Exponential Versus Hyperbolic Discounting of Delayed Outcomes: Risk and Waiting Time¹

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SYNOPSIS. Frequently, animals must choose between more immediate, smaller rewards and more delayed, but larger rewards. For example, they often must decide between accepting a smaller prey item versus continuing to search for a larger one, or between entering a leaner patch versus travelling to a richer patch that is further away. In both situations, choice of the more immediate, but smaller reward may be interpreted as implying that the value of the later reward is discounted; that is, the value of the later reward decreases as the delay to its receipt increases. This decrease in value may occur because of the increased risk involved in waiting for rewards, or because of the decreased rate of reward associated with increased waiting time. The present research attempts to determine the form of the relation between value and delay, and examines implications of this relation for mechanisms underlying risk-sensitive foraging.

Two accounts of the relation between value and delay have been proposed to describe the decrease in value resulting from increases in delay: an exponential model and a hyperbolic model. Our research demonstrates that, of the two, a hyperbola-like discounting model consistently explains more of the variance in temporal discounting data at the group level and, importantly, at the individual level as well. We show mathematically that the hyperbolic model shares fundamental features with models of prey and patch choice. In addition, the present review highlights the implications of a psychological perspective for the behavioral biology of risk-sensitive foraging, as well as the implications of an ecological perspective for the behavioral psychology of risk-sensitive choice and decision-making.

INTRODUCTION

Many aspects of behavior by both human and nonhuman animals suggest that the value of future rewards is discounted with time to their receipt. When an animal can engage in two different behaviors, either of which would produce a similar positive outcome except that one outcome would occur sooner than the other, the animal is likely to opt for the more immediate outcome. In fact, animals will often choose a smaller reward if it is available sooner over a larger reward that is not available until later, in spite of the fact that waiting for the larger reward

would maximize their rate of energy intake during experimental sessions (e.g., Rachlin and Green, 1972).

Consider two common situations, one in which an animal must decide whether to accept a smaller prey item or continue to search for a larger one, and another in which it must decide whether to travel to a richer patch that is further away or to a closer, but leaner patch. In both these situations, if choice of the smaller reward produces a lower overall reward rate, then preference for more immediate, but smaller rewards implies that the subjective value of a later reward is discounted; that is, the subjective value of the later reward decreases as the delay to its receipt increases. Discounting the value of future rewards may well be an adaptive response to the risks

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associated with waiting for delayed rewards (Kagel et al., 1986). After all, as delay to an outcome increases, the probability of receiving that outcome usually decreases. Thus, there is an implicit risk involved with delayed outcomes. With food, for example, there is an increasing likelihood of its spoiling; there also is an increasing likelihood that competitors might consume the food first, or that a predator might drive a foraging animal away from the food source.

The mathematical relation between subjective value and delay is termed a temporal discounting function. It may be important to determine the form of this discounting function for two reasons. First, different mathematical functions may lead to quantitatively (and even qualitatively) different predictions regarding behavior. Second, the form of the mathematical function may provide clues as to the mechanism underlying risk-sensitive behavior and the temporal discounting of future outcomes. For example, temporal discounting may reflect increases in the risk that a future reward will not be received as waiting time increases. As we will show, different mathematical functions assume different ways in which this risk changes with waiting time.

MATHEMATICAL MODELS OF DISCOUNTING

Two major models have been proposed to describe the temporal discounting of future outcomes. Economists studying human choice behavior have favored an exponential discounting model of the form

$$V = Ae^{-kD} \tag{1}$$

where V is the present, discounted value of a reward of amount A available after a delay of D units of time. The parameter k determines the rate at which value decreases with delay: a larger k is associated with steeper discounting, and a smaller k is associated with shallower discounting of the value of a future reward. The exponential decay function may be derived from the assumption that, with each additional unit of time that an animal must wait, there is a constant probability that something will occur to prevent the receipt of a reward. Under this assumption, a larger k implies either greater risk (i.e., a greater probability that

receipt will be prevented) or greater sensitivity (i.e., aversion) to risk, or both.

