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## Foraging Strategies in the Boreal Forest: An Analysis of Cree Hunting and Gathering

Bruce Winterhalder

### Introduction

Hunter-gatherers, or foragers, live in environments characterized by diverse and heterogeneously distributed resources. From the array of potential food species, foraging locations, and pathways, the forager can choose combinations which more or less effectively and efficiently procure subsistence. The forager's choices make up a strategy of adjustment to ecological conditions, an adaptive pattern resulting from evolutionary processes and the constraints of situation, time, and chance. Analysis of form and dynamics of these strategies in specified environmental situations is of interest not only to ecological anthropologists, but also to prehistoric archeologists and paleontologists studying the ecological circumstances affecting the evolution and expression of hunter-gatherer behavior. These strategies are the subject of the socioecological analysis presented in this chapter.

This chapter is intended as an analytic and empirical companion to the more theoretical and programmatic content of chapter 2, above. It is heuristic in intent. It attempts to evaluate the applicability of optimal foraging theory to human foraging behavior, and to assess the predictive reliability of hypotheses derived from particular models. These models provide alternative hypotheses for testing and clear guidelines about the kinds of information required to evaluate them. The structured nature of the approach means that confirmation or refutation can be used to reflect on the premises and constraints incorporated into the modeling effort.

The data are based on Cree hunting and gathering in a particular environment, the boreal forest of northern Ontario, but the analysis is directed to learning what the approach can help us to understand about foragers, and what an understanding of foragers can help us to appreciate about anthropological applications of the theory and methodology. The goal then is a general assessment of the usefulness of this theory to ecologically oriented anthropologists and prehistorians.

Throughout the analysis two questions are central to the proposed evaluation: Does use of this approach help in identifying the ecological variables affecting foraging behavior decisions? And, does the optimal foraging approach reliably specify the manner of their action?

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Study Orientation and Hypotheses Examined

The most general assumption invoked here is that adaptive processes produce behaviors which allow organisms to achieve specified goals efficiently and effectively. For human biocultural behavior the processes producing adaptations are not fully understood (cf. Durham 1976a; Thomas, Winterhalder, and McRae 1979). However, the assumption that behaviors develop toward optimization relative to adaptive goals is a reasonable one for building testable theory. The optimization assumption in the present instance is this: hunter-gatherers will develop behaviors which maximize the net rate of energy capture while foraging. This isolates energy capture as a measure of adaptation, and net acquisition rate as the criterion of success. Other measures--or "currencies" (Schoener 1971:369)--could be used, such as nutritional quality, and other assessment criteria adopted, such as an output-input (acquisition efficiency) ratio. But energy is measurable and of general significance, and the net rate criterion appears to be the best way of relating energy capture to adaptedness (Smith 1979b).

A case for the importance of maximizing the net rate of energy capture while foraging can take several forms: (a) the population may be constantly or periodically energy limited; (b) the population may be energy or time limited, in which case a high net rate of energy capture releases time for performance of essential activities besides foraging; or (c) the population may suffer a greater than average exposure to hazards while foraging, in which case improvement in the net rate of capture will reduce exposure to those hazards. Further, it is reasonable to suppose that hunters who survive to a large extent on a carnivorous diet readily obtain essential nutrients and minerals, so that in a first approximation the nutritional aspects of food resources can be overlooked.

There is ethnohistorical and dietary evidence to support the use of these assumptions in this study. Cree populations in the boreal forest faced periodic food shortages and occasional starvation throughout the historical fur trade period, and presumably before (Bishop 1974; Leacock 1973; Ray 1974; Rogers and Black 1976). When food supplies were adequate in quantity, evidence shows that the traditional Cree diet of meat, fish, and small amounts of vegetable matter provided sufficient amounts of minerals and vitamins (Berkes and Farkas 1978:156). This information confirms the proposition that periodic resource shortages had serious consequences in terms of energy for human foragers in this environment up to the early twentieth century, and consequently supports the expectation of finding foraging behaviors stressing energy efficiency.

The present analysis relies on the belief that these patterns have persisted into the present, when food shortages are not imminent, in part because the energy goal is substantially the same for the contemporary Cree hunter exercising personal skill in the capture of game. The desire to have leisure time within the village and to be with a family, to appear a competent and effective hunter and trapper, and to consume "healthy" bush food all contribute to the pressure to forage optimally, even though food may be available at a local store.

Given the assumption of maximization, a currency (energy), and a parameter (net capture rate), graphical or mathematical models can be constructed which produce hypotheses about foraging behavior. These models use qualities of resources and the environmental mosaic as independent variables (Pyke, Pulliam, and Charnov 1977; Schoener 1971). Tests of those hypotheses should identify ecological factors affecting behavior, or help to isolate historical constraints or competing goals which limit maximization with respect to particular behaviors or goals (Cody 1974).

The hypotheses examined here arise from models discussed in Winterhalder (chapter 2, above), and can be grouped under diet breadth, patch selectivity, and forager movement among patches.

#### Diet Breadth

Humans have evolved the capability to extract food energy and nutrients from a variety of plant and animal sources. This omnivory is expressed differently, and with differing degrees of selectivity, depending on habitat and situation. Optimal diet hypotheses attempt to determine the items, and, in general, the number of items, that will be included in an optimal forager's diet in given ecological circumstances.

In the diet breadth model (MacArthur 1972; MacArthur and Pianka 1966; Pianka 1978) resources are ranked by their value to the forager. Foraging is divided into two phases: search costs (time or energy) to encounter each unit of potential resource species, and the pursuit costs for each unit. Search and pursuit costs are the variables which carry into the model a variety of considerations, and their manipulation is the basis of hypothesis construction. The operational distinction between these foraging phases is this: all organisms are searched for concurrently (the environmental mosaic of resources is fine grained, Wiens 1976); but pursuit involves selection. An optimal diet is one that adds resources to those pursued in decreasing rank order until the last resource added creates a loss in the average pursuit costs that is not compensated by savings in average search costs, both measured per unit of resource captured. Factors which cause large or increasing search times will result in relatively broad, or increasingly broad, diet breadths. Conversely, a situation in which the forager has high or increasing pursuit costs will result respectively in a relatively narrow or decreasing diet breadth for the optimal forager.

Diet breadth, then, is the set of prey types that a forager will pursue if they are encountered during a search. If a sufficient time period or number of foraging trips is analyzed in given environmental conditions, diet breadth will be the same as the resources actually captured and consumed. By definition, in this study search costs end and pursuit costs begin when a species is located by sight or by definitive sign of its presence nearby. The operational distinction between search and pursuit in the model is that between the attempt to locate any of the species in the diet, and a commitment to capture a particular individual or group of individuals of that species. That transition most often occurs for the Cree when fresh tracks or some other sign (a beaver lodge, for instance) are located.

Application of this model requires information on the relative net energy value of prey species, and search and pursuit costs associated with each.

#### Patch Selectivity

Nearly all environments have an uneven distribution of resources. This almost ubiquitous spatial heterogeneity (Wiens 1976) can arise from habitat patchiness, from intraspecific social factors or habitat qualities affecting the dispersion of mobile prey, or directly from activities of the forager, such as localized depletion of prey. Environmental patchiness should affect the number and types of habitats within which a forager seeks resources, patterns of movement over the environmental mosaic, and the forager's influence on the resources themselves.

The patch selectivity model (MacArthur and Pianka 1966) assumes that the forager's effective resource habitat is discontinuous. There are a number of different patches, or patch types, each having a somewhat different quality. The organism moves over the landscape, randomly encountering patches, but is selective about the ones it forages within.

Patches are ranked by their quality to the forager. The foraging phases in this model are travel between patches (lost time and energy), and foraging time within patches which are harvested. The optimal forager includes patches in its foraging itinerary until the use of a low-quality patch lowers the average foraging return by an amount not compensated by the reduction in travel costs.

This model predicts that organisms living in a relatively small-scaled environmental mosaic will develop a broad use of habitats; they will be patch type generalists. Conversely, those exposed to a large-scaled resource environment will specialize and forage within relatively few habitats. As scale increases the optimum patch choice shifts toward specialization (Pianka 1978:266; Winterhalder, chapter 2, above).

The model in this case requires information on the relative value of patch types, and on the costs (per unit of resource captured) of traveling between and foraging within different types.

#### Movement among Habitats

The third set of hypotheses derive from the marginal value theorem (Charnov 1976a). This model complements the previous one in that it assumes the forager has already settled on an optimal set of patch types to harvest. The model posits that the net rate of harvest of a particular patch decreases, or is "depressed" (Charnov, Orians, and Hyatt 1976:247), with time. This happens because (a) the forager progressively depletes the resources in that locale; (b) the forager picks the more accessible resource initially and thus must harvest items increasingly difficult to locate or capture; or (c) the forager may inadvertently alert prey, which then emigrate or conceal themselves. The model predicts when, in terms of the depression curve for a particular patch type, the forager should leave that patch and search for one that is undepleted.

In this case two versions of the basic hypothesis, the second more strict in its test implications, can be considered: (1) Foragers abandon the harvest of patches or local resource aggregations prior to their depletion. (2) Foragers abandon each patch at the point at which its marginal return falls to the average habitat return. The second form of this hypothesis implies that in richer habitats, where the average foraging return is relatively high, patches will be abandoned sooner and depleted relatively less. In addition, the optimal forager leaves a trail of patches of uniform quality with respect to the resources it harvests from them.

In analyses using the marginal value theorem the following information is required: the average foraging return for the set of patches harvested, and the resource depression curve for each of the patches visited.

It should be apparent that the hypotheses developed in these models are generally qualitative rather than quantitative. Ideally they should be confirmed on a comparative rather than single-case basis. Given the exigencies of data collection and the complexity of the variables involved, the diet breadth model does not, for instance, allow one to hypothesize and test that the optimal strategy for organism *X* in circumstance *Y* is four resource items. Rather, diet breadth hypotheses are comparative in the following ways: (a) one can predict the change in foraging behavior as the organism moves from one environmental situation to another, spatially or temporally, or (b) one can predict foraging changes as the functional abilities of either the predator or the prey change with respect to search and pursuit costs and success. Despite this, in the present and most other analyses, some comparisons are only implicit.

The remainder of this chapter uses information gathered on Cree foraging to evaluate these models and hypotheses.

## Methods

### The Study Site

The data presented here are drawn from a year-long study (calendar year 1975) of hunting and gathering in the northern Ontario Cree community of Muskrat Dam Lake (Winterhalder 1977). The population of the community averaged about a hundred people, in two extended families and seventeen households. The community was initiated as an offshoot of Bearskin Lake ten years before fieldwork, in an area of the hunting ranges of some, but not all, contemporary residents. Currently the community is served by two small native-owned stores, selling foodstuffs, petroleum products, and a limited variety of hardware; an Anglican church with a native pastor; and a day school with a nonnative teacher. The nearest settlement is Round Lake (65 km air distance); intercommunity travel is usually by unscheduled, single-engine bush planes. The monetary income of the community is based on occasional wage labor (construction and fire fighting), some trapping, various grants (e.g., community development projects), and social services extended by the federal government of Canada (family allowance, unemployment, old age pensions).

In general social, cultural, and economic respects, Muskrat Dam Lake is similar to other Cree settlements in eastern boreal Canada (Black 1970; Dunning 1959; Rogers 1962). It differs from surrounding communities in being smaller, more recent in development, and somewhat more cohesive in social structure.

Snowmobiles are used in Muskrat Dam for winter travel and occasionally for searching for resources, but not for the pursuit of game. They allow a hunter to get away from the village, and perhaps to locate tracks along a river or lake shore, but hunting in the bush is done by snowshoe. Snowmobiles cannot be used off the hard-packed snow or ice surfaces of lakes and rivers unless a trail is packed in advance; they are too noisy to be useful in the direct location and pursuit of boreal forest animals. In summer, canoes with outboards replace snowmobiles to the same effect: they facilitate travel and increase search velocity, but they are not used for pursuit. The effects of these technologies on foraging will be examined below.

