



Original Article

Contingent trade-off decisions with feedbacks in cyclical environments: testing alternative theories

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Many animals make contingent decisions, such as when and where to feed, as trade-offs between growth and risk when these vary not only with activity and location but also 1) in cycles such as the daily light cycle and 2) with feedbacks due to competition. Theory can assume an individual decides whether and where to feed, at any point in the light cycle and under any new conditions, by predicting future conditions and maximizing an approximate measure of future fitness. We develop four such theories for stream trout and evaluate them by their ability to reproduce, in an individual-based model, seven patterns observed in real trout. The patterns concern how feeding in four circadian phases—dawn, day, dusk, and night—varies with predation risk, food availability, temperature, trout density, physical habitat, day length, and circadian cycles in food availability. We found that theory must consider the full circadian cycle: decisions at one phase must consider what happens in other phases. Three theories that do so could reproduce almost all the patterns, and their ability to let individuals adapt decisions over time produced higher average fitness than any fixed behavior cycle. Because individuals could adapt by selecting among habitat patches as well as activity, multiple behaviors produced similar fitness. Our most successful theories base selection of habitat and activity at each phase on memory of survival probabilities and growth rates experienced 1) in the three previous phases of the current day or 2) in each phase of several previous days.

Key words: activity selection, circadian rhythms, foraging, habitat selection, population models, theory, trade-off decisions, trout.

INTRODUCTION

Many animals make decisions in cyclical environments, with the best choice of behavior in one part of the cycle depending on what they do in other parts of the cycle. These decisions often involve trade-offs among objectives such as obtaining energy and avoiding predation. The decisions are also often *contingent*, in the sense that two decisions that strongly affect each other are made together. We address the common example of circadian foraging: making a contingent selection of activity (whether to feed or hide) and habitat (where to feed or hide) over the daily light cycle, considering how both feeding success and predation risk vary over the cycle.

These decisions produce circadian patterns in behavior driven by daily cycles in habitat variables such as light, temperature, and food availability, but also affected by factors such as habitat quality, competition, and individual state. Such cycles have been observed throughout the animal kingdom, including in insects (Whitford and Ettershank 1975), birds (Holmes et al. 1978; Brandt and Cresswell 2009), small (Levy et al. 2016) and large mammals (Klinka and Reimchen 2002), marine fish (Strand and Huse 2007), and the salmonid fish we model (Metcalf et al. 1998, 1999).

(The terminology related to 24-h cycles of light and dark can be confusing. We use the word “circadian” in reference to such cycles; “day” for the part of the cycle with sunlight, except when it clearly refers to a 24-h time period (e.g., “one-day”); and “diurnal,” “crepuscular,” and “nocturnal” for being active in day, dawn and dusk,

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and night, respectively. We also use the word “phase” for the four segments of the circadian cycle defined by light conditions: dawn, day, dusk, and night. “Circadian rhythm” here refers to the pattern of activity displayed by the model population through the 24-h cycle.)

We address theory for how individual animals make contingent foraging decisions in a cyclical environment. Furthermore, we address individual decisions in a population context: the options available to each individual, and their fitness value, depend on what competing individuals in the population decide to do. Specifically, we develop theory for how each unique individual decides, at the start of each phase of a circadian cycle, whether to feed or hide and which habitat patch to use for that activity (the “habitat and activity selection” behavior), when the number of patches and the growth and risk provided by each depends on the individual’s internal state and on unpredictable factors such as weather and the behavior of other individuals. This problem includes feedbacks at both the individual and population levels: the individual’s internal state is an outcome of its previous decisions (e.g., the extent to which it traded off growth to increase survival probability, which affects its size and energy reserves), while at the population level the decisions of each individual determine the resources they consume and make unavailable to others, how long they live, and how many offspring they have, all of which affect the availability of resources to competing individuals.

This habitat and activity selection problem can be addressed by applying fitness optimization theory. We can assume that each individual, at the start of each circadian phase, makes some prediction of the conditions they will be exposed to until a future time horizon and, therefore, what alternatives will be available and what the growth and risk associated with each are. Then we can use state-dependent fitness optimization theory (e.g., Houston and McNamara 1999; Clark and Mangel 2000) to optimize the individual’s behavior until the time horizon using techniques such as dynamic programming. Finally, we can assume that the individual executes the optimal behavior for the current time step. This prediction and optimization cycle can be repeated at the start of each circadian phase to consider the effects of unforeseen changes (from either environmental variability or feedbacks) that make the predictions inaccurate.

“State- and prediction-based theory” (SPT; Railsback and Harvey 2020) is an alternative that differs from such optimization theory only by using approximations to eliminate the need for dynamic programming optimization. These approximations typically include the individual deciding what to do each time step by assuming (incorrectly) that it will use the same behavior pattern until the time horizon and neglecting the effects of growth on future survival probability. SPT typically uses a “sliding” time horizon that remains a constant number of days in the future.

SPT has the advantages of being more tractable computationally and perhaps less likely to overestimate the cognitive abilities of real organisms, and can produce behavior very similar to optimization: Railsback and Harvey (2020) contrasted results of an SPT model of a simple forager problem to an optimization, finding that SPT produced behavior nearly as successful as optimization except when survival to the time horizon was very unlikely. Its use of simple predictions and approximations lets SPT produce good decisions while allowing the processes driving the decision (e.g., how expected fitness depends on energy reserves; how mortality risk depends on individual and habitat variables) to be complex in ways that would make dynamic programming optimization very challenging. The

sliding time horizon also avoids “terminal effects” of conventional optimization approaches that affect behavior as the time horizon approaches (e.g., Fiksen 1997). These characteristics of SPT make it useful for individual-based population models (IBMs) of complex, real-world management problems. Such IBMs can also serve as rigorous and challenging test beds for behavior theory (Grimm et al. 2005; Grimm and Railsback 2012).

A behavior can be modeled by a range of SPT-based theories that differ in complexity. In some cases, more complex theories cause IBMs to better reproduce empirical observations; in others, more complex theories are not better than simpler alternatives (Railsback and Harvey 2020). Alternative theories can be evaluated using the “pattern-oriented theory development cycle” (Grimm et al. 2005; Grimm and Railsback 2012): posing alternative theories as hypotheses; implementing them in an IBM that includes feedbacks of behavior, environmental variability, and other complexities; and contrasting and falsifying theories by how well they cause the population model to reproduce a variety of characteristic patterns observed in real individuals and populations.

Railsback et al. (2005) showed that SPT can produce realistic circadian rhythms in a population context with feedbacks and variable environments. In that application of SPT, each individual decides whether to feed or hide, in which one of many alternative habitat patches, at the start of each day and night. In this study we supplement those experiments by addressing a more complex decision. The model of Railsback et al. (2005) simplified the circadian cycle to only two phases, day and night, so the activity selection decision could be treated as selection among four alternatives: feeding in day and hiding at night, feeding at night and hiding in day, feeding day and night, or hiding day and night. However, representing only two phases oversimplifies many systems. For example, crepuscular periods have particular importance for many species: dawn and dusk can provide enough light to forage successfully while making foragers less visible to predators than during full daylight. Here, we seek theory applicable to any number of phases per circadian cycle while evaluating alternative theories by modeling four phases: night, dawn, day, and dusk.

We use stream populations of salmonid fish as a study system. Circadian variation in the behavior of stream salmonids has been studied well enough to document many of its complexities and their causal mechanisms. Circadian activity rhythms in stream salmonids appear driven by the effects of light on both feeding success and predation risk (Metcalfe et al. 1999). Salmonids are normally visual predators on small invertebrates drifting in the stream current; they can detect and capture prey at night but over smaller ranges. While salmonids face some nocturnal predators (e.g., owls, otters), often their most important predators (birds, especially mergansers) depend on daylight for prey detection (Harvey and Nakamoto 2013).

We start by identifying the patterns observed in circadian foraging behavior of stream salmonids used as criteria for testing and contrasting theory. Next, we briefly describe the IBM in which we test theory, focusing on the processes driving the foraging decision. Then we develop four alternative theories for how trout decide, at the start of each phase of a circadian cycle, whether to feed or hide and where to do so. Fourth, we describe the simulation experiments used to test theory and their results. Our results show how well each alternative theory, when implemented in the IBM, reproduces the observed patterns. Finally, we draw conclusions about appropriate levels of complexity for modeling circadian foraging decisions using SPT.

METHODS

Characteristic patterns in circadian behavior of salmonids

We first identified a diverse set of patterns observed in the circadian foraging behavior of real stream salmonids that characterize how this behavior varies with important drivers. We focus on four patterns that emerge from habitat and activity selection decisions; [Supplementary Material](#) defines and analyzes three additional patterns.

Pattern 1: More diurnal feeding when food availability or fish condition is low

[Metcalfé et al. \(1999\)](#) observed in a laboratory experiment that well-fed fish were active exclusively at night but as food availability decreased they became increasingly diurnal. [Metcalfé et al. \(1998\)](#) documented that the frequency of diurnal feeding increased as body condition decreased and starvation risk increased. [Orpwood et al. \(2006\)](#) observed less diurnal feeding when food was made more abundant.

