

Trait-mediated trophic interactions: is foraging theory keeping up?

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Many ecologists believe that there is a lack of foraging theory that works in community contexts, for populations of unique individuals each making trade-offs between food and risk that are subject to feedbacks from behavior of others. Such theory is necessary to reproduce the trait-mediated trophic interactions now recognized as widespread and strong. Game theory can address feedbacks but does not provide foraging theory for unique individuals in variable environments. ‘State- and prediction-based theory’ (SPT) is a new approach that combines existing trade-off methods with routine updating: individuals regularly predict future food availability and risk from current conditions to optimize a fitness measure. SPT can reproduce a variety of realistic foraging behaviors and trait-mediated trophic interactions with feedbacks, even when the environment is unpredictable.

Trait-mediated trophic interactions: a new challenge for foraging theory

Ever since the idea was expressed that evolution has equipped organisms with behaviors that can be represented as an optimization [1,2], foraging theory has been adapted to problems of increasing complexity. One jump in complexity was from decisions that optimize a single resource (typically, food intake or growth) to decisions that make trade-offs between growth and mortality risk. Now, a prominent challenge for foraging theory is jumping from strictly individual-level models to theory that considers feedbacks and integration across ecological levels. Instead of modeling decisions made by individuals in isolation, how do the individuals in a population or community make decisions when the alternatives available to them, and the consequences of their decisions, depend on the other individuals and their decisions? In such population and community contexts, community-level characteristics emerge from individual behavior; at the same time, individual behavior depends on emergent community-level characteristics, such as resource competition and predator distribution. This kind of integration across ecological levels (individual–population–community) and feedbacks of behavior are of intense interest in modern ecology [3,4].

The importance of integrating individual, population, and community levels is exemplified by ‘trait-mediated

trophic interactions’. Classical models of interaction among trophic levels, such as predator–prey population dynamics, assume that effects are ‘density mediated’: that is, the rate at which a predator population consumes prey depends on the density of predators (and prey). However, it is now widely accepted that predators also cause prey to modify their traits (e.g., behavior, life-history decisions, and morphology) to reduce predation risk. Trait modification to avoid predation typically has a cost of reduced growth or reproductive output. Hence, predators still affect prey populations, but the effects are trait mediated as well as density mediated.

Complex trophic interactions resulting from plasticity in individual traits, especially modification of foraging behavior to avoid predators, have been a popular topic over the past two decades [5]. Abrams [6] showed that predator-avoidance behavior invalidates the classical models of trophic interactions, and numerous empirical studies have shown that such trait plasticity is indeed common and capable of strongly affecting trophic interactions [5,7].

Foraging theory should be important for understanding and predicting trait-mediated interactions and integrating ecological levels: theory for how individuals decide when, where, and on what to feed, in response to variability in food resources, predation risk, and intraspecific competition, seems essential for understanding and predicting links and feedbacks among individuals at their population level and with both higher and lower trophic levels. However, there is concern in ecology that foraging theory is not keeping up in that there is no theory for foraging decisions that provides such understanding and prediction [4,8,9].

Foraging theory that can reproduce trait-mediated interactions is important for two reasons. First is so that the direction and strength of trait-mediated effects can be evaluated via bottom-up modeling. These effects are (as literature cited below shows) variable and context dependent, so evaluating them via empirical studies alone is challenging. Individual-based modeling, in which trophic interactions emerge ‘bottom up’ from individual behavior, is potentially a productive alternative, but only if such models are equipped with adequate foraging theory. The second reason is to develop foraging theory that can be used confidently in applications (e.g., conservation problems [10]) where trait plasticity is important. Foraging theory that reproduces observed trait-mediated trophic interactions should provide a

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deeper understanding of individual behavior and better models of the population- and community-level phenomena that emerge from behavior.