### Data Collection and Presentation

Data were gathered in three ways: (1) I participated in and directly recorded hunting, fishing, and trapping trips; (2) I discussed specific instances of foraging with recently returned hunters; and (3) I kept notes of hunting activities in the community and discussed procedures formally and informally with a group of diverse people. The first two sources of information are based on intensive work with six hunters. This sample covers ages eighteen to sixty, and was chosen to represent people of above average bush skills and hunting and trapping abilities, and who spent an above average time foraging. The data are not representative of the population in general, but come from experienced and committed hunters of different ages.

When directly observed, hunting activities were timed by wrist- and stopwatch in categories which differentiated tasks and energy expenditure levels. Foraging routes and the locations of significant events were recorded on topographic maps (1:250,000 scale) or on acetate sheets over a black-and-white air photo mosaic (1:59,000 scale). Discussion of the hunt--weather, tactics, animal behavior, clues as to location and movement of prey, and reasons for success and failure--was recorded, as were the type, number, and, in some cases, weight of game located and captured. In the case of nonobserved trips, the foragers provided similar but less detailed information, sometimes based on simple time diaries which they recorded for me. This information expanded the sample, but was invariably less com-

plete and detailed than that obtained by participation. The Cree educate young hunters by providing extensive experience with little verbal instruction; they were most comfortable, and my education was most productive, when I learned in the same way. Several older hunters were willing to discuss and be questioned about hunting at length (and through a translator), and thus provided historical information not otherwise obtainable.

The data presented here are selective with respect to the economic and in some cases ecological activity of the community. The focus is primarily on the foraging decisions made after a person has decided to hunt. This excludes analysis of decisions between hunting and other forms of productive activity, and it restricts attention to behavior of individuals or small groups of hunters, excluding community-level phenomena such as exchange of hunting and trapping products. More importantly, I will not consider the capital and immediate monetary costs and rewards of foraging associated with the use of outboard motors and canoes, snowmobiles, steel traps, repeating rifles and shotguns, and nylon fishing nets, and the sale of pelts. This can be done without compromising the present analytic focus because: (a) each of the hunters studied has, or has access to, the necessary equipment, purchased with wage earnings or social service payments; and (b) while the cost of fuel and ammunition may influence the overall amount of hunting, it does not strongly affect decisions to hunt particular species, in particular locations, with particular patterns of movement. Equipment, fuel, and ammunition costs are, therefore, fairly neutral factors with respect to the specific foraging decisions examined here, although they would certainly enter into a more complete human ecology analysis. The sale of pelts may have influenced the food quest in several specific ways, noted below. This selection of data is necessary to test the foraging hypotheses under evaluation.

It is also the case that the Cree are subject to, and observe, legal (provincial) restrictions on the trapping of fur bearers. They are, however, exempt by treaty from most regulations placed on sport hunters. As a result, game hunting regulations are not of large consequence to the data base used in this analysis.

#### Energy Calculations

The energy costs of foraging were calculated by timing foraging activities, assigning the activities to standardized energy expenditure levels for adult males or females (Dumin and Passmore 1967:47 and passim; Godin 1972), and aggregating the energy expenditure over the time, activities, and persons involved.

The energy value of various game species was determined using field measurements or published values of weights for the species in boreal Canada (e.g., Banfield 1974; Bellrose 1976; MacCay 1963), corrected in the case of larger, slow-growing species for the age structure of the harvest (NHRC 1976a). The composition and caloric value of various tissues for boreal species (Farmer, Ho, and Neilson 1971; Farmer and Neilson 1967; Ho, Farmer, and Neilson 1971; Mann, et al. 1962), the proportion by weight of the animal represented in these tissues (Kemp, unpub.; Spector 1956; Stewart and Stahl 1977; White 1953), and the tissues consumed under culturally prescribed "full use" were considered in calculating the caloric value of harvested organisms. Details of this procedure will be presented elsewhere (Winterhalder, in prep.); the caveat is stated here that the information available for these computations is partial and not always representative of the expected variation by season, sex, maturity, and health status of the animal. The net acquisition rate parameters used below are all calculated on a per forager basis, whether one or more persons participated in the activity. Energy values are expressed as kcal, or kcal/hr, as appropriate. Full details of the study location, sampling and recording procedures, and methods of calculation and data analysis can be found in Winterhalder (1977).

## Data and Results

### The Boreal Forest Environment

*Physical and climatic features.* The study area, Muskrat Dam Lake, is located on the Severn River. Geologically the area is in the Superior Province of the Precambrian Shield (Hewitt and Freeman 1972:72-85); floristically it is in the Northern Conifer Section of the Boreal Forest Region (Rowe 1972). The altitude is 300 m. The landscape is topographically muted and landforms are disoriented, a result of glacial disturbance (Bryson, et al. 1969), which left an irregular mosaic of subdued outcrops and glacial features (Prest 1965: 6-21). Moraines, kames, drumlins, and eskers separate kettle lakes in poorly drained depressions. Uplands rise 10-30 m above surrounding areas and represent either drift deposits or exposed Precambrian rock. These landforms constitute a small-scale irregular landscape.

The disorganized landforms, shallow slope toward Hudson Bay, and continuing isostatic uplift of Hudson Bay drainage basin have resulted in an impeded drainage (Andrews 1973:189; Terasmae 1970). Consequently much of the landscape is covered by numerous small lakes, or by hydrographic vegetation associations such as bogs or muskeg. Soils are mainly of the continental podsol type (Papadakis 1969). Specific soils are closely associated with landform features (Moir 1958:17; Rowe 1972; Tedrow 1970:203; Terasmae 1970).

The climate in winter is dominated by the dry, cold, and stable Arctic air masses (Bryson and Hare 1974:13). Days are short, typically clear and still, and acutely cold. Average nighttime lows and daytime highs are  $-29^{\circ}\text{C}$  and  $-19^{\circ}\text{C}$ , respectively. In summer the Arctic Frontal Zone is displaced north of Muskrat Dam Lake, to a position along the northern margin of the boreal forest. Air masses from the Pacific and Gulf regions mix frontally with Arctic air (Bryson 1966). Temperatures are warm, with an average daytime high of  $21^{\circ}\text{C}$  in July, and conditions typically are characterized by rain and thunderstorms, with occasional drizzle and fog. The pronounced seasonal cycle of the region is exemplary of a strong continental climate. Spring and fall mark the transition of the modal Arctic position from the southern to the northern margin of the boreal forest (Bryson 1966; Krebs and Barry 1970), and are characterized by cold, blustery weather. Hare and Hay (1974) and Hare and Thomas (1974) provide excellent summaries of the climate of this region.

Three secondary climatic features of this environment are of direct importance to foraging behavior, through their effects on game behavior, location, and accessibility to the Cree forager. These are freeze-up and break-up dates, snow cover profiles, and stream flow. These climatic features also show considerable year-to-year variability, variability which becomes important when evaluating the constancy of parameters incorporated into optimal foraging models.

The average and range of dates for initiation and conclusion of freeze-up and break-up are shown in figure 4.1. These environmental events are particularly important because they are phenological set points of the annual cycle, both for humans and for their prey, and because they mark the limits of a period of limited mobility, especially for humans.

Snow cover is the winter substrate of animals and humans (Formozov 1973; Pruitt 1970), and its depth and structure are critical to the movement of both over the boreal landscape. For instance, an increasingly deep snow cover, up to about 100 cm (chest height), progressively reduces the mobility of moose, an effect augmented by a crust on the snow (Coady 1974:423; LeResche 1974:406). But fairly deep snow and a light crust, or at least snow muffled by a light cover of powder, enhances the velocity and efficiency of human movement on snowshoes. As snow depth increases, moose are easier to pursue, but more difficult to



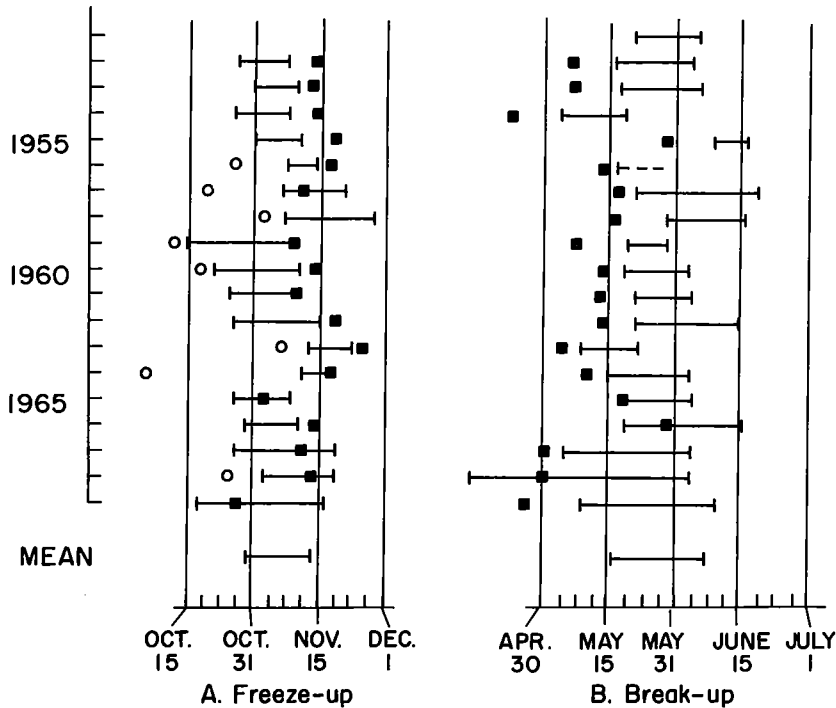


Figure 4.1. Freeze-up and Break-up Dates. (A) Freeze-up: The circles indicate the formation of ice that later melted completely; the horizontal lines show the interval between the formation of the first permanent ice and complete freeze-over, excepting permanently open areas such as falls; and the squares indicate that the ice became safe for light ground or air traffic. (B) Break-up: The squares indicate the time at which the ice became unsafe for light traffic; the horizontal lines represent the interval between the earliest date of the final thaw of the season (definite ice melt, cracks, movement or water puddles) and the disappearance of fixed or floating ice. Data from Allen and Cudbird (1971).

locate because they become confined to small feeding patches and do not leave long trails of easy-to-locate tracks (Bishop and Rausch 1974:571). The quality of the snow cover thus affects the ease and efficacy, and hence cost and likelihood of success, of searching for and pursuing moose. Variability from year to year in the snow cover (figure 4.2) causes variability in the parameters incorporated in the foraging models. Other examples could be given for different species, and the relationship discussed is one of greater detail, but the general significance to the human forager of variability in this secondary environmental factor should be evident.