Pattern 2: More diurnal and crepuscular feeding at higher temperatures

A number of studies have observed more salmonid feeding during higher light conditions—during day or crepuscular periods—at higher temperatures. For example, [Fraser et al. \(1993, 1995\)](#) conducted experiments in which they varied only temperature while controlling other variables that could contribute to seasonal differences in behavior. Over a range from <5 to >15 °C, higher temperatures produced slightly fewer fish feeding at night and many more feeding in day. [Breau et al. \(2007\)](#) observed in wild Atlantic salmon juveniles a strong positive relation between water temperature and the percentage of fish active in daytime, over temperatures between 13 and 24 °C. [Roy et al. \(2013\)](#) also observed wild Atlantic salmon juveniles and documented decreasing diurnal and crepuscular feeding as temperature decreased at the end of summer. This pattern is presumed driven by the increase with temperature in metabolic demands of fish and the food intake therefore needed to maintain body condition and avoid starvation.

Pattern 3: Effects of competition on circadian foraging

Competition can affect the prevalence of diurnal and nocturnal foraging and how circadian rhythms respond to other variables. [Harwood et al. \(2001\)](#) observed that competition with brown trout for preferred nocturnal feeding habitat caused juvenile Atlantic salmon to become more diurnal. [Alanärä et al. \(2001\)](#) found that dominant brown trout individuals all fed during crepuscular periods at low temperatures, but at higher temperatures the increased energetic demands increased the intensity of competition and caused some individuals to switch to nocturnal feeding. [Fingerle et al. \(2016\)](#) compared activity times in juvenile arctic charr at low and high densities; at both densities feeding was mainly nocturnal but at high densities there was more activity overall and especially more feeding in crepuscular periods. Because competition often interacts with other variables such as habitat availability, we consider this “pattern” reproduced simply when fish density affects foraging rhythms in some way.

Pattern 4: Circadian cycles of food availability affect foraging

The primary food of stream salmonids, invertebrate drift, is often most available during crepuscular or nocturnal periods ([Naman](#)

[et al. 2016](#)), which could make feeding during those phases relatively more beneficial. [Giroux et al. \(2000\)](#) observed a nocturnal peak in drift availability and a tendency for trout to feed when drift rates were higher. (Higher food availability at night is not universal; e.g., [Fingerle et al. 2016](#).)

The population model

The individual-based population model we use to test foraging theory is version 7 of inSTREAM, a family of salmonid IBMs that we have been developing and using for 20 years. [Supplementary Material](#) provides a full description and justification of the model as used here. InSTREAM includes many natural complexities, including spatial and temporal variation in habitat conditions and variation among individual trout in size, condition, and location. Therefore, it provides a virtual laboratory for testing ecological theory that is more complex and realistic than many laboratory experiments while eliminating the uncertainties of observing and measuring natural systems.

Entities and scales

Space is represented as a stream reach made up of patches. Flow, temperature, turbidity, and surface irradiance (light flux at the water surface) are reach-level habitat variables (varying over time but not among patches). The patches represent areas of relatively uniform habitat. Patches have dynamic variables for water depth and velocity (which depend on flow) and irradiance at mid-depth (a function of depth, turbidity, and surface irradiance), and separate static variables representing availability of cover for short-term escape, longer-term concealment, and reducing swimming costs of feeding. Time is represented as four time steps per day, one for each phase of the circadian cycle. The clock time at which these time steps begin is calculated from the latitude and date: dawn begins when the sun reaches 6° below the horizon and ends when the sun is 6° above the horizon; dusk begins and ends when the sun is 6° above and below the horizon.

Trout are represented as individual entities. Each model trout has variables for its length, weight, condition (the ratio of its weight to the weight of a healthy individual of the same length), and activity: whether it is feeding or hiding. Trout locations are represented as the patch that they feed or hide in.

Events and schedule

The first action executed each time step is habitat updates. If flow, temperature, and turbidity have changed since the previous time step, the new values are read from a file and variables that depend on these reach inputs are updated. (In the simulations here, these variables are either held constant or updated once per day, to make results easier to understand.) The surface irradiance is updated each time step, and calculated as the mean irradiance over the time step. Patch irradiance values are then updated.

Next, each trout executes the following three actions. The trout execute these in descending size order (largest to smallest) to represent the size-based dominance hierarchies widely observed in trout (e.g., [Hughes 1992](#)). Each trout completes all three actions before the next trout begins.

- **Habitat and activity selection:** The trout determines which patch to occupy and whether to feed or hide, using one of the alternative theories described below. Trout evaluate all patches within a radius that increases with trout length and not dry at the current flow, and move to the one providing the highest value of a fitness

measure. The fitness measure is based on the growth rates and survival probabilities that a trout would experience, which are explained below. (The model assumes no “site fidelity” or reluctance to move, a simplifying assumption whose realism could vary among species and individuals.)

- **Survival:** Whether a trout dies of each of several potential causes (especially, predation by terrestrial animals, predation by other fish, starvation) is treated as a stochastic event with the probability of survival a function of trout and habitat variables explained below. This action is turned off for most of the simulations used here to remove survival as a source of variation in results (individuals behave in response to risk but do not die).
- **Growth:** Trout length, weight, and condition are updated from the growth rate (which is negative when trout hide or have food intake less than energy costs) that results from their choice of patch and activity.

Growth

Like other salmonid energetics models, inSTREAM treats trout growth rate as a complex function of habitat and trout variables. Growth is modeled as the difference between gross energy intake from feeding and the energetic costs of metabolism and feeding. Trout can feed in two alternative modes: searching for benthic food and drift-feeding: holding a stationary position and capturing prey as it drifts past in the current. For trout of the size we model here, drift feeding is usually more profitable than searching. Drift food intake increases with the concentration of drifting prey and fish length (bigger fish can feed in faster water). Intake varies nonlinearly with velocity: higher velocity carries more prey past, but makes prey harder to capture; consequently, intake increases from zero at zero velocity to a maximum at an intermediate velocity that depends on fish length. Intake also depends nonlinearly on irradiance: at night light levels, reduced ability to see prey is assumed to reduce intake to approximately one quarter of day rates.

Metabolic energy costs increase with both swimming speed and temperature. The rate at which trout use energy increases at an increasing rate as swimming speed increases above about half of the maximum sustainable speed. Therefore, as patch velocity increases the benefits of higher drift rates are offset by sharply rising energy costs, so growth peaks at an intermediate velocity. Similarly, metabolic rates increase at an increasing rate as temperature rises above about 5 °C, so trout need higher food intake to maintain their weight at high temperatures.

Model trout that choose the hiding activity experience metabolic costs with zero swimming speed, and no energy intake from feeding. Therefore, they lose weight at a low rate that increases with temperature.

Starvation survival

InSTREAM models the probability of starvation survival as a function of body condition. If a model trout loses weight, its length remains unchanged so its body condition decreases. The probability of surviving starvation for a day is assumed to decrease at an increasing rate as condition decreases (Figure 1). Therefore, a steady rate of weight loss results in decreasing probability of daily survival, and the probability of surviving until the future time horizon we use (always 90 days in the future) decreases sharply as the rate of weight loss increases. However, trout are able to survive long periods of weight loss (Simpkins et al. 2003); our parameters

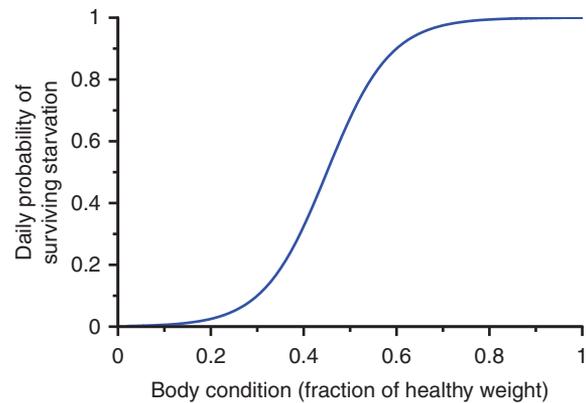


Figure 1

Logistic curve of starvation survival probability. Survival probability declines little as body weight falls to ~80% of healthy weight, given the trout’s length. If weight continues to decline, daily survival probability decreases rapidly. Consequently, the probability of surviving a period of weight loss depends strongly on the rate of weight loss and the length of the period; trout are likely to survive modest weight loss for prolonged periods.

produce a 50% probability of surviving 1% weight loss per day for 40 days. Compared with the common assumption in behavior theory that starvation happens at a deterministic threshold, this continuous relation between starvation survival probability and body condition is more realistic for fish and, very importantly, allows individuals to make good decisions even during periods when no alternatives offer adequate energy intake for long-term survival (Railsback and Harvey 2020).

Predation survival

InSTREAM simulates predation mortality as a stochastic event with the survival probability a deterministic function of trout and habitat variables. For the simulations used here, predation by terrestrial animals is the only important mortality risk other than starvation. InSTREAM assumes that such predators hunt mostly, but not entirely, by sight. Therefore, survival probability is assumed to increase as the irradiance in a trout’s patch decreases; compared to daytime values, the risk of daily mortality is approximately 70% lower during crepuscular phases and 80% lower at night. Depth also provides protection by making trout less visible and harder to catch from the surface; proximity to escape cover also reduces risk.

