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# Optimal Foraging on the Roof of the World: Himalayan Langurs and the Classical Prey Model

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*ABSTRACT* Optimal foraging theory has only been sporadically applied to nonhuman primates. The classical prey model, modified for patch choice, predicts a sliding "profitability threshold" for dropping patch types from the diet, preference for profitable foods, dietary niche breadth reduction as encounter rates increase, and that exploitation of a patch type is unrelated to its own abundance. We present results from a 1-year study testing these predictions with Himalayan langurs (*Semnopithecus entellus*) at Langtang National Park, Nepal. Behavioral data included continuous recording of feeding bouts and between-patch travel times. Encounter rates were estimated for 55 food types, which were analyzed for crude protein, lipid, free simple sugar, and fibers. Patch types were entered into the prey model algorithm for eight seasonal time periods and differing age-sex classes and nutritional currencies. Although the model consistently underestimated diet breadth, the majority of nonpredicted patch types represented rare foods. Profitability was positively related to annual/seasonal dietary contribution by organic matter estimates, whereas time estimates provided weaker relationships. Patch types utilized did not decrease with increasing encounter rates involving profitable foods, although low-ranking foods available year-round were taken predominantly when high-ranking foods were scarce. High-ranking foods were taken in close relation to encounter rates, while low-ranking foods were not. The utilization of an energetic currency generally resulted in closest conformation to model predictions, and it performed best when assumptions were most closely approximated. These results suggest that even simple models from foraging theory can provide a useful framework for the study of primate feeding behavior. Am J Phys Anthropol 000:000–000, 2009. ©2009 Wiley-Liss, Inc.

Optimal foraging theory (OFT) operates on the assumption that behavior has been molded by natural selection and uses mathematical models to predict animal feeding decisions (Stephens and Krebs, 1986). Although OFT, first developed in the 1960s and 1970s (Charnov and Orians, Unpublished manuscript; Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971), has engendered controversy (Gray, 1987; Perry and Pianka, 1997; Pierce and Ollason, 1987), few can deny its impact on behavioral ecology. Largely, descriptive work has been transformed into studies that convert measurable variables into quantitative, testable predictions concerning animal behavior. As a result, the breadth and applicability of its models continue to grow (Stephens et al., 2007). Foraging theory does not necessarily argue that animals are optimal; rather, it uses a mathematical tool (optimization) to denote how an animal *should* behave under specified conditions (Ydenberg et al., 2007). Often they do act as predicted (Nonacs, 2001; Sih and Christensen, 2001). In cases where OFT predictions are not supported, attention is directed toward novel lines of research and results in a more complete understanding of feeding behavior (Bulmer, 1994; Orians, 1980; Stephens and Krebs, 1986).

A seminal model in foraging theory is the classical prey model, variously called the attack, optimal diet, or contingency model, which predicts which foods in a set should be accepted by a forager under given conditions (MacArthur and Pianka, 1966; Schoener, 1971; Charnov, 1976; Stephens and Krebs, 1986). Food types are rank-ordered by energy or another currency divided by the handling time it takes to capture and consume them. The higher this value, the more profitable the food is considered. Food types, each of which has an associated mean energy content, handling time, and encounter rate, are then entered into the "prey algorithm" in the order of their profitability. As each new food type is entered, the algorithm gives the average rate of intake ($E_n/T$) if only this type and those of greater profitability were taken. The set of foods that results in the highest $E_n/T$ is considered the optimal diet. In short, when an animal comes upon a potential food item, the forager should exploit that item if its profitability is above the threshold $E_n/T$ value, but ignore it and continue searching if its profitability is below it.

Many animals, including many primates, exploit food *patches*, or aggregations of food (e.g., leaves on trees), as

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*Table 1. Assumptions of the classical prey model as applied to patch choice [after Stephens and Krebs (1986); see also Post (1984)]*

| Assumption | Description |
|---|---|
| Search and handling mutually exclusive | While exploiting a patch, animal does not search for or gather information on other patches. |
| Patches encountered sequentially | Patches are encountered one after another and are not alternatives. |
| Patches encountered randomly | Forager comes upon patches without prior knowledge or a predetermined travel path. |
| Complete information | Forager knows model variables such as encounter rates and patch identity/quality. |
| Homogeneous, fine-grained environment | Patches of similar type are not "clumped," but are evenly distributed in the environment. |

*Table 2. Predictions of the classical prey model as applied to patch choice [after Stephens and Krebs (1986)]*

| Prediction | Explanation and definitions | Notes |
|---|---|---|
| Profitability threshold for inclusion of patch types in diet | Only the set of patch types that results in the highest long-term currency gain over foraging time ($E_n/T$) should be exploited. "Currency" is generally defined as energy, but could represent any nutritional variable. Foraging time includes both time spent handling foods within patches and search time (travel between patches). Only patches with currency gains over time ($e/h$) higher than $E_n/T$ should be exploited. | Threshold moves up or down based on the nutritional values, handling times, and encounter rates associated with patch types. As long as these variables remain constant, the *zero-one rule* applies: a given patch type should either never be exploited or always be exploited when it is encountered. |
| Preference for more profitable patch types | "Profitability" is defined as average currency gained over time spent foraging in a specific patch type. More profitable patch types are ranked more highly than those of lower profitability, and less likely to be passed over while foraging. | Profitability is applied as a mean value associated with each patch type. In classic applications, does not take into account reduction in intake rates that may occur within patches as they are depleted (patch depression). |
| Increased selectivity as encounter rates with high-ranking patch types increase | When highly profitable patch types are abundant, a forager should specialize. When resources are scarce, and encounter rates with high-ranking patch types are low, the diet should expand to include less-profitable foods. | Diet breadth is generally measured using number of species exploited, controlling for season, if seasons vary significantly in the number of species available for consumption. |
| Inclusion of a patch type in the diet is not related to how often a forager encounters it | Whether or not a forager exploits a given patch type is only related to its profitability and the profitability and abundance (encounter rates with) foods of higher rank. | In practice, high-ranking patch types should be taken in close relation to their abundance, while those of low profitability should not. |

opposed to individual food items. There are two ways in which the classical prey model can be modified to predict patch choice. The first is a direct analogy where a patch is treated exactly like a prey item, and this approach does not consider patch depression (Schoener, 1974; Schoener, 1987; Stephens and Krebs, 1986, p. 34). Patch depression is a reduction in intake rate over time spent in a patch due to the depletion of food items, movement of prey, or other factors (Charnov et al., 1976). The second approach includes patch depression and solves concurrently for both patch choice and patch residence time (Stephens and Krebs, 1986). The first approach (direct analogy) is explored here (Tables 1 and 2), and the possible effects of depression on patch choice and departure will be investigated in later papers.

Human behavioral ecologists have applied variants of the classical prey model to modern human hunter-gatherers and, to a lesser extent, the archaeological record (Winterhalder and Smith, 1981; Smith, 1991; Kennett and Winterhalder, 2006). Hawkes et al. (1982), for example, used this approach to predict the caloric profitability threshold for food items to be included in the diet of Aché hunter gatherers (Kaplan and Hill, 1992). Kurland and Beckerman (1985), in a similar vein, used the model to argue that selection favored reciprocity and information exchange in early hominid evolution due to its effects on reducing search costs.

Interestingly, researchers of nonhuman primates have rarely applied OFT to their subjects, but this is not necessarily due to lack of interest. The data required to test these foraging models (e.g. intake rate) may be difficult to gather even in ideal field or captive situations, let alone with animals that are nocturnal, difficult to habituate, or living in high canopy. Although direct tests of OFT models are scarce (but see Grether et al., 1992; Altmann, 1998), a number of primatologists have referenced foraging theory as an a posteriori tool to explain observed behavior (e.g., Hamilton et al., 1978; Gaulin, 1979). Perhaps, the most direct application of the classical prey model to nonhuman primates involves work on patch quality and selection in Japanese macaques (*Macaca fuscata*) (Nakagawa, 1989, 1990) and orangutans (*Pongo pygmaeus*) (Baritell et al., 2009), and a review article on related topics covering the entire Order (Nakagawa, 1996). Quantitative testing of model predictions, however, coupled with estimation of all variables and food-type ranking, has yet to be undertaken with any nonhuman primate.

Here, we compare predictions of the classical prey model, modified for patch choice, with the behavior of

Himalayan gray langurs (*Semnopithecus entellus*) living at a high altitude (3,000–4,000 m) site at Langtang National Park, Nepal. The gray langur is a colobine monkey possessing a large, multichambered stomach with symbiotic gut microorganisms, which aid in the digestion of high-fiber foods (Bauchop and Martucci, 1968; Kay and Davies, 1994). Although colobines are popularly described as "leaf-eating monkeys," gray langurs have an eclectic, generalist diet that varies seasonally (Koenig and Borries, 2001), and this is particularly true of Himalayan populations (Curtin, 1982; Sayers and Norconk, 2008). This provides an ample opportunity to investigate predictions of the classical prey model as they pertain to behavioral shifts in response to changes in the abundance of foods. Field observations included continuous recording of feeding bouts and between-patch travel times, and laboratory work included standard nutritional analysis of langur foods. We apply a simple patch choice version of the classical prey model with corrections for search costs and use three nutritional currencies [kcal, kcal with a flat correction for neutral detergent fiber fermentation, and crude protein (CP)]. Because the classical prey model has not been fully applied to any nonhuman primate, we feel it is appropriate to begin with this simple, but potentially robust, model before moving to a more complex one with added constraints or nutritional variables (Grether et al., 1992; Kaplan and Hill, 1992).

## METHODS

### Study site and subjects

Langtang National Park is located in north-central Nepal on the Tibetan border, and the Langtang Valley between Ghore Tabela (3,033 m) and Langtang village (3,480 m) was our primary area of observation. Several vegetation types are present, all temperate or alpine, with different woody species characterizing each habitat type/elevation. On the north side of Langtang Khola (River), broadleaf trees and shrubs make up much of the woody plant cover, whereas the south side is largely coniferous forest. Other habitat types include cultivated and noncultivated fields, rockslides, and cliffs. A small human population is found at the village of Langtang. The climate is highly seasonal, with cold winters that include periodic snow cover, and a mild summer monsoon [see Sayers and Norconk (2008) for further details].

All observations reported here involve a single troop of Himalayan langurs. Members of this troop, once contacted, could generally be approached within 10 m, although this was in some cases not possible when the monkeys utilized cliff habitats or when rain/snow rendered human climbing difficult. Group size ranged from 27 to 33 individuals, with a modal number of 3 adult males and 10 adult females.

### Behavioral observations

All behavioral observations were dictated into an audio recorder between December 2002 and December 2003 and subsequently transcribed. A different focal individual was chosen for each sample day ($n = 53$), and data were collected on each food patch that was observed to be entered by this individual. The formal definition of a patch is given below. Focal individuals were rotated among nonadults ("juveniles"), adult females, and adult males. Because the length of time in which individuals could be followed varied extensively based on topography and weather, feeding data were collected from other individuals chosen at random whenever the focal animal was not visible. This occurred on most sample days. Whenever possible, individual identification was recorded.

When a target individual was observed to enter, or was already feeding in, a food patch, the following data were dictated into the recorder: food species, plant part ingested, the time and size of each bite, within-patch travel, and time of patch departure. Bite size refers to the number of food items (leaves, fruit, etc.) put into the mouth, and when number could not be determined, the average number of items per bite for that patch was later substituted. Periods when ingestion could not be observed were considered missing time and discarded (after Grether et al., 1992). When the focal individual left a patch, it was followed, whenever possible, until it entered another food patch, and recording ceased only when the individual stopped feeding or moving. When necessary, observations were aided by binoculars, or, rarely, a spotting scope. These data allow estimation of intake over time in a second-by-second fashion for each patch or patch type, as well as average travel time between food patches. In total, 402 langur patches were recorded (over 53 days distributed throughout a year) that included age-sex data and foods in which all nutritional analyses have been performed. Ninety-seven (97) between-patch travel times were estimated. Sample sizes were not equally distributed over the year, as weather conditions and the ranging behavior of the monkeys determined the likelihood and duration of contact with the troop. Seasonal (defined below) patch numbers/sample days were as follows: late winter (15/8), spring (71/9), late monsoon (9/2), fall 1 (35/5), fall 2 (54/8), fall 3 (73/8), fall 4 (113/11), and early winter (32/2).

Food types were collected and weighed wet, field dried, and after laboratory drying. Laboratory drying was completed at Peabody Museum, Harvard University. Plant identifications were conducted by plant scientists at the Central Department of Botany, Tribhuvan University, Kathmandu, Nepal.

### Nutritional analysis and currencies for the model

Nutrient (CP, water soluble carbohydrate, lipids, and hemicellulose) and non-nutrient (cellulose, cutin, lignin, and tannins) analyses were conducted by KS on 55 Himalayan langur food types at the Nutritional Ecology Laboratory in the Department of Anthropology, Peabody Museum, Harvard University (after Conklin-Brittain et al., 1998; Wrangham et al., 1998). CP was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce et al., 1958) instead of using the 4.3 conversion factor (Conklin-Brittain et al., 1999; Norconk and Conklin-Brittain, 2004).

The detergent system of fiber analysis (Goering and Van Soest, 1970) as modified by Robertson and van Soest (1980) was used to determine the neutral-detergent, or total cell wall fraction (NDF) that includes hemicellulose (HC), cellulose (Cs), sulfuric acid lignin (Ls), and cutin. Total ash, an estimate of overall mineral content, was measured in accordance with Williams (1984). Lipid content was measured using petroleum ether extraction for 4 days at room temperature, a modification of the method of the Association of Official Analytical Chemists (Williams, 1984). Free simple sugars (FSS) (formerly referred to as water soluble carbohydrates, Conklin-Brittain et al., 1998) were estimated using a phenol/sulfuric acid calorimetric assay developed by Dubois and colleagues (1956) and modified by Strickland and Parsons (1972), with sucrose as the standard. Total nonstructural carbohydrates (TNC) were calculated as follows: TNC = 100 − % NDF − % lipids − % CP − % ash (Conklin-Brittain et al., 1998). The results of the analyses are used as a percentage of organic matter (OM), which excludes inorganic materials.

Currencies for use in the foraging models include: (1) zero-fermentation metabolizable energy ($ME_O$, kcal/100 g OM) = (4 × % TNC) + (4 × % CP) + (9 × % lipids), (2) high-fermentation metabolizable energy ($ME_H$, kcal/100 g OM) = $ME_O$ + (2.0 × % NDF), and (3) CP (Conklin-Brittain et al., 2006; National Research Council, 2003).

