Rules of Thumb for Predation Hazard Assessment: Predictions from a Dynamic Model

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RULES OF THUMB FOR PREDATION HAZARD ASSESSMENT: PREDICTIONS FROM A DYNAMIC MODEL

Amos Bouskila* and Daniel T. Blumstein†

*Center for Population Biology, University of California, Davis, California 95616;
†Animal Behavior Graduate Group, c/o Department of Zoology, University of California,
Davis, California 95616

Abstract.—Before an animal can evaluate the benefits and costs associated with a particular behavior, it must first assess them. Since perfect information is impossible to acquire, it has been suggested that animals use simple rules of thumb to acquire information. The use of rules, however, may lead to substantially inaccurate perceptions. In this article, we present the results of a dynamic optimization model developed to study the opportunity for the evolution of rules of thumb for predation hazard assessment. There are four main conclusions from this model. First, selection will not always favor perfect estimates, if one assumes there is some cost in acquiring accurate information. There is a zone of tolerance where inaccurate perceptions perform just as well as perfect knowledge of predation hazard. This implies that animals need not have perfect, only sufficient, information in order to behave optimally. Second, this zone of tolerance is generally shifted toward overestimating predation hazard: animals that overestimate hazard will have a lower mortality than animals that underestimate hazard. Third, animals should attempt to track fluctuating predation hazard rather than act on the average predation hazard. Finally, the model is robust: several simplifying assumptions can be relaxed, and the same general conclusions are reached. We suggest instances where animals are using simple rules to assess predation hazard and outline an experimental protocol to study the use of rules of thumb for predation hazard assessment.

Animals require information in order to make decisions (Stephens and Krebs 1986; Mangel and Clark 1988; Stephens 1989; Mangel 1990). Acquiring completely accurate information may either be expensive (it takes much time or energy) or be beyond the sampling and perceptual capabilities of a given species. It is often assumed that animals use simple rules either to acquire information or to make decisions later. The use of assessment or decision rules by animals has been demonstrated in foraging (see, e.g., Pyke 1978; Barnard and Brown 1981; Bergelson 1985), kin recognition (Blaustein and O'Hara 1982), and habitat selection (Stamps 1988).

The importance of information has also been addressed using theoretical models. A common criticism of optimality models is that many assume perfect knowledge of a parameter (Stephens and Krebs 1986). To solve this problem, theoreticians have modeled the behavior of animals that are assumed to use rules for the acquisition of information, and the models study the effect of such rules on fitness (see, e.g., McNamara and Houston 1980, 1985; Pyke 1984). Although these rules

may lead to fitnesses that are near maximal, they often lead to lower fitnesses (Stephens and Krebs 1986).

The consequences of suboptimal strategies have been studied in different ways. McFarland and Houston (1981) concluded that animals using decision rules in the environment in which they evolved may exhibit nearly optimal behavior. Janetos and Cole (1981) compared the payoffs from optimality models to those based on simple rules and concluded that although optimal solutions always had higher payoffs than solutions based on rules, the magnitude of the difference was not that great. McNamara and Houston (1986) defined the canonical cost as a measure of the change in an animal's fitness incurred by a "wrong" decision. Mangel and Clark (1988) illustrated the cost of a suboptimal strategy by calculating the ratio of the fitness of an animal using a suboptimal strategy to the fitness of an animal using an optimal strategy. Roitberg (1990) analyzed the fitness of fruit flies that use inaccurate information about patch quality for oviposition. None of these studies deal with imperfect perceptions of predation risk.

Assessing predation hazard poses a problem similar to that of foraging or habitat choice. It differs in that acquiring or updating information by sampling may be fatal. Nevertheless, in order to make trade-offs between predation risks and benefits of a given behavior, animals must assess the magnitude of predation risks (see, e.g., Fraser and Huntingford 1986; Dill 1987; Brown 1988; Lima and Dill 1990). However, animals almost always have inadequate information to perceive actual risk. An individual that uses a perception of the probability of predation in its decision making may err by over- or underestimating the true probability of predation. Lima and Dill (1990) view predation risk as the result of a combination of several components, such as the probability of encountering a predator and the probabilities of being attacked, caught, and killed by it. Rather than focus on the assessment of each element that contributes to predation risk, we ask, What is the relationship between the magnitude of errors in the perception of predation hazard and fitness?

In this article, we use a dynamic optimization model to study how different errors in the perception of predation risk influence the fitness of a foraging organism. We assume that the use of rules of thumb for information acquisition is one of the processes that may generate incorrect perceptions. The model incorporates physiological constraints and is based on a trade-off between death from starvation and death from predation. We test the survival consequences of animals that make systematic errors in their perception of the true probability of predation yet behave as though they had perfect knowledge of predation risk.

