Discussion

Discussion on 'Movement rules for individual-based models of stream fish' [S.F. Railsback et al. 123 (1999) 73–89][☆]

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Dear Editor,

In a recent paper published in *Ecological Modelling*, Railsback et al. (1999) proposed a method for modeling movement rules for stream fishes that simplifies stochastic dynamic modeling techniques in an effort to design optimal movement rules amenable for use with individual based models (IBMs). Each day, individuals in the Railsback et al. model evaluate their expected survival to the end of the time horizon for all locations within a specified distance and move to the location with the highest value. Future fitness is defined as expected survival over a specified time horizon — the product of daily probabilities of not starving and daily probabilities of surviving non-starvation mortality. The high computational demands of dynamic programming required a number of simplifications to be made, including: (1) a restricted decision space; (2) a short time horizon; and (3) constant environmental conditions. Presumably these constraints could be relaxed as more computational power becomes available. We refer to this movement model as the Dynamic Programming (DP) model. This approach is not new and it, in fact, predated movement models that incorporate realistic perceptual constraints, as described in Tregenza's (1995) (p. 277) historical review of movement models.

Railsback et al. are critical of fish movement models based on departure rules that combine a fitness currency with a learning algorithm first described by Bernstein et al. (1988). Fish using this departure rule leave when the value of the present location falls below the expected value available elsewhere. Each individual maintains an estimate of the expected value based on its past experience. Once a decision to depart has been made, a new location is chosen at random. This approach has been used in a number of spatially explicit IBMs (Tyler and Rose 1997), including several for stream fishes (Jager et al., 1993; Clark and Rose, 1997; Van Winkle et al., 1997). We refer to this model as the Learning Algorithm (LA) model.

These models are distinguished by two main differences. First, the most fundamental difference between the models is the level of knowledge assumed to be available to individual fish. The DP model assumes that fish are omniscient, both in their knowledge of the surrounding environment in space and the future environment in time. In

the LA model, each individual obtains knowledge of the environment from exploration of locations visited in the past. The decision variable in the DP model is the destination, whereas the decision variable of the LA model is the decision to depart, followed by probabilistic choice of a destination. Second, the DP and LA models use a different fitness currency. The DP model in Railsback et al. used expected survival to a future date, while the LA models used the ratio of risk over growth or the expected growth (product of survival and growth). While we agree with Railsback et al. that previous modeling approaches have limitations, we feel that the proposed alternative has its own problems and leaves much to be desired as a means for modeling individual movement in a spatially-explicit environment. These limitations are described below.

1. Imperfect information

The DP and LA models assume different levels of knowledge and take very different approaches to decisions about departure and selection of a new location by fish. The DP model evaluates the future fitness of each simulated fish in all surrounding locations. Individuals rank locations by the fitness of the individual and choose the best location. There is a rich body of research on animal behavior that suggests that movement decisions do not typically result in animals selecting the best possible location (e.g. Krebs 1971). There are two main reasons that this does not occur. First, animals make movement decisions under uncertainty due to perceptual constraints (i.e. imperfect information). Second, always choosing the 'best' location is a short-sighted strategy because of the inherent conflict between gaining information to reduce uncertainty and being in the location with the highest short-term value.

Optimal decisions in a deterministic setting (e.g. by omniscient fish) are very different from those made under uncertainty (e.g. by real fish). Real fish have limited information obtained using imperfect senses from past experience in previously visited locations. For example, Marcotte and Browman (1986) suggested that perceptual constraints and cognitive limitations are a source of variance in foraging behavior in fishes. At high densities, optic tetanus renders fishes incapable of making foraging decisions, leading to a random diet. They claimed that abundant prey confuse predators, leading them to focus on one large prey type for perceptual reasons, not energetic ones. In a second example, Milinski (1988) noted that an animal that is unable to perceive differences in patch quality must choose a patch at random which leads more animals to over-use poor patches relative to predictions of the Ideal-Free distribution. Experiments with drift-feeding minnows show precisely this behavior (Tyler and Clapp, 1995). The uncertainty about habitat quality leads to what might be viewed as imperfectly optimal decisions (Janetos and Cole, 1981; Luttbeg and Schmitz, 2000).