In this review, we examine how well foraging theory is keeping up with the new understanding of trophic interactions: is there theory that can reproduce trait-mediated trophic interactions in bottom-up models of simple communities? We first define the problem specifically by identifying characteristic, well-documented trait-mediated interactions as a ‘test bed’ for foraging theory. If one implements a particular kind of foraging theory in an individual-based model with variation in food resources and risk over time and space, and competition among individuals, will the model reproduce these characteristic trophic interactions? We identify characteristics that foraging theory must have to reproduce the characteristic interactions and review examples of such theory. Finally, we discuss what this problem indicates about how ecologists think about, develop, and test theory for adaptive behaviors such as foraging.

Characteristic trait-mediated trophic interactions

The interest in trait-mediated trophic interactions has produced an extensive literature, common protocols for empirical experiments, and a widely used model system

and terminology (Box 1). The empirical evidence for interactions such as ‘non-consumptive effects’ and ‘trait-mediated indirect interactions’ (NCEs and TMII, respectively; Box 1) has been the subject of many studies and several influential reviews [5,7,11]. This literature identifies the following common patterns that seem to characterize trait-mediated trophic interactions; foraging theory that can produce these patterns is likely to explain and predict NCEs and TMII in general.

- Strong trait-mediated effects. Predator avoidance behavior can strongly reduce prey populations and their resource consumption, often by more than predation mortality itself does [5,7,11].
- Bottom-up effects. ‘Bottom-up’ TMII occur when changes in resource availability induce changes in prey behavior that then affect the rate of predation mortality [5,12]. The TMII appears at the predator level: consumption of prey by predators decreases as prey resource availability increases. (Without predator avoidance, higher resource availability would produce more prey and, therefore, increase consumption of prey by predators.)
- Prey density effects. The strength of NCEs and TMII can vary with density of prey because stronger competition for resources reduces the scope for prey

Box 1. Terminology and the tritrophic model system

Much of the theoretical (e.g., [6,7]) and empirical [5,40] work on indirect trophic interactions has used three-level (tritrophic) food chains as model systems. Furthermore, a common protocol has often been used to evaluate the strength of trophic interactions in both empirical and simulation experiments [5,7,41]. The terms and numerical measures used to define trait-mediated interactions have been debated [41]; here, we provide simple terms and measures that convey the essential concepts.

The tritrophic model system has at the top ‘predators’, which consume the middle level, ‘prey’, which in turn consume the ‘resource’. The common experimental protocol requires observing prey population status and resource consumption under three scenarios (Figure 1): ‘no predators’ (NP), in which there is no predation and prey perceive no risk; ‘with fear’ (WF), with prey perceiving and behaving to avoid predation risk but no actual predation mortality; and ‘with predators’ (WP), with prey perceiving and avoiding risk and predation actually occurring. Consumptive effects (CEs) are the effects of one level on the next lower level via direct consumption, not antipredator behavior. At the prey level, the CE due to predators is quantified as the fraction by which prey populations are reduced by actual predation (Equation I):

$$CE = \frac{N_{WF} - N_{WP}}{N_{NP}} \quad [I]$$

Non-consumptive effects (NCEs) are due to antipredator behavior alone (e.g., via reduced food intake and, hence, lower size and fecundity). In the tritrophic protocol, NCEs at the prey level are measured as the decrease in population due to predation avoidance (Equation II):

$$NCE = \frac{N_{NP} - N_{WF}}{N_{NP}} \quad [II]$$

The total effect of predators is the sum of CE and NCE (Equation III):

$$\frac{N_{NP} - N_{WP}}{N_{NP}} \quad [III]$$

Indirect effects occur between the top and bottom levels due to changes in the middle level. Indirect effects of predators on the resource level due to changes in prey density are termed ‘DMII’, often

evaluated as the (positive) change in resource population due to predation (Equation IV):

$$DMII = \frac{R_{WP} - R_{WF}}{R_{NP}} \quad [IV]$$

TMII are typically evaluated as the increase in resource due just to the predator-avoidance behavior of the prey (Equation V):

$$TMII = \frac{R_{WF} - R_{NP}}{R_{NP}} \quad [V]$$

Total indirect effects are the sum of DMII and TMII. (DMII and TMII are also sometimes evaluated as changes in resource consumption by prey, which decreases with predation and antipredator behavior; e.g., equations 5 and 6 of Luttbegg *et al.* [26].)