Psychologists studying both human and nonhuman animals have proposed a hyperbolic discounting function of the form

$$V = A/(1 + kD) \tag{2}$$

where *V*, *A*, and *D* have the same meaning as in Equation 1. As with the exponential decay function (Eq. 1), the larger the *k* parameter, the steeper the discounting of future rewards. Many psychologists favor the hyperbolic function because it is derived from the assumption that subjective value depends on the ratio of amount to time, consistent with the view that rates of reinforcement (and other biologically significant events) are fundamental determinants of behavior (*e.g.*, Rachlin, 1989).

This view is similar to that which underlies models of prey and patch choice. For behavioral psychologists, rate of reward is the currency for subjective value; for behavioral biologists, rate of energy intake is the currency for fitness. In both cases, it is rate (of reward in one case and energy intake in the other) that determines behavior. Whereas the hyperbolic discounting model predicts the point at which subjects will judge alternatives to be of equal subjective value, prey and patch choice models predict which alternative will lead to greater fitness. Nonetheless, despite the differences in their applications and the form in which they express their predictions (i.e., equations versus inequalities), we show in the Appendix that both models start from similar assumptions and lead to similar conclu-

Although part of the appeal of the hyperbolic model has been that it may be interpreted in terms of reward rate, the hyperbolic, like the exponential model, also may be conceptualized in terms of the risks associated with waiting for future rewards. The expected value (or utility) of a reward is equal to its amount multiplied by the probability (P) of its receipt, that is, $V = A \cdot P$. If P = 1/(1 + kD), then the expected value of a delayed reward is given by Equation 2. Similarly, Equation 1 can be conceptualized in terms of expected value with $P = e^{-kD}$.

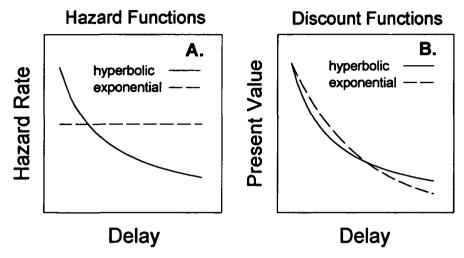


Fig. 1. Hazard and discount functions for the hyperbolic and exponential models.

Thus, the exponential and hyperbolic functions are similar in that both may be interpreted in terms of risk. However, they differ in their assumptions regarding the nature of the relation between risk and waiting time. As noted previously, the exponential function assumes that as an animal waits for a reward, the risk that something will occur at any given moment so as to prevent the reward's consumption remains constant. In contrast, the hyperbolic function implies that the risk that something will occur so as to prevent a delayed reward's consumption is initially greater, but that each unit of time added to the delay adds progressively less risk. The different assumptions regarding risk underlying the exponential and hyperbolic discounting functions may be visualized by reference to their hazard functions.

A hazard function describes mathematically the effect that increases in waiting time have on the risk that something will happen to prevent an event from occurring (Gross and Clark, 1975). In the context of temporal discounting, the hazard represents the probability that an event will occur at time t (or within some interval beginning at time t) to prevent receipt of a reward divided by the probability that no such event has yet occurred by time t. Hazard functions associated with the exponential and hyperbolic discounting functions are shown in Figure 1A. As may be seen, the hazard rate for the exponential discounting model is

constant: Each additional unit of waiting time adds a constant amount of additional risk. In contrast, the hazard rate for the hyperbolic discounting model decreases with time. In fact, this hazard rate decreases hyperbolically, with each additional unit of waiting time adding successively smaller amounts of risk. These differences in hazard rates are reflected in the fact that, as may be seen in Figure 1B, the hyperbolic discounting function predicts that value initially decreases at a faster rate but then decreases at a slower rate than would be predicted by an exponential function fit to the same data.

