

# Energetic behavioural-strategy prioritization of Clark's nutcrackers in whitebark pine communities: An agent-based modeling approach



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## ABSTRACT

While much is known about the relationship between Clark's nutcracker and whitebark pine, information on nutcracker energetic behavioural strategies – the driving factors behind nutcracker emigration – and the impact of nutcracker behaviour on whitebark pine communities remain uncertain. To investigate nutcracker energetic behaviour, we developed a spatially explicit agent-based model (ABM) to simulate the underlying behavioural mechanisms nutcrackers are most likely to employ during foraging in the South Cascades near Mt. Rainier, Washington. The ABM is comprised of cognitive nutcracker agents possessing memory and decision-making heuristics that act to optimize energy acquisition and loss. Environmental data layers for elevation and basal area of tree species were used to represent the landscape in terms of habitat and energy resources. We employed the *evaluation* approach for an organized sequence of model development and analysis, including: data evaluation, conceptual model evaluation, implementation, verification, model output verification (calibration consisting of comparison of parameters informed by nutcracker ecology to real-world empirical values; pattern-oriented modeling – POM), model analysis (sensitivity of model to changes in parameters and processes), and model output corroboration (use of POM to compare model output to real-world patterns from empirical investigations of nutcracker ecology, independent of calibration). Simulations were conducted on alternative nutcracker behavioural-energetic mechanism strategies by assigning different fitness-maximizing goals to agents. We found that an integrated energetic requirement (IER) mechanism, which includes both the short-term and long-term energetic needs of nutcracker agents to be the best-fit scenario. Our results affirm previous research that nutcrackers are responsive to changes in their energetic environment, and that they are capable of projecting energy budgets well into the future. The development of this ABM provides a basis for future research, such as a means to assess the driving conditions necessary for nutcrackers when choosing between a resident and emigrant strategy and as a planning tool to model nutcracker responses to potential landscape changes, which may facilitate long-term WBP conservation.

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## 1. Introduction

The Clark's nutcracker (*Nucifraga columbiana*, Corvidae), which has a year-round diet of fresh and stored conifer seeds, is the primary agent for seed dispersal in whitebark pine (*Pinus albicaulis*; WBP). As a result, WBP is regarded as an *obligate* mutualist of the nutcracker (Tomback and Linhart, 1990). Although regeneration in

WBP depends on seed-caching by the bird, the nutcracker is considered a *facultative* mutualist of WBP. Nutcrackers have the ability to assess local WBP cone abundance and adjust foraging strategies to accommodate other food sources, including other *Pinus* species (Tomback and Linhart, 1990; Tomback, 1998). Nutcrackers forage on WBP seeds during the summer and autumn seasons in most years, beginning prior to cone maturation and continuing until well after seeds have ripened, which generally occurs from mid-August to late September (Tomback, 1978a; Hutchins and Lanner, 1982). Several empirical investigations pertaining to nutcracker ecology have taken place. However knowledge gaps still remain, partic-

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ularly regarding nutcracker energetic behavioural strategies, the driving factors behind nutcracker emigration, and the manner in which nutcracker behaviour will be impacted by future changes in WBP communities. We define nutcracker emigration as the leaving of previous breeding grounds at irregular intervals to over-winter in other regions.

A promising strategy for investigating the behavioural processes of nutcrackers is through the examination of energetics: more specifically, how nutcrackers evaluate their current energetic state and prioritize short- and long-term energetic returns from food resources within their environment. Substantial evidence that nutcrackers make informed decisions regarding the energetic returns of food resources exists. For example, both [Tomback \(1978b\)](#) and [Vander Wall \(1988\)](#) found that nutcrackers modified their foraging behaviour by increasing foraging intensity after seeds ripened and can be extracted more easily. These same studies reported nutcrackers switching from one pine seed resource to another in a manner that optimized foraging gains or the energetic value of seeds stored. Further, [McKinney et al. \(2009\)](#) found that the frequency of occurrence of nutcrackers in WBP communities was strongly associated with annual WBP cone production, which had a positive linear relationship with live WBP basal area and thus a negative association with WBP tree mortality and rust infection. [Barringer et al. \(2012\)](#) also found a positive relationship between the frequency of nutcracker visitation and the magnitude of WBP cone production, although they note there is some probability of nutcracker visitation even in WBP stands that contain few cones. Nutcrackers are also capable of assessing potential long-term energetic deficiencies, such as those associated with breeding or the loss of seeds to predators, and mitigating these deficiencies by storing caches of seeds for future use ([Tomback, 1978a, 1982](#)). Given sufficient cone production, nutcrackers will cache up to five times their energetic requirement in WBP seeds ([Tomback, 1982](#)), highlighting the complexity of how nutcrackers forecast their own energetic needs, and revealing how the birds may balance their energetic requirements with those of potential offspring. Together, these findings suggest that nutcrackers are capable of assessing the energetic resources available on the landscape, and subsequently making informed foraging decisions regarding the optimization of energy consumption. However, what is not known about nutcracker foraging ecology is what low-level behavioural decision-making processes are most likely undertaken while displaying this flexible behaviour. In other words, how do nutcracker prioritize energetic requirements while foraging prior to caching? Is daily energetic requirement (DER) their priority? Do they balance their DER with their long-term energetic requirement (LTER) for an integrated energetic requirement (IER) approach? Can a random movement algorithm along with an LTER assessment characterize their foraging behaviour just as well as alternatives? While it would seem most probable that an IER approach would be the most robust and realistic based on what we know about nutcracker foraging ecology, thoroughly investigating behavioural decision-making processes used by nutcrackers are an essential step, since they will have a profound impact on their habitat selection, cache-site location and movement on the landscape.

Studies of the ecological linkages between bird species and habitat have traditionally been the domain of behavioural ecology, which uses models and empirical investigations that address the decision-making processes of individual birds in a relatively straightforward manner ([Railsback and Johnson, 2011](#)). For example, [Cruz-Angón et al. \(2008\)](#) studied habitat selection by Common Bush-Tanager (*Chlorospingus ophthalmicus*) and Golden-crowned Warbler (*Basileuterus culicivorus*) in a Mexican shade coffee plantation using a multi-state capture-recapture model, whereby individual birds were captured and re-sighted probabilities calculated for monthly survival, movement, and recapture. In contrast,

in this research we attempt to integrate the behavioral and ecological complexity confronted by individual nutcrackers in terms of prioritizing energetic returns. We do so by investigating the basis for their decisions, including energetic trade-offs and interactions. The patterns that emerge are integral to comprehensively addressing how nutcrackers prioritize their energetic needs, understanding how these decisions are mediated by their environment, and projecting how these decisions might impact WBP persistence. To this end, we used an approach in the tradition of individual-based ecology called agent-based models (ABMs) ([Grimm and Railsback, 2005](#)), wherein *agents* make decisions and compete for resources in a complex, dynamic, and stochastic environment. Several investigations have examined bird foraging using an individual-based ecological approach. For example, [Amano et al. \(2006\)](#) investigated decision-making and group-foraging benefits in geese (*Anser albifrons*) populations using a spatially explicit ABM that tracked the spatial distribution and dynamics of fat deposition by each individual. As another example, [Railsback and Johnson \(2011\)](#) utilized a spatially-explicit ABM to understand and predict how the relative area and spatial arrangement of several common habitat types affect local bird densities and the reduction of coffee berry borer (*Hypothenemus hampei*) infestation rates by birds. These studies highlight the utility of ABMs for modeling bird foraging behaviour and provide a backdrop against which we can build a model that incorporates the behavioural and ecological complexity of nutcracker energetics and space use.

We developed a spatially-explicit ABM to simulate summer nutcracker decision-making in the South Cascades, Washington, for the purpose of investigating their behavioural-energetic prioritization. The model was used to run simulations designed to provide insight into individual nutcracker decisions, and is designed to provide a logical behavioural mechanism platform that is rooted in state-based individual nutcracker energetics. Our objective is to determine which energetic behavioural strategy mechanism, i.e., Daily Energetic Requirement (Mechanism 1), Integrated Energetic Requirement (Mechanism 2), or Random (Mechanism 3) takes priority when it comes to nutcracker decision-making prior to caching. Using an ABM for this study is advantageous, since it allows us to capture the actions and interactions of individuals and their decisions in a realistic, dynamic environment, investigate hypothetical scenarios that bolster our understanding of the interplay in the ecosystem, and test the system to establish its level of robustness and sensitivity ([Grimm and Railsback, 2005](#)).

## 2. The model

The model was constructed using Netlogo v. 5.0.4 ([Wilensky, 1999](#)). We selected Netlogo for a number of reasons, including its ability to incorporate mobile agents acting concurrently across a grid space with behaviour dominated by local interactions over short time periods, its powerful programming language and extensive documentation, and its open-source software and large user community ([Railsback et al., 2006](#)). The overview, design concepts, and details (ODD) protocol was utilized here to standardize the descriptions of our model and make it more understandable and complete, as suggested by [Grimm et al. \(2010\)](#).

### 2.1. Purpose

The model simulates the movement and behaviour of Clark's nutcrackers in an energetic landscape representing the South Cascades, Washington, with the purpose of creating stochastic agents that reflect the behaviour and life-history of individual nutcrackers in a real-world context, informed by real-world landscape and evaluated with empirical data. Our detailed ABM design facilitates the

exploration of the influence of local individual energetic decision-making and movements on a range of population-level behaviours. The model aims to facilitate the corroboration of likely nutcracker energetic prioritization in scenarios that maintain spatial distribution and abundance of energetic resources, while altering slightly the individual behaviours of the nutcracker agents and comparing the model output with real-world patterns.

## 2.2. Entities, state variables and scales

In this model, nutcrackers are represented as a cognitive family unit agent of five nutcrackers, capable of assessing their internal state, environment and memory for the purposes of balancing their daily energetic need vs. their long-term reproductive energetic needs through the summer (mid-July to mid-August). An agent representative of a family unit of five is appropriate, since nutcrackers commonly have clutches of two to three eggs (Bent, 1946) and since nutcracker fledglings have an exceptionally long period of parental care compared to other passerines. Nutcrackers fledge in April and May (Tomback, 1998); however, they depend on their parents for food resources until mid-July to late August (13–14 weeks old) since their diet comprises seeds from caches made the previous fall and unripe pine seeds that require energy investment to acquire and offer less reward than ripe pine seeds (Vander Wall, 1988; Vander Wall and Hutchins, 1983).

Model architecture comprised a grid of 62,500 square cells (herein referred to as *patches*), each representing 3.24 ha and summing to a contiguous 2025 km<sup>2</sup> (45 km × 45 km). Models of basal area for WBP and ponderosa pine (*pinus ponderosa*; PP) derived through satellite imagery and analysis by the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) group were used to inform spatial distribution and abundance of available energy on the landscape. The datasets produced by LEMMA are described in detail in Ohmann and Gregory (2002). Each agent, representing family units of five nutcrackers, occupies a single patch within the grid at any one time. Each agent has: a unique identifier, a daily energetic requirement, a long-term energetic requirement, an energetic gain from WBP, a basal metabolic rate (amount of energy expended while at rest in a neutrally temperate environment; BMR), energetic costs for activities, a current energy level, speed, weight, a reference memory (i.e. long-term spatial distribution of patches and their remembered energy levels), and an episodic memory (i.e. short-term energy from patches observed while cruising over large distances) and location. The model includes nutcracker predator agents who appear in randomly-derived locations at randomly-derived times.

The environment, which influences how nutcracker agents make decisions, is defined by energetic parameters that capture the total energy available at each patch: determined by the species of pine present (WBP or PP) and the basal area of that species within the patch. Patches are characterized with three attributes: WBP energy, PP energy, and elevation. A nutcracker agent's reference memory initially consists of all the collective patches that contain energy levels greater than zero at the time of initialization. Reference memory is updated as new patches are visited. A nutcracker agent's episodic memory consists of all the collective patches that were visited during the last cruise. We define a cruise as a long range movement between patches whereby a nutcracker agent assesses the long-term energetic viability of the study area. Episodic memory is updated after every cruise. The foraging decisions of individual nutcracker agents are made on the basis of the energy level of each patch, along with their current energetic state, daily and long-term energy needs.

