Energy, information, and the evolution of migration

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Abstract

Migration has been an important model for the study of how organisms perceive their environments, share information with one another, and make decisions in light of physiological constraints and tradeoffs. Research on the navigation and collective behavior aspects of migration has primarily focused on how heritable genetic information allows migrants to use environmental cues to locate migration targets and how this information is shared among individuals. By contrast, work on physiological constraints and individual decision-making has largely focused on how individuals can maximize fitness by making decisions that affect the amount of energy or time required to complete migratory journeys given the constraints of physiological performance. While much progress has been made in both of these areas, no attempt has been made to synthesize them into a single modeling framework. Here, we use and agent-based simulation model to explore the evolution of sociality, navigation ability, physiology, and migration strategy. Simulations consistently produce populations comprised of individuals with low levels of socialization and high navigation abilities. Results also show that the relative importance of reaching a migratory site early relative to other migrants, versus reaching a migratory site with a large amount of stored fuel energy is key in determining the equilibrium phenotypes of migratory populations, influencing evolutionary trajectories of navigation ability, physiology, and migration strategy. Interestingly, under certain fitness scenarios, no equilibrium phenotype exists and populations undergo sustained oscillations between phenotypes. We speculate that the strong dependence of phenotype on fairly subtle changes in the fitness weight of time versus energy minimization may help explain why phenotypes of migratory animals appear to be so plastic over even short evolutionary timescales.

1 Introduction

Migration behavior is found across the tree of life and has been an important model for understanding environmental perception and biological navigation [1], collective behavior and information sharing [2], and life-history strategies in light of physiological constraints [3]. Work on navigation and collective behavior has primarily focused on how heritable genetic information allows migrants to use environmental cues to locate migration targets, and how the sharing of this information among individuals influences evolutionary processes at the population level [2]. By contrast, work on physiological performance and individual migration strategies has largely focused on how individuals can maximize fitness by making decisions that affect the amount of energy or time required to complete migratory journeys [4]. While the evolution and ecology of migratory organisms are clearly affected by both the capacity to successfully navigate over long distances and by the physiology and behavioral decisions of individual migrants, no attempt has been made to integrate these two aspects of migration into a single modeling framework.

Here, we use a simulation-based approach to model the migration and evolution of virtual migratory birds. We track the evolution of four key traits that are often studied separately but have not been studied in unison: socialization, navigation ability, fuel storage capacity, and migration speed. Socialization determines how strongly an individual migrant seeks to travel with conspecifics and provides a simple mechanism of information-sharing among individuals [5]. Navigation ability determines how strongly a migrant perceives and follows environmental cues that contain information about the location to which it is migrating [2]. Fuel storage capacity influences the distance a migrant can travel and its ability to survive harsh environmental conditions or competition for mates post-migration [4]. Migration speed is a central component of the two predominant behavioral strategies discussed in the migration literature: time minimization, and energy minimization [6, 7]. In the time minimization strategy, migrants attempt to travel as quickly as possible because