We assume that use of the hiding activity reduces predation risk by 90%. However, model trout cannot use hiding in patches lacking concealment cover. Concealment cover is represented via a patch variable for the number of places in the patch where an individual trout could hide, and each trout choosing to hide in a patch uses up one such place. This approach was chosen because field observations and laboratory experiments (Harvey and White 2016) have shown the reluctance of trout to share hiding space. Even when individuals are willing to share hiding space, availability of such space can affect activity selection (Larranaga and Steingrímsson 2015). Therefore, the prevalence of hiding at the population level can be limited by the availability of concealment cover.

Model implementation

InSTREAM 7 is implemented in the NetLogo platform for individual-based models (Wilensky 1999; Railsback and Grimm 2019). The code used here was thoroughly tested by using temporary output files to export the inputs and results of each

submodel and then comparing the results to independent implementations in Excel.

Alternative theories

Here we describe the four versions of SPT that we evaluate for modeling the habitat and activity selection decision. These are only a small initial set of alternatives chosen to provide informative contrasts in the key assumption that distinguishes SPT from previous approaches—how individuals predict future conditions—so they can motivate further theory refinement. All four versions share common characteristics of SPT (Railsback and Harvey 2020). At the start of each time step (each dawn, day, dusk, and night), trout decide which combination of habitat patch and activity (feeding vs. hiding) to use in a time step; under all theories they select the combination that would provide the highest value of a fitness measure that approximates the probability of surviving both predation and starvation until a future time (the time horizon), when starvation survival is a function of current condition and future growth rate.

The differences among our theory alternatives are in how individuals predict future growth rates and survival probabilities—the mental models that simulated trout use to predict future growth and survival. There is an extensive literature on how animals may predict future conditions and its consequences, both theoretical (Dall and Johnstone 2002; McNamara et al. 2016) and empirical (e.g., Bergeron et al. 2011; Fraker 2008). We explore the circadian behavior problem with a range of simple assumptions. The first theory uses an extremely simple prediction method that ignores the circadian cycle; the rest consider the cycle with increasing sophistication.

The fitness measures used in all theories represent future survival to the time horizon. To avoid additional complexity in results, we include no incentive for growth beyond that needed to avoid starvation. However, the theories are readily modified to include the value of growth when its contribution to fitness cannot be ignored (e.g., for juveniles the fitness measure includes the benefits of growing to reproductive size).

Theory A: Ignore circadian cycles

This is the simplest theory, included mainly for contrast to the more complex alternatives. Using it, fish predict their growth rate and survival probability until the time horizon by simply assuming growth and survival will continue at the values experienced at the current time step (the time step for which the animal is currently selecting habitat and activity). This assumption completely neglects the circadian light cycle.

At the start of each time step, each simulated trout evaluates each possible combination of patch and activity and calculates the current growth rate (G_C , g/d) and survival probability (P_C , probability of surviving predation for one day) it would obtain; these values depend on state variables of the patch (e.g., depth, velocity, hiding cover availability, temperature) and of the trout (length, weight). From these rates and the trout's current state, it calculates the fitness measure—its expected probability of surviving both predation and starvation until the time horizon—using the prediction that the current survival probability and growth rate would persist until the time horizon. This prediction is clearly wrong because it ignores the circadian cycle as well as future changes in growth and risk, but our experience is that simplistic predictions can often produce good decisions (Railsback and Harvey 2020).

The expected probability of surviving predation until the time horizon T days in the future is approximated simply as $P_T = P_C^T$.

The expected probability of surviving starvation until the time horizon is approximated by predicting the trout's length, weight, and body condition at the time horizon from G_C . First, weight at the time horizon is projected from the current weight and growth rate (W_C, G_C): $W_T = W_C + (T \times G_C)$. Then, the trout's condition factor at the time horizon (K_T) is projected from W_T and the current condition factor (K_C). If W_T is greater than the weight of a healthy trout (W_H ; weight of a trout with the same length and K of 1.0), then the trout is expected to have grown in length and have $K_T = 1.0$; otherwise, the trout's length is projected to remain unchanged (it remains underweight for its length) and K_T is set to W_T/W_H . Finally, the probability of surviving starvation until the time horizon (S_T) is approximated using the method of Railsback et al. (1999; also explained by Railsback and Harvey 2020), which uses the first moment of the logistic equation raised to the power T :

$$S_T = \left(\frac{1}{a} \ln \left(\frac{1 + \exp(aK_T + b)}{1 + \exp(aK_C + b)} \right) / (K_T - K_C) \right)^T$$

where a and b have values of -6.59 and 14.6 for the logistic relation between K and starvation survival discussed above, and K_C is the trout's current condition factor. (When K_T equals K_C , division by zero is avoided by setting S_T to the value of S from the logistic relation at K_C , raised to the power T ; this happens whenever K_C is 1.0 and G_C is positive.)

The fitness measure F , expected probability of surviving both predation and starvation until the time horizon, is evaluated simply as: $F = P_T S_T$.

Theory B: Constant prediction

This theory represents the entire circadian cycle but in an extremely simple way. The fitness measure is evaluated by using growth and survival rates over the day that ends with the current time step—not just those of the current time step—as the prediction of conditions until the time horizon. However, growth and survival over the parts of the circadian cycle preceding the current phase are represented simply as constant parameters. On each time step, the growth rate during all other phases of the circadian cycle is assumed to be $G_B = 0.0$ g/d (the trout is assumed to meet but not exceed its metabolic demands); and the survival probability is assumed to be $P_B = 0.995$, which corresponds to a survival rate of 63% over the 90-d time horizon. These values for the parameters G_B and P_B are somewhat arbitrary yet reasonably representative of long-term averages; to avoid bias, we did not attempt to calibrate them.

Mathematically, the constant prediction theory is like the first theory except for two changes that adjust the predicted daily growth rate and survival probability for the portion of a full day constituted by the current time step. In the equation for W_T , G_C is replaced by a one-day average growth rate calculated as: $G_D = (G_C \times d_C) + (G_B \times (1 - d_C))$ where d_C is the duration (d) of the current time step. In the equation for P_T , P_C is replaced by the survival probability over a full day: $P_D = P_C^{d_C} P_B^{(1-d_C)}$.

Theory C: One-day memory

The third theory differs from the first and second in using the growth rate and survival probability experienced throughout the most recent circadian cycle as the prediction of conditions until the time horizon. This theory therefore considers the full cycle and how feeding success and risks vary through it. For example, if an individual fed successfully during the most recent daytime, its daily starvation risk would be lower during the following dusk and night

phases, so hiding in those phases would become more attractive. (This theory is most like the two-phase theory of Railsback et al. 2005, but differs in a critical way: the previous theory assumed individuals decide what to do on one time step by considering all possible combinations of activity and habitat over a circadian cycle, whereas this theory considers only the activities and habitat actually used previously in the same day. This difference allows the number of phases per circadian cycle to be increased with negligible effects on the complexity of the algorithm and its computational effort.)

The one-day memory theory is evaluated like the constant prediction theory except that G_D and P_D are now calculated using experienced rates instead of constant parameters to represent growth and predation survival during previous phases of the one-day cycle. The model trout maintain a “memory” of the predation survival probabilities (P_i , for $i = 1-3$) and growth rates (G_i) they experienced with the habitat patch and activity they chose in each of the three phases preceding the current one. For example, when a trout is selecting habitat and activity at the start of a daytime phase, P_i and G_i are the predation survival probabilities and growth rates experienced in the previous dawn, night, and dusk phases. (At the start of a simulation, memory values for theories C and D are initialized to growth of 0.0 g/d and survival of 1.0.) Our assumption that individuals can sense the growth rates and predation risks they are (or could be) exposed to is widely used in behavioral ecology. Food intake is directly experienced by fish, but predation risk is not. However, there is strong evidence that trout, like many animals, estimate risk as a function of habitat variables (e.g., Fraser et al. 1993; Harvey and White 2017), indicating that this assumption, while clearly a simplification, is not unreasonable.

These memories are combined with the survival and growth rates for the alternatives being considered for the current phase to determine the overall rates for a full circadian cycle, adjusting for the duration of each phase. This combination for survival probability P_D is calculated as follows:

$$P_D = \left(\prod_{i=1}^3 (P_i)^{d_i} \right) (P_c)^{d_c}$$

where d_i are the durations of the previous three phases (as fractions of a day). The combined one-day growth rate G_D is calculated as follows:

$$G_D = \left(\sum_{i=1}^3 G_i d_i \right) + (G_c d_c).$$

Then P_T , S_T , and F are calculated exactly as for the first theory except that G_D and P_D replace G_C and P_C .

Theory D: Multiday memory

This theory is identical to the one-day memory theory except that previous phases are represented by the average conditions experienced with the patches occupied and activities used over the previous n days instead of only the conditions experienced in the current day. Here we arbitrarily use $n = 9$ days. Then in the equations for P_D and G_D , P_i and G_i are replaced by P_n and G_n , the mean survival probabilities and growth rates over the previous phases of the current day and previous n days.

The multiday memory theory is implemented by each simulated fish maintaining lists that contain the survival and growth values experienced during each circadian phase of the previous 9 days. The initial survival and growth values of 1.0 and 0.0 are replaced by actually experienced values over the first nine simulated days.

