

AN INDIVIDUAL-BASED MODEL FOR TRADITIONAL FORAGING BEHAVIOR: INVESTIGATING EFFECTS OF ENVIRONMENTAL FLUCTUATION

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ABSTRACT. We present an individual-based model to simulate the evolution of traditional foraging strategies in a fluctuating environment. The parameters and procedures are based on observed behavior of barnacle geese, *Branta leucopsis*, during spring staging off the coast of Helgeland, Norway. Within a temporally and spatially heterogeneous environment, goose movement is modeled according to state-dependent site selection decisions that maximize food intake. The aim of each individual is to optimize fitness (survival and reproduction) by gaining enough food (energy reserves) during 3 weeks of foraging to meet a threshold of energy necessary for successful reproduction. The geese return to the same islands each year and on a daily basis choose unoccupied sites according to their rank in the population-structured dominance hierarchy, memories of previously visited sites (tradition), past reproductive success, inherited genetic influence towards site faithfulness and/or site quality, and knowledge of the available biomass density. It is assumed that with each subsequent return to a specific location, increased familiarity of the area will benefit an individual through greater food acquisition by

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more efficient foraging practices. In the event of variable environmental conditions, geese are faced with a critical decision to return to previously visited sites or abandon tradition to explore for something better. It is shown that habitat quality plays an integral role in population dynamics. Beyond the scope of this paper, the evolution of foraging strategies that directly affect reproductive potential is shown to inevitably determine the resilience of the population over time (Kanarek [2006]). Further experiments are required for detailed results and analysis of specific circumstances that provoke the adaptation of certain behaviors. In general, this modeling approach has the potential to reveal significant insight into the emergence of stable responses to environmental disturbance.

KEY WORDS: Individual-based model, foraging behavior, site fidelity, environmental disturbance, barnacle geese.

1. Introduction. Studying the dynamics of an evolving system involves analyzing the governing behavior that influences individual performance (Krebs and Davies [1978, 1984, 1991, 1997]). Various strategies emerge over time, but those that become evolutionarily stable perpetuate optimal fitness and contribute the most to the gene pool (Wilson [1975], Dawkins [1976]). Mechanisms and principles that drive animal behavior directly relate to the quality of the environment. Recognizing specific conditions that generate immediate and emergent response is useful in understanding the overall efficacy of certain strategies. This paper addresses this notion through the development of an individual-based model for site selection of traditional foragers in a variable environment.

The ebb and flow of an ecosystem is fundamentally based on the complex interactions of behaviors employed by coexistent entities. Identifying individual traits provides keen insight into system-level patterns (Grimm and Railsback [2005]). Modeling state-dependent decisions of organisms in the context of a spatially and temporally heterogeneous environment will lead to a deeper understanding of the adaptive process. In this regard, methods and procedures were constructed that allow individuals to assess and weigh their available choices based on their location and current status, both physiologically and communally. These attributes include energy reserves, spatial memories, genetic disposition, dominance rank, reproductive success, and awareness of habitat quality. Simulating each individual in parallel with their unique characteristics, in addition to simplified rules for interaction (between

each other and their environment), can adequately model the dynamics of an ecosystem (Grimm and Railsback [2005]). This method is used to study site faithful foraging behavior in a fluctuating environment.

Knowledge of one's surroundings is evidently advantageous, being helpful in making decisions to optimize the response to a given situation. Many animals retain a spatial awareness and develop routines and customs from previous experience in seeking similar outcomes. This traditional behavior is thought to be an adaptive strategy due to the payoffs (Avital and Jablonka [2000]), which increase each time a routine is repeated. In the context of foraging, familiarity with an area develops with duration of residency and presumably leads to more efficient food acquisition (Black et al. [2006]). This strategy is often motivated by the expectation of certain results but may be due to limited awareness of potentially better alternatives. The combination of these factors plays an integral role in site selection behavior, especially with changing habitat quality. When resources deteriorate or disappear, the animal is faced with a decision about staying to make the most of a bad situation or setting off to explore for something different (Goss-Custard and Sutherland [1997], Sutherland et al. [2002]). With the pressure of temporal constraints (starvation, breeding, etc.), the choice will be based on whether the payoff at a new site may be greater than the benefit gained at the degraded but still familiar site. Determining circumstantial response in the practice or abandonment of traditional or routine foraging enables theoretical understanding of the interplay of environmental effects on behavior.

This model is intended for generalized application for the analysis of site-faithful foraging and the evolution of stable movement strategies, but has been developed based on the Svalbard population of barnacle geese, *Branta leucopsis* (Owen and Black [1989], Black and Owen [1995]). For 3 weeks in May, en route from their wintering area to the breeding grounds in Spitsbergen, the barnacle geese stop along the coast of Norway, on the archipelagos of the Helgeland district (Black et al. [1991]). This segment of the migration routine is devoted to accumulating fat reserves and nutrients critical to reproduction (Prop and Black [1998], Prop et al. [2003]). During this spring staging period, empirical observation reveals significant site fidelity in habitat selection (Black et al. [2006]); however, changes in the quality of their traditional staging grounds may lead to destabilizing effects on

the goose population (Black et al. [1991, 2006]). Increasing spring temperatures, changing agricultural practices, and other variable influences may cause habitat degradation, causing possible abandonment of traditional sites in favor of exploration and new colonization (Prop et al. [1998]). By modeling individual foraging behavior through specific state dependent procedures, we can begin to examine the complexity of tradition versus exploration.

