SIMULATION

SWAMP: An agent-based model for wetland and waterfowl conservation management
Matt L Miller, Kevin M Ringelman, Jeffrey C Schank and John M Eadie
SIMULATION 2014 90: 52 originally published online 26 November 2013
DOI: 10.1177/0037549713511864

SWAMP: An agent-based model for wetland and waterfowl conservation management

Matt L Miller[1,2], Kevin M Ringelman[1,3], Jeffrey C Schank[2] and John M Eadie[1]

Abstract
The management of North American waterfowl is widely recognized as a premier example of a successful conservation program. Conservation managers on the wintering grounds typically use simple estimates of food availability and population-wide cumulative energy demand to determine how many birds can be supported on a given landscape. When attempting to plan for future needs due to land reallocation, climate change, and other large-scale environmental changes, simple bioenergetic models may not capture important impacts on individual behavior, such as changes in metabolic costs due to increased travel-time and reduced food accessibility leading to non-linear declines in forager success. We describe the development of an agent-based model of foraging waterfowl that uses explicit individual behavior to generate more detailed and potentially more accurate insights into the impact of environmental changes on forager success and survival. While there is growing recognition of the potential utility of agent-based models in conservation planning, there has yet to be an attempt to formulate, validate, and communicate such a model for use as a decision support tool to guide habitat management conservation for wetlands in North America. Our model seeks to provide the foundational framework for such an effort. We predict that this model will be a useful tool for stakeholders making conservation management decisions.

1. Introduction

The primary goal of wildlife conservation and management is to provide sufficient habitat and food resources to support viable populations. In North America, waterfowl (family Anatidae; ducks and geese) are widely recognized as a premier example of a successful conservation program, as habitat conservation and harvest regulations have helped maintain populations for decades.[1] While there are sophisticated population-dynamics models for determining harvest quotas,[2] the explicit relationship between waterfowl population health and the quantity and quality of habitat is less well-known, especially in winter habitats. In the face of expanding human populations, urbanization, and climate change, there is a critical need to develop predictive models that explicitly link waterfowl habitat with waterfowl population dynamics.

Waterfowl managers are charged with maintaining sustainable populations of waterfowl. On wintering grounds, it is generally assumed that the amount of food available on the landscape is the limiting factor for populations.[3]

Thus, wildlife managers in these areas often focus on how environmental changes affect the amount of food available to foraging waterfowl. This is not a straightforward problem: human activity can affect success in contradictory ways, with commercial agriculture such as rice cultivation increasing food availability but diverting water away from natural wetlands and dedicated public refuges providing both increased habitat but also increased disturbance from hunters and bird-watchers. Increasing agricultural and residential development has raised concerns for the future of waterfowl and wetland conservation and has created a

[1]Department of Wildlife, Fish, and Conservation Biology, University of California, USA
[2]Psychology Department, University of California, USA
[3]Department of Entomology & Wildlife Ecology, University of Delaware, USA

Corresponding author:
Matt L Miller, Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, USA.
Email: hzmiller@ucdavis.edu

need for methods that allow conservation managers and other stakeholders to predict the effects of environmental changes on waterfowl populations. In this paper, we make the argument that new computational tools are required in the face of a changing environment and describe our development of a program that meets the emerging needs of conservation managers.

2. Waterfowl ecology and management

Currently, most of the tools used to predict conservation management outcomes rely on a standard bioenergetic approach that takes the average individual daily metabolic use for a species and multiplies it by the target population for that species; all of the species' requirements are then added together, and this is subtracted from the gross food calories available on the landscape (adjusted for spoilage and minimum accessible food density). If the net result is positive (supply exceeds demand), it is assumed that the modeled landscape can support the target population of waterfowl. These models, giving the number of ducks supported for a given number of days, are often referred to as duck-energy-day (DED) models.[3]

There are limitations to DED models, however. DED models are not spatially explicit, and thus do not account for changes in metabolic costs due to structural changes in the landscape. For instance, as water supplies become restricted and wetland refuges become dispersed due to land development, and as disturbance pressure (for example, hunting and bird-watching) becomes spatially concentrated, waterfowl may fly further, resulting in underestimates of daily energy expenditure (DEE). On the other hand, this pressure may cause waterfowl to roost in areas that were previously undesirable but more central to food resources; this could offset or even exceed any increases, possibly resulting in overestimates of DEE. DED models also do not estimate waterfowl body condition at the end of a season (which affects their ability to successfully migrate and breed) or time-budget impacts due to changes in food resource exploitation. Agent-based models, as spatially explicit, more behavior-driven, individual-based systems, are well-suited to providing such information.

Early in the development of spatial-depletion foraging models (reviewed by Sutherland[4]), explicit individual-level modeling was avoided due to the cost of computing resources needed for calculating the metabolic and behavioral outcomes of thousands of waterfowl. As computing power increased, some attempts were made to simulate foraging by considering smaller flocks within a population (see, for example, Thorn[5]). Within the past few years, computing power and available agent-based-modeling libraries have improved in speed and efficiency so that it is now possible to model realistically sized populations

with reasonable approximations of biologically plausible behavior on relatively inexpensive computers.

The convergence of affordable computing power with concerns about the accuracy of existing conservation-planning tools motivated us to develop an individual-level, agent-based model for waterfowl management planning. Indeed, as ecologists seek to more fully understand the linkages between individual-level processes and system-level patterns, the use of agent-based models in ecology has grown exponentially in the last decade.[6] Several agent-based models for other groups of animals have been developed (e.g., MORPH[7], a foraging modeling system applied to coastal birds foraging in estuarine environments;[8] Pettifor et al.'s model of migratory geese;[9] and EPICURE, a theoretical model of foraging with applications to human behaviour;[10] see review by McLane et al.[11]). These earlier models made advances on several fronts, and helped forge strong links between agent-based modeling (ABM), field ecology, and wildlife conservation. They set the stage, conceptually, for a move away from population-based management (focusing only on mean values of population metrics, such as average abundance, average survival, average habitat conditions, etc.) to a more realistic attempt to capture dynamics based on variation among individuals in their response over space and over time (individual-based ecology[6]).

There are now growing numbers of examples of agent-based models intended for applied use as conservation management tools (e.g., Ecolecon[12] for forestry management; ALMaSS[13] for management of animals in temperate European environments; coyote conservation management;[14] management strategies for coastal marine environments;[15] and several models that address human impacts on the landscape itself[16–18]). The utility of agent-based simulation tools in conservation management support is clearly being recognized. However, many of these management support tools are designed in such a way that they are limited to a single place and a single management concern.[19–24] Efforts to develop agent-based simulation models that can be applied to broader conservation planning decisions at a landscape scale are remarkably few.

The need for such an approach is particularly critical for wetland and waterfowl conservation planning, with the loss of over 50% of all wetlands in North America, and increasing encroachment by urbanization, oil and mineral development, agriculture, and water use. The release of the 2012 North American Waterfowl Management Plan[1] challenged managers to directly relate actions on the land, in terms of habitat loss or improvements, to changes in continental waterfowl population dynamics. This is a daunting task that lacks a clear modeling or decision support framework. We present here the first version of an agent-based simulation model to provide such a framework. Our approach is not without precedent – Mathevet and colleagues developed a management tool for

waterfowl conservation as impacted by farming and hunting practices in Southern France.[25] However, their model suffers the same limitations as other bioenergetic models in relying on a spatially located DED model (i.e., they did not model duck energetics behaviorally). We are unaware of any applications that have been developed for conservation management of North American waterfowl via water- and land-use planning that explicitly models waterfowl bioenergetics as emergent from spatial behavior.

In reviewing the state-of-the-art of simulation modeling in natural resources, and specifically in wetland conservation, we concluded that a new system, synthesizing these past accomplishments and written in a modern, fast language, could be implemented allowing complete flexibility as to the types of foragers and landscapes that could be modeled. Other desirable features of such a model include prediction of breeding and migration success, ability to incorporate spatially and temporally variable anthropogenic effects (e.g., hunting disturbance) and integration of Geographic Information System (GIS) data from other conservation stakeholders, such as water management agencies. In this paper, we describe the initial results of developing this system, which we refer to as *SWAMP* (Spatially explicit Waterbird Agent-based Model Program). We do not claim to advance the state-of-the-art in modeling and simulation per se; rather, the novelty of our study lies in the application of ABM to wetland and waterbird conservation and in a new way. We advance the state of the art by taking a well-established and accepted methodology and develop a simulation model to provide a unique application of wide-ranging continental significance.

3. Model objectives

Our overarching goal in creating SWAMP was to realistically model individual waterfowl foraging behavior on the wintering grounds. Waterfowl wintering in the Central Valley of California forage primarily on moist soil seeds found in natural and managed wetlands and on waste grain rice in flooded agricultural fields. These food plants are grown in the summer, the seeds fall off during the fall, and the land is flooded during the winter; thus, there is no regrowth of food resources during the wintering period, only depletion. Wintering waterfowl typically spend most of the day on large, managed refuges, often in non-hunted sanctuaries, then disperse from the refuge at night to forage in nearby moist soil and rice fields. We designed our model to approximate this biological system; individual waterfowl agents disperse from a central refuge at dusk and forage in discrete patches of moist soil seeds and flooded rice, and then return to the refuge at dawn. Waterfowl agents expend energy doing various activities and gain food energy from foraging, with the capacity to store any surplus as fat and metabolize lipid reserves when in energy deficit.