Three model designs were used to test the impact of energetic prioritization behaviour: the probable model that includes both short- and long-term energy balance prioritization and evaluation

in an integrated approach, the alternative model that only includes the prioritization and evaluation of short-term energy balance and a random/LTER model that includes only long-term energetic evaluation and whereby nutcracker agents moved randomly on the landscape. The model runs for 30 days (July 15–August 15, when pine energetic resources are ripening) with a time step of five minutes. A five-minute temporal resolution is fine enough to account for individual behaviours integral to the model without being too fine as to dramatically increase model processing times.

## 2.3. Process overview and scheduling

The process overview with major elements is displayed in Fig. 1. The process is performed for each nutcracker agent at random for every five-minute time step until the simulation is complete (i.e., 30 days have passed). There are eight major sub-models: *Behaviour Space*, *Setup*, *Go*, *Pre-Behavioural Mechanism*, *DER is Priority*, *IER is Priority*, *Random/LTER*, and *Post-Simulation Processing*.

The ABM utilizes the *Behaviour Space* within Netlogo to vary several global variables, which enables efficient calibration and repeated simulation runs. Once behavior space variables are set (Table 1) the model enters the *Setup* sub-model, where state variables and parameters are initialized. From *Setup*, the model enters the *Go* sub-model, which after every tick (5 min in real time) evaluates the number of ticks (time passed), then enters the *Pre-Behavioural Mechanism* sub-model, where initial questions regarding predation, internal energy, and time of day are made. After all decisions in the first sub-model are made, the model enters one of three subsequent sub-models, depending on the value of the *mechanism* behavior space variable (*DER*, *IER* or *Random/LTER*). Questions within these sub-models pertain to the current energetic state of the nutcracker agent, the energetic composition of its current patch, the status of the random cruise timer, the status of local and global patches to provide short-term energy, the status of the study area to provide long-term energy, and the decision to emigrate, depending on the sub-model entered. State variables are updated *asynchronously* (as soon as the value is calculated in the particular behaviour mechanism sub-model) with *patch-energy* and *patch-elevation* output to file (Table 1). Once the behavioural mechanism sub-model is complete, the model re-enters the *Go* sub-model and the process is repeated. After the simulation is complete, the model enters the *Post-Simulation Processing* sub-model where the values of several variables are output, including *time-spent-whitebark*, *time-spent-ponderosa*, *time-spent-other*, *median-all-net-energy*, and *num-emigrated*. As an option, the software can also export the location of nutcracker agents at each time step in the simulation.

## 2.4. Design concepts

### 2.4.1. Basic principles

Clark's nutcrackers display a flexible foraging ecology, altering their foraging intensity, prey choice, and geographic location to match the energetic resources available on the landscape (Vander Wall, 1988). The underlying premise of this model is to mimic this flexibility in foraging behaviour under the assumption that an individual nutcracker's internal energetic state will influence how it perceives its environment and therefore influence its decision-making process, i.e. its life history and behaviour is energy state-dependent. A thorough discussion on state-dependent life-history decision-making when it comes to individuals in a population can be found in Houston and McNamara (1992). A state-dependent behavioural approach is common when using ABMs to mimic the life history of animals on a landscape. For example, Semeniuk et al. (2012) also used this approach to investigate behavioural-ecological strategies of woodland caribou (*Rangifer*

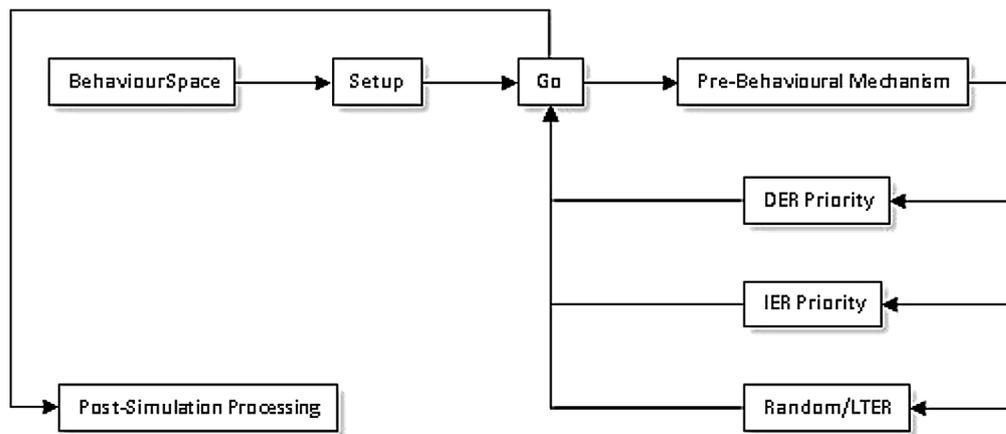


Fig. 1. Process overview for nutcracker ABM.

Table 1

Global and agent-scale variables used to initialize the model and used as output for evaluation.

Variable	Scale	Updated	Output	Description
num-nutcrackers	Global	Behaviour Space	Post-Simulation Processing	The number of nutcracker agents that are placed randomly on the landscape at the start of the simulation.
mechanism	Global	Behaviour Space	Post-Simulation Processing	One of three values ( <i>DER</i> , <i>IER</i> or <i>Random/LTER</i> ), specifying the behavioural mechanism sub-model entered once the <i>Pre-Behavioural Mechanism</i> sub-model is complete.
squirrel-reduction	Global	Behaviour Space	Post-Simulation Processing	The percentage reduction of cone abundance from squirrel predation initiated at the beginning of the simulation.
cruise-frequency	Global	Behaviour Space	Post-Simulation Processing	The frequency, in ticks, with which a nutcracker agent performs a random cruise.
predation-frequency	Global	Behaviour Space	Post-Simulation Processing	The frequency, in ticks, with which a predator appears on the landscape in a random location.
export-agent-locations?	Global	Behaviour Space	Post-Simulation Processing	If true, nutcracker locations will be exported in the <i>Post-Simulation Processing</i> sub-model
time-spent-whitebark	Global	Behavioural Mechanism	Post-Simulation Processing	The total cumulative time spent by all nutcracker agents in WBP patches.
time-spent-ponderosa	Global	Behavioural Mechanism	Post-Simulation Processing	The total cumulative time spent by all nutcracker agents in PP patches.
time-spent-other	Global	Behavioural Mechanism	Post-Simulation Processing	The total cumulative time spent by all nutcracker agents in non-WBP and non-PP patches.
median-all-net-energy	Global	Behavioural Mechanism	Post-Simulation Processing	The median net energy intake for all nutcracker agents.
num-emigrated	Global	Behavioural Mechanism	Post-Simulation Processing	The total number of nutcracker agents that emigrated.
patch-energy	Agent	Behavioural Mechanism	Post-Simulation Processing	The total energy available at the current patch.
patch-elevation	Agent	Behavioural Mechanism	Post-Simulation Processing	The elevation at the current patch.

*tarandus*) in Alberta, Canada using agent-based modeling. Through this energy state-dependent process, we seek to gain insight into the low-level behavioural decision-making processes that most likely influence nutcracker habitat-selection behavior. In other words, how do nutcracker prioritize energetic requirements while foraging? The model will provide a logical behavioural mechanism platform to move forward with rooted in state-based nutcracker energetics that will bolster our knowledge of nutcracker habitat selection and emigration behaviour and lead to information that can aid in the conservation of WBP.

#### 2.4.2. Emergence

Several model results are expected to emerge from the adaptive behaviours of individual nutcracker agents, which correspond to the following agent-scale and global scale variables outlined in Table 1: *time-spent-whitebark*, *time-spent-ponderosa*, *time-spent-other*, *median-all-net-energy*, and *num-emigrated*. These patterns are not hard-coded into the model, but rather emerge as the result of nutcracker-agent decisions and interactions. In addition, locations at each time step for each nutcracker agent also emerge, which are then post-processed to determine home ranges and probability of occurrence for various cone-abundance thresholds. Built-in model results that do not emerge are limited to the time-

dependent resting that nutcracker agents perform at night and certain behaviours that are implicit in each behavioural mechanism under investigation. This is essential in comparing the alternative behavioural mechanisms and while these behaviours are hard-coded, the model results are allowed to emerge, thus providing a means of comparison. These model results are expected to change based on energetic prioritization behaviour, therefore providing a measure of evaluation between behavioural model designs when comparing emergent model results to empirical patterns.

#### 2.4.3. Adaptation

Adaptive traits for nutcracker agents are related to the assessment of their internal energetic state, as well as the energetic state of their environment. Nutcracker agents have the ability to move to patches that maximize their energetic gain, and may ultimately leave the region if it cannot provide sufficient energetic returns. These traits seek to explicitly increase the energetic fitness of the nutcracker agent. Nutcracker agents follow different rules when making these decisions, depending on the behavioural mechanism. When DER is the priority, an evaluation of the nutcracker agent's success at meeting DER is undertaken, which if not sufficient, prompts foraging through a hierarchy of scales, whereby the energetic state of the individual is evaluated, followed by the energetic availability of the current cell, local cells and finally the entire study area. When IER is priority, the same evaluation for DER is undertaken by the nutcracker agent, but it is supplemented with an additional assessment of the region's ability to satisfy their long-term energetic needs. In addition to foraging movements, the nutcracker agent also perform *cruises* of its environment (both periodic and energetic state-based) to assess the region's ability to meet its energetic requirements. When the random/LTER behavioural mechanism is used, nutcrackers disregard their DER and focus only on whether their current patch can provide energy, traveling to other random patches if insufficient. While traveling (cruising) to random patches, they evaluate the region's ability to satisfy their long-term energetic needs.

#### 2.4.4. Objectives

Like adaptive traits, nutcracker-agent's objectives are dependent on the behavioural mechanism being tested. When DER is the priority, the nutcracker-agent's objective is to maintain its daily energetic requirement, which is the amount of energy needed to survive through the night. We assume the DER is a short-term energetic benefit. Success of this objective is measured by directly comparing the internal energy level of the nutcracker agent with its DER, which – if sufficient – enables the nutcracker agent to rest (roost). If not, the hierarchical foraging process begins and ultimately a decision on the negative outlook of the region's viability is made (emigration). When IER is the priority, the nutcracker-agent's objective is an integrated assessment of both short- and long-term energetic requirement: which is to maintain both the DER and the LTER. Success of the objective is measured in the same manner as for the DER, and through directly comparing the energy observed while cruising to the LTER. If energy availability is insufficient, then a decision on the negative outlook of the region's viability will be reached. When the random behavioural mechanism is used, the objective is simply to consume energy until a patch can no longer provide it. Success is measured by the evaluation of the energy level of the current patch, which if insufficient prompts a random movement. Once patches in memory fail to meet the DER of a nutcracker agent, then ultimately a decision on the negative outlook of the region's viability is made and the agent will emigrate.

#### 2.4.5. Learning

Adaptive traits change over time in the first two behavioural mechanism sub-models, *DER is priority* and *IER is priority*, how-

ever not in the *Random/LTER* behavioural mechanism sub-model. When DER is the priority, as a nutcracker agent forages and moves about the landscape, its reference memory is updated (how much energy is at each patch and where those patches are on the landscape in relation to the nutcracker agent). However, patches can have their energy depleted by other agents or seed predators during the simulation, and thus a nutcracker agent can return to a patch it thought was energy-rich, but not find the expected resources. Over time, nutcrackers will avoid these patches as they learn about the energy levels available at each of them. When IER is the priority, a nutcracker agent learns in the same manner as when DER is the priority, however it also learns about the region's ability to satisfy its long-term energetic

#### 2.4.6. Prediction

Prediction of future energy conditions on the landscape is not explicitly incorporated in the *DER is priority* behavioural mechanism sub-model, since the objective of nutcracker agents here is to meet their short-term (daily) energetic needs. However, emergent through this foraging process is a decision on the negative outlook of the region's viability. In terms of the *IER is priority* behavioural mechanism sub-model, however, nutcracker agents predict future conditions through the objective of meeting their long-term energetic needs. Nutcracker agents know how much energy they will need to survive the fall, winter, spring and early part of the next summer, and if their assessment of the landscape (*cruise*) cannot provide that, they decide that the region is not viable for them on a long-term basis and they emigrate. The random/LTER behavioural mechanism sub-model incorporates prediction in a similar manner to the *IER is priority* behavioural mechanism sub-model.

