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CANADIAN FUR BEARER CYCLES AND CREE-OJIBWA HUNTING AND TRAPPING PRACTICES

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The dramatic population fluctuations of fur bearers of the boreal regions of North America long have been a subject of biological curiosity. Pelt-count cycles of these species have received considerable analysis (Butler 1953; Cole 1951, 1954; Moran 1953a, 1953b, 1954; Rowan 1954; Leigh 1968; Bulmer 1974), and the lynx-hare case is presented in ecology texts as a classic example of cyclic predator-prey population interactions (Odum 1971; Wilson and Bossert 1971; Colinvaux 1973). The major data bases for these analyses, particularly in the early works (MacLulich 1937; Elton and Nicholson 1942a, 1942b; see also Bulmer 1974), have been pelt sale records kept by the Hudson's Bay Company and administrative agencies of the Canadian North.

An assumption consistently used in these studies is that pelt records accurately reflect the abundance of the harvested species (Elton and Nicholson 1942a, 1942b; Keith 1963). The most common statement is that pelt-counts are directly related, if not proportional, to population. Recent studies of human ecology in the boreal forest have led Weinstein (1977; see also Gilpin 1973; Winterhalder 1977) to question this assumption. Weinstein suggests that pelt-count cycles for lynx may be an artifact of the foraging practices of native hunters and trappers: "Thus the lynx records of the Hudson Bay Company may not reflect changes in the population density of lynx but short-term changes in the hunting strategy of trappers who sold their pelts to the Bay" (Weinstein 1977, p. 808). Weinstein points out that in years of hare abundance the lagomorph represents an ample food source, allowing trappers time to pursue fur species less valuable as food. Although lynx were eaten, the estimated edible portion of a single kill, 3.9 kg, is relatively small (Weinstein 1976) and the species too rare to be a significant food source. In contrast, in years of hare scarcity the priority of the food quest would reduce the amount of time available for pursuit of fur bearers not also valuable as food sources. If one assumes that a hare population cycle is primary and that hare played a major role in native diets, then it is easy to see how differential foraging tied to the hare population fluctuations could have produced systematic and more or less regular fluctuations in the harvest of nonlagomorph fur bearers. The harvest, or pelt-count, cycles for these species would not necessarily reflect changes in their actual population numbers.

In this paper I present evidence that this "differential foraging" hypothesis is correct, although it is probably more appropriately applied to fur bearing species other than lynx and hare. Ethnohistorical evidence (Bishop 1974; Rogers and Black 1976) and ecological studies of Cree-Ojibwa foraging practices in northern Ontario (Weinstein 1976; Winterhalder 1977) support the contention that the abundance of food species, primarily hare and moose, influenced native attention to fur trapping. At least when moose were absent, native trappers relied heavily on hare for food to provision fur bearer trapping. When hare were scarce, native trappers were often unable to pursue fur bearers. On the other hand, there is now evidence from direct censusing and field studies which demonstrates population cycles for some boreal species, especially hare and lynx (Nellis et al. 1972; Meslow and Keith 1968; Keith 1974; Brand et al. 1976). This evidence is independent of harvest statistics. Similar but less systematic information is available from earlier periods (Elton 1942; summary in Keith 1963).

Together the anthropological and field biology evidence indicate that Weinstein's hypothesis should be qualified to the extent that information exists independent of fur records to substantiate population cycles for the hare and lynx. The hypothesis should be extended to account for the possibility that hare-trapper interactions rather than population changes account for the cyclic pelt-counts for species such as fisher, marten, and muskrat.

For the remainder of the paper a "cyclic" fluctuation will be defined as "a pattern of numerical changes in which time intervals between successive highs and successive lows are significantly less variable and hence more predictable than in autocorrelated random fluctuations" (Keith 1974, p. 19). To represent a cycle, then, fluctuations must be of regular periodicity. Noncyclic changes will be designated periodic fluctuations or simply fluctuations.