In this paper, we present an overview of the model process by describing the main structural components that are essential for a realistic simulation of the system in question. The methods and procedures were ascertained from empirical evidence and inference, and are discussed and validated through the resulting observations. Within our general objective, the development of the artificial ecosystem has been corroborated with population-level trends and pattern-oriented analysis. By producing reasonable global dynamics, we ensue confidence in the effectiveness of the underlying properties and procedures of the model (Grimm and Railsback [2005]). We explore several realizations of population response to both consistent and fluctuating environmental conditions, in addition to the overall individual-level behavioral consequences. Success in capturing the essence of this ecological system merits further experimentation and investigation of specific hypotheses.

2. The Model. The model is based on discrete dynamic governing equations and state dependent procedures that optimize behavior at each time step as a result of an individual's current fitness. The Net-Logo programming environment provides a useful agent-based modeling platform in which the simulated system can be implemented (Wilensky [1999]). The program maintains the identity of each agent (individual geese) and processes them uniquely through each applicable routine. At each time step, individuals make fitness optimizing decisions according to their status within the population and the environment. The spatial structure has two scales, the archipelago comprising the entire spring staging area and a grid of patches within these islands. Decisions are made upon arrival at the staging area for a particular island (where they remain for the duration of the season) and then for a specific patch on that island that is projected to offer the most energy accumulation (expected payoff). Because the spring stopover is the primary focus of this model, the temporal arena consists of a

3-week period tracked with a 1-day time step, and the year is incremented at the beginning of the season. Beyond the focus of this model, the other aspects of the annual cycle (breeding and survival) are based on empirically derived probabilities and are updated prior to the geese returning to the staging area (Pettifor et al. [2000]). Thus, the model captures detailed behavior of foraging during this particular segment of the annual cycle by maintaining realistic life histories.

2.1 Environment. The model is setup by generating an archipelago to represent the staging environment. Separate islands vary in the amount and distribution of viable foraging habitat. The spatial structure is mapped by a gridwork of cells/patches, which can be occupied by one agent (goose) at a time. Each patch is ascribed a percentage of vegetative cover (amount of available biomass, shown in Figure 1) that is randomly distributed and smoothed with neighboring cells. The resulting value for each patch is recorded as the normal biomass density, which is used as the default amount of available biomass at the beginning of each year. Seasonal environmental fluctuation and daily growth and depletion are tracked through a current biomass variable associated with each patch. Whereas the daily growth is constant for all patches, depletion (with a specified decay rate) can be imposed on individual

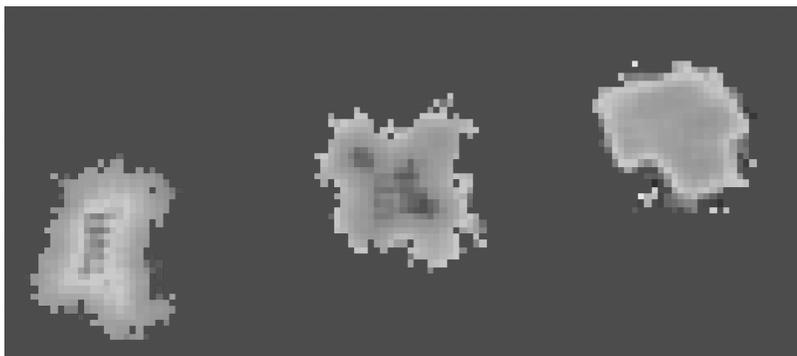


FIGURE 1. An example of the spatial element of the interface of the model. These islands are the foraging grounds during the 3 weeks of the spring staging. The vegetative density is depicted through color scale (darker = highest). In this case, patches along the coast of the left island are higher in biomass, the middle island becomes more lush toward the center, and the right island has the same distribution as the center one, less 20%.

sites or uniformly over an entire island. Site selection, movement decisions, and individual intake rate are predominantly based on the measure of biomass quality ($\beta_{i,j}$) for each specific patch.

The default layout for the simulated environment is fixed, as it has been found to support stable populations and maintains consistency between model runs. The habitat can then be altered for various experiments to observe behavioral responses. It is assumed that the main driving force behind habitat choice is the accumulation of sufficient energy to survive and reproduce (Black et al. [2006]). Seasonal climate changes and site deterioration instigate strategic alterations in movement between sites. Overall, these response behaviors to fluctuating quality of habitat are measured globally by genetic variation through natural selection promoting those individuals whose decisions inevitably allow for optimal fitness.

2.2 Geese. The primary individual attributes of the geese in this model are age, energy reserves and intake, genetic disposition, spatial memory of previously visited locations, and reproductive success. Barnacle geese form monogamous bonds at an early age (Choudhury and Black [1993], Black et al. [1996]), so each “individual” in the model represents a pair, and therefore collective behavior determines their overall fitness and success, as it would in the natural system. Otherwise, the model may be considered a female-only model because mating does not occur.

