

Efficiency Evaluation of Two Competing Foraging Modes under Different Conditions

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ABSTRACT: Various foraging modes are employed by predators in nature, ranging from ambush to active predation. Although the foraging mode may be limited by physiological constraints, other factors, such as prey behavior and distribution, may come into play. Using a simulation model, we tested to what extent the relative success of an ambush and an active predator changes as a function of the relative velocity and movement directionality of prey and active predator. In accordance with previous studies, we found that when both active predator and prey use nondirectional movement, the active mode is advantageous. However, as movement becomes more directional, this advantage diminishes gradually to 0. Previous theoretical studies assumed that animal movement is nondirectional; however, recent field observations show that in fact animal movement usually has some component of directionality. We therefore suggest that our simulation is a better predictor of encounter rates than previous studies. Furthermore, we show that as long as the active predator cannot move faster than its prey, it has little or no advantage over the ambush predator. However, as the active predator's velocity increases, its advantage increases sharply.

Keywords: foraging modes, predator-prey interactions, searching behavior, movement directionality.

Foraging mode is an important characterizing trait of predators and may correlate with a syndrome of behavioral, ecological, physiological, and morphological characteristics (Huey and Pianka 1981; McLaughlin 1989; Sih et al. 2004). Such a trait operating at the individual level may strongly influence community level interactions (e.g., Schmitz and Suttle 2001; Schmitz et al. 2004). Ambush

and active predation are considered to be the two extremes of the foraging mode spectrum (Eckhardt 1979; Perry 1999). Though we refer here only to those two extremes for simplicity, animals in fact possess some degree of flexibility in using different foraging modes as the environment changes. A fundamental question in evolutionary ecology is, under what circumstances does one foraging mode become advantageous over the other? Previous research has illustrated that predators may change their foraging mode according to various factors, such as variation in prey abundance (Formanowicz and Bradley 1987; Hirvonen 1999), opportunistic preferences for prey (Greef and Whiting 2000), and interspecific competition (Fausch et al. 1997).

Recent research has shown that the movement properties of foraging animals may have important implications for their success in locating prey (Fulton and Bellwood 2002) or in reaching specific patches (Hein et al. 2004). Moreover, when searching for hidden prey, certain searching patterns fit better than others (e.g., Benhamou 1992; Zollner and Lima 1999). Previous models evaluating the efficiency of different foraging modes (Gerristen and Strickler 1977; Werner and Anholt 1993) assumed that animals move in a strictly nondirectional way (i.e., random walk); however, such an assumption has considerable limitations. First, moving nondirectionally would result in redundant paths (Zollner and Lima 1999), and thus it is only rarely useful. Second, observations of animal movement show that directionality is the rule across different taxa, suggesting that strict nondirectional movement is not common in nature (e.g., Nakamura 1985; A. Bouskila, unpublished manuscript). Third, estimation of encounter rates using a model assuming random walk, such as the one developed by Werner and Anholt (1993), shows that the active predator should always have a higher encounter rate compared with the ambush predator. All of the above imply that the next logical stage in modeling encounter rates is to relax the assumption of random walk. Indeed, more modern theoretical literature uses a correlated random walk to analyze and model animal movement (e.g., Kareiva and Shigesada 1983; Benhamou 1992; Nolet and

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Table 1: List of directionality levels tested in the model

| No. | Probability of angle relative to previous move | | | | |
|-----|--|-------|-------|--------|-------|
| | 0° | ± 45° | ± 90° | ± 135° | 180° |
| 1 | 90% | 5% | ... | ... | ... |
| 2 | 80% | 10% | ... | ... | ... |
| 3 | 60% | 15% | 5% | ... | ... |
| 4 | 40% | 20% | 10% | ... | ... |
| 5 | 30% | 25% | 10% | ... | ... |
| 6 | 20% | 20% | 20% | ... | ... |
| 7 | 12.5% | 12.5% | 12.5% | 12.5% | 12.5% |

Note: From top to bottom, directionality level shifts from more directional to less directional. The fourth row indicates the standard directionality used in all other tests.

Mooij 2002). The goal of this study is to test how this change in the movement pattern affects the encounter rates of the active versus the ambush predators.

We used a grid-based simulation model to test the prey encounter rates of active and ambush predators as a function of the relative velocity and movement directionality of prey and active predator. Our model used a spectrum of correlated random walk rules of movement, from strictly nondirectional to almost directional movement, while abstracting the cost associated with searching.

