

# Predator and Prey Models with Flexible Individual Behavior and Imperfect Information

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**ABSTRACT:** To begin identifying what behavioral details might be needed to characterize community dynamics and stability, we examined the effect of prey behavioral responses to predation risk on community dynamics and stability. We considered the case of prey altering their foraging effort to trade off energy gain and predation risk. We used state-dependent dynamic optimization to calculate the optimal trade-off for four models of prey behaviorally responding to predation risk. We consider a fixed behavior model in which prey use constant levels of foraging effort and three flexible behavior models in which prey change their foraging effort according to their physiological state and their perceived level of predation risk. Flexible behavior was destabilizing at the community level as evidenced by higher predator-prey oscillations and lower community persistence times. The mechanisms by which prey estimated predation risk also affected community stability. We found that community dynamics resulting from prey with flexible behavior and fixed perception of risk approximated community dynamics resulting from prey with flexible behavior and perfect information about predation risk, however neither approximated the community dynamics resulting from prey with flexible behavior and flexible perception of risk. Thus, whether it might be possible to abstract complex behavior with simpler rules when modeling community dynamics depends on the prey's behavioral mechanisms, which are empirically poorly known.

*Keywords:* predator-prey interactions, predation risk, perception, individual behavior, Bayesian updating.

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Community ecology has a long tradition in which mathematical theory is formulated using generalized models

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describing species interactions (Kingsland 1987; Edelstein-Keshet 1988; Yodzis 1989). Such models offer compact ways to describe the complexity inherent in communities of many species (Yodzis 1996), but in doing so they often abstract considerable biological detail. Empirical research, however, is increasingly showing that one detail that may be critical to incorporate into models of species interactions in communities is the behavior of individuals responding to predation risk (Turner and Mittelbach 1990; Huang and Sih 1991; Werner and Anholt 1996; Beckerman et al. 1997; Peckarsky and McIntosh 1998; Schmitz 1998).

Theory has illuminated the ways behavior might affect community dynamics, but the focus usually has been on specific behavioral responses and ignored the mechanisms by which prey perceive predation risk (Ives and Dobson 1987; Abrams 1992; Krivan 1996; Fryxell and Lundberg 1997; Houston and McNamara 1997). For prey to respond behaviorally to risk of predation, they must detect or estimate the level of predation risk and respond to that perceived risk, which becomes an optimization problem that must be linked to models of community dynamics. In most previous theoretical analyses, the response to perception has not been analyzed. Rather, the models have been based on the assumption that prey have perfect knowledge of predation risk. For example, when prey behavior was incorporated into Lotka-Volterra equations as a response function to predation risk, predator avoidance behavior stabilized predator-prey systems (Ives and Dobson 1987). Two modeling assumptions contributed to this result. The model used continuous time, so destabilizing time lags caused by changing prey behavior were prevented or reduced. The model also assumed that prey perfectly perceived predation risk; thus, their behavioral responses were instantaneous, in conjunction with the continuous time assumption, and always retarded predator and prey population growth rates when risk was high. In another model, when prey behavior was modeled as a state-dependent response to predation risk and hunger using discrete time, predator avoidance behavior increased the rate of prey population growth and destabilized the predator-prey system (Houston and McNamara 1997). This model

too assumed that prey had perfect information about predation risk. An alternative formulation of the problem has been to ask how the existence of refuges that allow prey to behaviorally reduce predation risk affect predator-prey dynamics. The general conclusion has been that refuges can stabilize predator-prey systems (Sih 1987; Ruxton 1995; Krivan 1998), but this result depends on assumptions about how prey use refuges (McNair 1986).

Assumptions about perfect information probably are not realistic. Moreover, the level and clarity of information available to prey can affect their behavior and fitness (Bouskila and Blumstein 1992; Sih 1992). In variable environments, having perfect information about the risk of predation would require large expenditures of time and energy and would ultimately be limited by the reliability and clarity of the cues used to detect predation risk. Generally, individuals in variable environments have two options (Luttbeg and Warner 1999). They can assume that predation risk is constant and use a fixed estimate of predation risk when trading-off foraging benefits and predation costs, or they can gather information to assess the current level of predation risk and use their flexible estimate of predation risk when trading-off foraging benefits and predation costs.

The purpose of this study is to examine how flexible prey behavior and imperfect knowledge of predation risk affect the stability of predator-prey population dynamics. We wish to understand whether, and if so, how specific details at the level of individual behavior scale to the community level. Previous analytical studies examining effects of predation risk on community dynamics (e.g., Ives and Dobson 1987; Abrams 1992, 1995) take, as a given, that risk has a bearing on dynamics and proceed to characterize mathematically the function describing risk effects on prey foraging. We do not begin with a function describing linkages between risk and foraging, primarily because we would be merely guessing what such a function would look like for the range of behaviors explored here. Instead, we construct a series of models of optimal prey behavior in response to perceived predation risk and the prey's state variables. These models are based on plausible rules for perception. The models vary in whether prey use fixed behavior or behavior that flexibly responds to perceived predation risk and in whether prey detect predation risk perfectly or imperfectly. With each of the models, we simulate discrete predator-prey population dynamics as a consequence of prey exposure to predation risk and prey reproductive success. This approach allows us to explore whether unique dynamics emerge as a consequence of individual behavior and assess whether it is worth devoting future effort toward quantifying functions that can be incorporated into generalizable analytical models or whether it may be safe to abstract behavioral and perceptual details.

## Methods

### *Modeling Individual Behavior*

The motivation for our analyses comes from a desire to begin reconciling the relative importance of predation and predation risk on the long-term dynamics of prey populations and, accordingly, predator dynamics. The structure of the presented models are inspired by recent empirical work exploring how spider predators influence grasshopper behavior and population ecology (Beckerman et al. 1997; Rothley et al. 1997; Schmitz et al. 1997). Thus, our intent is not to provide a general explanation of the dynamics of all predator-prey systems. Rather, we focus on a class of prey-predator systems in which both prey and predator complete their life cycles within 1 yr, with no overlapping generations (typically arthropod species).

In such a class of system, prey emerge from eggs at the beginning of a foraging season and then develop through several instar stages. Prey become adults toward the end of the foraging season, at which time they mate, lay eggs, and then die because of senescence. The eggs remain dormant until the next foraging season. The rate at which prey pass through the various life-history stages is determined by their level of food intake. Prey that have high rates of food intake tend to pass through their life-cycle stages very rapidly, attain reproductive maturity sooner in the season, and tend to be more fecund than prey that have lower food intake. Predation risk can modify these life-history measures by altering prey foraging behavior. Prey facing predation risk tend to reduce their feeding activity in order to be vigilant, which imposes an important life-history cost. Consequently, prey must balance a trade-off between minimizing predation risk and maximizing food intake. The way prey choose to balance this trade-off will have an immediate bearing on their life-history schedule and, over the longer term, their population dynamics.