SWAMP development began by identifying specific objectives for the computational model satisfying the broad goals discussed above, followed by identifying which of these objectives could be met in the first version. Early in the process of discussing realistic behavioral decision models, we decided to develop the first version of SWAMP as a simpler version of the final model to ensure that the basic model could produce realistic outcomes and behaviors. Table 1 shows long-term objectives for SWAMP with the current version's realization of those objectives.

Goals implemented in the current version were considered necessary for ensuring realistic behaviors and outputs, determining if outcomes suggested differences between agent-based models and DED models, and developing an extensible substructure for future versions. Items deferred for the next version were considered to be necessary for a completely realized version of SWAMP that could be used for management planning. Those items deferred for future versions encompass improvements to our basic management tool to develop a more comprehensive system that might be useful in continent-wide planning for waterfowl and as a platform for modeling foragers of all types.

In this initial version, we set six targets for realistic behaviors and outputs that were selected to ensure both correct model function and reasonable biological output, given empirical data:

1. DEEs within the range observed in empirical data;
2. foragers able to survive for the season given a landscape approximating current ecological conditions in part of California's Central Valley and a realistic population;
3. foragers disperse to landscape foraging patches;
4. food resources depleted from patches throughout the season;
5. metabolic costs increase as the season progresses; and
6. foragers able to maintain body condition under conditions of abundant food availability, but not under conditions of severely reduced foraging habitat availability.

DEE, the ability to support foragers for a season, and the ability to maintain good body condition were evaluated quantitatively. We estimated DEE would fall between 170 and 280 kcal per day, the target being in the upper half of this estimate (that is, 225–280 kcal per day).[26] The number of days until the average forager could no longer meet its DEE with the food it could consume is referred to as *days to deficit* (DTD); a season was considered to be 150 days. Thus, if DTD was ≥ 150, individuals in the population could maintain good body condition through a season; if DTD was < 150, individuals in the population could not

Table 1. Spatially explicit Waterbird Agent-based Model Program (SWAMP) objectives and first version realization.

Ultimate objective	Realization in first version
1. Landscape-scale populations of foragers, > 1 million at a time	Local populations (~100,000 foragers); scaled to Butte Sink basin populations
2. Multiple realistic landscape types at appropriate ecological scales	Landscape types at sub-basin size: 10 km x 10 km; scaled to Butte Sink basin area
a. Structured simulated landscapes (regular grids)	Implemented
b. Stochastic simulated landscapes (pseudo-random grids)	Implemented
c. GIS landscapes from hydrological, climatological, and other geospatial models	*Not* implemented; deferred for *next* version
3. Density-dependent resource exploitation by foragers	Implemented via Holling's disc equation
4. Realistic forager metabolism	Implemented at time-step level (pro rata for partial time steps deferred for *next* version)
a. Energy requirements emergent from behavior instead of daily average estimates	Implemented for flight and foraging behavior; non-foraging/non-flight behavior metabolism modeled as a weighted average
b. Realistic constraints on gut capacity & digestion	Implemented
c. Realistic digestive metabolism of consumed items	Approximated daily with realistic efficiency factors
d. Separate lipid and glucose energy storage	Implemented
e. Composite food composition into carbohydrates, fats, and proteins	Deferred for a *future* version
5. Foraging agent decision-making based on behavioral models	Simple decision-making implemented
a. Initiation and termination of foraging bouts	Implemented by time of day and intake constraints
b. Foraging patch selection at bout initiation	Implemented via ideal-free distribution approximation or by random selection
c. Foraging patch switching during bout	*Not* implemented; deferred for *next* version
d. Home patch selection	*Not* implemented (single home refuge); deferred for *next* version
e. Migration time initiation	*Not* implemented; deferred for *future* version
6. Foraging patch dynamics	Implemented
a. Food depletion due to forager exploitation	Implemented
b. Food availability changes due to seasonal characteristics	*Not* implemented; deferred for *next* version
c. Food availability changes due to spoilage	*Not* implemented; deferred for *next* version
d. Food availability changes due to physical factors, such as inundation	*Not* implemented; inundation deferred for *next* version, other factors in discussion
e. Composite food availability within individual patches	Implemented
f. Patch accessibility changes due to physical factors, such as inundation	*Not* implemented; deferred for *future* version;
g. Patch desirability modifications due to human disturbance	*Not* implemented; deferred for *next* version;
7. Output metabolic and behavioral data for population and individuals on model steps and day totals	Implemented
a. Average and cumulative energy use	Implemented
b. Average and cumulative food energy consumption	Implemented
c. Average stored lipids	Implemented
d. Average time budgets	Implemented
e. Average food patch density by environment type	Implemented
f. Cumulative food mass and energy	Implemented

maintain good body condition. Forager dispersal, patch depletion, and increasing metabolic costs were judged qualitatively.

A further goal was to determine the sensitivity of several environmental and biological parameters. In particular, we expected the landscape's proportions of forageable habitat to be sensitive, as these are the primary inputs for conservation planning and management. We also explored biological parameters to determine which were sufficiently characterized for use in prediction and which require either further empirical study or continuing variation in future simulations.

4. Model description

Grimm et al.[27,28] suggest describing agent-based models for ecology in a consistent and thorough manner, and propose a format to accomplish this goal. We follow their ODD (Overview, Design, Details) protocol in Appendix A. We provide a brief synopsis in this section.

The SWAMP model was implemented in Java and MASON,[29] a library for the development of spatially explicit, agent-based models. We selected Java and MASON for their ability to handle a large number of agents efficiently, their capacity to integrate GIS data in
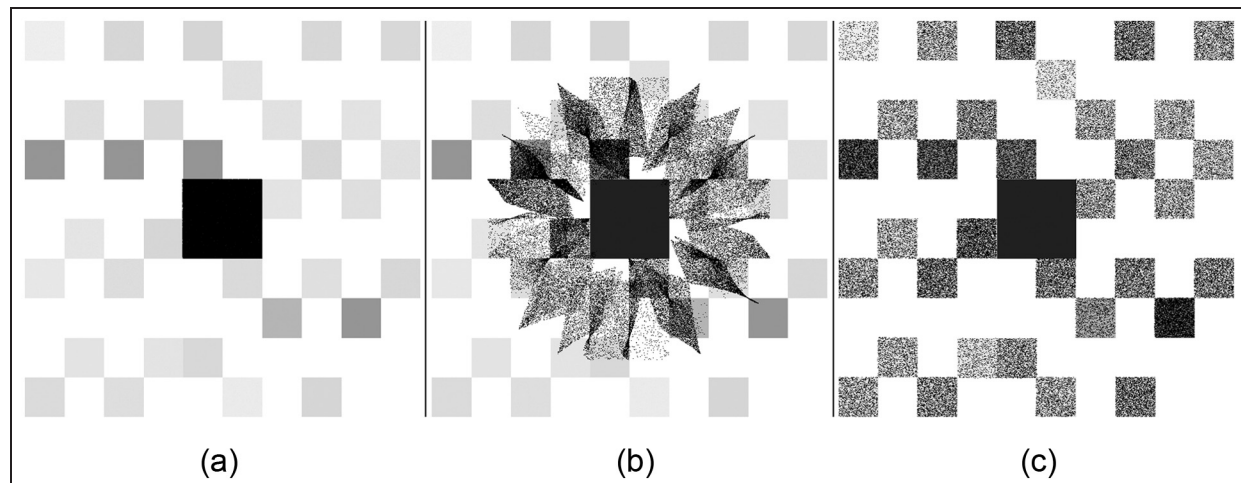
Figure 1. Graphical representation of a Spatially explicit Waterbird Agent-based Model Program (SWAMP) model during runtime. Black dots are individual birds, different shades represent different habitats, and white is unavailable habitat. In foraging habitats, a darker color represents increased food density. (a) The SWAMP model at initialization. The refuge appears black because it is almost entirely covered by roosting birds. (b) Birds begin to fly out on a foraging bout. Flocks emerge from many birds selecting the same foraging patch and departing at the same time; flock shape is an artifact of birds flying in straight lines from a rectilinear refuge to rectilinear targets. Some birds flying to foraging patches nearest the refuge have already landed within their target patches. (c) All birds have arrived at their target patches and are foraging; bird density is proportionate to food density within the patches.

future model versions, and their ability to run on different platforms. Java was selected due to its ease of cross-platform implementation; although Java's performance versus a compiled language such as C is a subject of some debate, there is evidence that Java offers competitive performance,[30] and is now being implemented in high-performance computing applications.[31] The choice to use MASON was driven by its widely recognized high performance in comparison to other modeling platforms, such as NetLogo,[32] as well as for its ability to integrate GIS and its growing support for distributed computing.

We developed code in the Eclipse integrated development environment and compiled it in Oracle's Java Standard Edition 7 compiler (version 1.7.0_03) as a runnable Java archive (JAR) file. We ran the simulation experiments described herein on a modeling farm of 12 identically configured Windows 7 machines with Intel i5 processors and 2GB of random-access memory (RAM). Model code was executed in Oracle's Java Runtime Environment SE 7 (version 1.7.0_03-b05).

