Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes

Julia E. Earl [a,*], Patrick A. Zollner [b,1]

[a] National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN 37996, USA
[b] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47906, USA

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ABSTRACT

Cross-ecosystem transfer of resources (spatial subsidies) can greatly impact recipient ecosystems. Many subsidies are actively moved by animals, which regularly transfer nutrients within and among ecosystems. Researchers have yet to integrate knowledge of animal movement and spatial subsidies to enhance predictions of subsidy spatial distribution and ecosystem effects. To examine this, we implemented a spatially explicit simulation model of animals that switch habitats due to behavioral or ontogenetic shifts. We explored how movement strategy (correlated random walk) and patterns of mortality risk affected the spatial distribution of living (consumer subsidies) and dead individuals (nutrient/energy subsidies). We ran models varying the correlation in a correlated random walk and explored four patterns of mortality risk: uniform mortality, higher mortality in the edge at the habitat boundary, a decreasing gradient and an increasing gradient of mortality risk as individuals move away from the boundary. For each scenario, we calculated the maximum extent, the distance of peak density and the peak density (a measure of maximum impact of the subsidy) of living and dead individuals. As expected, subsidy impact declined as deposition distance increased. Straighter movements resulted in deposition farther beyond the local habitat boundary with lower impact than more sinuous movements. Similarly, consumer subsidies were deposited farther from the boundary with lower impact than nutrient/energy subsidies. Patterns of mortality risk also affected the impact and deposition distance but to a lesser degree. Uniform mortality and increasing gradients of mortality risk deposited subsidies farther from the habitat boundary than did edge mortality and decreasing gradients. Edge mortality scenarios also resulted in higher densities of subsidies than other patterns of mortality risk. Our simulations represent a very simple, first attempt at using movement ecology to predict the spatial distribution and impacts of subsidies. More complex models and empirical tests are necessary to further assess movement ecology's utility for predicting subsidies.

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1. Introduction

Cross-ecosystem transfer of energy, materials, and various chemical compounds (spatial subsidies) can have profound effects on recipient ecosystems (Marczak et al., 2007; Polis et al., 1997). These fluxes are the major determinants of many economically important ecosystem services, including crop pollination (Kremen et al., 2007; Morandin and Winston, 2006) and pest control (Lundberg and Moberg, 2003). For example, ocean-derived nutrients in salmon fertilize inland forests in the Pacific northwest at a level that is similar to silvicultural fertilizer application (Quinn et al., 2009). Alternately, these chemical transfers can also result in major environmental degradation, such as that leading to the Gulf of Mexico dead zone (Rabalais et al., 2002) and the destruction of arctic ecosystems from agriculturally subsidized waterfowl (Jefferies et al., 2004). Recent evidence has shown that spatial subsidies can also move contaminants from impacted sites to unimpacted sites, creating potential problems for the management of waste disposal (Rasmussen and Zanden, 2004; Walters et al., 2008). With both positive and negative consequences of cross-ecosystem transfers, it would be useful to be able to predict the spatio-temporal distribution and effects of subsidies.

Many subsidies occur via active transport by animals. Animals, such as aquatic insects (Wesner, 2010), river otters (Ben-David

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* Corresponding author at: National Institute for Mathematical and Biological Synthesis, University of Tennessee, 1122 Volunteer Blvd. Suite 106, Knoxville, TN 37996, USA. Tel.: +1 865 974 4943; fax: +1 865 974 9300.
    E-mail addresses: jearl@nimbios.org (J.E. Earl), pzollner@purdue.edu (P.A. Zollner).
    [1] Tel.: +1 765 496 9495; fax: +1 765 496 2422.

et al., 1998), and bats (Duchamp et al., 2010), regularly move nutrients within and among ecosystems. The movement ecology of these animals determines where and when active subsidies are deposited. However, researchers have yet to integrate knowledge of animal movement ecology and spatial subsidies to enhance predictions of subsidy spatial distributions and ecosystem effects using dynamic models. McCoy et al. (2009) modeled predator subsidies with predator-prey models, but their predictions of the spatial pattern of subsidy deposition were based on a static distribution and did not incorporate movement data. In fact, most spatial subsidy models have been spatially implicit, examining trophic and nutrient dynamics in two interacting patches or one patch with a parameter for the input to that patch (Callaway and Hastings, 2002; Holdo et al., 2007; Leroux and Loreau, 2008; Loreau and Holt, 2004), despite the explicitly spatial nature of the research question (Massol et al., 2011). Spatially explicit individual-based models (IBMs) are particularly applicable to active subsidies, because they can simulate the movement behaviors of many individuals, which can be aggregated to summarize the spatio-temporal distribution of subsidies. Existing theoretical IBMs have examined the effectiveness of different search strategies for dispersing animals under different scenarios of landscape configuration, mortality risk, and perceptual ranges (Conradt et al., 2003; Zollner and Lima, 1999, 2005). These models could be used effectively to examine active subsidies if they were modified to keep track of the spatio-temporal distribution of living and dead individuals, representing consumer and nutrient/energy subsidies, respectively. Such dynamic movement models could predict active subsidies from animals with different movement ecologies, population dynamics and life histories (Chon et al., 2009). The use of those models, instead of static distributions, would allow for predictions of subsidy effects in both time and space.