EVALUATION OF DISCOUNTING MODELS

One aspect of our research has involved evaluating the hyperbolic and exponential models of discounting. Before presenting some recent data that bear on the empirical status of the two models, we first will consider an argument that had been presumed to definitively settle the question as to which model was correct. Both human and nonhuman animals exhibit preference reversals (e.g., Green et al., 1981; Green et al., 1994a; Kirby and Hermstein, 1995). That is, when an animal can engage in either of two different behaviors, one of which would lead to a smaller reward available sooner, the choice depends on the waiting time until the smaller, sooner reward. With a particular set of amounts and delays,

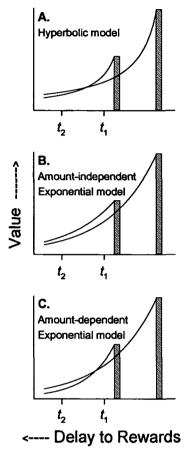


Fig. 2. Subjective value as a function of delay. Panels A and B depict the standard (i.e., amount-independent) hyperbolic and exponential models; Panel C depicts an amount-dependent exponential model. Cross-overs indicate points of preference reversal.

an animal may engage in the behavior leading to the smaller, sooner reward. However, if a sufficiently large amount of time is added to the delays to both rewards, then preference will reverse. That is, the animal will engage in the behavior leading to the larger, later reward.

The hyperbolic discounting model's account of the phenomenon of preference reversal is diagrammed in Figure 2A. The heights of the two solid bars represent the amounts of the two rewards, and the curved lines show how the subjective value of each of these rewards changes hyperbolically as a function of the delay until its receipt. As may be seen, when the delays are both relatively brief (e.g., when the choice is made

at time t₁), the value of the smaller reward is greater than that of the larger reward. However, when the delays are both relatively long (e.g., when the choice is made at time t2), the larger reward is the one of greater value. In contrast, the exponential discounting model predicts that preference will not reverse. This may be seen in Figure 2B where, when subjective value decreases exponentially, the smaller reward has the greater value regardless of when the choice is made (e.g., at both t_1 and t_2). (It should be noted that, according to the exponential model, if the amount of the larger reward were increased so that it had the greater value at t2, then it would also have greater value than the smaller reward at t₁.)

In modeling choice and decision-making by both human and nonhuman animals, researchers typically have assumed, explicitly or implicitly, that the rate of temporal discounting is independent of amount; that is, larger and smaller rewards are discounted at the same rate. The theoretical functions represented in Figures 2A and 2B are derived from this assumption of amount-independent discounting. The fact that with this assumption the hyperbolic model, but not the exponential model, correctly predicts preference reversals has been cited as a compelling reason for rejecting the exponential model.

Consider, however, what happens if the rate of temporal discounting is amount dependent, such that larger rewards are discounted less steeply than smaller rewards (i.e., k is inversely related to amount). A hyperbolic model incorporating amount-dependent discounting continues to predict preference reversals, although the point at which preference reverses is shifted. Importantly, if the assumption of amount-dependent discounting is incorporated in the exponential model, then this model also predicts preference reversals, as may be seen in Figure 2C.

Recent data demonstrate that the rate of temporal discounting is, in fact, amount dependent. More specifically, it has been shown in a number of studies that larger amounts are discounted less steeply than smaller amounts (e.g., Thaler, 1981; Raineri and Rachlin, 1993; Green et al. 1994b; Kir-

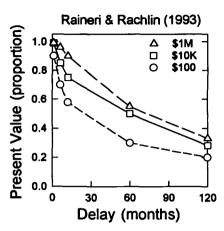


Fig. 3. Present, subjective value (expressed as a proportion of nominal value) as a function of delay, Data are taken from Raineri and Rachlin (1993), Experiment 1. Note the steeper discounting of smaller amounts.