4.1. Initialization

When the model started, the landscape was initialized as a 10 km by 10 km square with a 2 km by 2 km home refuge at the center. The remaining, non-refuge portion of the landscape was divided into 1 km by 1 km foraging or non-foraging patches arranged in order from top to bottom then from left to right in a regular pattern so that at each assignment the proportion of forageable patches matched the proportion specified in the setup parameters as closely as possible. Foraging patches contained food and were possible targets for foragers during foraging; non-foraging patches had no food and were never targets for foragers. Foraging patches could be either rice patches or moist soil patches; this determined what kind of food was present in the patch and the density of that food. Patches selected as foraging habitats were assigned as follows: the new patch would be a rice patch until the number of rice patches exceeded the specified rice proportion, at which point the new patch would be a moist soil patch. Figure 1(a) shows a representative landscape setup with forageable proportion at 0.35 and rice fields at 0.86 of the forageable landscape. Initial landscape values were based on reported field observations (Table 2); food items were also modeled based on reported values (Table 3). Note in Table 3 that *moist soil seed aggregate* refers to a combination of the primary seeds found in moist soils in the Central Valley represented as a weighted average. Some parameters varied for different experiments; the specific values used are discussed in Sections 5 and 6.

At the start of the simulation, 80,000 foragers were placed randomly in the refuge maintaining sufficient distance to prevent exceeding the maximum forager density within a 1 m radius. Each forager was assigned a lipid energy store from a normal distribution based on empirical data on waterfowl condition during winter in California's Central Valley.[33] Foragers began each simulation with an empty digestive tract; that is, the initial values for food eaten that day and non-lipid energy reserve were set to 0. The initial states of the foragers were based on reported values or were varied by experiment; some values not

Table 2. Initial patch parameters.

Parameter	Initial value	Units	Symbol	Source
Proportion of landscape forageable	Varied by experiment		p_F	(see text)
Proportion of forageable landscape as moist soil versus rice	Varied by experiment		p_M	(see text)
Moist soil patch food density	Drawn from normal distribution, $\mu = 58.5$, $\sigma = 6.6$	g/m^2	R_M	Naylor[34]
Rice patch food density	Drawn from normal distribution, $\mu = 33.3$, $\sigma = 2.2$	g/m^2	R_R	Eadie et al.[35]

Table 3. Initial food type parameters.

Parameter	Moist soil seed aggregate	Rice
True metabolizable energy[35] (kcal/g), ρ	3.4	3.53
Attack constant (m^2/s), α'	Varied by experiment	Varied by experiment
Handling time[4,5] (s), H_T	2.0	2.0

available in the literature were based on field observation (Table 4).

4.2. Model runtime

Flowcharts in Appendix B summarize overall model progress and individual forager behavior.

The basic agent for SWAMP is the forager. A forager has two high-level states: foraging and roosting. Foraging simulates the behavior of an animal that is hungry and motivated to acquire food, while roosting simulates the behavior of a satiated animal. In both states, the forager has a *target patch*. While roosting, this is the home refuge; while foraging, this is one of the foraging habitat patches (selection of a specific foraging patch is described below). If a forager is not on its target patch, it moves (modeling flight) in a straight line from its current location to the nearest point of the target patch; this is illustrated in Figure 1(b), which shows foragers heading from the refuge to their foraging patches at the beginning of a foraging bout. Otherwise, a forager performs the behavior for its current state as described below. At each time step, a forager expends the metabolic cost associated with its current behavior: when on its target patch, either foraging or non-foraging metabolic cost; when moving toward its target

Table 4. Initial forager parameters.

Parameter	Initial value	Units	Symbol	Source
Resting metabolic rate	0.0010643017	kcal/s	M_{Rest}	Miller & Eadie[36]
Flying metabolic rate	12.0 (m_{Fly}) $\times M_{Rest}$	kcal/s	M_{Fly}	Prange & Schmidt-Nielsen[37]; Schmidt-Nielsen[38]; King[39]
Foraging metabolic rate	Varied by experiment ($m_{For} \times M_{Rest}$)	kcal/s	M_{For}	(see text)
Non-foraging metabolic rate	Varied by experiment ($m_{NF} \times M_{Rest}$)	kcal/s	M_{NF}	(see text)
Daily food intake capacity	Varied by experiment	g	I_{max}	(see text)
Maximum lipid energy store	3148.25	kcal	E_{max}	Thomas[33]
Maximum forager density in refuge	1.0	m^{-2}	D_{ref}	(field observations)
Maximum forager density in foraging patches	1.0	m^{-2}	D_{for}	(field observations)
Earliest daily foraging time	18.0		T_{start}	Cox & Afton[40]; Fleskes et al.[41]
Latest daily foraging time	6.0		T_{end}	Cox & Afton[40]; Fleskes et al.[41]
Giving-up density	5.6	g/m^2	R_{GUD}	Naylor[34]; Central Valley Joint Venture[3]
Lipid energy store	Drawn from normal distribution, $\mu = 1349.25$, $\sigma = 179.9$	kcal	E	Thomas[33]
Mass of food eaten during current/most recent foraging bout	0.0	g	I	(see text)
Food energy consumed during current/most recent foraging bout	0.0	kcal	e	(see text)

patch, the flying metabolic cost. The final section, below, describes metabolic accounting details.

Patches are containers for food; foragers deplete patches' resources as they eat. Patches also provide food density (in mass per area) metrics to foragers currently exploiting their resources.

4.2.1. Foraging state. A forager is in its foraging state while actively seeking food to meet its metabolic demands. A contiguous time period during which the forager seeks food is a foraging bout. A foraging bout begins when the time of day is equal to or greater than the foraging start time (T_{start}) provided that the foraging end time (T_{end}) for the previous bout has already passed. A foraging bout can continue until T_{end}. A bout can also end earlier than T_{end} based upon its foraging success if one of two conditions are satisfied: (1) foragers have a daily food intake capacity (I_{max}) that limits the mass of food they can eat in one foraging bout; thus, if the forager's intake meets or exceeds I_{max} at any time step during a bout, the foraging bout ends; (2) foragers have a maximum lipid storage capacity (E_{max}) that limits the amount of food energy they can store; if the food energy taken in during a bout meets or exceeds the energy required to bring a forager's lipid reserves to E_{max}, the foraging bout ends.

While the forager is actively foraging, it consumes food from its current foraging patch at a rate that is dependent on the density of food available on that patch. SWAMP uses a type II functional response described by Holling's disc equation[42] in the simulations reported herein:

$$\frac{i}{t} = \frac{\alpha' R}{1 + \alpha' R H_T}, \tag{1}$$

in which i is amount of food eaten, t is elapsed time, α' is attack constant, R is the density of food in the patch, and H_T is handling time for a unit of food items. In this equation, attack constant is a measurement of search efficiency, expressed in area per time (m^2/s). Handling time (s) indicates the amount of time the unit of food must be manipulated by the forager after it is found. Elapsed time (s) is the length of the model time step; that is, the time interval over which food acquisition is occurring. The result is that foragers acquire food at a rate proportional to the available density of food items, modified by search and handling efficiency. Holling's disc equation has been frequently used to model waterfowl foraging on wetland grains[43–47] and other items. Holling's equation (1) is rearranged for the purposes of simulation as

$$i = \frac{\alpha' R t}{1 + \alpha' R H_T}. \tag{2}$$

The food consumed is immediately removed from the patch and is added to the forager's accounting system for

mass eaten during the bout (to effect I_{max}) and for energy taken in (to effect E_{max} and to provide non-lipid energy reserves; see below for metabolic details). Movement cost is included in the metabolic cost of foraging. If a patch's food density falls below a forager's giving up density due to forager exploitation, foragers continue utilizing the patch until the normal end of the foraging bout; however, such patches cannot be selected for the next bout. Competition between foragers is indirect: depletion of food resources by one forager reduces the efficiency of subsequent foragers on that patch, since in Equation (2), i decreases as R decreases.

At the beginning of a foraging bout (see Section 4.2.2), each forager selects a new foraging patch for that bout. The selection for the upcoming bout is independent of previous selections; indeed, the same patch can be selected more than once by a forager. The probability of selecting a patch is proportional to the density of food on that patch at the beginning of the upcoming bout.[48] Figure 1(c) shows foragers dispersed in foraging patches during a foraging bout.

4.2.2. Roosting state. A forager is in a roosting state while it is doing anything other than foraging or flying from roosting areas to foraging areas. This includes resting, swimming, courtship behaviors, short flights, sleep, and other behaviors. The metabolic cost of this state is modeled as the average of the costs of these behaviors weighted by the empirically observed time budget for the behaviors.[49] Table 5 shows the values for these behaviors; foraging behavior is omitted from the total since this is modeled in the foraging state. Although the model includes the metabolic cost of movement, the coordinates of individual foragers are not changed after arriving at the refuge to increase simulation speed (see below for metabolic details).

Foragers begin the simulation in the roosting state. Roosting ends and foraging begins on the first time step at which the time of day is later than T_{start} as long as the previous foraging bout's T_{end} has passed. When roosting ends, each individual forager selects a new foraging location. Roosting begins when the foraging state ends.

4.2.3. Food energy metabolism. Foragers have two reserves of food energy: non-lipid energy reserve and lipid stores. Non-lipid energy reserve is roughly analogous to blood glucose: carbohydrate energy from food first accumulates in this reserve and metabolic demand is first supplied from this reserve without lipid-conversion cost. Lipid stores explicitly model the forager's lipid reserves, that is, body fat.

When a forager removes a given mass of food from a foraging patch, the true metabolizable energy of that food mass is immediately placed in non-lipid energy reserve. All energy acquired in this way is maintained in non-lipid

Table 5. Non-foraging metabolic rate weighted average.

