



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



Adam J. McLane^{a,*}, Christina Semeniuk^b, Gregory J. McDermid^a, Diana F. Tomback^c,
Teresa Lorenz^d, Danielle Marceau^e

^a Department of Geography, University of Calgary, Calgary, Alberta, Canada

^b Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, Canada

^c Department of Integrative Biology, University of Colorado Denver, Denver, CO, USA

^d University of Idaho, Moscow, ID, USA

^e Schulich School of Engineering, University of Calgary, Calgary, Alberta, Canada

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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-

* Corresponding author.

E-mail address: ajmclane@ucalgary.ca (A.J. McLane).

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

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