When a model run is set up, an initial population is created with equal attributes but with varying ages. These ages are non-integer values so they can be easily used to rank the geese from oldest to youngest as part of a dominance hierarchy. Each year a goose returns to the staging area, their age is incremented by one with a maximum limit. In addition to dying of old age, mortality can occur as a result of starvation or other natural causes on or off the staging area. Each goose maintains its energy reserves as a function of daily food intake less daily energy expenditure. When the geese arrive at the staging grounds, each goose’s energy reserves are reset to reflect the energy expended in flight. Because the accumulation of sufficient energy reserves is necessary for successful reproduction (Prop et al. [2003]), breeding is determined by a preset mass threshold value of energy reserves. A goose will leave the staging grounds either when the threshold is reached or at the end

of the stopover period. Therefore, it is critical that the geese forage efficiently, as their primary goal is reproduction.

The intake rate of an individual goose depends on specific factors pertaining to the patch and the goose. Foremost, with regard to the patch, intake is a function proportional to the amount of biomass on a patch. More food available translates into a greater probability of finding food, which decreases as biomass is depleted. A goose remaining on a patch becomes more familiar with locating food there and therefore becomes more efficient in foraging on that patch. Thus, each day a goose stays on a particular patch, their potential intake rate increases (α_t derived from empirical data, Black et al. [2006]). In terms of individual variation, a goose's previous experience can also affect its foraging efficiency. Herein lies the essence of the "traditional" strategy. Each consecutive year a goose returns to the same patch, they increase their familiarity with the site and hence their ability to locate food, boosting their potential intake rate. Thus, experiential memory of a traditional patch affords a goose a slight benefit over spending time exploring an unknown location. The benefit follows an asymptotic function (ϕ_i), increasing with consecutive visits (i) on a yearly scale (discussed further in the Parameterization section). The relationship between tradition, daily residence, and available biomass on the intake rate is shown graphically in Figure 2, and the intake rate ($I_{t,i,j}$), current biomass ($\beta_{t,j}$), and energy reserves (E_t) are calculated for each day (t) on a specific patch (j) with the equations in Table 1.

When the geese initially arrive at the staging area, they proceed in choosing an island and then a patch on that island that will maximize their daily expected intake rate. The geese are ranked in a dominance hierarchy that determines the order in which they choose a patch, producing a despotic distribution (Black et al. [2006]). The older geese have seniority over the younger ones because of age, experience, and reproductive success. These terms are factored into the dominance ranking. At first arrival and over the course of the season, the geese adhere to this order each time they survey available patches and choose to move. An occupied patch prevents other geese from landing there, thus the hierarchical foraging ensures the senior geese maintain a competitive advantage for the best patches. A goose will remain on the patch until their intake rate drops below the amount that was initially available to them on that particular patch. "Birds migrate at a point when it is no

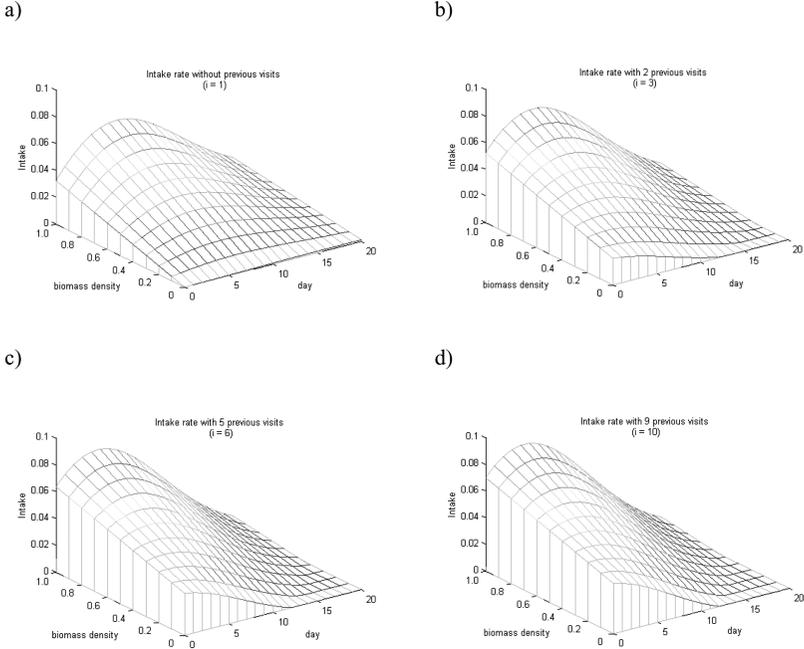


FIGURE 2. Daily intake rate at four instances of consecutive visitation, as a function of biomass density and daily residency. Graph (a) represents the first visit to a patch ($i = 1$), graph (b) represents two previous visits ($i = 3$), graph (c) is for five previous visits ($i = 6$), and (d) is an example of nine previous visits ($i = 10$).

longer profitable to remain in a particular area” (Prop et al. [2003]). Once a goose decides to leave a patch, it considers a number of factors in choosing where to go.