Behavior	Proportion time budget[a]	Multiplier to RMR	Weighted	Multiplier source
Sleep	0.52	1.1	0.572	Wooley & Owen[50]
Swimming & rest	0.16	1.4	0.224	Wooley & Owen[50]
Courtship	0.06	2.4	0.144	Albright et al.[51]
Flying	0.05	12.5	0.625	Wooley & Owen[50]
Diving	0.00	5.1	0.000	de Leeuw[52]
Surfacing	0.00	3.5	0.000	Wooley & Owen[50]
Preening	0.00	2.1	0.000	Albright et al.[51]
Aggression	0.00	1.8	0.000	Wooley & Owen[50]
Looking	0.00	1.4	0.000	Wooley & Owen[50]
Sum	0.79		1.565	
Weighted Average			1.981	

[a]Time budgets derived from Rave and Cordes.[49] Budget does not sum to 1.0 because foraging behavior is accounted for elsewhere and thus is not included here.
RMR: resting metabolic rate.

Table 6. First-round sensitivity test general linear model (GLM), days to deficit (DTD) = $a + b_1\alpha' + b_2 I_{max} + b_3 m_{For} + b_4 m_{NF}$

	Standardized coefficient (β)	Estimate	Standard error	t value	Probability $> |t|$ (p)
(Intercept)		2.038×10^2	2.097×10^1	9.719	<0.001
α'	0.7097	1.367×10^5	4.065×10^3	33.628	<0.001
I_{max}	0.0043	1.793×10^{-2}	8.892×10^{-2}	0.202	0.840
m_{For}	−0.0447	$−1.244 \times 10^1$	6.045	−2.058	0.040
m_{NF}	−0.1592	$−4.253 \times 10^1$	5.808	−7.323	<0.001

energy reserve (subject to removal by metabolic demand) through the current foraging bout and the subsequent roosting state. At the initiation of the *next* foraging bout, before the forager flies to the selected foraging patch, all non-lipid energy reserves are moved to lipid stores with a conversion rate that models the interconversion of glucose and lipids (blood glucose is converted to lipids at 16.747 kcal/g and lipids are converted back to blood glucose at 8.995 g/kcal; thus the interconversion efficiency is 0.537).[26] The lipid store has a maximum capacity, E_{max}.

The non-lipid energy reserve satisfies metabolic demand first. If that reserve is insufficient to meet the current demand, lipid stores satisfy the remaining demand. If both of these reserves reach 0 kcal, the forager dies.

5. Sensitivity analyses

A number of parameters of interest are either poorly characterized in the literature or have reported ranges that are quite large. To determine which of these needed to be further constrained, we conducted sensitivity analyses by varying these parameters across ranges suggested in the literature and measuring the effects on DTD. We first explored α', I_{max}, and metabolism in combination. We then tested α' in combination with a reduced set of metabolic ranges, based on the previous analysis, and with foraging habitat proportions. We found our ranges for α' in Thorn;[5] I_{max} in Sugden,[53] Clark and Gentle,[54] and Miller and

Newton;[26] all metabolic figures in Prange and Schmidt-Nielsen,[37] Schmidt-Nielsen,[38] and King;[39] landscape proportions vary from baseline reported by the Central Valley Joint Venture.[3] Varied parameters were provided as independent variables in a general linear model (GLM) with DTD as the dependent variable. We performed analysis in R. Degree of sensitivity was assessed from standardized regression coefficients.[55]

In the first sensitivity analysis, we systematically varied foraging parameters α' (0.00002, 0.0001, 0.0002, 0.0005, 0.001), I_{max} (80, 100, 120), and metabolism via m_{For} (2.5, 3.0) and m_{NF} (2.0, 2.25, 2.5, 2.75); combinations of m_{For} = 2.5 with m_{NF} = 2.75 were not explored because of our a priori assumption that foraging is more costly than non-foraging activity. For each parameter combination, 10 replications were run (Table 6). The attack constant was particularly sensitive (β = 0.7097, $p < 0.001$). Both non-foraging metabolism and foraging metabolism were sensitive, although we found that non-foraging metabolism ($\beta = −0.1592$, $p < 0.001$) had a larger effect than foraging metabolism ($\beta = −0.0447$, $p = 0.0398$). Daily food intake capacity was not sensitive ($\beta = 0.0043$, $p = 0.8402$).

In the second sensitivity analysis, we systematically varied α' (0.00002, 0.0002, 0.001), p_F (0.35, 0.25, 0.15), p_R (0.86, 0.43, 0.00) and thus p_M, and metabolism (m_{For} = 2.5, m_{NF} = 2.0 and m_{For} = 3.0, m_{NF} = 2.6). We chose values for p_R to simulate the current estimate of 86% rice fields[3] as well as scenarios in which rice area was halved

Table 7. Second-round sensitivity test general linear model (GLM).

|	Standardized coefficient (β)	Estimate	Standard error	t value	Probability $> |t|$ (p)
(Intercept)		31.577	16.022	1.971	0.049
α'	0.5535	1.393×10^5	6.031×10^3	23.107	<0.001
p_F	0.2541	3.562×10^2	9.247	8.693	<0.001
p_R	-0.3077	-9.732×10^1	4.097×10^1	-10.525	<0.001
m_{For}, m_{NF}[a]	-0.1314	-2.818×10^1	5.138	-5.486	<0.001

[a]m_{For} = 2.5, m_{NF} = 2.0 coded as 0 (*low metabolism*); m_{For} = 3.0, m_{NF} = 2.6 coded as 1 (*high metabolism*)

or eliminated entirely. For each parameter combination, we ran 25 replications. For the GLM, the metabolic levels were coded as 0 for low metabolism (m_{For} = 2.5, m_{NF} = 2.0) or 1 for high metabolism (m_{For} = 3.0, m_{NF} = 2.6). All parameters were sensitive (Table 7). The attack constant remained particularly sensitive (β = 0.5535); forageable landscape proportion (β = 0.2541) and forageable rice proportion (β = -0.3077) were also sensitive, with evidence that the latter has more effect than the former; metabolic level was moderately sensitive (β = -0.1314).

These analyses revealed that the attack constant (α') was an especially important predictor of population sustainability. Unfortunately, this parameter is poorly characterized in studies of overwintering waterfowl foraging on seeds,[47] so we further explored this variable to discover its range of sensitivity in association with changes in landscape composition. We systematically varied α' between 0.000025 and 0.0004 in increments of 0.000025 on two different foraging landscapes (p_F = 0.25, 0.35) while holding other variables constant (p_M = p_R = 0.5, m_{For} = 3.0, and m_{NF} = 2.5). For all parameter combinations, we ran 25 replications. Figure 2 illustrates the results. For the attack constant, very low values (< 0.0001) lead toward a situation in which individuals are not able to meet metabolic demands for a full season (150 days); larger values of α' (> 0.00025) approach asymptotes that depend on the amount of forageable landscape.

The primary manipulation of interest in the SWAMP model is landscape composition; therefore, it was expected that landscape proportion parameters would be sensitive. This was strongly supported in the sensitivity analyses.

Metabolic rates were sensitive. Even though foraging metabolic rates are higher, non-foraging metabolic rate is more sensitive. This is because foragers typically spend more time in non-foraging behavior than in foraging, except when resources have been significantly depleted (note that under our parameters foraging time can, at most, match non-foraging time and is usually lower). Thus, we continue to vary metabolic rates as parameters at levels producing reasonable DEEs (see Section 6). Current estimates of metabolic cost from empirical studies suggest that DEE for waterfowl with similar characteristics to those modeled should fall in the range of 170–280 kcal per day.[37–39,50] Since our experiments produced DEEs in
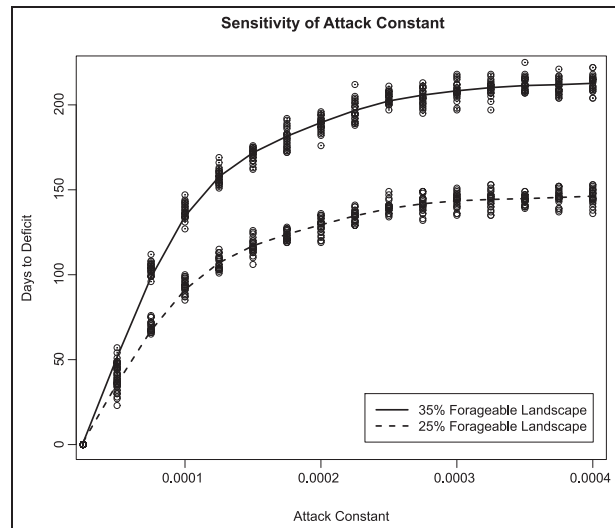
Figure 2. Effect of changing attack constant (α').

the middle of that range for m_{For} = 2.5, m_{NF} = 2.0, we selected this as a low metabolic level for further experiments; m_{For} = 3.0, m_{NF} = 2.5 produced DEEs near the top of the empirical range and was thus selected as the high metabolic level for further experiments.

Sensitivity analyses showed that I_{max} was not sensitive in our model; thus, for further experimentation it was set at 100 g per day, a value that Miller and Newton[26] suggest is reasonable and that allows foragers to accumulate an excess of food energy when environmental conditions are suitable.

6. Model validation

Validation targets were DEEs in the range of 170–280 kcal per day, DTD in excess of 150 days for simulations of current conditions, forager dispersal on foraging patches, depletion of patch food stores, increase in forager's metabolic cost throughout the season, and DTD falling below 150 days with reduced foraging habitat.

