



Food hoarding: future value in optimal foraging decisions

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Abstract

Traditionally, optimal foraging theory has been applied to situations in which a forager makes decisions about current resource consumption based on tradeoffs in resource attributes (e.g. caloric intake versus handling time). Food storage, which permits animals to manage the availability of food in space and time, adds a complex dimension to foraging decisions, and may influence the predictions of traditional foraging theory. One key question about the role of caching behavior in optimal foraging theory is the degree to which information about future value might influence foraging decisions. To investigate this question, we use a simple prey selection model that minimizes the time spent foraging and is modified to include food storage and changes in nutritional value through time. We used simulations to evaluate time spent in foraging activities per prey item and optimal foraging strategies (e.g. cache versus consume immediately) for 3125 parameter combinations, representing different abundance levels, handling times, and nutritional values. Using discriminant function analysis it was possible to distinguish situations where “caching” versus “immediate consumption” were optimal strategies with abundance as the single predictive variable. The circumstances where caching was optimal were characterized by a decline in prey abundance and an increase in nutritional value through time. These results provide a framework for identifying subtle differences in foraging behavior when future value is accounted for thereby improving our predictive understanding of how caching animals forage.

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1. Introduction

Optimal foraging theory has been applied to questions concerning (1) the choice by an animal of which food types to eat, (2) the choice of which patch type

to feed in, (3) the optimal time allocation for different patches, and (4) the optimal patterns and speed of movements of foragers (Pyke et al., 1977; Stephens and Krebs, 1986). Many theoretical and empirical studies have been devoted to the problem of prey choice (MacArthur and Pianka, 1966; Schoener, 1971; Pulliam, 1974; Pearson, 1974; Stephens and Krebs, 1986), but most of this work applies to foragers that consume food immediately or soon after returning to a central location. One general prediction of optimal foraging models is that a predator should continue to add increasingly less profitable items

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to its diet as long as this increases its overall rate of energy intake, but should ignore insufficiently profitable food types irrespective of their abundance (Werner and Hall, 1974; Krebs, 1978; Krebs and Davies, 1984). A second theoretical prediction is that consumers with handling times that are long relative to their search times should be specialists, and consumers with handling times that are typically short compared to search time should be generalists. We are interested in the extent to which caching behavior (i.e. food storage) might alter these theoretical predictions of traditional optimal foraging theory.

Dens, territories and food can be considered as commodities from an economic standpoint, whose future value could influence current decisions. In this context, future value refers to the value of a food item at the time of consumption (Gendron and Reichman, 1995). Foraging behavior often involves easily quantified values, where the future value of a food item might depend on the predictability and abundance of available food resources (Baum and Grant, 2001). A risk-sensitive forager might account for trade-offs between an uncertain future and current net value (DuBoway, 1997). Green et al. (1981) suggested that foragers prefer smaller, more immediate rewards when pursuit times are relatively small, but prefer larger, delayed rewards when pursuit times are large. Foraging processes may also be thought of as stochastic because animals face problems of information and risk (Oaten, 1977; Caraco, 1980; Gilliam et al., 1982; Stephens and Charnov, 1982; Cezilly and Benhamou, 1996). Kagel et al. (1986) suggest that preference for immediacy is a behavioral constraint on foraging. Deterministic approximations may be unrealistic when foragers are uncertain about changes in resource quality and when fitness depends on probabilities of benefits and costs.

For animals that gather resources for future use, information about the value of the resource when it is used, rather than simply when it is acquired, should be beneficial (Kagel et al., 1986; Gendron and Reichman, 1995). Many animals gather food when it is abundant and store it for periods when it is scarce or when foraging is costly or dangerous (Smith and Reichman, 1984; Vander Wall, 1990). Caching is a good example of a behavior for which animals would benefit by having the ability to incorporate future value into decisions about how to use resources (Andersson

and Krebs, 1978; Kotler et al., 1999). Specifically, animals that store sufficiently large quantities of food may be released from the constraint imposed by seasonal changes in food availability (Vander Wall, 1990). Another advantage of food storage is that it provides an opportunity to balance the relative values of various food items as they change through time (e.g. ripen, spoil). This ability to balance current and future value provides animals with a measure of control over their food supply in space and time, and has become an important adaptive strategy for circumventing problems of food limitation for many animals.