Our models are of a single predator species and a single prey species that exhibit annual lifecycles. For both species there is a 40-d foraging season and reproduction occurs at the end of the foraging season. We use state variable dynamic models to determine how individual prey should behave to maximize their gain in body mass while avoiding predation risk. Daily prey behavior is then placed into a simulation that tracks prey foraging success and encounters with predators over a season. At the end of the season, prey and predators reproduce with the magnitude of reproduction being based, respectively, on their body mass and the number of prey they have eaten. For prey that survive to the end of the season, the number of offspring produced equals

$$\text{prey offspring} = \frac{\text{mass}^{0.75}}{3}. \quad (1)$$

The exponent 0.75 is used to impose an allometric constraint on reproduction, and division by 3 reflects inefficient conversion of resources into offspring production. Predators produce offspring based on the number of prey they have eaten during the season according to the function

$$\text{predator offspring} = \frac{\text{prey eaten}}{3}. \quad (2)$$

We placed an upper limit of six offspring for predator reproduction, but the limit was very rarely reached.

#### *Individual-Level Foraging Effort and Success*

The foraging effort of prey determines their mass gain, their probability of encountering a predator, and the foraging success of their predators. Foraging effort represents either the relative effort an individual exerts when trading off foraging and vigilance or habitat shifts between resources that trade off foraging gains and predation risk. Distinguishing between these two possibilities is only important when looking at the effects of prey behavior on their resources. During each day of the season, each individual prey exerts one of six levels of foraging effort ( $\gamma$ ). The six levels of effort trade-off mass gain with predation risk and range from 0 to 1, at increments of 0.2. The mass gain for an individual prey increases with foraging effort according to the function

$$m(\gamma) = 2.5\gamma - 1, \quad (3)$$

where the forager is subject to a 1 mass unit metabolic cost and 2.5 is a constant chosen so that with maximum foraging effort a forager gains 1.5 net units of mass. Prey starve if their mass reaches 0 or less. The maximum mass a prey can attain was chosen to be 40. In our simulations, prey rarely reached the maximum body mass, because predation risk associated with that amount of mass gain is exceedingly high.

Our focus is on interactions between predators and prey, where prey face a nonzero risk of predation, and our analysis of dynamics stops whenever predators or prey go extinct in a simulation run. We assume that the probability that during a day a predator is in the prey's vicinity is determined by the number of predators ( $N$ ) present in the environment, but not by the prey's foraging effort, where

$$\text{for } N > 0 \quad \text{Prob(vicinity)} = (.05 + .005N) \quad (4)$$

with the probability of a predator being in the vicinity arbitrarily set to be  $\leq 0.7$  (the upper limit was never reached). We chose this step function to facilitate predators encountering enough prey to support reproduction, while limiting the rate of increasing predation risk. The probability that during a day the prey encountered a predator is affected by the prey's foraging effort and is

$$\text{Prob(encounter)} = \gamma \text{Prob(vicinity)}. \quad (5)$$

When a predator is encountered, the prey has a probability of escaping and surviving the encounter,  $\sigma$ . We arbitrarily set  $\sigma$  to equal 0.5. Thus, the probability of falling victim to predation during a day is

$$\text{Prob(predation)} = (1 - \sigma) \text{Prob(encounter)}. \quad (6)$$

#### *Models of Prey Behavior and Perception*

We constructed the following four models of prey behavior and perception. These models vary in whether or not prey respond behaviorally to changes in predation risk and whether and how they perceive predation risk. The models produce behavioral rules that we then place into simulations of population dynamics.

*Fixed Behavior Model.* Prey using fixed behavior exert the same foraging effort each day of the foraging season, independent of body mass, the level of predation risk, and day of the season. This assumption is identical to that of classical Lotka-Volterra models that examine predator-prey dynamics wholly at the community level.

*Flexible Behavior with Fixed Perception Model.* Prey using flexible behavior to balance foraging gains and predation risks need to perceive the current level of predation risk. In the next three models, we incorporate different assumptions for how prey perceive predation risk. In the first model we assume that prey have completely fixed perception of risk based on evolutionary history. This fixed perception is represented by a  $\beta$  distribution with two parameters,  $H$  and  $M$ , that do not vary. We use a  $\beta$  distribution as a way of estimating the binomial probability of prey encountering a predator (Hillborn and Mangel 1997). Using state variable dynamic models (Mangel and Clark 1988), we find the optimal foraging effort for each combination of prey's perception of predation risk, prey mass, and day in the season using a backward iteration procedure (see appendix for details on the flexible behavior models).

*Flexible Behavior with Flexible Perception Model.* The second way prey could perceive predation risk is through experience. In the second flexible behavior model, we assume that prey update their perception of risk as they either encounter or do not encounter predators. Individuals using flexible behavior with flexible perception of predation risk behave in the same manner as the previous model, but, in addition to invariant  $H$  and  $M$ , they track the number of days they have encountered or not encountered a predator, called “hit” and “miss.” The probability of encountering a predator in a day depends on the density of predators and the foraging effort of the prey. Therefore, a tally of days with encounters and without encounters with predators can be used to estimate the probability of encountering a predator. The tally of days with encounters and without encounters is forgotten at a fixed rate,  $\phi$  (see appendix). Using state variable dynamic models, we find the optimal foraging effort for each combination of the prey’s current perception of predation risk, prey mass, and day in the season using a backward iteration procedure.

*Flexible Behavior with Perfect Information Model.* The third way prey could perceive predation risk is by some means of perfect knowledge about the level of predation risk. While this assumption seems unrealistic, it is representative of the assumption made in classic behavioral ecological models of prey foraging in the presence of predation risk, that is, the omniscient forager (Stephens and Krebs 1986). Individuals using flexible behavior with perfect information on predation risk behave the same way as in the two previous models, but they know the actual risk of predation for each foraging effort. Using state variable dynamic models, we find the optimal foraging effort for each combination of actual risk of predation, prey mass, and day in the season using a backward iteration procedure.

#### *Searching for Optimal Parameters*

For each of the models, except the perfect information model, there are alternative parameter values that can influence the behavior of prey. For the fixed behavior model, individuals can utilize one of the six levels of foraging effort. For the fixed perception model, different fixed perceptions of predator risk ( $H$  and  $M$ ) can be used. For the flexible perception model, different rates of forgetting ( $\phi$ ) can be used.

For each model, we identified the parameter values that maximized individual prey reproductive success. For each alternative parameter value, we ran 5,000 realizations of prey experiencing an environment with 5, 10, 15, 20, or 25 predators (an approximation of the range of predator

populations produced by our simulations). We then selected the parameter values that produced the highest prey reproductive success (eq. [1]). For the fixed behavior model the best foraging effort was 0.6. For the fixed perception model, the best combination of  $H$  and  $M$  were 1 and 7. For the flexible perception model the best rate of forgetting ( $\phi$ ) was 0.92.

We then compared the successes of each model using its selected parameter values, in terms of prey reproductive success, a measure of individual fitness (table 1). A far more rigorous test of the relative optimality of the four models requires knowing the frequencies of environments (number of predators) that the prey encounter. It is not easy to obtain an explicit solution to this problem because the behavior of prey shapes their environment; prey behavior exposes them to predation risk, which determines predator foraging and reproductive success. Thus, for these models, the optimality of individual behavior involves not only how individuals perform in an environment but also what environments they form.