Stream flow, and the level of lakes and rivers, are the third important factor (figure 4.3). Among other things stream flow affects the distribution of fish, the migration of waterfowl (especially whether dabbling ducks will stop over in the Muskrat Dam area during migrations), and summer accessibility to game species and the habitat in general. The boreal landscape is an irregular pattern of uplands scattered in a matrix of lakes and streams, bogs and muskeg. Movement on water by canoe is fast and efficacious, but movement by foot through the bogs or muskeg is tortuously difficult. As a consequence of this and the shallow nature of the topography, changes in the level of lakes and small streams can open or

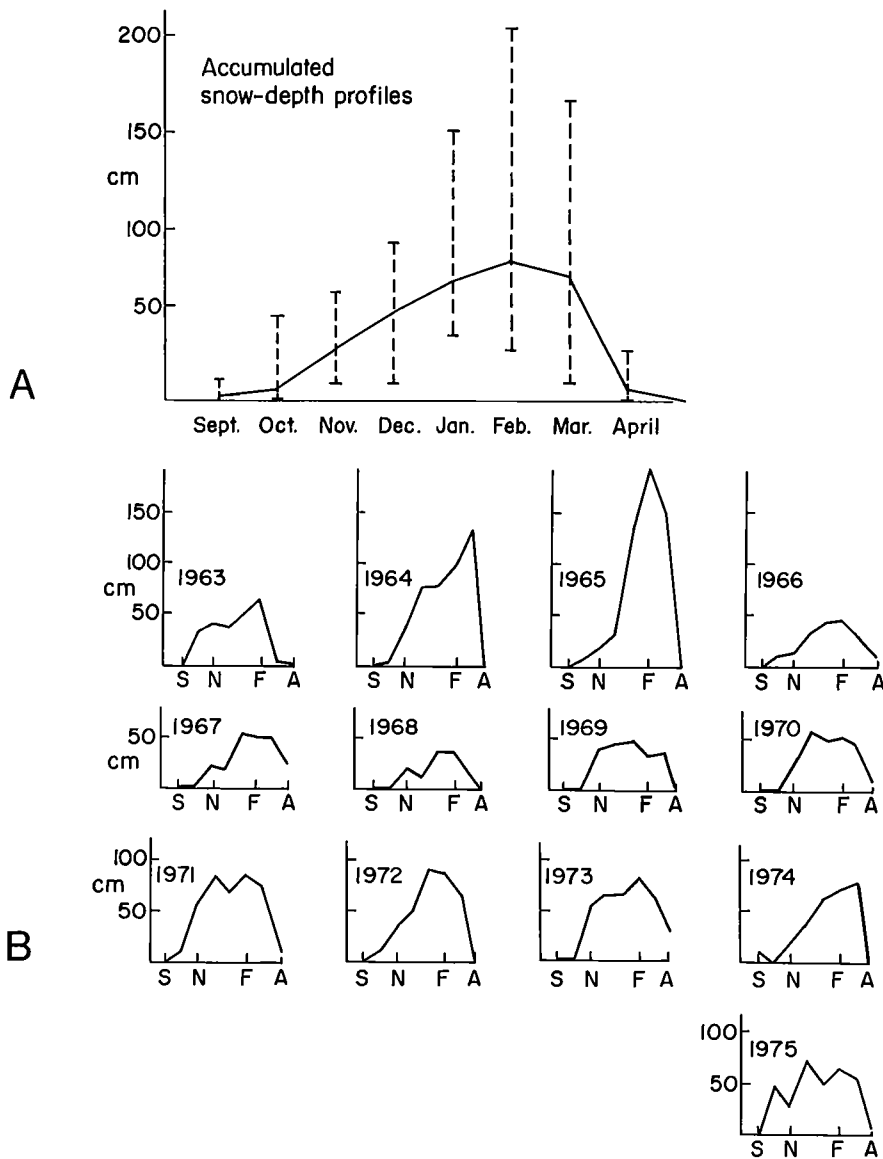


Figure 4.2. Annual Variability in the Accumulated Snow Depth Profile for Big Trout Lake, Ontario. (A) Monthly mean snow depth for the period 1963-75. The vertical dashed lines show the range of the monthly mean values. (B) Seasonal profiles for selected years. Data from Environment Canada, 1963-75.

close large areas to the only effective form of movement--canoe travel. Again, moose can provide an example of the effect of this factor on animal distributions and mobility. When summer water levels are high, moose can escape heat and insects and reach aquatic foods while well hidden in the extensive brushy bogs and muskegs lining streams and rivers. Low water, however, forces them to seek the deeper streams for the same reasons, where they are easily searched for and readily seen. Again, the importance of this secondary environmental factor is its high annual variability, especially in late summer and fall, and its effects on the parameters incorporated in foraging models.

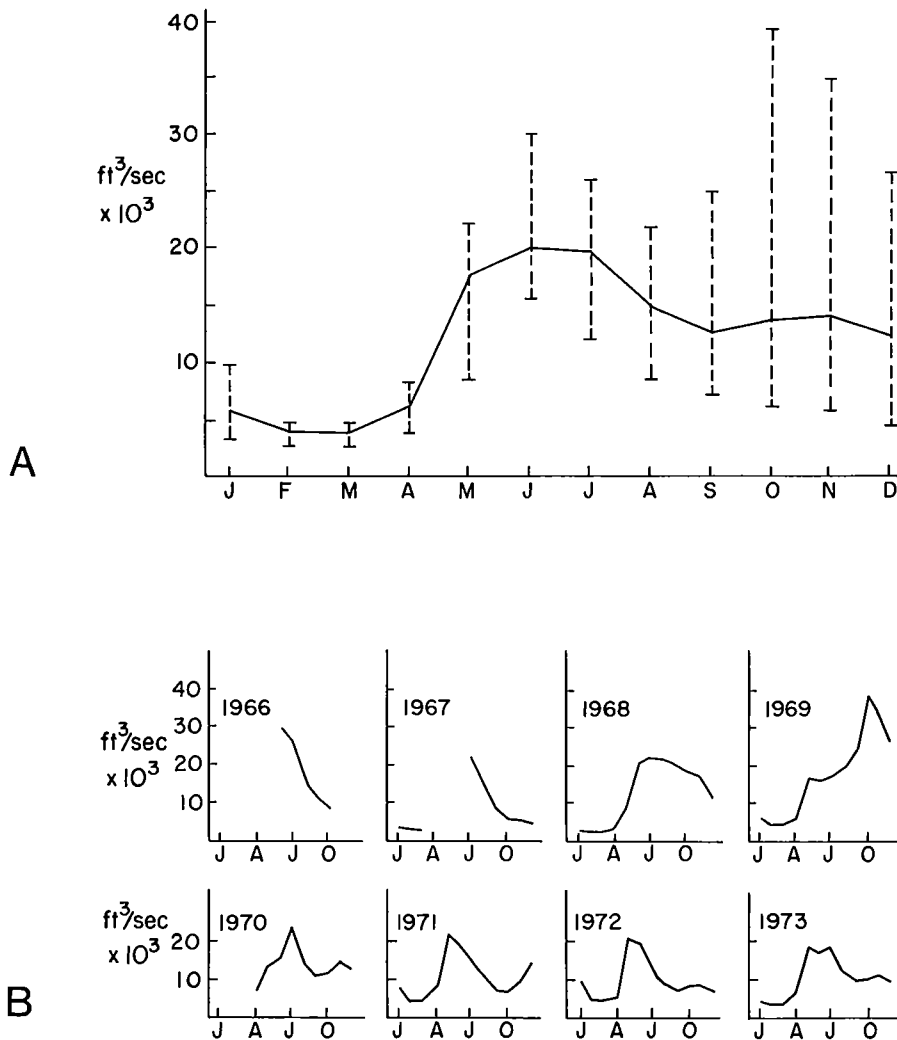


Figure 4.3. Annual Variability in Stream Flow. (A) Monthly mean discharge for the period 1966-73, measured at the outlet of Muskrat Dam Lake, on the Severn River. The vertical dashed lines show the range of monthly values. (B) Seasonal profiles for selected years. Source: Water Survey of Canada, Department of Environment, Guelph, Ontario.

*Flora: vegetation patchiness.* Two of the models analyzed here are concerned with a specific environmental property--spatial heterogeneity. The most obvious aspect of the boreal forest mosaic is the terrestrial-aquatic distinction. Topographic maps of the region show the forest to be studded with a myriad of small lakes, with a modal size in northern Ontario of  $1.6 \text{ km}^2$  (Ontario Department of Lands and Forests 1971:6). Secondly a complex and irregular, but distinct, set of vegetation patches is evident. The boundaries of these patches are defined by edaphic factors such as landform, soils, and drainage, and by ecological ones, primarily disturbance and succession. These patches differ in their species composition, physiognomy, and productivity, and consequently in the resources and shelter

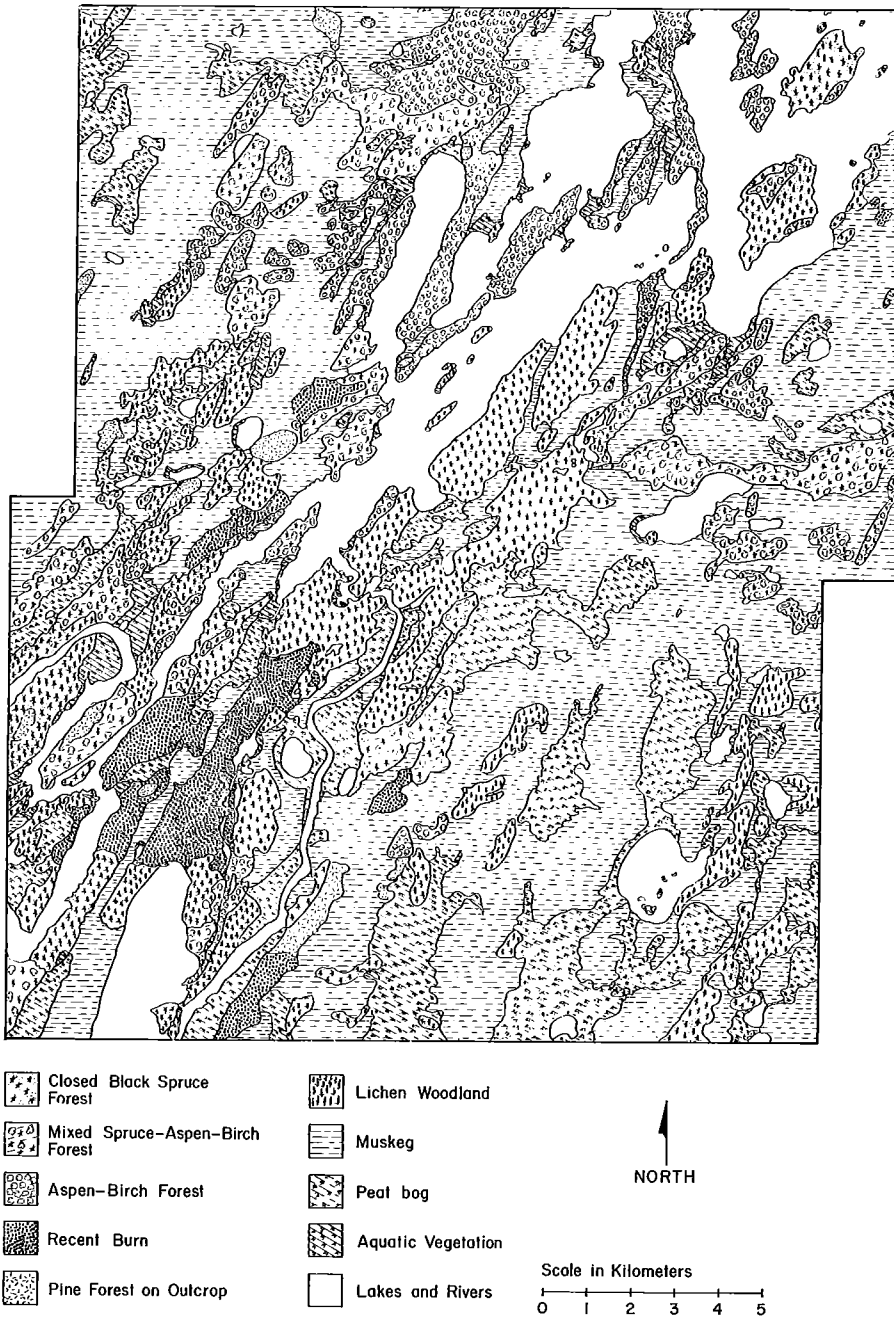


Figure 4.4. The Vegetation Mosaic. The definition and recognition of these associations are based on Ritchie's (1956 1958 1960) research in the Manitoba boreal forest, somewhat modified by field observations and by the work of the botanists Moir (1958) and Hustich (1957) within the Severn River drainage (see Winterhalder 1977:128-48). A stereoscopic interpretation of black and white air photos (provided by the National Airphoto Library, Survey and Mapping Branch, Energy Mines and Resources, Ottawa) was used in preparation of the map. The interpretation relied on (a) the author's familiarity with the area; (b) a series of low-level color air photos taken by the author at the autumn peak of vegetation color distinctions, which overlapped and could be correlated with the textural and tonal features of the high-altitude photos; and (c) reference to publications describing the preparation of similar maps of boreal forest vegetation (Larsen 1962 1972; Ritchie 1958).

they offer various animal species. Each has different qualities with respect to the game it attracts, and the impediments it places between forager and prey.