BACKGROUND

Hypotheses about the causes of pelt-count cycles are almost as numerous as writers on the subject (Elton 1924; Cox 1936; MacLulich 1937; Elton and Nicholson 1942b; Christian 1950; Moran 1953b; Grange 1965; Watt 1969). Importantly, these hypotheses give little attention to the role that the native trapper had in generating the harvest statistics that comprise the main data source. Biologists have argued against the possibility that pelt-count cycles are due to fluctuation of incentive related to prices (Elton and Nicholson 1942a, 1942b; Keith 1963), at least up to the early 1950s (Rowan 1954; Keith 1963). Other factors that might affect trapping and pelt production have likewise been minimized, including disease pandemics among trappers (Elton and Nicholson 1942b), inconsistencies in administrative recording of the pelts or changes in boundaries of the recording districts (Elton and Nicholson 1942b), and changes in the numbers of trappers or in the methods used (Moran 1953a). Until recently it has not been apparent that systematic pelt-count fluctuations may be partially independent of population density changes for some species, and that study of native foraging practices is

necessary in order to interpret the relationship between harvest statistics and population changes.

HARE SNARING AND THE DIFFERENTIAL FORAGING HYPOTHESIS

The differential foraging hypothesis requires three indirect kinds of evidence: (1) that hare were periodically important in the diet of native hunters and trappers; (2) that when abundant, hare could be effectively and efficiently harvested; and (3) that pelts could not be traded for significant quantities of food when primary food species (including hare) were scarce. These propositions underlie the suggestion that high densities of the lagomorph would "release" trappers to pursue species which make only small contributions to diet, despite their value as trade items.

First, there is good evidence that hare, when obtainable, played a major role in the diets of boreal forest peoples (Dunning 1959; Rogers 1967; Bishop 1974; Rogers and Black 1976). Especially during much of the nineteenth and early twentieth centuries, when moose were scarce or absent from northern Ontario (Bishop 1974; Winterhalder 1977), hare and fish were the major components of native diets. Low points in the hare cycle represented periods of great hardship (Bishop 1974; Rogers and Black 1976). Even when moose became abundant, families report living predominantly on hare during winters when the lagomorph was abundant (Winterhalder 1977).

Second, evidence indicates that hare are effectively and easily obtained by Cree foragers. Censuses of hare in northern Alberta boreal forest indicate peak densities of 1,150 hare/km², or a biomass of 1,725 kg/km² (summary in Winterhalder 1977). At the peak of population density the hare spread over the landscape, but during periods of lower density they aggregate in small patches of favorable vegetation (Keith 1966; Meslow and Keith 1968), maintaining local densities above that of surrounding areas. Cree foragers associate hare with these types of vegetation and know where such patches can be found (Rogers and Black 1976; Winterhalder 1977). Native trappers state that the catch from a snare line varies somewhat from day to day, depending mainly on the weather, but that the harvest is fairly reliable on a short-term basis.

In 1975 I measured the net acquisition rate (metabolic energy captured minus that invested, per unit time) of hare snaring to be 1,150 kcal/h (Winterhalder 1977). This measurement was made in the fall of the first year of recovery of the hare population from the low point in the cycle. Cree hunters had seen almost no sign of hare for the previous 3 yr, and even in 1975 the animals remained quite scarce.

Based on the measured costs of maintaining a snare line, and using estimates by Cree trappers of average catches during "good" hare years, I calculated that a net acquisition rate of about 5,230 kcal/h could be attained for time invested in hare snaring during years of hare abundance. These figures are based on analysis of snaring with stationary wire snares, a type not widely used prior to about 1910 (Rogers and Black 1976). In the nineteenth century and earlier many, if not all, trappers probably used a balance-pole with a snare loop constructed from string. (This type of snare lifts and chokes the hare before it can free itself by biting or

breaking the string.) The pole snare requires about half again as much time for its construction as a wire one, but assuming that other costs (traveling to and from and along the snare line, searching for sets, removing hare, and resetting the snare) remain the same, and that string and wire snares are equally effective, the use of balance pole snares would reduce the efficiencies cited above by less than 10%.

These figures make it clear that hare snaring, when the hare are abundant, would allow a trapper to provision himself and dependents with a relatively small investment of time and energy. This conclusion is supported by these further observations: Hare snaring was often an activity of women and adolescents, providing more time for the adult males, who did most of the fur trapping; and, when hare are abundant, hare snaring is an activity that can be pursued incidentally while other fur bearers are being sought (Rogers 1973; Winterhalder 1977).