In the model, the geese choose a patch by assigning a score to all the unoccupied possibilities on their respective island. For these simulations, the geese have “ideal” knowledge of their environment and the specific attributes of each patch (Fretwell and Lucas [1970], Sutherland [1983]). When evaluating a patch, a goose takes into account the available biomass, whether they have previously visited there, and their “innate” preference for these qualities. These preferences are manifested through genetic values that add weights (σ_{trad} , σ_{explore}) to the factors

TABLE 1. Equations and parameters describing the amount of food that an individual can intake at a patch ($I_{t,i,j}$) based on biomass availability, daily residency, and consecutive returns (tradition). That value is then converted to energy.

Equations and parameters	Value
Daily and intake rate	$I_{t,i,j} = \frac{(\alpha_t \beta_{t,j} + \phi_i)}{\gamma}$
Biomass	$\beta_{t,j} = \beta_{t-1,j} - \mathbf{I}_{t-1,i,j} + \eta$
Proportion of biomass consumed	$\alpha_t = \mu t + \theta$
Biomass consumed due to traditions	$\phi_i = \tau \left(\frac{i-1}{(i-1)+\nu} \right)$
Energy reserves	$E_t = E_{t-1} + (I_{t,i,j})\delta - \kappa$
Day	$t = 1, 2, \dots, 21$
Number of consecutive years at a patch	i
Patch/cell	j
Total number of days spent foraging	$\gamma = 20$
Energy conversion factor	$\delta = 40$
Consecutive yearly returns for a substantial effect of tradition on daily intake	$\nu = 3$
Fraction increase of biomass consumed per day	$\mu = 0.2$
Fraction of biomass consumed on arrival	$\theta = 0.65$
Maximum amount of biomass for consumption from tradition	$\tau = 2$
Energy expenditure per day	$\kappa = 1$
Daily growth of biomass	$\eta = 0.001$

affecting site selection that emphasize exploration for a high quality habitat and/or returning to a patch that they are familiar with (i.e., have visited in the previous season). These traits, when passed down to offspring, are subjected to possible random mutation. If the inherited preference of an individual enables higher reproductive success, the numerical value or weight of the genes will eventually be selected for and evolve through the population. These values are used in conjunction with their knowledge of the available food ($\beta_{t,j}$) as well as the

goose's memory of the patch ($\hat{\phi}_i$, more consecutive visits increases efficiency and is therefore beneficial). The memory of a location provides an individual with an expectation for their chances at finding available vegetation, which may not be the case in reality. For this reason, the term for tradition ($\hat{\phi}_i$) used in patch scoring is slightly different than the term (ϕ_i) used for the intake equation. When a goose surveys/scores the available patches, it factors in the number of years (i) it has visited there previously. When a goose has visited a patch for at least 10 years, it is assumed that it is unlikely that the goose will fail to return. Therefore, when a goose has nine previous consecutive visits to a particular site, the tradition term ($\hat{\phi}_i$) will reflect a scoring that is equivalent to a patch of maximum biomass density (a value of 1, because $\nu = 9$ and $\tau = 2$, see equation $\hat{\phi}_i$ in Table 2). The score will reflect the overall expected quality of a patch to the goose and is utilized in determining the best move by selecting the patch with the greatest overall score. The score is calculated by summing up the attributes of tradition, biomass, and reproductive success that each goose expects for each patch as shown in Table 2.

When a goose first arrives on the staging area, the scoring equation includes a term (ρ_s) to determine which island the goose will choose. At this point, each goose (except yearlings, which follow their parents) will survey all the patches on all the islands, not just those on the island where the goose will remain for the duration of the given season. Geese store a value for each island, which serves to indicate prior reproductive success. The value increments if the island enabled a goose to successfully acquire sufficient energy reserves to meet the reproductive threshold, or decrements otherwise. This is an important term in an individual's expected payoff because it suggests that adequate resources have been available previously, which therefore may enforce a decision to return, or conversely, it has the potential to diminish from future prospects.

After selecting an island and patch, the geese will take food according to the intake equation and update their energy reserves once a day. Following this daily update, all geese will decide, according to their present condition, whether to stay on their current patch, find a new patch, or leave the staging area to breed. These basic decision rules enable each goose to consistently optimize its fitness by maximizing energy reserves to ensure survival and promote reproductive success.

TABLE 2. The scoring equation and parameters based on the influences of tradition and biomass, as well as previous reproductive success (used only in initial island selection each year).

