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Theoretical Population Biology 71 (2007) 182–195

Theoretical Population Biology

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Sequential decision-making in a variable environment: Modeling elk movement in Yellowstone National Park as a dynamic game

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Received 9 March 2006
Available online 6 October 2006

Abstract

We develop a suite of models with varying complexity to predict elk movement behavior during the winter on the Northern Range of Yellowstone National Park (YNP). The models range from a simple representation of optimal patch choice to a dynamic game, and we show how the underlying theory in each is related by the presence or absence of state- and frequency-dependence. We compare predictions from each of the models for three variables that are of basic and applied interest: elk survival, aggregation, and use of habitat outside YNP. Our results suggest that despite low overall forage depletion in the winter, frequency-dependence is crucial to the predictions for elk movement and distribution. Furthermore, frequency-dependence interacts with mass-dependence in the predicted outcome of elk decision-making. We use these results to show how models that treat single movement decisions in isolation from the seasonal sequence of decisions are insufficient to capture landscape scale behavior.

Keywords: Dynamic programming; Foraging theory; Game theory; *Cervus elaphus*; Yellowstone National Park

1. Introduction

Ecologists rely on increasingly sophisticated models to predict the movement behavior and distribution of animals (reviewed in Grimm, 1999; Grimm and Railsback, 2005). These models range from individual-based simulations in which foragers follow predefined rules in response to environmental variation (e.g., Revilla et al., 2004; Jager et al., 2006), to relatively complicated algorithms that seek adaptive foraging strategies for individuals in a population of competitors (e.g., Huse and Giske, 1998; Alonzo and Mangel, 2001; Heinz and Strand, 2006). The development of these models has stimulated two related questions. First, what degree of model complexity is necessary to explain observed distribution and movement patterns of animals (Stephens et al., 2002; Jepsen et al., 2005)? Second, what is the relationship between these models and more basic ecological theory (Grimm, 1999)?

The link between individual-based models and basic optimal foraging theory is of particular interest to behavioral and landscape ecologists. Evolutionary ecologists have established a long tradition of analyzing foraging behavior as the outcome of adaptive processes at the individual level (Stephens and Krebs, 1986) and have developed a suite of theoretical constructs, such as optimal patch choice, residence time, and giving-up density (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976; Brown, 1988), the ideal free distribution (IFD) (Fretwell and Lucas, 1970; Sutherland, 1983), and density-dependent habitat selection theory (Morris, 2003; Jonzén et al., 2004). However, it is typically difficult to scale up the results of the basic models to guide the development and understanding of more complex landscape-level models (Lima

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0040-5809/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.tpb.2006.09.004

and Zollner, 1996; Bowler and Benton, 2005). This difficulty arises from the necessity to consider the fitness value of a sequence of decisions made by an individual in an environment that varies across large spatial and temporal scales. More specifically, how is the outcome of a single optimal movement decision (e.g., choosing the best neighboring grid cell at each time step in an individual-based population simulation) related to the sequence of decisions optimized as a whole? Similarly, how is the distribution at each time step predicted by an individual-based model related to the IFD?

We address the issues of model complexity and the link between behavioral ecology and landscape models in the context of a particular system, winter movement behavior of elk (*Cervus elaphus*) on the Northern Range of Yellowstone National Park (YNP), USA. Houston (1982) provides a detailed description of the natural system and its management history (see National Research Council, 2002 for more recent discussion). During the winter, elk move from high-elevation areas on the Northern Range to lower elevations inside and outside the park. Mobility and foraging can be severely limited by snow accumulation (Parker et al., 1984; Sweeney and Sweeney, 1984; Coughenour, 1994) and, because there is no regrowth of forage during the winter, an individual elk must contend with a dynamic pattern of competition from other grazers. A winter hunt imposes substantial mortality risk outside the park, and recent studies have suggested that the reintroduction of wolves to YNP in 1995 may have initiated a trophic cascade (Ripple and Beschta, 2004; Creel et al., 2005; Fortin et al., 2005a). Because this herd is closely intertwined with the local economy and management of YNP, predicting the movement of the elk is of applied as well as basic ecological interest (National Research Council, 2002).

We model landscape scale movement in the framework of a state-dependent game between members of the herd and optimize individual elk foraging decisions with the dynamic programming algorithm. The general technique has been used in the ecological literature to predict animal distributions (e.g., Alonzo and Mangel, 2001); however, our model is unique in this context in that we treat an individual forager's current location as a state variable. Although this feature is not conceptually novel, it is critical to predicting landscape scale movement of grazers because the large distance between potential foraging patches makes current location an important determinant of the payoff from moving to another location. Elk foraging on the Northern Range of YNP has been the subject of study at the level of small-scale adaptive foraging decisions and landscape scale patterns (e.g., Turner et al., 1993, 1994; Fortin et al., 2005a, b). Here, we place two simpler models of patch choice, state-dependent optimization and the IFD, in the common framework of the state-dependent game to address the link between adaptive behavior at the level of individual foragers and landscape scale patterns. We use each model to predict three specific features of elk winter movement that are of basic and applied interest: aggregation, use of habitat outside YNP, and survival through the winter. We ask not only what we would miss with the simpler optimal patch choice and IFD models, but also how state and frequency-dependent mechanisms interact in the more complex state-dependent game model to generate the predicted landscape level patterns.

2. Methods

The model framework consists of two distinct parts: (1) a representation of the natural system including elk energetics, snow accumulation, and forage availability; and (2) an optimization procedure to calculate the movement decisions that maximize individual fitness given the natural system. We use four variants of the optimization procedure to find sequences of movement decisions that maximize different fitness measures that are related within the framework of the full state-dependent game model. With the results of each of the four optimizations, we simulate the herd behavior in identical environmental conditions so we can compare the predicted herd movement and survival.

The optimizations find the sequence of moves between patches for an individual elk that starts the winter in any one of the patches. The four model variants that we consider incorporate different combinations of state- and frequency-dependence in the optimization (summarized in Table 1). The optimal behavior in all of the models depends on an individual's location at a given time step, which influences the movement cost to reach another patch. However, we conduct the optimization with and without individual mass (a measure of physiological condition) as a dynamic state variable. Similarly, we conduct the optimization with and without the influence of forage competition from the herd (frequency-dependence).

We selected mass- and frequency-dependence to include in our analysis for two reasons. First, although forage is depleted by the herd and survival and future reproductive success depend on individual mass, it is not obvious to

Table 1
Summary of models with (+) and without (−) frequency-dependence (FD) and mass-dependence (MD)

Model	FD	MD	Quantity maximized
1	−	−	Immediate payoff in the absence of forage depletion by competitors
2	+	−	Immediate payoff with forage depletion by competitors
3	−	+	Net payoff in the absence of forage depletion by competitors
4	+	+	Net payoff with forage depletion by competitors