#### *Simulating Population Dynamics*

The four models produce behavioral rules that prey utilize contingent on their situation. We examined how behavior and the mechanisms of perceiving predation risk translate into community-level dynamics by placing these behavioral rules into multiple season population simulations. In the simulations, prey and predator foraging success within a season determines their respective discrete densities at the beginning of the next season. Individual prey that avoid predation reproduce at the end of the season. Their reproductive success is determined by their final mass according to their fitness function (eq. [1]). When an individual prey is killed by predation, that predation success is randomly assigned to one of the predators. Predators produce offspring based on the number of prey they have eaten during the season according to equation (2). Prey and predators were only allowed to produce discrete off-

**Table 1:** Mean per capita reproduction by prey for the four models with different predator population sizes

Model	2	5	10	15	20	30	Geometric mean
Fixed behavior	1.62	1.36	.98	.73	.54	.29	.79
Fixed perception	1.85	1.49	1.06	.73	.55	.27	.83
Flexible perception	2.02	1.61	1.05	.74	.51	.24	.82
Perfect information	2.07	1.59	1.08	.78	.54	.28	.87

Note: Reproduction is presented for different predator population sizes, which create different levels of predation risk. Geometric means are for the six presented predator population sizes. Data are from 10,000 realizations of each model for each number of predators.

spring. Fractional values of offspring were randomly dropped or rounded up based on the magnitude of the fraction. Adult prey and predators die after reproduction, leaving their offspring to be the populations at the beginning of the next season.

We initialized each simulation with 40 prey and 10 predators and ran the simulations until either the prey or predator population went below 0 (extinct) or 250 seasons elapsed. We obtained 200 realizations for each of the four models and recorded persistence times, the number of seasons that both predator and prey populations persisted. We examined the frequency distribution of persistence times of predator-prey communities to understand how the models affected community stability. We collected sequences of prey and predator population sizes from simulations that lasted at least 20 seasons to produce phase plots and conduct autocorrelation analyses. We collected a single sequence of 250 seasons without an extinction for each of the models to examine the mean and range of prey and predator population sizes.

We varied several parameter values of the models and initial conditions of the simulation (table 2) to examine the sensitivity of patterns of persistence to our assumed values. We also explored the effects of density-dependent prey population growth on our results. Thus, in some

simulations, we introduced density dependence into prey population dynamics. We made mass gain for prey dependent on prey population sizes ( $Y$ ), so that

$$m(\gamma) = 2.5\gamma(1 - Y\mu) - 1, \tag{7}$$

with  $\mu$  being the magnitude of the density-dependent effect. The metabolic cost is unaffected by density dependence, but the amount of resources collected, which is converted into mass, is reduced by the number prey in the environment. We vary  $\mu$  to examine how this form of density dependence affects community persistence times of the models. The behavioral rules used by prey were not adjusted to the addition of density dependence, thus, prey were behaving as if density dependence was not occurring. However, for the flexible behavior models, the effects of density dependence on their body mass could indirectly change their behavior.

*Effects on Resources*

The alternative models affected the foraging behavior of prey. We looked at how these changes in prey behavior cascaded down to the resource level. Eight realizations of 25 or more seasons were obtained for each model. If for-

**Table 2:** Community persistence times with varied model parameters or starting conditions

Parameter or variable	Initial value	Changed value	Model (persistence times)			
			Fixed behavior	Fixed perception	Flexible perception	Perfect information
Baseline	...	...	54.4 <sup>a</sup>	29.8 <sup>a,b</sup>	16.5 <sup>a,b,c</sup>	27.9 <sup>a,c</sup>
Prey mass	2	6	35.5 <sup>a</sup>	29.5 <sup>a,b</sup>	18.9 <sup>a,b</sup>	23.9 <sup>a</sup>
Predator abundance	10	5	46.5 <sup>a</sup>	30.0 <sup>a,b</sup>	14.8 <sup>a,b,c</sup>	29.7 <sup>a,c</sup>
	10	15	57.9 <sup>a</sup>	28.2 <sup>a,b</sup>	16.8 <sup>a,b,c</sup>	28.1 <sup>a,c</sup>
Prey abundance	40	20	48.0 <sup>a</sup>	25.9 <sup>a</sup>	17.8 <sup>a,c</sup>	26.0 <sup>a,c</sup>
	40	60	51.2 <sup>a</sup>	30.1 <sup>a,b</sup>	16.7 <sup>a,b,c</sup>	26.3 <sup>a,c</sup>
Conversion efficiency:						
Prey → predators	1/3	1/2.5	38.0 <sup>a</sup>	22.7 <sup>a,b</sup>	14.8 <sup>a,b</sup>	19.7 <sup>a</sup>
	1/3	1/3.5	70.2 <sup>a</sup>	37.5 <sup>a,b</sup>	23.6 <sup>a,b,c</sup>	36.9 <sup>a,c</sup>
Resources → prey	1/3	1/2.5	25.3 <sup>a</sup>	17.0 <sup>a,b</sup>	12.3 <sup>a,b,c</sup>	19.0 <sup>a,c</sup>
	1/3	1/3.5	63.5 <sup>a</sup>	37.4 <sup>a,b</sup>	24.3 <sup>a,b,c</sup>	36.6 <sup>a,c</sup>
Escape probability	.5	.6	42.0 <sup>a</sup>	12.9 <sup>a,b</sup>	13.5 <sup>a,c</sup>	21.0 <sup>a,b,c</sup>
	.5	.4	32.0 <sup>a</sup>	25.0 <sup>a,b</sup>	13.4 <sup>a,b,c</sup>	20.3 <sup>a,c</sup>
Nonlinear $\gamma$	1	1.3	60.9 <sup>a</sup>	40.4 <sup>a,b</sup>	20.9 <sup>a,b,c</sup>	61.5 <sup>b,c</sup>
Density dependence	0	.0005	65.5 <sup>a</sup>	28.9 <sup>a</sup>	20.8 <sup>a,c</sup>	31.0 <sup>a,c</sup>
	0	.001	84.2 <sup>a</sup>	29.4 <sup>a</sup>	21.0 <sup>a</sup>	29.3 <sup>a</sup>
	0	.002	94.7 <sup>a</sup>	30.0 <sup>a,b</sup>	14.7 <sup>a,b,c</sup>	26.9 <sup>a,c</sup>

Note: Each mean is based on 200 realizations.

<sup>a</sup> Tukey tests: the fixed behavior model significantly different than any of the three flexible behavior models (df = 1,  $P < .05$ ).

<sup>b</sup> Tukey tests: the fixed perception model significantly different than the flexible perception or perfect information models (df = 1,  $P < .05$ ).

<sup>c</sup> Tukey tests: the flexible perception model significantly different than the perfect information model (df = 1,  $P < .05$ ).

aging effort represents the intensity of foraging on a single resource, then the total foraging effort for a season is the prey's impact on that single resource. Total foraging effort is the sum of individual days expended on each foraging effort times the magnitude of the foraging effort. If foraging effort represents the use of different resources, then the number of individual days per season allocated to the different foraging efforts is the impact prey had on each of their resources

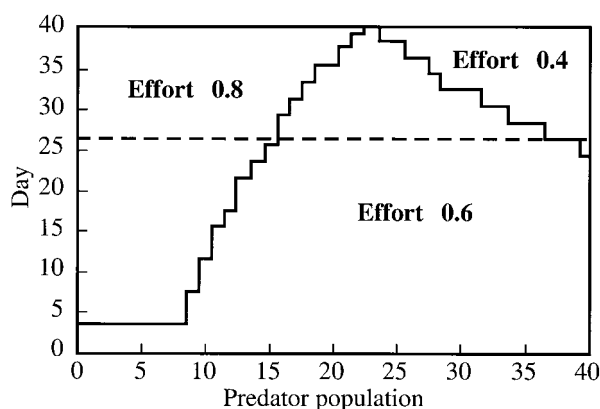
#### *Statistical Analyses*

To test whether the alternative models affected mean community persistence times, we first performed ANOVA. If from the ANOVA we concluded that persistence times were significantly affected by the models (which we always did), we then performed Tukey multiple comparisons for all combinations of models (Zar 1984). The same procedures were used to test whether the models affected average predator and prey population sizes. Autocorrelation analyses were performed for each of the models on a single 50-season sequence of prey population sizes. The analyses calculate the correlations between prey population sizes for seasons separated by different lengths of time and were performed using the S-Plus statistical package (Math Soft 1994).