Equations and parameters	Value
Score	$S_{i,j,s,t} = (\sigma_{\text{trad}} \phi_i) \lambda_1$ $+ (\sigma_{\text{explore}} \beta_{t,j}) \lambda_2 + \rho_s \lambda_3$
Expected benefit due to tradition	$\hat{\phi}_i = \hat{\tau} \left(\frac{i}{i+\hat{\nu}} \right)$
Biomass	$\beta_{t,j} = \beta_{t-1,j} - I_{t-1,i,j} + \eta$
Genetic value, predisposition toward influence of tradition	$\sigma_{\text{trad}} = 50$ (base value)
Genetic value, predisposition toward exploration	$\sigma_{\text{explore}} = 50$ (base value)
Previous reproductive success count	$\rho_s = 0$ (base value)
Measure of influence of tradition	$\lambda_1 = 0.5$
Measure of influence per biomass	$\lambda_2 = 0.5$
Measure of influence of prior reproductive success	$\lambda_3 = 0.3$
Consecutive yearly returns for a substantial effect of tradition	$\hat{\nu} = 9$
Maximum effect of tradition	$\hat{\tau} = 2$
Day	$i = 1, 2, \dots, 21$
Number of years at a patch	i
Patch/cell	j
Island	s

2.3 Validation. The model was run repeatedly with varying parameters to monitor and account for the range of possible behaviors. The patch scoring process and the intake equations were the priority in testing the model for appropriate results. The final equations and parameter values were determined when the model produced a stable population whose dynamics were consistent with those of the natural system. As mentioned previously, it was not the aim of this project to build an exact replica of a specific biological system; rather, the goal

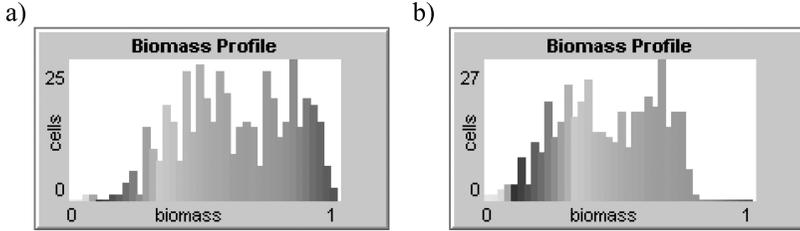


FIGURE 3. Frequency distribution of patches with available biomass (0 to 1). Part (a) describes the profile of the main island, and part (b) describes the alternate island. The coloration helps the graphical user interface (GUI) visually indicate the density of biomass at each patch.

was to create a realistic ecosystem where foraging behavior could be examined at a basic level. From a general perspective, it can be shown that the model can provide pragmatic conclusions of overall trends in strategic foraging for systems that retain an affinity toward site faithfulness. To this extent, pattern-oriented analysis provides validation of the model system through verification that the model can reproduce the patterns that it was designed to address by identifying and testing hypotheses about how individuals behave (Railsback [2001]). Because the fundamental focus of this study is to model the evolution of traditional foraging strategies, the ability of the model to represent patterns of traditional behavior and the factors that primarily influence the behavior have been observed with properly calibrated model procedures and parameters (as discussed in the following section).

2.4 Parameterization. Default values and controlled settings that were found to realistically simulate the system were maintained throughout the experimentation. The size and structure of the environment, as well as the global limits and weights for the geese, were kept constant. The spatial landscape is composed of two distinct islands where the geese choose to forage. The “main” island (where the initial geese traditionally go) maintains a cell count of 429 patches with a distribution of patches following the biomass profile shown in Figure 3a. The alternate island consists of 399 patches with a mean biomass that is reduced by 0.2% or 20% from that of the distribution of the main island (Figure 3b).

An initial population of 15 geese was chosen to allow for sufficient growth and stability (under optimal conditions). The ages of these individuals are normally distributed with a mean of 7 and standard deviation of 1. Because these agents have nothing inherited and lack previous experience, the model results are not meaningful until the population has adequate time to develop. The default values are set at 50 for both the tradition and exploration influence genes, and are tracked temporally. These values are initially set equal in order to balance the scoring equation (along with the other parameters) so that there is no innate preference in site selection for the first generation, causing initial decisions to be based solely on the available vegetation and consecutive visitation (without predisposition for one or the other). Subsequent generations will deviate from these base values as mutation (random floating point values from -1 to 1 that are added to the values) affects the genetic transmission from parent to offspring. Because the genetic values impact site selection, which inevitably influence survival and reproductive success, an evolutionary trend will tend to favor values that produce a stable population (Kanarek [2006]).

To this extent, the reproductive threshold becomes an important component of the emergent behavior through natural selection. For scenarios with an undisturbed environment and where habitat removal was simulated, this threshold was set at 70 units of energy, as a minimum amount of energetic reserves found to be attainable from a goose that is either able, within a season, to forage on patches with at least 80% vegetative density with no prior visitation, or a goose that has returned to the same patch of at least 60% biomass for 3 consecutive years. This numerically determined reproductive threshold maintains a small, competitive population with a tendency for site faithfulness, as suggested by the empirical evidence that the chance of reproductive success is increased after returning to the same sites in spring for at least 3 years (Black et al. [2006]).

The measures of influence in the patch scoring equation were also determined through rigorous calibration as they serve to keep the factors of site selection within a reasonable balance of each other. Referring back to the patch scoring equation, the model was run with each combination of global scalars from 0 to 1, incremented by 0.1. From these simulations, it was determined that the resultant behavior was not skewed toward one strategy or another at values where $\lambda_1 = 0.5$

(influence of tradition), $\lambda_2 = 0.5$ (influence of exploration), and $\lambda_3 = 0.3$ (influence of reproductive success). These terms allow the geese to take into account all relevant information within the model with the necessary emphasis to influence decisions based on expected payoff. The inclusion of environmental fluctuation provides a situation that may undermine this expectation.

