

Feeding under Predation Hazard: Testing Models of Adaptive Behavior with Stream Fish

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ABSTRACT: Many empirical studies support the premise that animals consider both the benefits of feeding and the cost of mortality when making behavioral decisions, and many theoretical studies predict animal behavior in the presence of a feeding-mortality trade-off. However, empirical work is lacking in studies that quantitatively assess alternative models. Using data from two sets of behavioral experiments examining stream minnows (bluehead chubs) foraging in the presence of sunfish predators (green sunfish), we assess, via statistical model fitting, the utility of four basic optimization models of foraging behavior. Our analysis of feeding and mortality of the minnows indicates that mortality is incurred so as to feed above maintenance requirements, that feeding rate is suppressed in response to the presence of predators, and that the balance of feeding against mortality can be estimated using a life-history parameter θ , interpreted theoretically as the marginal rate of substitution of mortality rate for growth rate. Our results indicate that both body size and age are probably involved in determining the value of θ , and we suggest that future studies should focus on estimating and understanding this parameter.

Keywords: foraging, predation, trade-off, models, fish, stream.

Ecologists have long recognized that the behaviors of individual animals can be used to predict patterns in populations (Sutherland 1996). Consequently, ecologists have been motivated to develop a conceptual framework for understanding and predicting animal behavior. Optimization methods, which leverage the principle that behavior is molded by natural selection, provide a conceptual framework for predicting animal behavior in a variety of

contexts (MacArthur and Pianka 1966; Fretwell and Lucas 1970; Charnov 1976; Mangel and Clark 1988; Perrin and Sibly 1993; Houston and McNamara 1999). Taken literally, the approach asserts that behavioral phenotypes that maximize Darwinian fitness should be the behavioral phenotypes that are observed in nature. Clearly, natural selection does not always overwhelm all other evolutionary processes, but the adaptationist approach has proved insightful as an explanation of phenotype (Houston and McNamara 1999; Kozłowski 1999; Pigliucci and Kaplan 2000).

Fitness is comprised of many components, such as feeding rate, mortality rate, and fecundity, all of which can be influenced by behavior. Many studies focus on behavioral effects on one fitness component, using feeding rate (e.g., Milinski 1979; Harper 1982), survivorship (e.g., Godin and Dugatkin 1996), or fecundity (e.g., Parker 1978) as a proxy for fitness (Stephens and Krebs 1986; Krebs and Davies 1993; Houston and McNamara 1999). However, in nature, it is unlikely that any particular behavior will maximize each fitness component taken alone; a bird might increase its foraging return only at the expense of alerting more predators to the location of its nest (e.g., Martin et al. 2000), or a juvenile fish might increase its feeding rate only at the cost of increasing its exposure to predators (e.g., Godin and Smith 1988; Werner and Hall 1988). These types of trade-offs have been widely studied in the literature (reviews in Lima and Dill 1990; Lima 1998), and the feeding-mortality trade-off in particular has been the focus of a large subset of this work. There is a voluminous empirical literature (Lima and Dill 1990; Lima 1998) showing that animals appear to weigh both feeding rate and mortality rate when making behavioral decisions (e.g., Milinski and Heller 1978; Sih 1980; Werner et al. 1983; Fraser and Gilliam 1987, 1992; Abrahams and Dill 1989; Kotler 1997; Dahlgren and Eggleston 2000), and there is also a substantial body of theory that addresses the quantitative manner in which animals may respond adaptively to the feeding-mortality trade-off and/or the ecological implications of such behaviors (Abrams 1982; Werner and Gilliam 1984; Gilliam and Fraser 1987; Ludwig and Rowe

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1990; Werner and Anholt 1993; Hugie and Dill 1994; Leonardsson and Johansson 1997; Brown et al. 1999; Houston and McNamara 1999). Yet the relationship between the variety of possible theoretical models and much of the available data is far from clear.

In this study, we address, using mechanistic modeling and laboratory experiments, the question of how animals (stream minnows) may balance, through adaptive behavior, opportunities for feeding versus an associated cost of mortality by predation. In designing this study, we adopted the approach advocated by Akaike (1974), Schwarz (1978), Hilborn and Mangel (1997), and others by proposing four alternative models a priori and assessing each model's fit to the data, adjusting for the number of parameters in each model. Model 1 posits that the animals behave so as to maximize their growth rate; this model is consistent with many "energy maximization" models of foraging. Model 2 posits that the animals behave so as to minimize their probability of death but are subject to the constraint that they at least maintain their current body mass (e.g., model 1 in Brown 1992). Models 1 and 2 might be viewed as "straw man" models unlikely to best describe the data, but we feel it is important to include these models when entering into a particular experimental system without extensive prior information because they represent behaviors that bracket the extremes of maximal growth (model 1) and zero growth (model 2). In contrast, models 3 and 4 offer the possibility of growth that is intermediate between maximal growth and zero growth by predicting behaviors that balance feeding against mortality but differ in their treatment of how reproductive value changes with size and age.

Methods

Experimental System

Our experimental system is a simple three-level food chain comprised of green sunfish (*Lepomis cyanellus*), bluehead chubs (*Nocomis leptocephalus*), and pelleted fish food (Hikari Cichlid-type floating baby pellets, 2.45 mg/pellet). Bluehead chubs and green sunfish occur in streams throughout the North Carolina Piedmont, which includes our study stream, Richland Creek (Wake County, N.C.), where we estimate their late summer densities to be 1.6 and 0.6 individuals/m², respectively, in our study reach (the study reach is 75 m long and, on average, 1.87 m wide; population abundances estimated by two-pass removal electrofishing; Seber and LeCren 1967). In our laboratory environment, green sunfish readily consume bluehead chubs, and bluehead chubs readily consume pellets, but green sunfish rarely or never consume pellets (see "Experiment 1" and "Experiment 2"). All experiments

took place during the summer of 2000 in a laboratory with the light cycle set to 14L : 10D and the water temperature set to 25°C.

Growth Experiment

Our goal is to understand how bluehead chubs may adaptively balance benefits of feeding on pellets against any associated mortality cost caused by predation by green sunfish. For many organisms, including fish, body size is often suggested as an important state variable because many salient biological features, including Darwinian fitness, may be described as functions of body size (Werner and Gilliam 1984; Houston and McNamara 1999). Optimization theory often explores the manner in which behavior affects fitness through its influence on growth rate; changes in body size and the feeding-mortality trade-off can also be studied as a growth-mortality trade-off. Accordingly, we conducted a growth experiment to quantify the dynamic relationship between feeding rate and growth rate for different body sizes of bluehead chubs feeding on pellets.

We captured 36 bluehead chubs from Richland Creek ranging in size from 33 to 78 mm total length (TL). After acclimating the fish to the laboratory environment for 3 d, we initiated a 21-d growth experiment in which bluehead chubs were weighed (wet mass) and measured (total length) and then housed individually in aerated 3-L tanks and supplied one of three daily rations of pellets (9.8, 19.6, or 39.2 mg). At 24-h intervals, we cleaned each tank, counting and removing all unconsumed pellets, and exchanged 1 L of tank water with filtered water from a central tank containing 200 L of biologically filtered water. After 21 d, we weighed and measured all individuals.

We estimated two parameters using the data from the growth experiment: k , an assimilation-conversion efficiency specifying the assimilation and conversion of pellet mass into bluehead chub biomass (unitless); and ω , a mass-specific maintenance rate specifying the loss of biomass attributable to all metabolic processes (1/d). Using these two parameters, we can model the growth rate, g , of a bluehead chub over the course of an experiment as

$$g = \frac{ds}{dt} = kf - \omega s,$$

where s is body size (mg wet mass), f is feeding rate (mg/d), and t is time (Kooijman 2000; Lika and Nisbet 2000). For a bluehead chub with initial size $s(0)$ following this model, its growth over the course of the experiment (i.e., change in body size, $s(t) - s(0)$) is

$$s(t) - s(0) = \left[\frac{kf}{\omega} - s(0) \right] [1 - \exp(-\omega t)]. \quad (1)$$

Initial body size, $s(0)$, and feeding rate, f , were experimentally manipulated by applying the ration treatments to individuals of varying body size; we used actual consumption of pellets for f if all pellets were not consumed. To estimate k and ω , we fit the model given by equation (1) to our measurements of growth via ordinary least squares, using $s(0)$ and f as covariates (the model is nonlinear in ω but linear in the parameters $\beta_f = k[1 - \exp(-\omega t)]/\omega$ and $\beta_s = [\exp(-\omega t) - 1]$). We use our estimates of k and ω in our optimization models (see “Alternative Optimization Models of Behavior”) to provide the link between feeding rate, growth rate, and fitness.