### **Results**

#### *Individual Behavior and Fitness*

The four models produced different patterns of individual behavior. For our baseline parameters and initial conditions, the fixed behavior model had prey using a 0.6 foraging effort, an intermediate balance between predation risk and foraging gains. The fixed perception model had prey using a 0.6 foraging effort for the first 27 d of the season and switching to a 0.8 foraging effort for the remainder of the season (fig. 1). The perfect information model created behavior that varied with predator population size (fig. 1). At low predator densities, prey used a 0.6 foraging effort during the early season and then switched to 0.8 foraging effort. At high predator densities, prey used a 0.6 foraging effort during the early season and then switched to 0.4 foraging effort. The model did not produce variation in behavior between individuals because we assumed that individuals had identical initial masses and identical knowledge of predation risk and that foraging was deterministic. The flexible perception model created prey behavior that varied with the individual's perception of predation risk, a product of predator population size, and the prey's mass. With the flexible perception model, prey moderately decreased the use of risky foraging



**Figure 1:** Regions of foraging efforts for the perfect information model are delineated by solid lines and shown for different predator population sizes. The regions of foraging efforts for the fixed perception model are delineated by the dashed line, with individuals using a 0.6 foraging effort up to day 27 and a 0.8 foraging effort after day 27, and are unaffected by predator population size.

efforts when larger predator populations were present (fig. 2A, 2B). In addition, the flexible perception model created prey behavior that varied between individuals. Individuals experienced different random encounters with predators, thus causing individuals to have different perceptions of predation risk and different behavior, and the different behavior caused body mass to vary between individuals, which then created more variation in behavior.

The foraging efforts of prey determine their exposure to predation risk and their mass gain. The fixed behavior model produced the highest rate of prey survival (fig. 3A) and the lowest final mass (fig. 3B) except at high predator densities, corresponding to the model's relatively cautious prey behavior. Starvation never occurs because of the assumption of deterministic foraging success; thus, changes in mortality were caused by predation. The fixed perception model produced slightly lower survival and slightly higher final mass than the fixed behavior model. The flexible perception model produced the lowest survival rate, which steadily decreased as predator numbers increased. It tended to produce the highest average final prey mass, but the decrease in final mass as predators increase reveals that the prey were perceiving and responding to different predator population sizes. At low predator numbers, the perfect information model had one of the lowest survival rates and a high final prey mass, but at high predator numbers the model had the highest survival rate and the lowest final prey mass, owing to more cautious prey behavior. This shows that the perfect information model responded to different predator population sizes.

Rates of survival and final prey masses produce per

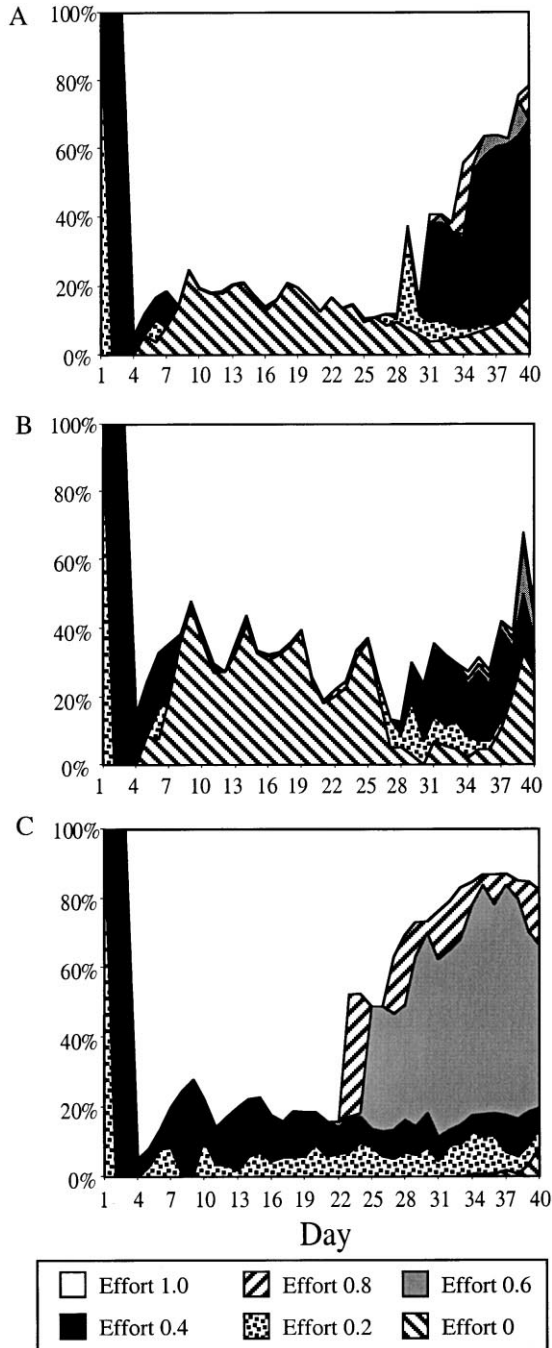


Figure 2: Frequencies of foraging efforts across a season for the flexible perception model with a predator population of (A) 10 and (B) 30, and (C) with a predator population of 10 and predation risk increasing exponentially with foraging effort.

capita prey reproductive success, a measure of individual fitness. Per capita reproductive success for all of the models decreased as predator population size increased (table 1). The fixed behavior model had the lowest geometric mean reproductive success and, for most predator population sizes, produced lower reproductive success than all of the flexible behavior models. The geometric mean is the most appropriate treatment of fitness when environments vary and one is looking at fitness over generations (Gillespie 1977). Thus, given the assumptions of the models, natural selection should favor prey using flexible behavior. The mechanism prey used to perceive predation risk also affected reproductive success. As expected, having perfect information about predation risk created the highest reproductive success in most cases and the highest geometric mean reproductive success. Flexible perception of predation risk tended to create higher reproductive success than fixed perception when few predators were present, but lower reproductive success when many predators were present. The geometric mean reproductive successes for the fixed perception and flexible perception models were very similar but highly sensitive to the frequency of environ-

