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Simulation of spatial movement that potentially maximizes assessment, presence, and defence in territorial and home-ranging animals, with special reference to territorial sex-changing fishes

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ABSTRACT

Question: Are there territory sizes, shapes, and movement rules that animals can use to maximize their presence for territorial and reproductive purposes?

Features of the model: Individual-oriented simulation model of a focal male, a female (his mate), and six other males in adjacent territories. Simulation variables were territory size and aspect (length-to-width ratio), velocity, step size, and potential movement angle. Each simulation represented 10,000 s of real time, and simulations were repeated until convergence on maximum mean encounter rates (MER) of a focal male with the female and other males was reached.

Ranges of variables: Simulations consisted of three velocities (0.05, 0.1, and 0.2 m·s⁻¹), three step sizes (time between movement decisions of 0.5, 1, and 2 s), 18 movement angles (20°, 40°, 60°, . . . 360°), four territory sizes (1, 10, 100, 400 m²), and four territory aspects (1, 2, 4, 8).

Conclusions: Random movement maximizes MER with a female only in small territories (e.g. 1 m²), but use of a simple correlated random walk strategy ('trajectory-swimming' in fishes) maximizes MER with both females and males for other territories, regardless of aspect. This form of movement also minimizes variability of MER; specifically, it gives a more reliable signal, or 'truth in advertising' of territoriality.

Keywords: computer model, fish, movement, swimming, territoriality.

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INTRODUCTION

Animals may have several tasks to perform when moving through space. In home-ranging animals, tasks may include assessment of resources, foraging, and interactions with conspecifics (Hayward, 2008; Loveridge *et al.*, 2009; Stradiotto *et al.*, 2009; Wasiolka *et al.*, 2009). In territorial animals, tasks may also include interactions with social-group members that share their territory, or defensive interactions with neighbours that potentially intrude into their territory for resources or mates (e.g. Grant, 1997; Sturmbauer *et al.*, 2008). Generally, papers on territoriality conclude that resources, their defence, and population density are the primary factors in determining territory size and shape (Schoener, 1983; Praw and Grant, 1999; Keeley, 2000; Imre *et al.*, 2004). However, the efficiency of energy use in the coverage of space while utilizing various resources may also potentially select for strategies of movement and use of space. The modelling of space use by animals (i.e. how they may optimize movement patterns and resource use in an ecological context) is a topic of recent interest (e.g. Scharf *et al.*, 2006; Chapman and Dytham, 2007; Duffy, 2011). Indeed, biologists have invented, and reinvented, ‘ideal gas’ models (variations on the theme of the classic physics models that predict collision rates) to predict rates of encounter between animals and a variety of their resources (Hutchinson and Waser, 2007).

In this paper, we present an agent-based, or individual-oriented, simulation model that is intended to become a general sub-model for a variety of biological situations in which an ‘ideal gas’ model would be suitable, but a less realistic alternative. The model may have potential to predict encounters in a variety of evolutionary and ecological settings where the ideal gas model would also have predictive power, for example encounter rates between individuals, between individuals in social groups, between mates, between social groups, or between predators and prey (reviewed in Hutchinson and Waser, 2007).

As a specific case to illustrate the use of the model, we simulate territoriality in sex-changing fishes. Territoriality in sex-changing fishes is especially interesting because in addition to defending resources from neighbours, they are also pressured by the potential loss of reproductive success when a social group member changes sex (e.g. Sakai *et al.*, 2001). Sex change is most commonly protogynous (i.e. female-first), but may also be protandrous (i.e. male-first) or even bi-directional (Munday *et al.*, 2010), depending on the ecological or social circumstances an individual experiences (Ross, 1990). Briefly, socially encountering or interacting with other individuals is known to stimulate sex change in fishes (Shapiro and Lubbock, 1980; Ross, 1990; Lutnesky, 1994; Lorenzi *et al.*, 2006). Presumably, such interactions with other social group members translate into proximate cues that stimulate the neuroendocrine control of sex change in fishes (for a recent review, see Godwin, 2010). Thus, if the proximate control of sex change is mediated through social interactions, factors such as territory size, territory shape, and swimming rules may influence not only resource defence, but sex change as well. We hypothesize that natural selection would favour individuals in social species that use rules of movement that efficiently defend a territory and promote interactions with other social group members (i.e. selection would be working on strategies to simultaneously optimize interactions concerning individuals both *between* and *within* social groups). For sex-changing fishes specifically, this would involve a swimming strategy that allows a male to defend a territory, and control the sex change of other social group members.

A simulation of the effectiveness of movement strategies is a good first step in testing this hypothesis because it will generate several predictions about the way animals may move in space based on the assumption that they were selected to minimize the energy consumed while maximizing their territorial and social presence at the same time. Furthermore,

movement patterns (distance moved, angle relative to last trajectory, velocity, etc.) in various territory shapes and sizes can be measured to test the robustness of the predictions and validity of the hypothesis.

Simulations and other studies of the ultimate or evolutionary causation of behavioural strategies are often undertaken (e.g. Walker and Cade, 2003; Poethke *et al.*, 2007), but simulations of the immediate or proximate causation for such strategies are not (Giske *et al.*, 1998; but see, for example, Pitt *et al.*, 2003; Ruxton and Bailey, 2005). However, simulations of proximate causation are necessary to eventually understand behaviour at the population level (e.g. Grimm, 1999). For sex-changing fishes specifically, ultimate causation of the phenomenon has been of interest for some time (Ghiselin, 1969; Warner, 1975; Iwasa, 1991; Hamaguchi *et al.*, 2002; Erisman *et al.*, 2009), but we take an unusual approach by simulating the proximate causation of their territorial movements. Understanding the space use of these fishes is necessary to fully understand the larger picture of how they may assess the potential of an environment for sex change. Furthermore, fully understanding the rules of sex change is necessary to understand how sex change may eventually influence their population dynamics, especially for those that are economically important fisheries organisms (Alonzo and Mangel, 2005).