A dynamic optimization model is most suitable for this type of problem because it enables the analysis of behavioral decisions responding to the internal state of the organism as well as to a perception of the external conditions (in our case, predation risk, which may vary over time). A dynamic model further enables the use of a stochastic approach that is required to reflect the probabilistic nature of the variables. We incorporate stochasticity in three ways: in the components of food reward, in the perceived predation risk, and in the real predation risk. Roitberg (1990) recently used a similar approach to study the costs of estimation errors in patch quality for ovipositing fruit flies.

TABLE 1

PARAMETERS AND INITIAL VALUES USED IN THE BASIC RUN OF THE MODEL

Symbol	Basic Run	Description
T	25	The final time (time horizon)
t	. . .	The current time unit, where $t < T$ and is measured discretely
α_i	1, 1	Energy expenditure in patch i, per unit time
λ_i	.15, .8	Probability of finding food in patch i, per unit time (in basic model)
$R\lambda_i$	. . .	Real probability of finding food in patch i, per unit time (in imperfect food knowledge model)
$E\lambda_i$	. . .	Probability of finding food in patch i, per unit time, as perceived by the forager (in imperfect food-knowledge model)
Y_i	1, 2	Amount of energy gain due to a foraging success in patch i
$R\beta_i$	.0001, .04	Real probability of getting killed by a predator in patch i, per unit time
$E\beta_i$	.0001, 0–.12	The probability of getting killed by a predator in patch i, per unit time, as perceived by the forager
$X(t)$	. . .	The state variable (energy reserves) at time t
x	. . .	Current value of the state variable $X(t)$
x_c	3	The critical value of $X_{(t)}$ below which the forager cannot survive
$i^*(x,t)$	. . .	The patch that maximizes expected future fitness for a forager with energy reserves x at time t based on its perceptions

NOTE.—Unless otherwise noted, these values were also used in the runs to produce the figures. Parameters with two numbers reflect the values in patch 1 and patch 2.

In the following sections, we list the assumptions and derive the model, discuss the results of a simple version of the model, and report on the results of relaxing some of the assumptions. Finally, we suggest experiments to test the use of rules of thumb in the perception of predation hazard.

THE MODEL

Our model is derived from a patch selection model described by Mangel and Clark (1988). The fundamental difference between our model and that of Mangel and Clark is that we force the animals to behave according to a perception of the probability of predation, rather than assume they have full information of this probability when making their decisions. We vary their perception around the true probability of predation. In this way, we can study the fitness consequences of incorrect perceptions of predation risk.

Derivation of the Model

Consider a forager facing a choice between two patches. Patch i can be characterized by the real probability of predation ($R\beta_i$), by the probability of finding food (λ_i), by the energetic value of the food (Y_i), and by the energy expenditure per unit time (α_i) for an animal staying in this patch. Table 1 summarizes the symbols used in the model and initial values of the parameters. In this model one patch is riskier, but it also has higher reward. Reward is a function of the probability of finding food and the value of the food. The state variable in this dynamic

model is energy reserves $X(t)$, and its dynamics are influenced by energy expenditure and by intake from food. The energy reserves of a forager change from x to x'_i when the forager spends one unit of time in patch i and finds food. Energy reserve x'_i is given by

$$x'_i = x - \alpha_i + Y_i. \tag{1}$$

Spending a unit time and not finding food leads to the following energy reserves:

$$x''_i = x - \alpha_i. \tag{2}$$

The calculated values of the energy reserves, x'_i and x''_i, are bounded between a maximum capacity and a lowest, critical level (x_c) that allows the animal to survive.

We assume the forager is in a nonreproductive period so that fitness can be identified with viability. We further assume that (1) food in the patches is not depleted, (2) there are no interactions between foraging individuals, and (3) there is no additional cost of moving to another patch. The relaxation of these assumptions can be easily added to such a model without major changes (Mangel and Clark 1988). We present other assumptions that we relaxed in later versions of the model after we derive the simple model.

Decisions about where to spend the next unit of time are made during each of the time units. Decisions continue until the time horizon $(t = T)$ is reached, which ends the foraging interval. For every patch, the forager weighs the consequences of three possible events (by their probability of occurrence): (1) the forager is killed by a predator (with a perceived probability $E\beta_i$), (2) the forager survives and finds food with probability λ_i, and (3) the forager survives and does not find food.