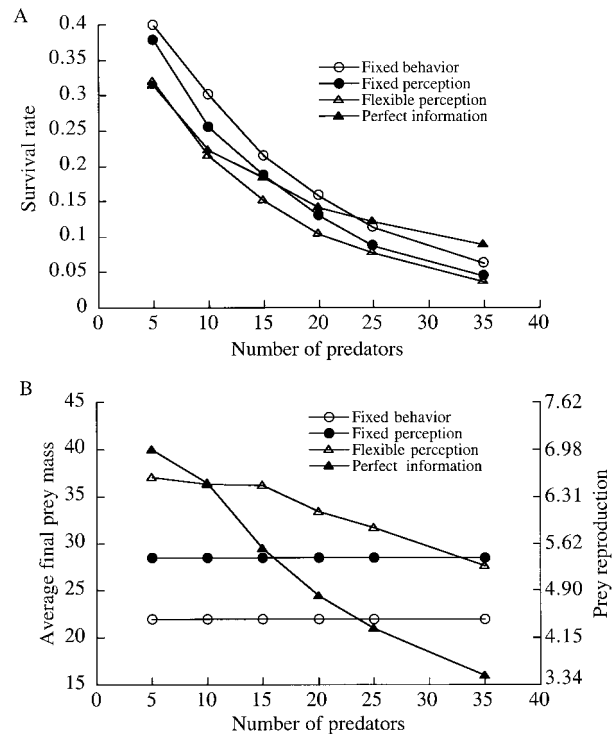


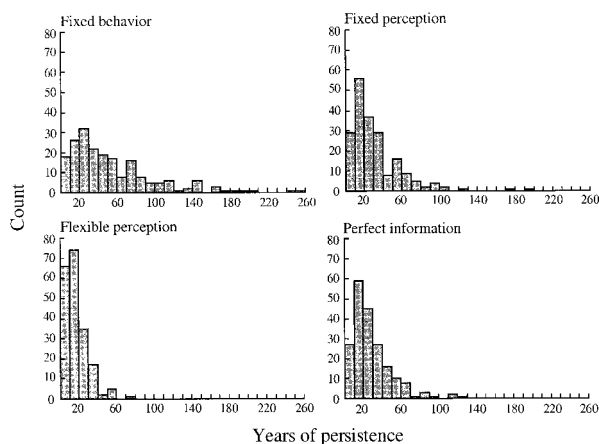
Figure 3: For the four models, (A) prey survival rates and (B) average final prey masses and prey reproduction associated with that average prey mass for different predator population sizes. Each point is the average from 5,000 realizations of a prey experiencing a foraging season with the given number of predators present.

ments with small or large predator populations. Without knowing the frequencies of these environments, no judgment can be made on whether natural selection would favor fixed or flexible perception.

#### *Community Persistence and Dynamics*

The models of prey behavior produced different levels of reproductive success for prey and for predators, through prey mortality. This influenced community dynamics to the extent that there were consistent, significant differences in community persistence time between the four models (ANOVA,  $df = 3$ ,  $P < .01$ ). For our baseline parameters, communities containing prey with fixed behavior had a significantly longer mean persistence time than each of the communities containing prey using the three models with flexible behavior (three Tukey tests,  $df = 1$ ,  $P < .01$  for each test; table 2; fig. 4). Within the flexible behavior models, the mean persistence time of communities containing prey with flexible perception was significantly lower (two Tukey tests,  $df = 1$ ,  $P < .01$  for each test) than communities containing prey with fixed perception or perfect information (table 2; fig. 4). Mean persistence times for communities containing prey with fixed perception or perfect information did not significantly differ (Tukey test,  $df = 1$ ,  $P > .05$ ) and were intermediate to communities with prey using the other two models (table 2; fig. 4). Thus, flexible prey behavior and flexible perception of predation risk both lowered the persistence time of communities.

Sensitivity analyses revealed that the pattern of fixed behavior creating the greatest community persistence and flexible perception creating the least community persistence was robust for the models. When we changed the initial prey mass, initial prey and predator abundances, and prey and predator conversion efficiencies, the same general pattern of fixed behavior having the longest persistence time and flexible perception having the shortest persistence time was preserved (table 2). Increasing the initial mass of prey caused the persistence times of the perfect information and the flexible perception models to no longer be significantly different, but the general pattern was preserved. Altering the initial predator abundance had very little effect on persistence times. Altering the initial prey abundance in one case caused a failure to find a significant difference between the persistence times of the fixed perception and flexible perception models, but the general pattern was preserved. Increasing the efficiency of the conversion of food into offspring for predators and prey lowered the persistence times of communities, and decreasing the efficiency increased persistence times. When the efficiency of predators was increased, there was a failure to find a significant difference between the persistence times of the perfect information and flexible perception



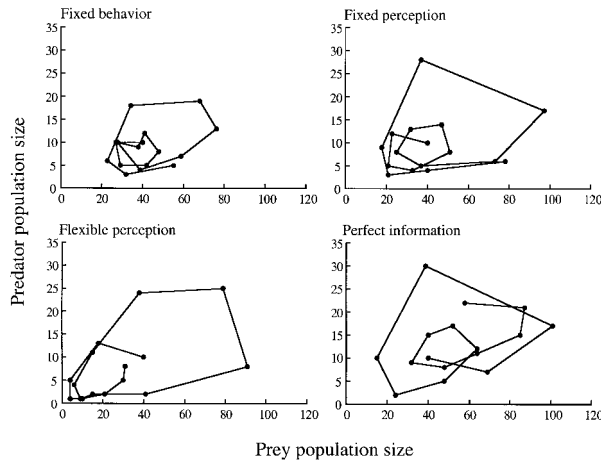
**Figure 4:** Community persistence time frequency plots for the four models.

models, but the general pattern was preserved. Changing the probability of escaping a predator affected the survival of prey, reproduction of predators, and the availability of information about predator population sizes. With those three concurrent effects, it is hard to interpret why the probability of escape affects the persistence of communities. Despite this difficulty, the pattern of persistence times for the four models tended to be maintained when escape probabilities were changed.

Our examination of prey behavior for the flexible perception model showed that foraging efforts were often either 0 or 1 (fig. 2A, 2B). To test whether this use of extreme foraging efforts caused our pattern of persistence times, we altered this pattern of behavior. We did this by making the effect of foraging effort ( $\gamma$ ) on the probability of encountering a predator increase exponentially, rather than linearly, with foraging effort being a power function in equation (5),  $\gamma^{1.3}$ . This resulted in prey using more intermediate foraging efforts (fig. 2C). The effect on persistence times was that the flexible perception model still produced the shortest persistence times and fixed behavior and perfect information models produced the longest persistence times (table 2). The destabilizing effects of flexible perception in initial simulations with linear effort then are not artifacts of prey using extreme foraging efforts.

The previous simulations had density-independent predator and prey population growth. Thus, observed persistence times could have been an artifact of not including a stabilizing density-dependent feedback (Kuno 1987). To explore this possibility, we simulated density dependence by reducing daily prey mass gain as a function of prey population size. Introducing density dependence increased the persistence of communities with fixed prey behavior consistent with expectations from classical theory (Kuno





**Figure 5:** Phase plots for the four models. Phase plots were selected based on representativeness of a sample of 10 plots for each model. Each plot begins with 40 prey and 10 predators, moves generally in a counter-clockwise motion, and has an imposed duration of 16 seasons.