(We address the effects of this initialization method in the first subsection of Results.)

Study site

The simulated reach (previously used by Harvey and Railsback 2007, 2012) spans 184 m of Little Jones Creek in northwestern California, where the stream drains 26 km² of second-growth forest. Dry-season streamflow is typically about 0.15 m³/s, whereas peak wet-season flows typically exceed 30 m³/s. At median flow, stream width averages 7.1 m and depth 33 cm. The channel gradient is moderately steep (about 2%). Abundant gravel substratum apparently limits the number of places providing concealment cover for large juvenile and adult trout; we estimated a total of 163 such hiding places in the reach at median streamflow. To eliminate strong effects of concealment cover limitation on results, the number of hiding places per patch was set to four times the estimated actual values.

Simulation experiments

The standard parameters and inputs used in simulation experiments are described here, while each experiment’s detailed design is described below with its results. Our simulation experiments were designed to limit variability due to factors other than the alternative behavior theories and the processes that drive them. All simulations were initialized with a population of 100 trout, sufficient to cause strong competition for good feeding sites. Many of the studies cited to support our characteristic patterns observed large juveniles, so we simulated trout of similar size: initial lengths were drawn randomly from a triangular distribution with minimum, mode, and maximum lengths of 8, 10, and 12 cm. The condition factor K was initialized to 1.0. To keep the number of fish constant during simulations, simulated mortality was deactivated even though fish still behaved to avoid risk.

InSTREAM is typically calibrated by adjusting parameters for food availability (concentration of drift food and production rate of search food, both assumed constant over time) and the overall intensity of terrestrial predation risk to produce realistic annual or seasonal rates of survival and growth. To avoid biasing the contrast of alternative behavior theories, we did not calibrate the model but instead used calibration parameter values from applications of earlier versions of inSTREAM to the same study site (e.g., Harvey and Railsback 2007, 2012). The final simulation experiment (“One-year simulations”) verified that these parameter values produced reasonable growth and survival rates.

Although inSTREAM is designed to predict effects of temporal variation in habitat conditions, these experiments used a steady stream flow (at the long-term median of 0.44 m³/s), a benign temperature of 10 °C, and a low turbidity of 5 NTUs. Simulations ran September 15–25, at a latitude of 42°N; because this period spans the fall equinox, day and night phases were both 10.9 h long, whereas dawn and dusk were both 1.1 h. We conducted 10 replicates (in which different random numbers were used to set initial trout lengths and locations) of each scenario.

RESULTS

Here we describe the simulation experiments used to test how well each of the four theories for habitat and activity selection could reproduce the characteristic patterns of observed circadian behavior, and explain the key results and differences among theories. But we

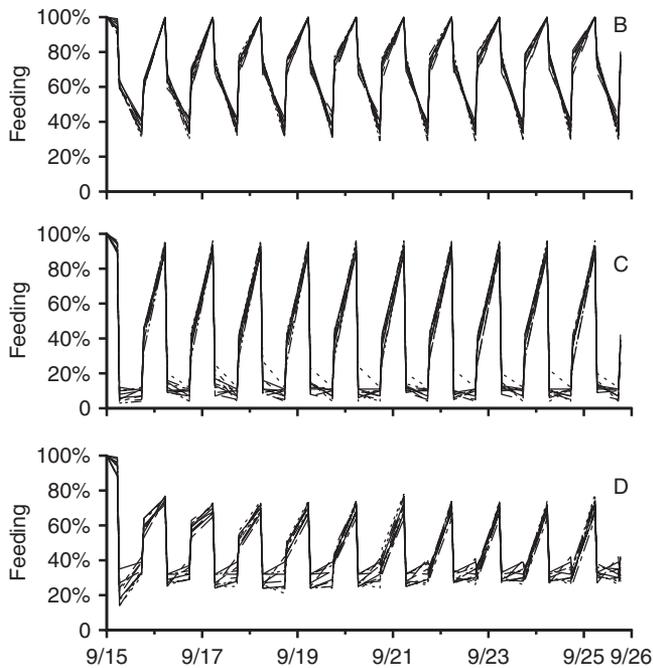


Figure 2

Percentage of simulated trout feeding over all time steps of the standard scenario, using theories B–D (constant prediction, one-day memory, multiday memory). Theory A (ignore circadian cycles) caused all trout to feed all the time. Separate lines represent each of 10 replicate simulations. *x* axis tick marks represent midnight.

start by exploring the behavior produced by each theory under the standard simulation scenario and end by contrasting the fitness provided by the theories under realistic simulation conditions.

Standard scenario

All four alternative theories caused the simulated trout to settle into consistent circadian feeding rhythms, within a few days (Figure 2). Even the multiday memory theory using memory from the previous 9 days produced consistent behavior by about the eighth day. Because of this consistency, we present most results in subsequent analyses by looking at behavior only during the final day of the simulation, as in Figure 3. Differences among replicate simulations were also small (Figure 2); therefore, in subsequent figures we display means over 10 replicates of each scenario but do not show error bars, to improve figure clarity.

The ignore circadian cycle theory caused all trout to feed all the time. This result is not surprising because it uses the extremely simple prediction that the individuals' current behavior would persist until the time horizon. Individuals always feed because when they consider hiding for a time step, they predict that they would hide until the time horizon 90 days in the future, which would place them at very high risk of starvation.

In contrast, the other three theories produced reasonable circadian feeding rhythms (Figure 3). The exact rhythms differed among the theories, but the most important characteristics were consistent across them: nocturnal feeding being dominant, and less feeding in daytime than in crepuscular periods (though this difference was small for the multiday memory theory). Crepuscular feeding is more common than diurnal presumably because it offers considerably lower risk due to lower light levels but also because a trout must feed in several crepuscular periods to obtain as much growth

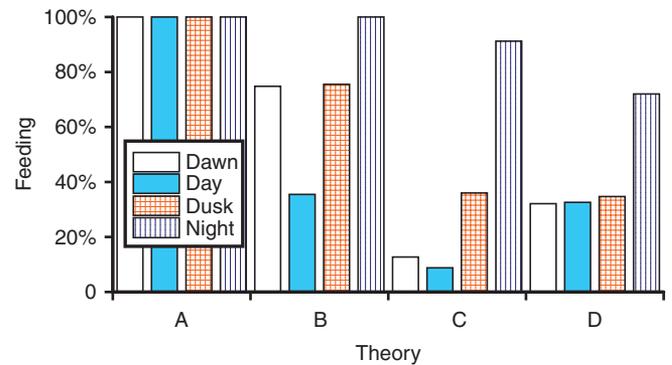


Figure 3

Percentage of trout feeding during each phase of the circadian cycle, for each theory, on the last simulated day of the standard scenario.

as in one daytime. The constant prediction theory produced more feeding overall than the one-day and multiday memory theories, presumably because it does not consider actual weight gain but always assumes zero growth in previous time steps. The constant prediction and multiday memory theories produced equal levels of feeding activity in dawn and dusk, but the one-day memory theory produced more feeding in dusk than dawn. This difference appears to be because the one-day memory theory produced less-frequent diurnal feeding so individuals more often had lower body condition entering dusk and thus had more incentive to feed.

How good is the behavior produced by the alternative theories, and how significant are the differences among theories? It is not trivial to answer these questions. Ideally, these approximate theories could be compared to an optimal solution, but competition among trout makes calculation of optimal behavior extremely cumbersome. (Because the model assumes a length-based hierarchy, optimization of these simulations that lack temporal variation in habitat could be possible by optimizing one individual at a time, from largest to smallest.)

We can evaluate the predicted behaviors by looking at their effects on the two components of individual fitness in our model: survival of predation and starvation. To quantify the first component, we used the probability of surviving predation (and the other non-starvation mortality risks) over the last full day of our 10-day simulations: the value of P_D as described above for the one-day memory theory, for the habitat and activity chosen on the last time step. As a measure of starvation survival, we used the body condition (K ; fraction of "healthy" weight at the end of the simulation, used as our driver of starvation) averaged over the last full day of the simulation, weighting values from each phase by the length of the phase. In contrast to the measure of predation survival, body condition inexactly indicates starvation survival, which is a complex and non-linear function of condition and future growth. We report the average values of these measures for the total of 1000 fish included in the 10 replicate simulations of each scenario.

Because it caused continual feeding, the ignore circadian cycle theory resulted in high body condition but substantially lower survival probability (Figure 4). (The difference between daily survival probability of 0.996 for this theory and 0.998 for the other theories may seem small, but these probabilities correspond to 23% vs. 48% probability of surviving a year.) Even though the other three theories produced different circadian feeding rhythms (Figure 3), they produced similar survival probabilities and only small differences in condition on the last day of the 10-day simulation. (The body

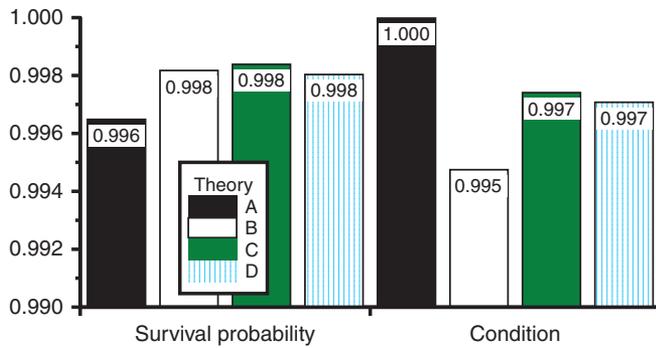


Figure 4 Daily survival probability (left) and body condition (right) of simulated trout on the last simulated day, in the standard scenario. Values are means over 100 simulated trout in each of 10 replicate simulations.

condition values of 0.995 for the constant prediction theory and 0.997 for one-day and multiday memory theories, if maintained steadily, produce one-year starvation survival probabilities of 88% and 89%.)

