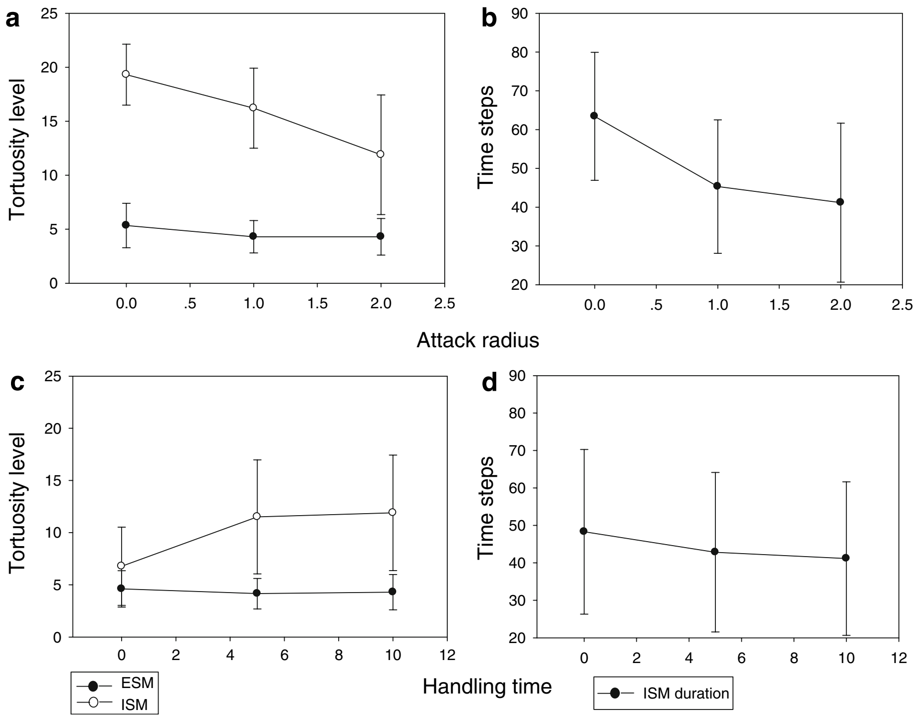

Fig. 4 The effect of the interaction between attack radius and handling time on searching tactic components (means of 100 replications of the GA ± 1 SD; $n = 100$): Increasing attack radius (0, 1 and 2 additional squares of detection range in each direction) while keeping handling time constant and long (10 time steps; **a**, **b**) and elongating handling time (0, 5 and 10 time steps of handling) while keeping attack radius high (two additional squares in each direction; **c**, **d**). The effect of increased attack radius on searching tactic components was consistent between long (Fig. 4**a**, **b**) and short (Fig. 3**a**, **b**) handling times. However, the effect of increased handling time on searching components was not consistent between low (Fig. 3**c**, **d**) and high (Fig. 4**c**, **d**) attack radius. Simulations were run for 1000 time steps, arena size was 100 × 100 squares, there were 5 patches of 16 × 16 squares, and the three traits (ESM, ISM and ISM duration) were obtained using a GA

distributed in a regular pattern, ISM is more directional than ESM, but under a clumped food pattern, ISM is much more tortuous than ESM.

A regular pattern of food is characterized by a negative auto-correlation among food items in space. Consequently, after encountering a food item an optimal forager should move away from it in a straight line because the chances of finding additional food items nearby are relatively low. Indeed, previous research has illustrated that such a pattern of quitting a food item in a direct line and paying little attention to the surrounding area could be a useful tactic when food is distributed in a regular pattern (Krakauer and Rodeiguez-Girones 1995), and items or patches are very distant (as in the case of hop aphids; Compton 2001). Additionally, it is analogous to leaving a patch in a straight line after exploiting it. The duration of the directional movement after leaving a patch should be determined by the overall density of food items, as our model shows. When food density is high, food items are closer to each other, and there is a need to use directional movement only for a short time period (smaller duration of ISM). Another interesting result was the change in ESM when the overall density was increased. Increased density had a positive effect on ESM tortuosity. This is probably because in rich areas it is better to search more carefully, using a more tortuous movement, as has also transpired from other theoretical and experimental studies (Motro and Shmida 1995; Zollner and Lima 1999).

When food is abundant and distributed in a random pattern, there is no difference between ESM and ISM. However, when food is scarce and randomly distributed, ISM is more tortuous than ESM. We hypothesized that in random pattern ESM will not significantly differ from ISM, but the results supported our hypothesis only partially. A possible explanation is that random pattern creates "pseudo-patches" (i.e., aggregations of food items), a phenomenon more dominant when food is scarce. Motro and Shmida (1995) claimed that bees can use near-far search (directional ESM and tortuous ISM) in random pattern as well, because the searching process itself produces some patchiness in the environment. This can be another possible explanation for the difference between ESM and ISM.

When searching in a clumped pattern, ISM is much more tortuous than ESM. This makes sense, since food is positively auto-correlated in space (when a food item is located this can be a good indicator that there is more food nearby). This finding is supported in theoretical (e.g., Benhamou 1992) and empirical studies (e.g., Nakamuta 1985; Mellgren and Roper 1986). The essential difference between searching in different food patterns is the sharpest when comparing regular and clumped patterns. This difference supports our hypothesis that a successful searching tactic in a specific food pattern may fail completely in another pattern.