Territorial-haremic fishes that change sex are numerous (Muñoz and Warner, 2004). Typically, males hold a territory that encompasses one to several females that may or may not hold separate territories within his larger territory (e.g. Moyer, 1991). In this initial study, we investigate how movement rules may optimize social group mean encounter rates and the detection of territory intruders in a protogynous (female-first) hermaphrodite. In our simulation, we equate optimization with maximization; we do not consider other functions the fish may have in their daily time-budgets in this simulation. We investigate how the variables of velocity, movement angle (i.e. trajectory), step size (i.e. how far a fish swims before the next 'decision' to change movement angle), territory size and aspect (length-to-width ratio) influence mean encounter rate. The results of our study yield *a priori* hypotheses that may be tested empirically. This is the first step in a new approach to the study of the proximate control of sex change in fishes. It may become a foundation for further studies incorporating more complexity such as studies involving game-theoretical approaches. The model described below follows an ODD methodology (*sensu* Grimm *et al.*, 2006).

THE MODEL

Purpose

This model investigated the influence of movement rules and territory shapes and sizes on encounter rates of a territorial individual with a social group member living within its territory, and with neighbours at territory borders. Specifically, we modelled swimming tactics that may be used by a territorial-haremic sex-changing fish. We used computer simulation (Java programming language within a Windows environment) to parametrically investigate the effects swimming rules have on mean encounter rates (MER) of territory holders (a focal male) with sex-change candidates (a single female within the focal male's territory) and six contiguous neighbour males as potential intruders (Fig. 1A). Many such fishes are female-first sex-changing fishes (protogynous fishes), where males are territorial, but share their territory with one to several females. Their presence may be communicated to others through encounter rates. The model focused on MER with neighbouring males and with a female with whom the male shared a territory. Mean encounter rates with

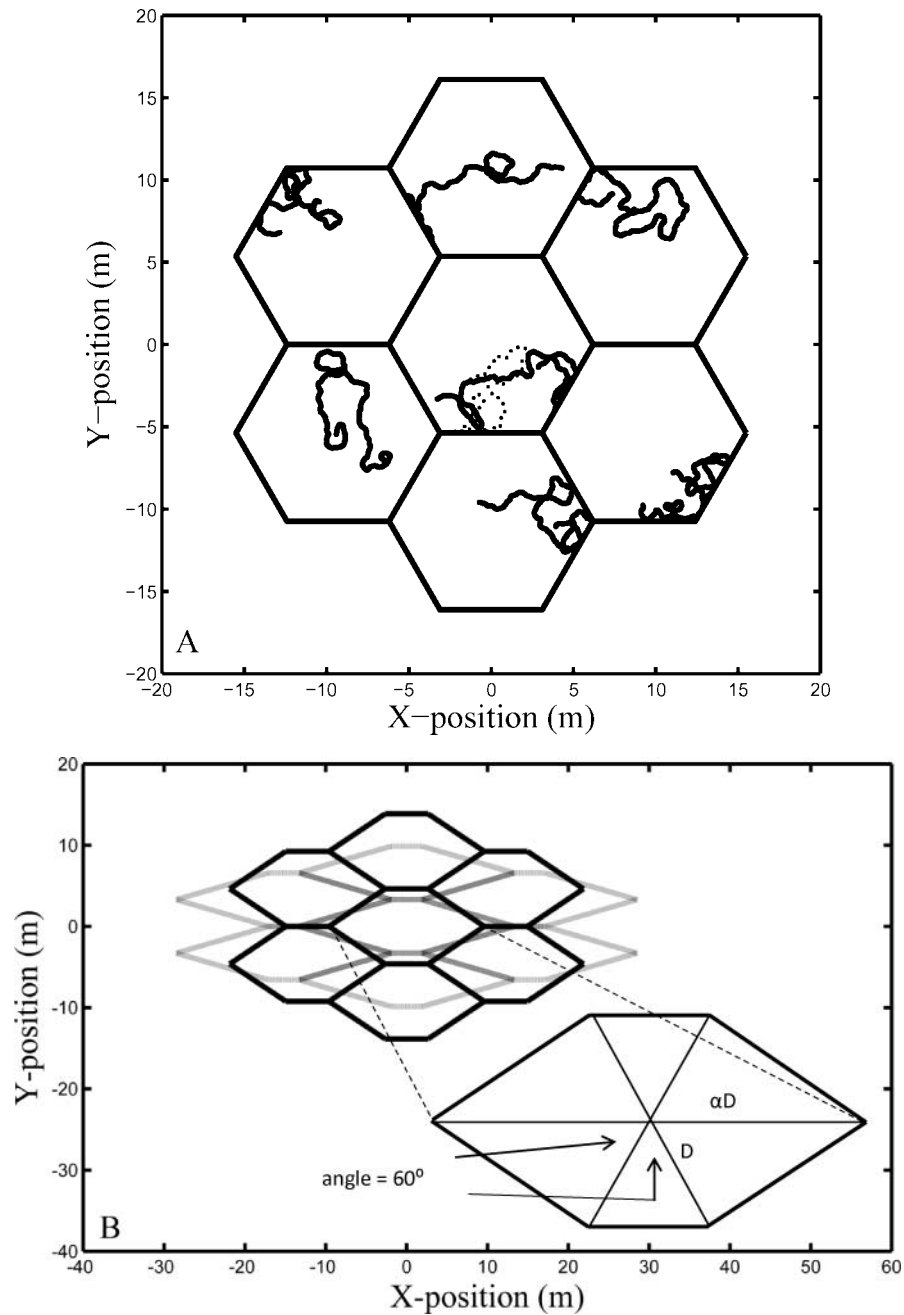


Fig. 1. (A) Example of swimming trajectories for a focal male (centre, solid line) and female (centre, dotted line), and six neighbouring males in contiguous territories. Territory sizes are 100 m^2 with an aspect of 1. All fish trajectories have a movement angle = 20° , velocity = $0.1 \text{ m} \cdot \text{s}^{-1}$, step size = 0.5 s , and show a simulation of 1000 steps. (B) Example of hexagonal packing of fish territories, regardless of aspect. Dark lines show a territory with an aspect of 2, lighter lines show an aspect of 4; interior angles remain at 60° regardless of aspect.

neighbour males may be important for territorial defence, while MER with the female may be important for reproduction, and in suppressing her from changing sex. We assume that swimming behaviour that maximizes MER with both sexes would be selected because it will best advertise male presence on a territory. We used six contiguous neighbours because we started with an assumption of a dense population, and territories in dense populations usually pack as hexagons (Wilson, 1975), but habitat utilization may depend on a variety of variables, including fish and habitat sizes and shapes (Woolnough *et al.*, 2009).