Previous models addressing the caching decision have treated foraging as a sequential decision that is related to available resources and in some cases, the state of the forager (e.g. Lucas and Walter, 1991; Brodin and Clark, 1997; Pravosudov and Lucas, 2000). These models, which rely on stochastic dynamic programming (SDP) approaches, were developed for state-dependent data (e.g. time-dependent risk sensitivity, cost of reserves, social dominance). For example, Clark (1994) found that the value of cache increases with reproductive value (which depends on age and condition). Brodin and Clark (1997) used an SDP model for birds and reported mass dependent costs to fat reserves. Pravosudov and Lucas (2000) found that, under favorable conditions, social interactions might cause both dominant and subordinate animals to accumulate more reserves due to competition. Collectively these studies suggest that state dependent models may be appropriate where data are available.

Although many taxa exhibit caching behavior (Vander Wall, 1990), the model we use was developed with animals such as woodrats (*Neotoma* sp.) in mind. State-dependent studies are rare for most mammals and nonexistent for woodrats, so we focus on extrinsic factors such as resource availability, handling time, and decomposition of prey. Woodrats are generalist herbivores whose handling times appear to be long relative to their search times. Woodrats are thought to be central place foragers, ranging from their houses to retrieve food and den-building material (McGinley, 1984). Previous studies indicate that woodrats take perishability into account when selecting food for long-term storage. For example, Post and Reichman (1991) conducted four experiments to determine whether *Neotoma floridana* differentially consumed and cached perishable and persistent food

under different conditions. Cache and winter diet analyses indicate that the perishable items are consumed early in the cache use period, whereas more persistent food types are consumed later (Post, 1991). Reichman (1988) reported that the caching behavior of woodrats changed in predictable ways according to the relative perishability of available food types. Similarly, Hadj-Chikh et al. (1996) found that gray squirrels consistently consumed acorns of high perishability and cached acorns of low perishability, without regard to handling time. With the ability to detect changes in the rate at which food items deteriorate or disappear and the costs of acquiring each type, an animal could potentially adjust the composition of its cache to produce the maximum benefit over the cache use period (Gendron and Reichman, 1995). In particular, animals should not store more of a food type than can be consumed before the remaining items of that type spoil.

In this paper, we analyze the extent to which future value must increase to override the value of immediate consumption. We hypothesize that caching animals face trade-offs in foraging between immediate consumption (i.e. increase probability of survival into the future) and caching food for later consumption (i.e. animals discount current rewards because future resources may be scarce). To address this question, we develop a simple prey selection model (Stephens and Krebs, 1986) to predict optimal foraging and food-storing behavior for one prey type that varies in quality between two time periods differing in food availability. Using our analytic model, we evaluate the range of strategies along this continuum under different levels of food availability and perishability. We consider these questions with respect to optimality of foraging decisions in the face of uncertainty, with the goal of characterizing the future value of resources for animals. Distinguishing the dynamic effects of contrasting modes of foraging behavior such as caching and immediate consumption will improve our predictive understanding of how caching animals forage.

2. Methods

2.1. Model description and parameter selection

We use a simple time-minimizing model that is modified to include food storage and decomposition.

In general, time-minimizers are thought to minimize the time required to gain a fixed ration of energy, while energy-maximizers maximize the amount of energy gained in a fixed time (Schoener, 1971). Both currencies are generally equivalent to rate maximization (Pyke et al., 1977), thus we adopt the simpler of the two as a first step in our analysis of foraging decisions. With a central place forager (e.g. woodrat) in mind, we assume that prey is encountered and returned to dens for either immediate consumption or storage. For simplicity we assume that an animal forages during two discrete but equal time periods, and that foraging decisions are made for a single prey item. The two time periods (e.g. season of high versus low food availability) may differ in prey abundance (a), where $1/a_1$ is the number seconds between prey encounters in the first time period, and $1/a_2$ is the number of seconds between encounters in the second time period. Handling time (h) refers to time spent handling and consuming food once in the central location (i.e. den), for each time period (immediate versus future). We consider h_1 as the handling time for prey to be consumed immediately and h_t as the handling time for prey attained during time period 1 to be consumed in time period 2. In time period 1, an animal may consume or cache an item, and in time period 2 animals may consume either cached or uncached items. Thus there are two strategies, and we assume that the optimal foraging strategy is the one that minimizes the time spent per item, and that an animal will not forage for more time than needed to meet energetic requirements.