Methods

The Model

We constructed a grid-based simulation model written in Matlab version 6.5. Grid-based simulations are simple to compute and were previously used to describe the movement of foragers in a two-dimensional space (e.g., Nolet and Mooij 2002). We used a “torus model” to cope with the problem of active predator or prey exiting the arena edges. According to this model, after exiting the arena, an individual immediately appears from the opposite side (Zollner and Lima 1999; Nolet and Mooij 2002). This type of model was used to maintain a fixed number of prey items in the arena, assuming that when the area is large enough, the prey density is relatively constant.

The model consisted of two predators, an ambush and an active predator, both of whom started at the same position in space at the center point of the arena (60 × 60 squares). Prey items were placed at the arena edges. The active predator and the prey moved simultaneously at the same time unit; they were not biased toward each other, and there was no interaction among animals. Prey items were allowed to occupy the same square simultaneously. The animal’s initial movement directionality was random. Afterward, the direction of movement changed according to a set of probabilities (table 1, fourth row). The ambush predator, on the other hand, never moved and remained

at the arena center. When a prey item was caught, the time to capture was recorded. The prey item was not removed, and the simulation continued until the other predator caught its first prey item. Each simulation was run 2,000 times, and the time to capture of the ambush predator was subtracted from the time to capture of the active predator. We used the percentile bootstrap test (Manly 1997) to estimate 95% confidence intervals. As accepted in such tests, the significance level was determined by examining the overlap in confidence limit intervals between treatments. In other words, only when there was no overlap between different treatments were the groups considered to be distinct. All procedures were performed using Matlab. The simulation code is available in a zip archive in the online edition of the *American Naturalist* or on request from the corresponding author.¹

In order to verify the simulation results, our results for nondirectional movement were compared with an analytical model predicting the encounter rates (Z) for a randomly moving prey and predator in two-dimensional space (Werner and Anholt 1993). This is a modification of Gerristen and Strickler’s (1977) three-dimensional model, $Z = 2rN(v^2 + s^2)^{1/2}$, where r is the perceptual radius of the predator, N is the predator density, v is the prey mean velocity, and s is the predator mean velocity. Since the equation is symmetric, meaning that predator and prey have the same probability of encountering each other, we used N as the prey density and not predator density and thus calculated the encounter rate of the predator and not of the prey. We compared the results of the analytical and the simulation models for four different scenarios: predator and prey move at the same velocity and predator moves two, four, or six times faster than prey.

Test 1: Influence of Prey Density

In all other procedures, our model used four prey items. However, to test whether prey density influences the relative success of the active or the ambush predator, we used the following prey densities: 4, 6, 8, 10, 12, 14, and 16 prey items. Prey items were always added at the arena edges in fixed locations.

Test 2: Influence of Arena Size

The original arena size was 60 × 60 squares. To test for the effect of arena size on the relative success of the active versus the ambush predator, the arena size was varied as follows: 20 × 20, 40 × 40, 60 × 60, 80 × 80, and 100 × 100 squares.

¹ Code that appears in the *American Naturalist* has not been peer-reviewed, nor does the journal provide support.