This model represents a first step in constructing a larger model that can be used to investigate how variables that influence encounter rates (see below) influence population rates of sex change and sex ratios in territorial-haremic fishes. Given that many of these fishes are species of economic interest, and that most are sexually dimorphic (males are larger), rates of sex change may be of great interest in both the biomass potentially harvested, and also the population's ability to recover (i.e. more female-biased populations will have lower biomass yet also have a greater potential for recovery). Although encounter rates are known to be influential in the proximate control of sex change in fishes, little is known regarding how they work or scale. A larger model could allow population-level predictions that could be useful for assessment of stock dynamics.

We chose to evaluate swimming patterns first because this individual-oriented simulation model can function as a sub-model for a larger population study. Its complexity is such that it requires evaluation, study, and discussion before one could go to the next step.

State variables and scales

The model comprised two hierarchical levels: individual and territory. Individuals were characterized by the following state variables: sex (male or female), identity of the territory where an individual lives (focal or neighbouring territory), velocity (0.05 , 0.1 , and $0.2 \text{ m} \cdot \text{s}^{-1}$), time between making direction changes (temporal step size, 0.5 , 1 , and 2 s), and direction of the next step relative to the forward direction (potential movement angle; 18 movement angles: 20° , 40° , 60° , . . . 360°). Although the ranges of territory sizes and aspects are not likely to be biologically reasonable for any one species of sex-changing fish (e.g. small damselfish through angelfishes), they are intended to cover most fishes and also the effects of extremes. Note that aspect is the ratio between territory length to width, where an aspect of 1 results in a regular hexagon, and territories with greater aspects keep the same area but we 'stretch' them along two sides of the hexagon (which is no longer regular) (Fig. 1B).

Operationally, we defined the aspect as the length of the longest diagonal of the hexagon divided by the length of the shortest diagonal of the hexagon, where a diagonal is a line traversing from vertex to vertex through the centre of the hexagon. To find these, we divided each hexagon into six triangles (Fig. 1B). At the centre of the hexagon, we forced the interior angles of each triangle to remain at 60° , while we allowed the internal angles of the triangles towards the periphery of the hexagon to vary as aspect changed. For example, to achieve a hexagon of a given area and aspect, we set the area to the desired state variable values for these terms. Then we use

$$A = \sqrt{3}D^2 \left(\alpha + \frac{1}{2} \right) \quad (1)$$

where A = area, α = aspect value, D = the length of the shortest half diagonal, and αD = the length of the longest half diagonal. We then solved equation (1) for

$$D = \sqrt{\frac{A}{\sqrt{3}\left(\alpha + \frac{1}{2}\right)}} \quad (2)$$

to achieve a hexagon of a given shape. As an example, Fig. 1B represents a hexagonal region with $A = 100 \text{ m}^2$ and $\alpha = 2$.

We considered hexagonal territories with four territory sizes (1, 10, 100, 400 m^2) and four territory aspects (1, 2, 4, 8). Regarding aspect, we used the pomacanthid angelfish, *Centropyge potteri*, to provide an approximate initial range to vary in the simulation. An extreme aspect (e.g. 8) could be caused by physical limitations such as a spur and groove habitat (M. Lutnesky, personal observation).

Process overview and scheduling

In this model, all fish use the same movement rules, and have the same schedule of movements. When moving, they move linearly between points of ‘decision’ at the end of each time step (see sub-models, below). We randomly placed the fish in their territories at the beginning of the simulation, and then moved them to their new positions by using a constant temporal step size (one of the state variables, see above) and constant rate of velocity (one of the state variables, see above). In addition, on each step, we required the fish’s new position to remain within its territory boundary. When a fish attempted to cross a boundary, the simulation culled the potential movement. Even when this occurred, the simulation used the angle of the potential (but unused) step as a starting point from which to choose a new angle. This process was repeated until a ‘legal’ (within territory) movement was made. Such border decisions were ‘no cost’ in the sense that time in the simulation was not used until an appropriate angle of movement was chosen. After all the fish performed a legal step, distances were calculated between the focal male and female, and between the focal male and the neighbouring males.

Territoriality was simulated with each combination of the variables, and each simulation represented 10,000 s of real time. Considering all combinations, the total number of simulations was approximately 19 million and the number of steps (i.e. movement decisions) was approximately 230 billion. Simulations were run until ‘noise’ due to variation was reduced by the large sample size (i.e. until MER curves became approximately smooth). The number of simulations was so large (3000 to 18,000, for territory sizes of 1 m^2 to 400 m^2 , respectively) that standard error was negligible. That is, standard error values were only about one 200th of the value of the mean when choosing among seven of the largest standard errors produced in the simulations. That is, they were so small that they would not even show on the figures when plotted. Significant differences in MER were assumed when functions were separated graphically. This requirement resulted in a different number of simulations for territories of different areas (ranging from 1.8 to 12 million simulations for territories of 1 m^2 to 400 m^2 , respectively), where number of simulations had to be increased for larger territory sizes (Table 1).

Java simulations were run simultaneously on the four processors of a quad-core personal computer (Dell Optiplex 780) to reduce turn-around time. To display results in a graphical format, MATLAB® was used to aggregate data outputted from a series of Java runs.