An interesting trend is the increase in ESM directionality as the patch density increases, which may be the result of a better distinction between patches and the surrounding inter-patch matrix. In other words, when patches are dense a forager using directional movement would hardly miss them. Additionally, as patch density increases ISM should be more tortuous. This is because when patches are rich and dense, the forager exploiting this food cluster would remain in the same area for a longer time period. The ISM duration decreases as the density in the patch increases. This result is unexpected, because foragers should stay more in high-density patches (i.e., longer ISM durations). We suggest that this reduction in ISM occurs in order to reduce the time lost while searching outside the patch during the ISM. ISM may bring the animal closer to the patch center and help it find additional food items, but it might also take it outside the patch, where there is no food (since food items are hidden). After not finding food for a fixed time (i.e., the ISM duration), the forager shifts back to ESM. When patch density is low, it is not optimal to shorten this fixed time, because it may also lead to an early departure from a patch. However, when patches are dense, the forager will keep encountering food items, reseting its ISM duration (again, in a rich environment characterized by patches of high density there should be a better distinction between those patches and the surrounding matrix). This phenomenon can alternatively be explained by diminishing returns, as described by Charnov (1976) and demonstrated experimentally on numerous occasions (e.g., Ovadia et al 2001): In rich habitat less time should be devoted to each patch as a result of diminishing returns.

An increase in the number of patches or an increase in patch area resulted in a decrease in each patch density. Consequently, animals decreased the ISM tortuostiy and increased the ESM tortuosity. This response is similar to the response when *decreasing* the overall density, also resulting in a reduction in patch density (see Fig. 2a in the opposite direction, from right to left). We conclude that when patches are more dilute it becomes less profitable to search intensively. However, ISM duration decreased when reducing each patch density, in contrary to its general increase when *decreasing* the overall density. It is possible that the difference between the three treatments is that increasing the patch number or area also resulted in an increase in the relative area occupied by food items in the arena. But at this point the mechanism causing this pattern—and hence its potential generality—is unclear.

Handling time and encounter rate are considered to be the basic elements of many foraging models (Ovadia et al 2001), and a trade-off between these two factors may often result in species coexistence. We show here that searching behavior is strongly influenced by attack radius, which is a major component of encounter rate. The decrease in ISM tortuosity as the attack radius increases is caused by the improved capability of the forager to locate food items nearby. The forager no longer needs to search intensively and has only to move in a relatively straight line through the patch in order to consume the maximal number of food items. Indeed, by allowing the foragers to have some attack radius we break some of the basic rules of the movement patterns as comprised of the three traits, ESM, ISM and ISM duration.

Handling time is a universal component of foraging, and may also influence the optimization in the simulation. An increase in handling time results in an increase in the duration of ISM. This is because a forager who suffers from long handling time has to stay longer in a patch in order to compensate for the long periods of time it spends handling the prey. Moreover, forcing the animal to have some handling time is equivalent to reducing the habitat profitability. Therefore, according to optimal foraging theory animals should stay more time in each patch (Charnov 1976). The relationship between handling time and other characteristics of foraging, such as attack rate and prey size, have been previously studied (e.g., Griffiths 1980; Ovadia et al 2001). Ovadia et al (2001) measured the handling time and encounter rate of two granivorous gerbil species which coexist sympatrically over a wide range of sandy habitats in the old world. They found that the larger gerbil species had a shorter handling time but also a lower seed encounter rate compared with the smaller gerbil species. They interpreted this to mean that the larger species may have an advantage at high food densities when most of the forager's time is spent handling seeds rather than searching for more seeds. But the smaller species may be at an advantage when food is scarce and when searching occupies most of the forager's time. The advantage that one species has over the other under different conditions may promote their coexistence over a wide range of resource densities. The interaction between handling time and attack radius shows that the three searching components react similarly to increased attack radius at low or high handling times. However, the response to increased handling time is not consistent between low and high attack radius. We interpret this to mean that at high levels of attack radius and handling time, the latter operates against the former in optimizing movement components. In other words, ISM becomes less tortuous.

Our model may have several implications for understanding prey behavior and the dynamic interactions between a predator and its prey. First, when the prey can actively select or change its location in space, there will be a considerable advantage for deviant individuals (as also suggested by Grünbaum 1998). For instance, when the prey population is distributed in clumps, a successful tactic may be to stay out of the clumps, because it is likely that the searching tactic of the predators has been adjusted adaptively to search within clumps (avoiding aggregation may be associated with reduced predation risk). Second, in a spatially heterogeneous environment, e.g., when some of the food is clumped while some is distributed in a regular pattern, a possible mechanism of coexistence among species or among different individuals of the same species might be segregation by searching behaviors. We suggest that animals searching differently in such an environment will succeed better than animals sharing the same searching behavior. Clearly, these two hypotheses should be further studied.

In summary, we used a simulation model and genetic algorithm to model animals searching in a landscape characterized by different spatial food patterns. Our model indicated that arriving at an optimal searching tactic requires the different modalities of searching behavior (i.e., ESM, ISM and ISM duration) to change adaptively as a function of food spatial distribution. To do so, an organism should have an innate spectrum of possible searching tactics, which it can modify according to the spatial arrangement of food items, or it should use a genetically fixed searching tactic that has been evolved in response to the specific pattern of the food it experiences. We interpret this to mean that animals with larger spectra of searching tactics should experience greater variance or seasonal changes in their food pattern than animals with narrow spectra of searching tactics. Finally, we suggest that using such a bottom-up evolutionary simulation approach may improve our understanding of how extrinsic and intrinsic factors interact to influence searching behavior at varying foraging scales.

Acknowledgements We thank Simon Benhamou and Tamar Keasar for their instructive comments on previous versions of the manuscript. We would also like to thank Ido Filin for his great help in improving the simulation program.

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