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Notes and Comments

How Movement Properties Affect Prey Encounter Rates of Ambush versus Active Predators: A Comment on Scharf et al.

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Movement properties of foraging animals are among the key determinants of foraging success (Zollner and Lima 1999). In a recent publication in this journal, Scharf et al. (2006) investigated the effect of movement velocity and directionality on predator-prey encounter rates while comparing ambush (sedentary) and active (mobile) predators, representing two extreme endpoints of the foraging-mode spectrum.

Scharf et al. were innovative in investigating the effect of differences in directionality between predators and their prey. Importantly, their simulations revealed that the advantage of active over ambush predators diminishes as the prey tends to move faster than the predator or in a more directional way. Yet they also reveal a very intriguing result: ambush predators were found to encounter prey more frequently than active predators if the prey tended to move as fast as the predator or along a directional path. This finding is surprising because it contradicts the consensus that benefits related to reduced predation risks and en-

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ergetic costs of movement are required for ambush predators to overcome the otherwise higher efficiency of active predators in encountering prey (Huey and Pianka 1981; Werner and Anholt 1993). In this comment, we identify the assumption in the Scharf et al. model that is responsible for this result. We show that a model relaxing this assumption, which we consider more compatible with the intended comparison between the two endpoint foraging strategies, not only eliminates this surprising result but also yields unequivocal and stronger evidence for Scharf et al.'s important conclusions.

Movement, the change in the location of an object over time, is a continuous phenomenon. Thus, the area scanned by an animal searching during any given time interval is a product of its velocity and its detection range (Hutchinson and Waser 2007). Scharf et al. employed a discrete spatiotemporal approach in which, during a single time step, a predator (or a prey) "disappears" from its current location (cell) and "reappears" in another cell. Thus, during the time step, no detection is possible regardless of the path traveled. This modeling method deviates from what is typically meant by a "mobile predator" in the literature: the classical conception (e.g., the one underlying the disk equation; Holling 1959) is that active predators can encounter prey during their moves. The assumption made by Scharf et al. introduces a bias against active predators. Consider, for example, a case in which a predator is located in cell (i, j) and a prey in the adjacent cell $(i + 1, j)$. The two animals then move toward each other, and by the next time step, they have switched locations: the predator is now located in cell $(i + 1, j)$ and the prey in cell (i, j). Indeed, this case represents, by definition, a predator-prey encounter, yet the Scharf et al. code does not count this case but enumerates only cases in which predator and prey both coincide in the same destination cell at the end of the time step.

Simulating predators that completely overlook prey or a prey's being completely transparent during their moves is, in our view, unrealistic and counterintuitive. Even if some examples for such behavior can be found, the as-

sumption made by Scharf et al. is incompatible with their intended comparison between the two endpoint foraging modes. This is because it discards a key difference between active and ambush foragers, portraying the active predators merely as ambush predators that do not move but appear in the simulated landscape in a manner determined by their directionality and velocity. Prey encounter rates of active predators are therefore underestimated in proportion to predator velocity. We relaxed this assumption by allowing a predator to detect prey during a given time step if a prey item has entered its detection range at any moment within this time step. It should be emphasized that our modification does not alter in any way the parameter defining the detection range of the predator (i.e., a single cell at any given time).

We implemented the above-mentioned procedure in the Scharf et al. code, using a domain of 100 × 100 cells with 10 prey items. The modified simulation code is available in a zip archive in the online edition of the *American Naturalist* or on request from the corresponding author.[1] Following Scharf et al., we recorded prey detection time for both active and ambush predators in the same simulation and estimated the 95% confidence interval of the mean difference in detection times, using the percentile bootstrap method (Manly 1997).

The revised simulations show that ambush predators do not encounter prey more frequently than active predators in any of the cases presented in Scharf et al.'s original simulations (figs. 1, 2). Furthermore, the hump-shaped pattern, with a distinct peak at the 1 : 1 predator-prey velocity ratio, reported by Scharf et al. disappears, and a clear (sigmoid) monotonic decline is predicted (fig. 1). Thus, our results provide stronger evidence for the general trend described by Scharf et al. of diminishing, though always negative, difference between active and ambush predator's prey detection time as prey moves faster than active predators (fig. 1) or along directional paths (fig. 2).

To conclude, our model results indicate that prey encounter rate is always higher in active than in ambush predators and that the opposite behavior reported under some circumstances by Scharf et al. is explained by their implementation of detection rules that discard a key difference between the two foraging strategies, introduce a bias against active predators, and are, in our view, also rather unrealistic. Regarding the method of individual-based modeling, we conclude that, as recommended by Grimm and Railsback (2005), it is indeed important not only to analyze the system-level behavior of an individual-based model but also to check whether the individual be-