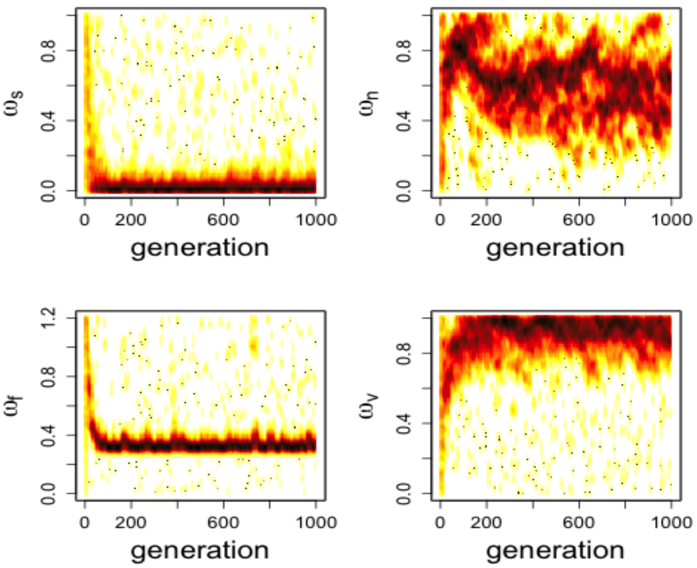

Figure 1: Evolution of migrant traits through time. Plot color indicates frequency of occurrence of a particular trait value (dark red indicates high frequency, light yellow indicates low frequency). Fitness contribution of energy and time are equal. All traits were uniformly distributed between their maximum and minimum values at the beginning of generation 1.

they benefit by reaching migration destination before other conspecifics. Under the energy minimization strategy, individuals minimize energy use so that they arrive at the migration destination with a surplus of stored fuel energy. We assume that heritable genetic attributes underlie these strategies.

Our simulations follow a population of migrants through 1000 generations. In each generation, individuals migrate toward a “target island” in response environmental cues, and interact with one another based on simple behavioral rules [5, 2]. After reaching the target island, individuals are selected for reproduction based on the time at which they arrive relative to other migrants (time component of fitness) and their physical condition upon arrival (energetic component, see Methods). The traits described above evolve through recombination and mutation and the frequency of phenotypes at the population level change over time. Simulations consistently produce populations consisting almost exclusively of individuals with low levels of socialization and high navigation abilities. Results also show that the relative importance of reaching a migratory site early relative to other migrants, versus reaching a migratory site with a large amount of stored fuel energy is key in determining the equilibrium phenotypes of migratory populations, influencing evolutionary trajectories of navigation ability, physiology, and migration strategy. Interestingly, under certain fitness scenarios, no equilibrium phenotype exists and populations undergo sustained oscillations between phenotypes. We speculate that the strong dependence of phenotype on fairly subtle changes in the fitness weight of time versus energy minimization may help explain why phenotypes of migratory animals appear to be so plastic over even short evolutionary timescales (e.g. [7, 8]).

2 Methods

We modeled the evolution of migration in an idealized bird species migrating across a two-dimensional landscape. At the beginning of each generation, N individuals were located within an area of size A, which was located at a distance of D units from a target island. Each individual had specific values of each of four heritable traits: a socialization coefficient (ω_s), navigation ability coefficient (ω_n), fuel storage coefficient (ω_f), and a speed coefficient (ω_v). Navigation ability determines how heavily migrants weight information about the location of the target island versus random errors in migratory direction. In this sense, individuals with high ω_n can be viewed as “good navigators”. The socialization coefficient determines how strongly individuals turn toward and match speed with other individuals in their immediate vicinity [2]. Individuals with high ω_s are highly social individuals that match the trajectories and speeds of neighboring individuals. The fuel coefficient, ω_f, determines the fraction of an individual’s total body mass that is composed of fuel that can be used to power migration. Individuals with high ω_f can fly for longer periods of time before exhausting their fuel supplies. The speed coefficient, ω_v, determines how rapidly individuals travel relative to their maximum range speeds (i.e. the speed that minimizes the amount of energy used per unit distance). Because there is a limit to the amount of power that a given mass of muscle can produce, we set a limit on the maximum power production of migrants. Because individuals with high ω_f are heavier than individuals with low ω_f, high ω_f individuals must devote more power toward remaining aloft and are thus not able to travel as quickly as low ω_f individuals. During each generation, individuals were allowed to migrate following a set of *behavioral rules* and a set of *energetic rules* (see Appendix A). Migration continued until all individuals either (1) reached