by and Marakovic, 1996). For example, Raineri and Rachlin (1993) and Green et al., (1994b) had human subjects make choices between delayed and immediate rewards, and the amount of an immediate reward equivalent in subjective value to a delayed reward was determined. Raineri and Rachlin studied the effect of delay on the present value of three amounts of delayed reward, and Green et al. studied three different age groups using two amounts. Figure 3 depicts data from the Raineri and Rachlin study. Data from young adults in the Green et al. study are shown Figure 4. In order to compare the results for different delayed amounts more easily, the amount of an immediate reward judged equivalent in value to a delayed reward (i.e., its present, subjective value) is expressed as a proportion of the amount of the delayed reward. As may be seen, the smaller the amount of the delayed reward, the more steeply it was discounted.

The evidence for amount-dependent discounting rates reopens the question of the form of the temporal discounting function, a question that many researchers thought had been answered by the fact that preferences reverse. Because an amount-dependent exponential model (Fig. 2C) does predict preference reversals, a different kind of approach to the question is needed. One approach is to compare how accurately the ex-

ponential and hyperbolic models describe the observed relation between present value and the waiting time to a delayed reward. Rachlin *et al.* (1991) showed that the hyperbolic model (Eq. 2) fit the group average data better than the exponential model (Eq. 1). However, the form of the function describing group data is not necessarily the same as the form of the function describing individual data (Sidman, 1952; Estes, 1956), and it is the form of the function that suggests the nature of the mechanism underlying the observed relation.

Therefore, we compared the fits of the exponential and hyperbolic models to data from individual subjects (Myerson and Green, 1995). The percentage of the variance in individual data explained by the hyperbolic model was typically more than 10% higher than that explained by the exponential model, and the difference between the R^2 s for fits of the two models to individual data was statistically significant.

The fits of the hyperbolic model to both individual and group data were significantly improved when the denominator of Equation 2 was raised to a power.

$$V = A/(1 + kD)^s \tag{3}$$

In terms of the expected value interpretation of the hyperbolic model, the parameter s represents nonlinear scaling of probability, or amount, or both. (Strictly speaking, Eq. 3 is not a hyperbola, but we shall continue to refer to it as a form of hyperbolic discounting model.) It should be noted that, as outlined in Myerson and Green (1995), the hyperbolic model is open to an alternative interpretation based on the rate at which choice opportunities are encountered. According to this interpretation, the parameter s again represents a nonlinear scaling factor, although in this case it is time (rather than probability) and amount that may be nonlinearly scaled.

Estimates of the s parameter based on fits of Equation 3 to both individual and group data were typically less than 1.0. When s is less than 1.0, this results in a flattening of the discount function as delay gets large. In terms of the expected value interpretation, the flattening of the discount function implies that the additional risk (or hazard) in-

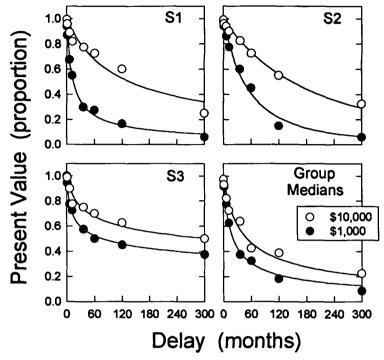


Fig. 4. Present, subjective value (expressed as a proportion of nominal value) as a function of delay. Data from three individuals (S1, S2, and S3) and the group median are taken from Myerson and Green (1995). The curves represent Equation 3 fit to the data for both amounts assuming a single exponent but amount-dependent discounting rates. Note that the smaller amount is discounted more than the larger amount.

curred with increases in delay is even less than that predicted by a simple hyperbola (Eq. 2), making the hyperbolic model represented by Equation 3 even less exponential-like.