Animals engage in exploratory behavior that results in latent learning (Alcock, 1977) (p. 216). Although exploration may not lead to an animal residing in best location in the short term, the information gained can improve future decisions. In the terminology of optimization theory, movement decisions are not 'greedy' algorithms in which animals only make movements to better locations. Rather, movements to locations with lower quality may ultimately be rewarded because they provide the animal with information about the landscape. As Stephens and Krebs (1986) note, incomplete information plays a central role in foraging theory and the methods available to animals to reduce ambiguity can be as important as the actual value of a location.

Ollason (1980) compared feeding experiments with birds against both an optimal foraging model and a learning model and was unable to distinguish between them. He summarized the value of learning models as follows:

"Perhaps the most important conclusion to be drawn from the analysis of the learning model is that to forage in a patchy environment in a way that approximates closely to optimality, an animal need not be omniscient; it does not need to sample; it does not need to perform numerical analyses to find the maxima of functions of many variables; all it needs to do is to remem-

ber and to leave each patch if it is not feeding as fast as it remembers doing.''

We believe that a learning algorithm is unlikely to always reach the same solution reached by an optimization that has access to information from a wider spatial area as well as that in the future, but we maintain that this is the best heuristic algorithm available to real organisms.

The LA model permits simulated fish to do their own real-time optimization, in which gaining information by exploring is part of the solution and individuals differ in their histories and knowledge of the surrounding habitat. No knowledge of future environment is assumed. Although animals have undoubtedly evolved some genetically hard-wired behaviors that anticipate highly predictable features of future environment (i.e. seasonality), the average fish does not have a crystal ball to guide its daily movements. Therefore, it is not clear to us that a DP modeling approach is appropriate.

2. Fitness currency

Expected survival is the fitness currency adopted by Railsback et al. This currency avoids the limitations of the 'minimize μ/G' rule when G is near zero, where $\mu =$ risk and $G =$ growth. The 'maximize expected survival' fitness currency has a more straightforward interpretation. This currency is state-dependent, allowing individuals with low energy reserves to make different decisions than individuals with high energy reserves.

Expected survival, as simulated by Railsback et al., does not include density- and frequency-dependent components of fitness. Many tests of habitat selection have shown that fish consider not only the resource availability in a habitat but also the demand on that resource (Milinski, 1979; Godin and Keenleyside, 1984; Power, 1984; Tyler, and Gilliam, 1995). In fact, the effects of competition on animal distributions have been the subject of habitat selection theory from the early formulations of the Ideal Free and Ideal Dominance distributions (Fretwell and Lucas, 1970). The LA model with its departure rule approach to modeling habitat selection allows fish to respond to changes

in local density that affect individual fitness. Any factor (e.g. environmental, population density, or anthropogenic change in the habitat) that affects the measure of fitness indirectly affects the departure decision of the model fish. The LA/departure rule approach to modeling fish habitat selection, thereby, allows for a flexible representation of frequency and/or density-dependent fitness.

We do not see alternative fitness currencies as a significant difference between the two approaches because alternative currencies can be substituted into either. For example, Van Winkle et al. (1997) generalized an earlier currency (predation risk/foraging intake) to include: (1) multiple mortality risks and (2) energetic costs as well as foraging potential. Railsback et al. explore reproductive potential as a component of future fitness as well. Both LA and DP can weigh the relative contributions of energetics (starvation risk or growth) and other influences on fitness, either through selection of the time horizon, T, or through the choice of a fitness currency. Railsback et al. argued that the importance of energetics (vs. survival) was unrealistically high in the LA models.

3. Field comparisons and future improvements

Railsback et al. present no comparisons of the predicted distributions from the two modeling approaches to field observations of fish distributions. They do suggest a field test that would distinguish the two models — Do fish ever move from a better location to a worse one? Without demonstrating improved predictive capability, we would argue against adopting the DP approach — or perhaps just gathering additional information first.

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