Foraging on the move

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Abstract— Many ungulate species embark on migrations where they are constantly foraging as they move. This means individuals have to simultaneously balance several demands: finding the best resources, maintaining the cohesion of the group, and migrating in a certain direction. While there is a vast literature on both flocking and optimal foraging, there has been no work done to understand how animals should trade off the decision to flock or forage (since it is difficult to do both simultaneously) during migration. To address this question, we developed an individual-based model and implemented a genetic algorithm to find the best decision-rule for switching between foraging and flocking, under a variety of parameter settings. The evolved rules converged both within simulations and across replicates. The evolved behavior decision thresholds were generally as would be expected from the model. One unexpected result was the possible existence of an optimal value for the ratio of energy gain from foraging to energy loss from flocking, per time step. The ratio is the same as is observed for real-world caribou and wildebeest.

Keywords: collective behavior, flocking, foraging theory, genetic algorithm, migration, social foraging, ungulates.

I. INTRODUCTION

Migration is one of the most visible phenomena in nature, seen across a huge variety of species, and usually involves many individuals, often traveling exceptionally long distances. In species that migrate collectively, individuals have to decide how to balance finding food, keeping up with their group, and making progress along their migratory route. The study of this type of migratory behavior draws on three areas that have been mostly disconnected to date: migration, foraging theory and group-living. We briefly discuss each area below.

There is a broad literature describing the migration patterns and routes of terrestrial mammals (see, e.g., Åkesson and Hedenström 2007, Berger 2004, Dingle 1996, Fryxell et al. 1988, Johnson et al. 2002). In contrast, there are few theoretical studies of migration and most of these are taxon-specific, with a bias towards birds and fishes (Bauer et al. 2009). The only existing modeling studies of terrestrial mammal migration focus on spatial patterns of movement. For example, Boone et al. (2006) found that migratory pathways of wildebeest derived using an evolutionary algorithm closely matched actual migration paths, suggesting that rainfall and vegetation are key determinants in wildebeest migratory behavior. Bergman et al. (1999) found that a correlated random walk model over predicted long-range displacement of migrating caribou. Gueron and Levin (1993) proposed a mathematical model for analyzing the wave front pattern during wildebeest migration and investigated the properties of spatial distribution and stability of the front using self-organization theory.

While the existing studies of mammalian migration are mainly focused on groups of animals, studies in classical foraging theory, in contrast, focus on a single individual. Classical foraging theory describes the payoffs that an individual receives from implementing different strategies for searching for and processing food. This body of theory predicts that animals will favor the strategy that delivers the highest gain, giving them the highest overall fitness payoff (Emlem 1966, MacArthur and Pianka 1966). There is a vast literature of optimal foraging behavior (e.g. Fretwell and Lucas 1969, Schoener 1971, Charnov 1976), which uses decision theory to predict the optimal foraging strategies when animals have some knowledge of the environment. Optimal foraging behavior predicts that animals will attempt to either maximize their rate of energy gain or minimize the time spent to obtain a fixed amount of energy (Schoener 1971). A time-minimizing approach implies that an animal is attempting to maximize time spent in other behaviors such as locomotion, reproduction or to minimize its exposure to temperature extremes and predators.

Many animals live in groups, which presents an additional level of complication for classic foraging theory. Animal groups are ubiquitous in nature and their formation comes with both costs and benefits. Groups provide individuals with a lower per-capita predation rate ('dilution effect'), shared information, and allow individuals to find both mates and resources more easily (Alexander 1974, Rubenstein 1978). However, groups tend to attract predators more easily than solitary individuals do, can increase the transmission rate of diseases, and lead to competition for resources (Alexander 1974, Hoogland and Sherman 1976). In theory, the size of an animal group should be determined by the payoff to an individual; at the equilibrium group size, the benefit to an individual of joining a group should be equal to that of being a loner (Sibly 1983). An individual's specific position within a group can have significant fitness consequences (see Krause 1994); individuals in the center of the group are often the safest from predation (Hamilton 1971), but those on the edge are in the best position to discover and exploit new food resources (Barta et al 1997). Some theoretical work has been done to combine foraging and group-living: what has been termed "social foraging" (see Giraldeau and Caraco 2000). Social foraging theory models how the consequence of an individual's foraging behavior can depend on both the individual's own actions and the behavior of other foragers. This theory also includes survival probabilities and risk-sensitivity, mainly using stochastic models of the individuals' behaviors (Giraldeau and Caraco 2000).