#### 2.4.7. Sensing

Individual extent to which nutcracker agents sense their internal energy level, the presence of other nutcracker agents, and the energy level of their current patch, neighbour patches, and all patches in the region depends on the behavioural mechanism being tested and the point in the decision flow within that sub-model. *Current patch energy* is sensed in all three behavioural mechanism sub-models near the beginning of the decision flow, while *neighbour patch energy* is sensed in both *DER is priority* and *IER is priority* sub-models, but not *Random/LTER*. Conspecifics are sensed in all three behavioural mechanism sub-models, as the number of agents on the current patch. All patches in the region are sensed (through memory) in both *IER is priority* and *Random/LTER*, but not *DER is priority*. Mechanisms by which agents obtain information are modeled explicitly.

#### 2.4.8. Interaction

Direct interaction between nutcracker agents occurs in the *DER is priority* and *IER is priority* behavioural mechanism sub-models, when an agent assesses the gain of a neighbouring patch based on two factors: the amount of energy available in that patch, and the number of competing conspecifics. Interactions are also indirect via competition for energetic resources beyond neighbouring patches. Direct interaction also occurs between predators and nutcracker agents when predators are within range. Predators within range of nutcracker agents are mobbed by the nutcracker and eliminated.

#### 2.4.9. Stochasticity

Four processes that include stochasticity are modeled. Within the *Setup* sub-model, nutcracker agents are positioned on the landscape at random locations. Within the *Go* sub-model, predators appear on the landscape depending on a random countdown timer, the frequency of which is determined by the *predation-frequency* variable, which is parameterized in *Behaviour Space*. Within the *IER is priority* behavioural mechanism sub-model, nutcracker agents

perform *spontaneous cruises*, depending on the status of a random countdown timer, the frequency of which is determined by the *cruise-frequency* variable parameterized in *Behaviour Space*. Also within the *IER is priority* behavioural mechanism sub-model, a nutcracker agent performs a *critical cruise* in a randomly-derived direction after DER is not met, and current, local and global patches could not provide energy. Within the *Random/LTER* behavioural mechanism sub-model, a nutcracker agent travels to a randomly-selected patch within its time-step flight range (21 patches) when its current patch cannot provide energy.

#### 2.4.10. Collectives

Individual nutcracker agents form aggregations of patches in two types of memory: reference and episodic. Reference memory refers to the map-like cognitive representation of the foraging environment, whereas episodic (or working) memory refers to sensory perceptual knowledge of recent experience retained for a short period of time (Olton, 1977; Bennett and Tang, 2006). Nutcrackers have remarkable spatial memory, demonstrating the ability to remember the locations of cache sites for seeds up to and surpassing 285 days (Balda and Kamil, 1989). Further, Gould et al. (2012) demonstrated that nutcrackers have the capacity for what they refer to as what-when-where (WWW) memory during cache recovery, indicating that they can recall what type of seed was deposited, when they deposited it and where exactly that deposit occurred. Nutcrackers have also displayed the usage of local landmarks when navigating a landscape, with the success of cache recovery reduced by the removal of landmarks in the interval between caching and recovering of seeds (Vander Wall, 1982). These studies highlight the importance of both reference and episodic memory for nutcracker foraging. In the context of this ABM, the reference memory of an agent comprises locations (patches) that contain profitable foraging for the agent, i.e. visited patches assessed while consuming seeds and visited patches assessed while cruising. Episodic memory comprises the comparison of the energy available at a given patch and that of the DER of the agent, as well as the comparison of the energy found while performing its last cruise compared to the LTER. An agent's episodic and reference memory is updated at every time step whenever the agent performs a cruise, consumes seeds or travels to patches stored in memory.

Nutcracker agent reference memory consists of all the collective patches that contain energy levels greater than zero at the time of initialization. Reference memory is updated as new patches are visited in the *DER is priority* sub-model and the *IER is priority* sub-model and affects nutcracker agents when they assess any global memory patches in terms of their ability to provide energy. Nutcracker agent episodic memory consists of all the collective patches that were visited during the last cruise. Episodic memory is updated after every cruise in the *IER is priority* sub-model and the *Random/LTER* sub-model and affects nutcracker agents when they assess the level of energy within those patches and compare it to their LTER.

#### 2.4.11. Observation

Several values are collected from the ABM for testing, which correspond to the following agent-scale and global-scale variables outlined in Table 1: *time-spent-whitebark*, *time-spent-ponderosa*, *time-spent-other*, *median-all-net-energy*, *num-emigrated*, *patch-energy*, and *patch-elevation*. In addition, locations for each nutcracker agent at each time step in the simulation are also collected, which can then be post-processed outside of the ABM to determine home ranges and used in conjunction with patch-energy levels to determine the probability of occurrence for various cone-abundance thresholds.

#### 2.5. Initialization

For each new run, the model cleared and reset all parameters, agents and environment data. Runs began with: a population of 500 nutcracker agents in random locations within the study area; a reduction of available energy at each cell of 85%, mimicking squirrel predation; cruise-frequency (for applicable behavioural mechanisms) selected stochastically within 12 h intervals; and predation frequency selected stochastically within 12 h intervals (determined through calibration; see Calibration and Evaluation section and Table 2).

Nutcracker agent weight (133.5 g) was set and determined as the average of the range of weights from juveniles to adults (106 g–160 g) and is used in determining energetic requirements (Tomback, 1998). Energetic requirement on a daily basis was set and calculated using previous empirical research. Tomback (1982) determined energetic requirements for nutcrackers based on basal metabolic rate (BMR) in the nutcracker thermos-neutral zone (20–30 °C). Summer-tested birds have a mean of 11.38 W/kg for minimum energetic needs and 15.98 W/kg for maximum energetic needs. Assuming that the average nutcracker in a family group will weigh approximately 133.5 g, it was determined that an agent in this model will require a minimum of 690.91 kJ each day to survive ( $0.1335 \text{ kg} * 11.38 * 10^{-3} \text{ kJ/s/kg} * 86,400 \text{ s}$ , multiplied by 5 birds) and a maximum of 921.59 kJ each day. This range was used in the ABM to correspond to the minimum and maximum thresholds that the agent strives to maintain. The BMR was also used to determine energetic costs for activity. The basal metabolic rate (BMR) of a Clark's nutcracker is 2.40 kJ per time step ( $690.91 \text{ kJ} * 300 \text{ s}/86400 \text{ s}$ ). Pravosudov and Lucas (2001) estimated the metabolic costs of different activities for food-caching passerines as follows: foraging/consumption –  $8 * \text{BMR}$  (19.20 kJ); resting –  $1.95 * \text{BMR}$  (4.68 kJ); and night resting –  $1 * \text{BMR}$  (2.40 kJ). In this ABM, costs of activity were set and an agent loses energy in accordance with these values. Cruising and flight to patches stored in memory resulted in a loss of energy at a rate of  $8 * \text{BMR}$  (19.20 kJ), since these activities would cause roughly equivalent energetic stress to nutcrackers than foraging. For predator mobbing, agents lost energy at a rate of  $10 * \text{BMR}$  (24.00 kJ), since this activity would cause more energetic stress to nutcrackers than foraging.

The energy required for winter survival (long-term energy) was set and also calculated according to previous empirical research. Extrapolating the daily energetic requirement for nutcrackers (Tomback, 1982) over summer, autumn, winter, and spring, a nutcracker agent would require a minimum of approximately 248,728 kJ to survive an entire year and a maximum of approximately 331,776 kJ. In the ABM, we set the LTER for each agent to match this 331,776 kJ, multiplied by five since it has been estimated that nutcrackers can cache up to five times their yearly energetic requirement when planning their energetic future (Tomback, 1982). Energetic gain for agents from WBP was set and determined through previous empirical research. Hutchins and Lanner (1982) observed that nutcrackers foraging on WBP seeds began with an average of 4.5 seeds/minute during mid-August. They also calculated that oven-dried WBP seeds weight on average 4.06 mg in early summer and 48.60 mg in late summer (mean 24.06 mg). In this ABM, we assumed that an agent can consume 22.5 seeds/min for WBP ( $4.5 \text{ seeds/min} * 5 \text{ nutcrackers}$ ), which corresponds to an energetic gain of 68.25 kJ per time step ( $5960 \text{ cal/g} * 24.06 \text{ mg/seed} * 22.5 \text{ seeds/min} * 5 \text{ min}$ ). Nutcracker agents do not consume PP in this model, but they incorporate the potential energy they could gain in the future from it when assessing the energy observed while cruising in the *IER is priority* and *Random/LTER* behavioural mechanism sub-models.

The distance within which a nutcracker agent will mob a predator if one is present was set to 360 m, which is equivalent to two

**Table 2**  
Parameters and values of the model.

State Variable or Parameter	Value	Source	Notes
Number of nutcracker agents	*500	This study	The scenario starts with 500 nutcracker agents
Reduction of energy on the landscape	*85%	This study	Energy is reduced uniformly by 85% to simulate squirrel predation
<b>Body Characteristics</b>			
Nutcracker agent speed	45 km/h	Vander Wall et al. (1981)	
Nutcracker agent weight	133.5g	Tomback (1998)	Range is 106–161 g
<b>Nutcracker Agent Energetics</b>			
Nutcracker agent daily energetic requirement	690.91–921.59 kJ	Tomback (1982)	0.1335 kg * 11.38 × 10 <sup>-3</sup> kJ/s/kg * 86,400 s, multiplied by 5 birds
Nutcracker agent long-term energetic requirement	1,658,880 kJ	Tomback (1982)	331,776 kJ * 5
Nutcracker agent energetic gain from WBP	68.25 kJ	Hutchins and Lanner (1982)	5960 cal/g * 24.06 mg/seed * 22.5 seeds/min * 5 min
Nutcracker BMR	2.40 kJ	Tomback (1982)	(690.91 kJ * 300 s)/86400 s, per time step
Nutcracker agent energetic cost of night rest	2.40 kJ	Pravosudov and Lucas (2001)	BMR
Nutcracker agent energetic cost of day rest	4.68 kJ	Pravosudov and Lucas (2001)	BMR * 1.95
Nutcracker agent energetic cost of consumption	19.20 kJ	Pravosudov and Lucas (2001)	BMR * 8
Nutcracker agent energetic cost of predator mobbing/crusing	24.00 kJ	Pravosudov and Lucas (2001)	BMR * 10
<b>Other ABM Parameters</b>			
Nutcracker agent predation distance	360 m	Unpublished data	2 * 180 m patch equivalent
Daily activity timer	12 h	Lorenz and Sullivan (2009)	144 ticks * 5 min/tick = 12 h; nutcrackers roost at night
Mechanism	DER, IER, Random/LTER	This study	Value is varied, depending on the behavioural mechanism tested
Random cruise timer	*12 h	This study	Nutcrackers cruise randomly once every 12 h during the day
Predation timer	*12 h	This study	Predation events occur randomly once every 12 h, day or night

\*Values were determined through calibration and sensitivity analysis.

patch distances and equals the approximate distance a nutcracker can reliably see predators (Tomback, personal communication). The daily activity timer was reset every 12 h, since nutcrackers in this region during this time of year appear to roost (rest at night) for this same time period (Lorenz and Sullivan, 2009).

## 2.6. Sub-models

### 2.6.1. Behaviour space

The *Behaviour Space* sub-model is where global variables are initialized. No other processes take place in this sub-model.

### 2.6.2. Setup

The *Setup* sub-model is where state variables and other model parameters are provided values prior to simulations taking place. In addition, elevation and WBP and PP energetic GIS layers are imported here and each patch is characterized with a value. Nutcrackers are created here and placed at random locations on the landscape. Timers for daytime countdown, predation and cruising are also initialized here.

### 2.6.3. Go

The *Go* sub-model evaluates the current time and if 30 days have not expired, permits the model to continue on to the *Pre-Behavioural Mechanism* sub-model. If 30 days have expired, the model is instead directed to the *Post-Simulation Processing* sub-model. Each model tick is equivalent to 5 min of real time.