Figure 4 shows data from three individual subjects as well as the group medians (Myerson and Green, 1995). The curves represent Equation 3 fit to the data using the same s parameter for both the larger and smaller rewards. Note that the smaller (\$1,000) reward was discounted more steeply than the larger (\$10,000) reward, and this was reflected in significantly larger estimates for the corresponding k parameters. The median R^2 for these fits of Equation 3 to the data from all 12 of the young adults who participated in the experiment was .978, and the R^2 for the fit to the group data was .984.

ECOLOGICAL AND PSYCHOLOGICAL PERSPECTIVES

The evidence that the subjective value of a future reward decreases with waiting time

is clear. Although the data presented in Figures 3 and 4 come from studies using human subjects and hypothetical rewards, other data suggest that the same principles may govern the behavior of nonhumans choosing between real rewards. For example, Mazur (1987) has shown that the hyperbolic model (Eq. 2) predicts the behavior of pigeons pecking keys to obtain larger or smaller rewards available after different delays. Rodriguez and Logue (1988) used the Mazur procedure in three experiments, one with pigeons and two with humans, and found that both species exhibited similar behavior. Although human decision making may, in some situations, involve processes unique to verbal organisms, the results to date show impressive correspondence in choice behavior across species as demonstrated by the ubiquity of hyperbolic discounting.

The discounting of delayed rewards is a robust behavioral phenomenon that may be viewed from both ecological and psychological perspectives. These perspectives are clearly not mutually exclusive; rather, they focus on or seek to explain different aspects of the phenomenon. Moreover, the ecological and psychological perspectives each provide important insights that may inform the other, thereby leading to a deeper understanding of temporal discounting and related aspects of animal choice behavior.

An ecological perspective would assume that the observed decrease in subjective value with increased delay reflects some contingency that exists in the environment. For example, an ecological perspective might assume that risk increases with waiting time, and would then focus on determining the source of that risk. As we have suggested, there are many possible sources of risk, including the risk that competitors will get to the food source first, the risk that food will have spoiled by the time it is obtained, or that prey will have vanished, as well as the risk that predators may interrupt foraging.

The goal of an ecological approach is to understand how the observed pattern of behavior contributes to fitness. In contrast, the goal of a psychological approach is to determine the proximate mechanisms that result in behavior. Thus, a psychological perspective might focus on the nature of the perceptual and decision-making processes involved in selecting between more immediate and more delayed rewards. For example, Equation 3 implies a nonlinear scaling of variables (i.e., time, probability or amount). Nonlinear scaling is a general perceptual phenomenon (Stevens, 1957) and, as such, suggests that at least some aspects of the temporal discounting process may have a correspondingly general explanation. one that goes beyond the specifics of choices between alternative rewards. Similarly, many foraging decisions involve memory of past experiences with different patches and types of prey, and there is always a risk of forgetting relevant information. Thus, a psychological perspective might focus on determining the variables influencing memory and the way that these variables affect decision making in foraging situations.

One of the exciting and valuable aspects

of this area of research is the potential interplay between these two perspectives. For example, an ecological perspective leads one to expect different rates of discounting in species adapted for different environments, and a psychological perspective suggests that differences in memory ability might be associated with differences in discounting rate. Together, the two perspectives raise the possibility that the memory ability and discounting behavior of species adapted for different environments may be related phenomena. Indeed, some memory limitations may actually be adaptations, in that there is a tradeoff between control of behavior by current conditions and the control exerted by previous experience. Rapidly fluctuating environments favor greater control by current input whereas more stable environments favor more control by long-term memory. Likewise, more rapidly changing environments may discourage waiting for delayed rewards whereas more stable environments may favor waiting if, by waiting, larger rewards can be obtained.