Let $F(x,t,T)$ be the forager's perceived maximum probability of survival, given its perception of predation risk, from time t to the time horizon T, given that its energy reserves at t are x. Based on the three possible events, we find

$$F_i(x,t,T) = (1 - E\beta_i) [\lambda_i F(x'_i, t + 1, T)$$
$$+ (1 - \lambda_i) F(x''_i, t+1, T)], \tag{3}$$

where x'_i and x''_i are given by equations (1) and (2).

The decisions of the forager in the model are based on the comparison of the fitness function in each of the two possible patches; the forager chooses the patch that will maximize its expected future fitness:

$$F(x,t,T) = \max_i F_i(x,t,T). \tag{4}$$

The perceived "optimal" decision is thus defined by $i^*(x,t)$: the patch that maximizes the expected future fitness for an animal at time t, with energy reserves x. Note that this is not really the optimal decision; rather, it is what the animal perceives as optimal.

The "optimal" decision for each given time unit and for each allowable level of energy reserves is made using backward induction (Houston et al. 1988; Mangel

and Clark 1988). At the time horizon ($t = T$), we define

$$F_i(x,T,T) = \begin{cases} 1 & \text{if } x > x_c \quad \text{(forager is alive)} \\ 0 & \text{if } x \leq x_c \quad \text{(forager died from starvation or predation)} . \end{cases} \quad (5)$$

When equations (3) and (4) are combined, the perceived expected future fitness for a forager at time $t = T - 1$ is thus given by

$$F(x,T - 1,T) = \max_i \{(1 - E\beta_i) [\lambda_i F(x_i',T,T)$$
$$+ (1 - \lambda_i) F(x_i'',T,T)]\} . \quad (6)$$

Since all the components on the right-hand side of the equation are known, we obtain the "optimal" patch, $i^*(x,T - 1)$, from equation (6). The model then moves backward one time unit at a time to obtain the "optimal" decision needed at each step to maximize the expected future fitness.

In this model the foraging interval is arbitrarily divided into 25 units of time. After computing and storing the decisions of the organism for the whole foraging interval, the model calculates the survival consequences of these decisions—the probability of survival for an animal choosing the "optimal" strategy $i^*(x,t)$. This probability is computed by

$$P_s(x,t,T) = (1 - R\beta_{i^*(x,t)}) [\lambda_{i^*(x,t)} P_s(x_{i^*(x,t)}',t + 1,T)$$
$$+ (1 - \lambda_{i^*(x,t)}) P_s(x_{i^*(x,t)}'', t + 1, T)] , \quad (7)$$

where $R\beta_{i^*(x,t)}$ is the real probability of predation to which the animals are exposed in patch $i^*(x,t)$. The range of values we used for $R\beta_i$ (0.005–0.05) includes values realistically encountered in nature (Prins and Iason 1989). Equation (7) was applied to all allowable levels of energy reserves using a backward iteration process. The survival at time T is known:

$$P_s(x,T,T) = \begin{cases} 1 & \text{if } x > x_c \quad \text{(forager is alive)} \\ 0 & \text{if } x \leq x_c \quad \text{(forager died from starvation or predation)} . \end{cases} \quad (8)$$

By iterating backward up to the first unit of time, we obtain the probability $P_s(x,1,T)$ that a forager with a given initial level of reserves survives to the end of the foraging interval.

Thus, the forager makes decisions that would be optimal given its perceptions of predation risk. However, in our model the decisions are based on erroneous perceptions. Note how this differs from other dynamic models. Other models often assume that the organism behaves optimally and that it knows the probabilities of events and the value of other parameters in the model (Houston et al. 1988; Mangel and Clark 1988; but see Roitberg 1990). The probability of predation ($E\beta_i$) that we used in the riskier patch during the process of decision making differed from the real value $R\beta_i$ in the survival iteration. This enabled us to test the consequences of perception errors on the survival of the animals.
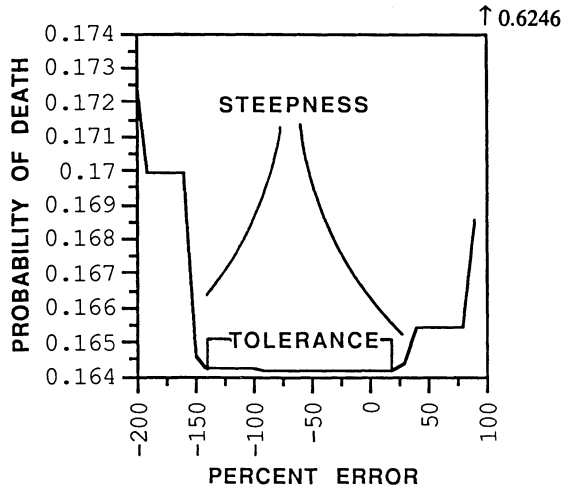
FIG 1.—Illustration of terms used in the text to describe figs. 2, 3, and 4. The figures plot the probability of death vs. the percent error in the perception of predation hazard. The tolerance refers to the generally flat range that forms the bottom of the curve. The steepness refers to the rate at which the probability of death increases with increased percent error and includes the remainder of the curve outside the range of tolerance. Figs. 1–4 do not include the points for 100% error because it was always very high and out of scale. Unless otherwise noted, the parameters in the plots are as in the basic run (see table 1). In this plot, $X(t = 0) = 10$.