Energy is a convenient currency that is applicable in many situations and has the added advantage that search costs can also be reported in kilocalories. Although nutritional analyses of colobine foods that include estimates of energetic value are rare, this variable has been suggested to be an important component of food selection for some colobines (Dasilva, 1994), and Himalayan langurs live in a marginal environment where energetic considerations are likely to be important (Sayers and Norconk, 2008). However, because of the foregut fermentation of colobine monkeys, they are likely able to derive more energy from fibrous foods than is suggested by the standard $ME_O$ equation (Kay and Davies, 1994). Conklin-Brittain and colleagues (2006) calculated $ME_H$ in chimpanzees, which can digest approximately half of the NDF in their diet through hindgut fermentation, as $ME_H = ME_O + (1.6 \times \%\ NDF)$. Foregut fermenters, however, show greater apparent digestibility of fiber than do hindgut fermenters (Edwards and Ullrey, 1999), with values of at least 68.9% of NDF (National Research Council, 2003). Therefore, here, we use $ME_H = ME_O + (2.0 \times \%\ NDF)$ as a conservative correction to account for colobine fermentation. There are likely to be problems with this "flat" correction applied equally to all food types, as foods with differing nutritional characteristics may be assimilated in differing fashions. However, at this point, very little is known about the differences in assimilation of different colobine foods, other than a general preference for lower-fiber leaves over higher fiber leaves (Waterman and Kool, 1994). We argue the "flat" correction is a reasonable starting point for the investigation of such questions.

CP has long been considered to play a role in diet choice for colobine monkeys (Milton, 1979; Wasserman and Chapman, 2003) and herbivores in general (Newman, 2007). Note from the above that CP is in itself a component of ME calculations and the two measurements may be correlated. A number of workers have found that a protein-to-fiber ratio is useful in predicting colobine leaf choice (Milton, 1979) or even biomass (Chapman et al., 2002). The primary limitation to the use of a ratio is that it is often unclear whether it is the numerator or denominator, or both, that is driving food selection, and thus we limit ourselves to CP in the foraging model.

## Seasonal time periods and age-sex categories

Eight seasonal time periods are used in the tests of model predictions. These were chosen on the basis of sample sizes as well as phenology (Sayers and Norconk, 2008): late winter (late December–March), spring (April–May), monsoon (September), fall 1–4 (October and November, divided into four 2-week samples), and early winter (early December). Ideally, encounter rates with patch types (i.e., food abundance) and the profitability of each patch type (i.e., nutritional quality) should remain constant throughout each time period in which the model is applied.

Age-sex categories are modified from Bishop (1975) and include adult males, adult females, and juveniles (nonadults). In some model applications, only data from a single adult male is considered. This single male was also the alpha male, which should reduce dominance effects on diet selection.

## Definition of a patch

In foraging theory, a patch is usually defined as an area of food concentration separated from other patches by areas with little or no food. *Sequential encounter* occurs when patches are met one after another (Table 1). *Simultaneous encounter*, a deviation from the assumptions of the model considered here, occurs when patches are met more-or-less at the same time (Stephens and Krebs, 1986). For this study, each tree, shrub, cultivated field or herb clump is generally considered a separate patch (see Astrom et al., 1990). There are, however, some situations that are somewhat ambiguous; for example, when multiple plants grow contiguously or more than one food type is found on a single plant. For this reason, we give the following formal definition of a patch:

1. A patch contains only one food type. A food type is the unit that is handled at one time. For example, if a monkey picks fruit from a tree and consumes both the flesh and seeds, this is considered one food type. If, however, a monkey eats fruit from a tree and then switches to eating leaves on the same tree, and they are not handled or consumed together, they are considered here as two food types from two patches encountered simultaneously. This "one food type rule" is used for analytical convenience and ease of interpretation; allowance for more than one food type within a patch will be considered elsewhere.
2. The travel time to a food source (e.g. a plant) must exceed the average between-item ingestion times from the previous food source to qualify as being two patches encountered sequentially. For example, if leaves in one shrub are consumed at an average rate of one leaf (or one leaf clump) every 10 s, the travel time to another shrub of the same species and food type must exceed 10 s to be considered a separate patch.
3. In cases where travel time to a food source (e.g. a plant) does not exceed the average between-item ingestion time from the previous food source, and they differ in species or food type, they are considered here as two patches encountered simultaneously.

Patch types as defined earlier were used for all calculations performed in this work.

## The model

Although there are a number of derivations of the classical prey model, we choose a modified version that treats patches as analogous to prey and include search costs (Schoener, 1974; Charnov, 1976; Paulissen, 1987; Schoener, 1987). The formula for the model is as follows:

$$\frac{E_{\mathrm{n}}}{T} = \frac{\sum(\lambda_i e_i) - C_{\mathrm{s}}}{1 + \sum \lambda_i h_i} \tag{1}$$

where $E_{\mathrm{n}}/T$ is the net energy (or other currency) acquired over time foraging, $\lambda_i$ is the encounter rate with patches of type $i$, $e_i$ is the mean energy (or other currency) acquired per patch of type $i$, $h_i$ is the mean time spent handling items in a patch of type $i$, and $C_{\mathrm{s}}$ is the cost of searching for food (kilocalories per second).

Encounter rates ($\lambda_i$) were determined by dividing the number of patches of type $i$ entered by total search time. Search time equals the average travel time between patches for that season × total number of patches (counting only those encountered sequentially) for that season. Only patches where at least one bite of food was taken were considered "encountered." Although this method only gives information on patch types that are exploited, it does provide an estimate of encounter rate based on actual animal observations and is the approach taken in some of the more detailed tests of the classical prey model (Paulissen, 1987). A preferable approach would be to record, over time, every patch that enters a forager's range of perception (e.g., within an arbitrary distance radius), although this was not possible in the present study. Encounter rates are expressed as patches per second of search time. The currency ($e_i$) is expressed as the mean kilocalories or grams OM (for CP) acquired while exploiting a patch of type $i$, and handling time ($h_i$) is expressed as the average number of seconds spent exploiting a patch of type $i$. For example, if a patch type on average yields 20 kcal per visit and is exploited an average of 100 s per visit, the profitability of this patch type ($e_i/h_i$) would equal 0.2 kcal/s (12 kcal/min). These mean values are calculated using all recorded patches regardless of residence time, or whether the complete patch session was recorded. Once again, missing time, when ingestion movements could not be seen, was discarded and not used in the calculation of $e_i$ or $h_i$. Raw data concerning the above variables are given in the Appendix section.

As much (though not all) between-patch travel in Himalayan langurs occurs on the ground, search costs ($C_{\mathrm{s}}$) were determined using a general equation for the mass-specific cost of terrestrial locomotion (Taylor et al., 1982):

$$\frac{E_{\mathrm{metab}}}{M_{\mathrm{b}}} = 10.7 M_{\mathrm{b}}^{-0.316} \times v_g \tag{2}$$

where $v_{\mathrm{g}}$ is velocity in meters per second and $\frac{E_{\mathrm{metab}}}{M_{\mathrm{b}}}$ has units of watts/kg, which were then converted to kilocalories. Zero-speed costs are not included. The average velocity was estimated at 1.25 m/s, considered a "comfortable walking speed" for most primates (Steudel-Numbers, 2003, p. 257). Weights of adult males were estimated at 19.5 kg, adult females 16.1 kg, and juveniles as 12.1 kg ([3/4] the weight of adult females) (from Bishop, 1975). Search costs are not included when utilizing CP as currency.

## Model predictions and statistics

*Prediction 1: Quantitative estimation of profitability threshold for dropping items from diet.* For each of eight seasonal time periods, patch types were entered into Equation 1 in the order of their profitability ($\mathrm{ME_O}$ or $\mathrm{ME_H}$ in mean kcal/second, CP in mean grams OM/second). Variables were entered into Eq. (1) with patches from (1) only juveniles, (2) only adult females, (3) only adult males, and (4) only a single adult male. As each patch type is entered for an age-sex class and season, the calculated $E_n/T$ reflects the average rate of gain while foraging. Only those patch types with average profitability ($e_i/h_i$) above the highest possible $E_n/T$ (the threshold value) are predicted to be included in the diet; all others should be rejected in favor of continued search. The proportion of the diet consisting of patch types with average profitability above the threshold (i.e., predicted in the optimal diet) and below the threshold (not predicted) were quantified for each application. The percent contribution of patch types in the diet was calculated using both OM (grams OM from patch type $i$/total grams OM from all patch types) and time (seconds spent feeding on patch type $i$/seconds spent feeding on all patch types). The model predicts that patch types with profitability lower than the maximum possible $E_n/T$ will not be exploited, or, in the manner expressed here, will make up 0% of the diet. A more direct test of the model would involve measuring the number of acceptances/rejections of patch types as they enter the range of an animal's perception, but, as noted earlier, it was not possible to gather this data. Because the classical prey model is designed to predict the behavior of a single forager and that the "optimal diet" may differ between individuals, it is expected that the application using data from only a single adult male will most closely fit the model (Krebs and McCleery, 1984).

### *Predictions 2–4 were tested using Spearman rank order correlations.*

*Prediction 2: More profitable patch types will be preferred.* Correlations were used to assess the relationship between patch type profitability by $\mathrm{ME_O}$, $\mathrm{ME_H}$, and CP and percent contribution to annual diet by both OM and time spent feeding. The latter is used as an indirect indicator of "preference." To account for temporal effects in food availability, correlations were also performed for all seasonal time periods where $\geq 5$ patch types were exploited.

*Prediction 3: Higher encounter rates with profitable foods will result in increased selectivity.* The patch types exploited by members of each age-sex class, and by one individual male, were divided into two categories, "high-ranking" (top half) or "low-ranking," (bottom half) based on their profitability across all patches and seasons by $\mathrm{ME_O}$, $\mathrm{ME_H}$, or CP. This method was used to estimate in general how many "rich" versus "poor" patch types were available in a given season. Encounter rates with high-ranking foods were then correlated with the number of patch types (species and plant part) and food parts (plant part only) taken during seasonal time periods. For the latter condition, plant part categories included (1) deciduous and herbaceous leaves, (2) evergreen leaves, (3) dormant leaf buds, (4) fruit and seeds, (5) soft underground storage organs, (6) hard or woody underground storage organs, (7) bark, and (8) flowers. The classical prey model, in general, predicts a negative correlation between the abundance of (encounter rate with) high-ranking foods and the number of patch types or plant parts included in the diet. However, this prediction may not hold if comparisons are made across seasons that differ markedly in the number of food types available for consumption [as in the Himalaya, Sayers and Norconk et al. (2008)]. For this reason, data were also qualitatively inspected to see if low-ranking foods available over much of the year were taken only when encounter rates with high-ranking foods were low, as predicted by the model.

*Prediction 4: Selectivity is not dependent on encounter rates with low-ranking patch types.* The encounter rates with low-ranking patch types and high-ranking patch types were correlated with the percent of the diet made up of low-ranking foods by OM and time. The model predicts no correlation between abundance of low-ranking patch types and their dietary contribution, but a negative correlation between the encounter rates with high-ranking patch types and the percentage of the diet involving low-ranking foods.

*Comparison of nutritional currencies.* For each age-sex class, conformation of langur behavior to model predictions was examined under $ME_O$, $ME_H$, and CP. For each prediction, currencies were given a rank of 1–3, with 1 = closest to model predictions and 3 = furthest from model predictions. For all the predictions discussed below, situations where rankings differed based on quantification method (e.g., OM versus time estimates of dietary contribution) were classed as ties. When ties occurred, rankings for all three currencies equaled six when summed. In cases where langur behavior differed quantitatively from model predictions, under all three currencies, they were ranked as ties. Overall rankings of currencies were based on averages across all predictions for each age-sex class.

For the quantitative threshold for dropping items from the diet, the percentage of foods in the predicted optimal diet was compared for each season and currency. This was performed both with and without the inclusion of search costs. The currency that included the highest percentage of diet in the predicted optimal set by OM and time spent feeding was given a rank of 1.

For the prediction that animals will prefer profitable foods, the strength of correlation between preference and patch type profitability was examined for each currency. Preference was ascertained by annual correlations between dietary contribution, by both OM and time, and the profitability of patch types (average caloric or protein gain over time) based on each the three currencies. The currency yielding the strongest positive correlation between dietary contribution and profitability was given the rank of 1. When ties occurred for annual contribution, currencies were ranked for all seasons with $\geq 5$ feeding sessions and overall rankings were based on averages from this sample.

For the prediction that inclusion in the diet is independent of encounter rate, two measures were examined: (1) the strength of the predicted negative correlation between encounter rates with high-ranking patch types and dietary contribution (by OM and time) of low-ranking foods, and (2) the predicted noncorrelation between encounter rates with low-ranking foods and their dietary inclusion (again, by both OM and time). The currency with the strongest correspondence to these predictions was given a rank of 1, with the following stipulations: for both (1) and (2), discrepancies between OM and time estimates were again considered ties, and for the latter, currencies were considered ties if there was not a significant positive correlation among them. The rankings for both (1) and (2) were then averaged.

*Deviations from model assumptions.* To quantify season-specific deviations from assumptions, we identified certain patch types that were exploited in a manner somewhat incongruent with the scenario depicted by the model (Table 1) by a single adult male. Herbaceous vegetation was considered the most-likely patch type category to deviate from the “exclusivity of search and handling” assumption. At Langtang, multiple herb species were often interspersed on the ground, providing situations where foragers, while feeding on one species, could evaluate (or “search” for) others. Large patch types (i.e., all excepting shrubs, herbs, and climbers) were considered more likely to deviate from the random encounter assumption. Trees of favored species and potato fields, for example, were revisited and in some cases, especially the latter, their locations appeared to influence group travel paths. It is presumed here that animals are less likely to remember the specific locations of individual patches of smaller size, such as shrubs, herbs, or climbers (but see Menzel, 1991). The seasonal percentages of definite simultaneous encounters, where animals exploited $\geq 1$ food type more-or-less at the same time (see “definition of a patch,” above), were recorded. Greater numbers of patch types exploited in a season were viewed as rendering the “complete information” assumption more unlikely. The model assumes that animals have knowledge of variables such as the encounter rate with a given patch type or its profitability, but in reality foragers must acquire such information through experience before converging on a “steady state” pattern of behavior (Staddon, 1983, p. 156). Psychological work suggests that animals can better remember food characteristics when there are fewer of them; that is, when there is less “interference” (p. 262). In addition, the number of woody habitats exploited per season was noted, with the assumption that feeding within one habitat is more likely to approximate the assumption of a fine-grained environment than multiple habitats.

All statistical tests are two-tailed with $P < 0.05$ and were performed in SPSS 13.0, SPSS 16.0, and Sigmaplot.