Figure 3 shows average DEE for α' = 0.0002 m^2/s, p_F = 0.35, p_R = 0.86, I_{max} = 100.0 g, and either low metabolism (m_{For} = 2.5, m_{NF} = 2.0) or high metabolism (m_{For} =

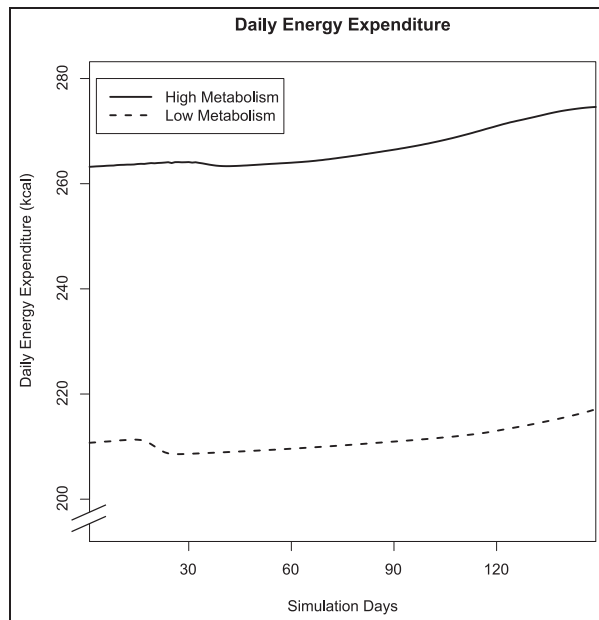**Figure 3.** Daily energy expenditure by model day (note that a portion of the *y*-axis is omitted).

Figure 4. Days to deficit (DTD) versus moist soil percentage in a 35% forageable landscape at target waterfowl populations.

3.0, m_{NF} = 2.6). The average DEE for low metabolism was 211.3 kcal per day (s.e. = 0.237) and for high metabolism was 266.8 kcal per day (s.e. = 0.218). Thus, both metabolic rates gave DEEs well within the target zone.

Figure 3 also demonstrates that metabolic demand generally increased through the season. For low metabolic rates, DEE at day 0 was 210.8 kcal per day (s.e. = 0.119) and at day 150 was 217.1 kcal per day (s.e. = 0.688), a small but clear increase. For high metabolic rates, the increase was larger: at day 0 DEE was 263.2 kcal per day (s.e. = 0.080) and at day 150 was 274.6 kcal per day (s.e. = 0.190). This meets our qualitative expectations for increasing energy use.

According to the Central Valley Joint Venture, forageable landscape (p_F) is about 35% of the Central Valley with commercial rice fields composing about 86% of that (p_R).[3] Scaling the target population to a 10 km by 10 km scale, as modeled, resulted in 80,000 foragers, the source of our initial population size. For the high metabolism rate (m_{For} = 3.0, m_{NF} = 2.6), our model suggests that target populations at current landscape metrics have a DTD of 132 (s.d. = 2); for the low metabolism rate (m_{For} = 2.5, m_{NF} = 2.0), the model suggests a DTD of 177 (s.d. = 4). Since empirical studies of Central Valley waterfowl show a slight decrease in lipid reserves late in the season,[33] and since the current waterfowl population is only 65% of the target population for the Central Valley,[3] we consider this result to closely match reasonable and realistic expectations and so provides further validation for our model. Decrease in landscape quality also imposes much shorter DTDs (see Figure 4), well below 150 days, as expected. In
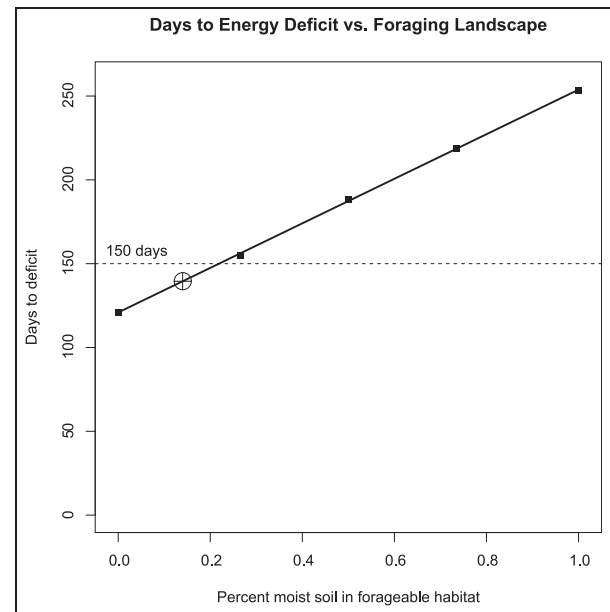
the figure, the cross-mark appears at the current percentage of moist soil habitats in the Central Valley; note that the model predicts that the current landscape may not be able to support target populations at maximum body condition.

Visual inspection of the graphical output of SWAMP confirmed that foragers were dispersing throughout the foraging habitat (see Figure 1(c)). Further confirmation came from examining patch uses statistics, which showed varying use of rice field versus moist soil across time, and average patch food density statistics, which decreased continuously throughout model time to slightly below the forager giving-up density as expected. This latter result also confirmed that foraging patches were being depleted by the foraging behavior.

A final result that we had not predicted a priori suggests that the model was producing a reasonable behavioral simulation. Flock-like structures emerged from foraging behavior (see Figure 1(b)): groups of foragers selecting the same patch flew to that patch together at the beginning of a foraging bout, and groups of foragers that finished foraging at the same time on a patch flew back to the refuge in smaller-sized groups. This appeared to resemble the foraging flock behavior observed in waterfowl.

7. Conservation applications

Having constrained sensitive parameters and validated that the model produces reasonable output under those constraints, in our final test of the model we provided SWAMP with a range of landscape modification scenarios to ensure that useful data was produced, in particular,

predictions about waterfowl survival under a number of different foraging habitat regimes (Figure 4). A full report of these results can be found elsewhere.[56]

8. Conclusion and future directions

Our development of SWAMP demonstrates that an agent-based model of individual waterfowl can be implemented to make conservation predictions and decisions. Our initial sensitivity analyses suggest that we need more accurate estimates of waterfowl metabolic rates and foraging efficiency to achieve more accurate predictions, but current estimates are yielding reasonable results. Even in this early version of SWAMP, there is ample evidence that an individual-behavioral approach provides important insights into waterfowl condition and survival: metabolic costs that emerge from behavior, estimation of body condition throughout the season, and prediction of metabolic balance. These results underscore the value of an agent-based approach in explicitly modeling the relationship between wildlife populations and environmental variables. Such spatially explicit, predictive simulation models are gaining in popularity in ecological disciplines, and we argue that they provide a powerful tool for the conservation and management of wildlife.

In the next version of SWAMP, we hope to provide more insight into the behavioral consequences of landscape changes allowing actual land management planning and forecasting. Key components for a new version include integrating GIS data to model the actual landscape, modeling changes in population due to within-season immigration, and modeling within-season changes in foraging patch availability due to water-use policy and human disturbance. We also hope to improve the sophistication of the forager model by integrating marginal-value foraging theory, including travel cost estimates in foraging patch selection, and adding reinforcement learning models for foraging strategies and memory for previously used foraging success. Of primary importance in our new model will be an improved interface; conservation management professionals will more easily be able to apply SWAMP's technology to scenario planning for their regions of responsibility.

References

1. North American Waterfowl Management Plan Committee. *North American waterfowl management plan 2012: people conserving waterfowl and wetlands*. Washington, DC: Fish and Wildlife Service; 2012.

2. Anderson MG, Caswell D, Eadie JM, et al. Report from the Joint Task Group for clarifying North American Waterfowl Management Plan population objectives and their use in harvest management. 2007.

3. Central Valley Joint Venture. *Central Valley Joint Venture implementation plan: conserving bird habitat*. Sacramento, CA: U.S. Fish and Wildlife Service, 2006.

4. Sutherland WJ. *From individual behaviour to population ecology*. New York: Oxford University Press, 1996.

5. Thorn A. Considerations in spatially explicit, individual based modeling of waterfowl foraging behaviors [thesis]. University of California, Davis, 2003.

6. Grimm V and Railsback SF. *Individual-based modeling and ecology*. Princeton, NJ: Princeton University Press, 2005.

7. Stillman RA. MORPH—an individual-based model to predict the effect of environmental change on foraging animal populations. *Ecol Model* 2008; 216: 265–276.

8. Stillman RA and Goss-Custard JD. Individual-based ecology of coastal birds. *Biol Rev Camb Philos Soc* 2010; 85: 413–434.

9. Pettifor RA, Caldow RWG, Rowcliffe JM, et al. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J Appl Ecol* 2000; 37(Supplement 1): 103–135.

10. Roberts ME and Goldstone RL. EPICURE: spatial and knowledge limitations in group foraging. *Adapt Behav* 2006; 14: 291–313.

11. McLane AJ, Semeniuk C, McDermid GJ, et al. The role of agent-based models in wildlife ecology and management. *Ecol Model* 2011; 222: 1544–1556.

12. Liu J. Ecolecon - an ecological economic-model for species conservation in complex forest landscapes. *Ecol Model* 1993; 70: 63–87.

13. Topping CJ, Hansen TS, Jensen TS, et al. ALMaSS, an agent-based model for animals in temperate European landscapes. *Ecol Model* 2003; 167: 65–82.

14. Conner MM, Ebinger MR and Knowlton FF. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecol Model* 2008; 219: 234–247.

15. McDonald AD, Little LR, Gray R, et al. An agent-based modelling approach to evaluation of multiple-use management strategies for coastal marine ecosystems. *Math Comput Simul* 2008; 78: 401–411.

16. Bennett VJ, Beard M, Zollner PA, et al. Understanding wildlife responses to human disturbance through simulation modelling: a management tool. *Ecol Complex* 2009; 6: 113–134.