Errors were defined as

$$\text{Error} = \frac{100 \, (R\beta_i - E\beta_i)}{R\beta_i}. \tag{9}$$

We considered 30 different values of errors, ranging from 100% (the most extreme error in this direction can be that the organism perceives no risk at all) to −200% (the organism perceives the predation risk twice as high as it really is). The negative errors could be much greater, but we chose to limit ourselves to −200% because, in most of the cases that we tested, the results beyond this value did not contribute new information.

In the basic model, we assumed that the forager is fully informed with respect to probabilities of finding food and that the errors occur only in the perception of predation hazard. This assumption is relaxed in later versions of the model (see Results from the Basic Model). Other assumptions that are relaxed later include a fixed value of predation risk during the entire foraging interval and an equal energy expenditure (α_i) in each patch.

Results from the Basic Model

We describe the results by plotting probability of death, $1 - P_s(x,1,T)$, versus the magnitude of errors in the perception of risk. When the forager makes no errors, mortality is minimized. However, there is a range of errors where an individual making errors has essentially the same probability of survival as one making no errors (fig. 1). This suggests that the opportunity for selection for
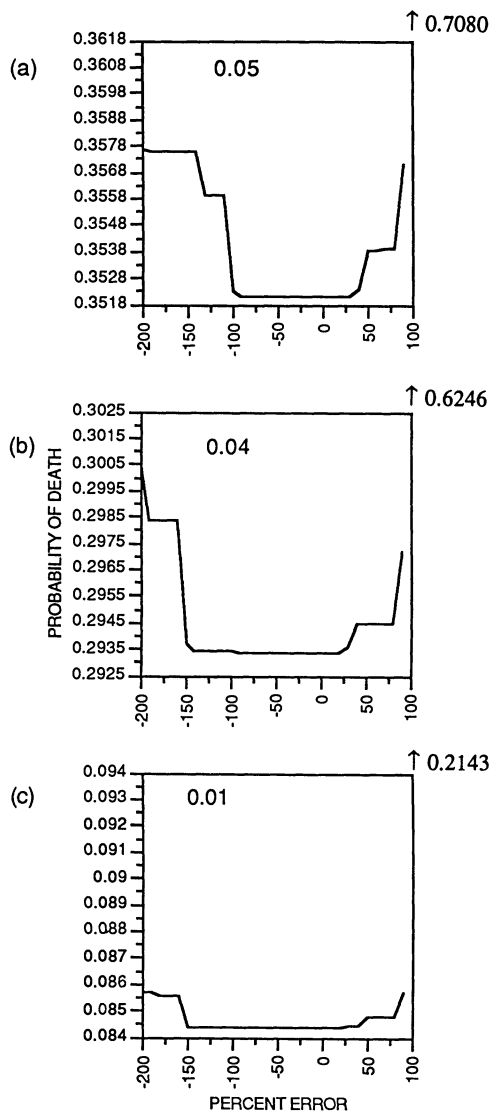
FIG. 2.—Probability of death vs. errors in the perception of predation risk. The true predation risk ($R\beta_i$) decreases from 0.05 to 0.01 in frames a–c. In these plots, $X(t = 0) = 13$.