### 2.6.4. Pre-behavioural mechanism

The decisions performed in the *Pre-Behavioural Mechanism* sub-model are outlined in Fig. 2. In this sub-model, a nutcracker agent evaluates its current energy level, and if it is below the threshold

(68.25 kJ- the amount of energy a nutcracker can obtain in a single time step), the nutcracker agent will die. If the current energy level is not below the threshold, the nutcracker agent evaluates the daytime timer. If the maximum daytime is reached, then the nutcracker agent will roost for the night. If the maximum daytime is not reached, the nutcracker agent checks to see if a predator is within range (2 patches). If so, it mobs the predator, expending energy but not dying. If no predator is within range, the model proceeds to one of three sub-models, depending on the value of the *mechanism* global variable: *DER is Priority*, *IER is Priority*, or *Random/LTER*.

### 2.6.5. DER is priority

The *DER is Priority* sub-model is the first of three behavioural mechanisms being tested as the most likely behavioural process performed by nutcrackers while foraging during the mid-summer (Fig. 3). The objective is for the nutcracker agent to prioritize meeting its DER only. First, the nutcracker agent compares its current energy level to the DER (based on the BMR). If it is met, the nutcracker agent rests and loses energy based on the BMR. Next, if the current patch can provide the DER, the agent will consume WBP seeds in its current location and will receive an energy increase (the patch will receive a corresponding decrease in energy). If the current patch does not meet the DER, the agent will then assess previously visited patches using its memory within a 3.78 km radius (equivalent to 21 patches, or the distance a nutcracker can fly over the time step) and determine if any of those can provide the DER (memory patch). If this is the case, the agent will go to the patch offering the maximum gain (a function of the amount of energy available and the amount of energy that will need to be expended travelling to that patch). If no patch in its immediate radius is acceptable, the agent will then assess all of its memory of patches

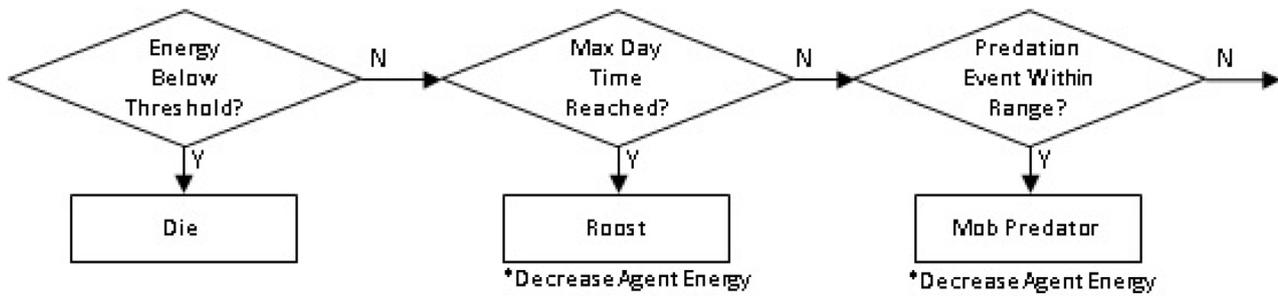


Fig. 2. Pre-behavioural mechanism sub-model.

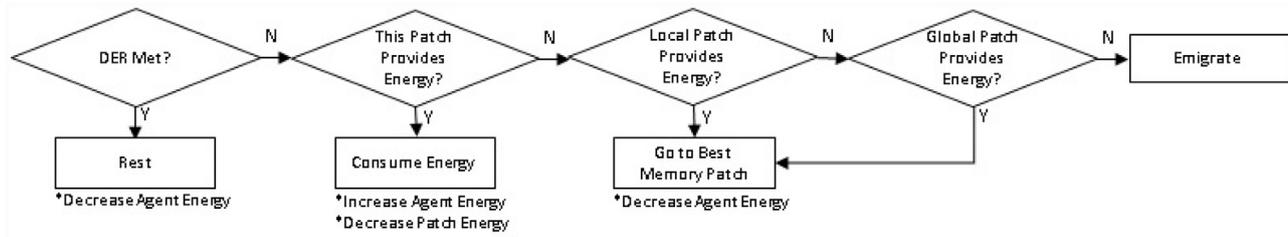


Fig. 3. DER is priority sub-model.

within the study area and proceed to the maximum gain patch using the same criteria as previous. If no patch in the study area is acceptable, the agent will select the emigrant strategy. The model then proceeds back to the *Go* sub-model, where the process repeats.

#### 2.6.6. IER is priority

The *IER is Priority* sub-model is the second of three behavioural mechanisms being tested as the most likely behavioural process performed by nutcrackers while foraging during the mid-summer (Fig. 4). The objective is for the nutcracker agent to *integrate* meeting both its DER and its LTER, based on the combination of the basal metabolic rate and the amount of energy a nutcracker will store and consume for future use. First, the nutcracker agent evaluates whether its DER is met. If this is the case, and sufficient time has not elapsed for a spontaneous cruise of its environment to occur, the agent will rest; otherwise it will cruise (choose a random heading and fly for the duration of the time step, searching and evaluating patch energy along the way). Cruising is an observed behaviour for nutcrackers that occurs in most populations during this time period and is thought to represent the assessment of cone crops (Barringer et al., 2012). If it is not the case that the DER is met, the agent evaluates its current patches ability to provide sufficient energetic resources for the time step. If this is the case, the agent will consume WBP seeds at its current location. If it is not the case, the agent will assess its memory patches in a 21 patch radius and travel to the maximum energetic gain patch available. If no local memory patch is available, the agent will then assess all its memory patches (global) and evaluate the maximum energetic gain patch available in the study area. If the agent can reach this memory patch without exhausting its current energetic resources, it will travel to the patch. If not, it will select the emigrant strategy. If no patch in the study area can provide sufficient energy, the agent will then assess its last cruise and determine whether or not the mean energetic gain (when extrapolated to the entire study area) can provide its LTER. If the agent finds that its last cruise was sufficient, the agent will perform another cruise to make sure the study area can, in fact, support its long term survival (critical cruise). If it is not the case, the agent will select the emigrant strategy. The model then proceeds back to the *Go* sub-model, where the process repeats.

#### 2.6.7. Random/LTER

The *Random/LTER* sub-model is the third of three behavioural mechanisms being tested as the most likely behavioural process performed by nutcrackers while foraging during the mid-summer (Fig. 5). First, the agent evaluates whether the current patch can provide the energy required for the duration of the time step (five minutes), based on the basal metabolic rate. If this is the case, the agent will remain at this patch and consume WBP seeds. If this is not the case, the agent will travel to a random patch within the distance it can travel over a time step (21 patches). While traveling to a random patch, the agent evaluates the amount of energy on the landscape and compares it to the LTER. If the amount of energy evaluated during this taxi does not exceed the LTER, the agent will select the emigrant strategy. The model then proceeds back to the *Go* sub-model, where the process repeats.

#### 2.6.8. Post-simulation processing

The *Post-Simulation Processing* sub-model is entered once the 30-day simulation is complete. As an option, nutcracker locations can be exported to a shapefile for post-processing. The global variables, *time-spent-whitebark*, *time-spent-ponderosa*, *time-spent-other*, *median-all-net-energy*, and *num-emigrated* are also output to a file for comparison with real-world values from empirical investigations.

### 3. Study area and input data

The study area is located near Mount Rainier in the South Cascades region of Washington, U.S.A, approximately 40 km to the west of Yakima (Fig. 6). The area comprises 2025 km<sup>2</sup> (45 km × 45 km square) of varied land covers, ranging from non-forested shrub-steppe in the eastern lowlands to wet mountain hemlock (*Tsuga mertensiana*) in the western ridges. Ponderosa pine (*Pinus ponderosa*; PP) and Douglas fir (*Pseudotsuga menziesii*) are the dominant tree species between 700 m and 1100 m of elevation, giving way to grand fir (*Abies grandis*) at elevations between 1100 m and 1500 m. WBP and mountain hemlock are dominant above 1500 m. Other tree species are present in lesser amounts, including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). The majority of the landscape in

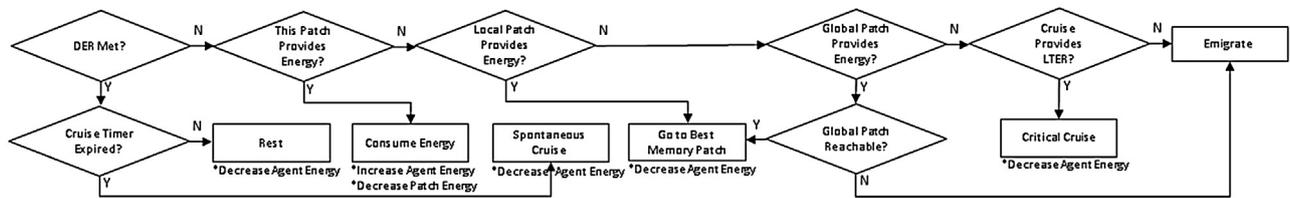


Fig. 4. IER is priority sub-model.

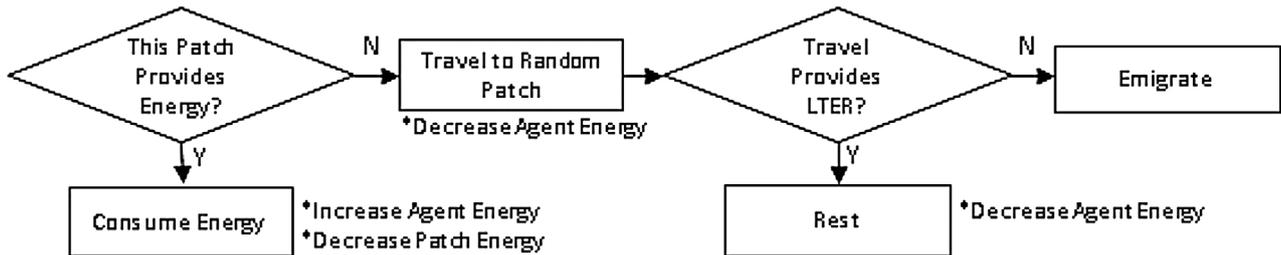


Fig. 5. Random/LTER sub-model.

the area of interest is administered by the Okanogan-Wenatchee National Forest and the Washington Department of Fish and Wildlife, and is either designated as wilderness or closed to motorized use.

The model uses three input datasets: elevation, basal area of WBP, and basal area of PP. Elevation was characterized through the use of a digital elevation model (DEM), acquired through the USGS National Elevation Dataset (Gesch et al., 2002). Datasets defining basal area of PP and WBP were selected out of the LEMMA group geodatabase as the two primary land covers and energetic resources available to nutcrackers (Ohmann and Gregory, 2002). Other energetic resources were excluded, based on the results of Lorenz and Sullivan (2009) who found that PP and WBP comprised the vast majority of foraging events for nutcrackers during the summer and autumn period in the same study area. For inclusion in the ABM, all geographic datasets were resampled to 180 × 180 m: a patch size chosen to optimize computational performance while still reflecting the biologically realistic size of a foraging patch for nutcrackers (Tomback, personal communication).

Spatial distributions of WBP and PP energetics were created, based on the following formula:

$$E_{Species} = ED \times W \times D_{Seeds} \times D_{Cones} \times A$$

where:  $E_{Species}$  is the energy available at a given patch for a given species,  $ED$  is the energetic density of a particular tree species' seed (measured in kJ/g),  $W$  is the seed weight for a given tree species (measured in grams per seed),  $D_{Seeds}$  is the density of seeds for a particular species (measured in seeds/cone),  $D_{Cones}$  is the density of cones per hectare (cones/ha), and  $A$  is the area of a patch in hectares (ha). The mean energetic density for PP is 5479 cal/g (Long, 1934) and the mean energetic density for WBP at this time of year is 5960 cal/g (Hutchins and Lanner, 1982). Krugman and Jenkinson (1974) determined the mean seed weight for PP, corresponding to 37.7 mg, and Hutchins and Lanner (1982) determined the mean seed weight for WBP during this time of year to be 24.06 mg. The mean number of seeds per cone for PP is estimated at 51 seeds (Snyder, 1993), while the mean number of seeds for WBP is estimated at 50 seeds (Hutchins and Lanner, 1982). McKinney et al. (2009) found a range of 218–2516 cones/ha for WBP, as well as a strong relationship between basal area and cone production. This relationship was also verified by Barringer et al. (2012). The relationship between basal area and cone production for PP is less established in this region, although cone production in PP has been

found to increase with tree diameter (Fowells and Schuber, 1956). Smith and Balda (1979) reported a range of 782–18,616 cones/ha for PP. For the purpose of this study, we assumed that cone production increases directly with basal area for both WBP and PP, using the ranges of cone density specified for each species. A virtual grid, at the spatial resolution of 180 m, was overlaid on the two energetic resource maps; each cell (patch) in the spatial environment was assigned an energetic score resultant from the combined energetic values of PP and WBP. WBP was made available to nutcracker agents as both a short- and long-term energetic resource, while PP was made available only as a long-term energetic resource, since nutcrackers are known to forage on the new PP cone crop beginning in late August and into the autumn months in this region (Torick, 1995).