With respect to the third proposition, until the twentieth century interior fur trappers could not exchange pelts for significant quantities of food (Bishop 1974; Ray 1974). Dry goods, metal implements, tea, tobacco, and in some cases alcohol were available, but it was a recurrent problem for trading companies to transport or obtain sufficient food provisions even to maintain trading post personnel. As a consequence European foods, including locally grown potatoes, were bartered to natives only rarely and usually in extreme circumstances. Native trappers seldom had the option of exchanging pelts for food; in times of shortage the pursuit of species highly ranked as food-producing resources had priority over those valuable mainly for their pelts.

HISTORICAL EVIDENCE

At the trough of the hare cycle the animals virtually disappear and hare trapping efforts cease. Densities at the low point in the cycle are estimated at 13 hare/km² (biomass 19.5 kg/km²; Winterhalder 1977). Archival evidence indicates directly that when hare were absent native trappers, preoccupied with the food quest, had little time for the trapping of species that provided pelts but little food. The following illustrations of this are taken from Bishop's (1974) ethnohistorical and ecological studies of the Ojibwa Indians living at Osnaburgh House, Ontario. Internal quotations are from traders' reports, drawn from Hudson's Bay Company Archives. In 1831 the trader wrote:

"... all of the Indians have med pour hunts the whole of them have starved all the winter and have prevented them from maken to good hunts as they would have don, ther are no martens on this quarter and no dear nor Rabits for the Indians to live on to enable them to pay ther debts or to Enable them to hunt other furs" [p. 183].

Referring to a date 20 yr later Bishop notes:

Hare were particularly scare near Osnaburgh in 1850 and on this account "the Indians will do very little... for want of them the Indians will pass away their time in hunting for food." They suffered so much from starvation that "not an Indian is Making any hunt in furs." The fur returns were reported to have been extraordinarily low, although fur bearers were not scarce. "The Indians, as they say, they

did nothing else but Angle Jackfish from day to day to Save their lives." Hare did not increase enough to allow Indians sufficient time to trap until 1853 [pp. 183–184].

Again, 10 yr later:

In 1856 and 1857, both trade and ecological conditions appear to have been at their optimum; however by 1861 hares were again scarce and Indians had to devote their time to the food quest. Although furred animals were relatively numerous that winter, the Indians "say that they cannot hunt furs for want of Rabbits for they say that ther is a few Martens on thir Lands but they cannot Make Traps for want of Provisions to live on" [pp. 203–204].

Finally, after another interval of about 10 yr:

During the late 1860's, when some food was available as a trade item at Osnaburgh, subsistence activities still prevailed over trapping. When "rabbits" were scarce Indians "were obligated to leave their lands and proceed where they would catch fish for a subsistence." The lack of food meant that Indians often shifted "about every now and again not looking for furs . . . never comes in their minds but hunting for the belly" [p. 184].

Bishop's analysis contains additional statements which indicate similar effects. Even as late as 1899, when some store foods were available and actual starvation became quite rare, a shortage of hare could disrupt trapping activities: "Indians are bringing poor hunts. They have been starving all spring. Rabbits being scarce." (Bishop 1974, p. 90).

THEORETICAL CONSIDERATIONS

Fur trade data are a valuable and unique source of long-term information on population processes in boreal species. Although pelt-count fluctuations are probably not in all cases directly related to population fluctuations, if the filtering represented by differential foraging is systematic, then pelt counts still provide good information on population densities. Optimal foraging theory applied to native trapping practices may provide the conceptual key to interpret pelt-count data in this manner. In a previous analysis (Winterhalder 1977) I have shown that in important respects Cree foraging strategies match those predicted by the optimal diet breadth model developed by MacArthur and Pianka (1966; Pianka 1974; MacArthur 1972). Important here is a corollary prediction of this and similar models: Once the forager has reached an optimum diet breadth (in the model derived from the rate of encounter with a spectrum of species and the costs of pursuing or handling each) it should not incorporate a potential resource species into its diet breadth simply because that species has increased in abundance (Krebs and Cowie 1976; Pyke et al. 1977). Diet breadth is dependent on the absolute abundance of species which the forager ranks highly, and not on the absolute abundance of low-ranking species, those outside of the existing diet breadth. In the short-term, in which diet breadth is fairly stable, the harvest of the optimal forager should not be sensitive to population fluctuations of "potential" prey. Conversely, if the absolute abundance of a highly-ranked food type decreased, the forager might begin harvesting the low-ranked food type even though its absolute population density had not changed.

