

## Prey Encounter Rate by Predators: Discussing the Realism of Grid-Based Models and How to Model the Predator's Foraging Mode: A Reply to Avgar et al.

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In an article in this journal (Scharf et al. 2006), we presented an individual-based model (IBM) whose aim was to investigate how gradual changes in the movement directionality and velocity of the predator and prey influence the relative hunting success of an active versus an ambush predator. Our main findings were as follows: (1) As the movements of the predator and prey become more directional, the relative hunting success of the active predator decreases and that of the ambush predator gradually improves. (2) Nondirectionally moving prey is better caught by a directionally than by a nondirectionally moving predator. (3) As expected from analytical models (e.g., Werner and Anholt 1993), an increase in the velocity of the active predator improves its relative hunting success. In their critique of our model, Avgar et al. (2008, in this issue) argued that the way in which we modeled the behavior of the active predator by using sequential actions (i.e., moving first and only then detecting/attacking prey) is problematic. They therefore modified the original code of our model to enable the predator to catch prey items while moving. Whereas in the original model the ambush predator had higher encounter rates than the active predator under some specific conditions, in the modified model this scenario never occurred. Avgar et al. noted that this

result better fits the expectations of previous analytical models.

Even with the modification of Avgar et al. (2008), none of the important patterns or trends presented in our study were qualitatively altered. First, the success of the ambush predator improves with increased directionality of both the active predator and prey, as compared to random-walk movement (fig. 2*a* in Avgar et al. 2008). Second, different combinations of directionality levels for the active predator and prey produce qualitatively the same results (fig. 2*b* in Avgar et al. 2008). Furthermore, even an additional minor trend was consistent between the two versions of the simulation: an increase in the active-predator velocity relative to the prey velocity results in an increase in the success of the active predator relative to the ambush predator (fig. 1*b* in Avgar et al. 2008). The only disagreement between the two versions of the model is presented in figure 1*a* in Avgar et al. (2008), in which our results show equal success between predators as the prey velocity increases relative to that of the active predator and Avgar et al. present a decrease in the relative success of the active predator. This difference did not, however, critically change the interpretation of the results: as the prey moves faster, the difference between the two predators diminishes, because encounter rates are influenced far more by prey velocity than by active-predator velocity. This latter point is not new (i.e., the velocities of prey and predator) and can be derived from earlier analytical models, such as those of Gerritsen and Strickler (1977) and Werner and Anholt (1993).

The above exposition thus suggests that the comment of Avgar et al. (2008) should be viewed not as critical but rather as a successful robustness analysis of our model (Grimm and Railsback 2005, p. 336), strengthening our sensitivity analysis. The outcome of a robustness analysis should be a general pattern and not a single value generated under a specific parameter combination. Furthermore, simulation models are simply an abstraction of reality and thus should provide only general quantitative predictions (Schmitz 2001). Meeting the criterion of being

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both general and realistic at the same time is difficult in this type of modeling framework, since the exact behavioral rules implemented in the model may affect some of the results (Murdoch et al. 1992), as happened here: a behavioral rule of the simulated animals was modified, and consequently the results obtained under specific parameter combinations changed in favor of the active predator in a way that mostly agrees with the trends and patterns presented in our article. Indeed, it is certainly not novel that a change in the order of events in simulations using discrete time and space may have some effect on the results (e.g., Ruxton 1996). Therefore, in designing an IBM, there are no “true” or “untrue” behavioral rules but only rules that are more or less adequate for specific systems (e.g., Schmitz 2001). Because our model was not calibrated to a specific system, such a discussion is premature.

We next explain why we disagree with the claim of Avgar et al. (2008) that the way we modeled active-predator behavior is either unrealistic or inappropriate. In grid-based simulation models, both space and time are simplified by treating them as discrete instead of continuous properties. Specifically, space is decomposed into grid cells, and the variation among cells but not the variation within each cell is emphasized (e.g., Bian 2003; Grimm and Railsback 2005, pp. 250–251). Furthermore, time is treated discontinuously, and the sequence of events should be chosen according to each specific system the model is calibrated for. Therefore, our computational method, by which predation is evaluated only from the predator’s location after prey and active predator move in each time step, is acceptable within the framework of grid-based simulation models. Moreover, grid-based models do not fully represent the spatial extent of individuals. For example, cells often represent individuals’ locations but not how much space they occupy (Grimm and Railsback 2005, pp. 250–251). Consequently, discussing the exact path traveled by animals between time steps is ineffective, since such a model represents only the individuals’ locations or change in locations over time steps. This is exactly how movement is represented in grid-based models (Bian 2003). Likewise, a time step model does not represent the velocity of an individual between time steps. Individuals just “jump” from one place at  $t$  to another place at  $t + 1$ . It is also already known that different discretizations of either space or time may lead to somewhat different results (Jetten et al. 2003). Finally, in contrary to the Avgar et al. claim that animals crossing each other should encounter, we suggest that there is no way to know whether a predator and a prey really overlapped on spatial or temporal scales that are finer than the grid cells and time steps. In other words, one can easily argue that their version of the model is exactly as unrealistic as ours.

In addition, it is important to note that in many systems, the movement of predators and/or prey is not continuous. Rather, it involves a series of movements and stops, and only during the latter can predators detect/attack prey. Such a search pattern is often referred to as “saltatory” (O’Brien et al. 1990; Cooper 2005) and is common in many systems of insects, spiders, fish, lizards, snakes, and birds (e.g., O’Brien et al. 1990; Gilbert 1997; Kramer and McLaughlin 2001; Schmitz and Suttle 2001; Bassett et al. 2007; Poole et al. 2007). Moreover, the way we modeled predator behavior may better fit predator-prey systems in which prey is small and cryptic or in which predators have a narrow attack range (e.g., Gendron and Staddon 1983; Nolet and Mooij 2002), meaning that only when the predator and the prey are close will an encounter occur. Thus, an ambush predator may indeed have higher encounter rates than the active predator, as our model suggested, and this may be especially relevant when the predator uses saltatory search or when the prey is cryptic (note that we neither set out to demonstrate this point as one of the goals of our original study nor developed a system-specific IBM). Furthermore, because the active predator can search while moving, it has an increased attack range (a product of both its velocity and its detection range). Therefore, it is not surprising that the encounter rate of the active predator increased, as we also showed (see fig. 1c in Scharf et al. 2006), and can be analytically calculated (Werner and Anholt 1993).

In summary, we claim here that the comment of Avgar et al. (2008) should be treated as a supporting robustness analysis of our model, since it strengthens our main conclusions. We agree that the modification of movement continuity may fit some predator-prey systems (of actively searching predators) better, while ours should fit other systems (of more discretely moving predators) better. Nevertheless, we disagree with the claim that the way we modeled predator behavior is unrealistic, because such a sequential behavior, consisting of movements followed by attacks, adequately describes many other systems in which prey is relatively cryptic or when an active predator uses a saltatory search pattern. Furthermore, grid-based models are not meant to be realistic to begin with, and our models surely have many other simplifying assumptions; each of them should be considered, but only after implementing the simulation in a specific model system (see also Scharf et al. 2006, p. 356). Therefore, all the discussion about the realism of this simulation model seems to us somehow ineffective.

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