We also evaluated the theories by comparing their fitness outcomes to those of 16 simulations that each forced all trout to use one of the 16 possible combinations of feeding and hiding over the four circadian phases. These simulations are not a way to find “optimal” behavior because 1) individual variation in size and competition means that different combinations are likely to be best for different individuals and 2) they did not allow switching among circadian rhythms, which could be more successful than following one continually. However, results of these 16 simulations (Figure 5) do provide a baseline for comparison to results produced by our theories. Eight of the behavior combinations produced mean survival probability equal or greater than those of the constant prediction, one-day memory, and multiday memory theories, and four produced condition equal or greater than those theories did. However, none of the combinations produced *both* survival probability and condition as high as those three theories did.

Pattern 1: More diurnal feeding when food availability or fish condition is low

We evaluated the ability of our theories to reproduce this pattern in two simulation experiments. First, the parameters for availability of drift and search food were varied from 0.2 to 3.0 times their standard values, in eight scenarios. In the second experiment, the starting condition factor *K* of simulated trout was varied, in five scenarios, from 0.5 to 1.0. Lower values of *K* place trout at higher risk of starvation so their trade-off decisions should more strongly emphasize energy acquisition.

In both of these experiments, the ignore circadian cycle theory produced feeding during all phases of the day, under all levels of food availability and body condition. Because of this inability to produce trade-off behaviors, we exclude this theory from the remaining analyses.

In the food availability experiment (left panels of Figure 6), the constant prediction theory did not produce the expected pattern: it resulted in nocturnal feeding at all food levels and no consistent increase in diurnal feeding as food availability decreased. The one-day and multiday memory theories produced similar results: as food availability decreased, diurnal and crepuscular feeding increased

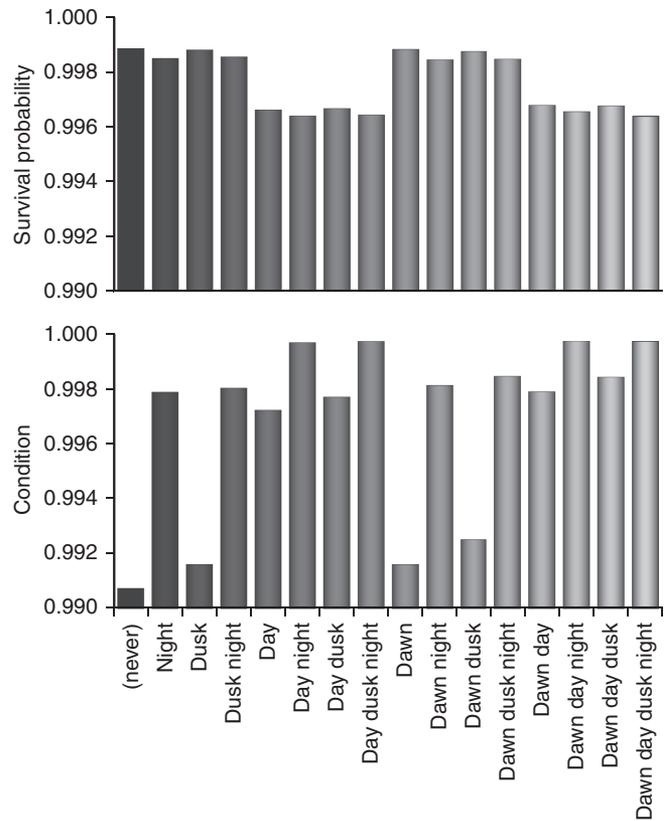


Figure 5 (Top) Daily survival probability and (bottom) body condition results of simulations forcing fish to use each of the 16 possible activity patterns. The bar labels indicate when the fish fed. Results are from the last day of 10-day simulations; means over 10 replicate simulations.

sharply while nocturnal feeding decreased. In the experiment that varied the starting value of *K* (right panels of Figure 6), the constant prediction theory again produced nocturnal feeding in all scenarios, with crepuscular and then diurnal feeding increasing as starting condition decreased. The one-day and multiday memory theories produced transitions from primarily nocturnal to primarily diurnal feeding as starting condition decreased, but different patterns in crepuscular feeding.

Pattern 2: More diurnal and crepuscular feeding at higher temperatures

We tested the ability of each alternative theory to reproduce this pattern by running the model 11 times using the standard inputs except for temperature, which was varied from 2 to 22 °C. Then, to evaluate the ability of model trout to respond to changes in temperature, we also simulated a temperature excursion: a period of 27 days in which temperatures were constant at 10 °C for 5 days, then decreased from 10 to 2 °C by 2 °C per day, increased by 2 °C per day to 20 °C, and then returned to 10 °C and held there for five more days. (Temperature changed at the start of the night phase.)

In the constant temperature simulations, the constant prediction, one-day memory, and multiday memory theories caused the model to reproduce the pattern, with diurnal feeding especially increasing with temperature (Figure 7). Under the constant prediction theory, all trout again always fed at night and often also during crepuscular

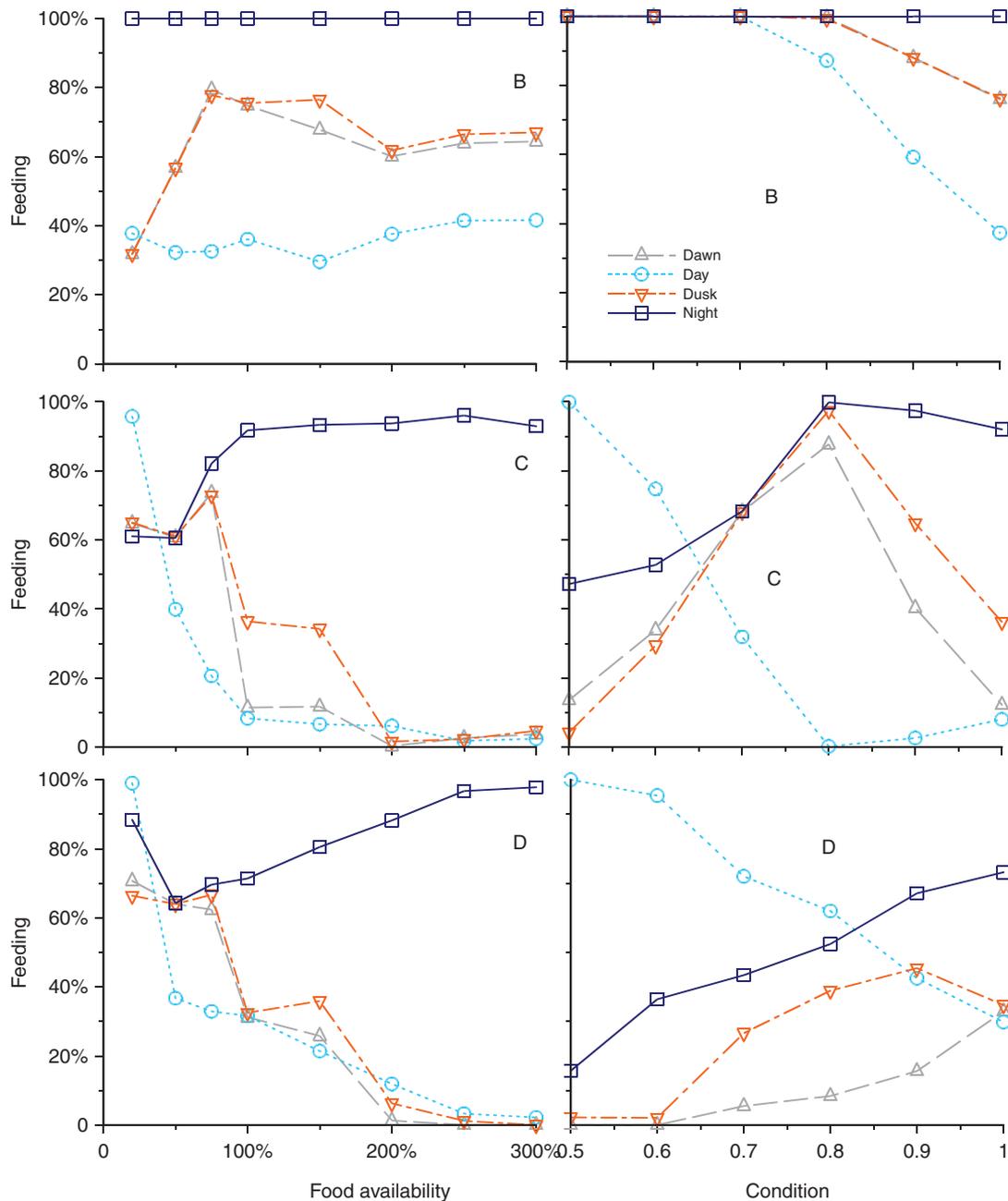


Figure 6

Response of feeding activity to (left) food availability, as percentage of standard availability of drift and search food, and (right) starting body condition K . The ignore circadian cycle theory is not shown because it produced feeding at all times in all scenarios.

periods. Diurnal feeding increased rapidly with temperature above 10 °C, and the frequency of crepuscular feeding increased rapidly at temperatures above 12 °C. Under the one-day and multiday memory theories, there was some diurnal feeding at all temperatures but mostly nocturnal feeding at temperatures below about 12 °C; as temperature increased further, feeding switched from primarily nocturnal to primarily diurnal. Presumably because crepuscular periods contribute relatively little to daily growth when food availability is constant, patterns in crepuscular feeding were more complex and less consistent.