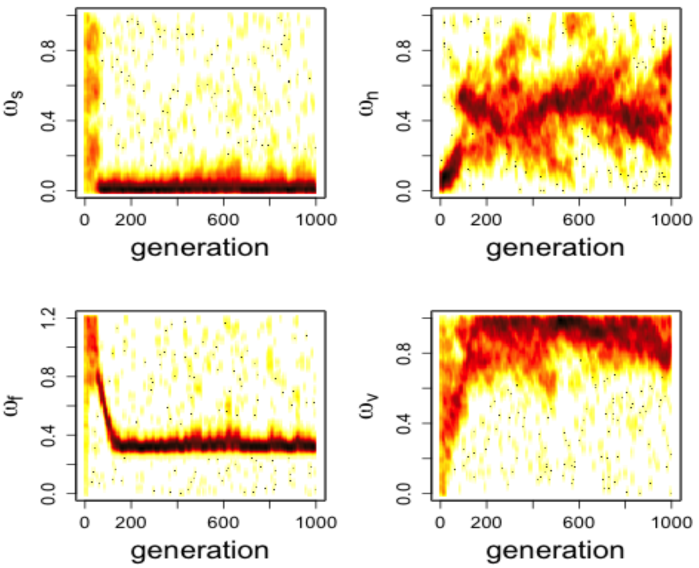

Figure 2: Evolution of migrants when navigation ability is initially low. plots as in figure 1. Initial trait values are the same as those shown in figure 1 except that ω_n was uniformly distributed between 0 and 0.1 in generation 1.

the target island or (2) ran out of stored fuel. At that point individuals were selected to reproduce from the population with probabilities proportional to their fitness at the end of the generation [2]. In each of these generations, trait values were allowed to change by re-combination and mutation. This process was repeated for 1000 generations.

To explore how sensitive our results were to initial conditions, we altered initial conditions in a number of simulations. To begin with, we constrained the initial distribution of trait values of navigation ability in the population to be uniform between 0 and 0.1, allowing values of the other three traits to be uniformly distributed between their minimum and maximum values. We repeated this simulation with the socialization trait uniformly distributed between 0.9 and 1. To determine whether socialization and fuel serve redundant roles, we ω_f to be 0.5, and repeated the simulation described above. Finally, to determine how the relative importance of arriving at the target island early versus arriving at the target island with fuel energy affected the outcome of evolution, we altered weighting coefficients on the fitness contributions of each of these terms (see Appendix A). We weighted both components equally, and explored the effect of a 5-fold and 10-fold difference in coefficients between the two components, resulting in a total of 5 fitness weighting combinations (1:1, 5:1,10:1,1:5, and 1:10).

3 Results and Discussion

When populations begin evolution with random values of each trait and the relative fitness contributions of time and energy are equal, populations quickly reach what appears to be a stable long-term equilibrium distribution in three of the four traits (figure 1). The socialization trait quickly approaches zero, whereas the navigation ability and migration speed traits quickly increase. Because we imposed the constraint that power production is limited in these migrants, there is a tradeoff between the maximum size of the fuel load that can be carried by a migrant and the speed at which that migrant can travel. Thus, as the speed trait increases, the fuel trait quickly decreases to a value that is close to the minimum required to reach the target island. It is apparent that the fuel trait increases drastically in early generations before dropping back down to approach its equilibrium value. This phenomenon is more clearly apparent when populations begin the simulation with low values of the navigation ability. In this case, the fuel trait increases to relatively high values for over 50 generations before decreasing toward its ultimate equilibrium value near 0.4 (figure 2). Starting with the same initial conditions but with values of socialization between 0.9 and 1 yielded similar results. The fact that fuel is positively selected for when navigation ability is low suggests a possible redundancy among these two traits; individuals that have more fuel can afford to make navigational errors because they can search for the target island for a longer period of time before running out of fuel. This is important when navigational errors are relatively large, but becomes less important as migrants evolve stronger navigation abilities. It is worth noting that socialization appears to play a similar role in models that do not include physiological variables like fuel (e.g. [2]). Is it possible then that the fuel variable in our simulations has taken over the role played by socialization in past models? We explored this possibility by fixing fuel and velocity and allowing only socialization and navigation ability to evolve. Although socialization ultimately approaches an equilibrium value very near zero, It does maintain a high value in the population for far longer in populations with fixed ω_f than in simulations in which all traits evolve. Positive values of socialization can be maintained in the population for even longer periods of time by increasing