The application of this kind of reasoning to Cree foraging requires the separa-

tion of species sought primarily for food from those sought primarily for pelts, with allowance for some intermediate examples. Food species, ranked roughly by their food value relative to the cost of pursuing and capturing them, would include moose, hare, beaver, fish, and muskrat. Fur bearing species would include lynx, otter, mink, marten, fisher, beaver, muskrat, and hare. The former are more abundant in biomass than the latter; they are also generally herbivores and contain the larger species. This separation reflects the dual economy of the native trapper; pelts could be bartered for goods supplied by a trader, but subsistence had to be gained independently.

Based on the indirect and direct evidence cited above, the following interactions are proposed to be characteristic of differential foraging. When highly ranked food resources, particularly moose and hare, were abundant they provided ample and efficiently obtained food. Male trappers therefore could concentrate on the second economy represented by the fur trade. As hare became scarce two things happened: (1) More attention was devoted to lower ranked food resources (e.g., fish and muskrats), which, because it lowered the overall efficiency of the food quest, (2) restricted male participation in the fur trade. For this reason pelt-counts for the carnivorous fur bearing species should cycle in parallel with the population abundance of hare.

Of the double-listed species, hare pelt-counts themselves should reflect, fairly accurately, population changes in this species. Beaver and muskrat both represent special cases. Beaver pelt-counts are seldom examined in the context of population cycle studies (e.g., Bulmer 1974), perhaps for reasons peculiar to the population dynamics and harvest of this species (Innis 1930), so little can be said about them in this context. Muskrat presumably represents an abundant but low-ranked food resource and simultaneously one of the less desirable fur bearing species. The model predicts that its harvest will cycle out of phase with that of hare. Similarly, muskrat population abundance can fluctuate without leaving evidence in its pelt-counts. As long as food resource species and more desirable fur bearers were abundant, muskrat may have been ignored by native trappers whatever its population density, or density changes.

While this brief description is highly simplified, it should be evident that optimal foraging theory provides (1) an analytic framework for investigating the variables central to the differential foraging hypothesis and (2) a key to systematic aspects of the relationship between pelt-counts and population density.

RELATED CONSIDERATIONS ON FUR BEARER CYCLES

The hypothesis presented here is consistent with a number of other properties of pelt-count and fur bearer population cycles that have been described in the literature.

First, this interpretation is consistent with the phase relationships demonstrated by Bulmer (1974) for pelt-count cycles. The peak abundance of pelts of most fur bearers occurs within the period when hare pelt-counts are high (i.e., the period during which harvest is expected if effort is directly related to hare densities). In his analysis Bulmer assumes that pelt-counts directly reflect population abun-

dance and argues that the phase relationships among the different species can be explained by food-chain effects tied to a primary cycle of hare population. Such food-chain effects can arise through a switch by predators to alternative prey species as densities of preferred prey decrease (Nellis et al. 1972; McInvaille and Keith 1974; Brand et al. 1976). Alternatively, species may compete with one another for use of common food resources (Rusch and Keith 1971; Keith 1974; Wolfe 1974). While Bulmer's analysis is plausible, much of the data he seeks to explain on a population basis may be a systematic artifact of differential foraging. The interaction between food-chain processes which affect population densities and differential foraging (a functional response by the human predator) in generating pelt-count statistics is a complex matter that will require extensive investigation.

Second, pelt-count cycles show up most clearly in fur records in the nineteenth century (Keith 1963; Leigh 1968; Bulmer 1974). This is a period during which moose and caribou were rare or absent from northern Ontario and possibly also from parts of Manitoba and Quebec (Bishop 1974; Winterhalder 1977). Without these important food sources the correlation between hare abundance and native attention to the fur trade should be strongest. In fact, the citations from Bishop (1974) given above come from this period. It is possible that the diminished magnitude and regularity of pelt harvest fluctuations in the eighteenth and twentieth centuries (Bulmer 1974) result partially from the fact that when hare were absent native trappers could subsist on the more stable moose (or beaver) populations while continuing to harvest carnivorous fur bearers. Other factors such as changing trade conditions and the quality of record keeping are presumably also involved. Elton and Swynnerton (1936; see also Elton and Nicholson 1942b) argue that diminished evidence of cyclicity in the marten during the twentieth century may be due to overtrapping and long-term depletion of the animal. Again, however, this could be entirely or partially a result of a diminishing influence of differential foraging as moose became reestablished in eastern boreal forest regions.