Our goal is to predict an animal's foraging and food-storing behavior over these two time periods and when only one resource is involved. That is, we ask what behavioral strategy will minimize the time spent foraging over the two time periods to achieve a fixed level of reward. For example, given a 2-day time period, this fixed level of reward may be defined based on the average daily caloric requirements for animals (Marcum et al., 1998), the average caloric value of prey items available, and a range of plausible encounter rates. For woodrats, we calculate the number of hours of foraging needed to meet daily caloric needs as well as caloric requirements from energy stores during periods of low food availability for a range of encounter rates (Appendix A). Our working assumption is that an animal seeks to minimize t_i , and time saved during foraging activities will minimize preda-

tion risk (Kotler et al., 1999) and may be used for other activities that may increase an animal's fitness. Starting with a simple prey selection model where the average time per item (t_i) is $1/a_1 + h$ (Stephens and Krebs, 1986), we consider the influence of the potential to cache (c) and change in value (p) by modifying this simple prey selection model (e.g. $1/a_1 c e^{-p} + h_t$). To evaluate the influence of these novel parameters, we develop a two-time-period prey selection model, where the average time per item for all foraging strategies is the cumulative average of time spent per item (t_i) for each strategy.

$$t_i = \frac{a_1(1-c)}{a_1(1-c) + a_1 c e^{-p} + a_2} \times \left(\frac{1}{a_1(1-c)} + h_1 \right) + \frac{a_1 c e^{-p}}{a_1(1-c) + a_1 c e^{-p} + a_2} \times \left(\frac{1}{a_1 c e^{-p}} + h_t \right) + \frac{a_2}{a_1(1-c) + a_1 c e^{-p} + a_2} \times \left(\frac{1}{a_2} + h_1 \right) \quad (1)$$

where c is the likelihood of caching, $1/a_1$ is number seconds between prey encounters in time period 1 (measure of prey abundance), $1/a_2$ is number seconds between prey encounters in time period 2 (measure of prey abundance), h_1 is handling time for prey to be consumed immediately (measure of prey quality), h_t is handling time for prey attained during time period 1 to be consumed in time period 2 (measure of prey quality), and p is the change in nutritional value between time periods 1 and 2.

The model assumes that animals have knowledge of the future value of food resources when making foraging decisions. The general form of this model is as follows. The first two terms of Eq. (1) represent foraging values for time period 1, where for a given encounter, an animal can either consume (first term) or cache (second term) a food item. The third term of Eq. (1) represents foraging values for time period 2 (i.e. future time). Food that is not immediately consumed ($1-c$) in the first term is cached (c) and this cached food may increase or decrease in value (p). We assume that p may influence the choice of whether to consume a prey item immediately ($1/a_1(1-c)e^{-p}$), or to store it for later consumption ($1/a_1 c e^{-p}$). We assume that p implicitly influences energy intake by an animal and thus the time required to meet daily energy needs. For example, prey items of a given value may

Table 1

Parameter values and combinations used in analytic model (Eqs. (1) and (2))

Parameter	Values considered	Cumulative number of parameter combinations
$1/a_1$	0, 2.0, 4.0, 6.0, 8.0	5
$1/a_2$	0, 2.0, 4.0, 6.0, 8.0	25
h_1	0.5, 1.5, 2.5, 3.5, 4.5	125
h_t	0.5, 1.5, 2.5, 3.5, 4.5	625
ρ	-1.0, -0.5, 0, 0.5, 1.0	3125

vary in h between the two time periods based on p (e.g. seed softens). Because h in our model is defined as time spent processing prey once in the den, p influences when, not whether, an item should be consumed. However, recognizing the uncertainty regarding these biological assumptions, we also conducted sensitivity analyses to consider the effect of handling time and decomposition explicitly influencing the decision to cache or consume immediately (Appendix B). The term h_1 applies to immediate consumption (terms 1 and 3), and h_t applies to consumption of cached items (term 2). Eq. (1) can then be simplified as

$$t_i = \frac{(1+h_1)a_1(1-c) + (1+h_t)a_1 c e^{-p} + (1+h_1)a_2}{a_1(1-c) + a_1 c e^{-p} + a_2} \quad (2)$$

Based on this model, t_i represents the sum of the three terms in the numerator; prey consumed in the first time period, prey cached in the first time period, and prey consumed in the second time period, respectively. We define our response variable as the foraging decision that minimizes t_i (e.g. t_i is either minimized for the decision to cache or eat). For example, immediate consumption is considered optimal when time is minimized for a caching likelihood of zero. We then examine the degree to which these response variables depend on the interaction between different abundance levels, handling times, and decomposition rates.