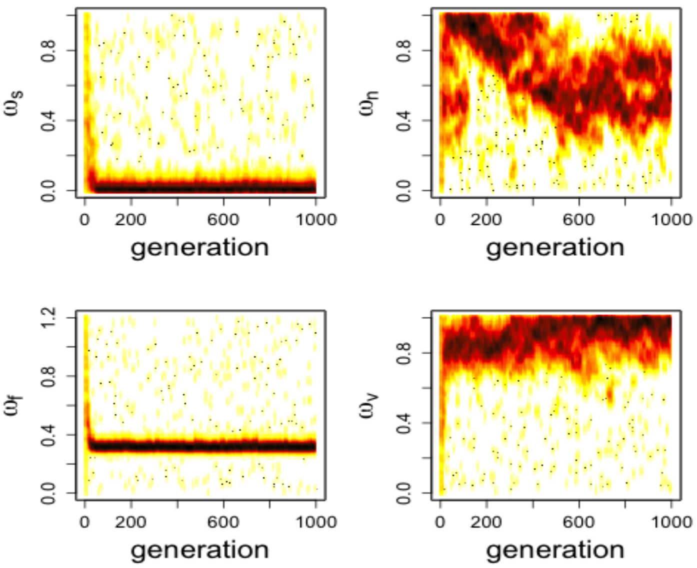

Figure 3: Evolution of migrants when the time component of fitness outweighs the energetic component by 10-fold. Plots and initial trait values as in figure 1.

the magnitude of random navigational errors. This is consistent with the hypothesis that fuel and socialization play somewhat redundant roles in allowing individuals with relatively weak navigation ability to reach the target despite navigational errors.

By manipulating the relative fitness contribution of time minimization versus energy maximization, we were able to alter the outcome of evolution. When weights were equal (figure 1) or time minimization was weighted more heavily than energy maximization (figure 4), populations tended to evolve toward states in which all individuals had low values of the fuel trait and high values of the speed trait. When energy maximization was weighted much more heavily than time minimization, populations quickly evolve toward high values of the fuel storage trait and intermediate values of the speed and navigation ability trait (figure 5). Interestingly, the navigation ability trait was less variable in this simulation than in other simulations and it stabilized more quickly to a value that was relatively low compared to its value in other simulations. Presumably, this is because high values of the navigation ability trait do cost migrants energy (see Appendix A). When the fitness benefit of arriving with high energy is heavily weighted, it appears that the modest energetic cost of navigation ability is enough to prevent this trait from equilibrating at high values.

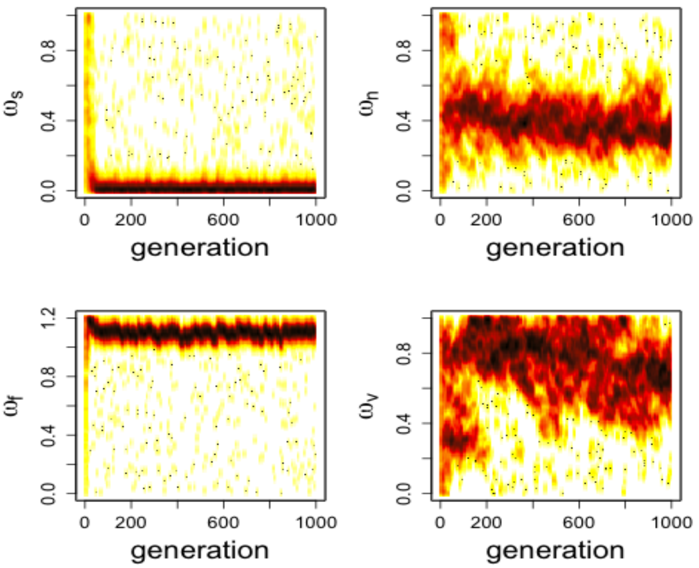

Figure 4: Evolution of migrants when the energetic component of fitness outweighs the time component by 10-fold. Plots and initial trait values as in figure 1.