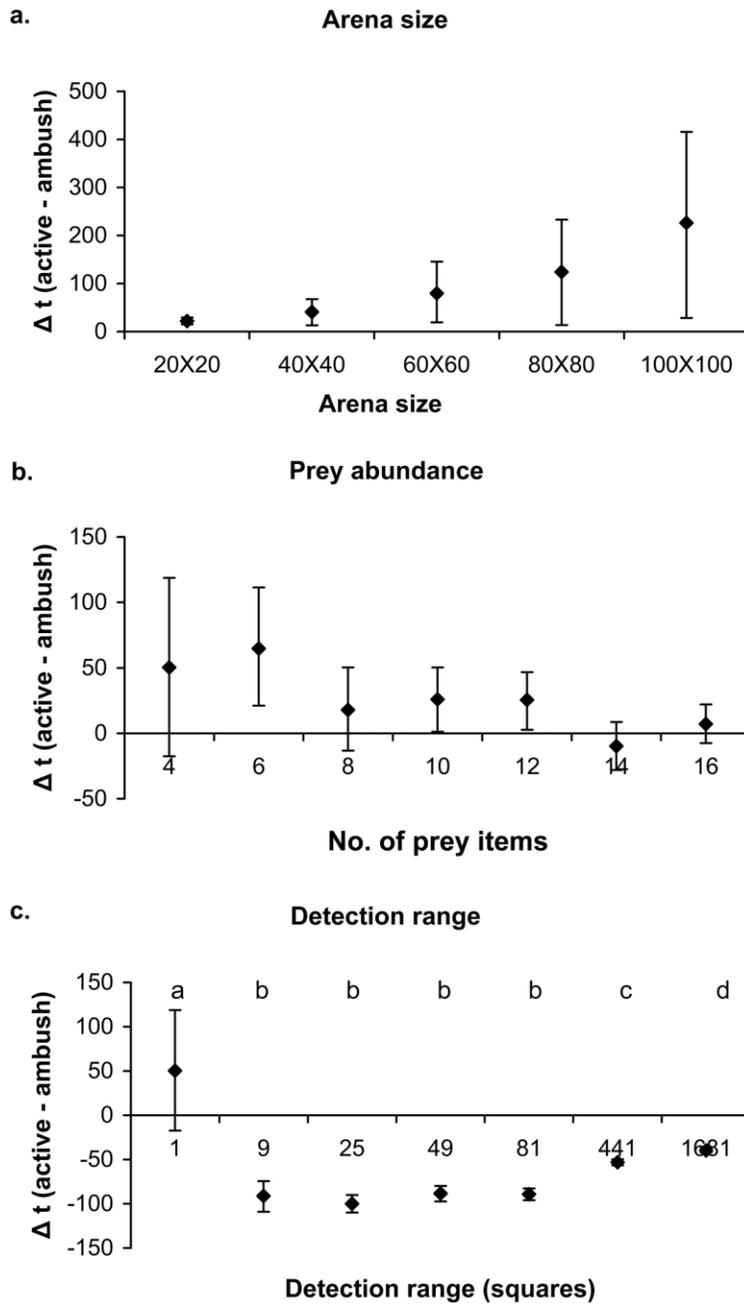


Figure 1: Relationship between the relative time to capture (active predator t_{capture} – ambush predator t_{capture}) and increasing prey abundance (a), increasing arena size (b), and increasing detection range (c) for both predators. Bootstrap tests did not detect significant effects ($P > .05$ for all cases) of either prey abundance or arena size. The advantage of the active predator showed an increase followed by a decrease (bootstrap test; different letters represent $P < .05$ in pairwise comparisons).

Test 3: Manipulation of Detection Range

In all other procedures, the detection range was minimal, meaning that predators could detect the prey only when it entered the square they occupied (detection range of

one square). To test for the effect of the detection range on the relative success of the predators, we manipulated the detection range as follows: 1, 9, 25, 81, 121, 441, and 1,681 squares, which enabled the predator to attack the prey from these larger distances.