Figure 4.4 is a vegetation association map, based on air photo analysis, which demonstrates the pattern of ten patch types which can be distinguished by their composition and physiognomy, and by their functional distinctions with respect to resources important to Cree foraging.

Table 4.1 is a quantitative analysis of the area depicted in figure 4.4. Several things stand out. First, fifty per cent of the area is muskeg or peat bogs, relatively unproductive habitats for terrestrial mammals and difficult ones for the Cree forager in summer. Another eighteen per cent is covered by water. The remainder of the habitat is upland patch types, for the most part in various stages of succession from recent burns to the climax association for this area--closed black spruce forest. The exceptions are the rarely occurring rock outcrops which support pine forests or lichen woodlands. Unlike the boreal forest areas of either Manitoba or Quebec, northwestern Ontario, for climatic and edaphic reasons (Ahti and Hepburn 1967:26-29, 52) does not have extensive areas of lichen woodland.

Table 4.1

Vegetation Patch Types: Number, Size, and Proportional Area

Patch Type	Number of Patches	Mean Size (km <sup>2</sup> )	Total Area (km <sup>2</sup> )	% of All Area	% of Upland (Successional) Area
Closed black spruce forest	74	.73	53.9	12	39
Mixed spruce-aspen-birch forest	55	.64	35.1	08	26
Aspen-birch forest	29	.76	22.1	05	16
Recent burn	10	1.38	13.8	03	10
Pine forest on rock outcrop	17	.14	2.4	01	03
Lichen woodland	13	.53	6.8	02	06
Muskeg	38	4.24	161.0	37	
Peat bog	57	.99	56.4	13	
Aquatic vegetation	38	.20	7.6	02	
Lakes and rivers					
Muskrat Dam Lake	1	63.10	63.1	14	
Others	54	.30	16.4	04	
Total	386		438.6	101	100

Note: The sizes of individual patches were calculated by placing a transparent point grid, calibrated on geometric shapes of known area, over the air photos used to prepare figure 4.4. A regression equation established the relationship between point counts for patches and their areas. Source: Winterhalder 1977:145.

The scale of heterogeneity of this habitat is important. The mean size of the productive upland patches is small (generally < 1 km<sup>2</sup>) relative to the range normally covered by a human forager. For instance, Rogers (1963:57) records family "hunting group" (3-5 families) areas of approximately 700 km<sup>2</sup> for the Pekangikum area of Ontario.

The vegetation mosaic presented in figure 4.4 is a dynamic one. The large areas of

muskeg, bogs, and fens have developed to their present state over a period of several thousand years (Terasmae 1970). But upland patch types have a high rate of repeated disturbance followed by succession. A given locality burns from natural causes every 100-150 years (Rowe and Scotter 1973:447; Viereck 1973:474). Away from population centers, lightning-caused fires predominate (Johnson and Rowe 1975:3; Viereck 1973:471). This ignition source guarantees the irregular distribution of early successional patches in space and time. Most fires are small: eighty-eight per cent of those in northern Saskatchewan burn less than forty-one hectares (Rowe and Scotter 1973:452). On this basis Rowe and Scotter (1973:453) state: "These figures suggest good reason for the patchiness of vegetation."

The greatest area, however, is burned by the rare, large fire:

But rarely do such conflagrations completely demolish the forest. Because of the vagaries of wind, and to some extent because of topography and the disposition of wetlands and water bodies, islands of undamaged vegetation escape. In fact some students of fire believe that the forest patchwork pattern is as much due to isolated remnants in a burned matrix as to spot fires in an unburned matrix.

[Rowe and Scotter 1973:453]

Wind throw and snow throw (Pruitt 1958:169; Ritchie 1956:528) can also create successional gaps in the shallowly rooted trees of the spruce-dominated climax forest.

The result of these disturbances is a small-scaled mosaic of vegetation patch types, even-aged and homogeneous in composition, abruptly and irregularly bounded (Ritchie 1956:532). The disturbances, and particularly fire, stimulate a flush of herbaceous and woody growth (Shafi and Yarranton 1973a 1973b), which represents quickly appearing and localized pockets of high and accessible productivity (Wright and Heinzelman 1973:324-25), attracting a variety of animal species.

Faunal succession follows plant succession, and there are optimum habitat or stages of plant succession for every animal species. Therefore, inasmuch as fire initiates and terminates succession it exerts both short-term and long-term effects . . . the conclusion must be that any influence tending toward diversifying the landscape at large and small scales will increase the diversity of the fauna as well as the population density of some species. By maintaining a mosaic pattern in the boreal forest, fire assists in the maintenance of diverse wildlife populations. [Rowe and Scotter 1973:457-58]

Within about fifty years a canopy forms and browse diversity decreases (Shafi and Yarranton 1973a:88). As noted earlier, the climax association, a spruce canopy over a feather moss mat, attracts few game species.

This vegetation dynamic has a scale roughly equivalent to the life span of the hunter, and draws the forager's attention closely to the microgeography of the vegetation landscape.

*Fauna: resource species population characteristics.* Currently the Cree of Muskrat Dam Lake depend entirely on fauna for their locally derived resources. Consequently the population and distributional characteristics of fish, waterfowl, and semiaquatic and terrestrial mammals are of central importance.

Table 4.2 summarizes, in highly condensed form, the population characteristics of major boreal forest resource species. This table is based on an extensive review of ecological and game management literature for this region, recorded in Winterhalder (1977). For the major species, biomass and density estimates, the stability of the population, the pattern of recurrence (recovery from depressions in population numbers), and the early winter group size are given.

Table 4.2  
Population Characteristics of Major Resource Species

	Biomass (kg/km <sup>2</sup> )	Density (No/100 km <sup>2</sup> )	Stability	Recurrence	Early Winter Group Size
Moose	17.2 (+ -)	5.6	Moderate	Irregular Short-term	680 kg (+ -) 1.8 individuals
Caribou	0.7 (+ -)	0.5	Moderate	Irregular Long-term	900 kg (+ -) 6 individuals
Beaver	20.9 (+ --)	185	Moderate	Irregular Short-term	100 kg (+ -) 5 individuals
Muskrat	34.2 (++ --)	3,800	Low	Cyclic--10 yr Irregular	0.9 kg individual
Hare	1,610 - 18.2	115,000 - 1,300	Low	Cyclic--10 yr	1.5 kg individual
Ruffed grouse	54.0 - 6.0	8,600 - 1,000	Low	Cyclic--10 yr	1.8 kg (+ -) 3 individuals
Spruce grouse	18.5 - Low	3,090 - Low	Low	Cyclic--10 yr	1.8 kg (+ -) 3 individuals
Fish	675		High		

Note: The +'s and -'s in parentheses are meant to indicate especially broad upper and lower boundaries of persistence relative to the estimate. The summary parameters used in this table (e.g., persistence, stability, and recurrence) are explained in Winterhalder 1980b. Source: Winterhalder 1977:275, with modification.

Several points stand out. The biomass of the large mammals, moose and caribou, is low compared with that of the smaller organisms. Cyclic, or periodic but irregular, population fluctuations are known to occur in all species, except fish. Fish populations are fairly stable according to records from commercial fisheries in the north (MacKay 1963). Northern Canadian mammals and game birds are known for their dramatic population fluctuations (Bulmer 1974; Elton 1942; Keith 1963; Winterhalder 1980a), documented in thorough historical records kept by the Hudson's Bay Company and its interior post traders, and more recently by the extensive zoological study which the cyclic fluctuations have stimulated (Keith 1974). As a result, a long-term record is available on this natural resource base, unlike that available for most other habitats.

The amplitude, frequency, and regularity of population fluctuations for these species are important to the boreal forager, and are indicated by each species' population stability and by the regularity and rate of its recurrence from points of low population density (table 4.2).

The final column of table 4.2 roughly indicates the dispersion pattern of each species as it is affected by sociality. Moose are predominantly solitary; woodland caribou are found in small herds. Beaver occur in family groups, regularly dispersed over the landscape because of territoriality and the fairly even availability of lodge sites. The remaining terrestrial mammals and game birds are either solitary or found in small groups during at least some seasons. With the exception of caribou, which are of negligible biomass in this region, none of these animals is aggregated into large groups. They are not, therefore, patchily distributed by virtue of social aggregation.

The habitat preferences of these species provide the key to their dispersion patterns (table 4.3). Each species is associated with only certain vegetation patch types. The Cree forager knows that each game species occupies certain landscape areas preferentially and can be found in specific types of habitats most of the time. Table 4.3 also indicates

Table 4.3

*Habitat Associations of Major Resource Species*

Resource	Patch or Vegetation Type Association	Notes
Moose Winter	Aspen-birch forest Recent burn Lake margins	Deep snowfall strengthens winter patch association
Summer	Aquatic vegetation Lake margins	Low water, heat, and insects strengthen summer patch association
Caribou Winter	Closed black spruce forest Pine forest on outcrop Lichen woodland	Deep snowfall strengthens winter patch association, especially for pine forest on outcrop
Summer	Peat bog	
Beaver	Aquatic vegetation Lake margins	
Muskrat	Aquatic vegetation	
Hare Winter	Aspen-birch forest Recent burn	Association with specific patch types increases during fall, winter, and spring, and when populations are low
Summer	Various	
Ruffed grouse	Aspen-birch forest Recent burn Lake margins	
Spruce grouse	Closed black spruce forest Spruce-aspen-birch forest	
Fish	Aquatic vegetation Open water	Association with the shallow water habitat is temperature influenced and increases in spring and fall and with spawning

Source: Winterhalder 1977:277.

that the associations change with the seasons, and that population density and secondary climatic factors can determine the probability that particular animals will be confined to distinct vegetation patches. For instance, as noted earlier, as winter snow depth increases, moose are increasingly confined within small areas offering abundant browse, because of the difficulty and high energy costs of movement between preferred patch types. And in summer, high temperatures, thick insects, and low water levels increase the chance that moose can be found in or near aquatic habitats. Resource patchiness for the Cree forager arises in the association of each animal species with particular vegetation patch types scattered over the boreal landscape.

The boreal forest presents a dramatic example of what is probably common to all habitats: regular and irregular fluctuations of the biomass of game species, with week synchronization among species. Each year the forager faces a somewhat different set of game densities. Over a period of decades it is unlikely that the same proportional distribution of population densities repeats. If the vagaries of resource densities are combined with those of the secondary climatic elements affecting foragers and game, and these are combined with changes in the environmental mosaic, an important conclusion emerges: on the scale of a hunter's life span, and at the detail at which foraging decisions are affected,



the constellation of environmental factors significant to foraging decisions is a nonrecurrent phenomenon.

Applicable Foraging Hypotheses

In terms of the models, then, these points emerge concerning the effective environment of the Cree forager:

- a. The boreal environment contains a large number of potential resources. Resource species are generally of fairly low density, scattered, and either solitary or in small groups. This leads to the expectation that the Cree will expend considerable energy searching for organisms, and, as a consequence, to the hypothesis that they have a generalized diet breadth.
- b. In addition, the resources available are patchily distributed. Thus, the environmental conditions assumed in the models for patch selection and movement in a heterogeneous environment are present. The scale (or grain) of the environmental mosaic is small relative to the usual range of a Cree forager, and a generalized use of patch types is hypothesized.

The analysis of Cree foraging in terms of time and energy investment and energy return provides information on the ranking of different resources or patch types, and on the relative costs of searching for and pursuing various species. An evaluation of foraging in terms of the energy currency is the basic content of the parameters of the models examined here. Table 4.4 presents the net acquisition rate and net acquisition rate per unit of pursuit time for the foraging activities measured in 1975. The measurements are differentiated by species and in some cases by season or capture technique. Figure 4.5 presents a composite seasonal profile of the foraging energetics of major resource species, also for the year 1975. The curves are complete for all species except beaver. For this organism data were insufficient to make the seasonal extrapolations.