When the fitness contribution of energy maximization outweighs that of time minimization by an intermediate amount (2-5-fold), populations do not reach stable equilibria in the fuel trait (figure 3). Rather, the fuel trait increases to high values in all individuals and then slowly decreases. Instead of stabilizing at a particular value, the population is invaded by a mutant with high fuel storage, which quickly achieves high frequency in the population leading to another slow decline in the mean value of the fuel trait until the population is invaded by a high-fuel mutant once more.

In all simulations, both the speed and navigation traits remain highly variable relative to the socialization and fuel traits. This is perhaps because selection on these traits is relatively weak above some threshold. For example, the navigation ability trait determines the relative weighting of environmental cues regarding the location of the target island relative to cues regarding the location of nearby migrants and random errors. However, when the value of the navigation ability trait is 0.5, information about the location of the target island is weighted 50-times more heavily than random errors. It may be that the relative weighting of errors is so low that further increase in this trait confers little advantage but also results in only very small detriments to fitness. Indeed, the equilibrium value of this trait can be increased and the variance decreased by simply increasing

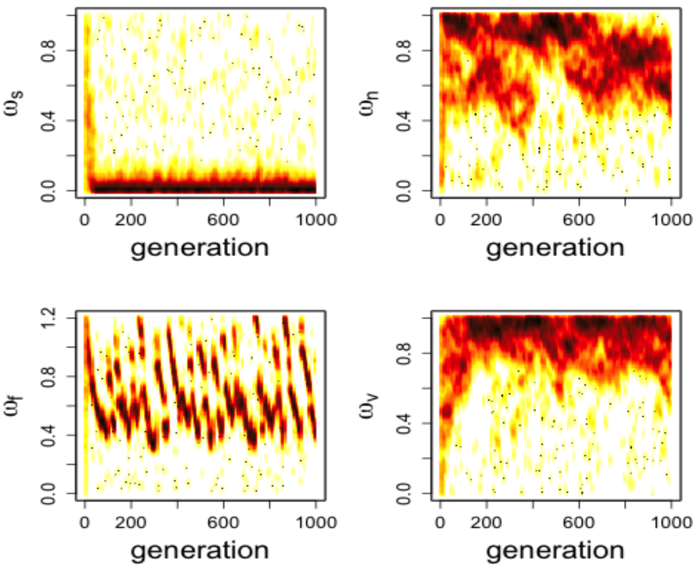

Figure 5: Evolution of migrants when the energetic component of fitness outweighs the time component by 2-fold. Plots as in figure 1. Plots and initial trait values as in figure 1.

the relative weighting of random navigational errors.

In summary, our results demonstrate that, under the conditions explored here, social interactions among migratory animals do not appear to play an important role in the evolutionary maintenance of migration behavior. This contrasts sharply with the results of past models. For example, Guttal and Couzin [2] observed that high values of socialization evolved under a wide variety of conditions in a simulation model of migratory evolution. One difference between our model and theirs is that migrants have the fuel trait and the ability to change migration speed in order to arrive at the target island before conspecifics. The fuel trait may serve a redundant role to that played by socialization. Another potentially important difference between our simulation and that described in [2] is that we do not impose a direct fitness cost of socialization or navigation ability. Indeed, the particular functions used to describe the relative fitness cost of socialization and navigation ability can alter the outcome of evolution, in some cases resulting in low values of socialization at the population level [2]. In our simulation, the fitness cost of socialization and navigation ability arise naturally through their effects on the rate of energy use of migrants. Individuals that are very social end up traveling at velocities that are non-optimal if they group with migrants that are different in size.