Table 1. Number of simulations and total simulation time as a function of territory size

Territory size (m ²)	Number of simulations	Number of time steps
1	1.8×10^6	2.1×10^{10}
10	1.9×10^6	2.3×10^{10}
100	3.9×10^6	4.5×10^{10}
400	1.2×10^7	1.4×10^{11}
Total	1.9×10^7	2.3×10^{11}

Note: Each simulation represents 10,000 s. The number of simulations for each territory size included all combinations of four aspects (1, 2, 4, and 8), three velocities (0.05, 0.1, and 0.2 m·s⁻¹), three time steps (0.5, 1, and 2 s), and 18 movement angles (20°, 40°, 60° . . . 360°).

Design concepts

Emergence

Swimming tactics that maximize encounter rates are potential emergent properties of the model; for example, low-movement angle swimming near borders, or ‘lap swimming’, was found to be the most efficient way for a fish to maximize encounter rates. Adaptation, fitness, and prediction are not applicable in this preliminary model (but they can be in a larger model).

Sensing

Regarding sensing, fish are assumed to ‘encounter’ another individual when they come within 0.5 m of each other in the model, regardless of borders. This distance was made a constant in the model. It was chosen as a first approximation (Lutnesky, 1994), but may vary in nature by species sensory abilities and environmental conditions. The simulation scored only one encounter when the encounter distance was within 0.5 m for consecutive steps in the simulation. Encounters were scored based on simple interpolation of trajectory, not only at the step intervals (see Avgar *et al.*, 2008). Examples of encounters are given in Fig. 2.

Interactions

Fish neither experience any changes in the state variables due to encountering other individuals, nor change trajectories based on encounters with other individuals, thus there are no interactions *per se* between fish in this preliminary model. Fish do, however, interact with territory boundaries. They change direction (see above), to stay within territory boundaries when they would potentially be crossed. A larger model (see above) could incorporate sex-change rules and rates of sex change based on encounter rates (i.e. a variable due to interactions between fish).

Stochasticity

The direction of movement within the state variable of movement angle (θ_m , see below) is chosen randomly from a uniform distribution with minimum value ($-\theta_m/2$, see below) and maximum value ($+\theta_m/2$, see below).

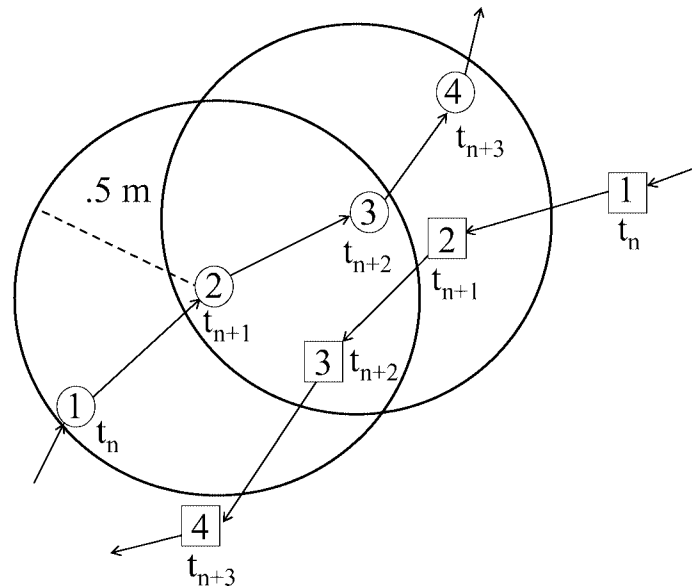


Fig. 2. Example of model parameters. Male trajectory (circles) and female trajectory (boxes) are illustrated in an encounter using an arbitrary movement angle through four steps in a simulation with an encounter radius of 0.5 m. The encounter with the female begins between t_{n+1} and t_{n+2} and ends between t_{n+2} and t_{n+3} . Note that the step size is the time between t_n and t_{n+1} . See ODD for movement protocol.

Observation

After each time step, the focal male's position is compared with the position of the alpha female and adjacent males. If the distance between the focal male and another fish is within 0.5 m, then an encounter is scored. The number of encounters for each simulation is stored in an array in the program and then written to a file upon completion of the simulation. The trajectory of any fish can thus be tracked for all time steps. When a simulation is completed, the output is written to a text file that can be read by MATLAB®; or a similar program.

Initialization

The central territory of each simulation is initially occupied by a focal male and an alpha female, while the six neighbouring territories are initially occupied by one neighbour male each. All fish are initially placed in each territory in a random location using Java's random number generator. Placement occurs by randomly selecting a position in an ellipse that inscribes the hexagonal territory until the position is contained in the hexagon. This process is repeated for each fish in the simulation, and these positions become the starting swimming position for each of these fish.

Input

All input values are set deterministically at the lowest value for each state variable when initializing the program. State variables are then changed by the program, and the program