accurate assessment or against inaccurate assessment will be weak, as long as errors fall within this range. Henceforth, we refer to this range as tolerance—a wide range of minimal selection implies a high tolerance for errors, whereas a narrow range implies little tolerance. This range is usually not symmetrical at approximately the zero error. The asymmetry may be toward overestimation (i.e., toward the negative errors; fig. 2a) or toward underestimation (positive errors; fig. 3). Later we analyze the factors that affect this shift. Note that the
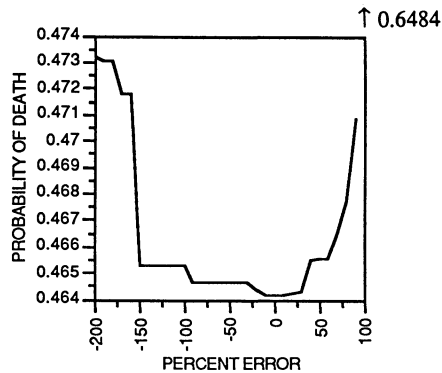
FIG. 3.—Probability of death vs. errors in the perception of predation risk. This illustrates the exceptional cases where there is a slight advantage to underestimating predation hazard. In this plot, $\alpha_1 = 3$ and $\alpha_2 = 3$, $Y_1 = 5$ and $Y_2 = 6$, and $X(t = 0) = 7$.

statistical meaning of estimation is not implied when we use the terms *over-* and *underestimate*.

There are two general properties of the mortality plots that are seen regardless of the direction in the shift of the range of tolerance: (1) The mortality at $+100\%$ error (the forager perceives no risk at all) is always much higher than at any other error. (2) The general shape of the plots is an asymmetrical parabola shifted toward the side that overestimates the real hazard. These properties are robust over wide ranges of parameters that we tested. In the following sections we discuss some of the effects of parameter values on the results.

Effect of predation level.—Three characteristics of the plots vary as predation level changes: tolerance, probability of death, and the steepness of the parabola (fig. 1).

As predation level increases, tolerance decreases (fig. 2). Thus, a higher predation level implies a stronger opportunity for selection for accurate assessments. Conversely, under low predation levels, an inaccurate rule would perform as well as a rule that acquired full information. Probability of death is correlated with predation level (fig. 2; note that the axis values of the probability of death change across figures). Animals thus may be even less likely to develop or to use accurate rules when predation risk is low.

A trade-off or phylogenetic constraint may force an animal to err in perceiving the true predation risk beyond the range of tolerance. Given a cost of accurate information (e.g., assessment takes more time), then the steepness of the curve beyond the range of tolerance is important. Steepness increases with predation risk (fig. 2). Thus, we predict strong selection under high predation for maintaining perception errors within the range of tolerance.

Effect of the state variable.—The state variable in our model is the energy reserves of the forager. We analyzed the model with foragers whose initial energy reserves ranged between 4 and 20 units of energy (where the cost of foraging, α_i, was one unit of energy). Figure 4 illustrates the relationship between initial energy reserves and the consequences of errors in the perception of risk. At low levels
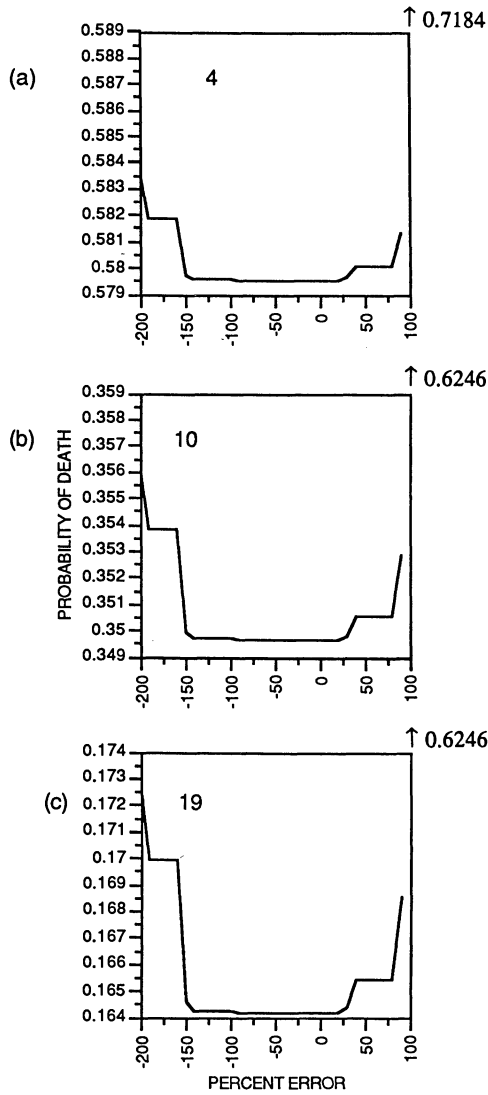
FIG. 4.—Probability of death vs. errors in the perception of predation risk. The starting value of the state variable (x) increases from 4 to 19 in frames a–c.

of energy reserves, mortality is much higher because of an increase in the probability of starvation. The steepness of the curves beyond the tolerance range increases with energy reserves. However, the level of energy reserves does not affect the range of tolerance. Tolerance remains constant at any given predation level for all values of the state variable.