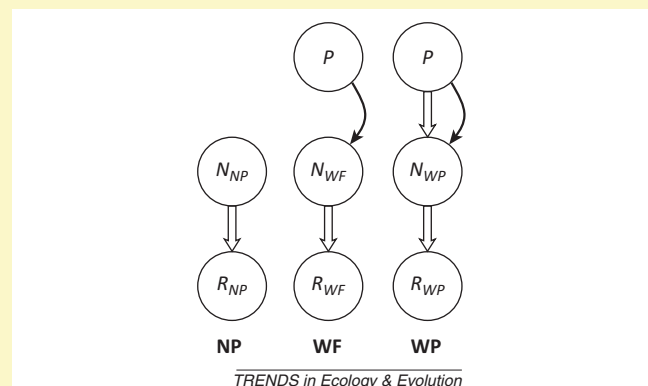


Figure 1. Interactions in the tritrophic model system and experimental protocol. P, N, and R are measures of population (e.g., biomass or abundance at the end of an experiment) for the predator, prey, and resource trophic levels, respectively. The wide vertical arrows represent consumption of a lower level by a higher level. The curved arrows represent nonconsumptive, trait-mediated effects, that is, changes in a lower level resulting from antipredator behavior in response to the higher level.

to further reduce feeding to avoid predators [13]. Predator avoidance behavior also can strongly reduce density dependence in growth: there is less competition among prey when they reduce feeding to avoid predators (e.g., [14]).

- **Environmental effects.** Environmental factors can alter trait-mediated effects [5]; in one example, nutrient levels affected the relationship between resource consumption and prey growth and, therefore, the strength of TMIs and NCEs [15]. Environmental factors that affect metabolic rates, such as temperature, can affect trait-mediated trophic interactions by altering the growth prey obtain from a unit of resource and the energy needed to avoid starvation (e.g., [16]).

These simple patterns make clear that foraging theory must have three characteristics if the patterns are to emerge from populations of individuals using the theory. First, theory obviously must make trade-offs between food intake and predation risk; such tradeoffs are the most basic driver of the patterns. Second, theory must be state based, with decisions depending on the energetic status and metabolic rate of the individual. Third, reproducing prey density effects requires theory that accommodates feedbacks of behavior. To model how prey individuals behave in response to their own population density, when that density depends on how they behave, theory must let individuals adapt and change their behavior in response to the behavior of others in their population. (In models with predators responding to prey behavior, foraging theory must also let prey respond to changes in predator behavior.) What is needed then is theory for how each individual in a population (or community) of unique, competing individuals chooses from day to day from among many foraging alternatives, when the risks and food intake from each alternative (and even the number of alternatives) varies with the state and previous behavior of the individual, the state and behavior of other individuals, unpredictable environmental variability, and the dynamics of adjacent trophic levels.

Is foraging theory up to the task?

Two of the three characteristics that we seek (the ability to make trade-offs between food intake and predation risk, which are also state-based) are well established in foraging theory [17]. The basic theoretical concept is that both food and survival of predation are fundamental elements of fitness, so trade-offs can be made by modeling how both affect a specific measure of fitness (e.g., probability of survival or expected reproductive output) over a future time horizon. Low food intake increases the probability of starvation and lowers fecundity, whereas predation risk reduces survival; therefore, animals can select the alternative that provides, for example, the highest expected reproductive output (the product of starvation survival probability, predation survival probability, and fecundity) at the start of the next reproductive season. This concept, with optimization techniques to find the best alternatives over the time horizon, has been formalized as a widely applicable type of theory [18–20] that we refer to as ‘dynamic state-variable modeling’ (DSVM).