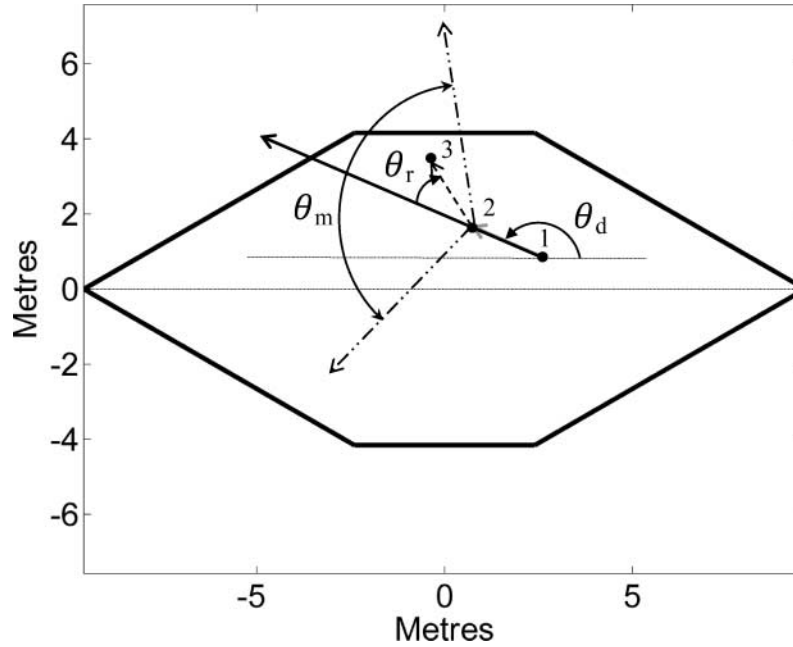


Fig. 3. Fish movement geometry. The fish moves from 1 (x_{n-1}, y_{n-1}) to 2 (x_n, y_n) to 3 (x_{n+1}, y_{n+1}) in this figure. θ_d represents the angle of movement relative to the longest axis of the hexagon (whose length is discussed in the text as aD). The solid arrow represents the ray of movement, and θ_m represents the state variable of movement angle. θ_r represents the randomly selected angle between the ray and the new direction of movement (simple dashed arrow).

reiterates the simulation, collecting data until all values of the state variables and their combinations have been run.

Sub-models

To move a fish from one location in a hexagonal territory to another, we used the following protocol: Imagine that the fish just moved from position (x_{n-1}, y_{n-1}) to (x_n, y_n) on its $(n-1)^{\text{st}}$ time step and is considering moving to its new position (x_{n+1}, y_{n+1}) on its n^{th} time step. We construct a ray (i.e. direction of movement) passing through (x_n, y_n) with its tail at (x_{n-1}, y_{n-1}). This defines the forward direction of movement for the fish, and allows definition of θ_d (movement angle), where θ_d is specified as the angle between a line parallel to the longest diagonal that passes through (x_{n-1}, y_{n-1}) (Fig. 3). Next, a new random movement direction is specified through selection of θ_r , an angle that is selected from a uniform distribution between $-\theta_m/2$ and $+\theta_m/2$, where θ_m is the movement angle (one of the state variables, see above). θ_r is thus the angle between the old ray and a new direction of movement (Fig. 3). The new movement angle will be $\theta_d + \theta_r$. The fish are moved to their new position by using a constant temporal step size (one of the state variables, see above), constant rate of velocity (one of the state variables, see above), and θ_d . Furthermore, on each step, the fish's new position is required to stay within its territory boundary.

RESULTS AND DISCUSSION

Territory size

Except in the smallest territory size (1 m^2), movement angle did not influence the MER of focal males much with females (i.e. potential sex-change candidates). However, their MER with male intruders was generally maximized by low movement angles. These patterns are shown in Fig. 4A and 4B, where we use a velocity of $0.1 \text{ m} \cdot \text{s}^{-1}$, aspect of 1, and time step of 0.5 s to illustrate the general relationships. Note that these general relationships also hold for other combinations not shown. Furthermore, the basic relationships of MER described below essentially hold for different velocities that scaled approximately linearly (not shown here). Interestingly, velocity is often modelled with a linear scale in deterministic models (Baird and Jumper, 1995; Giske *et al.*, 1998).

Movement angle

With a combined objective of encountering both interior females and intruder males, a low-movement angle strategy maximizes MER functions. This appears to be the best swimming strategy because changes in movement angle result in negligible changes in the MER of females. Even if more females were inside the territory to encounter, only the scale (total MER of all females) would change (roughly linearly with the number of females), but the movement angle would still not be influential. However, low-movement angle maximizes the MER with intruder males. Furthermore, if MER of the focal male was influenced by MER with intruder females (i.e. neighbouring females, something we did not model), this would only exaggerate the advantage of a low-movement angle swimming strategy for the male. Note that although differences occur in scale, the general relationships hold over different territory sizes (see above, and Fig. 4A, 4B).

Territory aspect

The influence of territory aspect on MER has an opposite effect for encounters with the female and encounters with the intruder males. Although the differences are small, MER is maximized internally with the female in a low-aspect territory (Fig. 5A), while MER is maximized with the intruding males in a high-aspect territory (Fig. 5B). Note that the overall influence of aspect on MER is not very large considering that an eight-fold change in aspect only results in at most about a two-fold change in MER.

Temporal step size

Temporal step size – that is, the amount of time swimming between movement ‘decisions’ – is analogous to the frequency of assessment a fish would do during territorial movements. Mean encounter rate with the female or the intruder males is maximized with the combination of low-movement angle and larger step size (i.e. less assessment) (Fig. 6A, 6B). In such a case, the fish eventually swim to the territory border and begin swimming laps. A low-angle (i.e. ‘trajectory-swimming’) rule would effectively keep them swimming near the territory border. This effectively makes a ‘doughnut’ out of the movement path (i.e. most swimming occurs along borders), and larger step sizes makes for thinner doughnuts. The combination of trajectory swimming and large step size may thus effectively reduce the