This results in higher rates of fuel use per unit distance and less energy upon arrival. The fitness cost of navigation ability is assumed to be related to the energetic cost of calling (see Appendix A). However, a similar energetic cost could result if good navigators occupy the most energetically costly positions in a migratory flock. Thus, while our model does impose an indirect fitness cost on increased navigation ability, this cost may be too small to result in positive selection for highly social individuals and negative selection.

While selection for socialization appears to be strongly negative regardless of the importance of time versus energy minimization, our model points to an important role of the relative fitness benefit of time minimization versus energy minimization in determining evolutionary trajectories of the other traits. It is particularly interesting to note that under certain fitness scenarios, no equilibrium phenotype exists and populations undergo sustained oscillations between phenotypes. We speculate that the strong dependence of phenotype on fairly subtle changes in the fitness weight of time versus energy minimization may help explain why phenotypes of migratory animals appear to be so plastic over even short evolutionary time periods. Our results show that integrating different aspects of migration biology into a single framework can yield new insights into the evolutionary possibilities that exist among migratory animals. We suggest that further insight will be gained by modifying the model presented here based on more accurate information regarding the fitness costs and benefits of the phenotypes of migratory organisms.

References

[1] Cochran, W. W., Mouritsen, H. & Wikelski, M. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **204**, 405–408 (2010).

[2] Guttal, V. & Couzin, I. D. Information use and the evolution of collective migration. *Proceedings of the National Academy of Sciences USA* **Online early edition** (2010).

[3] Bowlin, M. S. & Wikelski, M. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLoS One* **3**, e2154 (2008).

[4] Alerstam, T. & Hedenström, A. The development of bird migration theory. *Journal of Avian Biology* **29**, 343–369 (1998).

[5] Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516 (2005).

[6] Bowlin, M. S. *et al.* Grand challenges in migration biology. *Integrative and Comparative Biology* **50**, 261–279 (2010).

[7] Bearhop, S. *et al.* Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**, 502–504 (2005).

[8] Bisson, I., Safi, K. & Holland, R. Evidence for repeated evolution of migration in the largest family of bats. *PLoS One* **4**, e7504 (2009).

[9] Peters, R. H. *The Ecological Implications of Body Size* (Cambridge University Press, Cambridge, 1983).

[10] Ophir, A. G., Schrader, S. B. & Gillooly, J. F. Energetic cost of calling: General constraints and species-specific differences. *Journal of Evolutionary Biology* **online early publication** (2010).

[11] Pennycuick, C. J. *Modeling the Flying Bird* (Academic Press, 2008).

[12] Hein, A. M., Hou, C. & Gillooly, J. F. A general model to predict migration distance of running, swimming, and flying animals (2010). Unpublished manuscript.

[13] Alerstam, T., Hedenström, A. & Akesson, S. Long-distance migration: Evolution and determinants. *Oikos* **103**, 247–260 (2003).

4 Appendix A: Model Description

We modeled the evolution of migration in an idealized bird species migrating across a two-dimensional landscape over 1000 generations. At the beginning of each generation, N individuals were located within an area of size A, which was located at a distance of D units from a target island. N was set to 100 in all simulations shown here. Individuals migrate based on a set of behavioral and energetic rules, and are then allowed to reproduce according to a selection algorithm. The details of this process are described in the following sections. We relied heavily on the simulation model described by [2], although our model departs from this model in some important ways.