As previously mentioned, the geese benefit through their familiarity with a patch based on daily residence as well as yearly consecutive returns. The daily increase in the proportion of biomass consumed (α_t) was derived from empirical data (Black et al. [2006]) and applied in the context of the model, where on first arrival to a patch geese would intake a fraction, 0.65, of the available biomass (θ) at that location, with an increasing rate of nearly 0.20 (μ) per day (t). Tradition (being site faithful on a yearly basis ϕ_i) is included in the intake equation to provide an addition to the amount of food that may be acquired through an asymptotic function of consecutive returns to a specific patch. A similar term is taken into account during site selection in the scoring equation because a patch that has been previously visited is more desirable. Immediately when a goose lands on a patch, it stores the location and increments its memory of visits (i) by one; therefore to account for memory from prior visits (and not the current visit), one needs to be subtracted from (i) when using it for intake (ϕ_i) but not when surveying patches for expected payoff in the scoring equation ($\hat{\phi}_i$). The tradition function in the intake equation asymptotically approaches $\tau = 2$ and reaches half of this limit in the 4th year of consecutive visitation (when $\nu = 3$). These values were chosen carefully to provide a benefit for prior knowledge of a location and are based on empirical observation that geese who return to the same sites in spring for at least 3 years have an increased chance of reproductive success (Black et al. [2006]). The intake equation is a daily rate for the 20-day (γ) spring stopover period. When factored into the energy reserves (E_t), the intake value ($I_{t,i,j}$) is converted into energy by a multiplier $\delta = 40$, which is used to track and analyze individual fitness with respect to the reproductive threshold. After the geese update their energy reserves, the amount of biomass on a patch is reduced by the amount from the intake equation and grows back at 0.10% ($\eta = 0.001$) each day.

The temporal component of the program is the primary driving force of the model. It is subdivided into day, season (20 day stopover), and year, to ensure that the agents adhere to the schedule de rigueur. Mortality results from old age (geese will not live past 20 years of age), starvation (when an agent has no energy reserves), and other natural causes are pooled together and represented by an age-dependent mortality probability. According to the literature, there is a low survival probability for newborn geese prior to arriving at the wintering location (Pettifor et al. [2000], Black et al. [2006]). Therefore, geese less than 1 year of age are subject to 80% mortality, between 1 and 12 years geese are much more resilient and have a 5% death rate, and for those beyond age 12 there is a 20% mortality rate due to senescence. As predicted from hypotheses concerning the costs of reproduction, reproductive success has a negative effect on survival in this species (Black et al. [2006]), but for simplicity it is not modeled here.

With the turning of a year (after spring staging), the model is updated with births, deaths, and aging, which restructures the population and therefore the dominance hierarchy. When the geese arrive at the staging area, they are uniformly reduced to 15 units of energy in reserve. This assumption allows for the performance of each agent during the 3-week period to determine their subsequent success rather than confound the results with variable initial conditions. Similarly, for simplicity, the energy expenditure ($\kappa = 1$ unit per day) is equal for all individuals because it is assumed that patches on each island are reasonably close in proximity. In this regard, according to the intake equation, geese that remain site faithful for many years will reap a slight benefit even if the patch biomass is suddenly degraded because no time would have been spent exploring (essentially reducing the energy expenditure). Throughout a model simulation, geese make decisions according to their unique status, memories and disposition, and the aforementioned scoring and intake equations. Every individual in addition to the collective behavior can be tracked by the user through extensive data output.

2.5 Output. The model was built to output life histories of each individual in each simulation. The data are recorded in four separate files: daily statistics, annual statistics, lifetime summaries, and overall census reports. Individual goose identity is maintained through a

TABLE 3. Data output by file type. Daily, annual, and lifetime statistics are categorized by goose identification number and written in the end of each period.

Daily	Annual	Lifetime	Population
Year	Year	Age of death	Year
Day	Age	Year (birth and death)	Population count
Age	Island	Total reproductive success	Births
Island	Reproductive success count at island	Reproductive success for each island	Deaths
Patch coordinates	Energy reserves	Lifetime tradition count	Mean biomass of all patches
Current biomass of patch	Tradition count (sum of consecutive returns to patches)	Lifetime defection	Mean biomass for each island
Intake rate	Defection (sum of deviations from traditional patch)	Gene for tradition	
Energy reserves		Gene for exploration	

distinct value that is assigned to each goose at birth; therefore, these data can be assessed in chronological order. All of the characteristics of each individual are tracked and categorized by this method of identification. The specific information for each file type is shown in Table 3. Life histories (lifetime statistics) were generally the most useful in assessing model results.

2.6 Experiments. The aim of this model is addressed by simulating environmental fluctuation to investigate effects on traditional

foraging. Because this behavior is manifested through innate and learned decision mechanisms, experiments were designed to produce consequential response behavior. The results presented in this paper reflect the overall dynamics produced by habitat variation on this model species. Kanarek [2006] provides further experiments and analysis into the evolution of foraging strategies.