By living in groups and foraging socially, individuals gain a variety of benefits (see above), including being able to devote more time to foraging and less time to vigilance for dangers (Mangel and Clark 1986), examining how other individuals gain information about foraging locations by flocking with them (e.g. Clark and Mangel 1984), and exploring different foraging strategies with respect to the location within the flock (Barta et al 1997). However, there is no theoretical work on how foraging individuals should behave when they are in a group that is collectively moving, a behavior seen in many species of migratory ungulates, such as wildebeest and caribou. Individuals in this situation face a trade-off between foraging and keeping up with the group. Individuals that fail to forage will starve, and those that fail to keep up with the group will likely be picked off by predators (Hamilton 1971). This usually leads to a mixture of behaviors across the group; at any moment, some individuals are foraging and others are flocking and moving towards their migration destination (e.g. as seen in the Planet Earth "Plains" video of migrating caribou). Despite the scale of this phenomenon and the adequacy of existing models in specific subjects, our understanding of how migrating ungulates make decisions is still rather poor. Here we develop an individual based model to understand how ungulates balance tradeoffs between maximizing their energy intake and continuously moving with their group during long migrations.

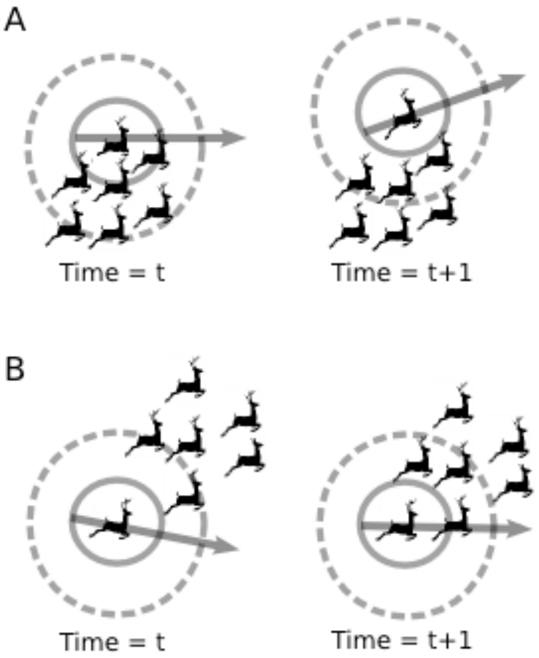

Figure 1: Shows an illustration of the flocking rules for one focal individual. Panel A demonstrates separate and B demonstrates align and cohere. The solid circle around the focal individual is the minimum separation distance, the larger dashed circle is the vision, and the arrow represents the heading.

II. METHODS

A. *Flocking*

We created a model in NetLogo to describe a group of migratory individuals that forage and flock as they move. The base of our model was the NetLogo demo model (Wilensky 1998) which is based on Craig Reynolds' Boids simulation (Reynolds 1987). The boids model assumes that an agent within a group moves based on two main rules. If there are other agents within a minimum separation distance radius, then the agent will turn to move away from these agents ('separate'; Figure 1, panel A), If there are no agents within the first radius, then the agent will align with ('align') and move towards ('cohere') any individuals within a second, larger radius (Figure 2, panel B). To simulate migration, where animals are moving together in a specific direction, we added another movement rule: after agents separate, align and cohere, they also all turn towards 'north' (positive y-direction). We set the parameters in this models to be the same for all simulations as follows: minimum-separation=0.5, vision=6.5, max-align-turn=7, max-cohere-turn=3.25, max-separate-turn=2, and max-north-turn=1.5.