17. Edwards VM and Smith S. Lessons from the application of decision-support tools in participatory management of the New Forest National Park, UK. *Environ Policy Gov* 2011; 21: 417–432.

18. Nikolic VV, Simonovic SP and Milicevic DB. Analytical support for integrated water resources management: a new method for addressing spatial and temporal variability. *Water Resour Manag* 2013; 27: 401–417.

19. An L, Linderman M, Qi J, et al. Exploring complexity in a human-environment system: an agent-based spatial model for multidisciplinary and multiscale integration. *Ann Assoc Am Geogr* 2005; 95: 54–79.

20. Dupont H, Mihoub JB, Becu N, et al. Modelling interactions between scavenger behaviour and farming practices: Impacts on scavenger population and ecosystem service efficiency. *Ecol Model* 2011; 222: 982–992.

21. Dupont H, Mihoub J-B, Bobbe S, et al. Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures. *J Appl Ecol*. 2012; 49: 404–411.

22. West AD, Stillman RA, Drewitt A, et al. WaderMORPH—a user-friendly individual-based model to advise shorebird policy and management. *Methods Ecol Evol* 2011; 2: 95–98.

23. Brady M, Sahrbacher C, Kellermann K, et al. An agent-based approach to modeling impacts of agricultural policy on land use, biodiversity and ecosystem services. *Landsc Ecol* 2012; 27: 1363–1381.

24. Chion C, Cantin G, Dionne S, et al. Spatiotemporal modelling for policy analysis: application to sustainable management of whale-watching activities. *Mar Pol* 2013; 38: 151–162.

25. Mathevet R, Bousquet F, Le Page C, et al. Agent-based simulations of interactions between duck population, farming decisions and leasing of hunting rights in the Camargue (Southern France). *Ecol Model* 2003; 165: 107–126.

26. Miller MR and Newton WE. Population energetics of northern pintails wintering in the Sacramento Valley, California. *J Wildlife Manage* 1999; 63: 1222.

27. Grimm V, Berger U, Bastiansen F, et al. A standard protocol for describing individual-based and agent-based models. *Ecol Model* 2006; 198: 115–126.

28. Grimm V, Berger U, DeAngelis DL, et al. The ODD protocol: a review and first update. *Ecol Model* 2010; 221: 2760–2768.

29. Luke S, Cioffi-Revilla C, Panait L, et al. MASON: a multiagent simulation environment. *Simulation* 2005; 81: 517–527.

30. Stein M and Geyer-Schulz A. A comparison of five programming languages in a graph clustering scenario. *J Univers Comput Sci* 2013; 19: 428–456.

31. Taboada GL, Ramos S, Expósito RR, et al. Java in the high performance computing arena: research, practice and experience. *Sci Comput Program* 2013; 78: 425–444.

32. Laclavík M, Dlugolinský Š, Šeleng M, et al. Agent-based simulation platform evaluation in the context of human behavior modeling. In: Dechesne F, Hattori H, Mors A, et al. (eds) *Advanced agent technology*. Berlin Heidelberg: Springer, 2012, pp.396–410.

33. Thomas DR. Assessment of waterfowl body condition to evaluate the effectiveness of the Central Valley Joint Venture [thesis]. University of California, Davis, 2004.

34. Naylor LW. Evaluating moist-soil seed production and management in Central Valley wetlands to determine habitat needs for waterfowl [thesis]. University of California, Davis, 1999.

35. Eadie JM, Elphick CS, Reinecke KJ, et al. Wildlife values of North American ricelands. In: Manley SW (ed.) *Conservation in ricelands of North America*. Stuttgart, AR: The Rice Foundation, 2008, pp.7–75.

36. Miller MR and Eadie JM. The allometric relationship between resting metabolic rate and body mass in wild waterfowl (Anatidae) and an application to estimation of winter habitat requirements. *Condor* 2006; 108: 166–177.

37. Prange HD and Schmidt-Nielsen K. The metabolic cost of swimming in ducks. *J Exp Biol* 1970; 53: 763–777.

38. Schmidt-Nielsen K. Locomotion: energy cost of swimming, flying, and running. *Science* 1972; 177: 222–228.

39. King JR (ed.) *Seasonal allocation of time and energy resources in birds*. Cambridge, MA: Nuttall Ornithological Club, 1974.

40. Cox RR and Afton AD. Evening flights of female Northern Pintails from a major roost site. *Condor* 1996; 98: 810–819.

41. Fleskes JP, Jarvis RL and Gilmer DS. Distribution and movements of female Northern Pintails radiotagged in San Joaquin Valley, California. *J Wildlife Manage* 2002; 66: 138.

42. Holling CS. Some characteristics of simple types of predation and parasitism. *Can Entomol* 1959; 91: 385–398.

43. Dolman PM and Sutherland WJ. Spatial patterns of depletion imposed by foraging vertebrates: theory, review and meta-analysis. *J Anim Ecol* 1997; 66: 481.

44. Fritz H, Durant D and Guillemain M. Shape and sources of variations of the functional response of wildfowl: an experiment with mallards, *Anas platyrhynchos*. *Oikos* 2001; 93: 488–496.

45. Durant D, Fritz H, Blais S, et al. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *J Anim Ecol* 2003; 72: 220–231.

46. Amano T, Ushiyama K, Fujita G, et al. Alleviating grazing damage by white-fronted geese: an optimal foraging approach. *J Appl Ecol* 2004; 41: 675–688.

47. Arzel C, Guillemain M, Gurd DB, et al. Experimental functional response and inter-individual variation in foraging rate of teal (*Anas crecca*). *Behav Process* 2007; 75: 66–71.

48. Fretwell SD and Lucas HLJ. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 1969; 19: 16–36.

49. Rave DP and Cordes CL. Time-activity budget of Northern Pintails using nonhunted rice fields in Southwest Louisiana. *J Field Ornithol* 1993; 64: 211–218.

50. Wooley JB and Owen RB. Energy costs of activity and daily energy expenditure in the Black Duck. *J Wildlife Manage* 1978; 42: 739.

51. Albright JJ, Owen RB and Corr PO. The effects of winter weather on the behavior and energy reserves of Black Ducks in Maine. *Trans Northeast Section Wildl Soc* 1983; 40: 118–128.

52. De Leeuw JJ. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in tufted ducks. *Can J Zool* 1996; 74: 2131–2142.

53. Sugden LG. Metabolizable energy of small grains for Mallards. *J Wildlife Manage* 1971; 35: 781.

54. Clark RG and Gentle GC. Estimates of grain passage time in captive mallards. *Can J Zool* 1990; 68: 2275–2279.

55. Howell DC. *Statistical methods for psychology*. 6th ed. Belmont, CA: Wadsworth, 2007.

56. Ringelman KM, Miller ML, Schank JC, et al. Conservation planning for wintering waterfowl in California: an agent-based approach. Unpublished manuscript, 2012.

Author biographies

Matt L Miller is a doctoral student in the biological psychology program at the University of California-Davis and was a researcher in the Department of Wildlife, Fish, and Conservation Biology at the University of California-Davis when this project was completed.

Kevin M Ringelman is a postdoctoral researcher for the Department of Entomology and Wildlife Ecology at the University of Delaware and was a doctoral candidate in the Department of Wildlife, Fish, and Conservation Biology at the University of California-Davis when this project was completed.

Jeffrey C Schank is a professor in the Department of Psychology at the University of California-Davis.

John M Eadie is the Dennis G. Raveling Professor of Waterfowl Biology and the chairperson of the Department of Wildlife, Fish, and Conservation Biology at the University of California-Davis.

Appendix A. Overview, Design, Details (ODD) model specification

A.1. Overview

A.1.1. Purpose. Our purpose in developing SWAMP was to produce a tool for wildlife management stakeholders to predict the effects of landscape changes on populations of foragers, specifically focused on waterfowl and other migratory birds. The current version provides validation of the general approach by comparing of metabolic measures with empirical values and determines via sensitivity analysis which biological inputs drive our results and may benefit from more accurate measurement.

A.1.2. Entities, state variables, and scale. The SWAMP model comprised three entities: foragers, patches, and an observer. Foragers were mobile and patches were stationary; the observer was a singleton instance that collected data at each time step and saved the data to a file or printed it to the screen.

A forager modeled an individual animal, specifically a waterbird approximating the dabbling ducks found in California's Central Valley during the overwintering season, closely resembling a Northern Pintail duck (*Anas acuta*). Two types of information described the forager state: fixed values, initialized and fixed at the start of the simulation (but may vary between individuals and/or simulation runs), and variables, which could change throughout the simulation. Fixed state values were flying metabolic rate (kcal per second); foraging metabolic rate

(kcal per second); non-foraging metabolic rate (kcal per second), which includes an omnibus, weighted average of all activities other than foraging and inter-patch flight; the maximum mass the forager could eat in one foraging bout (grams); the maximum number of calories the forager could store in lipid reserves (kcal); the food types the forager would eat; the maximum density of foragers tolerated in the refuge (per square meter), the maximum density of foragers tolerated in foraging habitats (per square meter); the rule the forager uses to begin foraging; the rule the forager uses to pick a foraging patch; the rule the forager uses to end foraging; the earliest time a time-based forager would start foraging (numeric time on a 24-hour clock); the latest time a time-based forager would stop foraging (numeric time on a 24-hour clock); and the food density below which a forager will no longer consider a patch eligible for foraging (grams per square meter). Variable values were location in Cartesian coordinates (meters); heading from due east (radians); the activity the forager was performing (foraging or roosting), which modeled the general motivational state in which different behaviors could be performed; the behavior the forager was engaged in (eating, distance flight, non-foraging) to satisfy its activity-determined goal; the forager's amount of lipid energy stores (kcal); the mass the forager had eaten on its latest foraging bout (grams); the food energy the forager had eaten on its latest foraging bout (kcal); and whether or not the forager was still alive.