4.1 Behavioral rules

At each time step an individual is allowed to change its heading depending on its location relative to (1) nearby conspecifics and (2) the target island. Collision avoidance has the highest priority, so if an individual is too close to another migrant, it will turn away, regardless of the location of other conspecifics or the target island. At any time step, t, the position and heading of the ith individual are given by the vectors $\mathbf{c}_i t$ and $\mathbf{v}_i(t)$, respectively. Individuals avoid colliding with other individuals by turning away from any individual within a small radius of avoidance, r_a, in the direction:

$$d_i(t+\Delta t) = -\sum_{j\neq i} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} \tag{1}$$

where $d_i(t+\Delta t)$ is the direction of travel during the next time step. If there are no other individuals located within r_a units of the ith migrant, the migrant's desired direction is given by

$$d_{si}(t+\Delta t) = \sum_{j\neq i} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} + \sum_{j=1}^{N} \frac{v_j(t)}{|v_j(t)|} \tag{2}$$

, which describes the tendency of individual i to move toward and align with other migrants within a local zone of socialization r_s. Ultimately, the desired direction of travel is a weighted mean of the individual's attraction toward other migrants, and its tendency to travel in the direction of the target island, weighted by the heritable socialization and navigation traits:

$$v_i(t+\Delta t) = \frac{\omega_{si}\hat{d}_{si}(t+\Delta t) + \omega_{ni}\hat{d}_{ni}(t+\Delta t) + \sigma_{ri}\hat{d}_{ri}(t+\Delta t)}{|\omega_{si}\hat{d}_{si}(t+\Delta t) + \omega_{ni}\hat{d}_{ni}(t+\Delta t) + \sigma_{ri}\hat{d}_{ri}(t+\Delta t)|} \tag{3}$$

Here ω_{ni} is navigation ability, ωsi is the socialization coefficient, and $\hat{d}_{ni}$ is the direction vector that points from the location of individual i toward the target island, and d_{ri} is a vector with random orientation to simulate navigational errors. The ˆ symbol denotes that vectors are normalized to unit length. Thus, the position of an individual at time $t + \Delta t$ is given by $c_i(t + \Delta t) = c_i(t) + s_i(t)v_i(t + \Delta t)\Delta t$, where $s_i(t)$ is speed. As in [2], individuals have a maximum turning rate of θ_{max} and can turn no more than $\theta_{max}\Delta t$ radians in a single time step. If the angle between current velocity and desired direction vectors is less than $\theta_{max}\Delta t$, the new direction of movement is equal to the desired direction. If $\theta_{max}\Delta t$ is less than this angle, they turn $\theta_{max}\Delta t$ radians toward the desired direction.

4.2 Energetic rules:

At the beginning of each generation, each individual starts with a fraction of fuel, f_{i0}. This fuel is depleted as the individuals migrate. The amount of energy stored in fuel that any time is given by

$$E_{it} = e\, f_{it}\, M_0 \qquad Joules \tag{4}$$

where e is the energy density of fuel (4.0×10^7 Joules kg^{-1}) [9]. Fuel is lost in two ways. First we assume that individuals that have information about the location of the target island (i.e. $\omega_n > 0$) must share this information via auditory communication with other migratory individuals. This results in an energetic cost due to sound production. Second, all individuals must expend energy to fly. The energy loss rate due to communication is given by

$$C_I(\omega_n) = \frac{7.3\, \omega_n}{\omega_{g\, max}} \qquad Watts \tag{5}$$

We assume that the cost of information sharing is a linear function of the amount of information shared (proportional to ω_n) and that the maximum rate of energy expenditure for communication is equal to maximal empirical rates observed in wild birds [10]. The energy loss rate used to power flight is given by

$$P_{fly} = 3.67 + 2.2[270(M_0 + M_0 f)^2 s^{-1} + 0.00173(M_0 + M_0 f)^{0.67} s^3]\ Watts \tag{6}$$