Factors influencing the shape of the curve.—In general, our model suggests that overestimating predation hazard is better than underestimating hazard. There
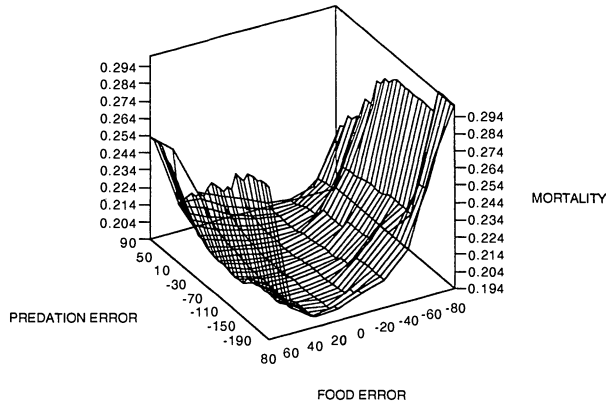
FIG. 5.—Changes in mortality as a function of errors in the perception of both predation risk, $R\beta_i$, and the probability of finding food, $R\lambda_i$. In this plot, $Y_1 = 1$ and $Y_2 = 3$, $R\lambda_i = 0.5$ and $E\lambda_i = 0.1 - 0.9$, and $X(t = 0) = 19$.

are, however, combinations of parameters that result in a more complex situation. In these cases, selection may favor animals taking risks when the magnitude of errors is small (i.e., the perceived risk is not far from the real predation risk). With larger errors, selection will favor animals overestimating hazard (fig. 3). However, even when these special cases occur, the advantage of underestimation is relatively weak. Mortality of overestimating animals is only slightly higher compared to that of underestimators when errors are small (compare mortalities when errors are -25% and $+25\%$ in fig. 3). At larger errors (e.g., when errors are -75% and $+75\%$), the general conclusion that overestimating predation risk is highly advantageous holds even in these special cases. Note, however, that these considerations are only relevant when there is a cost of reducing errors.

Relaxing the Assumptions

Perfect knowledge of food resources in patches.—Our simplifying assumption of perfect knowledge of food may be reasonable for specific cases (e.g., when food level is constant over several foraging intervals), but there are many cases where this assumption is not likely to be true. We thus introduced errors in the perception of the probability of finding food in the richer patch ($E\lambda_2$). The perceived probability of finding food ($E\lambda_2$) ranged between 0.9 and 0.1, while the real probability ($R\lambda_2$) was kept constant (0.5).

We studied the effect of varying both the errors in the perception of predation risk and the errors in the probability of finding food. For a range of values around the true probability of finding food, $R\lambda_2$, the results did not differ from the basic model: there is a tolerance for errors in the perception of predation risk. For the case illustrated in figure 5, the tolerance is between -20% and $+20\%$ in food errors and between -75% and $+75\%$ in predation errors. A less intuitive finding is that animals that underestimate food abundance would do better if they overestimate predation risk (fig. 5).

Random predation risk.—We randomized probability of predation because pre-

dation risk in nature is probably not always constant during the whole foraging period, as assumed in the basic model. We randomly assigned a level of risk at every unit of time. This may correspond to a case where predation hazard is proportional to a varying number of predators or to a case where the risk is correlated with environmental conditions that vary randomly (e.g., wind gusts; Jackson 1974). In order to obtain a random value for the predation risk, we used an algorithm similar to that which Press et al. (1986, p. 195) suggested as an improvement to system-supplied routines. The uniform deviates returned by the algorithm were bound by a specific range for each run. The lower limit of this range was set to the risk in the safer patch (always equal to 0.001 in these runs); the higher limit (and consequently the mean) varied between runs. In each time unit, the foragers were consistent in the rule they used, and they perceived the risk with the same percentage of error.

The results of this analysis generally agree with most of our conclusions from the basic model. There were two differences from the fixed predation risk model. First, the mortality calculated when predation is randomized is a bit lower than when predation is fixed on the mean predation level. This is because the effect of predation risk on mortality in the model turns out to be nonlinear, and the random values that are above the mean contribute less than those under it. Second, tolerance is always smaller when the risk is randomized than when it is fixed. These differences do not affect the main conclusions of the basic model.