**Net Acquisition Efficiencies, 1975**

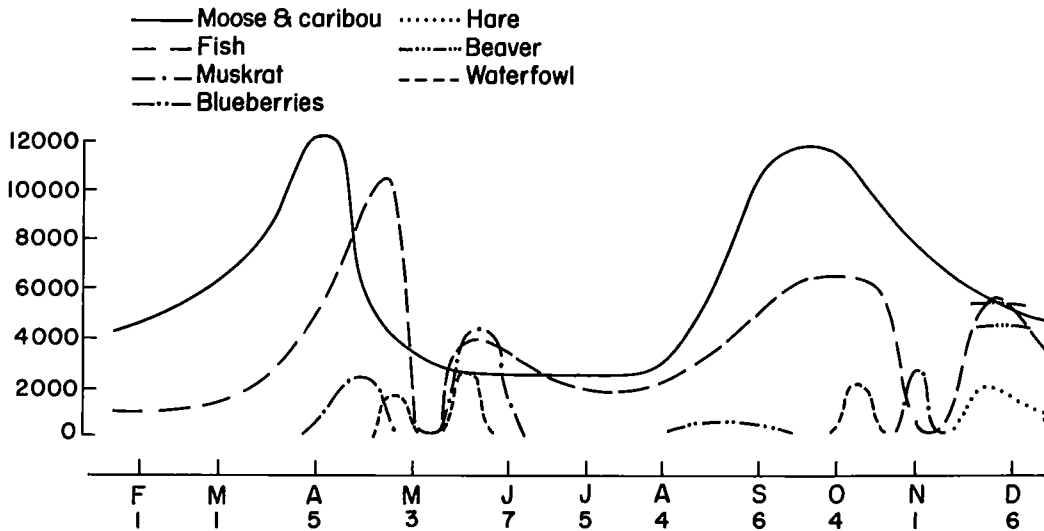


Figure 4.5. Seasonal Net Acquisition Efficiencies of Foraging for Various Resources. All of the curves are complete for the year, with the exception of beaver.

Table 4.4

## Measured Net Acquisition Rate of Foraging for Various Resources

Resource and Dates	Net Acquisition Rate (kcal/hr)	Net Acquisition Rate/Pursuit Time (kcal/hr) <sup>1</sup>
Moose and caribou <sup>2</sup>		
Winter	6,050	8,220
Early spring	11,950	25,140
Summer and fall	5,920	95,600
Fall (rut)	11,280	
Net fishing		
Winter, net 1	1,060	1,790
Spring, net 2	3,180	3,710
Spring, net 3	9,680	11,660
Summer, net 4	2,260	21,340
Summer, net 5	5,320	34,000
Fall, net 6	6,390	7,980
Hare snaring <sup>3</sup>		
Fall (measured)	1,900	8,260
Fall (hypothetical)	8,180	15,220

1. Calculation of this parameter required separation of search and pursuit costs. The working distinction between these two variables was not always evident, necessitating the following conventions (Winterhalder 1977:600-601):

All foraging costs up to the point of deciding to pursue a particular animal, or unit of organisms if it was a herd, flock, or other group, were designated as searching. Pursuit costs began when an animal was located visually, by tracks, or by some other indication of immediate presence, such as a fresh sign at a beaver lodge. The travel costs of returning to a village following a successful or unsuccessful pursuit were allotted to searching. It was always possible that another prey organism would be located and pursued. For large game the costs of processing and retrieval were designated as pursuit. If pursuit of an animal was resumed on a following day, the costs of reaching the site where pursuit left off were designated as search. Again, there was the possibility of locating a more promising animal for pursuit.

Traps, snares, and nets were handled similarly. All costs up to the point that a location was chosen for the capture device were allotted to searching. Such devices are often set in response to the same animal signs that would initiate active pursuit of other species. The costs of setting, maintaining and checking, and resetting the device were assigned to pursuit, but not travel costs to and from it. The decision to suspend generalized searching and to pursue a particular prey marks the functional distinction between search and pursuit for purposes of the model and the above conventions.

2. See figure 4.6.

3. The measured efficiency of snaring hare refers to 1975, the first year of hare population recovery from a cyclic low. Hare remained quite scarce and were snared only for several weeks in the fall, the peak of their seasonal density fluctuation. The hypothetical efficiency is based on measured costs of locating and maintaining a snare line, with both effort and returns adjusted to reflect reported catches during years of hare abundance.

Resource and Dates	Net Acquisition Rate (kcal/hr)	Net Acquisition Rate/Pursuit Time (kcal/hr) <sup>1</sup>
Muskrats <sup>4</sup>		
Spring trapping, case 1	250	1,280
Spring trapping, case 2	2,500	6,230
Fall hunting, case 1	2,370	4,740
Fall hunting, case 2	1,330	
Beaver <sup>5</sup>		
Early winter trapping	1,640	5,690
Early winter trapping (est.)	4,360	23,620
Early winter trapping (est.)	5,280	
Waterfowl		
Pre-break-up	720	3,000
Post-break-up	1,980	
Pre-freeze-up	1,190	
Game birds		
Grouse, case 1		1,740
Grouse, case 2		1,220
Vegetable foods		
Blueberries	250	650

4. The first case of spring muskrat trapping was described as unsuccessful; the second case is more representative of the expected efficiency of this type of foraging. Both instances of fall hunting fall within expected ranges of catch and effort.

5. The three values given for early winter beaver trapping represent three different cases. Time and energy costs, and returns, for the lowest efficiency case were measured in detail, but the effort was considered unsuccessful by the trapper. Consequently, two additional cases with more representative catches were recorded. The two estimated efficiencies then are calculated on the basis of known catches and reconstructed time and energy costs based on descriptions by the trappers involved.

Source: Winterhalder 1977:486.

The full data base for the energy measurements recorded in table 4.4 will be presented elsewhere. Figure 4.6 demonstrates how the energy efficiency curve was derived for moose and caribou. The bottom graph shows the distribution of the sample of analyzed hunting trips. The solid horizontal lines in the middle figure show the measured net acquisition rate and the duration for the sample. In this case the year was divided into a winter period of hunting on snowshoes (November through the beginning of March); a spring period in April (when a unique set of weather conditions produced a hard, powder-covered snow crust and unusually favorable hunting conditions); a lengthy summer and fall period (May through October) when moose were sought along waterways from canoes; and a brief period (during September) when the rut again created a highly favorable hunting situation. Differentiation of these intervals is thus based on seasonality and aspects of the environment or animal behavior which made hunting unique with respect to tactics and success. The dashed line interpolates a seasonal profile from those data, based on the measured levels and diverse sources of less quantitative information about the factors influencing the costs and success of moose hunting (Winterhalder 1977). The top graph shows the annual distribution of the community moose harvest (only some of these animals were captured on hunts represented in the energy analysis sample).

This particular curve for moose and caribou, and the similar curves drawn for other organisms (figure 4.5), are to some extent unique to the sample year, 1975. The April peak of energy efficiency derives in part from the peculiar weather and snow crust conditions of this period. Such a peak may not occur in other years. Similarly, the low efficiency of the summer sample stems in part from the unusually high water levels of 1975. Cree foragers watched the river carefully for signs that the flow would recede and improve their chances of finding moose. In a summer with lower water levels the energy efficiency of moose hunting could be considerably greater for reasons cited earlier. Similar idiosyncracies affect the costs of locating and pursuing each species, and although they are cited as peculiarities, the numerous sources of variability affecting the forager in this environment ensure that each year is one of peculiarities.

In a fine-grained search situation, as postulated for the diet breadth model, pursuit efficiency takes on special importance. An alternative statement of the main hypothesis of this model is as follows: When an organism is encountered it should be pursued if, and only if, in the same interval the forager is unlikely to encounter and capture an organism with a greater net return (MacArthur 1972:62). This allows organisms to be ranked for purposes of the model by the efficiency with which they can be pursued. This is important, because pursuit efficiency for *individual organisms* is much more easily derived from field data than is acquisition efficiency. Table 4.4, then, also gives the net acquisition rate per unit of pursuit time. With a few exceptions this parallels the general net acquisition rate.

#### Foraging Patterns in Relation to Those Hypothesized

In order to evaluate the optimal foraging predictions it is necessary to provide some general information on Cree hunting and gathering. The data used to construct figure 4.5 are based on isolated foraging trips. The net acquisition rate was determined from trips during which only one species was captured (although others would have been pursued had they been located), and, in effect, this sample draws on limited search success to isolate values for a particular species.

The important question in verifying the hypothesis of optimal diet breadth is not, What animals were successfully captured on a hunting trip? A given trip may result in the

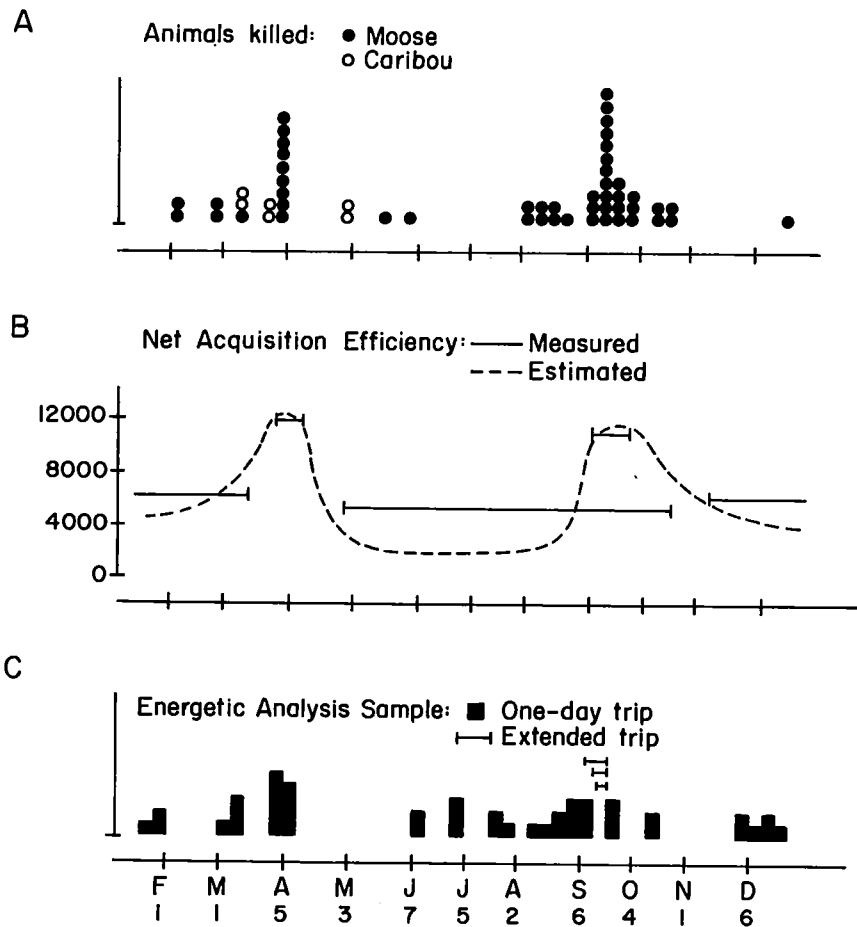


Figure 4.6. Calculations of Seasonal Energetics of Moose and Caribou Hunting. (A) Seasonal distribution, by week, of large game kills during 1975; (B) Measured and estimated net acquisition efficiency; (C) The energy analysis sample. The letters below the abscissa indicate months; the numbers the first date in each month that initiated a weekly sample period.

forager's encountering only a portion of the organisms in its actual diet breadth at that time. The appropriate question is, What organisms will the forager pursue if they are encountered? Determining this for nonhuman foragers is difficult. Anthropologists have the advantage of being able to ask. Or, even better, if differing technologies are used for various species then the equipment carried by the forager will be a fair clue to the organisms which will be pursued if located. The latter evidence is important in the Cree case. Each species (or species group in the case of waterfowl and fish) has its weapon, and although a hunter may say that the trip is for moose hunting, if a shotgun is included then ducks or geese will probably also be pursued if encountered. On a certain trip the forager may come back with the full complement of organisms being sought, but this is fairly rare.