The high frequency of crepuscular feeding at the lowest temperature under the one-day and multiday memory theories seems

surprising. This anomaly results from inSTREAM's assumption that maximum food consumption rate decreases with temperature and is very low at 2 °C. This assumption is based on observations that low temperatures slow physiological processes including digestion (e.g., Kepler et al. 2014). Apparently, food intake was so limited by the temperature effect on digestive rate that trout had to feed for additional time at 2 °C to meet even their reduced metabolic needs.

The temperature excursion experiment produced clear differences among theories (Figure 8). The constant prediction theory produced some response to the initial dip in temperature, with less diurnal and more crepuscular feeding during the dip, and the frequencies of diurnal and crepuscular feeding followed the

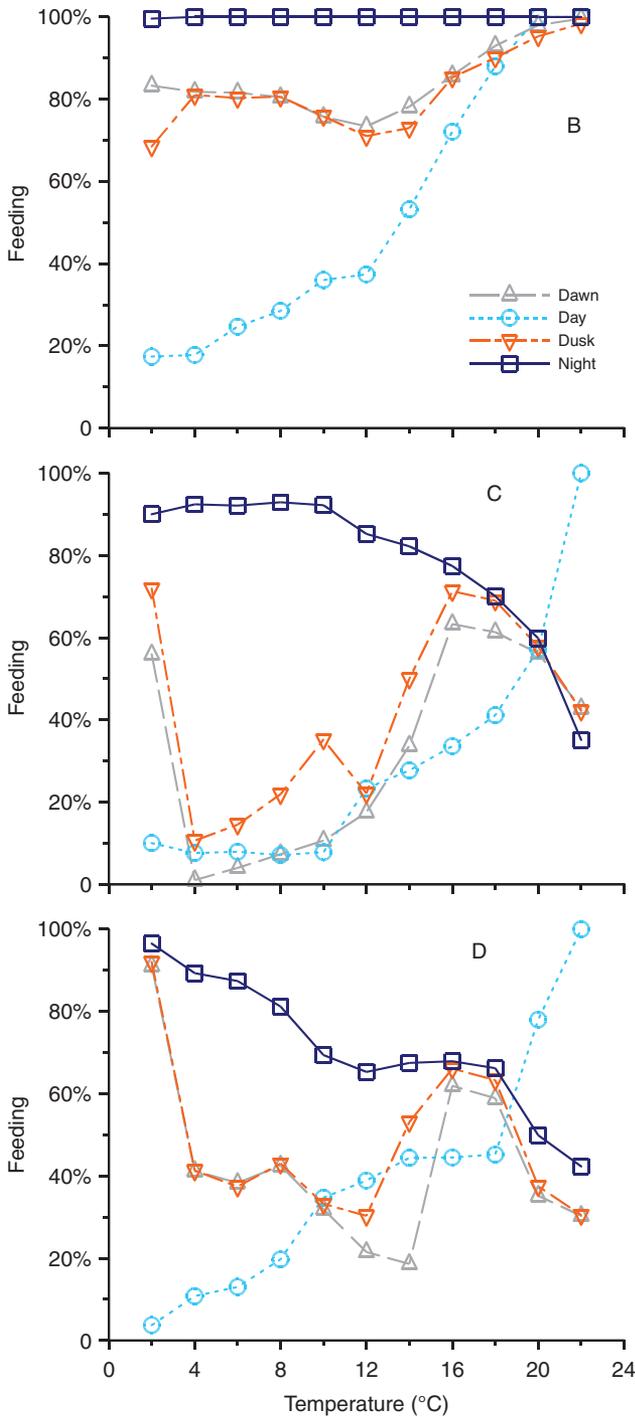


Figure 7 Percentage of trout feeding during each phase in simulations with temperatures from 2 to 22 °C, for theories (top to bottom) B–D (constant prediction, one-day memory, multiday memory).

subsequent temperature spike. The one-day memory theory produced a clearer response to the initial temperature dip, with dusk feeding decreasing as temperature dropped, then the increase in crepuscular feeding at the lowest temperature as observed in the constant-temperature experiment. During the temperature spike, the frequency of crepuscular feeding rose and fell with temperature, and diurnal feeding increased slightly at the highest temperature.

The multiday memory theory produced a response to the initial temperature dip but not until several days after it had ended. That theory also produced a delayed response to the spike.

Under the constant prediction and, especially, the one-day memory theory, the circadian rhythm did not return at the end of the experiment to its form at the beginning, apparently due to loss of body condition during the temperature spike (Figure 9). At the highest temperatures, model trout lost weight instead of assuming the predation risk needed to fully meet the higher metabolic demands. After temperatures decreased, the reduced condition caused the trout to feed more often during crepuscular phases (constant prediction) or diurnally (one-day memory) to regain weight.

Pattern 3: Feedbacks of competition on circadian foraging

We evaluated the ability of the alternative foraging theories to reproduce this pattern by varying the number of trout in the simulations from 5 to 500. Responses to trout abundance are complex and difficult to predict because they emerge from several processes, including competition for safe and productive feeding locations, which vary in abundance and location over the circadian cycle, and for concealment cover.

All theories except ignore circadian cycles produced strong effects of competition (Figure 10): as trout abundance increased from very low, feeding changed from primarily nocturnal to increasingly crepuscular and diurnal. The main difference among theories is again that the constant prediction theory caused all individuals to always feed at night, whereas the other theories did not.

Pattern 4: Circadian cycles of food availability affect foraging

We examined the extent to which the theories cause feeding activity to respond to increasing food availability during crepuscular periods. The simulation experiment varied the availability of food, only during dawn and dusk periods, from 0 to 10 times the standard value. Because the two crepuscular periods make up only about 9% of the day, these scenarios vary total food availability from 0.9 to 1.8 times that of the standard scenario.

The constant prediction theory produced a modest response in crepuscular feeding, but opposite the expected increase (Figure 11). Under this theory, a rhythm of always feeding at night and about 30% feeding in day appeared locked in, so higher food availability in crepuscular periods allowed the trout to meet their metabolic demands with less-frequent crepuscular feeding. The one-day memory theory produced the expected increase in crepuscular feeding—especially during dusk, presumably because it follows day, when trout rarely fed—and decreases in nocturnal and diurnal feeding, almost completely eliminating the need to feed during daytime. The multiday memory theory produced a response similar to that under one-day memory but with less increase in dusk feeding.

One-year simulations of realistic conditions

Our final exploration of the four alternative theories for activity and habitat selection simulated a full year (October 2000 through September 2001) using observed time series of flow, temperature, and turbidity as the input driving decisions. The mortality function was activated so that simulated trout could die of predation, starvation, or other less-likely causes. The primary output of interest was survival rate, measured as the percentage of the 100 initial trout that survived the year. We also looked at final mean length of trout as a measure

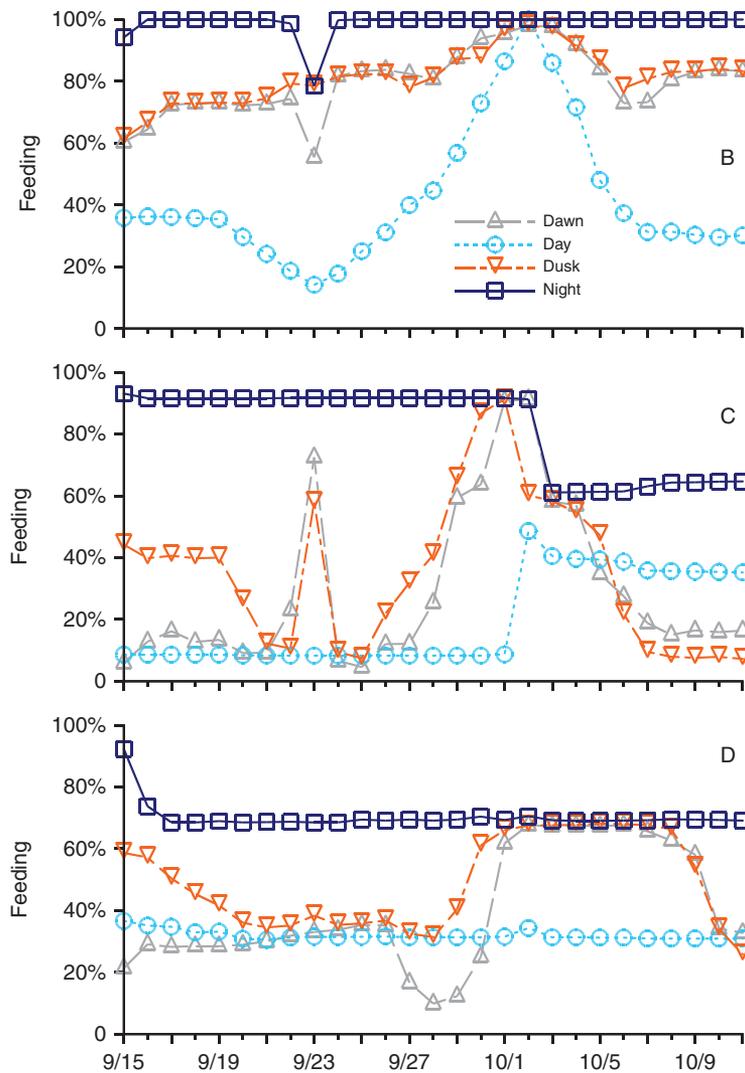


Figure 8 Results of the temperature excursion experiment: percentage of trout feeding in each phase of each simulated day, for (top to bottom) theories B–D.