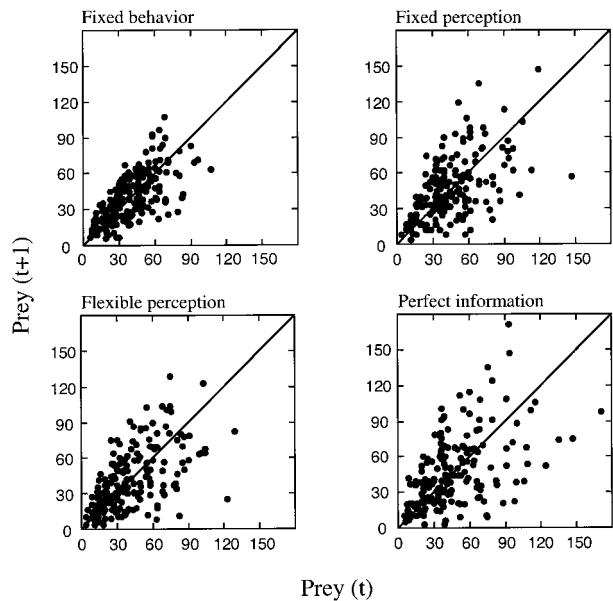
1987), but it had small effects on persistence times in the other communities. Thus, the pattern of fixed behavior creating the greatest community persistence times and flexible perception creating the least community persistence times was retained when we added one form of prey density dependence (table 2). Increasing density dependence may have caused a decrease in persistence times for flexible perception and perfect information models (table 2). A potential cause of this effect may have been that the four models prescribed behavior without incorporating the effects of density dependence on mass gain. Perhaps the two models with the most flexible behavior (flexible perception and perfect information) suffered lower persistence times because of suboptimal prey behavior.

Phase plots begin to reveal how the models affected community persistence. Each of the four models of prey behavior created oscillating prey and predator populations. Fixed prey behavior tended to create the slowest prey population growth and the smallest population oscillations (fig. 5). The three models with flexible prey behavior appear to have similar rates of prey population growth and each show examples of rapid prey growth. The three models appear to differ in their regions of oscillations. In the presented phase plots of the flexible behavior models, each plot reached a point where there were roughly 40 prey and 25 predators. The flexible perception model then proceeded dangerously close to prey extinction, while the other two models did not reach such low population sizes. This suggests that the flexible perception model's poor performance when predator populations are large (table

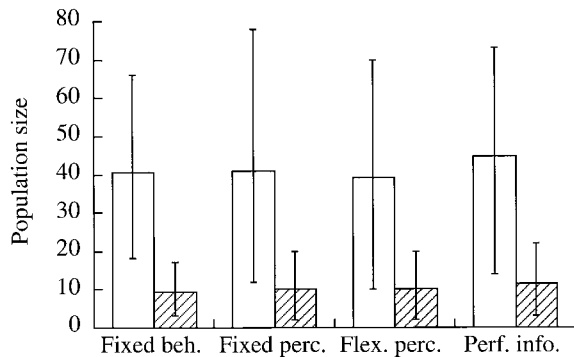
1) may lead to oscillations of a magnitude that lead to extinction.

To look more thoroughly at prey population growth rates for the four models, we plotted prey population sizes at the beginning of a season against prey population sizes at the beginning of the next season. As the phase plots suggest, the fixed behavior model produced smaller prey population changes in comparison to the other three models (fig. 6). Unlike the phase plots, these plots reveal differences in prey population growth rates for the three flexible behavior models. The fixed perception and flexible perception models produced intermediate prey population increases and decreases, and the perfect information model produced larger increases and decreases in prey population sizes (larger scatter from the line of equality).

The models produced slightly different means and ranges of prey and predator population sizes. The models did affect the mean predator and prey population sizes (fig. 7; two ANOVAs,  $df = 3, P < .01$  for each test). However, there were only significant differences between the mean prey populations of the perfect information model and the flexible perception model (Tukey test,  $df = 1, P < .05$ ) and the mean predator populations of the perfect information model and the fixed behavior model (Tukey



**Figure 6:** Scatterplot of prey population sizes at seasons  $t$  and  $t + 1$ . Data for each model is from 10 sequences with 20 seasons. The line of equality shows prey population sizes if they did not change between seasons. Fixed behavior created the smallest prey population changes (divergence from the line of equality was mean sum of squares [MSS] = 252), fixed perception and flexible perception created intermediate prey population changes (MSS = 531 and 549, respectively), and perfect information created the greatest prey population changes (MSS = 814).



**Figure 7:** Means and ninetieth and tenth percentiles of prey (open bars) and predator (hatched bars) population sizes for the four models. Data are from a single sequence of 250 seasons for each of the models.

test,  $df = 1$ ,  $P < .01$ ). The ninetieth and tenth percentiles give an estimate of the range of population sizes (fig. 7). The model with the greatest community persistence times, fixed behavior model, produced prey populations that did not range to high or low population sizes, and the model with the smallest community persistence times, flexible perception model, produced prey populations that ranged to small prey population sizes (fig. 7).

Autocorrelation analyses revealed few differences in the periodicity of prey populations for the four models. The fixed behavior model produced no regular periodicity, beyond a 4-yr initial time lag (fig. 8). The models with flexible behavior produced more regular periodicity, with oscillations ranging between 6 and 9 yr.

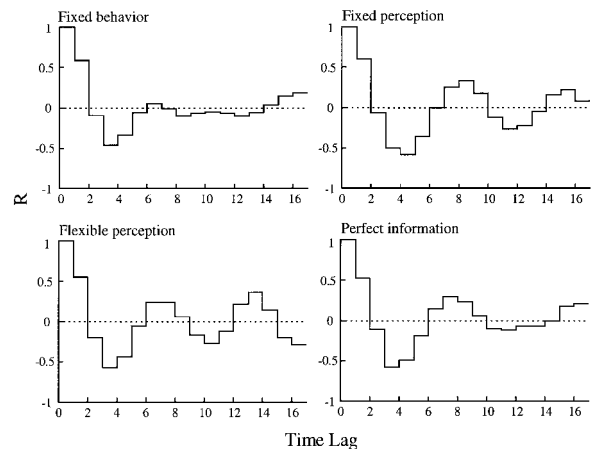
Whether or not it was safe to make different assumptions about prey behavior and perception depends on which trophic interaction one is examining. For example, flexible behavior models with fixed estimates or perfect information produced similar predator-prey dynamics; however, all of the models produced differing interactions between prey and the prey's resources, that is, food chain dynamics. The models varied in their distributions of foraging efforts and their total foraging efforts (table 3). The distributions of foraging efforts ranged from the fixed behavior model, which only used 0.6 foraging effort, and the flexible perception model, which used all available foraging efforts. And, the perfect information model used the 0.8 foraging effort more often than the fixed perception model, despite their similar predator-prey dynamics. Therefore, if foraging effort was the use of different resources, the perfect information model had a greater impact on the resource associated with the 0.8 foraging effort. The perfect information model created the largest total foraging effort reflecting its generally larger prey population size and its relatively aggressive foraging behavior.

If foraging effort was the intensity of foraging on a single resource, then the perfect information model caused the greatest impact on the resource. Understanding how prey behaviorally respond to predation risk may be paramount to understanding food chain dynamics. Thus, when judging the importance of differing assumptions, one has to confine their judgement to the trophic level they have examined.

## Discussion

A fundamental question for ecologists is whether the simplifying assumptions made in models sufficiently characterize the dynamics of their system. We are interested in how assumptions about the flexibility of prey behavior and the mechanisms of prey perceiving predation risk affect individual fitness and community dynamics. To begin forming answers to this question, we simulated the dynamics of a model predator-prey community in which prey have fixed behavior (as assumed by classical community-level models) and a model community containing prey with flexible behavior and perfect information about risk (as assumed by classical behavior ecology models). We used these models as benchmarks against which we compared the dynamics of models that incorporated flexible (imperfect) or fixed estimates of predation risk.