Behavioral Experiments

We conducted two sets of experiments, experiment 1 and experiment 2, in which we measured bluehead chub behavior in the presence of varying quantities of green sunfish predators and pellet food. The basic experimental setting for both sets of experiments consists of a 568-L oval stock tank (Rubbermaid Farm Tough 4245-00-GRAY livestock watering tank) containing 200 L of water and a concrete block (39.5 cm \times 19.4 cm \times 19.4 cm) placed on its side on the bottom of the tank. Two 14.3 \times 12.7 \times 19.4-cm holes in the concrete block served as a refuge for the green sunfish, and the top of the concrete block served as a partial refuge for the bluehead chubs since the water level was only a few centimeters above the surface of the block. For a given experimental trial, we placed green sunfish, bluehead chubs, and pellets, in that order, into a stock tank at 2200 hours when the laboratory lights shut off (bluehead chubs feed readily at night in the laboratory, and unpublished gut-contents data indicate that bluehead chubs feed at night in the field). Bluehead chubs were randomly selected from two community aquaria, and green sunfish were randomly assigned to predator treatments. The trials ran overnight at a light level of about 1 lux. At 0800 hours the next day (after 10 h), the experimental trial ended, the laboratory lights turned on, and all remaining bluehead chubs and pellets were counted. Thus, we measured two response variables per trial for both experiments: the number of bluehead chubs consumed by green sunfish and the mass of pellets consumed by bluehead chubs (each pellet has a mass of 2.45 mg on average). We ran four trials per night, with treatments randomly assigned to tanks.

We captured all bluehead chubs and green sunfish from Richland Creek. Except for experimental trials, we held the two species in separate aquaria in the laboratory. We

acclimated all fish to the laboratory environment (3-d acclimation to aquaria, 3-d acclimation to stock tanks, and 6-d acclimation to food supply) before the start of an experiment.

Experiment 1. Our first set of experiments used 65 1-yr-old, juvenile bluehead chubs (hatched during the spring of 1999; mean TL = 57.8 mm, SD = 5.5 mm, range = 47–66 mm) and six green sunfish (TL = 135, 140, 142, 149, 151, and 154 mm). The stock tanks contained one concrete block placed on its side and across the center of the oval tank. We applied one of three predator treatments (zero, one, or two green sunfish) and one of four pellet treatments (240-, 300-, 600-, or 750-mg pellets) to each experimental trial for a total of 12 treatment combinations. All trials received six bluehead chubs. Bluehead chubs not used in that night’s experimental trials were fed a maintenance ration of approximately 10 pellets each night. Each green sunfish was fed a ration of three female adult mosquitofish (*Gambusia holbrooki*) each morning. We repeated experimental trials until all 12 treatment combinations had been replicated four times. Because the relative errors varied across treatment combinations (relative error measured as standard error/mean), on each night thereafter, we repeated trials for the treatment combinations with the largest relative errors so as to homogenize the uncertainty across treatment combinations. We replicated each experimental trial four to nine times and ended the experiment after 71 experimental trials had been completed. We assessed the green sunfish’s propensity to consume pellets using control trials that isolated one green sunfish with 240 mg of pellets for 10 h overnight in the absence of bluehead chubs (five replicates). We found that green sunfish consumed no pellets in these trials. The average wet mass of bluehead chubs over the course of experiment 1 was 2,120 mg (for use in our mathematical models; see “Alternative Optimization Models of Behavior”).

Experiment 2. Our second set of experiments was designed to replicate experiment 1 using smaller, younger, juvenile bluehead chubs in a similar experimental setting. In experiment 2, we used 82 young-of-the-year (age 0) bluehead chubs (hatched during the spring of 2000; mean TL = 39.1 mm, SD = 3.1 mm, range = 33–45 mm) and three green sunfish (TL = 102, 104, and 108 mm). In these experiments, we included a foodless absolute refuge to facilitate a trade-off between feeding and mortality. Accordingly, we used a 0.6-cm mesh partition that is impermeable to green sunfish and floating pellets (solid barrier at the water’s surface) but permeable to bluehead chubs to divide the oval stock tanks into equal halves across the narrow axis. We applied one of two predator treatments (zero or one green sunfish) and one of four

pellet treatments (40-, 70-, 100-, or 160-mg pellets) to each experimental trial, adding pellets, green sunfish, and the concrete block to one randomly chosen half of the tank each night. All trials received four bluehead chubs placed into the half of the tank lacking pellets and green sunfish. We applied all eight of the treatment combinations except the one green sunfish and 100-mg pellet treatment combination for a total of seven treatment combinations (to focus our effort on the low and high pellet treatments). We repeated experimental trials until all seven treatment combinations had been replicated four times except for the 40 mg of pellets \times 0 green sunfish treatment, which was replicated only twice because it was apparent after two replicate trials that the bluehead chubs would probably consume all of the pellets on every trial. On each night thereafter, we repeated trials for the treatment combinations with the largest relative errors to homogenize uncertainty across treatment combinations. We replicated each experimental trial two to 12 times and ended the experiment after 51 experimental trials had been completed.

Bluehead chubs that were not used in a given night's experimental trials were fed a maintenance ration of about three pellets. Each morning, each green sunfish was fed a ration of two female adult mosquitofish. We assessed the green sunfish's propensity to consume pellets using control trials that isolated one green sunfish with 160 mg of pellets for 10 h overnight in the absence of bluehead chubs. The green sunfish sometimes consumed a small amount of pellets in these trials (mean = 2.9 mg, SE = 1.5 mg, seven replicates), but we considered such consumption to be negligible and ignore it in our calculations. The average wet mass of bluehead chubs over the course of experiment 1 was 597 mg (for use in our mathematical models; see "Alternative Optimization Models of Behavior").

Alternative Optimization Models of Behavior

We measured two response variables per trial in each experiment: the number of bluehead chubs consumed by green sunfish and the mass of pellets consumed by bluehead chubs. There are many hypothetical models that could feasibly describe the feeding rates and predation mortality of bluehead chubs in our experimental system, and we focus on a set of four foundational alternative models. In all of the models, we posit that bluehead chub feeding behavior in our experimental system can be quantified by a parameter ε that measures foraging effort (Abrams 1991; McNamara and Houston 1994). Foraging effort can depend on many factors, such as the proportion of time spent in foraging areas (Abrams 1982; Gilliam and Fraser 1987; Hügler and Dill 1994), searching speed (Werner and Anholt 1993; Leonardsson and Johansson 1997), or the proportion of time spent scanning for predators

while foraging (Brown et al. 1999). We do not explicitly model the behavioral components that determine foraging effort. Rather, we represent foraging effort with one parameter representing the rate at which bluehead chubs encounter pellet food. We posit that foraging effort, ε , can range between 0 and 1 and that it represents a proportion of the maximum encounter rate that can be achieved by bluehead chubs in our experimental system.

Our models specify the decline of pellets, $r(t)$ (mg), and bluehead chubs, $n(t)$ (number of individuals), over the course of the 10-h experimental trials. We assume that bluehead chubs consume pellets according to a Holling Type II functional response (Holling 1959) and that feeding rate is a nonlinear function of foraging effort, $f(\varepsilon)$. Therefore, the depletion of pellets over the course of an experimental trial is given by

$$\frac{dr}{dt} = -\frac{a\varepsilon r}{1 + a\varepsilon hr} n = -f(\varepsilon)n, \quad (2)$$

where the parameters a and h are the capture rate at maximum foraging effort ($1/h$) and the handling time (h/mg), respectively, for bluehead chubs feeding on pellets. We assume that green sunfish consume bluehead chubs according to a linear functional response and that the per capita mortality rate of bluehead chubs, $\mu(\varepsilon)$, is linear in ε . The depletion of bluehead chubs is given by

$$\frac{dn}{dt} = -\alpha\varepsilon pn = -\mu(\varepsilon)n, \quad (3)$$

where α is the predator capture rate at maximum bluehead chub foraging effort ($1/h$) and p is the number of green sunfish predators.