An alternative to the rule of constant error in the perception of the probability of predation can be a simple rule that assumes a fixed probability at the mean of the predation risk ($R\beta_2$), regardless of its fluctuations. The mortality associated with such an assessment rule was higher than is any other rule from the previous model. Only the animals that assumed no risk at all (error of $+100\%$) survived less than the animals with the averaging rule.

Unequal energy expenditure in patches.—The basic model assumes equal energy expenditure in both patches. This assumption may be valid for sit-and-wait predators, which do not expend additional energy searching for food beyond their expenditure in other activities (Schoener 1971). However, active foragers, especially when foraging in structurally different patches, may incur different energy expenditures in different patches. When we relax the assumption of equal energy costs, we still get the asymmetrical parabola; in general, overestimating hazard is still better than underestimating hazard. However, when energy expenditure is much higher in the patch with the greater resource, a finer examination of the data reveals another asymmetry. For a small range of errors around zero error, underestimators suffer a lower probability of predation than animals who overestimate risk. Outside this limited range of values, it is better to overestimate risk. The plot of error versus predation risk that we get has the same features as figure 3.

DISCUSSION

The consistent appearance of a zone of tolerance suggests that animals can acquire imperfect information about predation risk without any effect on fitness.

We assume rules of thumb are a source of perceptual errors. In the discussion, we discuss how the use of rules may produce errors in perception and consider predictions on the use of rules that follow the results of the model, then we suggest future empirical work as well as extensions from the foraging model that may shed light on the use of rules of thumb for information acquisition.

Possible Causes of Imperfect Information about Predation Risk

Rules of thumb for information acquisition are used by animals to evaluate cues (such as predator's body size) and to generate a perception of predation risk. Cues must have at least two different levels (e.g., large/small, fast/slow) and may be measured on a continuous or discrete scale. Thus, a potential rule might be stated: A large approaching object implies high risk. Under the same levels and a given rule, the perceived risk will always be the same. However, the true probabilities of predation that generate these perceptions may vary (e.g., the approaching predator may be satiated). This is one of the sources of perceptual errors.

Ethologists have long been interested in proximal cues used to elicit behavior (Stamps 1991). Thus, the literature contains many potential examples of cues used for predation hazard assessment. Because cues vary in the accuracy of the information they provide, they lead to different perceptual errors. For example, an auditory cue may be brief and contemporary with the presence of risk, whereas an olfactory cue may be present for a long period after the predator has left. The latter may provide an erroneous perception of predation risk because the actual time when the predator was present may be difficult to determine (see, e.g., Coss and Owings 1985; Petranka et al. 1987; Jedrzejewski and Jedrzejewska 1990). The most informative cue might be observing a conspecific interact with a predator. Examples of this are Levick's (1914) interpretation of penguins pushing a conspecific off an ice sheet to probe for leopard seals (*Hydurga leptonyx*) or Lima and Dill's (1990) suggestion that dominant tits (*Parus* spp.) may use subordinates as indicators of the presence and intentions of predators. Among less informative cues, accuracy might vary greatly. A cue that involves focusing on the behavior of the predator to assess the probability of attack (see, e.g., Helfman 1989) may be more relevant to the specific situation than a cue that focuses on a particular part of the predator's anatomy (Coss 1978; Karplus et al. 1982; Inglis et al. 1983). Some animals respond to conspecific alarm calls (Leger and Owings 1978; Seyfarth et al. 1980; Møller 1988). Such a cue may be misleading. Great tits (*Parus major*) may emit false alarm calls to increase their chances of acquiring food (Møller 1988). Finally, animals perceiving high risk in the presence of a factor that correlates with predation success (e.g., light intensity) may overestimate risk when the predator is not present (Kotler 1984; Endler 1987). The errors associated with each cue can be characterized by the accuracy of the cue as a measure of the probability of predation (i.e., by the distribution of the perceived risks around perfect knowledge). This distribution may be symmetrical or asymmetrical around perfect knowledge. Our model tests the fitness consequences of such errors.

Results and Predictions Based on the Analysis

An important observation that emerged from our analysis is that the behavior of animals using erroneous perceptions of predation risk may still result in nearly maximal fitness: animals making errors may experience identical or similar probabilities of death as animals that make no errors. The existence of a tolerance region parallels Roitberg's (1990) conclusions about the costs of errors and is consistent with other investigations into the cost of simple rules (see, e.g., Janetos and Cole 1981; McFarland and Houston 1981; McNamara and Houston 1985, 1987; Mangel and Clark 1988; Mangel 1990). However, animals assessing predation risk may incur extremely high costs (e.g., mortality) when acquiring information. Our model provides theoretical justification that constraints on optimal information acquisition (Roitberg 1985) may not necessarily prevent optimal performance.