DSVM generally involves four steps: (i) select a fitness measure and time horizon. The fitness measure is a mathematical expression of the fitness of an individual over the time horizon. The fitness measure has terms for key fitness elements, such as survival and fecundity. The choice of fitness measure and time horizon often depends on the life stage of the individual: for an adult in a non-reproductive period, the time horizon might be until the next reproductive cycle starts, with the fitness measure being the probability of survival (of predation and starvation) over the horizon. Once in the reproductive cycle, the horizon might be the time until reproduction, with the fitness measure including fecundity at, as well as survival to, the end of the time horizon. Juveniles might include growth to reproductive size in their fitness measure; (ii) identify the decision alternatives: what decision is the individual making and what are its possible choices? For example, individuals could decide which patch to forage in, with the alternatives being all patches within some radius; (iii) model how the fitness measure depends on the decision alternatives (e.g., the patches or food sources the individual chooses among). This typically requires modeling how food intake, energy costs, and risk vary among the alternatives, and how the fitness measure depends on growth and risk. The current state of the individual (energy reserves, size, etc.) typically is part of this model; and (iv) optimize the fitness measure by selecting the alternative, or sequence of alternatives over time, that provides the highest value over the time horizon. In standard DSVM [19,20], this step uses dynamic programming optimization.

The one characteristic that is needed in foraging theory to explain trait-mediated trophic interactions that is not provided by DSVM is the third one: the ability to accommodate feedbacks of behavior. In DSVM, the optimization that selects alternatives over the time horizon can only be solved if there is a limited number of alternatives, and the risks and benefits of each alternative are known. However, when modeling a population of competing individuals, the alternatives available to each individual depend on the behavior of the other individuals and so cannot be known in advance. In models of any realism, the number of potential future states approaches infinity. (In a trout model discussed below [21], each individual selects, twice per day for a lifespan of years, which cell to feed or hide in; the number of alternative cells ranges from a few to hundreds depending on the size of the individual, which is a product of past decisions. The food intake available in each cell depends on the number and size of other individuals using it, a feedback of the behavior and growth of other trout. Risks and food intake also depend on stream flow, temperature, and turbidity, which vary daily. The feedbacks of behavior and non-simplistic representation of habitat make it infeasible to even determine how many future states are available to an individual over its lifetime.) Hence, behavior feedbacks can make DSVM optimizations intractable and unrealistic, because real organisms continually adapt foraging behavior to changing conditions.

DSVM, similar to traditional foraging theory [1,2,22], has proven extremely useful as an individual-level theory: it models what an individual should do, assuming its future environment, including future food intake and risk,

Box 2. Modeling approaches that do not solve the trait-mediated interaction theory problem

Several approaches for modeling trade-offs between food intake and predation risk have proven useful for other problems, but do not address the specific problem we address here, that is, theory for how unique individuals make trade-off decisions when future alternatives are unforeseeable due to feedbacks of behavior.

Game theory

Many ecologists see problems involving feedbacks as inherently the realm of game theory (e.g., [20]) and related methods, such as 'adaptive dynamics' [42] and coupled equations for predator and prey populations with terms for behavior. Such methods have indeed been applied to foraging problems with feedbacks of behavior [43–46]. However, game theory addresses different questions than the ones we address here. Game theory applies to system-level questions, such as what behavior strategy is 'evolutionarily stable' or produces stable populations under specific population or community conditions, or how competing strategies coevolve, rather than addressing our question of how unique individuals make trade-offs in specific situations. Behavior and evolution are of course linked, but models for evolutionary questions require different simplifications (typically: identical individuals, stable populations, a static or predictable environment, or small numbers of simple strategies) than are useful in foraging models.

Empirical simulations

Some of the classic literature on trait-mediated trophic interactions used computer simulation based on detailed predator and prey behavior; for example, Schmitz simulated movement of grasshoppers and predatory spiders as the grasshopper prey attempted to obtain sufficient food while changing feeding strategy if a spider was detected [47,48]. These models can reproduce the trait-mediated interactions we address (e.g., [49]), but do not provide general, reusable theory for behavior. Decisions are not based on fitness-related assumptions about risk and energy intake, but instead are programmed responses to highly species-, behavior- and situation-specific conditions (e.g., stop feeding for one time step if a predator enters a detection radius).

