Simulation of movement that potentially maximizes assessment, presence, and defense in territorial animals with varying movement strategies

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ABSTRACT

Brown et al. (2011) published a simulation model that could be used as a sub-model for larger simulations (e.g. at the population level) to investigate how individuals may optimize territorial movements while sampling a territory for resources. In their example, a male fish guards a territory against neighbor males while interacting with a mate (the resource), but all individuals employed the same, matching (relative-movement), strategies. We contrast the results of this model with a model that allows individuals to use independent movement strategies. Using mean encounter rate (MER) between individuals, and the coefficient of variation (CV), as metrics, we found that in all but the smallest territories, of all aspects (length-to-width ratios), variant relative-movement strategies are not determinant in maximizing territorial presence (male–neighbor male interactions) or minimizing its variation. Directed movement (low-movement angle strategies) appears to accomplish this, regardless of behavior relative to others. In contrast, in small territories, directed movement does not optimize territorial presence, regardless of territory aspect, and mismatched relative-movement strategies are typically optimal. Social presence (within territory male–female interactions) is more complex. In larger territories, again a general pattern of a low-movement angle strategy was optimal. However, aspects and steps sizes (distances between movement decisions) became influential. Once again, directed movement appears to take on lesser importance in smaller territories. Concerning optimizing relative-movement strategies, matching, or no strategy, is optimal except for small, high aspect, territories. We conclude that a prudent approach in future efforts with the model will be to utilize a "top-down approach" by only removing the complexity involving varying movement strategies from simulations if they are found to be unnecessary for the situation simulated.

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1. Introduction

Many animals must assess resources while moving through space (e.g. Parker and Stewart, 1976; Thomson, 1981; Marzluff et al., 2004). Furthermore, territorial animals guard against potential intruders (e.g. Schultz and Switzer, 2001; Arnold et al., 2011; Pereira et al., 2014). Using simple rules, Brown et al. (2011) simulated how an animal moving through space could maximize its encounter rate with a resource while guarding against potential intruders. In an example application of the model, they found that fish using low-angle movement trajectories (direction of movement relative to the direction a fish was previously swimming), large step sizes (how far a fish swam between movement decisions), movement strategy maximized resource and potential intruder mean encounter rates (MERs) while simultaneously minimizing the coefficients of variation (CVs) in encounter rates, i.e. this movement strategy gave the strongest signal of territorial presence while the animal monitored the territory for resources.

The model may be generally applicable whenever a territorial animal is also invested in resource assessment. To show its potential, Brown et al. (2011) simulated the movement of a male fish as it encountered a female inside the territory (i.e. the resource, in this case, a mate), and neighboring males in six contiguous

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territories. While state variables of velocity (swimming speed), step size, and movement angle varied, all individuals in these initial simulations (investigating movement strategies in territories of different sizes and aspects) utilized the same movement strategies. Adams (2001) pointed out that game-theoretical approaches are needed to have a better understanding of territoriality, while Munday et al. (2006) mentioned the same for understanding sex change in fishes. In this paper, we again use a male fish interacting with a female (in a sex-changing species), with the male guarding its territory, to assess movement strategies. However, we allow movement strategies between (not within, see Section 2.1.3) the behavioral states of focal male, neighbor males, and the female, to vary independently, and thus we can evaluate movement strategies relative to different strategies potentially used by others.

The objective of this study, is to take the individual-oriented model of Brown et al. (2011), and test whether the predictions made in the model hold when individuals are allowed independent movement rules. The initial model is intended to be used as a sub-model for movement patterns in the development of an agent-based model (ABM, Railsback and Grimm, 2011), or more specifically, an individual-based ecological model (IBM, *sensu* Grimm and Railsback, 2005) toward a larger objective for an individual-based ecology (IBE) model. However, it is important before moving forward with such objectives to find if the basic sub-model to be used in the larger model is sound in its simplicity, or if a more complex model is necessary due to variation in movement strategies found between the alternative behavioral states (focal male, neighbor males, and females) in simulations.