, where the terms in parenthesis represent the mass of the ith individual at time t [11] , s is speed (see below) and values of morphological parameters have been estimated using established morphological scaling relationships [12]. Thus, the total rate of energy consumption is given by

$$P_{total} = C_I + P_{fly}\ Watts \tag{7}$$

4.3 Speed calculation:

In past models (e.g. [2]), $s_i(t)$ was assumed to be constant and identical for all individuals. However, different speeds are associated with different rates of energy use. We rely on results from aerodynamic theory [12], which show that a flying animal can approximately maximize its efficiency in terms of the number of meters traveled per unit of energy at any time, t by traveling at a speed given by the equation

$$s_{opt}(t) = 19.8M(t)^{0.33} \qquad meters/second \tag{8}$$

where $M(t)$ is body mass at time t. Individuals are allowed to adjust their speeds relative to this optimal speed based on the equation $s_{di} = s_{opt}\,i(1 + \omega_v)$, where s_{di} is the desired speed of travel of the ith individual. We assume that individuals balance the desire to travel at this speed, with the desire to cohere with other individuals. The speed of each individual is computed as

$$s_i(t + \Delta t) = \omega_s \frac{1}{n} \sum_k s_{opt,k}(t + \Delta t) + (1 - \omega_s) s_{di}(t + \Delta t) \tag{9}$$

where the summation is taken over all k individuals that are in the radius of socialization of the ith individual and n is the number of such individuals. In other words, the speed of an individual is computed by taking a weighted sum of the average speeds of its group and its optimal speed.

4.4 Fitness calculation

Each generation in a given simulation continues until all individuals either reach the target or run out of fuel. To calculate the fitness of each individual at the end of the generation, we relate the fuel remaining a when an individual reaches the target to fitness by the function

$$f(f_{it}) = \frac{2af_i(\tau)}{1 + f_i(\tau))} \tag{10}$$

, where $2a$ is the maximum fitness that can be contributed by fuel and $f_i(\tau)$ is the fuel fraction of the ith individual when it reaches the target at time, $t = \tau$. Migrants that arrive at the target early also get a boost in fitness [13], which is given by

$$g(t_i) = c\,(1 - \frac{t_i}{t_{max}}) \tag{11}$$

,where t_{max} is the time taken for the slowest migrant to reach the target and c is the maximum fitness that can be contributed by the time component of fitness. Total fitness of the i^{th} individual at the end of each generation is given by

$$F_i = f(E_{it}) + g(t_i) \tag{12}$$

for all individuals that reach the target and zero for individuals that run out of fuel before reaching the target. Parameters a and c determine the relative importance of time minimization versus fuel use minimization.

4.5 Selection algorithm

Following the completion of each generation, a subsequent population of size N is produced by selecting individuals from the current pool based on fitness differentials, with their heritable traits passed on through simulated recombination and mutation.

The fitness F_i of each individual is first normalized to the range $[0,1]$:

$$\hat{F}_i = \frac{F_i - F_{min}}{F_{max} - F_{min}} \tag{13}$$

To produce a new population of size N, for each new ‘offspring’ individual, two ‘parents’ are chosen using a roulette wheel selection algorithm. This can be envisaged as carving up a space into N regions proportional to each individual’s fitness and selecting a uniformly random point on this space. An individual i thus has a selection probability of:

$$p_i = \frac{\hat{F}_i}{\sum_{j=1}^{N} \hat{F}_j} \tag{14}$$

The heritable traits (ω_s, ω_n, ω_f, ω_v) of the offspring individual are selected randomly between those possessed by the parents, with equal probability $p = 0.5$.

To introduce variance into the subsequent generation, mutational effects are applied to the offspring’s trait values. With a very small probability p_{rad}, for each trait, a new uniformly random value ψ will be chosen within the range $[0,1]$. Otherwise, the existing value is ‘nudged’ by a small quantity ϵ, taken from a Gaussian distribution with mean 0, standard deviation 0.01.

$$\omega_{si} = \begin{cases} \psi & \text{if } \zeta < p_{rad} \\ \omega_{si} + \epsilon & \text{otherwise} \end{cases} \tag{15}$$

where ζ is a uniformly random distribution over $[0,1)$.