Because the solution for the optimal foraging decision is not attainable analytically, we could not analyze the model directly. Thus we adopt a simulation approach for our analysis and examined the model described by Eq. (2) for 3125 combinations of parameters (Table 1). We used simulations to evaluate time per item and optimal foraging strategies for different abundance levels, handling times, and nutritional value. For each parameter combination,

we numerically solved for the local minimum value for time per item and this value was used to determine the optimal foraging decision (i.e. consume or cache). Our analyses were restricted to parameter values based on empirical data reported in the literature. Specifically, we use values reported by Gendron and Reichman (1995) and developed from our field experience with woodrats. To determine values for $1/a_1$ and $1/a_2$, Gendron and Reichman use an indirect measure of density: the time between prey encounters. Shorter intervals between encounter rates are associated with higher density, and the encounter rate was set so that when the total abundance of prey was 5 million the animal encountered prey within its home range every second (Gendron and Reichman, 1995). Thus if prey abundance is increased, the time between encounters declined. Using this approach, values for $1/a_1$ and $1/a_2$ varied between 0 and 8.0 s per prey encounter, and h_1 and h_t varied between 0.5 and 4.5 s per prey item. Starting with the quadratic curves described by Gendron and Reichman (1995) for change in value (e.g. deterioration), we parameterized p as ranging between 1.0 and 1.0 because we were interested in the effects of changes in nutritional value (increasing or decreasing) on foraging decisions. Since we are concerned with how future value influences current decisions, we emphasize differences in abundance and handling times between the two time periods (e.g. a_1 , a_2 , h_1 and h_t are now $a_1 - a_2$, $h_1 - h_t$), where a_1 is in units of items per second, in our analyses.

2.2. Analysis of model output

Analyses were conducted in two stages. First, we asked which suites of model parameter combinations lead to caching being optimal, and identify model parameters that govern this decision. Second, we used a multivariate analysis to identify cases where caching is optimal, and examine this result in light of Eq. (2).

3. Results

Response curves demonstrating three possible realizations from our simulations for all parameter combinations are shown in Fig. 1. In all cases, response curves were linear. Based on our model, t_i is either: (1)

minimized at a caching value of 0 and the optimal decision is to consume prey immediately, (2) minimized at a caching value of 1 and the optimal decision is to cache, or (3) where there is no slope to the response curve there is no optimal decision. Below we describe the results of our simulations in the context of these potential outcomes.

We used discriminant function analysis to identify multivariate parameter combinations that best predicted cases where either immediate consumption or caching is optimal. The groupings for our discriminant function analysis were “cache”, “consume immediately” or “either” (i.e. there was no optimum), with the model parameters as potential classifying variables (Fig. 1). The parameter combinations displayed in Table 1 represent 3125 unique scenarios, of which caching was optimal for 1485, immediate consumption was optimal for 1515, and for 125 there was no optimum. When all three of the potential classifying variables were used to construct a discriminant function, 71% of the outcomes were correctly classified into the appropriate groups. More informatively, using only $a_1 - a_2$ as a classifying variable, it was possible to correctly classify 84% of the cases (Fig. 2). This classification did not change significantly in our sensitivity analysis (70% versus 71%, and 76% versus 84%), suggesting that our model is robust to a variety of biological assumptions. Using

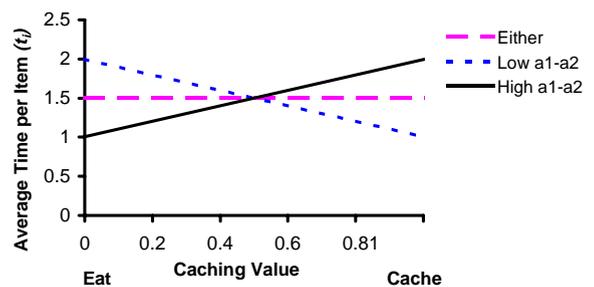


Fig. 1. Examples of response curves for three potential outcomes of simulation effort. t_i is either minimized at a caching value of 0, 1 or there is no slope to the response curve. Where t_i is minimized at a caching value of 0, the optimal decision is to consume prey immediately, where t_i is minimized at a caching value of 1, the optimal decision is to cache, and where there is no slope there is no optimal decision. “Negative $a_1 - a_2$ ” values are associated with an increase in encounter rate (prey abundance) between each time periods, while “positive” values are associated with a decrease in abundance between time periods.