Artificially evolved traits

Models of adaptive behaviors can be artificially evolved via computer simulation [50–52]. Behaviors are typically represented as artificial neural nets (but see [53]) and 'trained' via genetic algorithms to solve a specific problem, such as selecting among habitats that differ in risk, food availability, and competition. This approach is not considered here because it lacks two characteristics of theory. The models (trained neural nets) do not link decisions to risk and food intake in a way that is subject to ecological interpretation [53] and are not general: artificially evolved traits cannot be assumed useful for decisions or contexts except exactly those they were trained for.

is unaffected by its decision. What we seek instead is an across-level theory that models how each of the individuals of a population behaves as they interact with each other and with lower and higher trophic levels, concerning ourselves not only with individual behavior, but also with behavior of the entire system. (Box 2 discusses other approaches that also do not solve this particular foraging problem.) Is there foraging theory that, similar to DSVM, lets individuals make good risk-growth trade-offs while letting one model feedbacks by avoiding the assumption that future conditions are fixed?

State-based theory with prediction and updating

Several authors arrived at the same relatively simple solution to the inability of DSVM to accommodate feedbacks and uncertain futures, and showed that this solution is indeed the kind of theory that we seek. This solution involves two changes (Box 3). First, instead of making a one-time decision of what to do over an entire time horizon, individuals update their decision periodically as conditions change, as in traditional foraging theory. Second, instead

of assuming individuals know the growth and risk associated with each alternative over the entire time horizon, individuals make a prediction, possibly inaccurate, of the future conditions under each alternative behavior. Each time they update their decision, individuals first update their prediction by considering how their internal state (e.g., size or energy reserves) and external conditions (e.g., food availability, competition levels, or predator presence) have changed. Then, individuals re-evaluate their fitness measure for each alternative and possibly select a different alternative. We term this approach 'SPT' [21]. SPT has parallels to engineering feedback-and-control theory: individuals have a specific objective (fitness) function, use prediction and approximation to select behaviors estimated to maximize the objective, and update behaviors as conditions change.

Example 1: prey in a hypothetical tritrophic system

Luttbeg *et al.* [23] (see also [24]) simulated a hypothetical tritrophic system (as in Box 1) with prey individuals using foraging theory similar to DSVM except that they update

Box 3. State- and prediction-based foraging theory

SPT can be described as four steps executed by individuals when they update their decision (e.g., every day, or when triggered by changing conditions). As an example, we describe how these steps were implemented in an individual-based trout population model [28]. The simulated trout each execute the SPT steps each day, in order from the largest to the smallest individual to represent a feeding hierarchy. The foraging decision is which habitat cell (patch) to feed in.

- (i) Identify available alternatives, that is, the cells that the individual potentially could feed in. Trout consider cells within a radius that increases with their size. Individuals conduct steps (ii) and (iii) for each such cell.
- (ii) Individuals make the simplest possible prediction: that the habitat conditions of each cell (i.e., food availability, competition, temperature and hence metabolic costs, and predation risk) occurring on the current day will persist over the time horizon. The time horizon is always 90 days from the current day,

approximately the time it takes a trout in good condition to starve without food.

- (iii) The fitness measure is the expected survival of both predation and starvation over the time horizon if the individual spent the entire time horizon in the cell. (Assuming the individual spends the entire time horizon in the selected cell is incorrect but greatly simplifies the fitness measure and eliminates the need for a dynamic programming solution.) Expected survival of predation is simply S^{90} , with S the probability of surviving predation during the current day. Expected survival of starvation is a more complex function that depends on current energy reserves, food intake, and metabolic costs (which depend on size, temperature, and swimming speed).
- (iv) The trout moves to the cell providing the highest fitness measure, and its food consumption is subtracted from that remaining available in the cell for smaller individuals.

their decision at the start of each day. The foraging theory addresses the decision of what foraging effort to use each day of a 40-day life stage, with higher effort providing more food but higher predation risk. This decision is made to maximize a fitness measure that represents expected reproductive output as a combination of probability of surviving to the end of the 40-day time horizon and size at the end of the time horizon. In each daily update, individuals use the simple prediction that current predation risk will persist over the rest of the time horizon. Predation risk is size dependent, creating a feedback in behavior: the foraging decision of today depends on predation risk, which

depends on size, which depends on foraging behavior in previous days. However, this model does not represent competition or other interactions among prey individuals, so there are no feedbacks due to intraspecific processes.