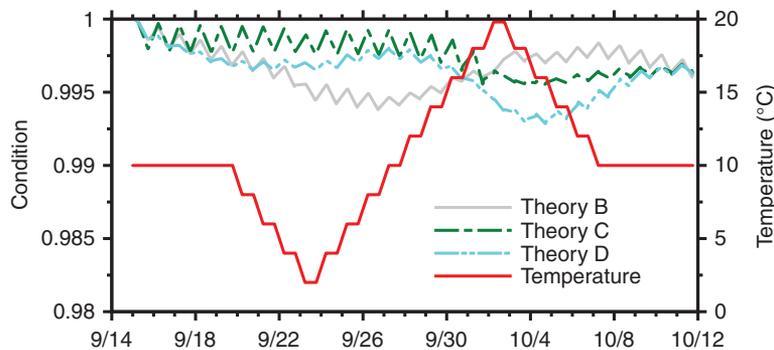


Figure 9 Time series of mean trout body condition during the temperature excursion experiment, for theories B–D. Low-amplitude circadian cycles in condition are apparent as fish alternate between feeding and hiding.

of growth; higher growth is not an indicator of decision success and in fact we did not expect model trout to grow much because the fitness measure used in all the theories seeks long-term survival only, not growth. However, growth does indicate how the trade-off between feeding and avoiding predation differed among theories.

The results (Figure 12) indicate that all four theories produced behavior sufficient for some individuals to survive for a year, though the one-day memory and multiday memory theories produced substantially higher survival than did the other two. As expected because it produced near-constant feeding, the ignore circadian cycle

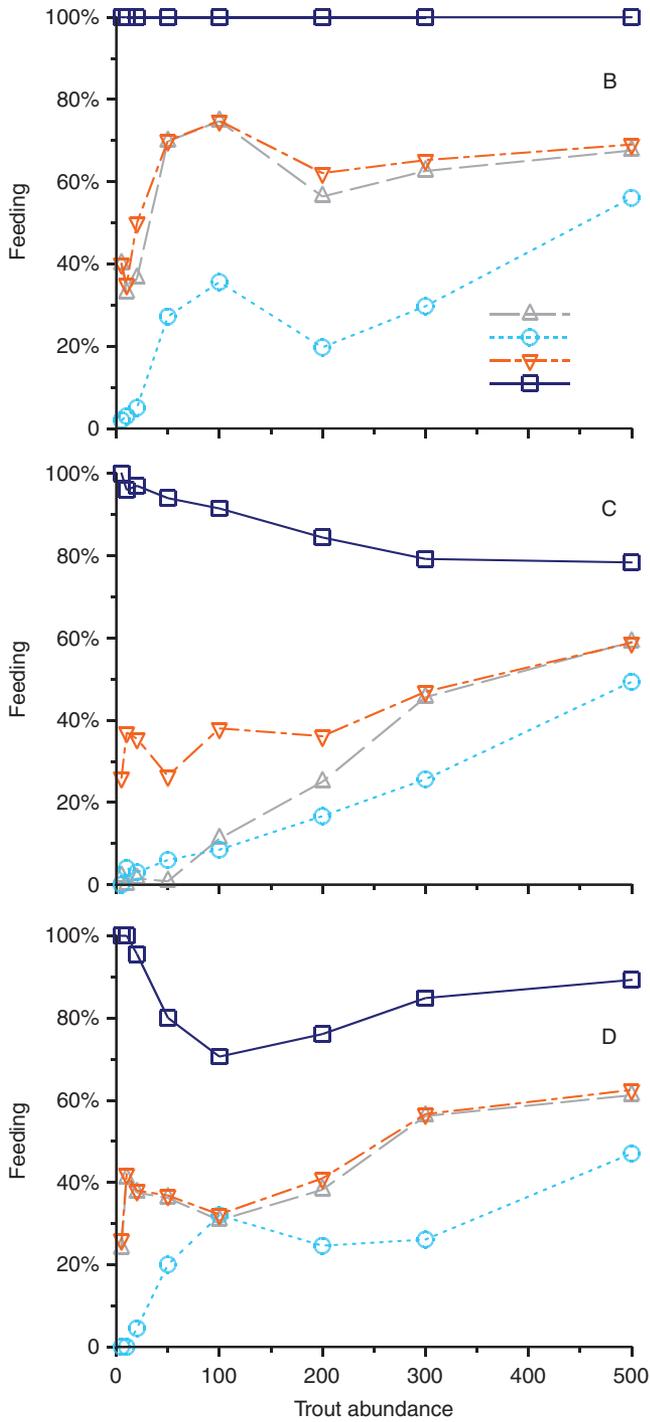


Figure 10 Competition experiment results: percentage of simulated trout feeding during each phase at simulated abundances of 5–500.

theory produced much lower survival than the others. The constant prediction theory produced both growth and survival lower than the one-day memory and multiday memory theories.

The constant prediction and multiday memory theories depend on parameters that are not in the other theories, cannot be estimated from data, and were not calibrated prior to these simulation experiments. An exploration of the constant prediction theory's parameters G_B and P_B indicated that, for 1-year

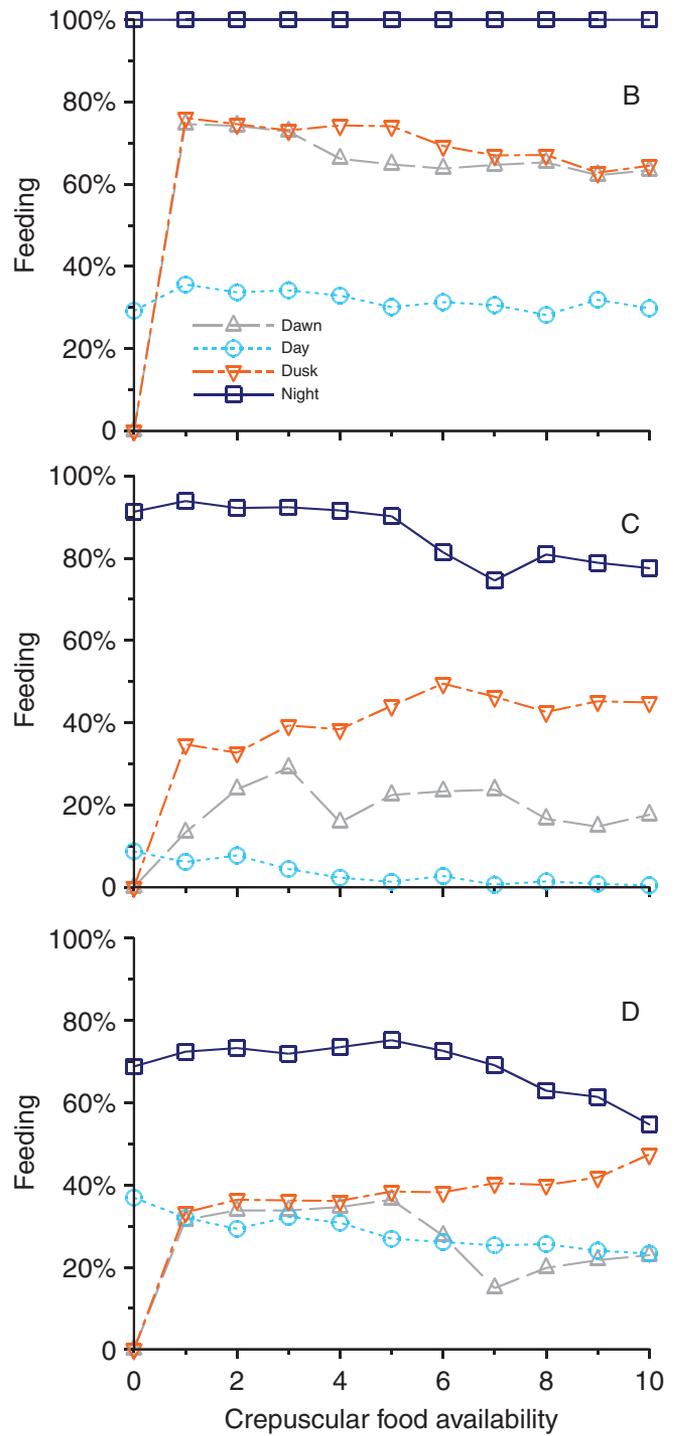


Figure 11 Crepuscular food availability experiment. The x axis is the factor by which standard food availability was multiplied during dawn and dusk.

simulations at our study site, higher survival was obtained when G_B was slightly negative. When G_B is negative, individuals decide whether to feed under the assumption that they lose weight in the other parts of the circadian cycle, which provides motivation to feed in the current phase. Varying the multiday memory theory's memory length n from 5 to 20 days produced no clear effect on survival over the year.