B. *Foraging behavior rules*

We modified this basic flocking model by including a foraging aspect. All agents in our model have an energy level that decreases as they spend energy moving, and increases as they acquire energy from foraging while stopped. At each time-step, every agent has to make a decision whether to forage or to flock. (Since animals such as caribou forage with their heads down, making it hard to see fellow herd-mates, we assume that it is impossible to forage and flock simultaneously.) We assume that agents make the decision of whether to flock or forage based on a simple threshold: if an agent's energy level is below a certain threshold (ForageT) it will start to forage, and if the number of agents within an agent's vision radius falls below a certain threshold (FlockT), it will start to flock. In the case where an agent is below both thresholds, we assume that flocking overrides foraging. If an agent decides to forage, it stops and increases its energy level by the amount 'energy-forage,' and continues to do so until its energy reaches the value 'full-energy' (set to 100 in our simulations). If an agent decides to flock it follows the movement rules described above (separate, align, cohere, and move north), takes a step forward, and decreases its energy level by the amount 'energy-move'.

C. *Mortality*

Agents can die in two ways, essentially from doing a poor job foraging or flocking. If an agent's energy level falls below a certain threshold, (we used 0 energy units for our simulations) it 'starves' and dies immediately. If an agent strays too far from the group, it can die of 'predation'. The probability of dying from predation, P, is a function of the number of other agents and agent can see and is given by

$$P = Exp\left(-\frac{F}{\lambda}\right)$$

per time step, where F is the number of other agents it can see, and λ is a constant. (set to 8 for our simulations) Therefore, if the agent can see no other agents, it is considered extremely susceptible to predation and will die immediately. The more agents it can see, the less likely it is to die from predation (fig. 2). Upon dying, agents are not immediately removed from the simulation, as this would change the flock's size and potentially its dynamics. The dead agents are removed from the population at the end of the generation in the genetic algorithm described below.

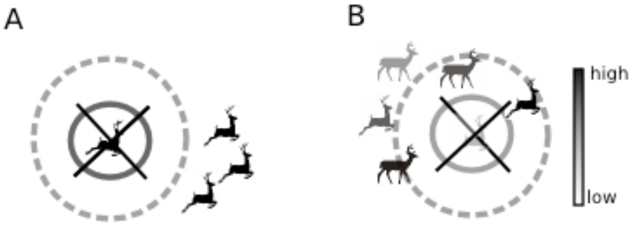

Figure 2: Illustration of the two ways an individual die: predation, or death by failing to flock (pane A) and starvation, or death by failing to forage (panel B). In panel B the shade of an individual represents its energy level.

D. *Selection*

We implemented a genetic algorithm to determine the optimal valuse of FlockT and ForageT, when an agent should decide to flock or forage. For a single run, N agents were created, each with a set of ForageT and FlockT threshold values drawn from a random distribution. The simulation was run for a single generation (which ended whenever either 20% of individuals die or 150 time-steps pass, whichever came first). At the end of a generation, N new agents were created and a new generation was restarted with fresh initial conditions. This process was repeated for 500 generations.

The only information passed between generations are the values of ForageT and FlockT. Each agent inherits its ForageT and FlockT values from a single 'parent' in the previous generation, with a small mutation rate (3% each). To determine which agents reproduce, first each agent from the previous generation is assigned a fitness, f,

$$f = \frac{N}{\max(N)} + \frac{E}{\max(E)}$$

where N is the time average over the generation of that agent's number of flockmates, E is the time average of that agent's energy, and $\max(N)$ and $\max(E)$ are the maximum values over all surviving agents in the population of these averages. Each agent then reproduces in proportion to its fitness. Agents that died during the course of a generation are not included in these calculations, and do not reproduce.