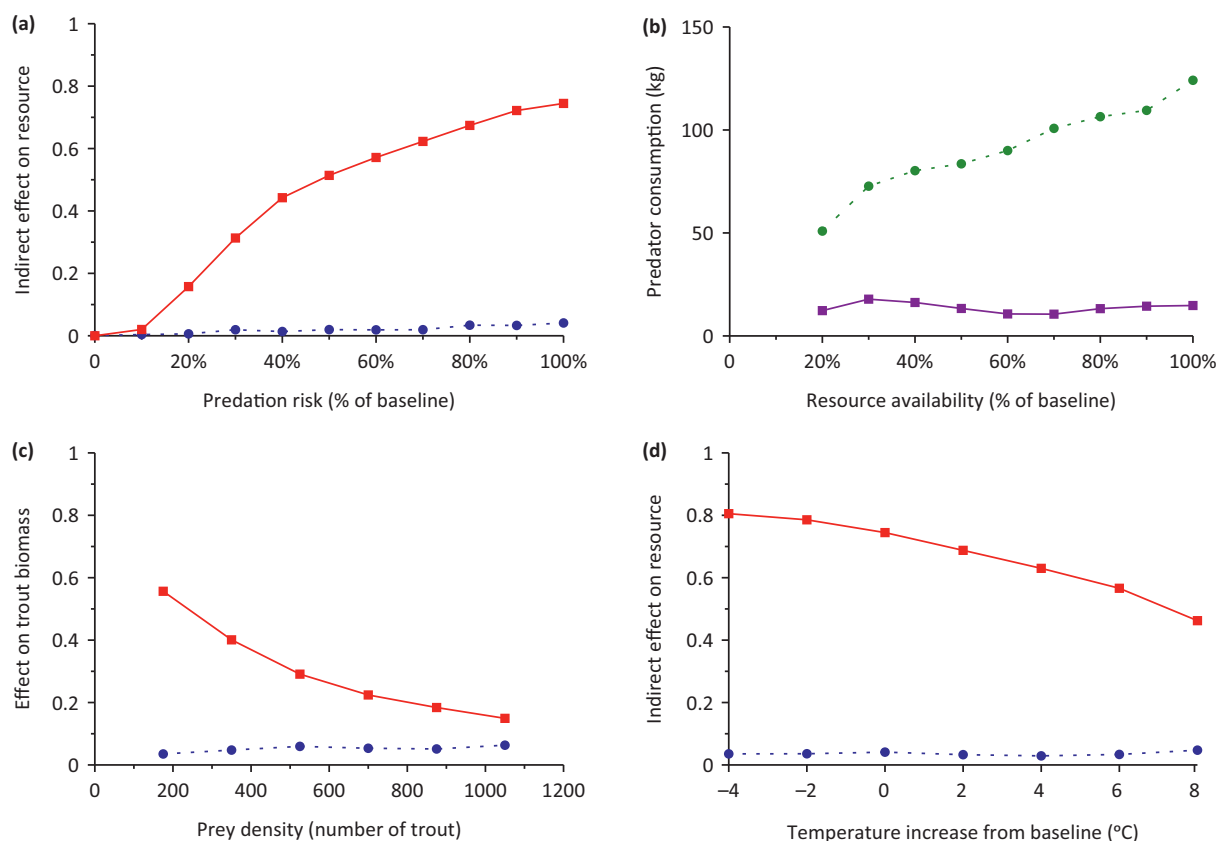
Luttbeg *et al.* [23] demonstrated that this model, using what is essentially SPT, could reproduce some of the characteristic trait-mediated trophic interactions identified above. They obtained TMIs far higher than density-mediated indirect interactions (DMIs), and found that TMIs were lower when resource was scarce because prey were less able to reduce foraging without risking starvation. They also found that trait-mediated effects of predation were stronger