Seasonally, the pattern of Cree hunting parallels fairly closely the acquisition efficiency ranking of prey species in figure 4.5 and table 4.4. Several examples will demonstrate this. In early winter trips (November-December), designated as beaver trapping,

Cree foragers also pursued (by trap, snare, or rifle) moose, grouse, and hare (in addition to the furbearers muskrat, mink, and otter). In the period shortly after break-up (late May, early June), the array of rifles and capture devices taken and the actual species pursued and captured indicated that, besides waterfowl, muskrats and beaver were pursued when located, and that moose would have been pursued if located in an accessible aquatic area. These species were potential prey, part of the diet breadth, along with the waterfowl and loons that were the express objects of the trips. Moose and caribou hunting trips usually focus on these animals in winter and early spring, but beaver snare wire is often included in the materials taken, and grouse will be shot (with a .22) if the noise is not likely to interfere with locating or pursuing moose. During summer trips, expressly for moose hunting, a shotgun is included, and adult waterfowl are hunted if encountered. Whatever the stated purpose of a foraging trip, the Cree hunter is rarely without a .30-.30 for moose.

Although the set of curves in figure 4.5 is assembled from hunting trips in which only one or a few species were captured, the diet breadth of the Cree forager closely parallels that suggested by the net acquisition efficiency rankings. On a hunting trip at a given point in the annual cycle the forager is prepared to pursue the set of species which have a net acquisition rate of roughly 1,500 kcal/hr or better. When the capture rate falls below this general value, dissatisfaction is expressed, and the pursuit of that species often stopped. The spring trapping of muskrats, and pre-break-up waterfowl hunting, are examples. The hare snare line, which had a net acquisition rate of 1,900 kcal/hr for a period of several weeks, was discontinued because hare were scarce, and it was felt that the success of the line would decline. For most of the year this foraging cutoff results in a moderate diet breadth.

Further confirmation of this point comes from table 4.5. The table gives four ways of ranking resources by their value to the forager in 1975: the actual harvest, biomass of the organisms, net acquisition rate, and the short-term reliability of capture once the organism is located. The table demonstrates that the rank order of the harvest corresponds more closely to that of the efficiency measure than it does to the biomass of the organisms present. Although this comparison overlooks much of the complexity of the situation, such as seasonal restrictions of some of the energy samples, these results are fairly striking. The net acquisition efficiency corresponds closely to the actual ranking of the harvest, and the harvest bears little relationship to biomass.

A familiarity with Cree hunting tactics provides substance and detail to this discussion. I will describe a foraging trip that occurred in late November, shortly after freeze-up. I accompanied another man. We traveled 12 km downriver by snowmobile and then left the snowmobiles to continue on snowshoe. The whole trip lasted 5 1/2 hours.

The trip was described as one for beaver trapping. But in the course of several hours we encountered tracks or sign of grouse, moose, wolf, hare, beaver, mink, otter, fisher, and muskrat. As each sign was located, the forager appraised the situation and decided whether or not to pursue the organism. The decisions were as follows: the grouse were shot with a .22; the moose was passed up, as the trail was old and the snow conditions poor for tracking it quietly; the wolf was passed up, because wolves move rapidly and although the trail was fresh, the wolf was probably distant; snares were set for the hare and beaver; and traps were set for the muskrat and otter. This example demonstrates the correspondence between the model parameters, especially the differentiation of search and pursuit, and the actual tactics of Cree hunting.

Table 4.5

Four Ways of Ranking Resource Species in the Boreal Forest by Their Value to the Forager

Biomass (kg/km <sup>2</sup> )	Harvest (kcalx10 <sup>6</sup> )	Activity and Net Acquisition Rate (kcal/hr)	Short-Term Reliability
Fish (675)	Moose (23.5)	Moose, spring (11,950) Moose, fall (11,280)	Fish (high)
Small mammals (110)	Beaver (6.9)	Fish, net 3 (9,680) Fish, net 6 (6,390)	Hare (mod-high)
Muskrat (34)	Fish (3.5)	Moose, winter (6,050) Moose, sum-fall (5,920)	Muskrat (mod)
Beaver (21)	Caribou (1.3)	Fish, net 5 (5,320) Beaver, est. (4,820)	Beaver (mod)
Hare (20)	Muskrat (0.4)	Fish, net 2 (3,180) Muskrat, trap 2 (2,500)	Spruce grouse (mod)
Moose (17)	Waterfowl (0.3)	Muskrat, hunt 1 (2,370) Fish, net 4 (2,260)	Ruffed grouse (mod)
Ruffed grouse (10)	Hare (0.2)	Waterfowl Post-break-up (1,980)	Waterfowl (mod-low)
Spruce grouse (10)	Ruffed grouse (?)	Hare, meas. (1,900) Beaver, meas. (1,640)	Moose (low)
Waterfowl (?)	Spruce grouse (?)	Muskrat (1,330) Waterfowl Pre-freeze-up (1,190)	Caribou (low)
Caribou (1)	Carnivores	Fish, net 1 (1,060)	
Carnivores	Small mammals	Waterfowl Pre-break-up (720)	
Passerine birds	Passerine birds	Muskrat, trap 1 (250) Grouse Grouse Blueberries (250)	

Note: The relatively high harvests of beaver and muskrat reflect their value as furbearers in addition to the food resources they provide. Source: Winterhalder 1977:501, with modification.

These results provide a basis for examining historical evidence of changes in diet breadth. The sequential adoption by the Cree of two sets of foraging technologies--the earlier acquisition of improved pursuit devices such as muskets and repeating rifles, traps, and nets, and the more recent introduction of motorized transport, snowmobiles, and outboards--provides important comparative information. The earlier technologies improved the efficiency of pursuing prey species; the later the efficiency of searching for prey (figure 4.7). Here I focus primarily on the more recent change, that affecting the mobility and velocity of the search phase of foraging.

The optimal diet breadth model produces the hypothesis that an increase in the efficiency of searching should result in a constriction of diet breadth. Snowmobiles and outboard motors provide that increase. On a packed snow surface over ice, snowmobiles can reach a velocity of 20 - 35 km/hr, whereas a man walking on snowshoes averages about 5 - 8 km/hr. A light outboard (10 hp) can push a canoe at 20 km/hr; the same canoe paddled over long distances moves at a much slower velocity. In the comparison being made we can look

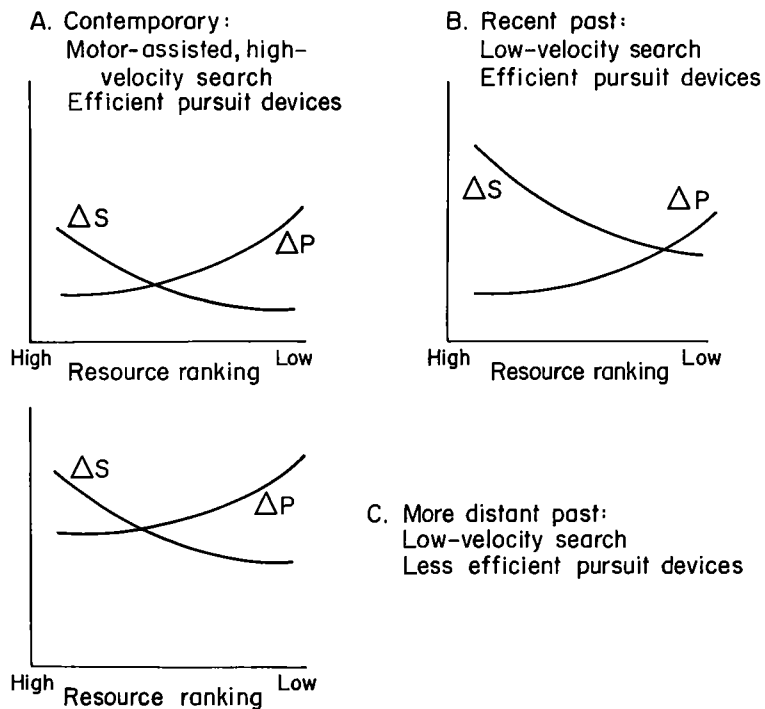


Figure 4.7. Optimal Diet Breadths Hypothesized for Three Historical Periods. (A) In the contemporary situation the use of outboard motors and snowmobiles and efficient steel traps, wire snares, and repeating rifles has kept search and pursuit costs low. Short-term diet breadth is fairly narrow in these circumstances. (B) Prior to the use of snowmobiles and outboard motors search velocity was lower and search costs in time and metabolic energy higher. Pursuit costs generally would have remained the same, leading to the prediction of a more generalized short-term diet during this period. (C) In the more distant past, prior to the widespread use of snare wire, steel traps, and repeating rifles, pursuit costs would be higher than in either the contemporary situation or the recent past. Again, the prediction is for a fairly narrow short-term diet breadth, one which does not necessarily include the same species as in case A.

to the period prior to the use of these devices as one of much slower search movements, leading to the hypothesis of a broader diet breadth. Outboards have come into use in northern Ontario within the past thirty years, and snowmobiles within the past 10-12 years, so that the changes they produced are well within the experience of older hunters and parts of the ethnographic record.

Several types of evidence confirm that the hypothesis accurately depicts this transition: Foragers state that access to snowmobiles and outboards, and increased ability to purchase fuel, have changed their hunting habits. There is a tendency to travel more and to do less looking for low-priority species. This comment, in the context of a discussion of moose hunting, is typical: "Before, I had to get by with just a little gas. I had to come back with something, like a beaver, or I didn't get any more gas. It was true for other animals too." The reduction in search time, and the reduced need of an immediate return, have limited the variety of animals sought on a given trip. Foragers with high mobility give little thought to traveling 30 km to a good location to look for moose, or to traveling that far to find moose tracks, while passing by evidence of other, less



valued, species. Foragers on snowshoes, or paddling a canoe, pursued such species long before these distances were traveled.

The hunting trip described above can be taken as indicative of an older style of foraging. A snowmobile was used to travel to a trail distant from the village, but the search and pursuit were done on snowshoe in areas not accessible to snowmobile travel. Velocity was slow, and a variety of animals were sought; the diet breadth was fairly wide. Older trappers comment that they always took a variety of traps and snares and used them for the different animals as they were located.

But ethnographic evidence is generally not of the right kind or of sufficient detail to determine the short-term diet breadth of boreal foragers. An exception is Rogers's weekly account (1973:table 4) of the game taken by a hunting group of Mistassini Cree with whom he traveled during the winter of 1953-54. At this time the Mistassini used outboards to travel between camps, but when hunting they paddled. Winter travel was by snowshoe, with the occasional assistance of a dogsled (Rogers 1973:7). In his report Rogers lumped fish species, and separated avian species into loons, geese, ducks, grouse, terns, and owls. Thirteen additional species were listed separately. Over a thirty-nine week period an average of five different species were captured each week. Presumably the diet breadth was larger than this; the game searched for and perhaps even located and pursued was more various than that captured in a given week. For instance, although moose were taken in only six of the sample weeks, it is probable that this animal was included in the diet breadth throughout the period. All of the species or species groups were harvested at some point, with the exception of weasel, fox, and tern.

The diet breadth of the foraging effort in this case is greater than that at Muskrat Dam Lake today, and species were taken that would not be taken today (e.g., squirrel, bear), even though encountered in the course of foraging. Again, this is consistent with the hypothesis. Other anthropologists working in northern Canada have observed that the introduction of snowmobiles has led to more specialized hunting (Hurlich, pers. comm.; McCormack, pers. comm.).

A fourth kind of evidence can be cited on this point--the qualities by which older Cree judge a hunter. One stands out: "A good hunter is someone who knows how to hunt all of the animals." People said that today the younger men know how to hunt or trap one or two animals, and that they are sometimes proficient at capturing those. But by an older standard this is not equated with being competent in the most desirable sense: "The good hunter . . . knows how to catch all of the animals, even if he isn't too good at any one of them." This is an evaluation made most emphatically by the older adults, and it lingers from a period when game was sought by snowshoe or paddle.