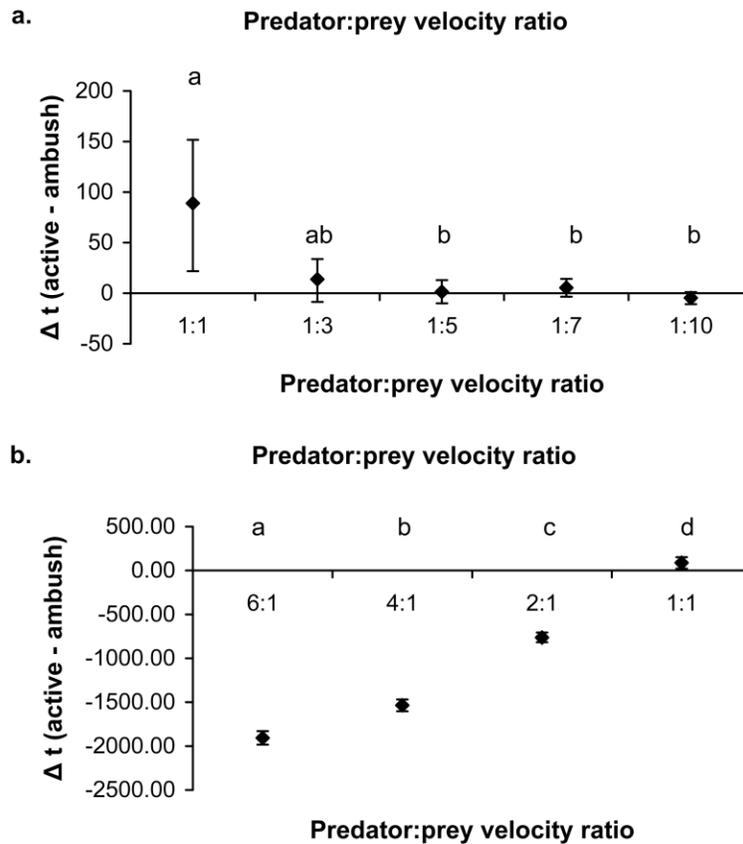


Figure 2: Relationship between the relative time to capture (active predator t_{capture} – ambush predator t_{capture}) and decreasing predator : prey velocity ratio (a) and increasing predator : prey velocity ratio (b). Decreasing predator : prey velocity ratio had no significant effect on relative time to capture (bootstrap tests; $P > .05$ for all cases). However, as predator : prey velocity ratio increased (b), the advantage of the active predator over the ambush one increased (bootstrap test; in all pairwise comparisons, $P < .05$; different letters indicate significant differences).

Test 4: Manipulation of the Relative Velocities of Prey and Mobile Predators

Relative velocity was manipulated while keeping all other factors constant. First, we checked the following velocity ratios between active predator and prey: 1 : 3, 1 : 5, 1 : 7, and 1 : 10 (the prey moves faster than the active predator). We then checked velocity ratios of 2 : 1, 4 : 1, and 6 : 1 (the active predator moves faster than the prey). Velocity did not change during each simulation run. When velocity ratio between active predator and prey was 1 : 1, all movements occurred simultaneously. However, when the velocity ratio was, for instance, 1 : 3 in favor of the prey, prey items moved three times in each step. The active predator movement occurred on the third movement of the prey.

Test 5: Manipulation of Movement Directionality

The degree of directionality of both active predator and prey was manipulated, shifting gradually from almost di-

rectional movement to strictly nondirectional movement (table 1). Next, we combined in one cycle a highly directional moving predator (table 1, first row) with a nondirectional moving prey item (table 1, seventh row), and vice versa: a nondirectional moving predator with a directional prey item.

Test 6: Sensitivity Analysis

In order to verify that neither the results regarding movement directionality nor the results regarding velocity could be affected by differences in arena size or prey density, directionality and velocity were tested under two additional conditions. We checked the differences between the relative success of active and ambush predators using different degrees of directionality in an arena of 20×20 and with a prey density of 12 prey items (our simulation generally used a 60×60 arena and four prey items). We also

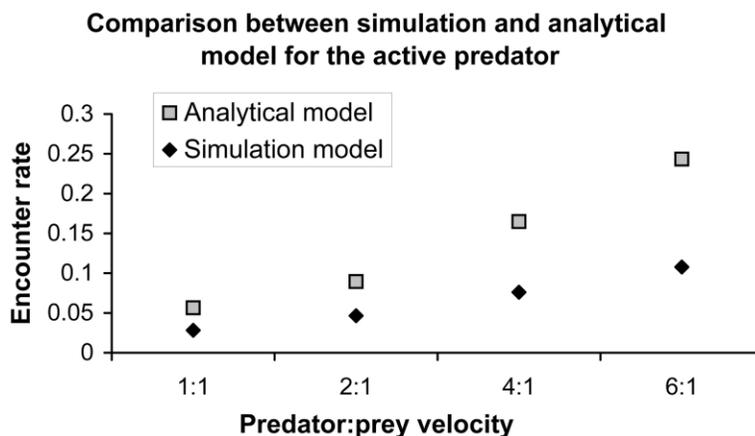


Figure 3: Positive correlation between predator velocity and encounter rates (t_{capture}^{-1}). Simulation results were qualitatively similar to an analytical model derived by Werner and Anholt (1993). We used an arena of 20×20 squares and assigned nondirectional movement to both the active predator and 12 prey items.

tested different ratios of velocity between the active predator and the prey under these two conditions.

Results

No significant effects of prey density (fig. 1*a*) and arena size (fig. 1*b*) were detected on the relative time to capture between the two foraging modes, suggesting that our model was not sensitive to these factors. Increasing detection range from a minimal range of one square to nine squares improved the time to capture of both predators, but the improvement of the active predator was much more prominent. Additional increase in the detection range caused no further change. When testing very high values of detection range (441 and 1,681 squares), the advantage of the active predator decreased (fig. 1*c*).

When prey velocity increased beyond the 1:1 ratio, almost no change in the relative time to capture was detected (fig. 2*a*). When the active predator and the prey had the same velocity, the ambush predator had a slight advantage over the active one; however, as prey velocity increased, this advantage declined. The difference in time to capture increased significantly as a function of increased predator velocity (fig. 2*b*). This means that when the active predator moves faster than its prey, there is an increasing advantage to the active predator over the ambush predator. Results for nondirectional movement when using different ratios of velocity were qualitatively consistent with those predicted by the analytical model of Werner and Anholt (1993; fig. 3).