Patches modeled different locations in the environment, either the home refuge, a forageable patch with a moist soil environment and foods, or a forageable patch with a rice field environment and food. In this version of SWAMP, patches were rectangular, axis-aligned areas with a uniform distribution of food across each individual patch. Fixed values were upper left corner in Cartesian coordinates (meters), lower right corner (meters), and patch type (refuge, moist soil foraging, rice foraging). The only variable value was amount of food contained on the patch (grams). The home refuge patch, 2 km by 2 km, was located in the center of the environment. Foraging patches, 1 km by 1 km, were uniformly spaced around the home refuge.

The observer served only to collect data and aggregate statistics across single days. Fixed values were the type of output (file or screen), the format (fixed-width or R formatted), and output file name. Variable values were cumulative daily measurements of gross food intake, gross metabolic demand for foragers, average time budgets for foragers, daily foraging habitat proportion, and forager mortality.

Food types (in the described model, rice and moist soil seed aggregate) encapsulate information about generic food resources that may appear in patches. As such, they are generic information about an environmental constituent instead of entities per se, but they do have fixed state

variables that are necessary for replication of a simulation and thus may be considered state variables for the simulation. These are true metabolizable energy (kcal per gram), search efficiency (Holling's attack constant,[42] square meters per second), and time required to handle a unit of food (seconds). Since only one forager type was modeled, each food type only had one value for each of these, but SWAMP allows different forager types to use different values.

A.1.3. Process overview and scheduling. After the model initialization, time moves forward in discrete steps of fixed size; in the analyses described herein, these steps simulate 15-minute increments, but SWAMP allows specification of time-step size to any real value. At each time step, foragers are shuffled into random order; the foragers perform their current action (non-foraging behaviors, flying to or from foraging habitats, or foraging) for the time step sequentially in the random order produced by shuffling. Note that at each time step, each forager also decides whether or not it will change action during that time step; this is performed at the beginning of the forager's turn. Patches did not step; as each forager interacted with a patch and ate food, the patch updated its amount of food. Thus, if two foragers were on the same patch, the one that foraged second during a time step would observe a lower food density due to the previous forager's depletion; note that the order of the foragers within the same patch could change during a foraging bout due to shuffling order at each step. The observer stepped last on each time step, after all of the foragers completed their turns.

A.2. Design concepts

A.2.1. Basic principles. The current version of SWAMP is based on simple foraging principles. When a foraging bout begins, foragers distribute themselves at random onto foraging patches in proportion to food density.[48] Foragers then eat food from the patch, acquiring resources at a rate dependent on food density within the patch, that is, as a type II functional response using Holling's disc equation.[42] Foraging continued until the forager reached one of three limits: it foraged a mass of food equal to its maximum daily intake limit, it foraged so many calories that it met its maximum lipid reserve, or it reached the time of day beyond which it would no longer forage. The forager's metabolism was strictly determined by the amount of time it spent engaging in activities. Food energy was converted to lipid reserves using a rate derived from standard glucose-lipid and lipid-glucose conversion rates (blood glucose to lipids at 16.747 kcal/g, lipids to blood glucose at 8.995 g/kcal; thus conversion factor of 0.537).[26] In the experiments described, we assumed these principles were sufficient for the results achieved; code was

implemented in such a way that future versions can explore other rules for the decision to begin foraging, the decision to end foraging, functional response, patch switching within a foraging bout, and patch selection (including variations based on distance to patch).

A.2.2. Emergence. Forager time budgets (proportion of time spent foraging, time flying between foraging habitats and the refuge, and time spent in other non-foraging behaviors) emerged dynamically from changes in food availability incurred by foraging depletion. This resulted in emergent metabolic costs. The amount of food foragers could acquire from the environment also changed across model time through depletion, although generally in a predictable fashion since the number of foragers on a patch during a given foraging bout was matched to resource density. Non-linearities in depletion emerged from various constraints: early in the season, foragers' daily intake capacity truncated foraging; mid-season, foragers' lipid storage capacity had a similar effect even earlier in a bout; and, in some models, at the end of the season, patches became unavailable as they fell below the foragers' giving-up density.[56]

The difference between food energy acquired and metabolic cost, the emergent energy balance, led to the ultimate measure of interest, DTD, that is, the number of days before the foragers' metabolic costs exceeded the amount of energy they could extract from the environment.

A.2.3. Adaptation. Foragers adapted to their environment by making foraging decisions based on changes in resource availability. Amount of time spent foraging was an important adaptation: as resources became less dense, the forager spent more time acquiring the target amount of food energy for that bout up to the maximum available time for foraging. Other adaptive behaviors were matching the number of foragers on patches to the patches' food density and excluding patches below the giving-up density from eligibility. Finally, foragers would not spend energy flying out of the refuge if all of the patches in the environment had fallen below the giving-up density.

A.2.4. Objectives. In the current version of SWAMP, foragers have one simple objective: to achieve and maintain their maximum store of lipids. Thus, as long as there was food in the environment in patches above the giving-up density, every day the foragers would fly out to forage food either to maintain the lipid storage maximum or to completely fill their gut (the daily intake limit) while increasing lipid reserve toward the lipid storage maximum.

A.2.5. Learning. Foragers did not have any facility for learning.

A.2.6. Prediction. Agents do not explicitly predict any outcomes in the described model. Agent behavior embodies two implicit predictions. In proportionally matching forager density to resource density in foraging patch selection, foragers implicitly predict that their foraging success will be inversely proportional to the number of foragers sharing the patch and directly proportional to the density of food resources. In excluding patches that have food resources below the giving-up density from foraging eligibility, foragers implicitly predict that food acquisition rates from such patches will not meet the energy required to forage within them.

A.2.7. Sensing. Foragers are capable of sensing each other and all of the patches in the environment. Foragers sense each other to prevent location in a place that exceeds their maximum threshold for forager density within the radius of one meter. Foragers sense the food type and density composition of all patches in the environment, as well as the distance and heading to every patch in the environment.

A.2.8. Interaction. Foragers do not interact with one another directly. Indirectly, foragers affect the foraging rate of other foragers in the same patch by slowly depleting the available food resources. Foragers also will not locate themselves in a position where the density of foragers exceeds their maximum density threshold within one meter. The density-proportional foraging patch selection rule can also be considered an implicit interaction: it models foragers varying the number of other foragers within a patch in proportion to the food density of that patch. Foragers interact with patches by removing food mass from them while foraging. Patches have no interactions outside of those imposed on them by the foragers.

A.2.9. Stochasticity. There are three phases of stochastic processes within SWAMP: initialization, before each step, and during each step. At initialization, foragers' initial lipid stores were set from a normal distribution and foragers' initial location within the refuge came from a bivariate uniform distribution; patches' initial food density came from a normal distribution dependent on patch type (moist soil or rice field). Before each time step, the order that foragers would perform in-step actions was shuffled using a uniform distribution. During time steps in which a foraging bout began, foragers (in the order determined prior to the step) picked patches in proportion to the food densities of the eligible foraging patches.

A.2.10. Collectives. Although apparent flocks emerged from the model in the form of foragers that picked the same foraging patch for a given foraging bout, such flocks were not represented programmatically, no flock-wise statistics were collected, and no analysis was done at the flock level. Flock membership had no effect on individual foragers and did not persist beyond one foraging bout since patch selection was independent between foraging bouts.

A.2.11. Observation. The observer agent aggregated and reported data. The observer made reports at two intervals, the model time step and the model day. At the model time step the observer reported the following measures for the time step just completed: mortality, total mortality to present, total food energy remaining on the landscape (kcal), total forager metabolic demand (kcal), total food intake by foragers (kcal), average forager metabolic demand (kcal), average forager intake (kcal), average forager lipid reserve (kcal), maximum forager lipid reserve (kcal), minimum forager lipid reserve (kcal), average food density in rice field patches (grams per square meter), and average food density in moist soil patches (grams per square meter). At the end of each model day, the observer reported the following measures for the day just completed: mortality, total mortality to date, total food energy remaining on the landscape (kcal), total forager daily metabolic demand (kcal), total forager daily food intake (kcal), average forager DEE (kcal), average forager daily food intake (kcal), average forager lipid reserve (kcal), proportion of foragers using rice patches, proportion of foragers using moist soil, time budget (percent foraging, flying, and other non-foraging), and total forager metabolic demand for the previous 15 days (kcal).

For the analyses reported in this paper, we used two metrics: average forager DEE and average forager daily food intake. The difference between daily intake and daily expenditure was calculated, and the number of days on which this figure remained positive was calculated to obtain the ultimate metric of interest, DTD, that is, the number of days before the average forager expended more energy than it acquired from foraging.

A.3. Details

A.3.1. Initialization. At simulation start (time 0), Table 2 (in the main text) shows initial patch values; patches were laid out in a regularly repeating pattern on the landscape (see Figure 1, main text). Certain values varied across model runs as noted in the table; actual values for the runs are reported in Sections 5 and 6 of this paper. Note that the actual layout of foraging patches varied depending on the proportion forageable and the proportion in rice versus moist soil; patches were tiled beginning in the upper left corner, then continuing down and across at intervals to achieve the desired proportions while skipping over the refuge allotment at the center of the landscape.