E. *Simulations*

We evolved values for ForageT and FlockT via model simulations using twelve different combinations of parameter settings. Ten replicates were run for each parameter setting combination, for a total of 120 simulation runs. Since it has been shown that individuals in larger groups can spend more time foraging and less time on the lookout for predators (Pulliam 1973, Cresswell 1994, Roberts 1996), we hypothesized that group size would be an important factor influencing evolved threshold values. We also thought that the relative values of energy-forage and energy-move might influence ForageT and FlockT. Few large ungulates have long-distance migrations, and those species that do are very efficient walkers; Fancy and White (1987) found that caribou and wildebeest have the lowest net cost of locomotion of all ungulates that they measured. This suggests that migration is an important selective pressure on locomotion efficiency. To examine the role of energetic cost, we held energy-move constant and varied the value of energy-forage.

We estimated parameter values from the literature to make our simulations as realistic as possible. The average size of a herd of wildebeest is 467 individuals (Fryxell et al. 1988) and of caribou is 450 individuals (Mahoney and Schafer 2002). However, these numbers can vary greatly; caribou herds of 417,000 individuals (Gunn et al. 1991) and wildebeest herds of over 1.3million (Sinclair 1995) have been recorded. Due to computational constraints, we were unable to simulate such large herd sizes, and ran simulations with 100, 300, and 500 individuals.

Energetic values were also estimated from the literature. A caribou walking horizontally in the snow spends about 1.696 kJ/(kg*km) (Johnson et al. 2002). Caribou weigh approximately 270 kilograms (Woodland Caribou (Osborn's Caribou)) 1996) and measure approximately 2 meters in length (Kuzyk et al 1999). Therefore an individual spends about (1.696kJ/kg/km)*(1km/1000m)*(272kg)*(2m)= 0.922kJ to move itself one body length. Plant matter has approximately 7.96 MJ/kg dried matter (Murray 1991), and wildebeest are estimated to take in about 0.3 grams per bite (Murray 1991). This means that an individual gets (0.3g/bite)*(1kg/1000g)*(7.96MJ/kg)*(1000kJ/MJ) = 2.388 kJ per bite. We assume that these values are representative of migratory ungulates and set energy-move to be 1 unit (kJ) and, assuming that a normal value of energy-forage is 2.5 units (kJ), we ran simulations under four different values for energy-forage (0.5, 1, 2.5, and 5 units).

III. RESULTS

Both ForageT and FlockT values converged across generations within a single simulation, for all simulation runs (Figure 3, left panels). In addition, FlockT and ForageT each converged to similar values across most simulations, with ForageT values converging much more tightly than FlockT values. All except two foraging thresholds converged to around 96 energy units, close to the full 100 energy units, as can be seen in Figure 3 (top panels). (These two outlier simulation runs were removed for the rest of the analysis since they dramatically altered the average threshold values.) The flocking thresholds converged to values in the range 10 to 60 flock mates, with most around 30, as per Figure 3 (bottom panels).

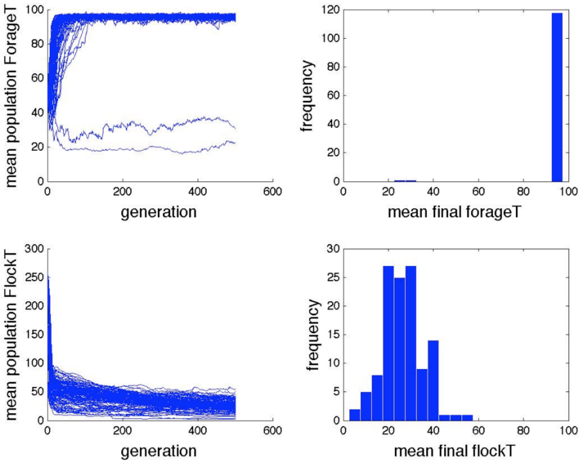

Figure 3: The left two panels show the mean population values for ForageT (top) and FlockT (bottom) at the end of each generation over the course of a single simulation. The right two panels show histograms of the final mean population ForageT and FlockT at the end of each simulation. Results shown are for all runs and all parameter-setting combinations (a total of 120).