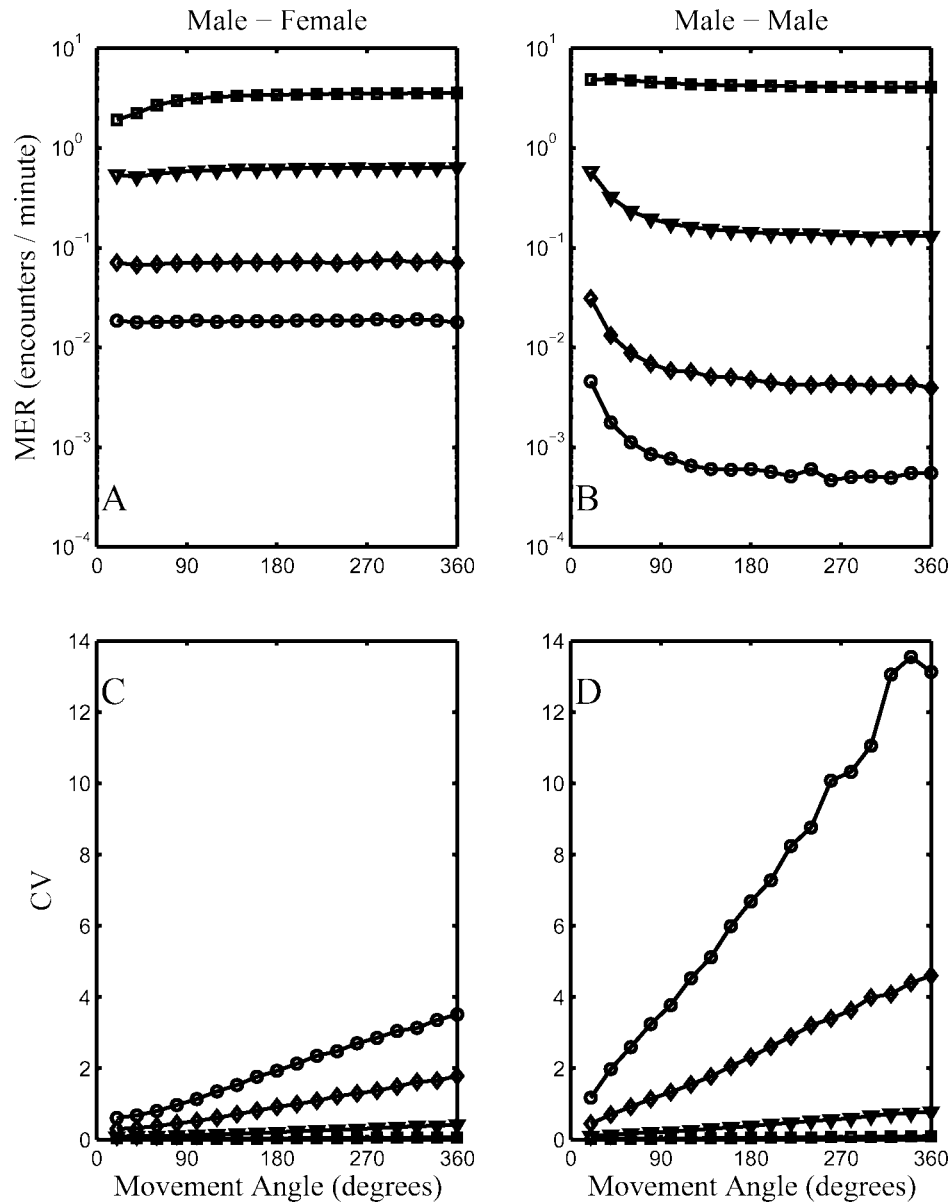


Fig. 4. Mean encounter rate (MER) as a function of movement angle for four different territory sizes (where square = 1 m², triangle = 10 m², diamond = 100 m², and circle = 400 m²) of a focal male and female with whom he shares a hexagonal territory (A), or the focal male and six contiguous neighbouring males (B). Standard deviation divided by MER (coefficient of variation, CV) for the male–female and male–male encounters is shown in panels (C) and (D), respectively. Aspect, velocity, and time step are held as constants of 1, 0.1 m·s⁻¹, and 0.5 s, respectively. All encounter distances are 0.5 m.