## RESULTS

### Quantitative estimation of profitability threshold for dropping items from diet

An example of patch type ranking and profitability threshold calculation [from Eq. (1)] is given in Table 3 for a single adult male using kilocalories ($ME_O$) as currency. The model predicts that all exploited patch types should be above the $E_n/T$ threshold (i.e., on Table 3, all patch types would be in bold face). Langurs, including this adult male, consistently exploited patch types that were, on average, poorer than the calculated profitability threshold. Patch types with average profitability below the thresholds, however, were generally taken only in small amounts, with just a few exceptions. The primary exception involves the mature leaves of *Cotoneaster frigidus*, which in fall 1 drops the overall foraging efficiency to a third of the optimal diet. Over all age-sex classes, the monkeys included patch types beneath the profitability threshold in 23/24 (95.8%) applications of the model (considering only seasons where $n \geq 5$ feeding sessions), and this rate of failure was the same regardless of the nutritional currency used (Figs. 1–4). The predicted optimal diet differed based on currency used in 16/24 (66.7%) of model applications. Although $ME_O$ and $ME_H$ differed from one another in only 7/24 (29.2%) of cases,

*Table 3. Seasonal patch types, overall rate of gain [$E_n/T$, calculated from Eq. (1)], and dietary contribution (% organic matter [OM] and feeding time) for a single adult male*

| Season | Patch type | $E_n/T$ (kcal/min) | % of diet (OM) | % of diet (time) |
|---|---|---|---|---|
| Spring | ***Zanthoxylum nepalense* YL/FL** | **1.617** | **86.3** | **73.6** |
| | *Rosa macrophylla* YL | 1.565 | 11.5 | 17.9 |
| | *Cotoneaster frigidus* YL | 1.471 | 2.2 | 8.6 |
| Fall 1 | ***Solanum tuberosum* USO** | **15.356** | **85.5** | **21.8** |
| | *Caragana gerardiana* seed | 15.213 | 1.4 | 1.3 |
| | *Rumex nepalensis* HL | 14.648 | 2.3 | 2.9 |
| | *Cotoneaster frigidus* ML | 5.748 | 10.8 | 74.0 |
| Fall 2 | ***Solanum tuberosum* USO** | **19.418** | **73.8** | **45.0** |
| | *Clematis montana* ML | 18.739 | 6.6 | 6.5 |
| | *Rumex nepalensis* HL | 18.488 | 0.9 | 1.3 |
| | *Hippophae rhamnoides* ML | 16.573 | 6.5 | 10.6 |
| | *Elsholtzia fruticosa* FL | 15.745 | 3.1 | 5.7 |
| | *Caragana gerardiana* seed | 15.532 | 0.5 | 1.4 |
| | *Theropogon pallidus* HF | 15.405 | 0.4 | 0.9 |
| | *Raphanus sativus* HL | 15.297 | 0.2 | 0.7 |
| | *Malva* sp. HL | 12.385 | 7.5 | 24.1 |
| | Compositae HL | 12.321 | 0.2 | 0.7 |
| | *Fagopyrum esculentum* HL | 12.308 | 0.0 | 0.1 |
| | *Hippophae rhamnoides* UF | 12.052 | 0.2 | 2.3 |
| | *Cotoneaster frigidus* ML | 11.967 | 0.1 | 0.8 |
| Fall 4 | ***Hippophae rhamnoides* ML** | **3.173** | **9.1** | **2.7** |
| | ***Caragana gerardiana* seed** | **3.419** | **0.5** | **0.2** |
| | ***Sorbus cuspidata* RF** | **7.603** | **23.3** | **5.9** |
| | ***Solanum tuberosum* USO** | **8.281** | **44.1** | **45.4** |
| | *Cotoneaster frigidus* RF | 7.984 | 3.3 | 4.2 |
| | *Allium wallichii* HF | 7.957 | 0.2 | 0.4 |
| | *Cotoneaster frigidus* ML | 6.300 | 17.9 | 35.3 |
| | *Euphorbia* sp. RF | 6.190 | 1.2 | 3.3 |
| | *Cotoneaster acuminatus* RF | 6.143 | 0.3 | 1.1 |
| | *Berberis aristata* RF | 6.066 | 0.1 | 1.5 |
| Early winter | ***Hippophae rhamnoides* ML** | **3.783** | **55.0** | **22.5** |
| | ***Caragana gerardiana* seed** | **4.202** | **20.4** | **29.6** |
| | *Aconogonum molle* USO | 4.010 | 6.1 | 11.8 |
| | *Cotoneaster frigidus* RF | 3.734 | 14.1 | 22.9 |
| | *Cotoneaster frigidus* ML | 3.618 | 3.4 | 9.2 |
| | *Cotoneaster frigidus* LB | 3.530 | 0.9 | 4.1 |

Patch types listed in order of their profitability with kilocalories over time ($ME_O$) utilized as currency. $E_n/T$ shows the rate of gain if only that patch type and those of greater profitability were taken; patch types included in the predicted optimal diet for each season are given in bold face. Only seasons with $\geq$5 feeding sessions are shown. YL, young leaf; ML, mature leaf; HL, herb leaf; RF, ripe fruit; UF, unripe fruit; HF, herb fruit; LB, leaf bud; USO, underground storage organ.

the CP predicted diet differed from $ME_O$ and $ME_H$ in 16/24 (66.7%) and 14/24 (58.3%) of applications, respectively.

The diet of a single adult male, which resembles the pooled age-sex results, shows seasonal differences in the extent to which the model could account for observed feeding behavior (see Fig. 4). The model performed best in spring, where, under all three currencies, only one food type was predicted in the optimal diet. This item, consisting of clusters of *Zanthoxylum nepalense* young leaf and flowers (handled and ingested together), made up 86.3% of dietary OM and represented 73.6% of foraging time. For other seasons, however, the model failed to varying degrees based on the currency entered into Eq. (1) and/or the method used to quantify diet. Most strikingly, under both energetic and CP currencies, this male spent considerable amounts of time exploiting patch types not predicted in the optimal diet.

## More profitable patch types will be preferred

The model predicts a positive correlation between average patch profitability ($e_i/h_i$) and exploitation. For grouped age-sex classes (juveniles, adult females, and adult males), contribution of food types to annual diet by percentage OM was positively related to $ME_O$, $ME_H$, and CP profitability (Table 4). Conversely, annual percent feeding time was not significantly correlated with profitability with the exception of $ME_O$ in the adult male category. Seasonal contribution to diet by percentage OM was, in general, positively correlated with profitability under all three currencies. Significant positive seasonal relationships between feeding time and profitability, however, were the exception rather than the rule.

For the single adult male, annual OM contribution was positively related to profitability under all three currencies (Table 4). Correlation coefficients between annual feeding time and profitability were also positive, but not statistically significant. Within seasons, significant positive relationships were detected between OM contribution and $ME_O$ and/or $ME_H$ profitability. A significant positive relationship between feeding time and $ME_O$ or $ME_H$ profitability was apparent in two of three seasons. CP profitability was not significantly correlated with seasonal percentages by either OM or feeding time.

## Higher encounter rates with profitable foods will result in increased selectivity

Under the model, diet breadth is expected to decrease as food abundance increases. Contrary to expectations,

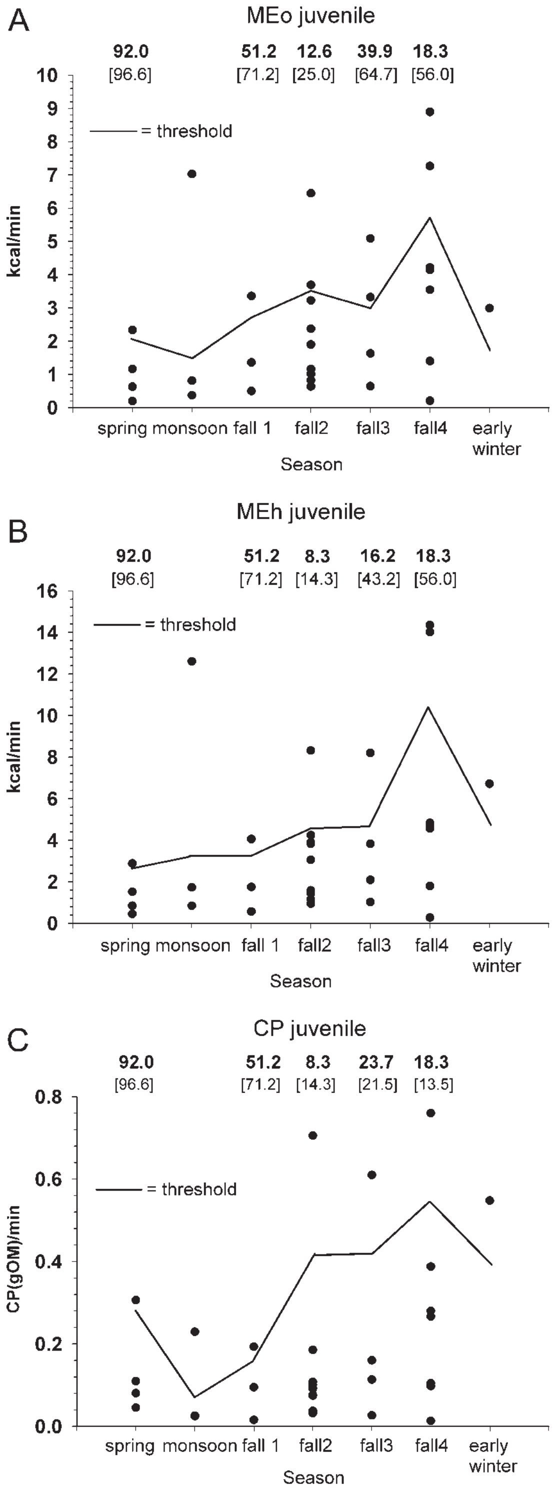

**Fig. 1.** The seasonal mean profitability of patch types exploited (data points) and calculated $E_n/T$ threshold for inclusion in diet (line) for juveniles under three different nutritional currencies. For all seasons with $n \geq 5$ feeding sessions, the percentage of feeding time spent on foods in the predicted set (above the threshold) is given at the top of the figure, with the percentage organic matter (OM) of diet above the threshold in brackets. 1A, zero-fermentation metabolizable energy (MEo) as currency; 1B, high-fermentation metabolizable energy (MEh) as currency; 1C, crude protein (CP) as currency.

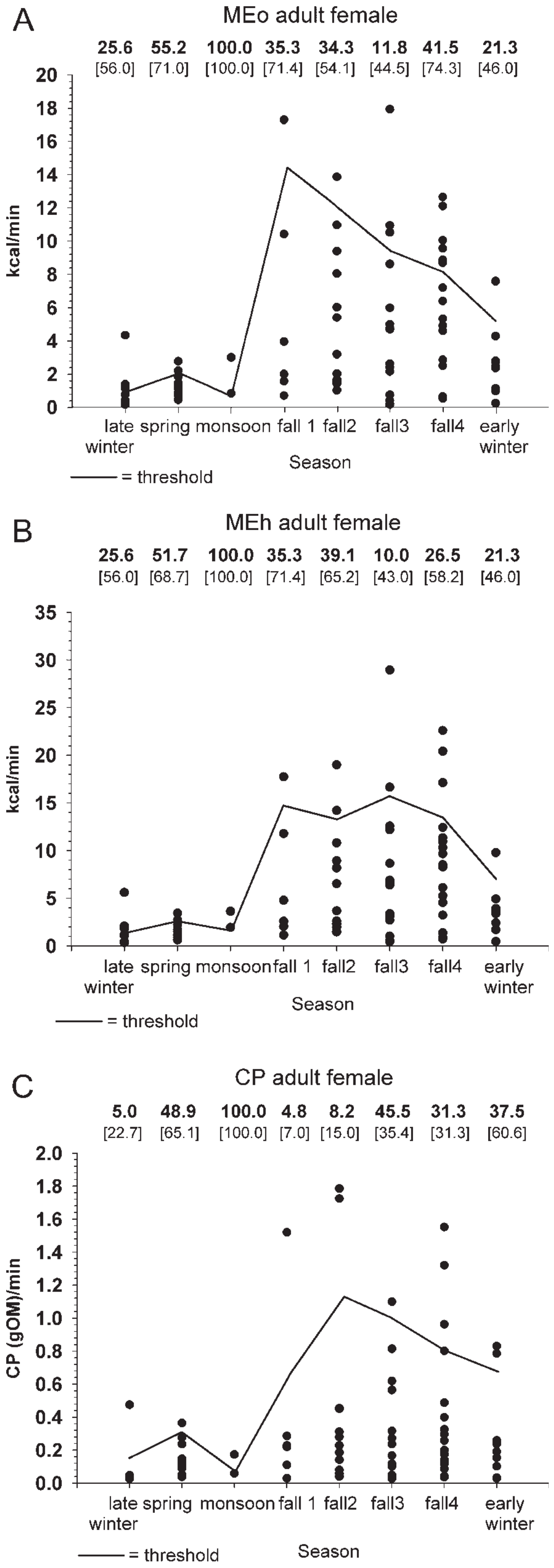

**Fig. 2.** The seasonal mean profitability of patch types exploited and calculated $E_n/T$ threshold for inclusion in diet for adult females under three different nutritional currencies. The notation and description are as in Figure 1.

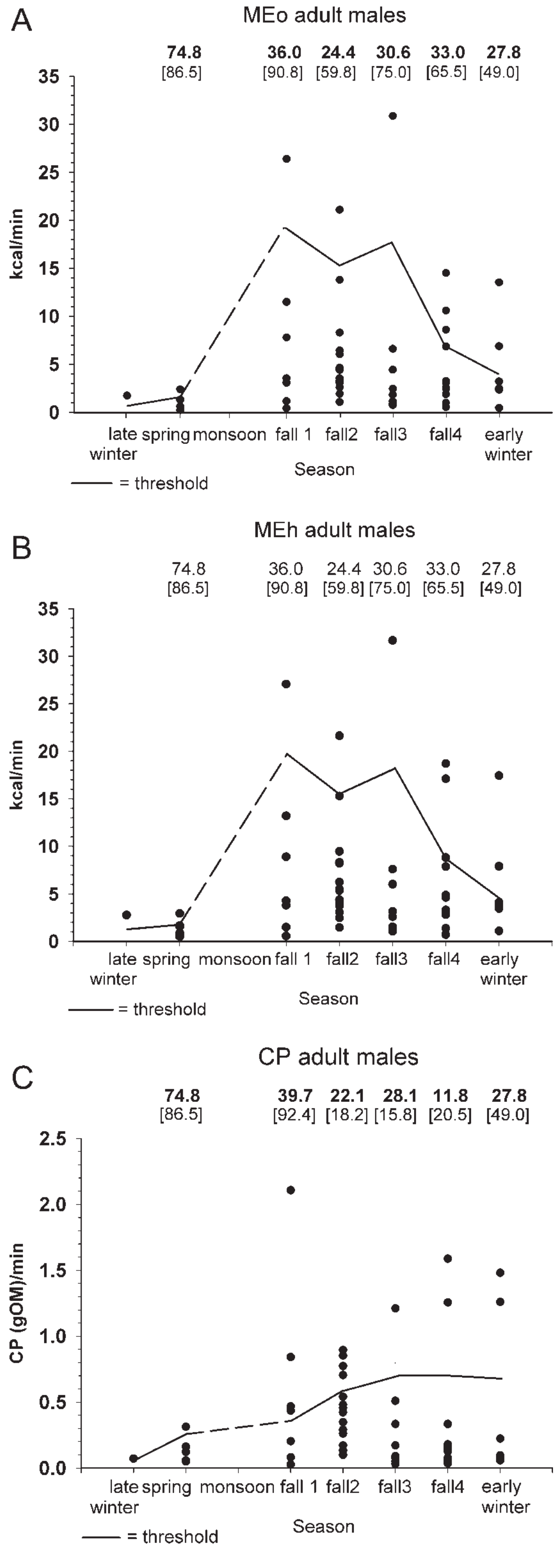

**Fig. 3.** The seasonal mean profitability of patch types exploited and calculated $E_n/T$ threshold for inclusion in diet for adult males under three different nutritional currencies. The notation and description are as in Figure 1.