Figures 4 and 5 show the mean population values of ForageT and FlockT separated by population size and energy-forage values. Each line is the threshold value averaged across 10 replicates with the same parameter settings. There seems to be little difference in the ForageT value evolved with different population sizes or different foraging energy gain values, whereas FlockT varies across different parameter settings. ForageT convergence across different energy-forage values is tightest for large population sizes (Figure 4, top panels). In contrast, FlockT converges most rapidly for small population sizes (Figure 4, bottom panels). ForageT and FlockT converge most consistently across population size for low energy levels (Figure 4 and 5, top panels). Interestingly, there is the greatest difference in FlockT values with different population sizes for an energy-forage value of 2.5 units, the most realistic value (Figure 5, bottom panel, second from right; see also Discussion).

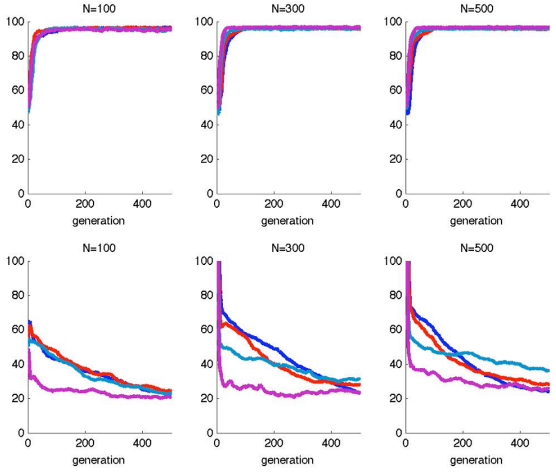

Figure 4: The mean population values for ForageT (top panels) and FlockT (bottom panels) across generations within a simulation run, averaged across all simulation runs for each parameter setting combination, grouped by population size. Left panels are for N=100, middle panels are N=300, and right panels are N=500. Blue lines are simulations with energy-forage(EF)=0.5, red are with EF=1.0, turquoise with EF=2.5, and purple with EF=5.0.

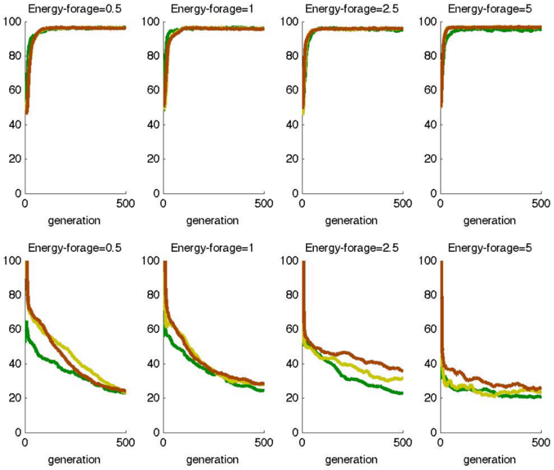

Figure 5: The mean population values for ForageT (top panels) and FlockT (bottom panels) across generations within a simulation run, averaged across all simulation runs for each parameter setting combination, grouped by energy-forage value. Far left panels are for energy-forage(EF)=0.5, left panels are EF=1.0, right panels are EF=3.5, and far right panels are EF=5.0. Green lines are simulation with N=100, yellow lines are with N=300, and brown with N=500.

Figure 6 shows the mean FlockT and ForageT values for different values of energy-forage and population size. There are no clear trends for mean ForageT value. Mean FlockT seems to peak at 2.5units as a function of energy-forage for populations with 300 and 500 individuals, with lower values for 0.5 and 5units (bottom left panel). The mean flocking threshold appears to increase as population size increases for three out of four energy forage values, a trend not seen as clearly at any other energy-forage value. (bottom right panel). None of the trends are significant with 95% confidence intervals, although this is only with ten replicates.