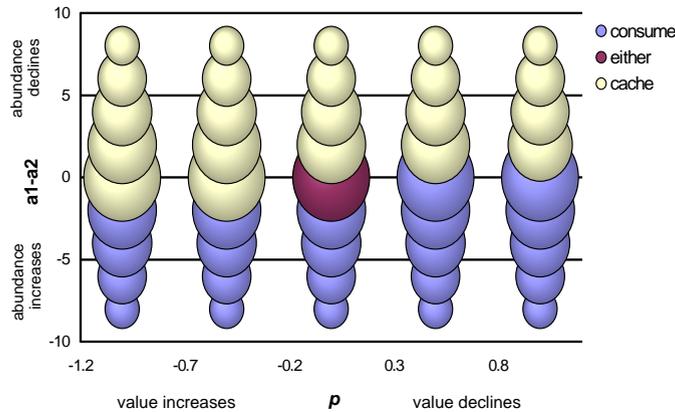


Fig. 2. Distribution of foraging decisions for combinations of abundance and decomposition, representing 3125 distinct parameter combinations. Bubble size is proportional to frequency of occurrence for outcomes in parameter space (consume, cache, either). Abundance is the primary determinant of foraging decisions, where positive $a_1 - a_2$ values (i.e. abundance declines) are highly correlated with decisions to cache and negative $a_1 - a_2$ (i.e. abundance increases) values are correlated with decisions to consume immediately. A less pronounced tendency to cache when decomposition rate increases (i.e. nutritional value increases) is also evident.

discriminant function analysis, it is often possible to achieve effective classification with fewer variables (Johnson and Wichern, 1998; Fischer, 1936). It should be noted that negative $a_1 - a_2$ and $h_1 - h_t$ values are associated with an increase in encounter rate (prey abundance) and handling time between each time period, while positive values are associated with a decrease in abundance and handling time between time periods. Similarly, negative p values represent an increase in value and positive p values represent a decline in value through time.

The cases where caching was optimal were characterized by a positive $a_1 - a_2$ as compared those where immediate consumption was optimal ($a_1 - a_2 = 3.3$ for caching group versus -3.3 for immediate consumption group), by a slight increase in nutritional value ($p = -0.13$ for caching group versus 0.14 for the immediate consumption group), and by no difference in $h_1 - h_t$ (Fig. 1, Tables 2 and 3). These values did not differ significantly for our sensitivity analysis (e.g. $a_1 - a_2 = 3.1$ for caching group versus -2.8 for immediate consumption group, $p = -0.2$ for caching group versus 0.22 for the immediate consumption group, and by no difference in $h_1 - h_t$). In other words, our model predicts a strong tendency to cache where abundance declines, and an even more pronounced tendency to cache where nutritional value increased between the two time periods (Fig. 2).

Table 2

Group means of discriminant function analysis for multivariate parameter combinations leading to decision to cache

	Consume immediately	Cache
$a_1 - a_2$	-3.3	3.3
$h_1 - h_t$	0	0
ρt	0.13	-0.14
Number of cases	1515	1485

Seventy-one percent of cases were correctly classified using three model parameters.

Table 3

Outcome of classification using discriminant function analysis for parameter combinations leading to the decision to cache using only $a_1 - a_2$ as a classifying variable

	Predicted consumed	Predicted either	Predicted cached
Observed consumed	1250	250	15
Observed either	0	125	0
Observed cached	0	250	1235
Number of cases	1250	625	1250

Group means for these variables are identical to those indicated in Table 2. With only this one predictor variable, 84% of cases were correctly classified.

4. Discussion

Perishability is an important consideration faced by animals that store food. While previous models

have suggested that information from the past influences prey choice decisions (Hirvonen et al., 1999), our results show that information about the future value of food items would likely improve caching decisions. In the context of optimal foraging behavior for caching animals, we consider Kagel et al.'s (1986) thesis that the value of a food item eaten now is greater than one eaten later. Using a simple analytic model, we examined optimal foraging and caching decisions for different levels of abundance, handling time and changes in values. For a wide range of parameter values, response curves were linear. The decline in abundance and increase in nutritional value that characterized cases where caching was optimal makes sense intuitively: animals store food when they expect prey abundance to diminish or the nutritional value of prey items to increase with time. One non-intuitive result was that changes in handling time had virtually no influence on foraging decisions. The increased percent of correctly classified outcomes for a reduced number of parameters suggests that $h_1 - h_t$ may obscure explanatory power of $a_1 - a_2$. It is interesting that change in abundance so accurately predicts foraging decisions when other factors are also involved (e.g. handling time and decomposition).