Box 4. Characteristic trait-mediated trophic interactions emerge from SPT

The trout model of Railsback *et al.* [25] simulates a three-level food chain in a virtual environment of relatively realistic complexity. Foraging behavior is represented at the prey (trout) level; 350 individual trout are simulated. Predators are represented only as risk that varies with characteristics of habitat cells (e.g., depth or hiding cover) and prey (e.g., body size, whether feeding or hiding). The resource level is represented as a rate of trout food availability that varies among habitat cells and over time (as a function of river flow). Hence, we implemented a variation of the experimental protocol described in Box 1.

To focus on behavior instead of demographics (and to correspond with the empirical literature, which most often uses

within-generation experiments), we simulated a 4-month period outside the reproductive cycle. Prey population N is represented as total trout biomass, which varies due to growth and mortality of individuals. The predator population is represented by the daily risk it poses to prey. TMIs and DMIs on the resource level are represented as biomass of resource consumed by trout, using equations 5 and 6 of Luttbeg *et al.* [26]. Simulation experiments show that this model with SPT for foraging reproduces four characteristic trait-mediated trophic interactions (Figure I).



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Figure I. Simulation experiments demonstrate that a trout model using state- and prediction-based theory 'SPT' can reproduce characteristic interactions (see 'Characteristic trait-mediated trophic interactions' section in main text). **(a)** As predation risk increased above zero, trait-mediated indirect interactions (TMIs; unbroken red line) on resource consumption were much stronger than density-mediated indirect interactions (DMIs; broken blue line) because trout adapted by feeding at night instead of during the day. **(b)** Strong bottom-up TMIs: without predator avoidance behavior (broken green line), predator consumption of trout increased with increasing resource availability. With behavior (unbroken purple line), increasing resource availability let trout reduce predation by feeding less often or at night. **(c)** As trout density increased, non-consumptive effects (NCEs; unbroken red line) decreased because competition gives trout less scope to avoid predators by reducing feeding effort, compared with consumptive effects (CEs, broken blue line). **(d)** TMIs (unbroken red line) decreased with water temperature; metabolic demands increase with temperature, giving trout less scope to avoid predators by reducing feeding, compared with DMIs (broken blue line).

later in the life stage, because prey were already large enough to reproduce successfully and so could reduce feeding with less effect on expected fitness.

Example 2: stream trout populations

Railsback *et al.* [21,25,26] applied SPT to foraging behavior in a simulated stream trout population, which enabled the authors to test how well models using the theory reproduce a variety of complex foraging behaviors observed in real trout. In the first experiment [26], the daily foraging decision was to select a habitat patch for foraging, with predation risk and growth potential varying among patches and changing over time due to daily variation in flow and temperature (Box 3). Feedbacks of foraging behavior result from (i) competition for food via a size-based hierarchy, with larger individuals having access to more patches and more food in each patch; and (ii) growth and predation risks of individuals depending on their size. The simulation experiment showed that SPT let the model reproduce observed responses in foraging habitat selection to changes in resource availability, predation risk, competition levels, and temperature (which affects metabolic demands), and that simpler theory, such as maximizing growth, did not.

In a second experiment, the trout model was modified to represent a more complex foraging decision: choosing when as well as where to feed [21]. SPT was adapted to model how trout individuals decide whether to feed during the daytime or at night, when both food intake and risk are lower. Hence, nocturnal feeding is a predator-avoidance behavior that reduces food intake. At the start of each day and night, the model trout update their predictions of growth and risk for both daytime and nocturnal feeding (in the best available habitat) and decide whether to feed or hide. From this model emerged complex dynamics such as (i) more daytime feeding when temperature is higher, due to higher energy demands; (ii) more daytime feeding by juveniles, whose fitness is more growth dependent than that of adults; (iii) more daytime feeding when trout abundance is high, due to food competition; (iv) more daytime feeding when food resources are reduced; and (v) dependence of diel feeding patterns on availability of good habitat for feeding or hiding [21].