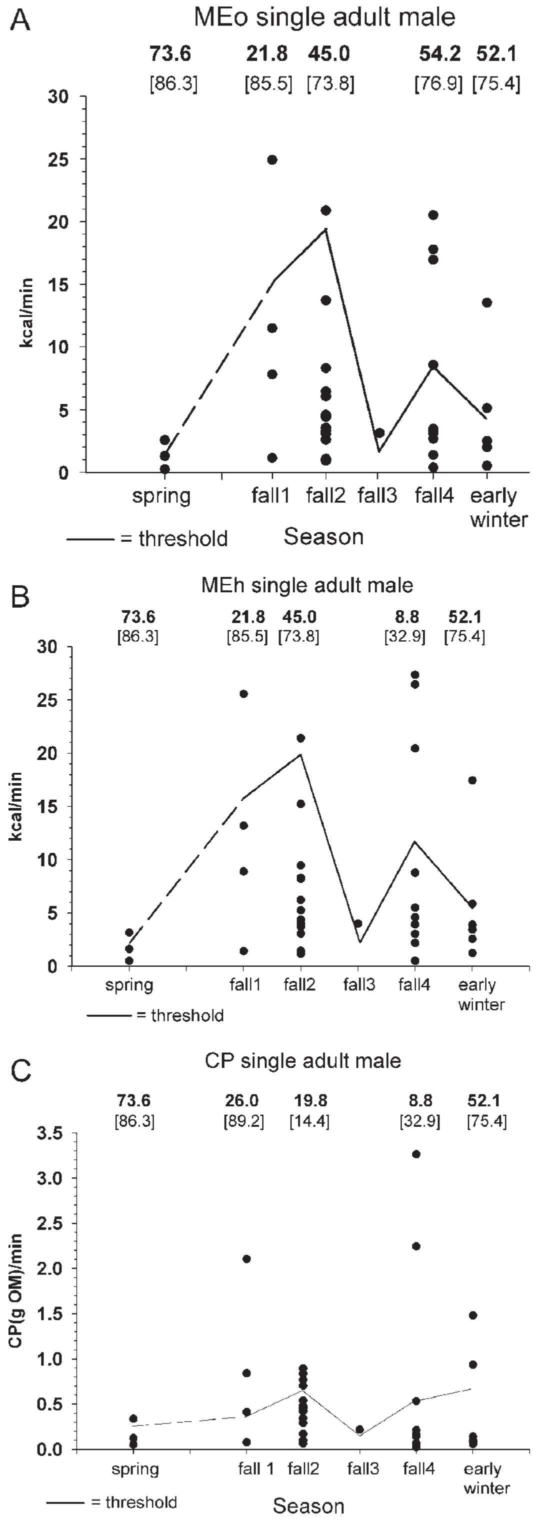

**Fig. 4.** The seasonal mean profitability of patch types exploited and calculated $E_n/T$ threshold for inclusion in diet for a single adult male under three different nutritional currencies. The notation and description are as in Figure 1.

neither the number of patch types nor plant parts exploited by grouped age-sex classes or a single adult male were significantly related to seasonal encounter rates of high ranking foods under any currency (Table 5). This is likely related to the fact that many profitable foods were available simultaneously in the fall seasons,

*Table 4. Spearman rank order correlation coefficients between contribution to diet of patch types (by % organic matter [OM] or % feeding time) and patch type profitability by age-sex class and season*

| | | % OM | | | % Time | | |
|---|---|---|---|---|---|---|---|
| | $n$ | $\mathrm{ME_O}$ | $\mathrm{ME_H}$ | CP | $\mathrm{ME_O}$ | $\mathrm{ME_H}$ | CP |
| JJ | | | | | | | |
| Annual | 23 | 0.77** | 0.72** | 0.67** | 0.35 | 0.27 | 0.37 |
| Fall 2 | 9 | 0.85** | 0.85** | 0.88** | 0.48 | 0.48 | 0.82** |
| Fall 4 | 7 | 0.96** | 0.96** | 0.43 | −0.07 | −0.07 | −0.14 |
| ♀♀ | | | | | | | |
| Annual | 47 | 0.51** | 0.54** | 0.49** | −0.06 | −0.06 | 0.00 |
| Late winter | 7 | 0.21 | 0.25 | 0.50 | −0.68 | −0.64 | −0.21 |
| Spring | 11 | 0.56 | 0.62* | 0.67* | 0.36 | 0.36 | 0.54 |
| Fall 1 | 6 | 0.89* | 0.89* | 0.77 | 0.26 | 0.26 | −0.03 |
| Fall 2 | 12 | 0.83** | 0.83** | 0.49 | 0.69* | 0.64* | 0.29 |
| Fall 3 | 14 | 0.69** | 0.66** | 0.75** | −0.10 | −0.22 | −0.01 |
| Fall 4 | 17 | 0.51* | 0.57* | 0.67** | −0.03 | −0.01 | 0.25 |
| Early winter | 9 | 0.50 | 0.57 | 0.63 | 0.27 | 0.30 | 0.45 |
| ♂♂ | | | | | | | |
| Annual | 30 | 0.64** | 0.63** | 0.47** | 0.36* | 0.35 | 0.20 |
| Spring | 6 | 1.00** | 0.94** | 0.83* | 1.00** | 0.94** | 0.83* |
| Fall 1 | 7 | 0.50 | 0.50 | −0.04 | −0.25 | −0.25 | −0.75 |
| Fall 2 | 14 | 0.49 | 0.42 | 0.08 | 0.24 | 0.14 | −0.02 |
| Fall 3 | 8 | 0.81* | 0.81* | 0.79* | 0.62 | 0.62 | 0.60 |
| Fall 4 | 11 | 0.66* | 0.70* | 0.61* | −0.01 | 0.02 | 0.04 |
| Early winter | 6 | 0.77 | 0.83* | 0.77 | 0.49 | 0.60 | 0.54 |
| ♂ | | | | | | | |
| Annual | 24 | 0.66** | 0.70** | 0.53** | 0.33 | 0.36 | 0.27 |
| Fall 2 | 13 | 0.78** | 0.73** | 0.46 | 0.59* | 0.53 | 0.24 |
| Fall 4 | 10 | 0.55 | 0.64* | 0.39 | 0.08 | 0.20 | −0.07 |
| Early winter | 6 | 0.94** | 1.00** | 0.71 | 0.71 | 0.83* | 0.49 |

Only seasons where ≥5 food types were taken are shown. JJ, all juveniles; ♀♀, all females; ♂♂, all adult males; ♂, one adult male; $\mathrm{ME_O}$, zero-fermentation metabolizable energy; $\mathrm{ME_H}$, high-fermentation metabolizable energy; CP, crude protein.
* , significant at the 0.05 level; ** , significant at the 0.01 level.

while in the winter and spring seasons there were fewer food types of any kind available (Sayers and Norconk, 2008).

Nevertheless, qualitative inspection of data from all age-sex classes (Appendix section) and nonseasonal foods suggests that this prediction was partially supported when food availability is considered. Certain food items that were considered of low profitability under all currencies, such as *Gaultheria* evergreen mature leaves and petioles and *Elsholtzia fruticosa* woody roots, were available throughout the year but taken almost exclusively when encounter rates with high-ranking foods were lowest (late winter).

### Selectivity is not dependent on encounter rates with low-ranking patch types

The model predicts no correlation between encounter rates with low-ranking patch types and their inclusion in the diet. In addition, it predicts a negative correlation between encounter rates with high-ranking foods and the proportion of the diet consisting of low-ranking foods. For grouped data, juvenile foraging behavior most clearly ran counter to model predictions (Table 6). Encounter rates with low-ranking foods were positively related to feeding time on low-ranking foods irrespective of currency, and encounter rates with high-ranking foods did not show a significant negative correlation with the contribution of low-ranking foods by either OM or time. In fact, for juveniles, encounter rates with high-ranking foods were less-closely related to dietary contribution than low-ranking foods.

The behavior of adult females was consistent with the model under $\mathrm{ME_O}$ (Table 6). Using this currency, encounter rates with low-ranking foods were not significantly related to the dietary contribution of low-ranking foods, whereas the encounter rates with high-ranking foods showed a strong positive relation to the contribution of high-ranking foods by both OM and time. For adult males, similar agreement with the model was detected under both $\mathrm{ME_O}$ and $\mathrm{ME_H}$. For both adult sexes in the pooled data set, the utilization of CP as currency provided slightly weaker conformation to model predictions, as low-ranking foods as described by this currency were taken in closer proportion to their encounter rates.

Results from a single adult male were generally consistent with the model (Table 6). Seasonal encounter rate with low-ranking foods, under all three currencies, was not significantly related to percent contribution of low-ranking foods. Also as predicted, a significant negative relationship was detected between encounter rate with high-ranking foods (under both $\mathrm{ME_O}$ and CP) and OM contribution of low-ranking foods. Correlation coefficients concerning encounter rates of high-ranking foods and percentage of time feeding on low-ranking foods were negative but not statistically significant.

### Comparison of nutritional currencies

Data from grouped age-sex classes and a single adult male most closely approximated classical prey model predictions using $\mathrm{ME_O}$ as currency (Table 7). However, for the "threshold" prediction, search costs were only included in the models for $\mathrm{ME_O}$ and $\mathrm{ME_H}$, and increasing search costs can result in a broader predicted diet (Lifjeld and Slagsvold, 1988). When search costs were removed, CP resulted in greatest conformation for pooled adult females, and $\mathrm{ME_O}$ for juveniles, pooled adult males, and a single adult male.

### Deviations from model assumptions

All age-sex classes engaged in foraging behavior that likely resulted in deviations from model assumptions, e.g., 78 of 402 patches (19.4%) involved definite simultaneous encounters. Recall that the model predicts the behavior of a forager encountering patches sequentially (Table 1). For a single adult male, the lowest degree of deviation from model assumptions occurred in spring, and this was also the season in which the model was most successful in predicting diet (Table 8).

## DISCUSSION

A likely reason that few primatologists have used OFT is that the assumptions and variables of its models have been questioned. Although these critiques in some cases possess merit, we argue that the drawbacks have been greatly exaggerated (Table 9). Although the classical prey model, for example, sidesteps a number of relevant parameters, such as the effects of variance and feeding

*Table 5. Spearman rank order correlation coefficients between seasonal encounter rates with high-ranking patch types ($\lambda_{high}$) under three currencies and the number of food types or plant parts included in the diet*

| | $\lambda_{high}$ | | | | $\lambda_{high}$ | | | | $\lambda_{high}$ | | | | $\lambda_{high}$ | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | JJ | ME$_O$ | ME$_H$ | CP | ♀♀ | ME$_O$ | ME$_H$ | CP | ♂♂ | ME$_O$ | ME$_H$ | CP | ♂ | ME$_O$ | ME$_H$ | CP |
| Food types | $n = 5$ | 0.31 | 0.31 | −0.15 | $n = 8$ | 0.17 | 0.17 | 0.17 | $n = 6$ | 0.75 | 0.75 | 0.75 | $n = 5$ | 0.70 | 0.70 | 0.10 |
| Plant parts | | −0.26 | −0.26 | 0.37 | | −0.16 | −0.17 | −0.16 | | 0.29 | 0.29 | 0.10 | | 0.53 | 0.53 | −0.16 |

Shown are all seasons with ≥5 feeding sessions for that age sex-class; sample size reflects number of seasons that meet this criteria.

*Table 6. Spearman rank order correlation coefficients between seasonal encounter rates with high or low-ranking patch types under three currencies and proportion of organic matter (OM) and feeding (time) devoted to low-ranking patch types*

| | $\lambda_{high}$ | | | $\lambda_{low}$ | | |
|---|---|---|---|---|---|---|
| | ME$_O$ | ME$_H$ | CP | ME$_O$ | ME$_H$ | CP |
| JJ ($n = 5$) | | | | | | |
| % low OM | −0.20 | −0.20 | −0.20 | 0.60 | 0.60 | 0.80 |
| % low time | −0.20 | −0.20 | −0.70 | 0.90* | 0.90* | 1.00** |
| % high OM | 0.20 | 0.20 | 0.20 | −0.60 | −0.60 | −0.80 |
| % high time | 0.20 | 0.20 | 0.70 | −0.90* | −0.90* | −1.00** |
| ♀♀ ($n = 8$) | | | | | | |
| % low OM | −0.79* | −0.69 | −0.79* | 0.43 | 0.76* | 0.76* |
| % low time | −0.83* | −0.52 | −0.79* | 0.10 | 0.62 | 0.62 |
| % high OM | 0.79* | 0.69 | 0.79* | −0.43 | −0.76* | −0.76* |
| % high time | 0.83* | 0.52 | 0.79* | −0.10 | −0.62 | −0.62 |
| ♂♂ ($n = 6$) | | | | | | |
| % low OM | −0.83* | −0.83* | −0.89* | 0.14 | 0.20 | 0.71 |
| % low time | −0.94** | −0.94** | −0.54 | 0.26 | 0.43 | 0.94** |
| % high OM | 0.83* | 0.83* | 0.89* | −0.14 | −0.20 | −0.71 |
| % high time | 0.94* | 0.94* | 0.54 | −0.26 | −0.43 | −0.94** |
| ♂ ($n = 5$) | | | | | | |
| % low OM | −1.00** | −0.70 | −0.90** | 0.00 | 0.30 | −0.70 |
| % low time | −0.70 | −0.30 | −0.70 | 0.30 | 0.70 | −0.10 |
| % high OM | 1.00** | 0.70 | 0.90* | 0.00 | −0.30 | 0.70 |
| % high time | 0.70 | 0.30 | 0.70 | −0.30 | −0.70 | 0.10 |

* significant at the 0.05 level.
** significant at the 0.01 level.

competition, it touches on the primary ones and could add significantly to our knowledge of primate feeding behavior. For example, a wealth of studies have demonstrated the influence of travel time (search time) between food items or patches on the decisions animals make in regards to what foods to eat and when to leave a given patch [reviewed in Nonacs (2001) and Sih and Christensen (2001)]. Yet this seemingly critical variable, a staple of even the most basic OFT models, has only rarely been addressed in primate feeding studies (e.g., Rapaport, 1995, 1998; interpatch distance, Suarez, 2006). In an extensive review of tests, it has been noted that predictions from the classical prey and other optimal diet models are most often upheld in foragers that feed on immobile prey (e.g., fruit and leaves), a category which would accommodate the diets of many primates. In addition, the model appears to be fairly robust and often withstands violations of some of its assumptions (Sih and Christensen, 2001). All models are by definition abstractions of nature, and simpler and more generalized models can gain in power what they lack in precision.