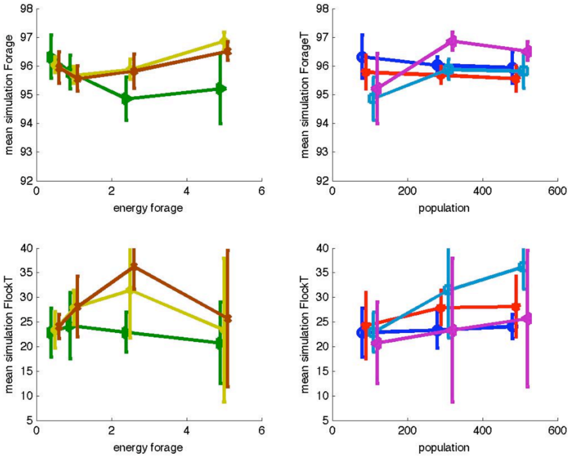

Figure 6: The mean population vales for ForageT (top panels) and FlockT (bottom panels) at the end of a simulation run, averaged across all simulation runs for each parameter setting combination. Left panels give vales as a function of energy-forage. Green lines are simulation with N=100, yellow lines are with N=300, and brown with N=500. Right panels give values as a function of population size. Blue lines are simulations with energy-forage(EF)=0.5, red are with EF=1.0, turquoise with EF=2.5, and purple with EF=5.0. Error bars are one standard deviation above and below the mean value.

Since FlockT and ForageT are inherited together and have the potential to coevolve, we might expect to see a clear trend when plotting one versus the other, however this is not the case (Figure 7). FlockT and ForageT values cluster tightly, but do not show any clear pattern with either population size or energy-forage.

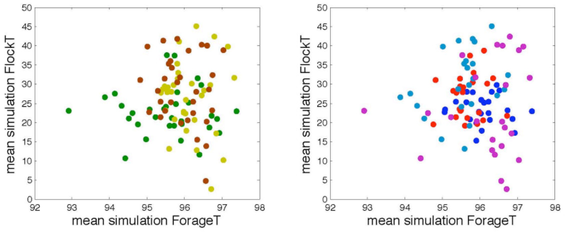

Figure 7: The mean population values of FlockT vs ForageT for each simulation. Left panel shows values sorted by population size with green dots for simulations with N=100, yellow for N=300, and brown N=500. Right panel shows values sorted by energy-forage values with blue dots for simulations with energy-forage(EF)=0.5, red for EF=1.0,

IV. DISCUSSION

In our simulations the evolved values of FlockT and ForageT seemed to converge well within a run, and converge consistently across replicates. This suggests that the genetic algorithm and selection rules implemented in our model were successful in making the evolved threshold values converge. The convergence of ForageT was much stronger than that of FlockT, both within replicates of the same parameter settings, and even across different parameter settings. This is especially interesting given that the flocking rule overrides the foraging rule in our model (i.e. if an individual has both low energy and few neighbors it will choose to flock instead of forage). The better convergence of ForageT may be because the mortality and behavior rules for foraging are all deterministic, whereas the mortality rule for flocking (death from predation) is stochastic. This may make convergence of behavior to avoid death from predation (i.e. FlockT) more difficult.

Out of the 120 simulations that were run, the values for ForageT and FlockT each converged to very similar values in 118 cases. The two exceptions were both simulations with a population size of 100, one with an energy-forage value of 0.5 units and the other with a value of1 energy unit. Over the duration of the simulation, the ForageT values for these populations remained around 20 or 30 energy units. ForageT was similar for all individuals within the population (not shown); there were not two sub-populations with different threshold values. These low threshold values are only possible since in the above simulations flocking behavior overrode foraging behavior; if it did not, the individuals would continue feeding for ~70 time steps (for foraging energy of 1) and be most likely left behind the flock. Thus although the genetic algorithm evolved most ForageT values towards one dominant equilibrium, it appears other values can be generated. These two exceptional trajectories had the lowest populations size considered. In general, ForageT converged best for the largest population size (Figure 4, top panels). This could be simply because large populations have more individuals exploring the space of possible threshold values. In contrast, the convergence of FlockT is largely independent of population size (Figure 4, bottom panels). Genetic drift, which acts more strongly in smaller populations, could also account for these two outliers.