Flexible behavior and perfect information about the level of predation risk both tended to increase the average number of offspring produced by prey (table 1), so at the level of individual fitness, the assumptions did have effects. At the community level, flexible prey behavior lowered the persistence times of communities. How prey perceived predation risk had complex effects on community per-



**Figure 8:** Autocorrelation plots for the four models. Analyses for each model are based on a single sequence of prey population sizes for 50 seasons.

**Table 3:** Distribution of foraging efforts and the total foraging efforts for the four models

Model	0	.2	.4	.6	.8	1.0	Total
Fixed behavior	0	0	0	914	0	0	548
Fixed perception	0	0	0	713	167	0	561
Flexible perception	106	51	153	3	1	508	582
Perfect information	0	0	4	460	440	0	629

Note: Eight realizations of 25 or more seasons were obtained for each model. The reported values are the average number of individual days expended on each foraging effort. The density of prey, the rate at which they are lost to predation, and their foraging decisions contribute to the distribution of foraging efforts. Total foraging effort is the sum of individual days expended on each foraging effort times the magnitude of the foraging effort.

sistence. Prey that had perfect information about predation risk or fixed perception of predation risk yielded similar community persistence times, despite differences in average individual fitness. Prey that estimated predation risk based on flexible perception had lower community persistence times than the two other flexible behavior models. Therefore, based on community persistence times, one might conclude that it is safe to assume that fixed perception of predation risk model and perfect information about predation risk are reasonable approximations of each other. However, neither was a reasonable approximation of the flexible perception model. To decide which assumption about perception of predation risk is most appropriate will require empirically determining how prey perceive predation risk.

A combination of factors caused models with flexible behavior to have lower community persistence times. Flexible behavior increased the average fitness of individuals (table 1). This led to more rapid changes in prey population sizes than models without flexible behavior (fig. 6). In addition, the discrete, seasonal structure of our models introduced a time lag between prey population changes and predator population changes. Thus, increases in prey populations typically led to increases in predator populations in the subsequent season. This lag led to the potential extinction of the prey population because of the sharp numerical response of the predator population in response to abundant prey and then the potential extinction of the predator population because of the subsequent rapid decline of the prey population because of overexploitation. This explanation is supported by the decrease in persistence times that occurred when we increased the conversion efficiencies of predators and prey and by the increase in persistence times that occurred when we decreased the conversion efficiencies of predators and prey (table 2).

Ives and Dobson (1987) found prey behavior to be stabilizing. We believe that their results differed from ours because of differences between discrete and continuous

models, the assumption of perfect information about predation risk, and the assumption of density-dependent prey population growth. Ives and Dobson's models used continuous time, which eliminated time lags between prey and predator population changes. This eliminates the destabilizing effects of rapidly changing prey populations that we found. In addition, their assumption of perfect information eliminates a second time lag between changes in predation risk and behavioral responses of prey. With perfect information about predation risk, prey can immediately and perfectly respond to changes in predation risk. Thus, increases in predation risk will always lead to increases in antipredator behavior and stabilizing reductions in predator and prey population growth rates (Ives and Dobson 1987). However, if prey estimate predation risk based on experience, even with a continuous time model, there will be time lags between changes in predation risk and prey detecting these changes and, thus, there will be time lags between prey and predator population changes. In addition, with imperfect information sampling, errors will occur, causing incorrect estimates of predation risk. Thus, without perfect information antipredator behavior will not reliably retard predator population growth, and destabilizing discordance between predator and prey population changes will occur. It would be interesting to see if a continuous time model with imperfect information would find prey behavior to be stabilizing. Finally, the assumption of density-dependent prey population growth, which Ives and Dobson assumed, reduces the magnitude of rapid prey population growth and, thus, eliminates one of the destabilizing aspects of flexible prey behavior.

Given our previous argument that increased prey population growth was destabilizing, the perfect information model, the model with the highest individual prey fitness, would be expected to have the lowest persistence time. However, the flexible perception model had the lowest community persistence time. The reason for this outcome lies in how prey responded to adverse environments. When predator population sizes were large, prey using the perfect information model were better at adjusting to the increased predation risk than prey using the flexible perception model (fig. 3; table 1). The perfect information model increased the chance that some prey would survive and reproduce during seasons with large predator populations, thus, avoiding extinction and increasing persistence of the community. The flexible perception model did respond to high predator numbers, but not very well. The models use of encounters to estimate predation risk exposed prey to risk before high risk could be perceived. Thus, the flexible perception model had the lowest persistence time because it combined prey population growth that put the system in peril with a reduced capacity to survive perilous seasons. The similar persistence times of

the fixed perception and perfect information models appear to be coincidental. The fixed perception model had slower prey population growth that contributed to longer persistence times, and the perfect information model had better behavioral responses to high predation risk that contributed to longer persistence times. The lesson is that how prey perceive predation risk can determine the relative timing of behavioral responses and population changes.

We have seen that flexible behavior and flexible perception decrease community persistence times. However, there are alternative behavioral mechanisms for flexible behavior and perception. So, models with different assumptions might produce different conclusions. For example, for flexible perception, we assumed individuals estimate their predation risk based on daily encounters with predators. The result was a strategy that responded to changes in predation risk, but the speed and magnitude of the response was poor. Perhaps, if more accurate and timely cues of predation risk were available, flexible perception could better respond to high predation risk and, thus, cause greater community stability. Information about predation risk available to prey must vary between habitats and locations. Potentially, within a predator-prey system we should be able to identify situations in which more or less information is available to prey and then measure how persistence times or population variability are affected by the availability of information. The reality is, however, that very little is known empirically about how prey use information to trade off energy gain and predation risk, that is, which model adequately describes the real behavior. Thus, in addition to investigating how prey should use information to interpret predation risk (Abrams 1994,

1995; Bouskila and Blumstein 1992), we should be identifying empirically how individuals do use information. Results from such experiments would provide important insight on how to structure community-level models of predator-prey interactions.

Our analysis supports previous conclusions that community-level models that do not account for prey behavior produce different dynamics than models that embody behavioral detail (Abrams 1984, 1992; Ives and Dobson 1987; Werner and Anholt 1996; Schmitz and Booth 1997). Some assumptions about prey behavior and how they perceive predation risk may produce similar community dynamics, but other assumptions had significantly different effects on community dynamics. And, assumptions that had similar effects on community persistence times had different effects on resources. Thus, choosing which assumptions to incorporate into predator-prey models will require a better empirical understanding of the behavioral and cognitive capabilities of prey. Hopefully, our analysis of the community-level consequences of prey behavior will motivate more empirical research on how prey perceive and behaviorally respond to changes in predation risk.

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## APPENDIX

### Flexible Behavior with Fixed Perception Model

Fixed perception is represented by a  $\beta$  distribution with two parameters,  $H$  and  $M$ , that do not vary. The probability distribution that prey perceive as the probability that a predator is in their vicinity is

$$\text{Prob}[\text{Prob}(\text{vicinity}) = x] = \frac{x^{H-1}(x-1)^{M-1}}{\sum_{x=0.02}^{0.98} x^{H-1}(x-1)^{M-1}}, \quad (\text{A1})$$

with  $0 \leq x \leq 1$ . The probability is calculated for  $x$  from 0.02 to 0.98 at increments of 0.04, and the denominator normalizes the distribution to sum to 1. Equation (A1) essentially states that the prey's perception that the probability a predator is in its vicinity increases as  $H$  increases. The prey's perceived probability of encountering a predator and the probability of falling victim to a predator follow the same form as equations (5) and (6), but use the value  $x$  for the estimated probability that a predator is in the vicinity.