Although Himalayan langurs generally exploited patch types not predicted by the classical prey model, in most cases these were rare foods taken only sporadically within a season. For example, *Cotoneaster frigidus* leaf buds were sometimes consumed in the fall, but not on every occasion when foragers entered a tree of this species. In this respect, such foods represent partial preferences. These are deviations from the zero-one rule, which states that foods should always be taken or never be taken when they are encountered, as long as environmental conditions remain constant (Stephens and Krebs, 1986). Partial preferences have been observed in almost all tests of the model, both in laboratory and field (Sih and Christensen, 2001). There are a number of reasons for partial preferences, several of which are relevant to this study (Table 10). Most of the patch types that were exploited, but not predicted, were relatively rare foods whose consumption could hypothetically be explained as, for example, cases of patch sampling or the obtaining of rare nutrients.

Several foods taken beneath the threshold, however, were not merely "partial preferences," but were routinely and consistently exploited. The most striking example involves the mature leaves of *Cotoneaster frigidus*, an abundant woody plant. This was ranked first or second by annual feeding time for all age-sex classes, and in scan samples taken concurrently represented the highest percentage of feeding records over an annual cycle (Sayers and Norconk, 2008). In no case was this resource predicted to be a part of the optimal diet for any age-sex class, season, or currency. One possibility is that our nutritional sample is not representative of the average quality of *Cotoneaster frigidus*, or that some other quality associated with this food type renders it a preferred item. It is also likely that Himalayan langurs perceive their environment as poorer than suggested by the calculations used in this study; that is, in the context of the model, the "thresholds" should be lower than those depicted on Figures 1–4. For example, increasing search costs result in a broader predicted diet, and it is likely that the general equation used here (Taylor et al., 1982) underestimates them. The Himalayan environment is characterized by extreme changes in topography, whereas the langurs must negotiate during travel and which makes movement more costly than would be expected in flatter terrain (Sprague, 2000). In a similar vein, underestimates of search time or overestimates of the encounter rates with high-ranking foods would also result in a narrower predicted diet than actually would be observed (Kaplan and Hill, 1992; Winterhalder et al., 1988). It is in this regard that nonrandom encounter could cause violations from model predictions. Revisiting patches will result in an exaggerated estimate of encounter rates and, if it is a high-ranking food, could result in an overly narrow predicted diet breadth. Potato fields, for example, were revisited in the fall months. It is also important to point out that when variation in patch profitability is low, the costs of moderate deviation from the predicted optimal diet may be minor, although that was not the case with some nonpredicted patch types considered here, such as *Cotoneaster frigidus*.

*Table 7. Comparison of results from the three currencies ($ME_O$, $ME_H$, and CP) utilized here in relation to the classical prey model*

| | JJ | | | ♀♀ | | | ♂♂ | | | ♂ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $ME_O$ | $ME_H$ | CP | $ME_O$ | $ME_H$ | CP | $ME_O$ | $ME_H$ | CP | $ME_O$ | $ME_H$ | CP |
| Threshold | 1 | 2.5 | 2.5 | 1 | 2 | 3 | 1.5 | 1.5 | 3 | 1 | 2.5 | 2.5 |
| Profitability | – | – | – | 2.5 | 2.5 | 1 | 1 | 2 | 3 | 2 | 1 | 3 |
| Increased selectivity | – | – | – | – | – | – | – | – | – | – | – | – |
| Independence | – | – | – | 1.5 | 3 | 1.5 | – | – | – | 1.5 | 3 | 1.5 |
| Overall | ✓ | | | ✓ | | * | ✓ | | | ✓ | | |

1, closest to model predictions and 3, furthest from model predictions. Blank cells represent ties across all currencies and check-marks (✓) indicate the currency to which the model best conforms over all predictions. An asterisk (*) indicates the currency, if different from above, that conformed best to model predictions when search costs were removed from $ME_O$ and $ME_H$ threshold calculations.

*Table 8. Seasonal comparisons of likely deviation and compliance with model assumptions compared with success of the model in predicting diet for a single adult male*

| Assumption | Measure of deviation | Spring | Fall 1 | Fall 2 | Fall 4 | Early winter |
|---|---|---|---|---|---|---|
| Search and handling mutually exclusive | % herb | 0 | 25.0 | 40.0 | 3.8 | 0 |
| Sequential encounter | % simultaneous | 0 | 25.0 | 80.0 | 15.4 | 22.2 |
| Random encounter | % trees and cultivated fields[a] | 14.3 | 62.5 | 40.0 | 80.8 | 66.7 |
| Complete information | # food types | 3 | 4 | 13 | 10 | 6 |
| Homogeneous, fine-grained environment | # woody habitat types | 1 | 2 | 1 | 2 | 2 |
| Least deviation from model assumptions | | ✓ | | | | |
| Highest percentage of diet predicted | | ✓ | | | | |

[a] In other words, large patch types, which do not include herbaceous plants, shrubs, or climbers. Justification in text.

Other predictions of the model were generally qualitatively or quantitatively upheld. Strong positive correlations were detected between patch type profitability and OM contribution to diet, whereas correlations between profitability and feeding time were generally positive but weaker. This suggests that "profitability" as defined in the classical prey model—but not necessarily as perceived by the animals—is driven largely by intake rate, at least with regards to the Himalayan langur data set (see also Schulke et al., 2006). Foods of low profitability that were available over the entire year were generally taken only when encounter rates with profitable patch types were lowest. With the exception of juveniles, high-ranking foods were taken in close relation to their abundance, while low-ranking foods were not. The deviation of juveniles in this respect may be related to dominance effects, whereas high-ranking patches are disproportionately unavailable to them, or simply reflect that they are in a process of learning to forage efficiently (Pulliam, 1981).

In general, langur behavior was closest to that predicted by the model using a standard energetic currency ($ME_O$), although CP performed slightly better for grouped adult females when search costs were removed. These findings run counter to some of the colobine literature, which argues for the primacy of CP in colobine food selection. Wasserman and Chapman (2003), for example, found no correlation between the energy content of food and foraging effort, and a positive relationship between protein-to-fiber content and foraging effort, in red colobus (*Procolobus badius*) and guerezas (*Colobus guereza*) at Kibale, Uganda. In addition, they found that estimates of energy consumption were higher than estimates of expenditure for these monkeys and suggested that energy was of minor importance. Although this certainly may be the case, we do not accept their conclusion that these results demonstrate "the importance of protein over other nutritional characters" (p. 657) or eliminate energetic considerations altogether. Our reasons include (1) Wasserman and Chapman looked only at the protein-to-fiber ratio, not CP alone, (2) in their calculations of energy consumption, intake rates for plant parts were not estimated directly, but taken from studies of howler monkeys, (3) they assumed that surplus energy is unnecessary, an unlikely scenario in a stochastic environment (Stephens and Krebs, 1986), and (4) in any event, they provided no evidence to suggest that CP is a limiting variable (Oftedal et al., 1991). Although protein is generally positively related, and dietary fiber negatively related, to food selection in colobines, it is still an open question as to the relative importance of each of these variables. Fewer studies still have examined calories or intake rate, again making it difficult to ascertain their general importance to colobine food selection. In this study, the predicted protein-maximizing and energy-maximizing diets generally (67% of applications) either differed only by one patch type, or were identical.

Contrary to expectations, metabolizable energy with a correction for fermentation ($ME_H$) did not unilaterally outperform the energetic currency without this correction ($ME_O$). Undoubtedly, being able to ferment higher amounts of fiber than other primates influences colobine food choice, and leaves (stereotypically a high-fiber food) make up a significant proportion of the diet at most study sites (Kirkpatrick, 1999). Nonetheless, colobines have consistently shown a preference for lower-fiber over higher fiber leaves (Davies et al., 1988; Fashing et al., 2007). One interpretation of this is that fiber exerts a "sliding scale" on colobine food preference. At low levels, fiber may be nearly completely digested, while at high levels fiber will subtract from food value either through incomplete digestion, an increase in gut retention time, or the overproduction of volatile fatty acids which could alter fore-stomach pH (Lambert, 1998). Unfortunately, few data currently exist to test this hypothesis or to

*Table 9. Criticisms of classical OFT models*

| Criticism | Explanation | Comments |
|---|---|---|
| Primate diets are too complex from a nutritional standpoint to be accounted for by maximizing one variable such as energy or protein (Glander, 1981, p. 157–158; Milton, 1979; Richard, 1985). | Many animals face the problem of balancing critical nutrients, toxins and digestion inhibitors, rendering classical OFT models inapplicable. | In many cases, one variable may be sufficient to describe the general feeding patterns of a given animal.[a] Some primates may be able to detoxify certain compounds or simply avoid plants containing them (Waterman and Kool, 1994). At a reductionist level, toxins or digestion inhibitors could simply be subtracted from overall food value, e.g., total energy yield minus the energy expended in detoxification or digestion (see Newman, 2007). |
| Classical OFT models assume a "fine-grained environment" where resources are evenly distributed and encountered in proportion to their abundance in the environment. This in unlikely in most primate habitats (Post, 1984). | Many animals actually inhabit a "coarse-grained environment" where the encounter rate with a given resource changes as they enter different parts of their range. | If sample sizes allow, OFT models such as the classical prey model can be applied separately to different parts of the environment that have variable resource abundances (Stephens and Krebs, 1986). Little evidence exists to suggest that primates deviate from this assumption more than other vertebrates to which OFT models have been applied. |
| Maximization models fall prey to a "fast-food fallacy," predicting "diets that are quickly consumed but well below the animal's consumption capacity for foods and their components, including energy" (Altmann, 1998, p. 157–158). | Altmann (1998) illustrates with the hypothetical example of an animal that has met its nutrient requirements for the day and then feeds on the most profitable food type until it can no longer be eaten (e.g., it is rare in the environment). Would not a rate-maximizing forager then refuse to feed on the second-most-profitable food, as this would lower average intake rate? | In the classical prey model, the decision variable is whether or not to exploit a food type when encountered. It does not predict time spent feeding; it is generally assumed that animals will forage when they are hungry. In the hypothetical example, the encounter rate with the most profitable food type is low or has dropped to zero, and the diet would be predicted to include or expand to include the second-most-profitable food type.[b] |
| Classical OFT models are simplistic and do not account for all of the variables that influence feeding behavior (see Janson and Vogel, 2006). | Variance in prey quantity or quality, hunger, predator avoidance, feeding competition, etc. are not considered in classical OFT models (Mangel and Clark, 1988; Houston and McNamara, 1999; Caraco, 1981; Clark and Mangel, 2000; Giraldeau and Caraco, 2000). | Simple modifications on the classical OFT models address some of these shortcomings. Nonetheless, the simpler the biological model, and the more easily it can be applied across taxa, the more heuristic value it garners (Stephens et al., 2007). |

[a] For example, energy shortfall as yearlings was found to account for 96% of variability in fecundity and 81% in reproductive success for yellow baboon (*Papio cynocephalus*) females (Altmann, 1998). Although it is possible that energy alone would make a reasonable currency for maximization in yellow baboons, Altmann does not make this contention. Also, maximizing one nutrient may maximize many if they are correlated between food types (Glander, 1981; Stephens and Krebs, 1986).

[b] The fast-food fallacy is a valid objection within models which assume that an animal can cease foraging as long as its minimum requirements for the day are met. This is not an assumption of the classical prey model. In addition, OFT applications generally examine many foraging decisions simultaneously (maximizing long-term intake rate), again a scenario to which the fast-food fallacy does not apply (Altmann, 1998; Stephens and Krebs, 1986).

develop a more specific energetic currency for colobine monkeys that includes variables such as item-specific assimilation (National Research Council, 2003). Elucidating such factors should be one long-term goal for applications of OFT to primates.

Schoener (1987) noted several potential problems for applying the classical prey model to patch choice, as performed here. One potential problem is that patches (such as trees in this study) are less likely to be encountered randomly than individual prey items (such as a solitary grasshopper) and can result in departure from model predictions. Another is that patches can be depleted and a forager may alter the profitability of a patch while exploiting it. In this study, all patch types were assigned a mean value with no account taken of decreases in intake rate over time (patch depression). In other words, the patch type approach is more likely to result in deviations from the assumptions of the prey model than the standard usage, but modifications can be incorporated in situations where patch depression is found to be important (Stephens and Krebs, 1986).

In a wide-ranging review, Sih and Christensen (2001) noted that the classical prey model has proven to be quite robust (even in patch choice applications) and often withstands deviations from the assumptions of the model. In this study, however, the model performed best in spring, when fewer of these assumptions were violated and the animals were "playing the same game as the model" (Stephens and Krebs, 1986, p. 204). Future applications of OFT to nonhuman primates should also attempt to determine which assumptions are being violated and its effects on model performance. The results given here suggest that such violations should be examined, but need not discourage primatologists from utilizing this powerful body of theory.