We lack detailed empirical information concerning the functions $f(\varepsilon)$ and $\mu(\varepsilon)$ and adopt the expressions in equations (2) and (3) because they are simple, are employed in the literature (e.g., Abrams 1982, 1991; Houston and McNamara 1989; Werner and Anholt 1993; Leonardsson and Johansson 1997), and produce a convex growth-mortality trade-off (models with a concave or linear trade-off provide poor fits to our data). This convex function describes the growth-mortality trade-off: growth rate and mortality rate increase simultaneously as foraging effort increases from 0 to 1 (fig. 1).

We consider different optimization models that specify bluehead chub foraging effort based on growth rate (or, equivalently, feeding rate) and mortality rate. These optimization models operate under the premise that behaviors evolve so as to maximize fitness. Here we note that organisms within a population are not identical (i.e., individuals can be classified into different categories or states according to age, body size, spatial position, parasite load,

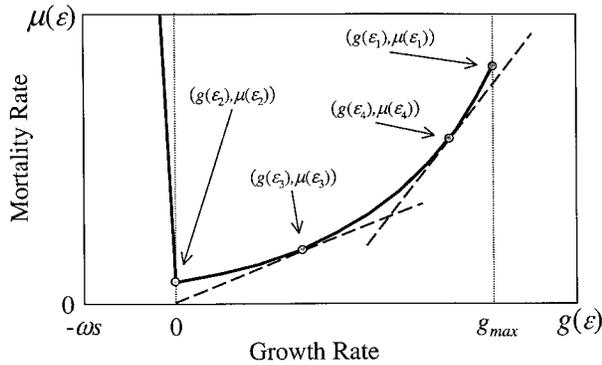


Figure 1: Graphical illustration of the foraging behavior (ϵ = foraging effort) predicted by the four alternative optimization models when there is a convex trade-off between growth rate and mortality rate. Model 1 predicts that bluehead chubs forage with maximum effort so that $\epsilon_1 = 1$ and growth rate is maximized at $g = g_{max}$. Model 2 predicts a foraging effort that exactly meets maintenance needs, resulting in $g(\epsilon_2) = 0$. The dashed lines tangent to the curve identify optimal foraging efforts for models 3 and 4. Model 3 predicts that bluehead chubs forage so as to minimize the ratio of mortality rate to growth rate (i.e., minimize $\mu(\epsilon) : g(\epsilon)$). Model 4 predicts a foraging effort that maximizes a linear combination of growth rate and mortality rate according to a dynamic programming equation (eq. [4]) or, equivalently, that minimizes $(\mu + z) : g$, where $z = -(\partial V^*/\partial t)/V^*$, V^* = reproductive value, and t = age.

energetic condition, etc.), and we rely on the set of optimization literature that models behavior in state-structured populations (e.g., Werner and Gilliam 1984; Mangel and Clark 1988; Houston and McNamara 1999) as our conceptual foundation. Many authors have discussed alternative representations of fitness in optimization models (e.g., Abrams 1991; Brown et al. 1996; Houston and McNamara 1999; Kozłowski 1999).

We take reproductive value, V , as our basic metric of fitness. Our general model assumes that the population is structured by body size, s , and age, t , so that reproductive value is a function of body size and age (i.e., $V = V(s, t)$); for a cohort of individuals with the same birthday, our age variable t can represent the effects of time on reproductive value acting through both aging per se and time of year per se. Introductions to the theory and literature on which our general optimization model is based can be found in Houston and McNamara (1999). Under this assumption, the reproductive value of a juvenile animal in a stable population changes over time according to

$$-\frac{\partial V}{\partial t} = \frac{\partial V}{\partial s}g(\epsilon) - \mu(\epsilon)V,$$

where $g(\epsilon)$ is the growth rate, or change in body size per time (Houston and McNamara 1989; Ludwig and Rowe

1990; McNamara and Houston 1994). Optimal behaviors maximize fitness by maximizing the right-hand side of this equation at every age t . This optimization is equivalent to maximizing reproductive value at each age. Behavior of bluehead chubs is determined by foraging effort, ϵ , so optimal behaviors satisfy the dynamic programming equation

$$-\frac{\partial V^*}{\partial t} = \max_{\epsilon} \left(\frac{\partial V^*}{\partial s}g(\epsilon) - \mu(\epsilon)V^* \right), \quad (4)$$

where $V^* = V^*(s, t)$ is the reproductive value of a bluehead chub at size s and age t that behaves optimally over the remainder of its lifetime.

We now discuss four possible models of foraging effort. All of the models assume that bluehead chubs forage with maximum effort so that $\epsilon = 1$ when predation hazard is 0 (i.e., when green sunfish predators are absent), but the models differ in their predicted foraging efforts when predators are present. In all four models, we assume that we can approximate bluehead chub fitness as density and frequency independent. Density independence applies because the instantaneous rates of feeding and mortality for bluehead chubs, as written in equations (2) and (3), do not depend on bluehead chub abundance. Density independence is not an unreasonable assumption for our experimental system because, averaging across trials with green sunfish predators, bluehead chub abundance varies by <1 individual over the duration of a trial (on average, only 0.60 and 0.84 bluehead chubs were killed in these trials in experiments 1 and 2, respectively). Frequency independence applies if the foraging effort, and therefore fitness, of a given bluehead chub does not depend on the foraging efforts of other bluehead chubs. Our models can still represent situations with frequency dependence even if they do not explicitly model the process. If all bluehead chubs adopt the same foraging effort, then the foraging effort parameter ϵ represents this effort exactly. Alternatively, if there is among-individual variability in foraging effort among bluehead chubs, then the parameter ϵ represents a weighted average of the individual foraging efforts. Finally, if green sunfish predators adjust their predation rate in response to changes in bluehead chub foraging effort, then the capture rate parameter α represents an average capture rate, with the average taken over the duration of a trial. We do not have data that would justify the explicit inclusion of density- and frequency-dependent effects in our analysis, but our models are not necessarily inconsistent with these effects; they provide a foundation to which these kinds of complexities could be added in future studies.

Model 1 ($\epsilon = 1$ regardless of predator presence or ab-

sence) is the classic growth, or energy, maximization model that is a foundation of foraging theory (Stephens and Krebs 1986; Krebs and Davies 1993). It can also arise when a growth-mortality trade-off does not exist or if $\partial V^*/\partial s$ is sufficiently large in comparison with V^* in equation (4). The resultant growth and mortality rates predicted for model 1 are $g(\varepsilon_1)$ and $\mu(\varepsilon_1)$ (fig. 1).

Model 2 (e.g., model 1 in Brown 1992) assumes that bluehead chubs fix foraging effort so as exactly to meet maintenance costs ($g(\varepsilon) = 0$) when predators are present. Model 2 can also arise from equation (4) if $\partial V^*/\partial s$ is sufficiently small in comparison with V^* . Model 2 specifies foraging effort as $\varepsilon_2 = 1$ when green sunfish are absent and

$$\varepsilon_2 = \frac{\omega s}{ar(k - \omega sh)}$$

(i.e., the ε such that $g(\varepsilon) = 0$) when green sunfish are present, with resultant growth and mortality rates $g(\varepsilon_2)$ and $\mu(\varepsilon_2)$ in figure 1. Model 2 can be thought of as minimizing mortality rate when green sunfish are present.