ForageT values, in general, converged less strongly for higher energy-forage values. For high values of energy-forage, an individual's energy level is changing by large intervals per time step, which may make convergence to a specific value difficult. These large fluctuations in threshold could also contribute towards preventing the foraging energy thresholds settling into the apparently marginally stable, low threshold exceptional equilibria noted above. The dependence of the FlockT convergence on energy-forage values is less clear (Figures 5, bottom panels), although it is worst for the highest energy-forage values. It is plausible that instability in one threshold may lead to instability in another.

The average trial ForageT values span just over two energy units (Figure 6, top panels). One apparent trend is the lower foraging threshold at large foraging energy gain for the smallest population size. Even this trend, however, is small (differences in energy of 0.7 and 1.5 units compared to foraging energy gains per time step of 2.5 and 5 units, respectively) and unlikely to be significant.

The average final flocking thresholds summarized by Figure 6 (bottom panels) show that for large foraging energy gains, smaller population sizes led to smaller flocking thresholds. If individuals gain a lot of energy at each time step, then they can afford to react faster to possible death from predation with small populations, and therefore use a high flocking threshold. For large populations this risk of death from as predation isn't as high. Interestingly, the evolved foraging thresholds are their highest (which presumably means there are the fewest deaths from predation) when energy-forage is 2.5 energy units. This approximately corresponds, in scaled units, to the actual foraging energy gain for caribou and wildebeest. This may be evidence of a natural optimum that real-world evolution has already found. The optimum is not statistically significant due to the small number of replicates; further simulations would be required to confirm this optimum.

One key component which we have yet to address is whether a population of individuals using the FlockT and ForageT behavioral rules that we have evolved would be able to succesfully migrate. To test this we will set up simulations where individuals have the FlockT and ForageT values evolved above and see if the population is able to travel a typical migration distance (200km for wildebeest; Åkesson and Hedenström 2007) with a relatively realistic mortality rate. This should be tested for all of the combinations of parameter settings that were used above. One predicted result is that migration will not be successful (i.e. there will be complete mortality) when the energetic cost of moving is high relative to the energy gained by foraging (for low energy-forage values).

The above simulations currently do not evolve the foraging energy gain; this could be an interesting direction for future work. Dependence, or lack thereof, of optimal foraging energy gain on other parameters such as population size could also be investigated. Different 'patterns' of migration also occur for different ungulates, for example 'stringy' wildebeest movement and 'flowing' caribou movement. Obtaining these different patterns by varying parameters of the model could be investigated.

Other modifications to the model could include investigating conditions for fragmentation or geometrical changes of a herd. Past theoretical work suggests that fragmentation occurs more easily when individuals are heterogeneous in their walking speeds (Gueron et al. 1993), which in our model would correspond to heterogeneous ratios of foraging energy gain to flocking energy loss. In our model, the migration rate is fixed by the ratio of energy gained per time step from foraging to the energy lost per time step by moving, which determines the fraction of time an individual must spend foraging. Geometrical changes have previously been shown to be dependent on the average speeds of individuals (Gueron et al. 1996). The dependence of an individual's position within a flock on their energy levels (Parrish 1999), or on their current mode of behavior (flocking or foraging), could also be investigated.

V. CONCLUSIONS

The behavior of migrating ungulate flocks with individuals switching between flocking and foraging behavior was simulated with an individual-based model. The genetic algorithm applied to the flocking and foraging thresholds gave reproducible values for these behavioral thresholds. The flock population size and the energy gained per time step from foraging were also varied. The tightness of the genetic algorithm's convergence varied to some degree with these parameters. That the evolved foraging threshold was highest when the foraging energy gain was 2.5 energy units, and that real-world ungulates have this foraging energy gain, may be evidence of an optimal strategy. Confirming this optimum could be the subject of future work. Other investigations and modifications could include: investigating individual heterogeneity or global parameter settings for inducing fragmentation or geometric changes of the herd; including local interactions with the environment (different resource qualities); and investigating the dependence of flock position on the individual's current conditions and behavior. Whether the evolved thresholds give rise to realistic mortality rates for real-world flocks could be a useful evaluation of the model.

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