*Table 10. Potential causes of partial preferences, with application to the present study*

| Cause of partial preferences | Description | Relevance to present study, and other notes |
|---|---|---|
| Discrimination errors (Krebs and McCleery, 1984) | Different food types may be confused by the forager. Also, the extent to which the taxonomy of food types used by researchers (e.g., biological species and plant part) corresponds to that used by the subjects is little known (see Menzel, 1997). | In late winter at Langtang, deciduous plants are largely or completely devoid of leaves, and discriminating between certain types of bark or woody roots may be difficult. The same may apply to plant parts of differing species within the same genera. However, this is not likely to be a major cause of partial preferences, and studies have shown that primates' knowledge of their habitat can be substantial (Janson and Byrne, 2007; Menzel, 1991, 1997). |
| Long-term learning (Krebs and McCleery, 1984) | Accurate estimate of model variables may only be possible after many days of exposure to similar conditions. | In highly seasonal habitats such as Langtang, conditions may change so rapidly that estimates of patch type abundance or quality are one-step behind the environment, in a cognitive analogue of the "Red Queen's hypothesis" (see Kamil, 1983; Van Valen, 1973). |
| Inherent variation in the animal (Krebs and McCleery, 1984) | Changes in the internal clock of a forager may cause deviations from model predictions. | Unknown |
| Runs of bad luck (Krebs and McCleery, 1984) | If the animal uses a short-term rule to determine encounter rates, habitat quality may be underestimated after repeated exposure to unprofitable foods. | Unknown |
| Simultaneous encounters (Engen and Stenseth, 1984; Krebs and McCleery, 1984) | Food items or patches are encountered at the same time rather than sequentially. | A minimum of 19.4% of Himalayan langur feeding sessions involved undoubted simultaneous encounters.[a] The model performed best in spring, when the lowest percentage of simultaneous encounters was recorded. |
| Averaging across individuals (Krebs and McCleery, 1984) | Model is designed to predict the behavior of a single individual. | While likely a major reason for partial preferences in the pooled age-sex categories, partial preferences were also noted for a single adult male. |
| Nutritional requirements and anti-feedant avoidance (Westoby, 1978) | Animal may take variable amounts of foods with low e/h that are high in certain macronutrients or minerals, or take only limited amounts of foods with qualitative or quantitative plant defenses (e.g., Fashing et al., 2007). | In most cases, no simple nutritional rationale has yet been found for those variables for which we have data, including crude protein, free simple sugars, lipids, fiber fractions, and condensed and hydrolizable tannins. It has been noted that high-starch diets fed to captive primates, in particular foregut fermenters like colobines, can lead to excessive fermentation, stomach problems, and in extreme cases even death (National Research Council, 2003). This may be a possible explanation for the expansion of the diet beyond potatoes in the fall applications, when this resource was in many cases the only patch type predicted.[b] Although mineral analyses have not yet been completed, the langurs were observed licking rocks, possibly for sodium (Sayers and Norconk, 2008). |
| Differential predation danger associated with differing patch types (Brown and Kotler, 2007) | A patch with highly profitable food may be underexploited if a forager is more exposed to predators while feeding in it. | While feeding in potato fields, Himalayan langurs were exposed to potential aerial predators and also to local farmers wielding sling-shots and stones (Brown and Kotler, 2007). |

*Table 10. (Continued)*

| Cause of partial preferences | Description | Relevance to present study, and other notes |
|---|---|---|
| Sampling (Lima, 1984) | Foragers may take small amounts of foods to gain information about them, which is a deviation from the "complete information" assumption.[c] | Himalayan langurs were observed taste-testing *Sorbus cuspidata* fruit before acceptance or rejection.[d] |
| Local but not global omniscience (Berec and Křivan, 2000) | The classical prey model presumes that animals are "globally omniscient," and know encounter rates with food items or patches within the entire area that they range in for the period the model is applied. In models where it is assumed that foragers are limited to knowledge within the range of their perception, partial preferences are predicted. | Nonhuman primates likely possess knowledge between the extremes of global and local omniscience (Tomasello and Call, 1997). In what manner primates estimate encounter rates with food patches (abundance) is little known. |

[a] The actual percentage may exceed this, as any situation in which two patches are detected at the same time (e.g., visually identifying a nearby and distant shrub of differing species) can be considered simultaneous encounters.

[b] However, the large quantities of potatoes taken suggest that the effects of starch are limited for gray langurs, at least over a 2-month period.

[c] Such sampling, whether by taste, touch, prolonged visual inspection or smell, has been observed in other primates (*Alouatta palliata*, Glander, 1981; Dominy et al., 2001; *Ateles geoffroyi* and *Saimiri sciureus*, Laska et al., 2007; *Pithecia pithecia*, Norconk, personal observation) and may be especially important in situations where nutritional quality of a "food type" varies spatially or temporally between plants of the same species or even within a single plant (Houle et al., 2007).

[d] Patch sampling is also a possible explanation for rare foods that appear to have little nutritional value. This point should be considered carefully in putative cases of primate medicinal plant use.

Even simple models may have relevance to nonhuman primate foraging behavior (Barton and Whiten, 1994). Although students of primate diet argue for approaches of greater and greater complexity (Felton et al., 2009), it is possible, and perhaps likely, that quantifying only several key variables from foraging theory (e.g., energy or protein gain, handling time, and travel time) would be sufficient to explain much of the variance in primate feeding behavior. In this study, the classical prey model was applied to seasonal time periods from weeks to months in length, and it is probable that at study sites where a single individual could be followed for entire days, the model could be doubly informative. Given the temporal and spatial heterogeneity of primate habitats, we would suggest applying the model freshly on a weekly or even daily basis to individual primates and habitat types if sample sizes allow. Although not applied here, recent game-theory applications attempting to predict the behavior of social foragers appear to be especially relevant to group-living primates and hopefully will generate enthusiasm among primate researchers (Giraldeau and Caraco, 2000; di Bitetti and Janson, 2001). Unfortunately, there are no social models as general as those from classical foraging theory, at least pertaining to diet choice. To date, the classical prey model has proven to be informative in animals as diverse as invertebrates and human hunter-gatherers (Stephens and Krebs, 1986; Sih and Christensen, 2001), and it is hoped that this study will encourage further applications of patch choice and exploitation models to other primates.

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## APPENDIX

Variables used in Eq. (1) to estimate the profitability threshold for dropping items from the diet, arranged by season, age-sex classification, and plant part. Encounter rates ($\lambda_i$) are given in patches ($n$) per second of search time (search time = total estimated travel time between patches for the sample). Handling times ($h_i$) are given in seconds. For the three alternative currencies, zero-fermentation metabolizable energy ($\mathrm{ME_O}$) and high-fermentation metabolizable energy ($ME_H$) are given in kilocalories and crude protein (CP) in grams organic matter. Profitability is presented as currency per minute over all patches for that food type and season [(currency/$h_i$) × 60]. Currency and handling times were entered into Eq. (1) as mean values per patch (e.g., $\sum h_i/n$). Food types for each season and age-sex class are listed in order of $\mathrm{ME_O}$ profitability. *Abbreviations:* m. leaf, mature leaf; y. leaf, young leaf; USO (hard), underground storage organ with woody texture; USO (soft), other textures. Fruits include both pulp and seeds unless noted otherwise.

| Species | Part | *n* | $\lambda$ *i* | $\sum$ MEO | $\sum$ MEH | $\sum$ CP | $\sum h_i$ | $\frac{\text{MEO}}{\text{min}}$ | $\frac{\text{MEH}}{\text{min}}$ | $\frac{\text{CP}}{\text{min}}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Late winter adult females | | | | | | | | | | |
| Search time = 635 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00158 | 19.94 | 25.72 | 2.18 | 276 | 4.34 | 5.60 | 0.4753 |
| *Cotoneaster frigidus* | Bark | 1 | 0.00158 | 3.82 | 5.71 | 0.11 | 165 | 1.39 | 2.07 | 0.0407 |
| *Cotoneaster frigidus* | Ripe fruit | 3 | 0.00473 | 18.45 | 29.34 | 0.76 | 965 | 1.15 | 1.82 | 0.0471 |
| *Gaultheria* sp. | Petiole | 1 | 0.00158 | 0.69 | 1.03 | 0.02 | 53 | 0.78 | 1.16 | 0.0259 |
| *Elsholtzia fruticosa* | USO (hard) | 2 | 0.00315 | 6.68 | 17.17 | 0.41 | 948 | 0.42 | 1.09 | 0.0259 |
| *Hippophae rhamnoides* | Leaf bud | 1 | 0.00158 | 3.99 | 7.52 | 0.56 | 1314 | 0.18 | 0.34 | 0.0256 |
| *Gaultheria* sp. | m. leaf | 4 | 0.00630 | 5.18 | 12.75 | 0.81 | 1777 | 0.17 | 0.43 | 0.0274 |
| Late winter adult males | | | | | | | | | | |
| Search time = 115 s | | | | | | | | | | |
| *Cotoneaster frigidus* | Ripe fruit | 2 | 0.01733 | 9.19 | 14.62 | 0.38 | 317 | 1.74 | 2.77 | 0.0713 |
| Spring juveniles | | | | | | | | | | |
| Search time = 247 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | y. leaf/flower | 7 | 0.02832 | 106.03 | 131.13 | 13.93 | 2730 | 2.33 | 2.88 | 0.3062 |
| *Jasminum humile* | Leaf bud | 1 | 0.00405 | 2.32 | 3.03 | 0.22 | 120 | 1.16 | 1.52 | 0.1097 |
| *Clematis montana* | y. leaf | 1 | 0.00405 | 0.52 | 0.71 | 0.07 | 50 | 0.63 | 0.85 | 0.0804 |
| *Cotoneaster frigidus* | y. leaf | 2 | 0.00809 | 0.22 | 0.50 | 0.05 | 67 | 0.20 | 0.45 | 0.0451 |
| Spring adult females | | | | | | | | | | |
| Search time = 725 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | y. leaf/flower | 19 | 0.02622 | 152.49 | 188.59 | 20.04 | 3296 | 2.78 | 3.43 | 0.3647 |
| *Jasminum humile* | y. leaf | 2 | 0.00276 | 15.65 | 17.91 | 1.04 | 425 | 2.21 | 2.53 | 0.1472 |
| *Clematis montana* | y. leaf | 1 | 0.00138 | 2.97 | 4.01 | 0.38 | 97 | 1.84 | 2.49 | 0.2361 |
| *Sorbus cuspidata* | Leaf bud | 1 | 0.00138 | 1.14 | 1.69 | 0.04 | 46 | 1.48 | 2.19 | 0.0515 |
| *Rosa macrophylla* | y. leaf | 7 | 0.00966 | 19.83 | 25.67 | 1.91 | 921 | 1.29 | 1.67 | 0.1242 |
| *Salix tetrasperma* | Flower | 1 | 0.00138 | 3.87 | 8.47 | 0.86 | 188 | 1.23 | 2.70 | 0.2757 |
| *Jasminum humile* | Leaf bud | 5 | 0.00690 | 15.28 | 20.02 | 1.45 | 808 | 1.14 | 1.49 | 0.1075 |
| Compositae | Herb leaf | 2 | 0.00276 | 6.28 | 8.21 | 0.86 | 428 | 0.88 | 1.15 | 0.1213 |
| *Berberis aristata* | y. leaf | 1 | 0.00138 | 1.26 | 1.49 | 0.15 | 105 | 0.72 | 0.85 | 0.0881 |
| *Cotoneaster frigidus* | y. leaf | 2 | 0.00276 | 3.17 | 7.21 | 0.73 | 401 | 0.47 | 1.08 | 0.1085 |
| *Rosa sericea* | y. leaf | 1 | 0.00138 | 0.18 | 0.25 | 0.02 | 24 | 0.45 | 0.63 | 0.0373 |
| Spring adult males | | | | | | | | | | |
| Search time = 630 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | y. leaf/flower | 13 | 0.02064 | 99.89 | 123.54 | 13.13 | 2519 | 2.38 | 2.94 | 0.3126 |
| *Berberis aristata* | y. leaf | 1 | 0.00159 | 11.17 | 13.27 | 1.37 | 511 | 1.31 | 1.56 | 0.1610 |
| *Rosa macrophylla* | y. leaf | 1 | 0.00159 | 2.56 | 3.32 | 0.25 | 120 | 1.28 | 1.66 | 0.1232 |
| *Rosa sericea* | y. leaf | 1 | 0.00159 | 1.01 | 1.39 | 0.08 | 98 | 0.62 | 0.85 | 0.0505 |
| *Jasminum humile* | Leaf bud | 1 | 0.00159 | 0.62 | 0.81 | 0.06 | 61 | 0.61 | 0.80 | 0.0575 |
| *Cotoneaster frigidus* | y. leaf | 1 | 0.00159 | 0.22 | 0.50 | 0.05 | 57 | 0.23 | 0.52 | 0.0523 |
| Spring one adult male | | | | | | | | | | |
| Search time = 151 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | y. leaf/flower | 5 | 0.03305 | 21.07 | 26.06 | 2.77 | 494 | 2.56 | 3.17 | 0.3365 |
| *Rosa macrophylla* | y. leaf | 1 | 0.00661 | 2.56 | 3.32 | 0.25 | 120 | 1.28 | 1.66 | 0.1232 |
| *Cotoneaster frigidus* | y. leaf | 1 | 0.00661 | 0.22 | 0.50 | 0.05 | 57 | 0.23 | 0.52 | 0.0523 |
| Monsoon juveniles | | | | | | | | | | |
| Search time = 74 s | | | | | | | | | | |
| *Sorbus cuspidata* | Unripe fruit | 1 | 0.01348 | 4.00 | 7.17 | 0.13 | 34 | 7.03 | 12.60 | 0.2291 |
| *Tsuga dumosa* | Bark | 1 | 0.01348 | 0.72 | 1.56 | 0.02 | 54 | 0.81 | 1.73 | 0.0247 |
| Unidentified tree sp. 54 | Fruit | 2 | 0.02697 | 3.69 | 8.38 | 0.26 | 596 | 0.37 | 0.84 | 0.0260 |
| Monsoon adult females | | | | | | | | | | |
| Search time = 93 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | m. leaf | 1 | 0.01079 | 1.85 | 2.24 | 0.11 | 37 | 3.00 | 3.63 | 0.1729 |
| Unidentified tree sp. 54 | Fruit | 4 | 0.04315 | 8.09 | 18.39 | 0.57 | 574 | 0.85 | 1.92 | 0.0593 |
| Fall 1 juveniles | | | | | | | | | | |
| Search time = 196 s | | | | | | | | | | |
| *Zanthoxylum nepalense* | m. leaf | 5 | 0.02552 | 60.22 | 72.71 | 3.46 | 1077 | 3.36 | 4.05 | 0.1930 |
| *Cotoneaster frigidus* | m. leaf | 1 | 0.00510 | 21.36 | 27.46 | 1.49 | 945 | 1.36 | 1.74 | 0.0947 |
| *Rosa macrophylla* | m. leaf | 1 | 0.00510 | 0.67 | 0.76 | 0.02 | 80 | 0.50 | 0.57 | 0.0154 |
| Fall 1 adult females | | | | | | | | | | |
| Search time = 109 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 2 | 0.01832 | 170.32 | 174.66 | 2.81 | 591 | 17.30 | 17.74 | 0.2855 |
| *Malva* sp. | Herb leaf | 1 | 0.00916 | 13.97 | 15.79 | 2.04 | 80 | 10.42 | 11.77 | 1.5201 |
| *Zanthoxylum nepalense* | m. leaf | 2 | 0.01832 | 18.54 | 22.38 | 1.07 | 280 | 3.97 | 4.79 | 0.2281 |
| *Hippophae rhamnoides* | m. leaf | 2 | 0.01832 | 5.4 | 6.97 | 0.59 | 161 | 2.01 | 2.59 | 0.2196 |
| *Cotoneaster frigidus* | m. leaf | 4 | 0.03664 | 10.77 | 13.85 | 0.75 | 409 | 1.58 | 2.03 | 0.1103 |
| *Cotoneaster frigidus* | Ripe fruit | 1 | 0.00916 | 1.77 | 2.82 | 0.07 | 149 | 0.71 | 1.13 | 0.0292 |
| Fall 1 adult males | | | | | | | | | | |
| Search time = 289 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 3 | 0.01037 | 373.92 | 383.45 | 6.17 | 850 | 26.39 | 27.06 | 0.4354 |
| *Caragana gerardiana* | Seed | 1 | 0.00346 | 2.71 | 3.12 | 0.50 | 14 | 11.49 | 13.21 | 2.1069 |