Nutcrackers (18 in total) were radio-tracked during July and August of 2008, with their locations recorded (Lorenz, Unpublished). For a detailed description of radio-tracking methods, please refer to Lorenz and Sullivan (2009). Radio-tracked nutcracker (telemetry) data was analyzed and compared to model output for model corroboration.

#### 4. Model output verification (calibration)

Ambiguity and confusion of terminology surrounding model evaluation lead us to embrace the procedure of *evaluation* as outlined by Augusiak et al. (2014). The fourth element of this procedure entails *model output verification*, whereby model output is compared to data and patterns that guide model design and help calibrate the model. In this investigation, we employed pattern-oriented modeling (POM; Grimm et al., 1996, 2005; Grimm and Railsback, 2012) where nutcracker ecology informed model parameters and patterns from empirical investigations were directly compared model output (Table 2: Parameters and values of the model). Where no published data existed, author DFT provided expert field knowledge from extensive studies of nutcrackers in and around the Cascades (Tomback, Personal Communication). The number of nutcracker agents, energy reduction in each cell due to squirrel predation rates, nutcracker predator frequency, and nutcracker cruise frequency are parameters that required calibration. To accomplish this, the number of nutcracker agents was varied between 50 and 1000, energy reduction due to squirrel predation rates were varied between 60% and 99%, and nutcracker predator frequency and nutcracker cruise frequency was varied

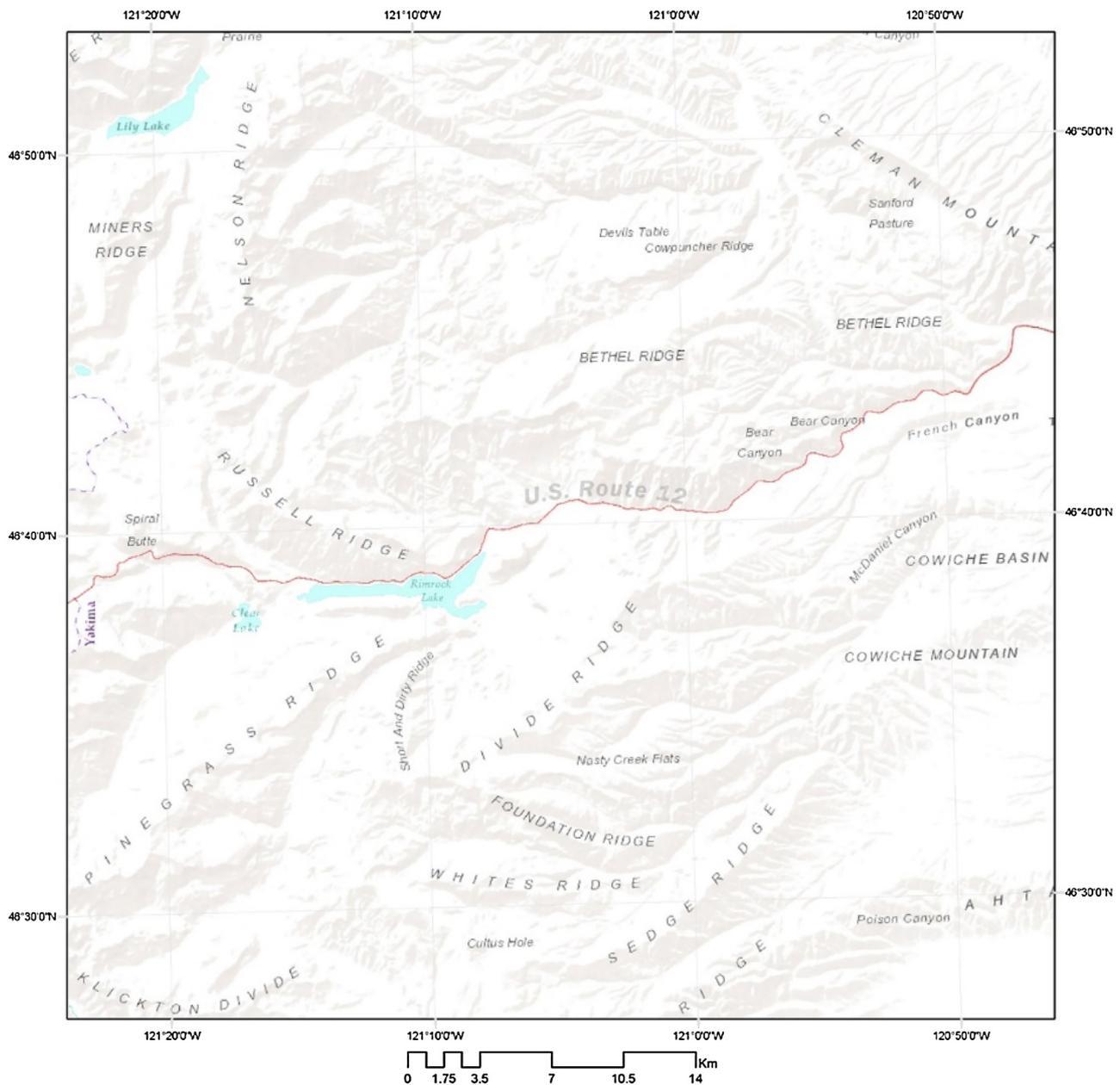


Fig. 6. Study area in the Cascades near Mount Rainer, Washington (Data: ESRI).

between once per hour to once per week. Each parameter was held constant while the others were varied through their full range. Percentage of daily energy budget for foraging, the number of nutcrackers emigrated and the number of nutcrackers that perished, along with flock sizes were monitored and compared to empirically derived values.

Extrapolating foraging times from Lorenz (2009), nutcrackers foraged for 38.29 min/h to 38.29 mins every 6 h, which equates to a range of 1.28 h every day to 7.66 h every day (10%–64% of daily activity budget). Therefore, simulations should produce percentage of daily activity budget within this range. No study of nutcracker emigration behaviour has observed complete residency during this time period (mid-late summer). Complete emigration has been observed, however only under extreme circumstances where entire cone crop failures occurred. Within the study area, estimated of cones cones/ha are far beyond cone crop failure levels, therefore

complete emigration is extremely unlikely. Further, Lorenz (2009) found that 67% of the nutcrackers that she radio tagged and followed could be defined as emigrants and 16% died for a total of 83% non-living, although this number seems high based on what we know about nutcrackers preferring a resident strategy. With all of this information taken into account, simulations should produce non-living rates between 16% and 83% (living rates 17%–84%). Vander Wall et al. (1981) found it very rare for nutcrackers to forage in flocks greater than 25 birds. Thus, no more than five nutcracker agents should not occur in the same patch at any given time. A model with 500 nutcracker agents, 85% reduction of energy due to squirrel predation rates, cruise frequency of once every 12 h, and predatory frequency of once every 12 h produced the most realistic results over all three behavioural mechanisms tested, with values matching closely to calibration patterns outlined above.

## 5. Model analysis (sensitivity)

The fifth element of the *evaluation* procedure of Augusiak et al. (2014) entails model analysis, whereby the sensitivity of the model to changes in parameters and process formulations is evaluated. We conducted a hierarchical sensitivity analysis whereby sensitivity to processes was performed through evaluation of each behavioural mechanism under investigation and the sensitivity to parameters was performed using results of simulations ran while calibrating. The model was sensitive to processes in that changing the behavioural mechanism resulted in changes nutcracker emigration and mortality, with the overall ABM being most sensitive to the processes within the *Random/LTER* behavioural mechanism. Memory was not explicitly tested for sensitivity. Through the calibration process for the number of nutcracker agents, energy reduction in each cell due to squirrel predation rates, nutcracker predator frequency, and nutcracker cruise frequency, we monitored the impact of the values of these parameters on the number of nutcracker agents that emigrated and the number of nutcracker agents that perished, enabling the evaluation of the sensitivity of emigration and mortality to population (competition) and landscape energetics. The model was most sensitive to changes in landscape energetics, although it was also sensitive to large changes in nutcracker population.

## 6. Post-processing

Once the simulations were complete, the locations exported from the model were post-processed in ArcGIS (Redlands, CA). Elevation statistics and home ranges using a minimum convex polygons (MCPs) algorithm were calculated for each nutcracker agent, with minimum, maximum, and median values determined. Elevation and MCP statistics were also calculated from real-world locations of nutcrackers through telemetry data, and were compared to model output. Patch-energy values recorded by each nutcracker at each time step were also post-processed to create frequency distributions of nutcracker visitation for energy categories (seed/cone abundance). Due to the large amount of data, visitations were normalized by occurrence of energy categories. Patterns from post-processing, along with the other global variables output from the model, were compared to data from empirical investigations.

## 7. Model output corroboration and behavioural mechanism evaluation

The sixth element of the *evaluation* procedure of Augusiak et al. (2014) entails model output corroboration, whereby model output is compared to patterns not used in model development. We conducted model output corroboration using POM and compared model output to six patterns: 1) preference for WBP; 2) nutcrackers maintained net energy; 3) preference for resident strategy; 4) cone threshold exists; 5) 100% MCP for individual nutcrackers; and 6) elevation use of all nutcrackers (Table 3). We used cumulative performance of pattern matching and absolute difference compared to real-world values to determine which behavioural mechanism best corroborated real-world patterns and thus was the most appropriate mechanism to assume moving forward. Orders of magnitude between absolute values for each behavioural mechanism were also compared to assess the degree of performance, if any. Pattern descriptions are below.

### 7.1. Pattern 1: nutcrackers display a preference for habitat where WBP is more abundant

WBP and nutcrackers have co-evolved, with selection working on each species over time, modifying from progenitors in favour of characteristics that benefit one another (Lanner, 1999). This process has facilitated a general condition whereby nutcrackers favour WBP over other food resources, and display preference for WBP habitat. Researchers have observed this phenomenon in multiple study areas, including the Sierra Nevada (Tomback, 1978b), the Bridger-Teton National Forest (Hutchins and Lanner, 1982), Glacier National Park (Maier, 2012), and the Cascades (Lorenz and Sullivan, 2009). Since WBP is more abundant, nutcracker agents should spend more than 50% of their time in WBP patches, however they should not spend 100% of their time in WBP patches, either since these studies never show complete use of WBP in time-budgets.

### 7.2. Pattern 2: nutcrackers carry little in the way of fat reserves, thus maintaining a median daily net energy balance close to zero

Nutcrackers are considered food-hoarding birds (Tomback, 1978b), hiding food in caches for extended periods of time and returning to these locations with incredible accuracy (Balda and Kamil, 1989). This evolutionary trait makes the storage of fat reserves within the bird of little value, especially over longer timer periods. In fact, Schaming (2015) found that nutcrackers tend to carry as little as 0% body fat and as much as 5% body fat. For these reasons, it seems logical to assume that nutcrackers will maintain a median daily net energy balance near zero or slightly higher than zero in order to not put on large fat reserves. Since the BMR for nutcracker agents is 690.91 kJ in this ABM, a realistic net energetic gain over the 30-day simulation would be 34.54 kJ (5%). Anything above that would not match this pattern.