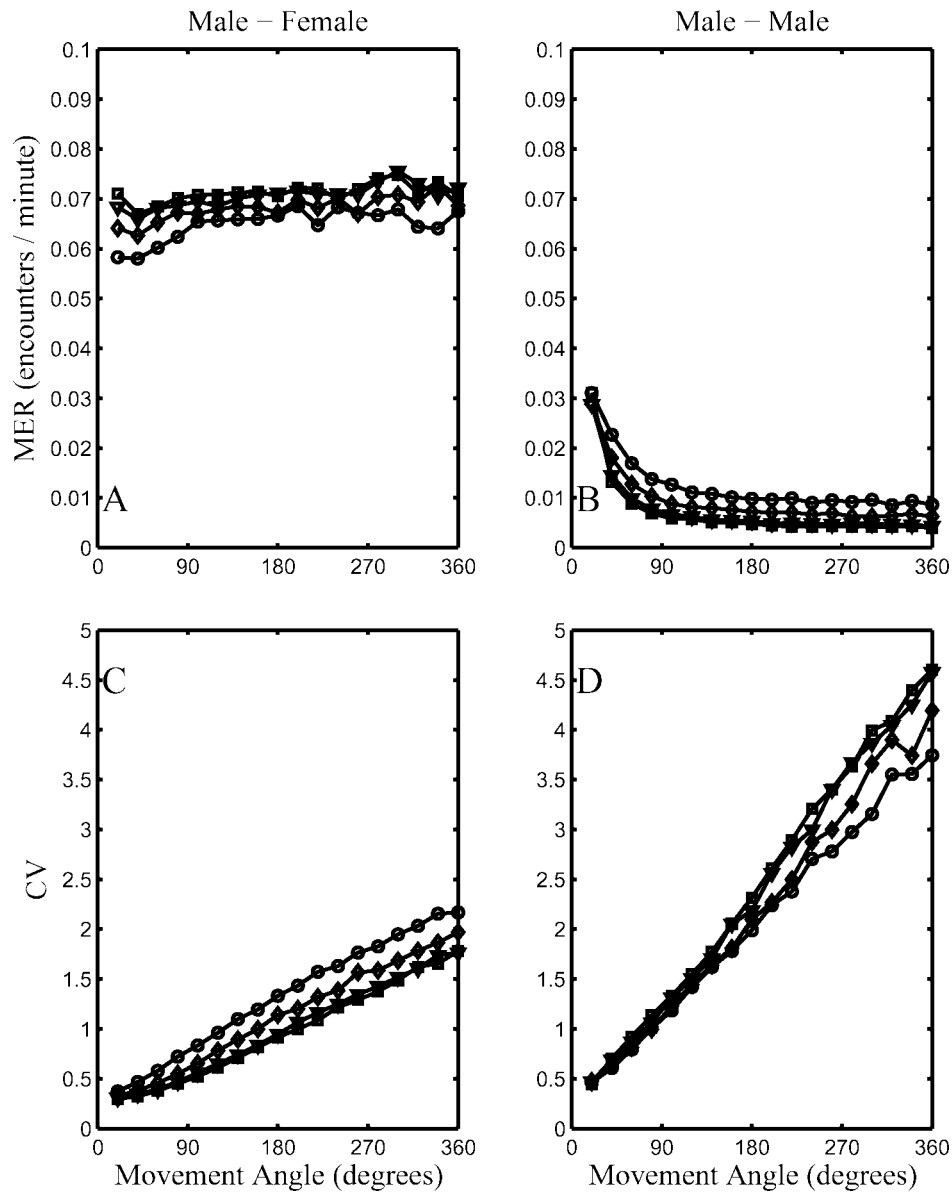


Fig. 5. Mean encounter rate (MER) as a function of movement angle for four different territory aspects (where square = 1, triangle = 2, diamond = 4, and circle = 8) of a focal male and female with whom he shares a hexagonal territory (A), or the focal male and six contiguous neighbouring males (B). Standard deviation divided by MER (coefficient of variation, CV) for the male–female and male–male encounters is shown in panels (C) and (D), respectively. Territory size, velocity, and time step are held as constants of 100 m^2 , $0.1 \text{ m} \cdot \text{s}^{-1}$, and 0.5 s , respectively. All encounter distances are 0.5 m .

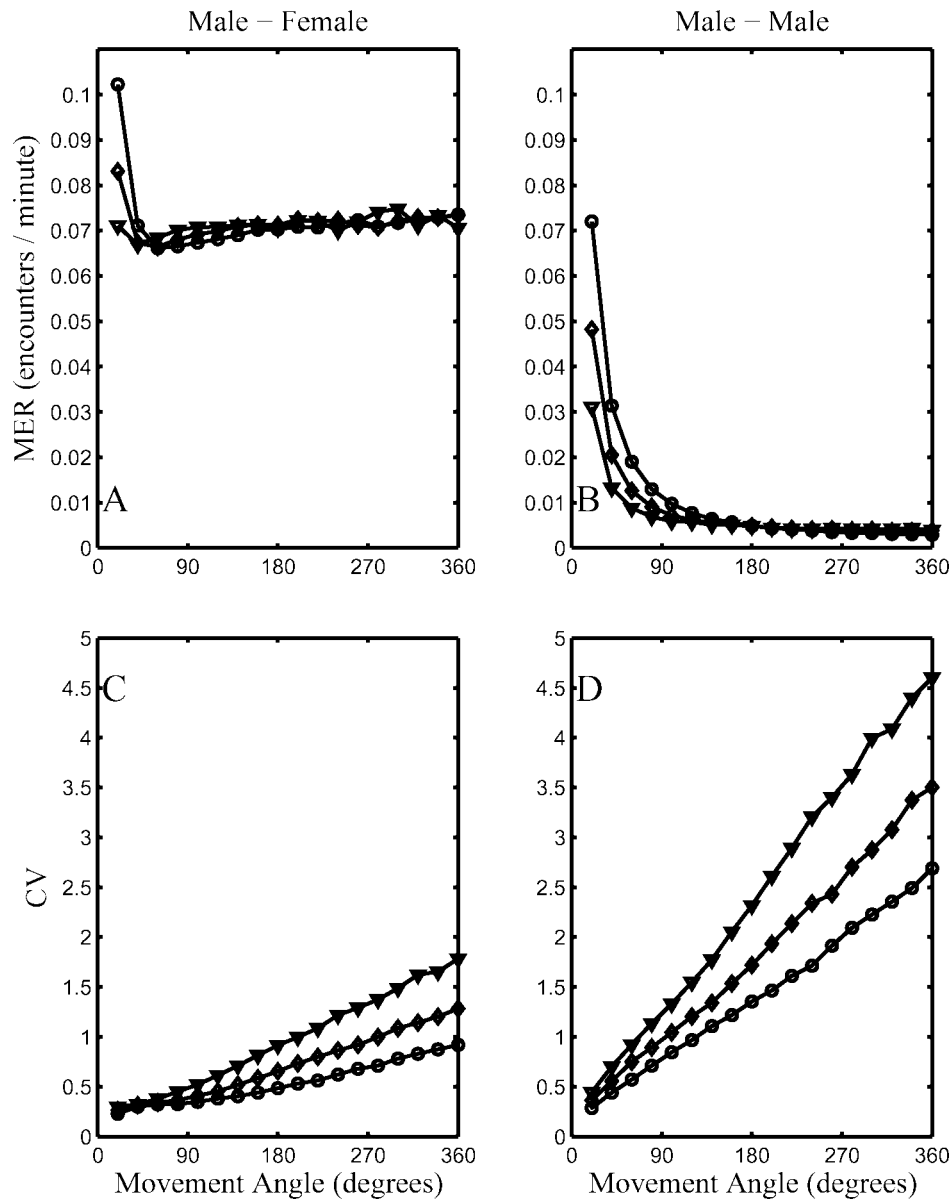


Fig. 6. Mean encounter rate (MER) as a function of movement angle for three different step sizes (where triangle = 0.5 s, diamond = 1 s, and circle = 2 s) of a focal male and female with whom he shares a hexagonal territory (A), or the focal male and six contiguous neighbouring males (B). Standard deviation divided by MER (coefficient of variation, CV) for the male–female and male–male encounters is shown in panels (C) and (D), respectively. Territory size, aspect, and velocity are held as constants of 100 m^2 , 1, and $0.1 \text{ m} \cdot \text{s}^{-1}$, respectively. All encounter distances are 0.5 m.

effort of territoriality (i.e. reduce the frequency of 'decisions' necessary to assess the status of territorial integrity).

Note that we also find that beyond movement angles of about 50° for male–female encounters, and about 150° for male–male encounters, there is negligible influence based on different step sizes (Fig. 6A, 6B).