Third, peaks of muskrat pelt counts tend to come between those for hare (Bulmer 1974). This could mean simply that native hunters drew heavily on the less desirable muskrat as a food source, and as a source of income through the sale of pelts, when hare were scarce. It is not necessary to assume that high muskrat pelt production reflects periods of greater muskrat abundance. This species may represent a low-ranked resource that moved into and out of "diet breadth" as higher ranked food species changed in absolute abundance.

Muskrat do undergo large periodic fluctuations in numbers related to irregular environmental conditions (Elton and Nicholson 1942a; Errington 1954, 1963; Bishop 1974; Ray 1974), but it has been possible to establish cyclicity in muskrat pelt data only for certain data sets and time periods. Elton and Nicholson (1942a, p. 100), analyzing muskrat pelts from the Northern Department found "... rather irregular fluctuations from 1821 to 1848... more regular fluctuations from 1848 to 1913, with a conspicuous major cycle of about 10 years..." This is just the pattern one would expect if the nineteenth century disappearance of moose accentuated

the relationship between hare populations and fur harvests. Elton and Nicholson (1942a, p. 106) also note that Innis (1930) ". . . was inclined to attribute the cycle [of muskrat] to the combined effects of a real cycle in numbers with a periodically increased trapping caused by the corresponding cyclical scarcity of more valuable furs" (see also Ray 1974). The view of Innis closely parallels that suggested here.

As a final point, Keith (1974) has presented a model of the lynx-hare population cycle which is based on extensive and long-term field observations of the interactions of these species. The population fluctuations documented by Keith are quite similar to those evident in the historical pelt-count record, with the exception that the measured amplitude of population changes is less than that suggested by fur returns (L. B. Keith, personal communication). The close relationship between pelt-count cycles and population cycles for lynx and hare can be explained by their high value as fur bearer and food resource, respectively. The foraging models cited earlier predict that the harvest of highly ranked species should parallel abundance. Further, the observations by Keith document the assumption, made earlier, that the hare population cycle actually occurs and can therefore act as a primary cause of differential foraging by native trappers.

SUMMARY

Hutchinson (1975) has recently suggested that the study of population cycles is one area of ecological inquiry where theory and data have not always interacted to produce satisfactory explanations. One difficulty may be that a major part of the data available, fur trade statistics, provides evidence of a different kind than has been, until recently, assumed.

In this paper I have attempted to substantiate in qualified form a hypothesis presented by Weinstein (1977) and independently by Winterhalder (1977) pertinent to this difficulty. It states that cyclic or fluctuating pelt counts of boreal region species are partially a result of differential foraging by native trappers, and for many species are not directly indicative of population fluctuations. Three conditions necessary to this interpretation were established: (1) Hare were important in the diet of the Cree-Ojibwa, (2) they could be effectively and efficiently obtained when abundant, and (3) the quest for food-producing species, including hare, had priority to the native trapper because pelts could not generally be exchanged for food. Ethnohistorical evidence provides direct accounts of the postulated relationship. An optimal foraging model was briefly introduced to elaborate the hypothesis. This theory provides an appropriate framework for investigating this topic, and possibly also a key for retrieving population data from fur trade harvest statistics. It was shown that the differential foraging hypothesis is consistent with a number of observed properties of pelt-count cycles, including the apparent similarity in all respects except amplitude, between pelt-counts and actual population fluctuations in lynx and hare.

The hypothesis suggested here is important for the statistical analysis of peltcount cycles, and it raises questions about the reality of population cycles which are inferred predominantly or solely from fur record data. Despite this there is ample evidence demonstrating population cycles for hare and lynx, cycles which presumably have correlative food-chain effects on other species, including humans.

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