There is, then, good evidence to substantiate the hypothesis that diet breadth was wider prior to the use of snowmobiles and outboards.

A third and earlier situation can be envisioned, without motorized transport, but also without the pursuit efficiency afforded by repeating rifles, steel traps, and nylon fishnets (figure 4.7). In the nineteenth century and earlier, the bow and arrow, muzzle-loading rifle, pole snares, handwoven nets, weir fish traps, and deadfall traps were used. These are all technologies which are either less effective or less convenient to use, or which require greater effort in construction or maintenance than present devices and techniques. Relative to the contemporary situation, it would have been a period when high search costs (due to the absence of motorized transport) were matched by fairly high pursuit costs. In this circumstance the diet breadth model predicts a constriction in diet breadth, coupled generally with less efficient foraging.

I have not yet tested this hypothesis, although the extensive ethnohistorical (and ethnoecological) evidence available for the Canadian North makes it probable that information is available for at least a partial confirmation or refutation.

The patch use model produced the hypothesis of a generalized use of the habitat mosaic. In fact, the foraging behavior of the Cree does not fully bear this out. Foraging itineraries touch on relatively few patch types. In part this is owing to the high mobility of contemporary hunters. Snowmobiles and outboards greatly reduce the cost of travel between productive patches. This reduction, which does not affect hunting costs, should favor specialization, and it appears to do so. Cree foragers know the location of favorable patches and can travel to them quickly. As with diet breadth, there is some evidence that Cree hunters sought resources in a broader variety of patch types prior to motorized transport and when the food quest was more important. Older hunters, for instance, recall that caribou were pursued into bogs and fens, a practice now abandoned because of its difficulty. But some other factors operate as well, making the predictions of the patch use model less reliable ones.

The impression of somewhat restricted habitat use is based partly on this observation: Cree seek particular prey species in fewer patch types than the species are known to inhabit at a given time. For example, it is known that moose frequent certain habitat areas near water in the summer, but they are sought only in or from the aquatic habitat. The limitation in this and other cases is a physical one: hunters avoid some patch types (e.g., bogs or muskeg) either because of the difficulty and high cost of moving about there, or because the noise of doing so, and the limited visibility (as in brushy areas), preclude finding an unaltered animal. The patch use model assumes that different patch types are homogeneous with respect to travel costs and the physical impediments they create for search and pursuit tactics, but this is not the case in the boreal forest. Different habitat types are unequal with respect to travel or foraging conditions.

In practice, however, the main reason that this model is less satisfactory arises from the implications of tracking. For some smaller species, such as muskrat, the Cree forager moves in the patch-to-patch fashion envisioned in the model. These animals are localized in discrete habitats, mainly the aquatic vegetation found in shallow, sheltered areas along river and lake shorelines. However, in the case of moose and caribou and some of the widely foraging carnivores (the furbearers), the prey species themselves move from patch to patch. Moose, for instance, will enter a small feeding patch and spend several days there, but move with regularity between such patches. In these instances the Cree forager, rather than seeking to locate the animal within a patch, searches instead for tracks located between patches. The Cree adopt an "interstice" foraging pattern. They follow the creeks and lakes of the drainage pattern, moving along the matrix which surrounds the more productive upland patch types.

The difference between a patch-to-patch and an interstice pattern is illustrated in figure 4.8. Moose move between patches fairly frequently relative to the duration of the trail they leave behind, and the number of animals is low compared with the number of patches they might inhabit. The Cree forager's tactic in this circumstance is to attempt to cross and thus discover old trails rather than to locate the moose directly within a patch.

This pattern has advantages besides shortening the travel route of the forager. With or without motorized transport, it is much easier to travel on the ice and hardpacked snow (or on the water) of streams and lakes than to enter the brushy upland habitats where the

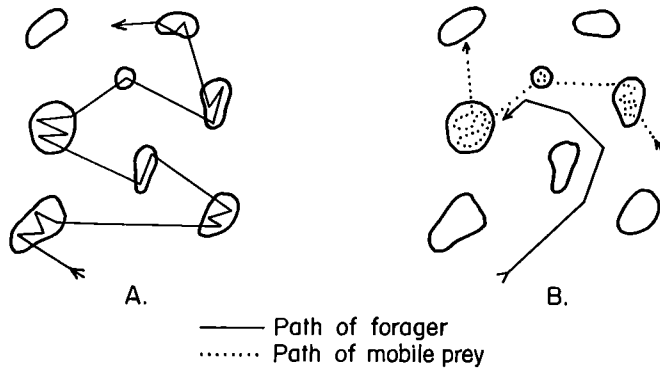


Figure 4.8. Alternative Foraging Tactics in a Patchy Environment. (A) In the MacArthur and Pianka (1966) model it is assumed that the forager moves from patch to patch in search of prey. (B) This research suggests a somewhat different model, in which the forager seeks mobile prey by moving in the interstices of the patches being visited by the resource organism. This kind of adaptation arises when prey spend time within, but regularly move among, small patches; the prey organisms (or groups if they are aggregated) are not abundant relative to the number of patches they are associated with; the forager relies on locating tracks or a trail as part of its search procedure.

snows are deep and soft and movement is slower and more costly. Second, for many prey species it is essential to anticipate the location of an unseen animal before the final stages of the pursuit. For example, a successful moose hunter must know the animal's location before coming too close to it. This is done by searching for tracks in habitats that the animal is traversing (rather than feeding in) and then adjusting the pursuit tactics to the location of feeding patches which the animal is likely to visit. Cree foragers have developed this technique to a high level of skill.

The interstice pattern presumably applies for any carnivore that preys on organisms that (a) themselves respond to patchy habitats of small grain size; and (b) move between patches in a regular manner. Because the pattern of interstice movement partially obviates the assumptions of the patch use model, it illustrates the importance of examining the constraints built into the models with field observations, and the value of field evidence to modeling in general. It should be possible to define the conditions under which the patch-to-patch pattern would, optimally, switch to the interstice pattern. The number and size of patches, the density of prey, the time prey animals spend within a patch, the frequency of movement between patches, and the life span of the trail left behind would be key variables.

The data gathered on Cree foraging are not sufficient to make a quantitative test of the marginal value theorem. They do provide anecdotal support for the hypothesis that foragers leave patches before they are depleted of the resource(s) being sought there. Thus, in 1975 visits to patches to snare hare were stopped in the late fall in favor of other foraging activities, even though the patches continued to produce animals. Referring to previous years, foragers described abandoning a snareline set around a felled tree for a fresh location, even though the original site continued to be productive. During spring trapping, only the most favorable muskrat push-ups were chosen for trap sets, and then the trapper moved to another patch to pursue only the most promising set locations. In the

fall, muskrat are shot with .22s as they sit on the newly formed ice mats found over aquatic habitats along river banks. Several animals would be taken from each area, but a patch was abandoned when the muskrats became scarce (but not entirely depleted) in favor of other patches where they were more abundant because not recently hunted. Finally, although a beaver house may have 3-5 underwater shoots (openings), snares are set at only two or three of these, suggesting that the return is greater on two snares at the next beaver house than on the additional snares at a house which already has some. In each of these examples the forager moved to the next patch before exhausting the resources or capture opportunities of the one being foraged. This is the pattern suggested by the marginal value theorem, but how closely the marginal return at the point of a decision to move on approximates the average return from the habitat is not known.

### Discussion

#### Theory Assumptions, Models, and Tests of the Hypotheses

The models and variables applied in this specific analysis of Cree foraging are general ones. Search and pursuit time, patchiness, prey stabilities and distributions are variables --"sufficient parameters" in Levins's (1966) phrase--with wide applicability. Thus the broader lessons of these results apply beyond the temporal and geographic limits of ethnographic analysis in the boreal forest. It may also be true that some of the more specific points--for example, about nonrecurrence of the forager's environment--are similarly general.

The choice of an energy currency to measure subsistence goals produced good results. Energy effectively subsumed the complex set of variables that go into a forager's appraisal of resource opportunities: the size and quality of game species; their nutritional value; and the social rewards of their capture. And, for analysis of foraging, energy gave a fairly complete accounting of both sides of the cost-benefit ratios central to optimal foraging theory. Cultural constraints on energy optimization did not prove critical, although it should be stressed that these hypotheses were chosen for examination precisely to minimize this type of constraint.

The results obtained in the energy analysis of contemporary Cree foraging and the data available from historical sources confirm the hypotheses of the optimal diet breadth model. The dynamic expressed in the model itself conforms well to the practice of Cree foraging. This appears to be a model, with some qualifications noted below, that can be reliably applied in anthropological research.

The hypotheses about patch selectivity performed less well. The original model structure assumes a homogeneous space with respect to travel, and does not allow for alternate foraging patterns based on tracking of mobile prey. The first problem could be unique to the boreal forest; other biomes may have patch types less differentiated in these respects. The problem of tracking, however, may prove to be a more general deficiency of the model. Assessment of these qualifications will require more analyses in different environments.

Qualitative evidence supports the marginal value theorem, but the data are not complete enough to confirm the hypothesis in its stronger form. Unlike the models that make dichotomous, or simple, qualitative predictions (generalized versus specialized diet breadth; dispersed versus aggregated settlement pattern), this model focuses on a decision point in the middle of a range of complicated values. Given the complexities of foraging, and the vagaries of data collection, this type of hypothesis is less amenable to verification.

For the marginal value theorem it is useful to emphasize that most of its assumptions

(see below) and constraints, and the goals the model assumes, are indirectly confirmed by this research. The data *suggest* that the hypothesis is a reliable one.

The time interval used to assess foraging in this study--one year--is short given the temporal scale of human foraging activities and the dynamic qualities of the boreal forest over time intervals longer than the seasonal one. Three situations were identified which may compromise the validity of short assessment intervals (Winterhalder, chapter 2, above) --the effects of extended foraging in a limited area; delay of harvest for resources which are used exclusively; and investment in exploration. Although the general importance of these situations cannot be judged from the present study, two comments can be made. First, there is an obvious example of delay of harvest in the boreal forest: the beaver. Beaver lodges and their resident populations are visible, and sufficiently permanent in location and stable in number, that Cree foragers "manage" the harvest of those over which they have exclusive control. This is an alternative explanation for the use of fewer snares than there are snare locations at a beaver lodge, a practice cited above as possibly confirming the marginal value theorem. Second, although the dynamic quality of the boreal habitat, and particularly of its patch structure, makes exploration important, two considerations diminish the impact of this requirement on short-term foraging optimization: (a) By the time that a Cree forager is recognized as proficient, long experience within a given range has provided him or her with detailed knowledge of it. This is particularly evident in the density of ecologically and historically informative names which are applied to the micro-geography (Winterhalder, unpubl.). (b) Because of the extensive nature of searching, and the fine grain of the habitat structure, considerable information can be maintained incidentally to the regular foraging effort. Occasionally a forager deviates to check on a beaver lodge or notice how the browse is growing on a recent burn, but for the most part this information can remain current without much special effort. The maintenance of extensive habitat information by experienced foragers entails little cost exclusive of foraging itself.

The intimate knowledge the Cree forager has of an area raises a question about the random search assumption of these models. With the exception of beaver, the mobility and dispersal of prey and their association with a fine-grained habitat make the random prey encounter assumption a reasonable one. This is not the case, however, for patches. Cree foragers know the distribution of patches in their hunting areas closely. They can often choose foraging pathways which avoid encountering patch types which are not productive in a given situation. This does not compromise the applicability of either the patch use model or the marginal value theorem, provided that the effect of nonrandom searching on the model parameters is noted. In both cases habitat knowledge decreases the travel time which would otherwise be lost in encounters with unproductive patches. This implies greater specialization. In terms of the marginal value theorem, because the average return over the set of patches visited is somewhat greater, each patch should be abandoned somewhat sooner along the depression curve.