Territorial and social presence

Whether defending against territorial intruders, courting females, or discouraging their sex change, the male must maintain a 'presence' on the territory (i.e. advertise he is there by encountering other individuals). We think the appropriate metric to examine variability in territorial and social presence is the coefficient of variation, CV (Hilborn and Mangel, 1997), of encounter rates (i.e. the standard deviation of the encounter rate divided by MER). Otherwise, if looking at only standard deviation or standard error alone, it could increase simply by changes in velocity, area, etc. Such changes may also be important (i.e. a way to increase signal strength through increases in MER), but the focus of this part of our discussion regards how a fish may increase signal strength through minimizing error. The CV thus represents a metric of the predictability of territorial and social presence. We interpret a low CV in encounter rate to represent strong constancy in territorial and social advertising (i.e. 'truth in advertising' to would-be intruders or sex-change candidates, the potential competitors to the male).

Examination of the CV of encounters shows that low movement angles (i.e. trajectory swimming) generally reduced the CV for all territory sizes, aspects, and step sizes (Figs. 4C, 4D, 5C, 5D, 6C, 6D). Furthermore, the CV is reduced more prominently in smaller-sized territories (Fig. 4C, 4D). Thus, in this simulation, a fish both maximizes MER and minimizes CV (i.e. maximizes territorial and social presence) through the employment of a low-angle swimming strategy (i.e. trajectory swimming) in a smaller-sized territory. Note that such a swimming strategy may increase the amount of 'lap swimming' around territory borders, a phenomenon observed in at least one sex-changing fish, *Centropyge potteri* (Lutnesky, 1992).

Interestingly, the aspect of the territory has opposite effects on the CV of encounter rates with the female (social presence) or with the contiguous neighbour males (territorial presence). The CV is reduced when encountering females in low-aspect territories (Fig. 5C), but decreased in high-aspect territories when encountering neighbouring males (Fig. 5D). We think the CV of encountering neighbouring males is decreased due to the increase of the perimeter-to-area ratio in high-aspect territories. That is, the area that is too distant from a territory border to encounter the neighbour males is minimized in high-aspect territories. We think this is why high-aspect territories minimize the CV of encounter with neighbouring males using higher movement angles. However, this effect of aspect is negligible at low movement angles (below a movement angle of about 120° ; Fig. 5D). We have already pointed out that a low-movement angle swimming strategy is advantageous due to MER (see above). If a fish were employing a low-angle movement strategy, a low-aspect territory may be advantageous due to the reduced CV of encounter with females (Fig. 5C). We think this occurs due to the potential range of encounter distances involved. For example, high-aspect territories result in a greater CV due to the larger potential distances between independently moving fish. Thus, if reduction in the CV of encounter is critical, low-aspect territories appear advantageous. Interestingly, territories in high-density fish populations

often pack as regular hexagons – that is, they appear as low-aspect territories (e.g. Barlow, 1974; Covich, 1976).

As was the case with MER, larger step size (i.e. less assessment and fewer decisions) is optimal in that it reduces the CV when encountering either females or males (Fig. 6C, 6D). We think that larger step size is complementary with a low-angle movement strategy because fewer decisions result in fewer changes in direction.

SYNTHESIS

This simulation represents an initial effort at an individual behavioural model (IBM) for the basic movement patterns in animals. However, by the definitions of Grimm and Railsback (2005), our model would presently be defined as individual-oriented, not individual-based. The model will become an IBM in modelling individual-based ecology (IBE) if it is taken to a population level and includes resource use and adaptation. We think an obvious first application would be to model the proximate control of sex change in fishes via encounter rates (*sensu* Lutnesky, 1994). However, the basic rules for movement and territoriality have the potential for much broader application (e.g. whenever an individual must monitor resources on the inside of a territory, and for potential intruders into that territory). Furthermore, even such divergent animals as wolves use similar patterns of movement [i.e. ‘rotational’ space use on a territory (Jedrzejewski *et al.*, 2001)], which may be similar to the ‘lap swimming’ described above, yet in a different time scale.

Our simulation is a first approximation for a complex topic, and allows the isolation and subsequent understanding of the basic dynamics of territorial movement. This understanding will be essential in constructing higher-order hypotheses about how animal movement is tied to fitness. However, our basic model lacks a game-theoretical approach (i.e. how potentially different tactics by males, females, and intruders may influence the simulation). Indeed, Adams (2001) suggested that there is a need for models involving game theory that show how these interactions may influence territory size (i.e. the logical next step in encounter-rate modelling). However, given the results of this study, we suspect that a correlated random walk (*sensu* Hutchinson and Waser, 2007) that results in low-movement angle, or a trajectory-swimming strategy, will likely maximize MER and minimize CV in territorial advertisement regardless of alternative strategies due to the heavy influence of territory borders on encounter rates. Once an IBM is constructed, contiguous IBMs can be joined for higher-level population studies (Huse and Giske, 1998; Grimm, 1999; Adams, 2001). The results of this, and other such simulations, can form the basis of *a priori* hypotheses with predictions that can be tested empirically (Table 2). To our knowledge, this is the first simulation of a movement strategy in which an individual needs to simultaneously manage both social group members and territorial intruders.

In conclusion, we hypothesize that MER is affected by a combination of border contact rates and effective territory coverage rates. As shown in the simulation, this characteristic of territoriality appears to be more important for defence against intruders than for contact with social group members (but see the influence of territory aspect, above), and characteristics of territories may be influenced more by defence than resource use (Eason, 1992). For sex-changing fishes, a simple test of whether males respond to females as resources (e.g. mates) or potential competitors (e.g. as sex-change candidates), or both, would be to look for significant differences in the swimming strategies used by territorial sex-changing and gonochoristic fishes.

Table 2. *A priori* hypotheses generated by the model

State variable	Territorial presence		Social presence	
	Max. MER	Min. CV	Max. MER	Min. CV
Movement angle	Low	Low	?	Low
Territory size	Small	Small	Small	Small
Aspect	High	High	Low	Low
Step size	Large	Large	Large	Large

Note: These are movement strategies predicted to maximize the mean encounter rate (MER) and minimize the coefficient of variation (CV) for territorial presence (male–male encounter) and social presence (male–female encounter).

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