Model 3 (Werner and Gilliam 1984) offers a way to predict optimal growth rates that are intermediate between zero growth and maximal growth, and it predicts that bluehead chubs adjust foraging effort so as to minimize the ratio of mortality rate to growth rate, $\mu(\varepsilon) : g(\varepsilon)$, depicted by rates $g(\varepsilon_3)$ and $\mu(\varepsilon_3)$ in figure 1. This model follows from equation (4) for the case $\partial V^*/\partial t = 0$, making the simplifying assumption that reproductive value depends only on body size and not on age or time of year. If we assume that $\partial V^*/\partial s > 0$ and $V^* > 0$ and treat those quantities as constants, the general principle for using equation (4) is to choose ε so as to maximize $(\partial V^*/\partial s)g(\varepsilon) - \mu(\varepsilon)V^*$ or, equivalently, to maximize $\theta g(\varepsilon) - \mu(\varepsilon)$, where $\theta = (\partial V^*/\partial s)(1/V^*)$. However, setting $\partial V^*/\partial t = 0$ yields the additional insight that not only is $\theta g(\varepsilon) - \mu(\varepsilon)$ maximized but also the maximal value is equal to 0. Graphically, this means that the solution is shown by a line tangent to the curve in figure 1, with slope θ and passing through the origin. Werner and Gilliam (1984) used that observation to restate the solution as choosing the behavior that minimizes the value of $\mu(\varepsilon) : g(\varepsilon)$, found graphically by finding the value of ε at the tangent produced by taking the smallest slope of a straight line through the origin such that this line still touches the graph of $\mu(\varepsilon)$ versus $g(\varepsilon)$ (fig. 1). Bluehead chubs that adopt this strategy maximize their probability of surviving to each body size. Model 3 specifies foraging effort as $\varepsilon_3 = 1$ when green sunfish are absent and

$$\varepsilon_3 = \begin{cases} 1 & \text{if } r < \sqrt{\frac{\omega s}{kh}} \frac{1}{a(1 - \sqrt{\omega sh/k})} \\ \sqrt{\frac{\omega s}{kh}} \frac{1}{ar(1 - \sqrt{\omega sh/k})} & \text{otherwise,} \end{cases}$$

when green sunfish are present. If the optimal solution according to model 3 is intermediate between zero and maximal growth, all the following are equal at the optimal, tangent point in figure 1: $\partial \mu/\partial g$, μ/g , and θ .

Model 4 specifies foraging effort from the general model in equation (4) (Houston and McNamara 1989; Ludwig and Rowe 1990; McNamara and Houston 1994), subject to the constraint that $g(\varepsilon) \geq 0$. As in model 3, model 4 maximizes a linear combination of growth rate and mortality rate, $\theta g(\varepsilon) - \mu(\varepsilon)$. However, in model 4, we do not assume that $\partial V^*/\partial t = 0$, so the slope of the tangent line need not produce a line that includes the origin; model 4 requires estimation of one additional parameter, θ itself, to depict the optimal solution in figure 4. Model 4 specifies foraging effort as $\varepsilon_4 = 1$ when green sunfish are absent and

$$\varepsilon_4 = \begin{cases} \frac{\omega s}{ar(k - \omega sh)} & \text{if } r < \frac{\alpha p}{ka\theta} \\ \left(\sqrt{\frac{ka\theta r}{\alpha p}} - 1 \right) \frac{1}{ahr} & \text{if } \frac{\alpha p}{ka\theta} < r < \frac{\alpha p(1 +ahr)^2}{ka\theta} \\ 1 & \text{otherwise,} \end{cases}$$

when green sunfish are present. The parameter θ (1/mg) is the marginal rate of substitution (MRS) of mortality rate for growth rate, and it specifies the relative contributions of growth and mortality to fitness. If the optimal solution according to model 4 is intermediate between zero and maximal growth, all the following are equal at the optimal, tangent point in figure 4: $\partial \mu/\partial g$, $[\mu - (\partial V^*/\partial t)/V^*]/g$, and θ .

Statistical Model Selection

Our experimental treatments vary the initial mass of pellets, $r(0)$, and the number of green sunfish, p , in each trial. The initial number of bluehead chubs, $n(0)$, is given and is constant across treatment combinations within each set of experiments ($n(0) = 6$ in experiment 1 and $n(0) = 4$ in experiment 2). Our two observed response variables, which we treat as random variables, are the mass of pellets consumed by bluehead chubs, $R_c(t)$, and the number of bluehead chubs consumed by green sunfish, $N_c(t)$. The differential equations (eq. [2], [3]) describe the depletion

of pellets and bluehead chubs over the course of the trials given $r(0)$, $n(0)$, p , and values for foraging effort, ε , where foraging effort over the course of a trial is determined by one of the four alternative optimization models. Foraging effort may depend on the growth parameters k and ω and the body size, s , of bluehead chubs. In the models, we assume that all individual bluehead chubs within a set of experiments have identical and constant body sizes over the duration of the experiments (i.e., $s = 2,120$ mg in fits to experiment 1 data and $s = 597$ mg in fits to experiment 2 data; surviving bluehead chubs grew an average of 1.1 and 1.7 mm TL over the course of experiment 1 and experiment 2, respectively). Moreover, we assume that all parameters (a , h , α , and λ in models 1–3 and a , h , α , λ , and θ in model 4; λ is a covariance parameter defined below) are constant during each trial and across all treatments within each set of experiments. The parameters are assumed to differ across our two sets of independent experiments, experiment 1 and experiment 2, because the experimental conditions and the body sizes of the fish differ between the two sets of experiments.

Hence, each of the four optimization models produces a prediction of the mass of pellets consumed, $r_c(t) = r(0) - r(t)$, and the number of bluehead chubs consumed, $n_c(t) = n(0) - n(t)$, for any given treatment combination. That is, for a given treatment combination for one of the sets of experiments, the i th optimization model predicts that $r(t)$ and $n(t)$ change according to equations (2) and (3) with foraging effort ε_i , giving solutions for the amounts of pellets ($r_i(t)$) and bluehead chubs ($n_i(t)$) remaining at the end of a trial, so that the predicted rates of consumption of pellets and bluehead chubs are $r_{c,i}(t) = r(0) - r_i(t)$ and $n_{c,i}(t) = n(0) - n_i(t)$, respectively.

We model the stochastic variability in the outcomes of our experimental trials by assuming that the observed value of bluehead chubs consumed for a given treatment combination, $N_{c,i}(t)$, follows a binomial distribution with marginal probability density $\Pi_n(n_{c,i}(t))$ determined by

$$N_{c,i}(t) \sim \text{binomial}\left(p, \frac{n_{c,i}(t)}{p}\right)$$

for experiment 1 and

$$N_{c,i}(t) \sim \text{binomial}\left(2, \frac{n_{c,i}(t)}{2}\right)$$

for experiment 2 because at most p bluehead chubs were actually consumed in any trial in experiment 1 and at most two bluehead chubs were actually consumed in any trial in experiment 2. We assume that the observed value of pellets consumed for a given treatment combination,

$R_{c,i}(t)$, has a binomial distribution conditional on $n_{c,i}(t)$ with probability density $\Pi_{r|n}(r_{c,i}(t)|n_{c,i}(t))$ determined by

$$R_{c,i}(t) \sim \text{binomial}\left(r_i(0), \frac{r_{c,i}(t)}{r_i(0)} + \lambda_i \frac{N_{c,i}(t) - n_{c,i}(t)}{r_i(0)}\right),$$

where

$$\lambda_i = \text{corr}(R_{c,i}(t), N_{c,i}(t)) \sqrt{\frac{\text{Var}(R_{c,i}(t))}{\text{Var}(N_{c,i}(t))}}$$

is a measure of the within-treatment covariance between $R_{c,i}(t)$ and $N_{c,i}(t)$ and is proportional to the correlation coefficient, $\text{corr}(R_{c,i}(t), N_{c,i}(t))$. Accordingly, $R_{c,i}(t)$ and $N_{c,i}(t)$ have the joint probability density

$$\Pi(r_{c,i}(t), n_{c,i}(t)) = \Pi_{r|n}(r_{c,i}(t)|n_{c,i}(t))\Pi_n(n_{c,i}(t)), \quad (5)$$

with expectations $E(R_{c,i}(t)) = r_{c,i}(t)$ and $E(N_{c,i}(t)) = n_{c,i}(t)$. We use this statistical model because our data are counts and it is a computationally tractable analogy to the joint density predicted using a stochastic version of equations (2) and (3).