The optimal foraging effort for each combination of prey mass and day in the season is determined using a backward iteration procedure for state variable dynamic models (Mangel and Clark 1988). The terminal fitness function for prey that survive to the end of the season (for all of the models) is equation (1). For any day  $d$  before the end of the

season, expected fitness for a given level of foraging effort is summed over the perceived probability distribution of possible values of  $x$ ,

$$f(\text{mass}, H, M, d) = \sum_{x=0.02}^{0.98} \text{Prob}[\text{Prob}(\text{vicinity}) = x][1 - \text{Prob}(\text{predation})]f[\text{mass} + m(\gamma), H, M, d + 1]. \quad (\text{A2})$$

This was done instead of using the expected value of  $x$ , because of nonlinear predator effects. This function represents the prey’s perceived probability of not being killed by a predator multiplied by the prey’s expected fitness, given the mass change associated with its foraging effort and advancing to the next day in the season. Fitness is calculated for each of the six potential foraging efforts for each combination of day and body mass. The foraging effort with the highest expected fitness is recorded as the optimal behavior and the expected fitness is recorded for the given combination of mass and day,

$$f(\text{mass}, H, M, d) = \max_{\gamma} f(\text{mass}, H, M, d). \quad (\text{A3})$$

### Flexible Behavior with Flexible Perception Model

Individuals using flexible behavior with flexible perception of predation risk track of the number of days they have encountered or not encountered a predator, called “hit” and “miss.” The information a prey gains from an encounter or nonencounter with a predator is assumed to vary with foraging effort. The rationale for this is that individuals that expend less foraging effort are less likely to encounter a predator. So, when an individual expending low foraging effort does encounter a predator, that experience is a greater indication of high predator densities than when encountering a predator during high foraging effort. When a predator is encountered during a day (encounters cannot occur when  $\gamma = 0$ ), their tally of days with an encounter with a predator increases,

$$\text{hit}_{t+1} = \text{hit}_t + 6 - 5\gamma, \quad (\text{A4})$$

and  $1 \leq \text{hit} \leq 15$ . The upper limit, 15, was arbitrarily set and the lower limit, 1, is necessary for proper specification of a  $\beta$  distribution. Equation (A4) specifies that with a minimal foraging effort of 0.2, a forager adds five to its tally of hits if it encounters a predator. If a forager expends a maximal effort of 1, that same encounter with a predator produces the addition of one hit.

This same logic applies when an individual does not encounter a predator during a day. Individuals that expend less foraging effort are less likely to encounter a predator. Thus, when a predator is not encountered during low foraging effort that experience is less of an indication of low predator density than when a predator is not encountered during high foraging effort. When a predator is not encountered,

$$\text{miss}_{t+1} = \text{miss}_t + 5\gamma, \quad (\text{A5})$$

where  $1 \leq \text{miss} \leq 15$ .

We assumed that individuals are incapable of remembering all of their experiences. We, therefore, reduce an individual’s cumulative count of hits and misses using a rate of forgetting ( $\phi$ ) such that at the end of each day,

$$\text{hit}_{t+1} = \phi \text{hit}_{t+1}, \quad (\text{A6a})$$

$$\text{miss}_{t+1} = \phi \text{miss}_{t+1}. \quad (\text{A6b})$$

Allowing foragers to forget reduces the length of time that an individual’s behavior is shaped by a set of experiences. We varied the rate at which individuals forget to identify an optimal rate of forgetting based on individual fitness.

Individuals using flexible perception, in addition to their experience, can have fixed baseline perception of predation risk,  $H$  and  $M$ , onto which experience is added. However, we assumed  $H$  and  $M$  were 0 for this model. The probability distribution that prey perceive as the probability that a predator is in their vicinity is,

$$\text{Prob}[\text{Prob}(\text{vicinity}) = x] = \frac{x^{\text{hit}_t+H-1}(x-1)^{\text{miss}_t+M-1}}{\sum_{x=0.02}^{0.98} x^{\text{hit}_t+H-1}(x-1)^{\text{miss}_t+M-1}}, \quad (\text{A7})$$

with  $0 \leq x \leq 1$ . The probabilities are calculated for  $x$  from 0.02 to 0.98 at increments of 0.04 and the denominator normalizes the distribution to sum to 1. The prey's perceived probability of encountering a predator and the probability of falling victim to a predator follow the same form as equations (5) and (6) but use the value  $x$  for the estimated probability that a predator is in the vicinity. In addition, the probability of encountering a predator and surviving is

$$\text{Prob}(\text{survived encounter}) = \sigma \text{Prob}(\text{encounter}). \quad (\text{A8})$$

For any day  $d$  before the end of the season, the expected fitness for a given level of foraging effort is

$$\begin{aligned} f(\text{mass}, \text{hit}_d, \text{miss}_d, d) &= \sum_{x=0.02}^{0.98} \text{Prob}[\text{Prob}(\text{vicinity}) = x][1 - \text{Prob}(\text{predation})] \\ &\quad \{ \text{Prob}(\text{survived encounter})f[\text{mass} + m(\gamma), \text{hit}_{t+1}, \text{miss}_{t+1}, d + 1] \\ &\quad + [1 - \text{Prob}(\text{encounter})]f[\text{mass} + m(\gamma), \text{hit}_{t+1}, \text{miss}_{t+1}, d + 1] \}. \end{aligned} \quad (\text{A9})$$

The  $\text{hit}_{t+1}$  and  $\text{miss}_{t+1}$  terms in the first half of (A9) are updated based on an encounter with predators (eqq. [A4] and [A6]). The  $\text{hit}_{t+1}$  and  $\text{miss}_{t+1}$  terms in the second half of (A9) are updated based on a nonencounter with predators (eqq. [A5] and [A6]). Fitness is calculated for each of the six potential foraging efforts for each combination of mass, hit, miss, and day using backward iteration. The foraging effort with the highest expected fitness is recorded as the optimal behavior and the expected fitness is recorded for the given combination of mass, day, hit, and miss:

$$f(\text{mass}, \text{hit}_d, \text{miss}_d, d) = \max_{\gamma} f(\text{mass}, \text{hit}_d, \text{miss}_d, d). \quad (\text{A10})$$

### Flexible Behavior with Perfect Information Model

Individuals using flexible behavior with perfect information know the actual risk of predation for each foraging effort. This risk varies between seasons, but not within seasons. For any day  $d$  before the end of the season, the expected fitness for a given level of foraging effort is

$$f(\text{mass}, N, d) = [1 - \text{Prob}(\text{predation})]f[\text{mass} + m(\gamma), N, d + 1], \quad (\text{A11})$$

with  $N$  being predator population size and the probability of predation being the actual probability (eq. [6]). The foraging effort with the highest expected fitness is recorded as the optimal behavior for the given combination of mass,  $N$ , and day,

$$f(\text{mass}, N, d) = \max_{\gamma} f(\text{mass}, N, d). \quad (\text{A12})$$

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