These experiments show that foraging theory with prediction and updating can produce the kinds of individual adaptive behavior that produce NCEs and TMIs, even in reasonably realistic contexts, with future food and risk conditions variable and unknown as well as subject to feedbacks from behavior. In fact, the four characteristic trait-mediated trophic interactions we identified above all emerge from foraging theory in the trout model of Railsback *et al.* [21] (Box 4).

What is really new about state- and prediction-based modeling?

Trait-mediated trophic interactions are important because they focus ecology on the kinds of complexity that are critical to understanding how real ecosystems work, although these are challenging to model [27]. Many of these interactions emerge from foraging behavior, so foraging theory that can reproduce TMIs and NCEs in bottom-up population models is essential for understanding both individual behavior and the community dynamics that arise from behavior. SPT

appears to be useful for this foraging problem; how does it change the way one thinks about foraging theory?

Fitness optimization trade-offs in a traditional updating context

SPT is a modification of DSVM that lets one take advantage of the ability of DSVM to model growth–risk trade-offs, but within the traditional optimal foraging context of individuals that routinely update their decision as their internal state and external conditions change (e.g., [1,2,22]). Using SPT, individuals update their foraging decision by predicting growth and predation risk for the alternatives available to them; the prediction considers current conditions as affected by recent behavior of other individuals. Decisions are then made by ‘optimizing’ (perhaps approximately) a fitness measure over a time horizon. This process of prediction and updating enables individuals to respond to feedbacks of their own behavior and the behavior of competitors (and possibly predators and food resources), and also lets individuals respond adaptively to other changes in their environment. SPT appears to provide a useful, general method to model foraging in a way that both produces and responds to complex population- and community-level dynamics, such as trait-mediated trophic interactions.

Similar to DSVM, SPT can also be applied to trade-off-based adaptive decisions other than foraging, such as life-history strategy and morphologic adaptation. For example, Stephens *et al.* [28] modeled a dispersal decision by marmots using the elements of SPT: periodic evaluation of a fitness measure using state-based assumptions (i.e., predictions) about future survival and reproductive success.

Research issues: prediction, and optimization or approximation of fitness measures

The use of SPT raises several research issues to new prominence. First is how to represent prediction. Explicit prediction is the key new element of SPT that enables its use when future conditions are uncertain and subject to feedbacks. Prediction is fundamental to decision-making, and has long been recognized as important to adaptive behavior in ecology [29,30]. The SPT applications reviewed here indicate that even an extremely simple, and usually wrong, prediction (that current conditions will continue over the time horizon) can produce usefully realistic behavior when updated frequently. However, many organisms are undoubtedly capable of better prediction. How would the response of a model animal to a weather or predation event change if, instead of assuming current conditions persist over a time horizon, it predicts that conditions will revert toward normal? Prediction is modeling the future, so models are needed of how organisms model their environment. A small but growing literature addresses how organisms use genetic traits, memory, environmental cues, and so on, to anticipate future conditions (or behave as if they do; e.g., [31–33]). Example ways to model such mechanisms include assuming individuals simply follow pre-determined rules for prediction, and using Bayesian updating to represent how past events alter expected probabilities of future events [34]. Deciding how to represent prediction is an important step in applying SPT that remains largely unexplored.

A second research issue is how to optimize fitness measures over their time horizons. Luttbegg *et al.* [23] used the kind of dynamic programming technique associated with DSVM, whereas Railsback *et al.* [25,26] simplified the optimization by basing it on the (incorrect but useful) assumption that individuals use the same alternative for the entire time horizon. Differences in behavior resulting from these two approaches have not been explored.

Finally, this review illustrates the use of individual-based simulation models and observed patterns to test foraging theory (including models of prediction) more comprehensively. This technique of 'pattern-oriented modeling' [35–37] facilitates the contrast and falsification of alternative theories (e.g., [26,38,39]) and, therefore, use of the scientific method to find useful foraging theory for specific ecological situations.

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