Given this stochastic model of our experimental data, we fit the four alternative optimization models to the data from experiments 1 and 2 via maximum likelihood using the joint density defined in equation (5) (Casella and Berger 1990; Hilborn and Mangel 1997). We implemented the optimization routine `fmincon` in the software application Matlab to maximize the likelihood (Coleman et al. 1999). Solutions to the differential equations in equations (2) and (3) and those used to obtain the gradient required in `fmincon` were solved using a fourth order Runge-Kutta scheme with a fixed step size (Kincaid and Cheney 1996).

Because the models differ in their number of parameters, we computed Schwarz's Information Criterion (SIC) for each model fit to each data set to compare the alternative models. That is, models 1–3 have parameters a , h , α , and λ , but model 4 has these same four parameters plus a fifth parameter, θ . The SIC is an asymptotic model selection criterion with a Bayesian foundation that incorporates both the model's fit to the data and the model's number of parameters (Schwarz 1978). The SIC for model i fit to the data from one of the experiments with a total of m experimental trials is

$$\text{SIC}_i = -2L_i + \log_e(m)q_i,$$

where L_i is the \log_e -likelihood of model i and q_i is the number of parameters in model i . The SIC decreases as the \log_e -likelihood increases (i.e., as the model fit to the data improves) and decreases as the number of parameters

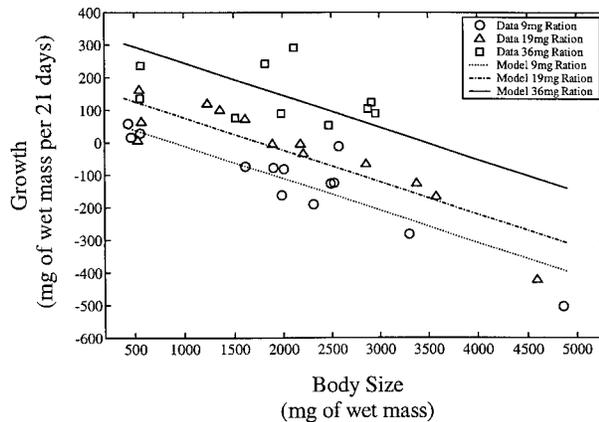


Figure 2: Predictions of the growth model described by equation (1) and the data from the growth experiment. Each data point corresponds to an individual bluehead chub.

decreases (i.e., as the model becomes more parsimonious). Thus, smaller values of SIC_i in comparison with SIC_j provide support for model i in comparison with model j as a model of the data, and we use the SIC to make this kind of inference in our analysis. We use the SIC rather than some other model selection criteria because it can select the correct model with high probability when sample sizes are large (i.e., it is asymptotically consistent) and it is less likely to select models with more parameters (i.e., it is less prone to overfitting) in comparison with some other criteria (McQuarrie and Tsai 1998).

Results

Growth Experiment

The growth model specified in equation (1) with parameters k and ω explained a significant amount of the variation in the data from the growth experiment ($F = 80.46$, $df = 2, 34$, $P < .001$). In particular, the specification of instantaneous growth rate as linear in feeding rate and body size provides a good fit to the data (fig. 2). We take the estimates (95% confidence intervals), 0.455 (0.3785, 0.5302) and 0.005 (0.0041, 0.0058), as values for the parameters k (unitless) and ω (1/d), respectively, in fitting our optimization models below. We also fit a more general four-parameter model that specifies k and ω as allometric functions of body size, and we found that it does not explain any more variation in the data than the two-parameter model given by equation (1) (i.e., the likelihoods for these two models are identical).

Behavioral Experiments

The results from both experiments 1 and 2 with our corresponding statistical analysis indicate that bluehead chubs forage so as to balance the benefits of growth versus the cost of predation mortality. Moreover, our statistical ranking of the models using the data from the experiments results in the following order of the models from worst to best (highest SIC to lowest SIC): model 2, model 1, model 3, and model 4. This ranking of the models holds if the data from the two experiments are considered separately or pooled (table 1), indicating that our result is applicable to both young-of-the-year and 1-yr-old bluehead chubs. Furthermore, application of the Akaike Information Criterion (Akaike 1974), another commonly used model selection criterion, results in the same rankings.

Optimization model 1 (statistical rank of 3 with the second highest SIC) lacks any behavioral flexibility and predicts that bluehead chubs forage with maximum effort so as to maximize growth rate regardless of the number of pellets or green sunfish present. However, our analysis indicates that bluehead chubs behaviorally decrease their pellet consumption in the presence of green sunfish. Indeed, model 1 cannot explain all of the variation in pellet consumption across green sunfish treatments (fig. 3a, 3b), and it overestimates the mortality of bluehead chubs by green sunfish (fig. 3c, 3d). Model 1 does account for some of the variation in pellet consumption across green sunfish treatments via depletion effects. Specifically, bluehead chub mortality increases with increasing numbers of green sunfish, resulting in fewer individuals to consume pellets and thereby decreasing pellet consumption. Even with depletion effects, model 1 remains a poor predictor of both response variables in both experiments.

Optimization model 2 (statistical rank of 4 with highest SIC) predicts that bluehead chubs forage with maximum effort in the absence of green sunfish but forage so as just to meet maintenance requirements when green sunfish are present. However, our data indicate that in the presence of green sunfish, bluehead chubs consume pellets at a rate above their maintenance requirements (fig. 4a, 4b) while incurring an associated mortality cost (fig. 4c, 4d); this il-

Table 1: Values of the Schwarz Information Criterion (SIC) for each of the four models for each data set

Model	Experiment 1	Experiment 2	Both experiments
1	450.7	314.7	764.0
2	4,901.8	1,457.2	6,357.6
3	131.4	189.7	319.7
4	0	0	0

Note: Lower values of the SIC indicate that the model provides a more parsimonious fit to the data. The values have been standardized within each column so that the model with the lowest SIC value is set to 0.