Appendix *(Continued)*

| Species | Part | $n$ | $\lambda i$ | $\sum$ MEO | $\sum$ MEH | $\sum$ CP | $\sum hi$ | $\frac{\text{MEO}}{\text{min}}$ | $\frac{\text{MEH}}{\text{min}}$ | $\frac{\text{CP}}{\text{min}}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Rumex nepalensis*? | Herb leaf | 2 | 0.00691 | 4.12 | 4.70 | 0.44 | 32 | 7.80 | 8.90 | 0.8410 |
| *Zanthoxylum nepalense* | m. leaf | 1 | 0.00346 | 17.05 | 20.59 | 0.98 | 290 | 3.53 | 4.26 | 0.2029 |
| *Raphanus sativus* | Herb leaf | 2 | 0.00691 | 2.14 | 2.65 | 0.33 | 42 | 3.06 | 3.79 | 0.4670 |
| *Cotoneaster frigidus* | m. leaf | 6 | 0.02074 | 18.96 | 24.38 | 1.32 | 978 | 1.16 | 1.50 | 0.0812 |
| *Berberis aristata* | Ripe fruit | 1 | 0.00346 | 1.11 | 1.48 | 0.07 | 159 | 0.42 | 0.56 | 0.0271 |
| Fall 1 one adult male | | | | | | | | | | |
| Search time = 134 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 1 | 0.00745 | 98.02 | 100.51 | 1.62 | 236 | 24.93 | 25.56 | 0.4113 |
| *Caragana gerardiana* | Seed | 1 | 0.00745 | 2.71 | 3.12 | 0.50 | 14 | 11.49 | 13.21 | 2.1069 |
| *Rumex nepalensis*? | Herb leaf | 2 | 0.01490 | 4.12 | 4.70 | 0.44 | 32 | 7.80 | 8.90 | 0.8410 |
| *Cotoneaster frigidus* | m. leaf | 4 | 0.02979 | 15.13 | 19.45 | 1.06 | 802 | 1.13 | 1.45 | 0.0790 |
| Fall 2 juvenile | | | | | | | | | | |
| Search time = 159 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00628 | 25.27 | 32.60 | 2.77 | 235 | 6.45 | 8.31 | 0.7055 |
| *Euphorbia* sp. | Ripe fruit | 1 | 0.00628 | 10.78 | 12.37 | 0.27 | 175 | 3.69 | 4.24 | 0.0918 |
| *Zanthoxylum nepalense* | m. leaf | 2 | 0.01255 | 14.83 | 17.90 | 0.85 | 276 | 3.23 | 3.89 | 0.1855 |
| *Sorbus cuspidata* | Ripe fruit | 1 | 0.00628 | 2.61 | 4.21 | 0.08 | 66 | 2.37 | 3.83 | 0.0746 |
| *Cotoneaster acuminatus* | Ripe fruit | 1 | 0.00628 | 3.34 | 5.39 | 0.13 | 106 | 1.90 | 3.06 | 0.0761 |
| *Hippophae rhamnoides* | Ripe fruit | 1 | 0.00628 | 9.30 | 12.69 | 0.86 | 480 | 1.16 | 1.59 | 0.1075 |
| *Aconogonum molle* | Herb leaf | 1 | 0.00628 | 2.77 | 3.96 | 0.28 | 165 | 1.01 | 1.44 | 0.1009 |
| *Theropogon pallidus* | Herb fruit | 1 | 0.00628 | 1.77 | 2.51 | 0.07 | 129 | 0.82 | 1.16 | 0.0320 |
| *Aconogonum molle* | Herb flower | 1 | 0.00628 | 0.13 | 0.19 | 0.01 | 12 | 0.64 | 0.95 | 0.0371 |
| Fall 2 adult females | | | | | | | | | | |
| Search time = 161 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 2 | 0.01245 | 283.86 | 291.09 | 4.68 | 1228 | 13.86 | 14.22 | 0.2288 |
| *Saussurea* sp. | USO (soft) | 1 | 0.00622 | 31.42 | 54.42 | 5.12 | 172 | 10.97 | 19.00 | 1.7857 |
| *Caragana gerardiana* | Seed | 1 | 0.00622 | 18.98 | 21.81 | 3.48 | 121 | 9.40 | 10.81 | 1.7247 |
| *Clematis Montana* | m. leaf | 2 | 0.01245 | 20.65 | 22.92 | 1.16 | 154 | 8.04 | 8.93 | 0.4508 |
| *Elsholtzia fruticosa* | Flower | 1 | 0.00622 | 9.09 | 12.36 | 0.69 | 91 | 6.02 | 8.19 | 0.4545 |
| *Zanthoxylum nepalense* | m. leaf | 1 | 0.00622 | 26.32 | 31.78 | 1.51 | 292 | 5.41 | 6.53 | 0.3110 |
| *Euphorbia sp.* | Ripe fruit | 3 | 0.01867 | 60.13 | 69.03 | 1.50 | 1128 | 3.20 | 3.67 | 0.0796 |
| *Cotoneaster frigidus* | m. leaf | 1 | 0.00622 | 5.11 | 6.57 | 0.36 | 151 | 2.03 | 2.61 | 0.1415 |
| *Fagopyrum esculentum* | Herb leaf | 1 | 0.00622 | 2.80 | 3.33 | 0.31 | 101 | 1.66 | 1.98 | 0.1864 |
| *Fagopyrum esculentum* | Herb flower | 1 | 0.00622 | 2.64 | 4.53 | 0.47 | 102 | 1.55 | 2.67 | 0.2798 |
| *Cotoneaster acuminatus* | Ripe fruit | 1 | 0.00622 | 0.35 | 0.57 | 0.01 | 15 | 1.43 | 2.30 | 0.0574 |
| *Theropogon pallidus* | Herb fruit | 1 | 0.00622 | 0.41 | 0.58 | 0.02 | 24 | 1.04 | 1.47 | 0.0403 |
| Fall 2 adult males | | | | | | | | | | |
| Search time = 494 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 4 | 0.00810 | 519.14 | 532.36 | 8.57 | 1477 | 21.09 | 21.63 | 0.3481 |
| *Clematis montana* | m. leaf | 2 | 0.00405 | 61.93 | 68.74 | 3.47 | 270 | 13.78 | 15.30 | 0.7725 |
| *Rumex nepalensis*? | Herb leaf | 1 | 0.00203 | 5.67 | 6.46 | 0.61 | 41 | 8.30 | 9.46 | 0.8947 |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00203 | 34.50 | 44.49 | 3.78 | 321 | 6.44 | 8.31 | 0.7049 |
| *Elsholtzia fruticosa* | Flower | 1 | 0.00203 | 17.36 | 23.60 | 1.31 | 172 | 6.04 | 8.21 | 0.4558 |
| *Caragana gerardiana* | Seed | 4 | 0.00810 | 54.76 | 62.95 | 10.04 | 708 | 4.64 | 5.34 | 0.8516 |
| *Zanthoxylum nepalense* | m. leaf | 2 | 0.00405 | 47.45 | 57.30 | 2.73 | 626 | 4.55 | 5.49 | 0.2617 |
| *Theropogon pallidus* | Herb fruit | 1 | 0.00203 | 1.91 | 2.70 | 0.07 | 26 | 4.40 | 6.24 | 0.1714 |
| *Raphanus sativus* | Herb leaf | 1 | 0.00203 | 1.22 | 1.51 | 0.19 | 21 | 3.54 | 4.38 | 0.5404 |
| *Malva* sp. | Herb leaf | 1 | 0.00203 | 40.15 | 45.38 | 5.86 | 732 | 3.29 | 3.72 | 0.4805 |
| *Compositae* | Herb leaf | 1 | 0.00203 | 1.06 | 1.39 | 0.15 | 21 | 3.07 | 4.02 | 0.4227 |
| *Fagopyrum esculentum* | Herb leaf | 1 | 0.00203 | 0.18 | 0.21 | 0.02 | 4 | 2.59 | 3.08 | 0.2904 |
| *Cotoneaster frigidus* | m. leaf | 7 | 0.01418 | 49.95 | 64.21 | 3.49 | 1561 | 1.92 | 2.47 | 0.1340 |
| *Hippophae rhamnoides* | Unripe fruit | 1 | 0.00203 | 1.26 | 1.72 | 0.12 | 71 | 1.07 | 1.46 | 0.0990 |
| Fall 2 one adult male | | | | | | | | | | |
| Search time = 96 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 3 | 0.03124 | 475.57 | 487.68 | 7.85 | 1366 | 20.89 | 21.42 | 0.3446 |
| *Clematis montana* | m. leaf | 1 | 0.01041 | 45.15 | 50.12 | 2.53 | 198 | 13.71 | 15.22 | 0.7687 |
| *Rumex nepalensis*? | Herb leaf | 1 | 0.01041 | 5.67 | 6.46 | 0.61 | 41 | 8.30 | 9.46 | 0.8947 |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.01041 | 34.50 | 44.49 | 3.78 | 321 | 6.44 | 8.31 | 0.7049 |
| *Elsholtzia fruticosa* | Flower | 1 | 0.01041 | 17.36 | 23.60 | 1.31 | 172 | 6.04 | 8.21 | 0.4558 |
| *Caragana gerardiana* | Seed | 1 | 0.01041 | 3.25 | 3.74 | 0.60 | 43 | 4.58 | 5.26 | 0.8396 |
| *Theropogon pallidus* | Herb fruit | 1 | 0.01041 | 1.91 | 2.70 | 0.07 | 26 | 4.40 | 6.24 | 0.1714 |
| *Raphanus sativus* | Herb leaf | 1 | 0.01041 | 1.22 | 1.51 | 0.19 | 21 | 3.54 | 4.38 | 0.5404 |
| *Malva* sp. | Herb leaf | 1 | 0.01041 | 40.15 | 45.38 | 5.86 | 732 | 3.29 | 3.72 | 0.4805 |
| *Compositae* | Herb leaf | 1 | 0.01041 | 1.06 | 1.39 | 0.15 | 21 | 3.07 | 4.02 | 0.4227 |
| *Fagopyrum esculentum* | Herb leaf | 1 | 0.01041 | 0.18 | 0.21 | 0.02 | 4 | 2.59 | 3.08 | 0.2904 |
| *Hippophae rhamnoides* | Unripe fruit | 1 | 0.01041 | 1.26 | 1.72 | 0.12 | 71 | 1.07 | 1.46 | 0.0990 |
| *Cotoneaster frigidus* | m. leaf | 1 | 0.01041 | 0.37 | 0.47 | 0.03 | 24 | 0.92 | 1.18 | 0.0639 |