At simulation start, 80,000 foragers were created. Table 4 (in the main text) shows initial forager parameters. Again, certain values varied across model runs as described in Sections 5 and 6. Note that we report metabolic rates for behaviors as multiples of the resting metabolic rate; the multiplier is indicated as *m* in the remainder of this paper. Foragers were assigned random locations within the refuge patch in such a way that no forager had forager density exceeding its maximum refuge density threshold within a one meter radius.

Table 3 (in the main text) shows initial values for food types.

Model time started on day 0, representing the beginning of the overwintering season for waterfowl in the Central Valley of California, at midnight (0.0 hours).

A.3.2. Input data. The described version of SWAMP did not have any data stream input.

A.3.3. Submodels. As noted previously, patches simply keep track of their total food mass and the observer provides output for data accumulated and reported at intervals. Thus, foragers are the only entities that implement a submodel more complex than accumulating variables and is the only system described in this section.

Foragers have two basic modes of behavior that can be thought of as modeling motivational states: foraging and non-foraging. The latter mode encompasses all of the activities that the forager engages in when it is not attempting to meet its metabolic needs by locating food and eating it. Each of these states is a submodel, since their behaviors and decision-making processes are different. The decision to switch to one of these states is made while in the other state, so initialization for a state occurs at the end of the other state; since foraging requires more initialization, we treat the non-foraging submodel first so that foraging setup is explained before the details of the foraging submodel. Following the description of these submodels, we explain the flying and the metabolism submodels, which are shared by both the non-foraging and foraging submodels.

A.3.3.1. Non-foraging submodel. The forager checks to see if it is on its refuge patch; if it is not, it must fly there, so it flies toward its refuge patch (perhaps continuing previous progress toward that goal) by moving toward the refuge's nearest point and metabolizes energy at the flying metabolic rate. If the forager is on its refuge patch, it tests to see if the current time is equal to or later than the next eligible foraging time (the start time of the next foraging bout); if it is not, it metabolizes energy at the non-foraging metabolic rate. If it is time to start foraging, the forager converts any remaining non-lipid energy reserves to lipid storage, resets the foraging bout accumulators for mass and energy eaten to 0, selects an eligible foraging patch as its target with probability proportional to food density on the patches, establishes its heading toward the selected patch, switches to foraging mode, and immediately goes on to complete the behavior mandated by the foraging submodel. If there are no eligible foraging patches because all patches are below the giving-up density, the forager sets the next eligible foraging time to the foraging start time following the next foraging end time (that is, the start of the next bout after the current one) and remains in non-foraging mode.

A.3.3.2. Foraging submodel. The forager checks to see if it is on its current target foraging patch; if it is not, it must fly there to forage by moving along its current heading toward the nearest point of the target patch at flying velocity and metabolizing energy at the flying metabolic rate. The forager then checks to see if any of the following *exit conditions* are true: the next foraging ending time has been reached or exceeded; the mass of food eaten in the current bout has met or exceeded the maximum daily food intake mass; or the food energy acquired in the current bout, if converted to lipid energy storage, would cause the lipid storage to meet or exceed the maximum lipid energy storage. If all exit conditions are false, the forager removes from the patch the amount of food specified by Holling's disc equation:[42]

$$i = \frac{\alpha' R t}{1 + \alpha' R H_t},$$ (A1)

in which *i* is the amount eaten, *α'* is attack constant (search efficiency), *R* is density of food on the patch, *t* is the length of the model time step, and H_T is handling time for food. The forager adds *i* to the current bout mass intake, *I*, and the food energy contained in *i* to the food energy for the current bout, that is:

$$e = e + i\rho.$$ (A2)

The forager then metabolizes energy at the foraging metabolic rate. If one or more of the exit conditions are true, the forager establishes its heading toward the nearest point of its refuge patch, switches its mode to non-foraging, and immediately goes on to complete the behavior mandated by the non-foraging submodel.

A.3.3.3. Flying submodel. The flying submodel describes the method by which foragers travel in the non-foraging and foraging submodels to a *target patch*, either the refuge or the selected foraging patch, respectively. Movement within a target patch is included in the metabolic costs of foraging and non-foraging behaviors, but to increase model speed, SWAMP does not change the physical location of foragers once they have arrived at a target patch. Flying is simulated by the forager moving the lesser of the distance to the furthest point along its heading within the target

patch or the product of the forager's flying speed and the model time step; that is, the forager will only fly as far as its modeled speed allows, ending at a point in the target patch. When the forager arrives inside its target patch, it determines if the forager density at its current location within a 1 meter radius is below the forager's density threshold for foraging patches. If so, the forager remains in its current location; otherwise, or if the forager's last move would have caused it to overshoot the further edge of its target patch, it moves to a random location within the patch that is below the density threshold.

A.3.3.4. Metabolism submodel. The forager uses energy on each model time step during which it is alive. Foragers have two pools of energy to satisfy their metabolic requirements: the *non-lipid energy reserve*, which is roughly analogous to blood glucose, and the *lipid energy store*, which models food energy stored in body fat. Foragers start with

a non-lipid energy reserve of 0 and an initial lipid energy store greater than 0 drawn from a normal distribution. During a foraging bout, the energy value of the food that is eaten is immediately added to the non-lipid energy reserve. Any energy that remains from the previous foraging bout's non-lipid energy reserve is converted to lipid energy storage at the beginning of the next foraging bout using a standard conversion factor (0.537; see Section A.2.1 for details). The non-lipid energy reserve supplies metabolic costs first. If the non-lipid energy reserve is insufficient to meet the metabolic costs of the current time step, the lipid energy store supplies remainder. If this is also insufficient (that is, non-lipid energy reserve and lipid energy store together would be less than or equal to zero after the current time step), the forager dies; that is, its alive state variable is set to *false*, it is removed from the model spatial field, the mortality counters are incremented, and the forager is removed from the model schedule so that it will not step again.
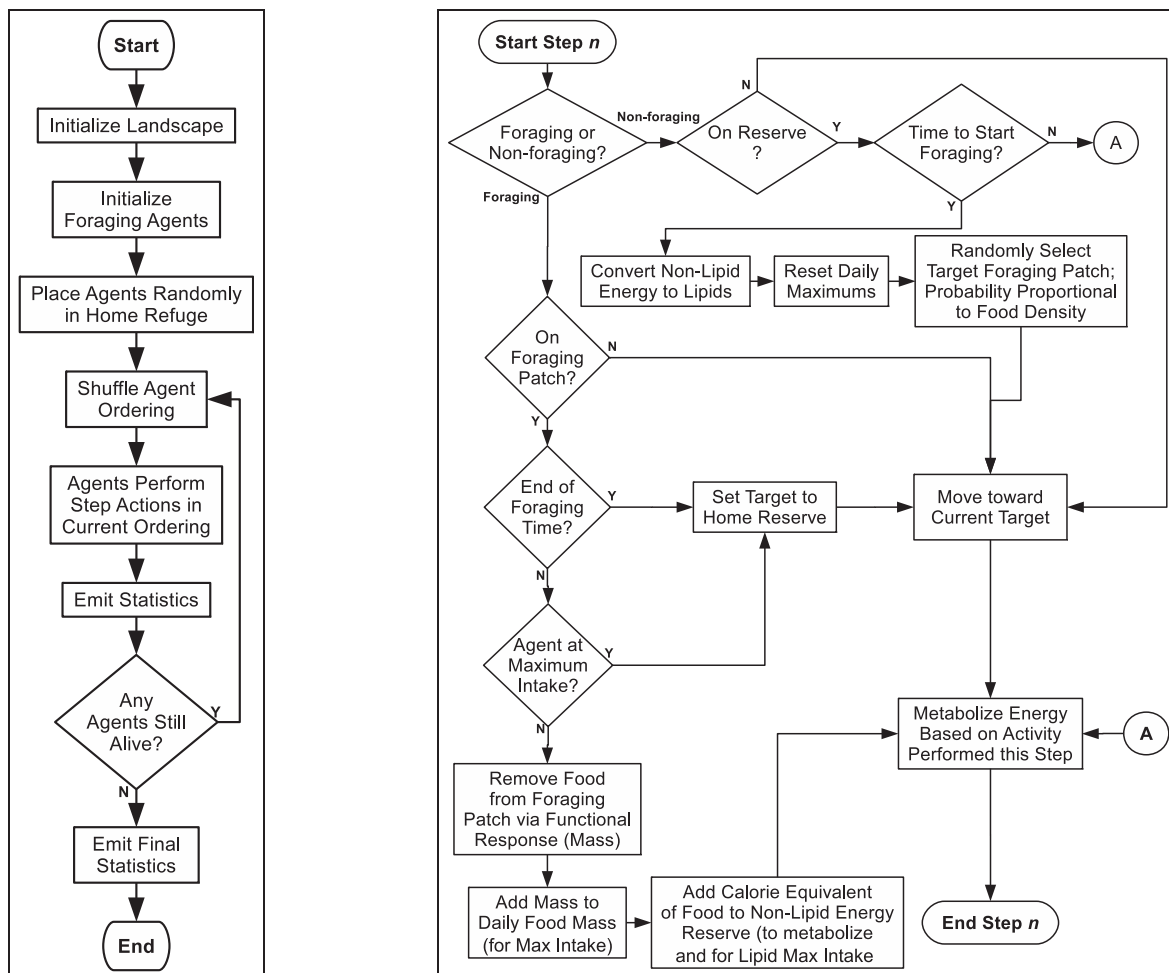
Appendix B. Forager flowcharts

Figure B1. Main program loop flowchart.

Figure B2. Agent step flowchart.