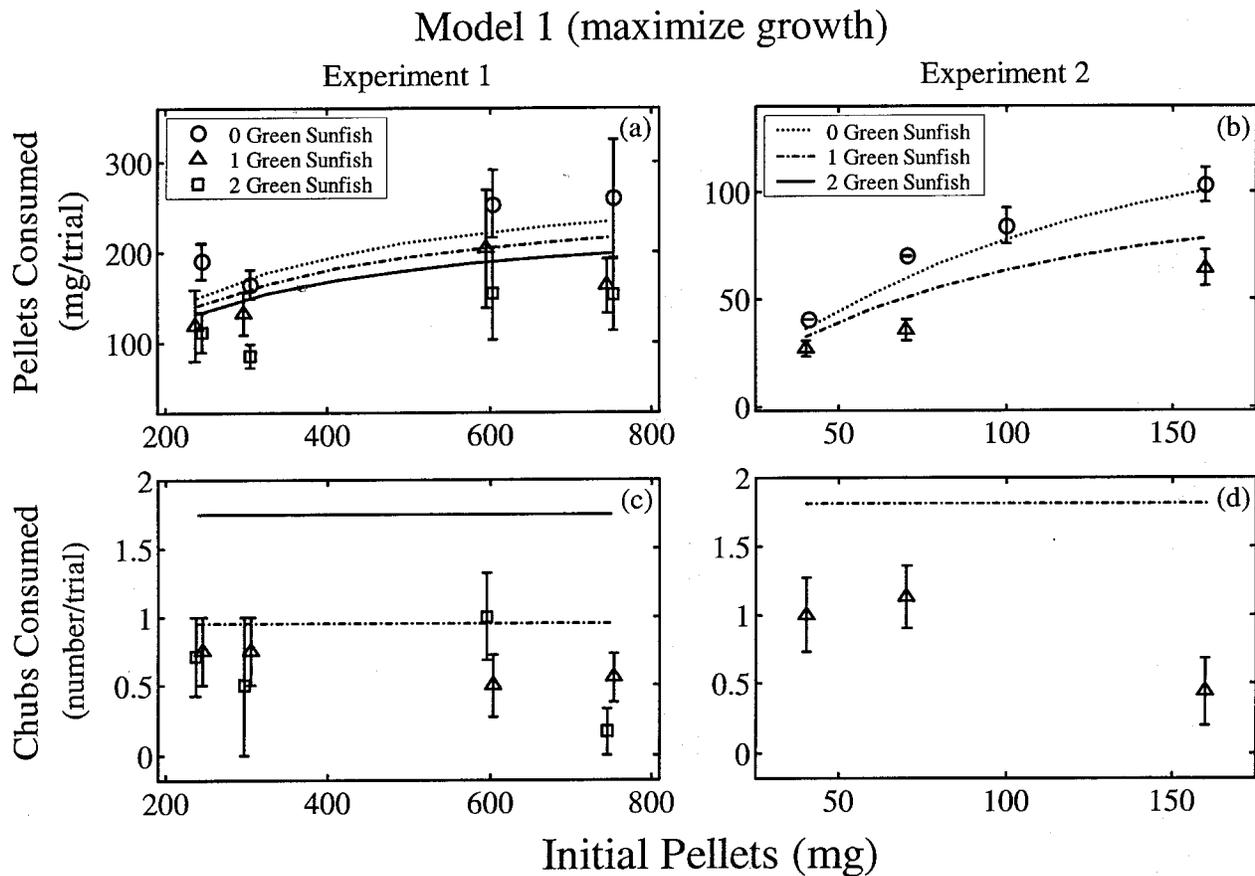


Figure 3: Fits of optimization model 1 to the bivariate data from experiments 1 (*a, c*) and 2 (*b, d*). Model 1 predicts that bluehead chubs maximize foraging effort in all treatments. The two response variables, pellets consumed by bluehead chubs (*a, b*) and bluehead chubs consumed by their predator (*c, d*), are plotted against initial pellet treatments for different levels of the predator (green sunfish) treatment. Symbols indicate data (treatment means with standard errors, slightly offset for clarity), and lines indicate model predictions.

illustrates the importance for bluehead chubs of maintaining positive growth rather than just avoiding predation.

Optimization model 3 (statistical rank of 2 with second lowest SIC) predicts that bluehead chubs forage with some intermediate level of effort by minimizing the ratio of mortality rate to growth rate. Accordingly, in comparison with models 1 and 2, model 3 provides a better fit to the data by correctly predicting the approximate magnitude of the decrease in pellet consumption in the presence of green sunfish (fig. 5*a, 5b*) and more closely approximating the observed numbers of bluehead chubs consumed (fig. 5*c, 5d*). However, model 3 predicts an almost constant feeding rate over the duration of a trial and thus tends to overestimate pellet consumption at low initial pellets and to underestimate pellet consumption at high initial pellets. Furthermore, model 3 underestimates the mortality of bluehead chubs across all treatments. These results indicate that model 3 is superior to models 1 and 2 because model

3 predicts a foraging effort intermediate between 0 and 1 that balances the growth-mortality trade-off in some fashion. However, model 3 fails to explain some features of the data that result in systematic deviations in the model fit.

Of the four models we consider, model 4 (statistical rank of 1 with lowest SIC) provides the best fit to the data by providing a good description of the pellets consumed and bluehead chubs consumed from both experiments. However, model 4 has an additional parameter θ , and we should ask whether the improvement is worth it in two senses. The first sense is whether the extra parameter results in a qualitative improvement in fit to some feature(s) of the data. We feel it does. In comparison with model 3, model 4 predicts that pellet consumption increases with initial pellets in the presence of green sunfish (fig. 6*a, 6b*), and it also predicts the approximate magnitude of the numbers of bluehead chubs consumed across all treat-

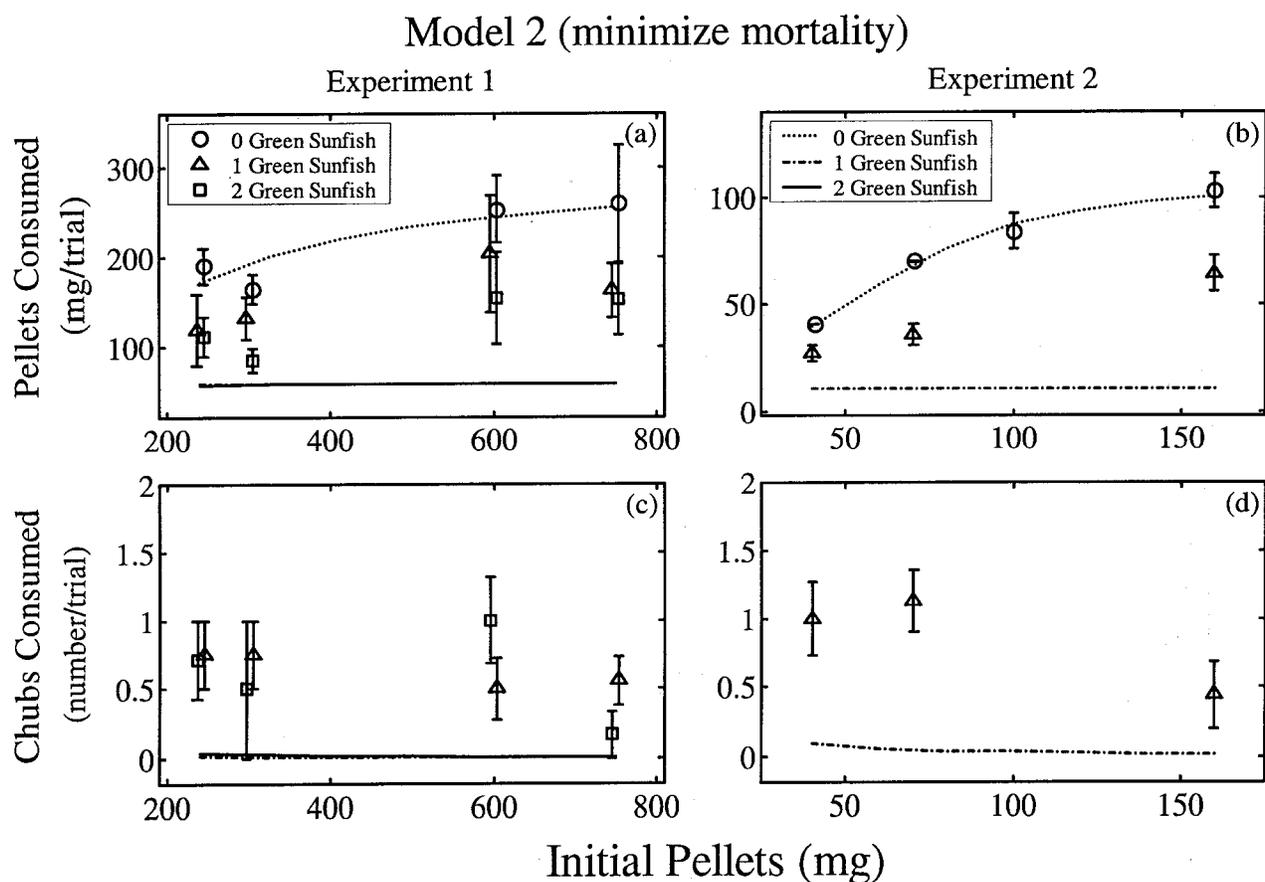


Figure 4: Fits of optimization model 2 to the bivariate data from experiments 1 and 2. Model 2 predicts that bluehead chubs adjust their foraging effort in the presence of the predator (green sunfish) so as to meet maintenance costs exactly. For experiment 1, the model's predictions for two predators nearly overlie the prediction for one predator.

ments (fig. 6c, 6d). The second sense is the statistical assessment via the SIC. Model 4 has the lowest SIC value, indicating that among the four models we consider, model 4 is the best overall representation of the data despite having one more parameter than models 1–3.

Discussion

The fits of the models to the data and our statistical ranking of the models by the SIC indicate several conclusions. First, model 1, which lacks any behavioral flexibility, is a poor description of the data, indicating that the inclusion of behavioral flexibility is crucial to understanding our experimental food chain. Second, models 3 and 4 are both preferable in terms of the SIC to models 1 and 2, indicating that models with behavior that balances benefits of growth against the threat of death are better descriptions of bluehead chub behavior than models emphasizing growth or

mortality alone. Third, model 4 has a lower SIC than model 3, indicating that modeling bluehead chub reproductive value as a function of body size and age gave a significantly better statistical fit to the data than modeling bluehead chub reproductive value as a function of body size alone (assuming that the bluehead chub population growth rate is 0; see below). Model 4 can account for time-related changes in reproductive value, such as those that may result from age-specific and seasonal effects on fitness components—effects that are not included in model 3.