Animals that cache may have an adaptive advantage in environments with variable conditions. There have been suggestions in the literature that woodrats consider future value by taking perishability into account when caching food (Reichman, 1988). However, data are not available to determine the degree to which woodrats alter foraging and caching patterns based on prey abundance and decomposition as predicted by our model. Our model provides a basis for further empirical studies of tradeoffs between short- and long-term benefits. Parameter values used in our model are also measurable in the field or in controlled experiments. Further, with knowledge of the food types cached and their nutritional value, we could predict the amounts cached and inventory strategies employed for individual animals such as woodrats.

Our results should be interpreted carefully. While our model examines tradeoffs in foraging decisions occurring in two discrete time periods, optimal behavior over a longer time horizon may be different

if there is time-dependence in risk sensitivity (Clark, 1994). Further, it is possible that over longer time horizons, optimal decisions reflect a trade-off between predation risk and energy gain. We assumed time minimization as a proxy for costs associated with reserves, however SDP models may allow more explicit inclusion of time-dependent risk sensitivity. Empirical data on state-dependent foraging is needed in order to develop more sophisticated SDP models. Future studies should also explore a variety of different model formulations (e.g. energy-maximizing strategy, two prey items) in which optimal food-storage is quantified.

Long-term foraging optimization strategies may be determined by (1) foraging specialization, (2) availability of preferred prey, and (3) fat storage or caching of food items (DuBow, 1997). While none of the strategies examined were optimal under all conditions, our analyses indicate that prey abundance dominates as an explanatory factor underlying optimal food storage decisions. This is a qualitative difference between optimal foraging theory with and without caching. Our results represent a useful first step in considering the extent to which caching behavior might extend the theoretical predictions of classic optimal foraging theory. With this work as a basis, we plan to continue with empirical and theoretical investigations with the goal of improving our understanding of the ability of animals to respond to information about the future value of resources. For example, we hope to test the predictions that change in food abundance and quality influence the propensity of a small mammal to cache. Future studies should also include measurement of state dependence (e.g. reproductive value) in order to parameterize more sophisticated state-dependent models.

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Appendix A. Number of hours needed for foraging for plausible range of encounter rates and average caloric values (cal) for wood rat prey

Average food value (cal)	Encounter rate							
	1	0.5	0.33	0.25	0.2	0.17	0.143	0.125
10	1.3	2.59	3.89	10.37	19.45	62.23	136.12	497.81
20	0.65	1.3	1.94	5.18	9.72	31.11	68.05	248.85
30	0.43	0.86	1.3	3.46	6.48	20.75	45.38	165.97
40	0.32	0.65	0.97	2.59	4.86	15.56	34.04	124.48
50	0.26	0.52	0.78	2.07	3.89	12.44	27.21	99.52
60	0.22	0.43	0.65	1.73	3.24	10.37	22.69	82.99
70	0.19	0.37	0.56	1.48	2.78	8.89	19.45	71.15
80	0.16	0.32	0.49	1.3	2.43	7.77	17	62.19

Calculation based on a daily energy requirement of 35,000kcal and the assumption that 3/4 of the period animals face low food availability.

Appendix B. Modification of Eqs. (1) and (2) used for sensitivity analysis, where handling time and decomposition explicitly influence the decision to cache or consume immediately

$$t_i = \frac{a_1(1-c)}{a_1(1-c) + a_1c e^{-p} + a_2} \times \left(\frac{1}{a_1(1-c)} + h_1(1-c) \right) + \frac{a_1c e^{-p}}{a_1(1-c) + a_1c e^{-p} + a_2} \\ \times \left(\frac{1}{a_1c e^{-p}} + h_1(c e^{-p}) \right) + \frac{a_2}{a_1(1-c) + a_1c e^{-p} + a_2} \times \left(\frac{1}{a_2} + h_1 \right)$$

$$t_i = \frac{(1+h_1)(1-c)a_1(1-c) + (1+ht)a_1c e^{-p}c e^{-p} + (1+h_1)a_2}{a_1(1-c) + a_1c e^{-p} + a_2}$$

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