Appendix *(Continued)*

| Species | Part | *n* | $\lambda\ i$ | $\sum$ MEO | $\sum$ MEH | $\sum$ CP | $\sum hi$ | $\frac{\text{MEO}}{\text{min}}$ | $\frac{\text{MEH}}{\text{min}}$ | $\frac{\text{CP}}{\text{min}}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Fall 3 juveniles | | | | | | | | | | |
| Search time = 203 s | | | | | | | | | | |
| *Sorbus cuspidata* | Ripe fruit | 3 | 0.01481 | 27.78 | 44.83 | 0.87 | 328 | 5.08 | 8.21 | 0.1600 |
| *Caragana gerardiana* | Seed | 2 | 0.00987 | 26.57 | 30.54 | 4.87 | 479 | 3.32 | 3.82 | 0.6098 |
| *Cotoneaster frigidus* | m. leaf | 4 | 0.01974 | 31.22 | 40.13 | 2.18 | 1152 | 1.63 | 2.09 | 0.1135 |
| *Cotoneaster frigidus* | Ripe fruit | 1 | 0.00494 | 0.68 | 1.08 | 0.03 | 64 | 0.64 | 1.02 | 0.0264 |
| Fall 3 adult females | | | | | | | | | | |
| Search time = 618 s | | | | | | | | | | |
| *Sorbus cuspidata* | Ripe fruit | 5 | 0.00809 | 242.86 | 391.90 | 7.64 | 812 | 17.94 | 28.95 | 0.5645 |
| *Euphorbia* sp. | Ripe fruit | 1 | 0.00162 | 4.96 | 5.69 | 0.12 | 27 | 10.95 | 12.57 | 0.2724 |
| *Myrsine semiserrata* | m. leaf | 1 | 0.00162 | 40.84 | 47.25 | 2.40 | 233 | 10.52 | 12.17 | 0.6185 |
| *Rosa sericea* | Ripe fruit | 1 | 0.00162 | 13.63 | 26.31 | 0.50 | 95 | 8.63 | 16.66 | 0.3165 |
| *Caragana gerardiana* | Seed | 10 | 0.01617 | 412.04 | 473.69 | 75.58 | 4125 | 5.99 | 6.89 | 1.0995 |
| *Saussurea* sp. | USO soft | 1 | 0.00162 | 6.28 | 10.88 | 1.02 | 75 | 5.00 | 8.66 | 0.8145 |
| *Vibernum cotinifolium* | Ripe fruit | 1 | 0.00162 | 7.59 | 10.16 | 0.19 | 95 | 4.77 | 6.39 | 0.1182 |
| *Allium wallichii* | Herb fruit | 2 | 0.00323 | 14.65 | 20.71 | 0.73 | 187 | 4.70 | 6.65 | 0.2358 |
| *Solanum tuberosum* | USO (soft) | 1 | 0.00162 | 11.83 | 12.13 | 0.20 | 269 | 2.64 | 2.71 | 0.0436 |
| *Cotoneaster frigidus* | m. leaf | 13 | 0.02102 | 98.34 | 126.43 | 6.86 | 2453 | 2.40 | 3.09 | 0.1678 |
| *Gaultheria* sp. | Fruit | 1 | 0.00162 | 2.96 | 4.64 | 0.14 | 82 | 2.17 | 3.40 | 0.1008 |
| *Berberis aristata* | Ripe fruit | 1 | 0.00162 | 2.95 | 3.95 | 0.19 | 233 | 0.76 | 1.02 | 0.0491 |
| *Rubia manjith* | Herb fruit | 2 | 0.00323 | 1.65 | 2.30 | 0.11 | 239 | 0.41 | 0.58 | 0.0285 |
| *Gaultheria* sp. | m. leaf | 1 | 0.00162 | 0.40 | 0.98 | 0.06 | 137 | 0.17 | 0.43 | 0.0274 |
| Fall 3 adult male | | | | | | | | | | |
| Search time = 481 s | | | | | | | | | | |
| *Solanum tuberosum* | USO (soft) | 2 | 0.00416 | 370.29 | 379.72 | 6.11 | 720 | 30.87 | 31.66 | 0.5095 |
| *Caragana gerardiana* | Seed | 6 | 0.01248 | 72.65 | 83.52 | 13.33 | 660 | 6.60 | 7.59 | 1.2113 |
| *Elsholtzia fruticosa* | Flower | 2 | 0.00416 | 7.44 | 10.12 | 0.56 | 101 | 4.43 | 6.02 | 0.3341 |
| *Cotoneaster frigidus* | m. leaf | 6 | 0.01248 | 15.50 | 19.93 | 1.08 | 379 | 2.45 | 3.15 | 0.1711 |
| *Allium wallichii* | Herb fruit | 2 | 0.00416 | 1.26 | 1.78 | 0.06 | 41 | 1.83 | 2.58 | 0.0916 |
| *Berberis aristata* | Ripe fruit | 2 | 0.00416 | 2.57 | 3.44 | 0.17 | 136 | 1.14 | 1.52 | 0.0735 |
| *Aconogonum molle*? | Herb flower | 1 | 0.00208 | 0.13 | 0.20 | 0.01 | 9 | 0.90 | 1.34 | 0.0524 |
| *Theropogon pallidus* | Herb fruit | 1 | 0.00208 | 3.81 | 5.40 | 0.15 | 306 | 0.75 | 1.06 | 0.0291 |
| Fall 3 one adult male | | | | | | | | | | |
| Search time = 72 s | | | | | | | | | | |
| *Cotoneaster frigidus* | m. leaf | 3 | 0.04159 | 7.12 | 9.15 | 0.50 | 137 | 3.12 | 4.01 | 0.2177 |
| Fall 4 juvenile | | | | | | | | | | |
| Search time = 208 s | | | | | | | | | | |
| *Sorbus cuspidata* | Ripe fruit | 1 | 0.00482 | 36.46 | 58.84 | 1.15 | 246 | 8.89 | 14.35 | 0.2799 |
| *Rosa sericea* | Ripe fruit | 1 | 0.00482 | 47.10 | 90.89 | 1.73 | 389 | 7.26 | 14.02 | 0.2663 |
| *Euphorbia* sp. | Ripe fruit | 3 | 0.01445 | 62.07 | 71.25 | 1.54 | 884 | 4.21 | 4.83 | 0.1048 |
| *Caragana gerardiana* | Seed | 1 | 0.00482 | 43.91 | 50.49 | 8.06 | 636 | 4.14 | 4.76 | 0.7598 |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00482 | 14.96 | 19.29 | 1.64 | 253 | 3.54 | 4.57 | 0.3875 |
| *Cotoneaster frigidus* | m. leaf | 2 | 0.00963 | 5.66 | 7.28 | 0.39 | 243 | 1.40 | 1.80 | 0.0975 |
| *Berberis aristata* | Ripe fruit | 6 | 0.02889 | 2.80 | 3.75 | 0.18 | 826 | 0.20 | 0.27 | 0.0131 |
| Fall 4 adult females | | | | | | | | | | |
| Search time = 548 s | | | | | | | | | | |
| *Sorbus cuspidata* | Ripe fruit | 2 | 0.00365 | 189.80 | 306.29 | 5.97 | 900 | 12.66 | 20.43 | 0.3984 |
| *Solanum tuberosum* | USO (soft) | 1 | 0.00182 | 26.02 | 26.68 | 0.43 | 129 | 12.12 | 12.43 | 0.2000 |
| *Caragana gerardiana* | USO (hard) | 2 | 0.00365 | 28.01 | 63.01 | 4.33 | 167 | 10.05 | 22.60 | 1.5526 |
| *Rosa macrophylla* | m. leaf | 1 | 0.00182 | 2.00 | 2.29 | 0.06 | 13 | 9.57 | 10.94 | 0.2963 |
| *Rosa sericea* | Ripe fruit | 1 | 0.00182 | 4.96 | 9.57 | 0.18 | 34 | 8.87 | 17.12 | 0.3254 |
| *Hippophae rhamnoides* | m. leaf | 2 | 0.00365 | 65.39 | 84.33 | 7.16 | 446 | 8.80 | 11.35 | 0.9629 |
| *Clematis montana* | m. leaf | 1 | 0.00182 | 5.16 | 5.73 | 0.29 | 36 | 8.70 | 9.66 | 0.4878 |
| *Caragana gerardiana* | Seed | 4 | 0.00730 | 43.37 | 49.86 | 7.96 | 361 | 7.20 | 8.28 | 1.3210 |
| *Cotoneaster acuminatus* | Ripe fruit | 1 | 0.00182 | 7.92 | 10.05 | 0.32 | 74 | 6.40 | 10.32 | 0.2569 |
| *Euphorbia* sp. | Ripe fruit | 1 | 0.00182 | 4.96 | 5.69 | 0.12 | 56 | 5.33 | 6.12 | 0.1326 |
| *Saussurea* sp. | USO (soft) | 2 | 0.00365 | 26.93 | 46.64 | 4.38 | 328 | 4.92 | 8.53 | 0.8017 |
| *Jasminum humile* | m. leaf | 2 | 0.00365 | 4.70 | 5.35 | 0.14 | 61 | 4.61 | 5.26 | 0.1409 |
| *Cotoneaster frigidus* | Ripe fruit | 2 | 0.00365 | 6.32 | 10.05 | 0.26 | 133 | 2.86 | 4.55 | 0.1173 |
| *Cotoneaster frigidus* | m. leaf | 8 | 0.01459 | 40.31 | 51.82 | 2.81 | 965 | 2.51 | 3.22 | 0.1749 |
| *Berberis aristata* | Ripe fruit | 1 | 0.00182 | 3.19 | 4.27 | 0.21 | 293 | 0.65 | 0.87 | 0.0422 |
| *Cotoneaster frigidus* | Leaf bud | 1 | 0.00182 | 0.90 | 2.18 | 0.14 | 95 | 0.56 | 1.38 | 0.0878 |
| *Rubia manjith* | Herb fruit | 1 | 0.00182 | 0.59 | 0.81 | 0.04 | 66 | 0.53 | 0.74 | 0.0365 |
| Fall 4 adult males | | | | | | | | | | |
| Search time = 1528 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 4 | 0.00262 | 133.35 | 171.99 | 14.60 | 552 | 14.50 | 18.71 | 1.5876 |
| *Sorbus cuspidata* | Ripe fruit | 3 | 0.00196 | 203.14 | 327.80 | 6.39 | 1150 | 10.60 | 17.10 | 0.3336 |
| *Solanum tuberosum* | USO (soft) | 7 | 0.00458 | 384.81 | 394.61 | 6.35 | 2684 | 8.60 | 8.82 | 0.1419 |
| *Caragana gerardiana* | Seed | 6 | 0.00393 | 116.02 | 133.38 | 21.28 | 1016 | 6.85 | 7.87 | 1.2564 |
| *Allium wallichii* | Herb fruit | 1 | 0.00065 | 1.26 | 1.78 | 0.06 | 23 | 3.26 | 4.61 | 0.1635 |

Appendix *(Continued)*

| Species | Part | $n$ | $\lambda\ i$ | $\sum$ MEO | $\sum$ MEH | $\sum$ CP | $\sum hi$ | $\frac{\text{MEO}}{\text{min}}$ | $\frac{\text{MEH}}{\text{min}}$ | $\frac{\text{CP}}{\text{min}}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cotoneaster frigidus* | Ripe fruit | 5 | 0.00327 | 43.75 | 69.59 | 1.80 | 857 | 3.06 | 4.87 | 0.1257 |
| *Cotoneaster frigidus* | m. leaf | 20 | 0.01309 | 171.07 | 219.93 | 11.94 | 3988 | 2.57 | 3.31 | 0.1796 |
| *Euphorbia* sp. | Ripe fruit | 3 | 0.00196 | 17.67 | 20.29 | 0.44 | 434 | 2.44 | 2.80 | 0.0607 |
| *Cotoneaster acuminatus* | Ripe fruit | 3 | 0.00196 | 10.21 | 16.45 | 0.41 | 326 | 1.88 | 3.03 | 0.0755 |
| *Rubia manjith* | Herb fruit | 7 | 0.00458 | 17.40 | 24.18 | 1.20 | 1062 | 0.98 | 1.37 | 0.0676 |
| *Berberis aristata* | Ripe fruit | 6 | 0.00393 | 10.72 | 14.36 | 0.69 | 1194 | 0.54 | 0.72 | 0.0348 |
| Fall 4 one adult male | | | | | | | | | | |
| Search time = 591 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 2 | 0.00338 | 54.00 | 69.65 | 5.91 | 158 | 20.51 | 26.45 | 2.2446 |
| *Caragana gerardiana* | Unripe fruit | 1 | 0.00169 | 3.80 | 4.36 | 0.70 | 13 | 17.79 | 20.45 | 3.2631 |
| *Sorbus cuspidata* | Ripe fruit | 1 | 0.00169 | 96.36 | 155.50 | 3.03 | 341 | 16.94 | 27.34 | 0.5333 |
| *Solanum tuberosum* | USO (soft) | 6 | 0.01015 | 377.55 | 387.17 | 6.23 | 2645 | 8.56 | 8.78 | 0.1413 |
| *Cotoneaster frigidus* | Ripe fruit | 2 | 0.00338 | 14.29 | 22.73 | 0.59 | 247 | 3.47 | 5.52 | 0.1424 |
| *Allium wallichii* | Herb fruit | 1 | 0.00169 | 1.26 | 1.78 | 0.06 | 23 | 3.26 | 4.61 | 0.1635 |
| *Cotoneaster frigidus* | m. leaf | 9 | 0.01523 | 104.87 | 134.82 | 7.32 | 2055 | 3.06 | 3.94 | 0.2136 |
| *Euphorbia* sp. | Ripe fruit | 1 | 0.00169 | 8.41 | 9.65 | 0.21 | 189 | 2.66 | 3.06 | 0.0662 |
| *Cotoneaster acuminatus* | Ripe fruit | 2 | 0.00338 | 1.41 | 2.27 | 0.06 | 61 | 1.38 | 2.22 | 0.0552 |
| *Berberis aristata* | Ripe fruit | 1 | 0.00169 | 0.55 | 0.74 | 0.04 | 86 | 0.38 | 0.51 | 0.0249 |
| Early winter juveniles | | | | | | | | | | |
| Search time = 44 s | | | | | | | | | | |
| *Caragana gerardiana* | USO (hard) | 1 | 0.02275 | 5.80 | 13.05 | 1.06 | 117 | 2.99 | 6.72 | 0.5479 |
| Early winter adult females | | | | | | | | | | |
| Search time = 131 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00764 | 47.08 | 60.71 | 5.15 | 372 | 7.59 | 9.79 | 0.8304 |
| *Caragana gerardiana* | Seed | 3 | 0.02292 | 20.06 | 23.06 | 3.68 | 281 | 4.28 | 4.92 | 0.7857 |
| *Hippophae rhamnoides* | Ripe fruit | 1 | 0.00764 | 0.30 | 0.40 | 0.03 | 6 | 2.80 | 3.82 | 0.2587 |
| *Cotoneaster frigidus* | m. leaf | 2 | 0.01528 | 10.55 | 13.56 | 0.74 | 232 | 2.73 | 3.51 | 0.1907 |
| *Cotoneaster frigidus* | Ripe fruit | 1 | 0.00764 | 3.81 | 6.06 | 0.16 | 93 | 2.47 | 3.93 | 0.1013 |
| *Aconogonum molle* | Herb leaf | 1 | 0.00764 | 11.86 | 16.98 | 1.19 | 300 | 2.37 | 3.39 | 0.2376 |
| *Cotoneaster frigidus* | Bark | 1 | 0.00764 | 0.24 | 0.36 | 0.01 | 13 | 1.14 | 1.71 | 0.0335 |
| *Cotoneaster frigidus* | Leaf bud | 2 | 0.01528 | 3.04 | 7.41 | 0.47 | 184 | 0.99 | 2.42 | 0.1546 |
| *Viburnum erubescens* | Ripe fruit | 2 | 0.01528 | 1.13 | 2.00 | 0.12 | 264 | 0.26 | 0.46 | 0.0281 |
| Early winter adult males | | | | | | | | | | |
| Search time = 665 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00150 | 51.17 | 66.00 | 5.60 | 227 | 13.53 | 17.45 | 1.4805 |
| *Caragana gerardiana* | Seed | 3 | 0.00451 | 54.22 | 62.33 | 9.94 | 474 | 6.87 | 7.90 | 1.2601 |
| *Cotoneaster frigidus* | m. leaf | 6 | 0.00902 | 72.34 | 92.99 | 5.05 | 1355 | 3.20 | 4.12 | 0.2236 |
| *Aconogonum molle* | USO (hard) | 1 | 0.00150 | 4.95 | 6.89 | 0.12 | 120 | 2.48 | 3.46 | 0.0584 |
| *Cotoneaster frigidus* | Ripe fruit | 3 | 0.00451 | 11.16 | 17.75 | 0.46 | 286 | 2.34 | 3.72 | 0.0960 |
| *Cotoneaster frigidus* | Leaf bud | 3 | 0.00451 | 0.43 | 1.04 | 0.07 | 57 | 0.45 | 1.10 | 0.0701 |
| Early winter one adult male | | | | | | | | | | |
| Search time = 422 s | | | | | | | | | | |
| *Hippophae rhamnoides* | m. leaf | 1 | 0.00237 | 51.17 | 66.00 | 5.60 | 227 | 13.53 | 17.45 | 1.4805 |
| *Caragana gerardiana* | Seed | 2 | 0.00474 | 25.48 | 29.29 | 4.67 | 299 | 5.11 | 5.88 | 0.9374 |
| *Aconogonum molle* | USO (hard) | 1 | 0.00237 | 4.95 | 6.89 | 0.12 | 120 | 2.48 | 3.46 | 0.0584 |
| *Cotoneaster frigidus* | Ripe fruit | 2 | 0.00474 | 9.48 | 15.08 | 0.39 | 231 | 2.46 | 3.92 | 0.1010 |
| *Cotoneaster frigidus* | m. leaf | 1 | 0.00237 | 3.10 | 3.99 | 0.22 | 93 | 2.00 | 2.57 | 0.1397 |
| *Cotoneaster frigidus* | Leaf bud | 2 | 0.00474 | 0.35 | 0.85 | 0.05 | 41 | 0.51 | 1.25 | 0.0799 |

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