The fits of model 4 to the data also allow us to study the resulting estimates of the parameter θ , the marginal rate of substitution (MRS) of mortality rate for growth rate. Large values for the MRS indicate a greater value placed on growth in comparison with avoidance of death. The MRS thus provides a conceptual connection between behavior and life history. Based on the definition of the

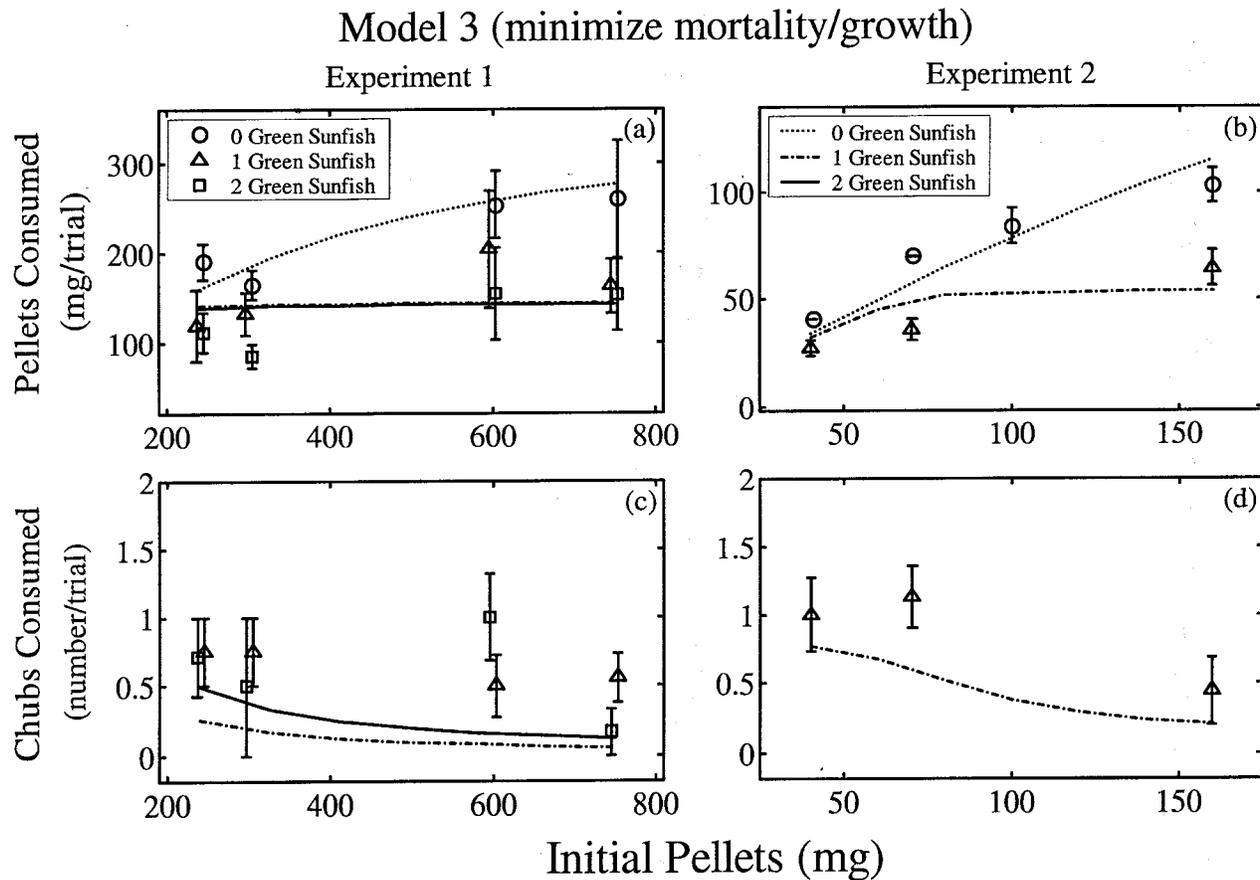


Figure 5: Fits of optimization model 3 to the bivariate data from experiments 1 and 2. Model 3 predicts that bluehead chubs adjust foraging effort so as to minimize the ratio of mortality rate to growth rate (i.e., minimize $\mu(\epsilon) : g(\epsilon)$). Model 3 predicts nearly identical results for pellets consumed across predator levels 1 and 2, so the lines for these values overlap substantially.

MRS as $\theta = (\partial V^*/\partial s)/(1/V^*)$, we might expect that young bluehead chubs of small body size would place more value on growth in comparison with mortality than older, larger bluehead chubs with higher reproductive value (e.g., Houston and McNamara 1999). Our estimates of the MRS for young-of-the-year (fish from experiment 2) and 1-yr-old (fish from experiment 1) bluehead chubs support this idea. We estimate the MRS (95% confidence intervals computed using likelihood ratios) to be 0.1194/mg (0.0993, 0.1446) and 0.0297/mg (0.0262, 0.0341) for young-of-the-year and 1-yr-old bluehead chubs, respectively. Moreover, the results from our experiments and our observations of bluehead chub behavior in the lab corroborate this idea. Averaging across treatments with green sunfish present, the young-of-the-year bluehead chubs in experiment 2 fed at higher rates (four times vs. 2.5 times maintenance requirement) and incurred higher rates of mortality (0.2/trial vs. 0.1/trial) in comparison with their 1-yr-old coun-

terparts in experiment 1, even though prey:predator length ratios were similar in both experiments (0.37 in experiment 2 vs. 0.40 in experiment 1). This comparison is only approximate because other factors, in addition to the age and size of bluehead chubs, probably differed across the two experiments.

While the data from our empirical example make a convincing case for the appropriateness of model 4 in comparison with the three alternatives, model 4 requires an estimate of the MRS—an estimate that provides additional insight and accuracy of predictions but that can also be difficult or impossible to obtain, especially in field settings. Accordingly, if empirical estimates of the MRS are lacking, model 3 can be used provisionally until sufficient data are available to make a rigorous inference regarding the appropriateness of model 3 in comparison with model 4. In comparison with model 1 and model 2, model 3 has the substantial advantage of being a practical way