The relative time to capture decreased significantly as the movement directionality of both prey and active predator decreased. In other words, as the movement of both

prey and active predator became less directional, the time to encounter of the ambush predator increased in comparison with that of the active predator (fig. 4*a*).

We next combined highly directional moving prey with a randomly moving predator (hereafter referred to as “direct prey–random predator”) and vice versa (hereafter referred to as “random prey–direct predator”). These two scenarios were contrasted with the strictly nondirectional movement scenario of both active predator and prey (table 1). The relative time to capture of random prey–direct predator was much lower than that of direct prey–random predator (fig. 4*b*). When the prey movement was directional, there was no influence of predator directionality on encounter rates. In other words, only when prey movement is nondirectional would a predator adopting directional movement have an advantage over a predator adopting nondirectional movement.

The results regarding the effect of directionality and velocity on relative time to capture were consistent across arena sizes and prey densities, suggesting that our model is not sensitive to these parameters.

Discussion

Our simulation model highlights two interesting points. First, if an active predator cannot move faster than its prey, the encounter rate is mainly influenced by the prey velocity. Second, previous analytical models that assumed nondirectional movement showed that active predators have higher encounter rates than ambush predators (Werner and Anholt 1993). We found that active predators do indeed have higher prey encounter rates than ambush predators when predator movement is nondirectional, but

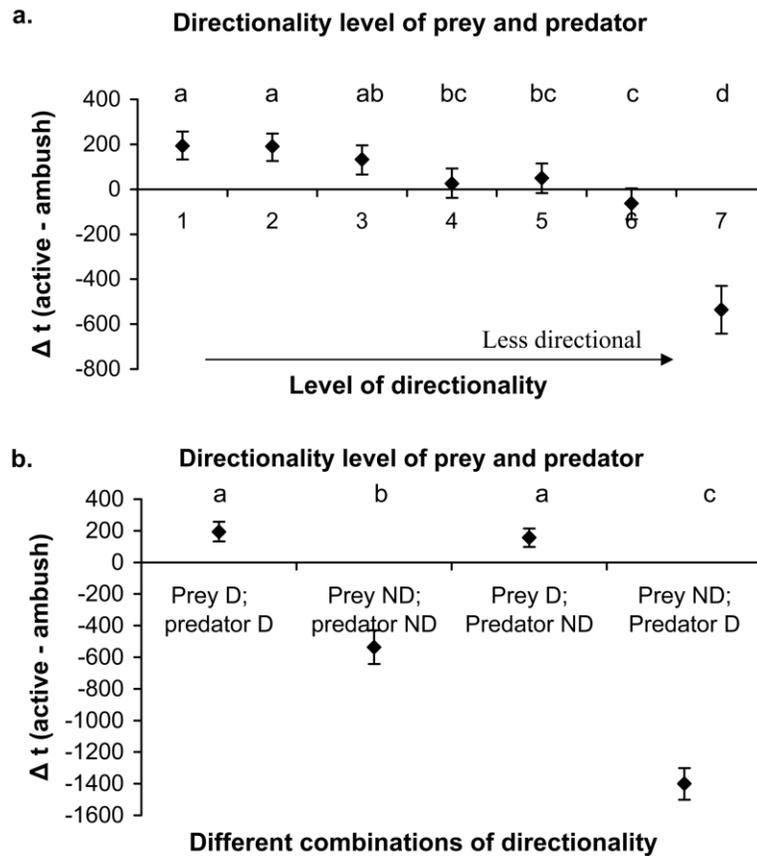


Figure 4: Relationship between the relative time to capture (active predator t_{capture} – ambush predator t_{capture}) and movement directionality (as shown in table 1). In most pairwise tests, $P < .05$ (P values were estimated using bootstrap tests). *a*, Decreased directionality results in an increase in the relative success of the active predator ($P < .05$ for most cases). *b*, Different combinations of prey and predator movement directionality: *D* = directional movement; *ND* = nondirectional movement. When prey moved directionally, encounter rates were not significantly influenced by predator movement directionality. In other words, when prey moves nondirectionally, the predator would do better to adopt a directional form of movement. Different letters indicate significant differences ($P < .05$).

we also found that as predator movement becomes more directional, this difference in encounter rates disappears. Animals rarely use strictly nondirectional movement; we thus suggest that our model is a better predictor of their encounter rates with prey. Moreover, it can explain benefits associated with the ambush strategy.