### 7.3. Pattern 3: a resident strategy is a preferred strategy over an emigrant strategy for most nutcrackers

Vander Wall et al. (1981) identified that nutcrackers choose one of two strategies when it comes to foraging and geographic fidelity: resident and emigrant, based on observations of birds in northern Utah and eastern Nevada. They found it was more common for a nutcracker to choose a resident strategy over an emigrant strategy, especially in areas where multiple species of conifer seeds are available in low to moderate levels. The costs and uncertainties of emigration, combined with the potential benefits of site-related dominance and familiarity with local terrain, food resources, and predators outweigh the potential gains of emigration for most nutcrackers. Nonetheless, an emigrant strategy was found to be successful for some nutcrackers, as evidence of successful breeding exists in newly established areas with emigrant birds. Lorenz and Sullivan (2009) also witnessed both resident and emigrant strategies in nutcrackers in the Cascades, concluding that the resident strategy is the preferred strategy. Nutcracker agents should emigrate when the predicted long-term energetic returns on the landscape decline below what is required for them to survive throughout the year. Residents should exceed 50% of total agents.

### 7.4. Pattern 4: a threshold of cone density exists on the landscape, below which the probability of nutcracker occurrence drops off drastically

McKinney et al. (2009) were the first to investigate a threshold of cone abundance on the landscape, below which nutcrackers would cease to exploit WBP as an energetic resource. Their findings, conducted at three sites across the Rocky Mountains, indicate that there is a threshold below which there is a rapid decline in

**Table 3**  
Behavioural/spatiotemporal patterns observed in real-world nutcracker communities used for model output corroboration.

Pattern	Description	Source (s)
Preference for WBP (1)	Nutcrackers display a preference for habitat where WBP is more abundant	Maier (2012)
Nutcrackers maintain net energy (2)	Nutcrackers maintain a median daily net energy balance close to zero	Schaming (2015)
Resident strategy is preferred (3)	Nutcrackers prefer a resident strategy over an emigrant strategy	Lorenz and Sullivan (2009)
Cone threshold exists (4)	A threshold of cone density exists, below which nutcracker occurrence is low	McKinney et al. (2009); Barringer et al. (2012)
100% MCP for individual nutcrackers (5)	MCP of locations for each individual nutcracker; min, max and median sizes	Lorenz and Sullivan (2009)
Elevation use of all nutcrackers (6)	Minimum, maximum and median elevation	Lorenz and Sullivan (2009)

the frequency of nutcracker occurrence, and thus probability of seed dispersal: when cone production declines from 700 to 300 cones/ha, frequency of occurrence declines from 0.4 to 0.1 and probability of seed dispersal from 0.7 to 0.3. Further, they estimate that no nutcracker visitation will occur when cone production drops below 130 cones/ha. Barringer et al. (2012) also found that as WBP cone production decreases, so too does the probability of occurrence of nutcrackers, although they did not conclude that a null-occurrence threshold exists. The reason for a lack of null occurrence with low cone production most likely has to do with nutcrackers ability/desire to “cruise” the landscape periodically in search of energetic resources, meaning that they may visit WBP patches even if those patches have little to no WBP before they move on. Specific values for cones/ha will undoubtedly vary across years/study areas when it comes to probability of occurrence for nutcrackers. What appears to be common though, is that some threshold for cones/ha exists in every situation where the probability of occurrence will sharply drop. We expect the probability of occurrence for nutcracker agents to drop sharply at some threshold occurring at less than 1000 cones/ha, although this may be a liberal estimate.

#### 7.5. Pattern 5: 100% minimum convex polygon (MCP) area for individuals

The calculation of 100% MCPs is an accepted procedure for determining the home range or spatial extent of individuals (see Patterson et al., 1991; Lorenz et al., 2011 for examples). The spatial extent of individuals is important, since it indicates where on the landscape those individuals have travelled and potentially what habitats are in use. Although absolute home range size can be an interesting and important metric, the mean MCP area is more appropriate in this investigation, since we deal with stochastic spatial extent output from the ABM. Directly comparing 100% MCPs for all individuals that emerge from the model to those generated from real-world nutcracker locations provides a robust metric for comparing habitat use in term of foraging. Large home ranges are indicative of nutcrackers having to travel large distances, be it in search of food, or cruising, or both. We expect to see a range of home range sizes, since stochasticity exists in nutcracker movement in response to internal and external energetic factors

#### 7.6. Pattern 6: elevation used by all individuals

Using the spatial location information as well as elevation from the acquired DEM of the study area, elevation above sea level for each nutcracker at each recorded location is determined. Elevation information from ABM output can be directly compared to these elevation values. Directly comparing the emergent elevation values for all individuals from the model to those generated from real-world nutcracker locations provides a robust metric for comparing space use. Nutcrackers use high elevations during this time period, since that is where WBP is abundant. We would expect to see a range of elevation usage, due to stochastic movements, however the bulk of usage should be within the elevation range of WBP.

## 8. Results

Table 4 outlines the results of the model output corroboration POM procedure that was performed on the three alternative behavioural mechanisms we tested: DER, IER, and Random/LTER. Pattern 1, *nutcrackers display a preference for WBP*, was measured through using the metric WBP patch visitation percentage. All three behavioural mechanisms display overwhelming preference for WBP: 94% for IER and 100% for both DER and Random/LTER. Pattern 2, *nutcrackers maintain a net energy balance close to zero*, was measured through use of the metric median net energy intake for all nutcrackers. While the DER behavioural mechanism produced a small median net energy gain over the simulation (37.1 kJ), the IER behavioural mechanism produced a number closest to zero (4.21 kJ), although both values were within the 5% range. The median net energy gain for the Random/LTER behavioural mechanism was quite large (7821.47 kJ). Pattern 3, *preference for resident strategy*, was measured through use of the metric *residency percentage*. Both the DER and IER had high percentage of residency: 100% and 84%, respectively. The Random/LTER behaviour mechanism had 0% residency. Pattern 4, *a cone threshold exists below which visitation markedly decreases*, was measured using the metric of frequency of visitation at a particular threshold of cone abundance. All three behavioural mechanisms display a large drop in frequency of occurrence at the 25 cones/ha threshold, indicating that no behavioural mechanism can be favoured for this pattern. Pattern 5, *100% MCP for all individual nutcrackers*, was measured through calculating the MCP for all individual agents and comparing the minimum, maximum, and median values with those calculated from the MCPs from the real-world nutcrackers observed in the Cascades. No behavioural mechanism reproduced the patterns from the real-world data exactly; however the IER model was the closest of the three, with a minimum home range size of 9.37 km<sup>2</sup>, a maximum home range size of 497.00 km<sup>2</sup>, and a median home range size of 264.63 km<sup>2</sup>. The corresponding values for the real-world home range data were 7.01 km<sup>2</sup>, 472.00 km<sup>2</sup>, and 191.15 km<sup>2</sup>, respectively. Pattern 6, *elevation use of all nutcrackers*, was measured by calculating the minimum, maximum and median elevation values for all nutcracker agents and comparing those with the calculated values from the real-world nutcrackers observed in the Cascades. Much like the home range analysis, no behavioral mechanism exactly reproduced the real-world data; however the IER mechanism was again the closest by comparison, with a minimum elevation of 691 m, a maximum elevation of 2120 m, and a median elevation of 1438 m. The corresponding values for the real-world elevation use were 710 m, 2036 m, and 1429 m, respectively.

Table 5 summarizes the results of the ranking of each alternative behavioural mechanism for each pattern from the model when compared to the real-world observed patterns through the model output corroboration procedure. The IER behavioural mechanism received the lowest total score (212.84) and thus the highest overall rank (1) for absolute difference pattern matching with the real-world observed patterns. The DER behavioural mechanism received the second highest total score (1117.02) and thus the second highest overall rank (2), however its absolute difference from real-world patterns differed from the IER mechanism by an order of magni-

**Table 4**  
Results of model output corroboration and behavioural mechanism evaluation.

Pattern	Pattern Evaluation Metric	DER	IER	Random/LTER	Observed
1	WBP Patch-Visit (%)	100	94	100	50–99%
2	Median Net Energy Intake (kJ)	37.10	4.21	7821.47	<34.54 kJ
3	Nutcracker Residency (%)	100	84	0	50–99%
4	135 cones/ha (%)	100	100	100	1000 cones/ha
	100 cones/ha (%)	99	99	99	–
	75 cones/ha (%)	87	90	99	–
	50 cones/ha (%)	59	47	90	–
	25 cones/ha (%)	37	32	17	–
	15 cones/ha (%)	19	22	16	–
	5 cones/ha (%)	10	12	14	–
5	Minimum Home range (km <sup>2</sup> )	0.00	9.37	1707.90	7.01
	Maximum Home range (km <sup>2</sup> )	32.80	497.00	2005.39	472.00
	Median Home range (km <sup>2</sup> )	7.90	264.63	1959.52	191.15
6	Minimum Elevation (m)	661	691	454	710
	Maximum Elevation (m)	2139	2120	2323	2036
	Median Elevation (m)	1815	1438	1374	1429

**Table 5**  
Results of ranking alternative behavioural mechanisms with how well (absolute difference) they match real-world observed patterns. Highest total score corresponds to highest absolute difference between values output from the model and patterns from real-world empirical investigations. Lowest scoring mechanism is also the most valid, since all mechanisms were compared via POM.

Mechanism	Patterns						Overall Ranking (Total Score)
	1	2	3	4	5	6	
DER	1 (1)	2 (2.56)	1 (1)	1 (0)	2 (629.46)	2 (538)	2 (1172.02)
IER	1 (0)	1 (0)	1 (0)	1 (0)	1 (100.84)	1 (112)	1 (212.84)
Random/LTER	1 (1)	3 (7785.73)	3 (50)	1 (0)	3 (5002.65)	2 (598)	3 (13437.38)

tude of 5.24. The Random/LTER behavioural mechanism received the highest total score (13437.38) and thus the lowest overall rank (3), with its absolute difference from real-world patterns differing from the IER mechanism by an order of magnitude of 63.13.

Fig. 7 displays an example of spatial output from the ABM. A nutcracker agent flight path is shown generated from time-stamped locations of the agent during the simulation, along with MCPs generated from those same locations. MCPs were used to define homeranges for nutcracker agents, which are an essential tool in defining scale for nutcracker agent behaviour.