Fairly specialized use of habitat patches is the case for Cree foraging: the efficiency gained by knowing patch locations complements that of motorized transport for covering the intervening spaces. As noted earlier, the results obtained here are not sufficiently detailed to make a quantitative test of the effect of habitat knowledge on the marginal value theorem. In the case of muskrat hunting, cited earlier, when the hunter decided to leave one patch, the next productive location was already in mind.

Another factor not considered explicitly in foraging strategy theory, but of

immediate concern in Cree foraging decisions, is short-term risk with respect to a return on foraging effort. Moose and hare are examples. In some instances moose will have a higher net energy efficiency than hare, but, even so, a hunter could go for days or weeks without successfully capturing a moose. In contrast, a few hare will, with fair regularity, turn up in a snare line each night. Although possibly of lower efficiency, a foraging effort invested in hare snaring will produce food consistently and with less risk of shortages on a day-to-day basis. Grouse provide a second example. Although the net acquisition rate for their pursuit is fairly low by Cree standards (table 4.4), if grouse are encountered in the course of moose hunting they are usually shot. Grouse are reliably captured, and at the end of the day it is sometimes better to have a few grouse than an abstract vision of an efficiently sought but elusive moose.

Other things being equal, species with a low short-term risk of capture failure will be ranked preferentially to those with a higher risk. In the boreal forest, and perhaps elsewhere, these tend to be the smaller herbivores (table 4.5).

It should be evident by now that although the independent variables in these models are environmental, their action cannot be understood in complete ignorance of the specifics of foraging. It is not heterogeneity, the size or density of prey, or prey distribution *per se* that generate hypotheses, but rather these environmental parameters as they relate to foraging. The "independent" environmental variables become relevant with sufficient empirical understanding of foraging behavior to evaluate their relationship to the models. For example, prey must be ranked according to energy costs and benefits, and this involves evaluation of the forager's behavioral and technological capabilities for capturing each animal. Although the models and parameters are based on highly generalized ecological parameters, these parameters can be utilized only with some knowledge about the skills and behavior of the foragers.

Finally, there is a question of the independence of models, or alternatively, of the interrelationships among separate "decision sets" (see Winterhalder, chapter 2, above). Diet breadth and use of a patchy environment are the decision sets covered in this report. Actually, the information provided here does not suggest clear general conclusions concerning their adequacy or importance relative to one another. Are these decision sets conceptually appropriate? And if the decision sets are in conflict, which will take precedence? In this analysis the small grain size of the habitat structure does not diverge strongly from the fine-grained assumption of the diet breadth model, making it difficult to appraise these questions. Cree foragers *are* excluded from certain habitats that contain resources within their diet breadth, but the causes of this may be specific to the boreal forest. Indeed, it may not be feasible to seek a general resolution to these questions.

In the environmental analysis I stressed two sets of properties in the boreal forest that are highly variable and that directly affect foraging: secondary features of the environment (freeze-up and break-up, snow conditions, stream and lake levels), and the strong fluctuations in animal populations. The analysis of moose foraging gave several examples of how these environmental factors affect foraging, examples that could be multiplied for moose and extended to other species. It is apparent that the parameters of foraging models may be dynamic in ways not appreciated in the model itself, and any long-term view of foraging must take this into account. The search costs and pursuit costs of individual species may vary seasonally and on the longer term, with effects on diet selectivity and breadth. As the environment of the boreal forest is nonrecurrent, so too on a year-to-year basis are the details of foraging. This situation does not reduce the value of the foraging model, but it does indicate that such models should not be applied in static interpretations based

on a normative description of the environment (Winterhalder 1980b). Indeed, a virtue of these models is that they allow predictions to track such environmental variability.

Some experience with the details of Cree foraging, combined with analysis and interpretation using optimal foraging models, makes it possible to predict with some confidence the effect on foraging behavior of diverse environmental situations which may occur in the boreal forest. Optimal foraging strategy models provide that capacity by virtue of their realism and dynamic incorporation of a limited set of apposite environmental variables.

This analysis has demonstrated that the optimal foraging approach, the form of specific models, and the constraints contained in their structure and parameters are heuristically valuable for the analysis of human foraging behavior. Several hypotheses gained support, and others did not, for reasons which became evident during analysis, and which are informative in their own right. It is important to be candid about the strength of the case. Much of the field data were consumed in identifying the correct hypotheses, and in estimating model parameters. In an ideal scientific world independent data would be used to test hypotheses, but that has not always been possible in this chapter. There is another shortcoming of the energy efficiency results presented--I was able to measure the efficiency only of activities that were actually performed. Although considerable evidence indicates that they ceased to be performed because efficiency decreased below a certain point, short of experimental intervention, direct demonstration of this is impossible. For instance, while the biomass of very small mammals in the boreal forest is quite high (109 kg/km<sup>2</sup> for 4 species--squirrel, shrew, and two voles--in Alaskan boreal forest [Grodzinski 1971]), presumably they cannot be captured with sufficient efficiency for the Cree forager to pursue them. Ecological information can be developed to make this a reasonable argument, but for obvious reasons direct energy measurements are impossible.

What has emerged, then, is a strong case for analytic efficacy, for the use of the optimal foraging approach as a research procedure which can produce reliable predictions with conscientious application.

#### Implications for Archeology and Paleontology

Foraging strategy models have a variety of implications for interpretations of prehistoric human ecology, and for data gathering and analysis in prehistoric archeology. The support that the optimal foraging strategy approach has received here and in the rest of this volume charter a guarded license for application of this reasoning in prehistoric contexts. Caution is necessary because this theory, like other forms of adaptive optimization arguments (e.g., sociobiology), can readily stimulate the production of "just-so" stories (S. J. Gould 1978; Lewontin 1979b) of questionable analytic merit. Nevertheless, some points can be developed with fair reliability, and are an improvement over the more intuitive assertions which permeate the literature, and with which foraging strategy hypotheses sometimes differ.

Optimal foraging models can apparently predict the effects of technological changes such as the introduction of firearms or motorized transport, because these have specifiable impacts on model parameters. They should also be applicable to the analysis of other technological and morphological changes where similar foraging effects can be specified, such as alterations in stone tools or the development of bipedalism.

Perhaps the most important point is this: optimal foraging models do help identify the environmental variables affecting foraging behavior (see Sih 1979) and the manner of their action, and should do so in diverse situations.

There are a number of such possible variables: the relative abundances of game

species; their absolute abundances; the size of the available organisms; or the distribution or behavior of the organisms. Analyses of hunter-gatherer behavior are not consistent in the importance assigned to the variables mentioned. Archeologists and others (e.g., Simenstad, et al. 1978:405) sometimes assume, for instance, that harvest is proportional to biomass. These foraging models make it clear that prey abundance is only indirectly involved in foraging decisions. The effectiveness of searching for prey, and especially the costs of pursuing and capturing different species, are also determining parameters. In particular, changes in the abundance of species ranked outside of a diet breadth in a given situation should have no effect on whether or not they are included in the diet. And an increase in the abundance of highly ranked species may decrease diet breadth, but the forager will drop species from the diet in rank order, even though their particular abundances may not have changed.

Another common assumption, that larger species are always more efficiently hunted than smaller ones, is not supported by this research. In years in which hare are abundant, for instance, their net acquisition rate per unit of pursuit time (15,220 kcal/hr) is almost twice that recorded for moose (8,220 kcal/hr).

The approach developed here isolates a limited set of variables, and directly establishes their relevance to foraging behavior. It is evident in considering wider use of these models that we need to develop measurements of the energetics of different foraging activities in diverse environments; of the costs of travel and manufacture and use of pursuit technologies for different prey species; of the energy and nutritional value of various game species; and of the effectiveness and short-term risk of various foraging tactics. The literature records too little quantitative information of sufficient detail on any of these points.

The models used here examine very specific aspects of the behavior of individual foragers. I suggest that this microecological approach and data gathering are necessary to develop correct interpretations of the macroecological topics frequently discussed in ethnographic and prehistoric analyses. Several examples can be cited.

The optimal hunter in a fine-grained environment takes a variety of game species determined by the conjunction of prey ranking and search and pursuit costs. If the optimal diet breadth is fairly broad, efficiency is achieved only if each hunter or contiguous hunting group is general in its hunting. In this circumstance individual specialization and camp exchange will not achieve the same end. Thus in fine-grained environments there is an ecological or energy disadvantage to the "division of labor" often postulated to be the basis of hominid sociality. In contrast, the ability to specialize and then exchange goods at a central location may be of advantage in a coarse-grained environment, with separate foragers behaving optimally by seeking resources in a few geographically separated and ecologically distinct types of patches.

The patch use model demonstrates that if a situation arises which compels highly efficient foraging, such as diminished resource availability due to environmental changes or to competition from other species, the optimal forager may restrict the portion of habitat it uses. Habitat selectivity is thus critical to archeological applications of the carrying capacity concept, or to paleontological applications of the competitive exclusion principle. For instance, Wolpoff (1971 1976) argues that competition between two hominid species will necessarily select for more generalized use of resources and habitat. This increased competition, in his view, will result in the inevitable extinction of one species. Foraging behavior models--in particular the "compression hypothesis" (MacArthur and Pianka



1966)--produce the opposite prediction (see Winterhalder 1980c n.d.c). Further, foraging models outline the specific types of dietary "character divergence" which are likely to result.

The marginal value theorem has similar implications. For instance, it indicates that the foraging behaviors implied in the Pleistocene extinction ("overkill") hypothesis (P. S. Martin 1973), as applied to the North American megafauna, are not likely. The overkill hypothesis posits highly efficient hunters moving through a heterogeneous environment of abundant and easily pursued game. The marginal value theorem indicates that this is just the situation in which localized depletion of game populations does not occur. Efficient Pleistocene hunters entering the North American continent would have skimmed the most easily obtained animals from a location before moving on. With high average habitat returns, an optimal forager moves out of a given patch early along the depression curve (see figure 2.2) and leaves behind a breeding stock. This theorem, incidentally, may help explain the apparently very rapid migration over, and hence population of, the continent.

The apparent population stability of hunter-gatherers may be due to a related consideration. It is sometimes stated that hunters developed behaviors which promoted the management of game species and hence their conservation. The marginal value theorem makes it apparent that it would be difficult for hunters to act otherwise. Most environments are heterogeneous to some degree (Wiens 1976). The forager attempting to deplete localized populations fully must act in a manner that is not energy efficient in order to do so. The marginal costs of fully "depressing" the resources of a patch and thereby depleting the breeding stock are high compared with those of moving to the next patch to continue foraging. In effect, conservation may (among other things) be the *incidental* effect of efficient foraging in a heterogeneous habitat. A consequence of this is a reduced possibility of crashes in human population due to serious decreases in game supplies.

While these are brief and somewhat speculative examples, they demonstrate the potential of applying carefully verified foraging models to interpretations of prehistoric hunter-gatherer behavior.

#### Conclusions

Optimal foraging theory can link theory and field data of diverse sources in a program to improve both; it is an operational approach to analysis of hunter-gatherer behavior. The models examined here provided, for the most part, a reliable analysis of the ecological factors affecting Cree behavior. The approach has some important kinds of generality; it can be applied in ethnographic or prehistoric situations; and it can be applied to topics other than those discussed here (e.g., territoriality and group formation). It is versatile and should help to organize the rather disparate sources of information available to anthropologists for inferring the adaptations of early hominid species (e.g., primate and social carnivore behavior; ethnography of hunter-gatherers; archeological information). In general the results presented here begin to substantiate the optimistic assessment of these models presented in chapter 2, above.

Careful testing of this theory is important to its use. Some model hypotheses have emerged in this analysis as more reliable than others. The diet breadth model and hypotheses were confirmed here without major qualifications; the patch use model, in contrast, made assumptions about the structure of the forager's environment, and about the tactics of foraging itself, that were not appropriate. This work, in combination with other analyses using these models, can eventually be used to illuminate the peculiarities of individual

models and to evaluate them by their reliability in circumstances where information is incomplete, as in most archeological or paleontological analysis. Wider application of this approach will require the production of types of data which are not routinely generated in research on human ecology, ethnographic or prehistoric.