We again model a sex-changing fish as an example of how this model may be utilized. There is a world-wide collapse of fishery stocks (e.g. Myers et al., 1997; Pinsky et al., 2011; Burgess et al., 2013). Few assessments of fishery stocks consider the impact that sex-changing fishes may have on our ability to manage these natural resources (but see Huntsman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004, 2005; Hamilton et al., 2007). As a step in the right direction, Heppel et al. (2006) model management options for a protogynous fish with fishing mortality, but even in these models sex change is probabilistically set according to population data on size or age (McGovern et al., 1998), rather than on social organization or behavior often known to stimulate sex change (Ross, 1990). Difficulties may occur if (1) models are loaded with data on sex change probabilities from a specific population if changes to the population, including from fishing mortality, changes the probability of sex change (Alonzo et al., 2008), or (2) if a homogenization of sex change probabilities from several populations, or times, are lumped such that the model produced does not predict impacts specific to a population, or time, for the population needing management. An IBE in which sex change is tied to proximate causation due to behavioral interactions (Lutnesky, 1994) may help in our understanding of this pressing problem. Understanding the strengths and weaknesses of a behavioral sub-model that can be used in larger simulations addressing problems of population dynamics is necessary before proceeding to larger objectives.

Although the results of our simulation may have more general applicability, we acknowledge that each problem investigated in such a simulation may be quite different from others, even with an overarching objective for a territory holder to both monitor territorial resources and potential intruders. For example, our territorial "resource," i.e. the female that moves within the territory, could easily have been a moving or static food resource, distributed in clumped, random, or even distributions (Molles, 2013), with varying rates of renewal. Tests of any such simulations for the importance of independent strategies would be necessary before more simple sub-models could be used in larger simulations.

2. Methods

2.1. Model

2.1.1. Model description

To accomplish our objective, we used the basic model of Brown et al. (2011). The model employs the ODD methodology of Grimm et al. (2006), and the reader should see Brown et al. (2011) for a detailed description of the model. Briefly, for general understanding, the simulation examines the mean encounter rate (MER) of a male fish that encounters its mate, a female fish, inside a hexagonal territory that can vary in area (1, 10, 100, and 400 m^2); aspect, i.e. length to width ratio of the territory (1, 2, 4, and 8); and simulation step size, i.e. the time used between movement decisions (0.5, 1.0, and 2.0 s). As he travels in his territory, the male also encounters six neighboring males at the borders of the territory. Although real encounter distances likely vary in nature due to sensory perception, and stimulation of variables important to the neuroendocrine regulation of socially-controlled sex change (e.g. Lamm et al., 2015), we used a constant 0.5 m encounter distance in the simulation as a first approximation to provide a signal in our investigation. Because the encounter distance remains constant, and territory size changes in the investigation, a de facto sensitivity of the encounter distance can be examined (see the 1 m^2 territory size results, below). We used three movement velocities in the simulation (0.05, 0.1, and 0.2 m s^{-1}), but we found that MERs scaled linearly with velocity, and thus we only reported the results for the 0.1 m s^{-1} case. In this investigation, we limit velocity to only the 0.1 m s^{-1} case. We recognize that having individuals employ different velocities can result in MER frequency versus duration trade-offs (Lutnesky & Brown, unpublished), e.g. encounters become more frequent, but last less time, with increases in velocity. While this may turn out to be of interest in the future, at this point in time there is no evidence regarding the potential importance of the trade-off, so we limit our simulation to a single velocity.

2.1.2. Model implementation

For general understanding of the model, fish were randomly placed within a territory, and then moved according to state-variable parameters of territory area, step-size, and movement angle in 20° increments (where 18 movement angles where possible, up to 360°, i.e., 20°, 40°, 60°,. . ., and 360°). When fish attempted to move across boundaries, the simulation culled the potential movements. The simulation only used the angle of the unused potential step as a starting point to choose a new angle. When a 'legal' (within territory) movement was made, the simulation continued. This process was 'no cost,' i.e. time in the simulation was not used until a legal movement was chosen. After all fish made legal movements, distances were calculated between the focal male and all other fish in the simulation, i.e. the female, and the neighboring males. Encounters were recorded if fish were within 0.5 m of each other. However, encounters were scored based on simple interpolation of trajectory, not just at the step intervals (see Scharf et al., 2006; Avgar et al., 2008).

While the simulation of Brown et al. (2011) can be run on a personal computer, examination of all variables simultaneously, i.e. the objective in this paper, makes for a large simulation requiring time on a supercomputer. To that end, we acquired supercomputer time. Briefly, the simulation was run in batch mode (batch file started each run on a single node using a different input file) on the Hrothgar Cluster at the High Performance Computing Center at Texas Tech University. Each run was submitted to a serial processor (3.0 GHz Nehalem processor with 16 GB of memory) with a particular aspect (1, 2, 4, or 8), area (1, 10, 100, or 400 m^2) and time step (0.5, 1, or 2 s). The runs were executed approximately simultaneously (in parallel) on different processors. To save run time, we