## 9. Discussion and conclusions

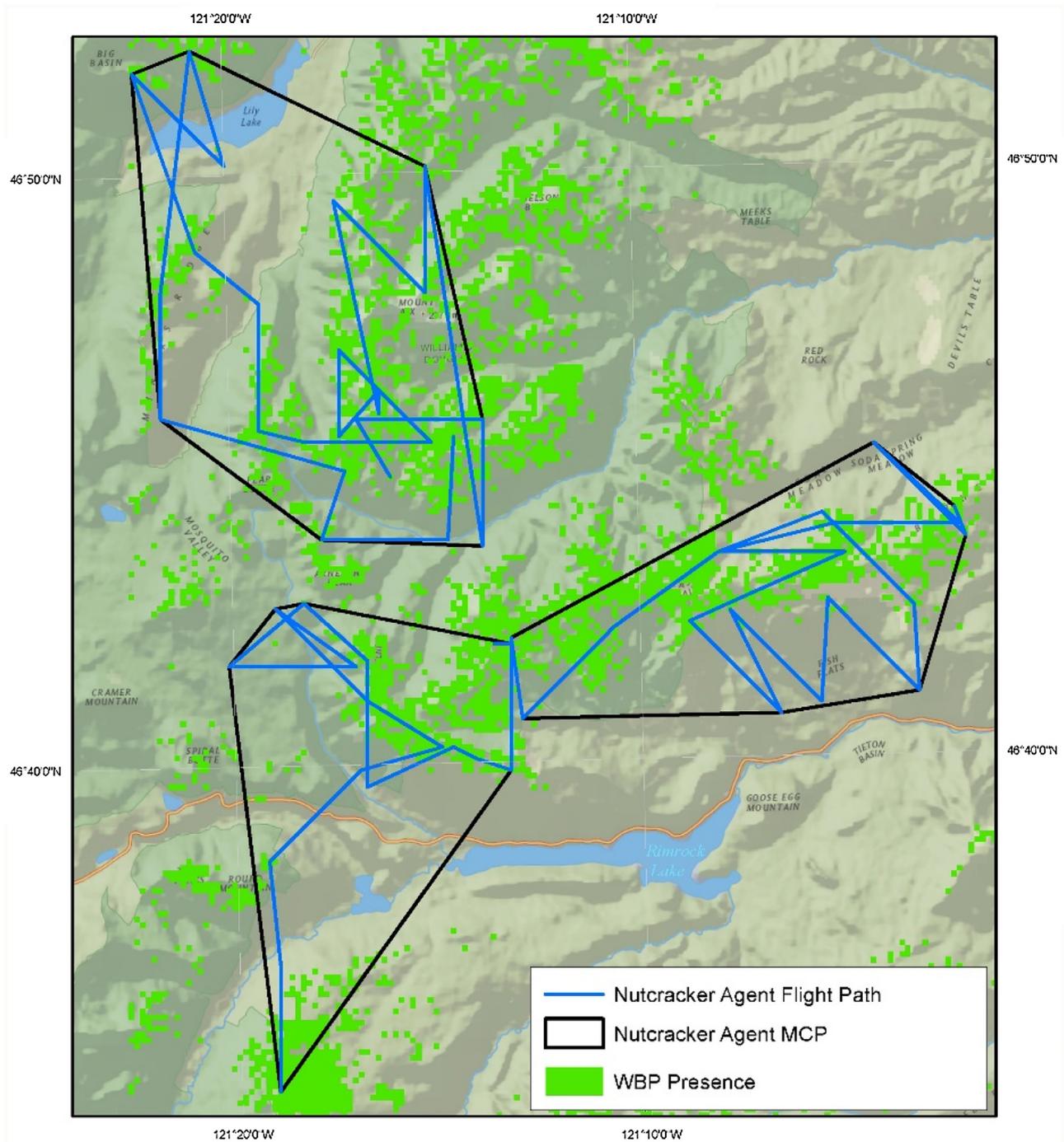
A comparative pattern analysis of bio-energetic and spatio-temporal patterns emergent from alternative nutcracker behavioural mechanisms with those observed from real-world investigations on nutcracker ecology reveals that an integrated energetic approach (IER) is best. Herein, we highlight the success of the IER approach against the alternatives through pattern-matching performance and discuss the driving factors behind successful pattern symmetry.

### 9.1. Pattern comparison

Research shows that a general condition exists whereby nutcrackers favor WBP over other food resources and display preference for WBP habitat, albeit never at the complete exclusion of usage of other habitat types (e.g. Tomback, 1978b; Hutchins and Lanner, 1982; Lorenz and Sullivan, 2009; Maier, 2012). Our analysis shows that both the DER and Random/LTER behavioural mechanism models over-estimate the preference towards WBP, with each mechanism excluding the use of patches that contain PP and patches that contain no energetic resource. The focus of both the DER and Random/LTER behavioural mechanisms is on short-term energetic returns, excluding explicit cruising behaviours and

the evaluation of long-term energy on the landscape. With WBP as the only short-term energetic resource available to the agents during the simulation, these results align with what we would expect: complete usage of WBP patches at the exclusion of all other options. The IER behaviour mechanism produces a strong preference for WBP patches, aligning with empirical research, however it also shows that nutcracker agents use patches with no WBP (PP and null energy patches) through cruising behaviour. The assessment of these non-WBP patches by nutcracker agents highlights the existence of optimization behaviour in the IER behavioural mechanism, since it is the cumulative energetic return of all patches visited through cruising that allows the nutcracker agents to assess the long-term energetic vitality of the study area. While it was assumed that a preference for WBP would be the case (it was the only short-term food source available), the results using the IER mechanism show that the nutcracker agents engage in the use of other habitats and thus other optimization behaviours. While the total available energy on the landscape was the same for all three mechanisms over time, by integrating both short-term and long-term energetic requirements and by assessing local and regional energy availability, the IER mechanisms was able to optimize short- and long-term returns for nutcracker agents, whereas the other two mechanisms were unable to do so. This aligns with adaptive behaviours of nutcrackers in the real world and gives us confidence in the IER behavioural mechanism.

It is commonplace for nutcrackers to have nearly 0% body fat and no more than 5% body fat throughout the year (Schaming, 2015). The costs of maintaining high body fat reserves for nutcrackers have not been extensively studied, however several potential costs that have been identified for birds in general, and may include mass-dependent metabolism, mass-dependent predation risk, mass-dependent risk of injury, mass-dependent foraging, pathological costs, or reproductive costs (Witter and Cuthill, 1993). All of these costs may play a role in explaining low fat reserves in nutcrackers. Alternatively, low fat reserves in nutcrackers may



**Fig. 7.** Example of nutcracker agent flight path (blue) and MCP based on nutcracker agent locations (black) in and around cells of available energy from WBP presence (green). Base map source: ESRI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be the result of lost opportunity cost, with nutcrackers choosing to forage on less fatty and energy-rich resources at the expense of other items that provide higher returns. This explanation seems less plausible, however, since nutcrackers have demonstrated energy optimization behaviours such as increasing foraging intensity after seeds have ripened, switching from one pine seed resource to another to maximize energetic gains (Vander Wall, 1988), and a preference for WBP which provides the highest energetic return per unit mass available to them. Additionally, maintaining fat reserves may be of little benefit to nutcrackers, since they have highly adaptive food-hoarding behaviours allowing them to store energy for future use externally in caches instead of internally

as fat (Tomback, 1978b). Conversely, externally storing energetic resources (caching) also poses its own set of challenges in that the location of caches may be forgotten, caches could be pilfered by conspecifics or other seed competitors, it takes energetic resources to fly to caching sites and to search for and return to those sites, and in time of low seed production there may be marginal reserves to cache. However, it would seem that nutcrackers mitigate these risks through: a highly-developed hippocampus that allows them to remember cache locations with incredible accuracy (Balda and Kamil, 1992); by potentially participating in reciprocal pilferage (see Vander Wall and Jenkins, 2003), whereby pilferage is not as damaging as it might otherwise be because many interspecific and

all intraspecific cache pilferers also cache food; by altering their foraging intensity, prey choice, and geographic location to match the energetic resources available on the landscape (Vander Wall, 1988), and eventually emigrating from a region when it appears to be no longer viable for long-term survival (eg. Vander Wall et al., 1981).

Our analysis reveals that a very large net energy balance of 7821.47 kJ emerged from the Random/LTER behavioural mechanism, which would equate to a higher than 5% body fat increase over the simulation (daily energy requirement is 690.91 kJ, multiplied by 30 days is 20,727.30 kJ; 7821.47 divided by 20,727.30 K is 38% body fat). Body fat percentages that emerge from the DER and IER mechanisms were  $1.79 \times 10^{-3}\%$  and  $2.03 \times 10^{-4}\%$ , respectively. Net energy balances (and as a result body fat percentages) over the simulation were the result of combined daily activity (day/night resting metabolism, foraging, predator mobbing, and cruising), reducing the energy level of an agent and the gain from consumption of WBP increasing its energy. Without any limitations placed on a nutcracker agent's internal energy levels under the Random/LTER behavioural mechanism, it comes as little surprise that net energy levels and body fat percentage were high. Under the DER mechanism, as well as the IER mechanism, nutcracker agents evaluate their internal energetic state and stop consumption of WBP seeds when their daily energetic requirement is reached. Increased stochastic predation events could be the cause of the lower body fat emergent from the IER behavioural mechanism, however, the likely cause is the decrease in energy level as a result of cruising which was not included in the DER mechanism. While body fat percentages emergent from the DER and IER mechanisms are both within the observed range, the IER behavioural mechanism better optimizes net energy.

Lorenz and Sullivan (2009) found that a resident strategy is the preferred strategy for nutcrackers in the Cascades. The costs and uncertainties of emigration, combined with the potential benefits of site-related dominance and familiarity with local terrain, food resources, and predators outweigh the potential gains of emigration for most nutcrackers (Vander Wall et al., 1981). We expect that some nutcrackers would choose to emigrate, especially when faced with low energy values on the landscape and a waning internal energetic situation; however, not all would choose to leave. Conversely, not all nutcrackers would choose to stay since energetic returns vary over the landscape, in particular with stronger competition from conspecifics in some areas and spatial heterogeneity of resources. Our analysis shows complete residency (all nutcracker agents choosing remaining in the study area) and no residency (no nutcracker agents remaining in the study area) emergent from the DER behavioural mechanism and the Random/LTER mechanism, respectively. Since the choice of an emigrant strategy through use of the Random/LTER mechanism results from the evaluation of the energy of patches visited only after the current patch has been depleted and in a random direction, it comes of little surprise that all nutcracker agents would eventually choose to emigrate under this behavioural approach. Conversely, the choice of an emigrant strategy through use of the DER mechanism results from the inability of the current patch and any memory patch to provide enough short-term energy, which fails to not only incorporate long-term energy requirements, but also to rely on the memory of patch abundance that may have changed since the agent's last visitation. Emergent from the simulation using the IER behavioural mechanism is the pattern that while most nutcracker agents chose a resident strategy (84%), some also chose an emigrant strategy. Choosing an emigrant strategy under this mechanism can emerge at any time, since nutcracker agents can cruise and evaluate long-term energy stochastically, not only when their current patch is not providing their daily energetic needs. The underpinnings of the IER behavioural mechanism are that nutcracker agents must integrate

short-term and long-term energetic requirements, which in this study area would suggest that is optimized by most by choosing a resident strategy over an emigrant one.

McKinney et al. (2009) found that there is a threshold of cone density ( $\sim 1000$  cones/ha) below which there is a rapid decline in the frequency of nutcracker visitation occurrence and predicted that a cone density of 130 cones/ha would cease visitation by nutcrackers completely. Barringer et al. (2012) also identified a cone density threshold below which probabilities of nutcracker visitation occurrence rapidly decline, albeit much lower at 50 cones/ha, and also with visitations taking place at densities as low as 0 cones/ha. Scott (2013) also determined nutcracker probability of visitation occurrence exists in areas with very low cone density. Emergent from all three behavioural mechanisms in our analysis are rapid declines in probability of visitation occurrence, with these declines occurring at 50 cones/ha for the IER and DER mechanisms and at 25 cones/ha for the Random/LTER mechanism. Direct comparison of thresholds between regions, studies, years, and seasons is very difficult since a variety of factors could be influencing nutcracker behaviour. As such, it is difficult to say which behavioural mechanism matches the patterns observed in real-world studies best. However, all three mimic the general pattern of a drop in frequency of occurrence at some (realistic) threshold.

Large differences existed between minimum, maximum, and median home range area for all three behavioural mechanisms. Emergent from the DER mechanism were home ranges that are very small in comparison to home ranges from real-world observed nutcrackers and those from the other behavioural mechanisms, highlighting the fact that nutcracker agents did not travel large distances throughout the simulation. This most likely is due to the fact that agents using this behavioural mechanism do not cruise their landscape periodically and thus, unless their current patch does not provide them with their energetic needs, they do not travel large distances. Conversely, emergent from the Random/LTER behavioural mechanism were home ranges that are very large in comparison to those from real-world observed nutcrackers and those from the other behavioural mechanisms. While no specific cruise behaviour was incorporated into the Random/LTER mechanism, agents were able to traverse several patches while on the way to a new patch, which provided a pseudo-cruise behaviour and lead to the emergence of large distances travelled over the simulation. Emergent from the IER behavioural mechanism were home range values comparable to those calculated from real-world nutcrackers, albeit slightly larger for all three metrics (minimum, maximum, and median). Reasons for these differences are difficult to ascertain, although one solution might stem from sampling frequency differences between the telemetry data and the model. Telemetry data was used to determine the home ranges for the real-world nutcrackers, which and was not completely comprehensive throughout the sampling time period. Dedicated studies tracking the space use of nutcrackers might provide more information on the mechanisms as to why these differences occur.