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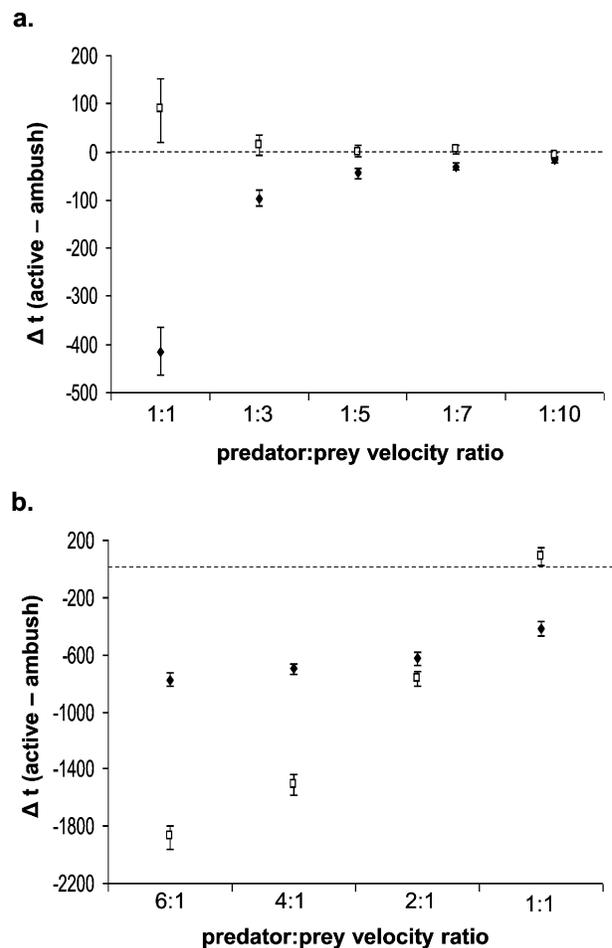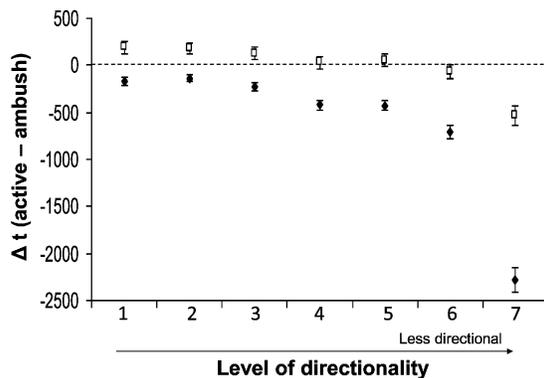

Figure 1: Mean difference in prey detection time between active and ambush predators under different predator-prey velocity ratios. Squares represent the results reported by Scharf et al. (2006; their fig. 2). Diamonds represent results obtained from the revised model, in which all differences are significantly smaller than 0, suggesting that active predators are always more efficient than ambush predators in encountering prey. Directionality is set to 4 (see Scharf et al. 2006). Error bars represent 95% confidence bounds.

havior is represented in a realistic way. Moreover, subtle details of model assumptions are usually hidden in verbal model descriptions, and so we consider it essential to include, as Scharf et al. did, the code implementing the model.

The diminishing differences in prey encounter rate between ambush and active predators when the prey moves faster or in a more directional way, found by both original and revised simulations, suggest that even minor energetic/survival costs of movement may bestow selective advantage to ambush predators. Note that the difference between the original and revised simulations can be related to the degree to which predators may overlook their prey while on

a. Directionality level of prey and predator

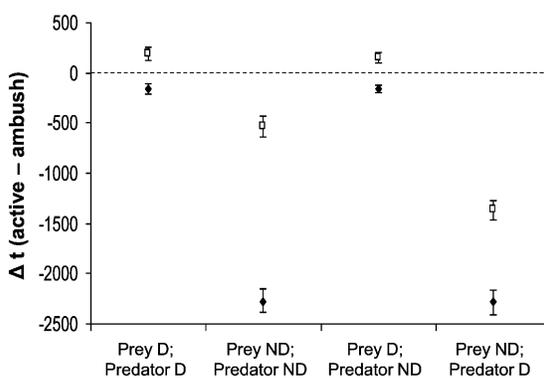## b. Different combinations of directionality

Figure 2: Mean difference in prey detection time between active and ambush predators at different levels of movement directionality (*a*, 7 designates pure random walk, while 1 designates a highly correlated random walk) and at different combinations of directionality of prey and predators (*b*, D = directional; ND = nondirectional; see Scharf et al. 2006 for more details). Squares represent the results reported by Scharf et al. (2006, fig. 4). Diamonds represent results of the revised simulation, in which all differences are significantly smaller than 0, suggesting that active predators are always more efficient in encountering prey than ambush predators. Predator-prey velocity ratio is 1 : 1. Error bars represent 95% confidence bounds.

the move (completely in the original code, not at all in the revised code). Thus, the general differences between the results suggest that conditions distracting the attention of mobile predators or making their prey less conspicuous can determine the relative efficiencies of these two extreme foraging strategies. In order to improve our understanding of animal movements and foraging strategies, perception quality effects of this kind, already discussed in the literature (Hutchinson and Waser 2007), should be given more attention.

Acknowledgments

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