There was a clear dichotomy regarding velocity ratio: the optimal strategy for predators that cannot move as fast as their prey is the ambush one, because predator velocity is negligible as long as it is below prey velocity. However, if the predator is able to move faster than its prey, the encounter rate of the active predator increases, and adopting the active mode becomes preferable. Clearly, this pattern might be weakened by the costs associated with increased predator velocity (e.g., metabolic costs and predation risk). Our results support Huey and Pianka's (1981) hypothesis that if the prey moves fast, it is better

to be a sit-and-wait (ambush) predator. It is important to note that such a dichotomy has been largely ignored in the ecological literature (but see Gerristen and Strickler 1977; Werner and Anholt 1993). When the prey moves twice as fast as the active predator, it has the same effect on the encounter rate of both predators. In contrast, increasing the active predator's velocity affects only its encounter rate, without contributing anything to the success of the ambush predator.

The improvement in the performance of the active predator when slightly increasing the detection range is not predicted by Werner and Anholt's (1993) model. We suggest that this is caused by a faster approach of the active predator to the prey compared with the ambush predator, which does not move. The active predator with a higher detection range does not have to intercept a prey item but instead simply has to move sufficiently close to it in order

to capture it. However, at very high detection ranges (441 or 1,681 squares), the foraging mode is less relevant, because prey items can be located from large distances.

Our simulation model did not reveal any link between prey density (as reflected in changing prey number or arena size) and relative success of the active versus the ambush predator. These results are consistent with the analytical model of Werner and Anholt (1993), which predicts that a change in either arena size or prey number should not bring about a change in the relative success of active and ambush predators. It is also consistent with a study by Greef and Whiting (2000), who reported that a lizard foraging on insects adopts a sedentary foraging mode, regardless of its prey density. However, reports from other studies (e.g., Jaeger and Barnard 1981; Formanowicz and Bradley 1987; Hirvonen 1999) are not consistent with this pattern. When we examine each foraging mode separately, we find a positive correlation between prey abundance and the absolute predator encounter rate with prey. Therefore, it would be advantageous to adopt a sedentary strategy when food is abundant, especially owing to the additional costs associated with moving.

We show that when searching for nondirectional moving prey, it is more useful to use relatively directional movement (fig. 4*b*). This is because when predator and prey movement is nondirectional, the predator will approach the prey very slowly. This pattern is analogous with previous reports suggesting that ambush predators mostly capture active prey while active predators mostly capture sedentary prey (Eckhardt 1979; Huey and Pianka 1981; Riechert and Luczek 1982; Greef and Whiting 2000). Our results are also in accordance with the simulation results of Zollner and Lima (1999), who showed that an exhaustive (i.e., nondirectional) search in a uniform landscape is not a useful strategy. However, when the opposite is true, and prey employs directional movement and active predator employs nondirectional movement, the results do not differ from a situation in which both prey and active predator employ a directional type of movement. We suggest a possible connection between the preferred foraging mode of the predator and the directionality level of the prey. There is some evidence of animals searching in straight lines when the prey is aggregated and/or sedentary (e.g., ladybird beetles searching for aphids; Nakamura 1985). Fulton and Bellwood (2002) reached similar conclusions: the foraging path depends on the prey distribution—small patches are most efficiently explored by moving in straight lines, while large homogenous patches are better explored through high turning rates.

Our model has several simplifying assumptions. First, the prey distribution is random, whereas in reality prey is very often clumped. Second, the predator is not attracted to the prey, nor does the prey try to avoid the predator.

Third, we assume a homogenous landscape. Fourth, costs derived from the mobile strategy (energetic cost, risk of predation, etc.) can be safely abstracted. Fifth, the foraging mode does not affect the probability of successfully attacking a prey item. Since our aim was to compare the time to encounter of active and ambush predators, the additional cost of the active strategy would be important only when the active strategy is apparently preferred. Relaxing these assumptions could result in more complex models, which may bring about a deeper insight into the use of these two strategies.

Grimm and Railsback (2005, p. 57) suggest that the search for a general theory of how ecological systems function may be more productive when using individual-based models. In such models, system properties emerge from individual behavior and interactions, which are much easier to follow and understand. In this individual-based model, we used a few prior assumptions and incorporated only basic properties of animal behavior. The strength of this model is in its generality and simplicity, and thus it may have implications for various systems.

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