Much like the analysis of the home ranges, the analysis of elevation use reveals large differences between elevation values (minimum, maximum, and median) for all three behavioural mechanisms. Emergent from the Random/LTER mechanism were elevation values that are wide ranging in comparison to those from observational data and those from the other behavioural mechanisms. The nutcracker agents in this mechanism moved all over the landscape, covering nearly the entire range of elevation in the process (as is apparent from the home range metrics). Emergent from the DER mechanism were elevation values that are more similar to the IER mechanism, with the exception of the median value. This indicates that while nutcracker agents covered nearly the same range of elevations between the two behavioural mechanisms, nutcracker agents spent more time at higher elevations

using the DER mechanism as compared to the IER mechanism. This again is most likely due to the fact that nutcracker agents using the DER mechanism do not cruise and therefore stay in areas of high WBP abundance, which occurs at higher elevations. While the emergent elevation range for the IER mechanism is slightly outside of the range of real-world observed elevation values, the median values closely match. This suggests that the IER mechanism closely mimics elevation use of real-world data in the Cascades (due to where WBP grows – at high elevations). Differences could be attributed to stochasticity in cruising frequency and elevation.

## 9.2. Nutcracker emigration and conservation of whitebark pine

The success of our IER behavioural mechanism provides a robust state-dependent behavioural approach for modeling nutcracker foraging and provides a backdrop against which we can build scenarios that incorporate the behavioural and ecological complexity of nutcracker energetics and space use. An application of particular interest, conservation of WBP, represents one such avenue for future research that is made possible by our IER behavioural mechanism ABM. WBP, a keystone and foundation species located in high elevation western forests, plays a central role in promoting biodiversity, community development and watershed protection (Tomback et al., 2001; Tomback and Achuff, 2010). WBP is a species on the decline, with losses due to infestations of blister rust and mountain pine beetle, increased competition due to fire exclusion, and climate change which limits habitat suitability and exacerbates all other potential threats (Tomback et al., 2001; Tomback and Achuff, 2010). Several agencies have listed or made WBP a candidate as *endangered* (IUCN Red List of Threatened Species - Mahalovich and Stritch 2013; Species at Risk Act – Government of Canada 2012; Endangered Species Act – U.S. Fish and Wildlife Service, 2011). These agencies recommend that significant efforts be invested in assessment and restoration of WBP to prevent extinction.

Key to restoration of WBP is the continuance of seed dispersal of WBP seeds by Clark's nutcracker, an occurrence that is only possible if large numbers of nutcrackers in a region choose a resident life-history strategy. Alternatively, nutcrackers can choose another life history strategy: emigration. Both strategies seem to be employed by nutcrackers in response to variable and ephemeral food supply (Vander Wall et al., 1981). Understanding the driving factors behind choosing one of these alternative life-history strategies could provide clues as to the conditions necessary to maintain seed dispersal of WBP by nutcrackers, and thus, the long term persistence of WBP on the landscape. Further, armed with a robust model that accurately replicates nutcracker energetics and the potential driving factors behind emigrant strategies in nutcrackers, our ABM approach can be extended as a scenario-planning tool. Using the ABM and through consideration of multiple potential landscapes (both current and future) in a spatially explicit context, we can model nutcracker spatio-temporal, bio-energetic, and emigration responses to changes in WBP habitat. This process of scenario planning can offer managers a method for creating more resilient conservation policies by increasing understanding of key uncertainties, incorporating alternative perspectives, and providing greater resilience to unexpected outcomes for conservation decisions (McLane et al., 2011; Chapter 2). These two endeavors: driving factors of Clark's nutcracker choice between a resident or emigrant strategy, and WBP scenario-planning for conservation represent the next phases of our research focus.

Using a POM approach, we suggest that nutcrackers integrate both short-term (daily) and long-term (yearly) energetic constraints on the landscape when making decisions regarding energetic fitness. The success of our IER behavioural mechanism affirms previous research that nutcrackers are responsive to

changes in their energetic environment, and that nutcrackers are capable of projecting energy budgets well into the future. In addition, the development of this ABM represents a means to assess the driving conditions necessary for nutcrackers when choosing between a resident and emigrant strategy. These factors, along with the use of the ABM as a planning tool through which we can model nutcracker responses to potential landscape changes, may help facilitate the long-term conservation of WBP.

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## References

- Amano, T., Ushiyama, K., Moriguchi, S., Fujita, G., Higuchi, H., 2006. Decision-making in group foragers with incomplete information: test of individual-based model in Geese. *Ecol. Monogr.* 76, 601–616.
- Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to 'evaluation': a review of terminology and a practical approach. *Ecol. Model.* 280, 117–128.
- Balda, R.P., Kamil, A.C., 1989. A comparative study of cache recovery by three corvid species. *Anim. Behav.* 38, 486–495.
- Barringer, L.E., Tomback, D.F., Wunder, M.B., McKinney, S.T., 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker. *PLoS One* 7.
- Bennett, D.A., Tang, W., 2006. Modelling adaptive, spatially aware, and mobile agents: elk migration in Yellowstone. *Int. J. Geogr. Inf. Sci.* 20, 1039–1066.
- Bent, A.C., 1946. Life Histories of North American Jays, Crows and Titmice (United States National Museum Bulletin v. 191, Washington).
- Cruz-Angón, A., Sillett, T.S., Greenberg, R., 2008. An experimental study of habitat selection by birds in a coffee plantation. *Ecology* 89, 921–927.
- Fowells, H.A., Schuber, G.H., 1956. *Seed Crops of Forest Trees in the Pine Region of California*.
- Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M., Tyler, D., 2002. The national elevation dataset. *Photogramm. Eng. Remote Sens.* 68, 5.
- Gould, K.L., Ort, A.J., Kamil, A.C., 2012. Do Clark's nutcrackers demonstrate what-where-when memory on a cache-recovery task? *Anim. Cogn.* 15, 37–44.
- Grimm, V., Railsback, S.F., 2005. Individual-based modeling and ecology. *Individ.-Based Model. Ecol.*, 1–428, i–xvi.
- Grimm, V., Railsback, S.F., 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Philos. Trans. R. Soc. B* 367, 298–310.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., Wissel, C., 1996. Pattern-oriented modelling in population ecology. *Sci. Total Environ.* 183, 151–166.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol A review and first update. *Ecol. Model.* 221, 2760–2768.
- Houston, A.I., McNamara, J.M., 1992. Phenotypic plasticity as a state-dependent life-history decision. *Evol. Ecol.* 6, 243–253.
- Hutchins, H.E., Lanner, R.M., 1982. The central role of Clark nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55, 192–201.
- Krugman, S.L., Jenkinson, J.L., 1974. *Pinus, Seeds of Woody Plants in the United States*. 45 ed.
- Lanner, R.M., 1999. Made for each other: Clark's Nutcracker and the Whitebark Pine. *IV International Conifer Conference* 615, 121–125.
- Long, F.L., 1934. Application of calorimetric methods to ecological research. *Plant Physiol.* 9, 323–337.
- Lorenz, T.J., Sullivan, K.A., 2009. Seasonal differences in space use by Clark's Nutcrackers in the Cascade Range. *The Condor* 111, 326–340.
- Lorenz, T.J., Sullivan, K.A., Bakian, A.V., Aubry, C.A., 2011. Cache-site selection in Clark's nutcracker ( *Nucifraga columbiana*). *Auk* 128, 237–247.
- Lorenz, T.J., 2009. *Linking Space Use and Behavior in Clark's Nutcracker*. Thesis. Utah State University.
- Mahalovich, M., Stritch, L., 2013. *Pinus albicaulis*. In: *The IUCN Red List of Threatened Species*.
- Maier, M., 2012. Clark's Nutcracker Seed Harvest Patterns in Glacier National Park and a Novel Method for Monitoring Whitebark Pine Cones. *Biology*. Utah State University (p. 67).
- McKinney, S.T., Fiedler, C.E., Tomback, D.F., 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. *Ecol. Appl.* 19, 597–607.

- McLane, A.J., Semeniuk, C., McDermid, G.J., Marceau, D.J., 2011. The role of agent-based models in wildlife ecology and management. *Ecol. Model.* 222, 1544–1556.
- Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Can. J. For. Res.-Revue Canadienne De Recherche Forestiere* 32, 725–741.
- Olton, D.S., 1977. Spatial memory. *Sci. Am.* 236, 82.
- Patterson, I.J., Cavallini, P., Rolando, A., 1991. Density, range size and diet of the european jay *garrulus-glandarius* in the Maremma natural park, Tuscany, Italy, in the summer and autumn. *Ornis Scand.* 22, 79–87.
- Pravosudov, V.V., Lucas, J.R., 2001. Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. *Behav. Ecol. Sociobiol.* 50, 239–250.
- Railsback, S.F., Johnson, M.D., 2011. Pattern-oriented modeling of bird foraging and pest control in coffee farms. *Ecol. Model.* 222, 3305–3319.
- Railsback, S.F., Lytinen, S.L., Jackson, S.K., 2006. Agent-based simulation platforms: review and development recommendations. *Simulation* 82, 609–623.
- Schaming, T.D., 2015. Population-Wide failure to breed in the Clark's nutcracker (*Nucifraga columbiana*). *PLoS One* 10.
- Scott, J.D., 2013. Clark's Nutcracker Occurrence, Whitebark Pine Stand Health, and Cone Production in the Waterton-glacier International Peace Park, Biology. University of Colorado.
- Semeniuk, C.A.D., Musiani, M., Hebblewhite, M., Grindal, S., Marceau, D.J., 2012. Incorporating behavioral-ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape. *Ecol. Model.* 243, 18–32.
- Smith, C.C., Balda, R.P., 1979. Competition among insects, birds and mammals for conifer seeds. *Am. Zool.* 19, 1065–1083.
- Snyder, M.A., 1993. Interactions between Aberts squirrel and ponderosa pine- the relationship between selective herbivory and host-plant fitness. *Am. Nat.* 141, 866–879.
- Tomback, D.F., Achuff, P., 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *For. Pathol.* 40, 186–225.
- Tomback, D.F., Linhart, Y.B., 1990. The evolution of bird-dispersed pines. *Evol. Ecol.* 4, 185–219.
- Tomback, D.F., Arno, S.F., Keane, R.E., 2001. Whitebark Pine Communities: Ecology and Restoration. Island Press.
- Tomback, D.F., 1978a. Foraging strategies of Clark's nutcracker. *Living Bird* 16, 123–161.
- Tomback, D.F., 1978b. The behavioural ecology of the Clark's nutcracker *Nucifraga columbiana* in the eastern Sierra Nevada. *Diss. Abstr. Int. B Sci. Eng.* 38, 3030.
- Tomback, D.F., 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *J. Anim. Ecol.* 451–467.
- Tomback, D.F., 1998. Clark's nutcracker. *Birds North Am.* 331, 1–24.
- Torick, L.L., 1995. The Interaction Between Clark's Nutcracker and Ponderosa Pine a Wind-dispersed Pine: Energy Efficiency and Multi-genet Growth Forms. U.S. F.a.W. Service, 2011. Endangered and Threatened Wildlife and Plants; 12-month Finding on a Petition to List *Pinus Albicaulis* as Endangered or Threatened with Critical Habitat, vol. 76. Fish and Wildlife Service, Interior Federal Register, Cheyenne, Wyoming, pp. 42631–42654 (no. 136).
- Vander Wall, S.B., Hutchins, H.E., 1983. Dependence of Clark's Nutcracker, *Nucifraga columbiana*, on conifer seeds during the post-fledging period. *Can. Field-Nat. Ottawa ON* 97, 208–214.
- Vander Wall, S.B., Jenkins, S.H., 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behav. Ecol.* 14, 656–667.
- Vander Wall, S.B., Hoffman, S.W., Potts, W.K., 1981. Emigration behavior of clarks nutcracker *nucifraga-columbiana*. *Condor* 83, 162–170.
- Vander Wall, S.B., 1982. An experimental analysis of cache recovery in Clark's nutcracker. *Anim. Behav.* 30, 84–94.
- Vander Wall, S.B., 1988. Foraging of clark's nutcrackers on rapidly changing pine seed resources. *Condor* 90, 621–631.
- Wilensky, U., 1999. Netlogo, 5.0.4 ed. Northwestern University. Center for Connected Learning and Computer-Based Modelling.
- Witter, M.S., Cuthill, I.C., 1993. The ecological costs of avian fat storage. *Philos. Trans. R. Soc. B: Biol. Sci.* 340, 73–92.