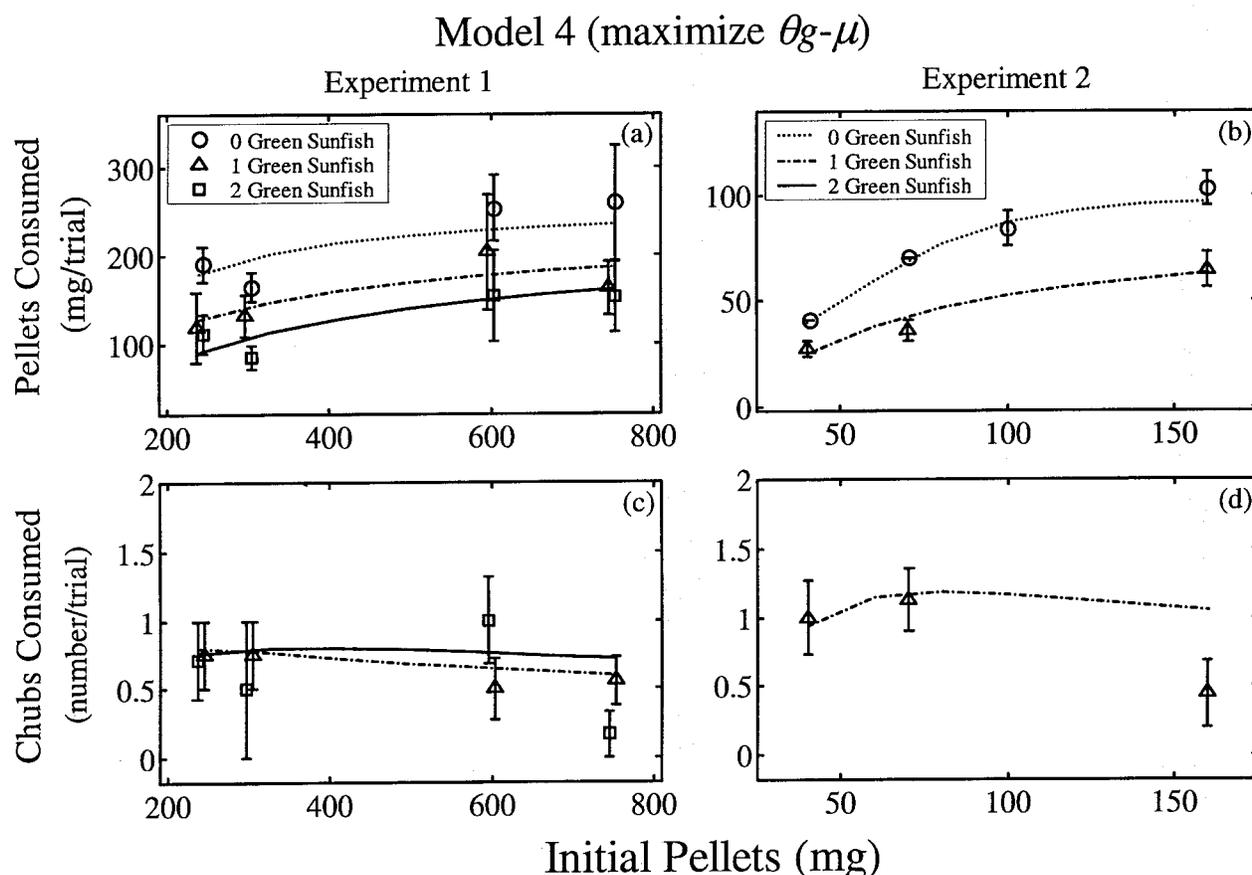


Figure 6: Fits of optimization model 4 to the bivariate data from experiments 1 and 2. Model 4 predicts that bluehead chubs adjust foraging effort so as to maximize a linear combination of growth rate and mortality rate given by a dynamic programming equation or, equivalently, to minimize $(\mu + z) : g$, where $z = -(\partial V^*/\partial t)/V^*$, V^* = reproductive value, and t = age.

to specify a predicted growth rate intermediate between zero and maximal, but it lacks the fuller accuracy that model 4 affords.

A large number of empirical studies have addressed the topic of feeding-mortality trade-offs (Lima and Dill 1990; Lima 1998). Abrahams and Dill (1989) and Nonacs and Dill (1990) used titration-type methods in laboratory habitats to study the trade-off between feeding rate and mortality rate and computed measures of the amount of mortality animals are willing to incur so as to obtain food. Houston and McNamara (1999) discuss how to interpret the results of these kinds of titration experiments in terms of the kinds of models that we test here, including the relevance of the MRS. Kotler (1997) and Mitchell et al. (1990) studied the foraging of desert gerbils and show that feeding rate maximization (our model 1) is a better description of their behavioral data than mortality rate minimization (our model 2). Their results are similar to our result that model 1 is superior to model 2 for bluehead

chubs. Other studies have considered the optimization hypothesis underlying model 3, that is, that foragers should behave so as to minimize the ratio of mortality rate to growth rate, $\mu : g$. Gilliam and Fraser (1987) reported that habitat selection by juvenile creek chubs in an experimental stream was consistent with a minimize $\mu : f$ hypothesis (minimize $\mu : f$ can be related to, but is not identical to, minimize $\mu : g$) and inconsistent with growth maximization and mortality minimization (i.e., feeding to obtain a fixed ration). Dahlgren and Eggleston (2000) obtained a similar result in their field study of ontogenetic habitat shifts in Nassau grouper. Using approximate calculations, Turner and Mittelbach (1990) argue that the foraging behavior of bluegill sunfish in experimental ponds is consistent with the minimize $\mu : f$ hypothesis. All of these studies and many others (Lima and Dill 1990; Lima 1998) show that animals consider both feeding rate and mortality rate when making behavioral decisions.

Many other avenues for future research are available.

For example, we considered only one state variable, body size, in our theoretical treatment, and additional state variables such as level of energetic reserves or parasite load could be considered. Also, we framed the models around the concept of foraging effort, ε , but did not attempt explicitly to measure foraging effort except as it was inferred by our measurements of feeding rate and mortality rate; direct measurements of metrics of foraging effort such as swimming speed and activity (Werner and Anholt 1993; Johansson and Leonardsson 1998; Anholt et al. 2000) would improve our ability to test among more detailed hypotheses. Extensions to explicit consideration of frequency dependence have revolved around an “equalize $\mu : f$ ” idea (Gilliam and Fraser 1988; Hugie and Dill 1994; Sih 1998), but explicit tests are lacking (Sih 1998). Also in its infancy are intriguing theoretical predictions about how optimal behavior in a given time or place depends on conditions in a different time and/or place (Gilliam and Fraser 1987; Gilliam 1990; McNamara and Houston 1994; Lima and Bednekoff 1999). For example, we consider an animal splitting its time between an energetically poor but relatively safe habitat (a “refuge”) and a second, hazardous habitat. The enhancement of food in the refuge, which seemingly takes pressure off the animal to forage in a hazardous way in the second habitat, can instead be predicted actually to induce more hazardous behavior by the animal when it is in the second habitat (Gilliam 1990). Finally, many earlier studies designed experiments that minimized or eliminated the depletion of foragers and/or their prey over the course of experimental trials. Some consequences of these efforts are that the duration of trials is of the order of minutes with a nonzero predation hazard (e.g., Gilliam and Fraser 1987; Abrahams and Dill 1989; Johansson and Leonardsson 1998), the trial duration is longer with 0 or negligible predation hazard (e.g., Sih 1980; Anholt et al. 2000), or the trials are short and have a negligible predation hazard (e.g., Milinski and Heller 1978; Godin and Dugatkin 1996). However, as our analysis demonstrates, eliminating depletion is not necessary to test among quantitative hypotheses when the depletion process can be explicitly modeled in the statistical analysis. In fact, measurements of depletion can be viewed as providing additional information over longer time intervals.

In our models and specifically equation (4), we modeled optimal behavior as occurring in a population that is neither increasing nor decreasing, that is, with population growth rate $r = 0$ (here, we do not italicize r purely to distinguish it from our previous use of italicized r to denote resource level in our models); considering cases where r is not 0 has the consequence of substituting $\mu(\varepsilon) + r$ for $\mu(\varepsilon)$ in equation (4), representing the effect of dilution (for $r > 0$) of the individual’s future offspring in a larger future population; for declining populations ($r < 0$), the

effect reverses. In this case, model 3 becomes “minimize $(\mu + r) : g$ ” (Werner and Gilliam 1984), with the vertical intercept in figure 1 being $-r$ rather than 0, and resultant higher optimal growth and mortality for $r > 0$, where r is treated as a parameter in the calculation of the optimal behavior. This variant on model 3 then takes the same form as model 4, that is, both models can be expressed as “minimize $(\mu + z) : g$,” where $z = 0$ in model 3, $z = r$ in model 3 augmented to include r , $z = r - b/V^*$ for adults with b representing instantaneous fecundity (Werner and Gilliam 1984), $z = (-\partial V^*/\partial t)/V^*$ in model 4, or $z = r - b/V^* - (\partial V^*/\partial t)/V^*$ if all three extensions are included. The vertical intercept of these models is $-z$ in figure 1, and at optimal solutions intermediate between zero and maximal growth, $\partial\mu/\partial g$, $(\mu + z)/g$, and θ are all equal. Hence, we can think of z as a “bias function” that specifies what systematic deviations we find, or expect to find, from the simpler “minimize $\mu : g$ ” heuristic. Studies focusing on estimates of z and/or θ might be useful tools in testing hypotheses in a wide variety of ecological and evolutionary settings. Such efforts remain important, given the strong role that behavioral flexibility plays in the ecology of populations and communities (e.g., Rosenzweig and Abramsky 1997; Post et al. 1999).

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