Here, we present simulations on the spatial distribution of active subsidies from a simple theoretical IBM of the dispersal phase of animals with an ontogenetic or behavioral habitat shift during their life cycle. Animals with ontogenetic or behavioral habitat shifts are one type of active subsidy scenario and a good starting place for theoretical models, because they represent a very simple case where the nutrient/energy subsidies derive from individual mortality (not excretion) and animals typically cross the boundary between ecosystems only once during the dispersal phase (e.g. aquatic insects, pond-breeding amphibians, some migratory fish). In this model, individuals move into the virtual landscape from one side, representing their previous habitat, and individual movements are simulated using a correlated random walk (CRW). We systematically varied movement strategy (the degree of correlation in a random walk) and movement costs (non-starvation risks per step and spatial variation in these risks). We chose this simple case as a starting point to predict the spatio-temporal distribution of living and dead individuals, a first examination of how movement ecology might affect subsidy deposition. Dead individuals (nutrient/energy subsidies) deposit energy, nutrients and/or contaminants. Living individuals (consumer subsidies) transfer their metabolic demands to the adult habitat and, through trophic interactions, act as consumers (more specifically herbivores, omnivores, detritivores or predators, depending on the animal being considered) potentially capable of causing top-down effects. We predicted that straighter movements would deposit subsidies further beyond the habitat boundary and with lower potential impact (measured as the maximum density of individuals on the landscape) than more sinuous movements. We also expected edge mortality and decreasing mortality risk gradients to deposit nutrient/energy subsidies (dead individuals) closer to the habitat boundary with more concentrated effects than uniform mortality or increasing mortality risk gradients, which would deposit nutrient/energy subsidies further with less concentrated effects. Finally, we predicted
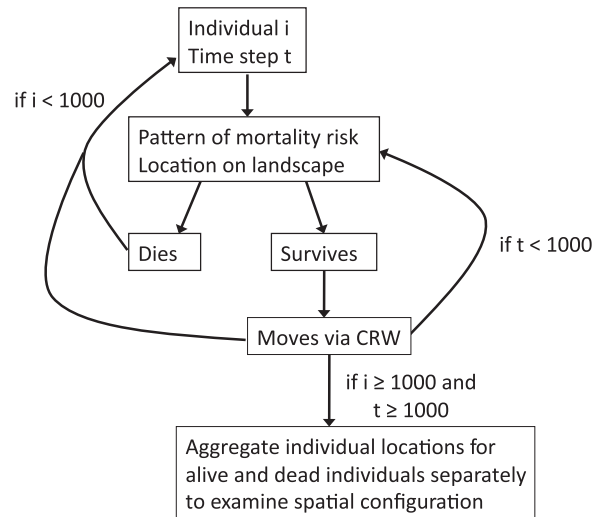

Fig. 1. Schematic of the flow of the model.

that consumer subsidies would be deposited farther than nutrient/energy subsidies, because living individuals would take more steps on average than dead individuals.

2. Material and methods

2.1. Model design and purpose

The main purpose of this model was to investigate how animal movement strategies and movement costs (patterns of mortality risk in this case) affect the spatial distribution of animal transported subsidies. In this theoretical model, we considered the very simple case where animals grow in one habitat (the natal habitat) and then move into a second habitat (adult habitat) and can die during the movement phase. This model examines the population only during the movement phase in the adult habitat, assuming that other portions of the life history, such as growth and reproduction, would take place over a longer time scale than considered in the model. Dead animals represent a nutrient, energy, and possibly a contaminant subsidy to the adult habitat, and individuals that survive represent a consumer subsidy to the adult habitat. We separately track both nutrient/energy and consumer subsidies in the model. We assume for simplicity that the location of death is where the subsidy is deposited. Clearly there are many cases where scavengers may move carcasses or predators may consume nutrients that are deposited elsewhere, but we considered these to be scenarios of added complexity that could be investigated in future studies. Also, predators often consume only a portion of the subsidized prey, leaving unpalatable portions of the carcass that can have large local impacts on microbial communities and nutrients in soil, water and/or primary producers that can persist for years (Bump et al., 2009; Danell et al., 2002).

Time is treated as discrete and is defined as the time it takes an individual to take one step forward on the landscape (see Matlab code in Online Appendix A). The model is run for 1000 time steps; i.e. if an animal does not die during the simulation, it will take 1000 steps across the landscape (Fig. 1). The landscape is represented continuously in two dimensions on an (x, y) grid, is uniform (except for changes in mortality risk, described below), and the adult habitat includes 0–1000 units on the X-axis and −1000 to 1000 units on the Y-axis. Thus, individuals do not leave the adult habitat during the model run. Also, individuals may not cross back into the natal habitat, because it is assumed that individuals have transformed or grown into adults at the start of the simulation and they move