Indeed, memory and discounting may even be causally related. It is possible that if adaptation to a rapidly changing environment leads to steep discounting, then there is little advantage to having a good memory. Alternatively, it may be that the memory limitations associated with adaptation to a particular environment may themselves form a significant source of risk. That is, the waiting time represents a retention interval (to use a psychological term), and the longer the retention interval, the greater the likelihood of forgetting single events, causeeffect relations, and response sequences or skills (Spear and Riccio, 1994). For example, as retention intervals increase, animals are more likely to forget the location of a particular prey item or food cache (e.g., Hitchcock and Sherry, 1990). The possibility of such forgetting may contribute to discounting the value of delayed rewards.

A number of variables have been shown to influence the rate of temporal discounting. First, as already discussed, there is the fact that the rate at which a reward is discounted depends on its size. Second, although we have presented only the results for the young adults who participated in the

Green et al. (1994b) study, orderly discounting functions were observed in data from children and older adults as well. Importantly, the rate at which rewards were discounted decreased with the age of the participants. Third, we have recently reported that discounting rate is also sensitive to income level, as exemplified by our finding that upper-income subjects discounted future rewards at a much lower rate than lower-income subjects (Green et al., 1996).

Consideration of these variables points up the interrelation between ecological and psychological studies and may suggest useful hypotheses regarding ultimate and proximate determinants of risk-sensitive animal behavior. With respect to the effect of reward amount, for example, two possibilities may be considered. First, from an ecological perspective, is there some way in which there is less risk associated with waiting for a large reward than for a small reward? Second, from a psychological perspective, are larger rewards more salient so that information regarding them is less susceptible to memory loss?

With respect to the effect of income, does the steeper discounting of delayed rewards by low income humans reflect a greater risk of shortfall in such necessities as food, heat, or medicine? Are the greater risks associated with low income analogous to the greater risk of energy shortfall for animals foraging in winter? With respect to the greater discounting rate observed in children, do the young of other species also show steeper discounting than adults, and does this reflect extra risks associated with inexperience? Interestingly, although older animals would be expected to be at greater predation risk during foraging, leading to the expectation that they would show higher rates of discounting than younger adults of the same species, elderly humans do not discount delayed rewards more steeply than younger adults (Green et al., 1994b; Green et al., 1996).

The risks involved in foraging undoubtedly change across the life span, and there may be concurrent changes in the rate at which animals discount delayed rewards. Knowing whether the change in discounting rate across the life span in nonhuman

animals follows a similar trajectory to that observed in humans would help focus the search for causes of age-related changes. If the trajectories in different species are similar, the search might focus on aspects of organisms' interaction with their environment that are common to many species; if the trajectories are dissimilar, the search might be better focused on aspects of interactions with the environment that differ across species.

CONCLUSION

The research in our laboratory reviewed here has been largely concerned with how delayed outcomes influence behavior. A key to understanding this influence may be found in the form of the relation between the value of a reward and the delay to its receipt. Of the two major forms of discounting function that have been proposed, an exponential model and a hyperbolic model, our research demonstrates that a hyperbola-like discounting function provides a better account. Hyperbolas and hyperbola-like functions (Eqs. 2 and 3) predict the preference reversals that are a key characteristic of choice between delayed rewards. Although preference reversals do not clearly discriminate between exponential and hyperbolic models, we have shown that the hyperbolic model consistently explains more of the variance in temporal discounting data at the group level and, more importantly, at the level of individual performances as well.

An important focus of future research should be discriminating between rate and risk interpretations of the hyperbolic model. Although historically the risk interpretation of temporal discounting has been associated with an exponential model (i.e., with a constant hazard rate), we have argued that a hyperbolic model can also be interpreted in terms of risk. From an ecological perspective, such an interpretation predicts that the foraging environment is one in which the hazard rate decreases with increases in waiting time. The risk interpretation further predicts that the rate of temporal discounting will vary depending on the characteristics of a species' environment as well as how that environment impacts individuals at different stages in their life history. Whether one adopts a risk or a rate interpretation, an adequate explanation of why the discounting function is hyperbolic in form must take into account the fact that discounting rate varies inversely with amount. Regardless of the interpretation and the explanation, research on temporal discounting highlights the rich interplay possible between psychological and ecological approaches to choice behavior.