All experimental simulations use the parameters described above and listed in Tables 1 and 2 to produce the resultant model behavior. The control environment maintains the default spatial structure (described in the environment and parameterization sections). This is an unperturbed simulation that represents behavior under optimal conditions. Other experiments included some level of environmental fluctuation, where every viable patch on the main island was subjected to some variation in the normal biomass density. Such events have been observed in some of the Norwegian archipelagos that experienced large numbers of over wintering water voles that temporarily removed and destroyed grassland vegetation (Prop et al. [1998]). To simulate this type of scenario, a period of degradation or blight (i.e., removal of vegetation) was imposed over the course of 1, 5, and 10 years, all beginning at year 250 to allow for a stable population to become established. For each of these periods, the habitat quality was fully (100%) reduced at a rate according to the duration of blight. After this period, the biomass was returned to its normal density, returning with a 10% annual growth rate.

Twenty-five replicates were done for all experiment scenarios, and each simulation was set to run for 500 years. The output was examined for variability within and between the model simulations, and averaged for the graphical results. The primary aim was to observe the viability of a site-faithful population.

3. Results. The general population patterns clearly indicate dependence on the condition of the available habitat. The majority of simulations sustained steady population growth eventually showing small fluctuations about a stable equilibrium; however, extinction occasionally occurred in the worst circumstances. During periods of optimal conditions, the average population would plateau and fluctuate at near 60 individuals (Figure 4a). In trial runs where the initial population was set greater than 60, it was noted that density-dependent effects

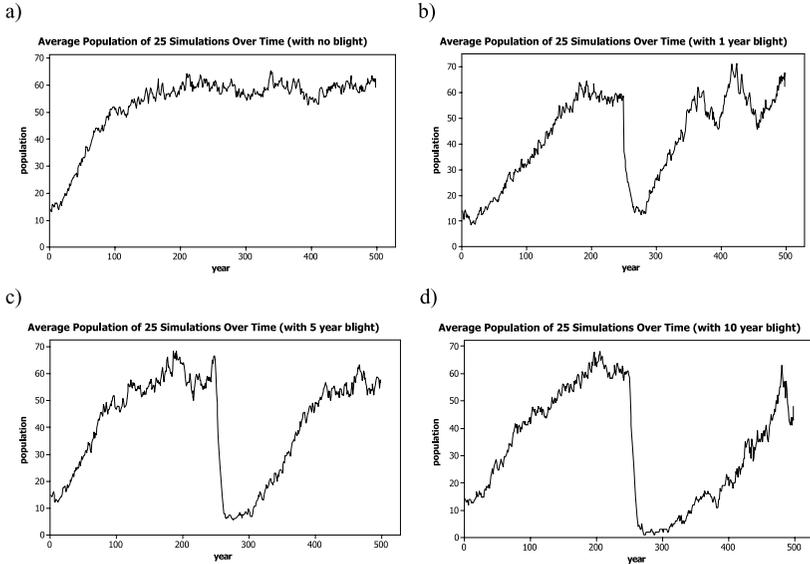


FIGURE 4. Graphs of population versus time averaged for all the model replicates for (a) optimal conditions, (b) 1 year of full biomass depletion, (c) 5 years of full depletion, and (d) 10 years of blight.

inherent to spatially explicit individual-based models caused the population to decline and hover around 60 (which can be considered a stable limit for this particular amount of available habitat). In the experiments that included any amount of environmental degradation (at year 250), the population obviously declined during the period of limited vegetation; however, in almost all cases the population recovered and grew steadily, approaching what appears to be a stable population level by the 500th year (Figures 4b–4d). The recovery progress was slow in most cases due to the specified 10% annual recovery growth rate for the biomass, in addition to some geese needing to familiarize themselves with new foraging grounds. Overall, removal of any proportion of the habitat had an initial negative effect on the equilibrium population, similar to the results of Pettifor et al. [2000], whose annual model for the Svalbard population of the barnacle goose shows that

any removal of habitat resulted in a proportional reduction in the size of the population.

In all model runs, the correlation of tradition, energy, and reproductive success was observed. As the geese aged and built experience, becoming more dominant in their competitive ability, they had more opportunity to choose among the best possible sites. This led to energy reserves that were proportional with age and therefore increases in reproductive success (measured in an increased number of offspring) (Figure 5), regardless of the foraging strategy employed (basing decisions more on tradition versus exploration). Under the circumstances, site fidelity (measured through counts of consecutive visits to specific patches) generally developed with age and experience (Figure 5 is for optimal conditions; however, similar trends possessing a wider variance between individuals at each age were found under circumstances of habitat removal). In years of severely degraded habitat, geese failed to meet the required energy reserve reproductive threshold, which resulted in very few births, in addition to a dramatic decrease in survival. The reduction in these numbers could be attributed to individuals failing to deviate from locations that lacked the necessary sustenance or not being able to occupy new sites of significantly greater quality. Further investigation into the evolution of the genetic influences by Kanarek [2006] helps to substantiate these observations.