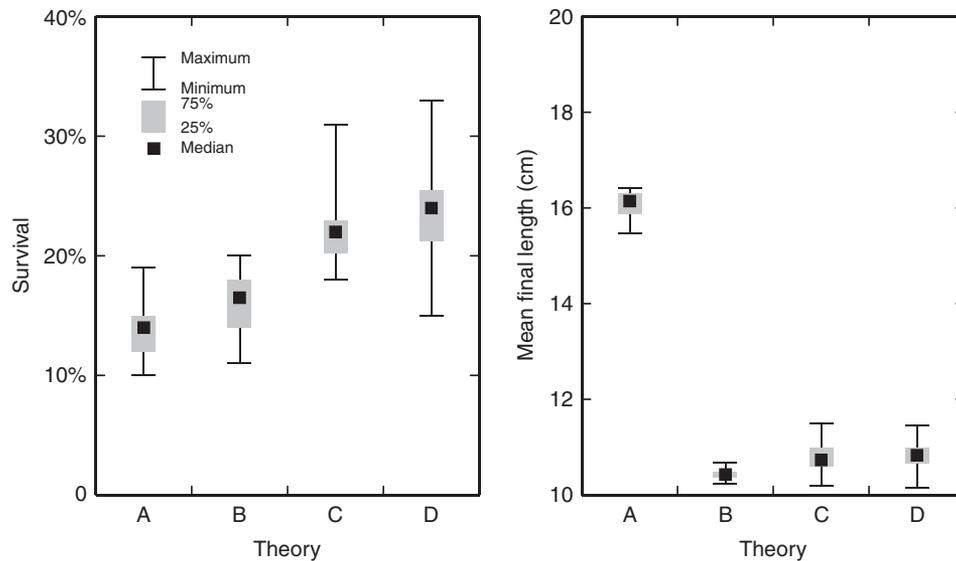


Figure 12

Survival and growth in the 1-year simulations. Left: percentage of 100 initial trout that survived for 1 year. Right: mean final length of surviving trout (initial mean length was 10 cm). Because survival is partially stochastic, plots display the distribution of results over 10 replicate simulations.

Table 1

Summary of the pattern-oriented theory tests^a

Pattern	Theory			
	A: Ignore circadian cycles	B: Constant prediction	C: One-day memory	D: Multiday memory
1: More diurnal feeding when food availability or fish condition is low	–	–	+	+
2: More diurnal and crepuscular feeding at higher temperatures	–	+	+	+
3: Feedbacks of competition on circadian foraging	–	+	+	+
4: Circadian cycles of food availability affect foraging	–	–	+	+
5: Less diurnal feeding under higher predation risk	~	+	~	+
6: Physical habitat affects circadian foraging	–	+	+	+
7: Day length affects circadian foraging	–	+	+	+

^aPatterns 5–7 are analyzed in [Supplementary Material](#). Explanation of symbols: + means that the pattern was robustly reproduced by the theory, ~ means that the theory neither robustly reproduced nor contradicted the pattern, and – means that the theory produced results contradicting the pattern.

DISCUSSION

The kind of behavior we address is widely recognized as essential to all levels of ecology. Trade-off decisions are not just important as individual behavior, but can also affect population-, community-, and ecosystem-level dynamics through mechanisms such as nonconsumptive trophic interactions. Modeling trade-off behaviors of diverse individuals in IBMs that contain natural complexities such as competition and environmental variability can provide unique insights into population and community dynamics, yet doing so remains a challenge (Railsback and Harvey 2013).

We applied four versions of SPT, of increasing complexity, to this challenge. We then treated the theories as alternative hypotheses in a pattern-oriented theory development cycle (Grimm et al. 2005; Grimm and Railsback 2005), testing their ability to reproduce, in our trout IBM, a variety of patterns observed in real systems. Because we focused on qualitative patterns instead of quantitative model results, we were able to test theory without calibrating—and potentially biasing—the model to a particular study site.

Our simulation experiments indicate that the three SPT theories that consider the full circadian cycle could all produce usefully realistic behavioral responses to a wide variety of conditions and relatively high survival in long-term simulations with realistic habitat variability (Table 1). In contrast, the ignore circadian cycle theory consistently produced unrealistic behavior. This difference supports our first two general conclusions: 1) SPT can produce successful circadian habitat and activity selection decisions in a population context that includes feedbacks, but 2) it is essential for the theory to consider the full circadian cycle: decisions at each phase must consider what happens at other times of day.

Our third general conclusion is supported by results of the experiment in which we compared results of the four theory alternatives to results when model individuals were forced to use fixed circadian activity rhythms (Figure 5) while still choosing the best habitat each time step. We found that our theories that let individuals update their decisions each time step in response to their current state and environment (which in this experiment changed only due to competition with others for food and concealment cover) produced higher

individual fitness (approximated as the combination of survival and condition) than any of the fixed rhythms. Therefore, we conclude that highest fitness is provided not by a fixed circadian behavior pattern but instead by the ability of individuals to adapt over time. Two mechanisms might explain this conclusion. First, individuals can avoid competition by feeding when fewer others are feeding, so an activity pattern best for most of the population may not be best for some individuals, especially in a dominance hierarchy. Second, even for an isolated individual the best behavior pattern could include variation among days, for example by feeding only every other night.

All our theories except ignore circadian cycles produced adaptive behavior that reproduced the observed patterns and provided high individual fitness, even though they often produced quite different circadian activity rhythms. The one-day memory and multiday memory theories especially produced, in many experiments, different rhythms but similar survival and condition results. Our fourth conclusion therefore is that, at least in the system we modeled, a variety of circadian activity rhythms may be nearly equally good. The interactions among activity, habitat, and competition contribute to the similar fitness offered by various alternatives. For example, when competition for feeding habitat at night would force use of relatively risky habitat, it may be almost as safe and more energetically profitable to feed in a safer patch during day. Such trade-offs were particularly clear in simulations (not presented here) we made of a large, deep river: as we increased predation risk, for example, model trout responded not only by increased nocturnal feeding but also by feeding diurnally in deeper habitat.

Which theory is best? Here we summarize what we learned about each. The ignore circadian cycle theory uses the prediction that current conditions will persist until the time horizon; this prediction has worked well for habitat selection behavior in models without circadian cycles (Railsback and Harvey 2002, 2020), but it does not appear useful for the contingent behaviors of activity and habitat selection or for cyclical environments.

The constant prediction theory is the simplest that considers the full circadian cycle. It caused the IBM to reproduce all of our evaluation patterns except patterns 1 and 4. However, in many experiments, its behavior was less responsive, especially in consistently producing nocturnal feeding in all individuals. Experiments not presented here indicate that universal nocturnal feeding was not hardwired by this theory; it does not occur when individuals assume they lose rather than just maintain weight in phases other than the current one. This theory also produced substantially lower survival in the full-year simulation. The simplicity of this theory is appealing and it may deserve consideration for especially simple models. However, its dependence on two unmeasurable parameters (growth and survival assumed for phases other than the current one) is a clear disadvantage.

The one-day memory and multiday memory theories differ only in the amount of recent experience individuals use to predict future conditions. They both caused the IBM to reproduce the seven evaluation patterns (Table 1), at least over some ranges. In some cases, the two theories produced surprisingly different circadian rhythms with similar overall fitness. However, the temperature excursion experiment (Figure 8) showed that the multiday memory theory can produce behavior that lags behind environmental drivers, which does not seem realistic or adaptive. On the other hand, that theory could keep short-term events from biasing decisions too strongly. The relative benefits of the one-day and multiday memory theories will depend on patterns of variation in environmental drivers.

(A theory that discounts older memories could be developed and evaluated as a compromise between these two.)

This study illustrates how behavior theory can be evaluated not just at the individual level but by the population- and higher-level dynamics it produces. Implementing foraging theory in an IBM and examining its higher-level effects via simulation has several benefits. First, it forces the theorist and the theory to confront the natural complexities in the IBM, making it more likely that the theory is applicable to reality. Second, simulation allows us to confront alternative theories with a more comprehensive range of tests than is typically feasible through experiments on real organisms. We used a wide range of observations from the literature, at both the individual and population levels, instead of conducting new field or laboratory studies. Most importantly, this approach can result in theory and models useful for understanding and predicting how the dynamics of real populations and communities emerge from individual behavior.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

Supplementary material provides a complete description of the stream trout model, and description and analysis of the three additional patterns included in Table 1.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Railsback (2020).

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