Additionally, when predation risk varies, it is better to assess with error than not to attempt to track changes in predation risk. In our model, animals that used an averaging rule performed very poorly.

The asymmetrical mortality in our model should lead to selection for biased perceptions (Kendall and Stuart 1979), if we assume the cost of rules is proportional to their accuracy. Roitberg (1990) used a dynamic model to study oviposition site selection in fruit flies. He, too, found an asymmetrical opportunity for selection as well as benefits for overestimation (in this case of site quality). Bayesian models that focus on information acquisition and updating provide an example of a mechanism that may lead to biased perceptions for the value of a parameter.

We suggest that, within a certain range of values in the model, it is better to have biased rules that lead to overestimating predation hazard than those that lead to underestimating predation hazard. Bank voles (*Clethrionomis glareolus*) may use a biased rule that overestimates hazard. Jedrzejewski and Jedrzejewska (1990) exposed bank voles to pens with a weasel (*Mustela nivalis*) or with only weasel scent. The voles avoided the pens equally. This suggests that a rule that overestimates risk, such as equating odor with high predation risk, may have been used by the voles.

The magnitude of selection against assessment errors seems weakly influenced by the initial level of reserves. Animals that started with low reserves had moderate slopes beyond the tolerance range; thus, we expect little selection for the use of accurate rules that fall in that range. Alternatively, animals that began with high levels of reserves suffered a higher proportion of death due to predation. Thus, there was a greater opportunity for selection for precise rules in those individuals. This is reflected by the steepness seen in figure 2.

The main conclusions from our model were robust with respect to a wide range of parameters and to several relaxed assumptions. Based on the results of our model, we make three predictions about the present form of rules of thumb used for predation hazard assessment and the evolution of such rules. (1) We predict that animals will attempt to track fluctuations in predation risk despite inaccuracies in assessment. (2) We predict that rules that overestimate predation risk will

be more common than rules that underestimate risk. The results of the model show that overestimation should lead to low mortality even when these rules provide inaccurate information. The selection against underestimation implies that, if an animal minimizes the cost associated with accurate assessment, it must do so by overestimating. (3) Based on our model, we predict that animals that evolved in an environment with high predation risk will have rules that provide quantitatively better perceptions of predation risk than animals that evolved in environments with less predation risk. The fitness function gets steeper and the tolerance narrower as predation risk increases. Thus, animals with inaccurate rules should be eliminated as predation risk increases.

Future Empirical Work

In order to study biases in rules of thumb empirically for predation hazard assessment, one must compare the animal's perception of predation risk with the true probability of predation for several different true predation risks. To evaluate perception errors, one must (1) have the ability to calculate the true probability of predation in the experimental setting, (2) manipulate the true probability of predation (e.g., by adding predators, by changing the motivation or ability of the predators, by using more vulnerable prey), (3) quantify the prey animal's perception of risk (three methods have been used to study this indirectly: giving-up densities [Brown 1988], energetic equivalence [Abrahams and Dill 1989; Nonacs and Dill 1990], and Todd and Cowie's [1990] operant technique), and (4) compare the animal's perception of risk with the true probability of predation for each manipulated predation risk.

Extensions from Foraging Models

Our results suggest that animals need not have perfect, only sufficient, information in order to behave optimally. A common criticism of optimality models is that many assume perfect knowledge of a parameter (Stephens and Krebs 1986). Several ways have been proposed whereby animals may perfect perceptions about important parameters (e.g., Mangel [1990] discussed a Bayesian approach, whereas McNamara and Houston [1985] proposed learning rules). In certain circumstances, sampling may be difficult or hazardous: animals may not be able to learn from their mistakes. We suggest that perfecting knowledge about predation risk may not be required as long as an animal's perception of risk is within the zone of tolerance.

The foraging model we developed is a way to visualize the trade-off of predation perception errors and other potential benefits. It is likely that animals may trade off predation hazard with a plethora of behaviors other than foraging, including reproductive behaviors, territorial behaviors, movement, play, grooming, allogrooming, mobbing, parental or alloparental care, and so on. To model any trade-off dynamically, one must first identify a common currency-state variable. This permits the visualization of both costs and benefits and directly relates them to fitness. Foraging behavior is initially appealing, for one can experimentally measure the energetic costs of predation risk (see, e.g., Abrahams and Dill 1989). The conclusions from a simple model, such as one involving the trade-off between

predation and foraging behavior, may shed some light on the effect of perception errors with more complicated trade-offs.

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