4. Discussion. As predicted from model assumptions, the results suggest that under severe habitat deterioration, individual foraging performance is hindered, which has an effect on the acquisition of energy necessary to reproduce and in some cases to survive. As seen in the aftermath of the water vole invasion, those geese that remained on the affected archipelagos failed to breed for a number of years until the vegetation recovered (Prop and Black [1998]). It is those individuals who are capable of strategically adapting to environmental changes and consequentially optimize their fitness who eventually influence the gene pool. Some individuals, however, may benefit from maintaining their once successful routine in the hope that the environment recovers within an acceptable amount of time. By not deviating from the familiar sites, in the event of the return of suitable habitat, those geese will not have to spend time learning about their new surroundings in order to maximize intake. To this extent, empirical observation indicates

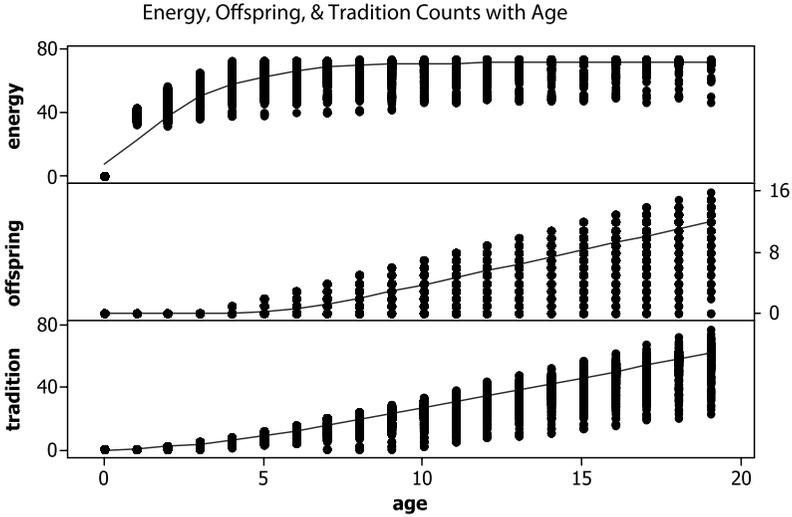


FIGURE 5. Without environmental degradation, this is the range of individuals at each age with their energy reserves, total offspring (lifetime reproductive success), and tradition (counts of consecutive returns). The locally weighted scatterplot smoother (Lowess) provides an idea of the correlative relationships (with a degree of 0.5 and 2 iterations of smoothing).

that the chance of reproductive success is increased after returning to the same sites in spring for at least 3 years (Black et al. [2006]). The model generates this effect primarily in younger geese that are unable to occupy patches that provide sufficient energy gain due to the dominance hierarchy. When an individual forages on a mediocre site or a site for the first time, they most likely will not be able to meet the energy threshold required to reproduce. The model assumptions for the benefit of practicing a traditional strategy, increased efficiency through familiarity (Figure 2), have an impact on decisions for site selection.

“The intake rate that individuals experience will depend upon a complex interaction of the quality of the chosen patch, its foraging efficiency, the amount of competition within the patch and its susceptibility to interference” (Goss-Custard and Sutherland [1997]). Our modeling approach reflects this dynamic behavior as a bottom-up

simulation of the effect on the total population of the factors that uniquely influence the fitness of each organism. The algorithm for site selection pivots on a simple weighted judgment based on learned behavior/experience, instinct/genetic preference, physical and societal status, and the resources available. If a decision propagates one's survival to a subsequent time step, its outcome inevitably contributes to the model's emergent behavior. The resultant patterns at the population level provide insight into the significance of the underlying mechanisms and thus serve to enhance our awareness of the system dynamics, animal behavior, and overall ecological progression. Based on these findings and model predictions, we can develop approaches for the management and conservation of this and similar populations.

We believe that our model realistically captures the essential biological features of foraging animals. The implications of habitat loss have been previously illustrated through population-based models in addition to those that incorporate individual variation (Sutherland and Dolman [1994], Goss-Custard et al. [1996a, 1996b], Pettifor et al. [2000]). Density dependent effects have also been extensively demonstrated (Lang et al. [1998], Rowcliffe et al. [1999]). The effects of energy on reproductive success (Prop and Black [1998], Prop et al. [2003]) and dominance (Caldow et al. [1999]) with respect to distribution, site selection, or resource accumulation have also been sufficiently documented. Our findings fit well with the conclusions of similar modeling efforts expounded in the literature. The inclusion of tradition in the context of foraging (and not just breeding) has recently been explored. Matthiopoulos et al. [2005] noted that different types of population dynamics and patterns of colonization occur, depending on the strength of site fidelity. Although it is known that site-faithful behavior can be maladaptive under temporally and spatially heterogeneous environments (Coch et al. [1993], Schmidt [2004], Matthiopoulos et al. [2005]), questions of the underlying mechanism have yet to be thoroughly considered. This model will enable further investigation into traditional foraging strategies with the genetic evolution of behavioral traits combined with other mitigating factors that influence site selection.

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