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APPENDIX

We show here that an interpretation of the hyperbolic model based on choice between rates of reward is fundamentally similar to models of foraging based on Holling's (1959) disc equation (a fuller discussion of such foraging models is presented in Stephens and Krebs, 1986). In the hyperbolic discounting model, choice is determined by overall rates of reward whereas in foraging models, choice is determined by net rates of energy intake. Where energy content is proportional to reward magnitude, energy intake and reward rates covary directly; accordingly, we shall use *R* to represent both.

If D represents the delay from the point at which the choice is made until the reward is received, and m represents the time interval between receipt of the reward and the next choice opportunity, then the total inter-reward interval equals (m + D). Similarly, D may represent search time, and m may represent handling time; then the total foraging time per item equals (m + D). In both cases, the net rate (of reward or energy intake) is given by amount divided by total time per reward item.

$$R = A/(m+D), (A1)$$

where A represents the amount of energy or magnitude of a reward.

When the energy costs of searching are negligible, A1 is analogous to Holling's (1959) disc equation for the net rate of energy intake. The disc equation provides the basis for a number of prey and patch choice models (for a brief tutorial, see Stephens and Krebs, 1986). Noting that encounter rate (λ) in the disc equation is the reciprocal of D (i.e., the reciprocal of the average search time), the equivalence of A1 and the disc equation becomes apparent if one substitutes $1/\lambda$

for D, and then multiplies both the numerator and the denominator of the right side of A1 by λ .

If a reward is available immediately (i.e., a prey item has just been encountered), and thus D=0, then R is simply equal to A/m. When the overall rate for a reward available immediately equals the overall rate for a delayed reward (i.e., a prey item requiring further search).

$$A_i/m_i = A_d/(m_d + D), \tag{A2}$$

where the subscripts i and d denote the immediate and delayed rewards. Multiplying both sides by m_i and then dividing both the numerator and denominator of the right-hand side by m_i , yields

$$A_i = A_d/[(m_d/m_i) + (D/m_i)].$$
 (A3)

A3 describes a hyperbolic relation between the amount of an immediate reward and the time until receipt of a delayed reward when the overall rates of both rewards are equal.

The relationship of A3 to the hyperbolic model (Eq. 2) is apparent if one considers the special case where m is the same for both immediate and delayed rewards. This would be true, for example, if two rewards require equal handling times because they differ in caloric content but not in size, or if the interval between receipt of a reward and the next choice opportunity was independent of amount. If $m = m_i = m_d$, then A3 simplifies to

$$A_i = A_d/(1 + D/m).$$
 (A4)

Substituting k for 1/m results in Eq. 2, the hyperbolic

discounting function. (When m_i does not equal m_d , as in A3, the shape of the discounting function is the same as in A4, but the function is displaced along the X-axis.)

Equations 2 and A4 specify the point at which subjects will judge the immediate and delayed reward, or the prev item that has just been encountered and the item requiring additional search, to be of equal value. Behavioral psychologists have developed models (such as the hyperbolic discounting model) that predict such equivalence points. In contrast, behavioral biologists have developed models (such as the prey choice model) to predict nonequivalence, for example, whether to accept a prey item or continue searching. To see the relation between the preceding derivation of the hyperbolic discounting model and a prey choice model such as that described in Stephens and Krebs (1986), note that Equation A3 implies that the value of the immediate and delayed rewards would be unequal if the amount of either reward or the waiting time to the delayed reward were changed. Under these circumstances, subjects would choose the reward of higher value, that is, they would follow the decision rule: if

$$A/m > A/(m + D), \tag{A5a}$$

choose the immediate reward; if

$$A/m < A_d/(m+D), \tag{A5b}$$

choose the delayed reward. This is equivalent to a prey choice model in which animals choose the alternative that maximizes their net rate of energy intake.