

BEAVER CENTRAL PLACE FORAGING

Literature Review, Model, and Field Test

by

© William J. Dalton

A Graduate Thesis Submitted

In Partial Fulfillment of the Requirements
for the Degree of Master of Science in Forestry

Lakehead University
School of Forestry
Thunder Bay, Ontario

October, 1984

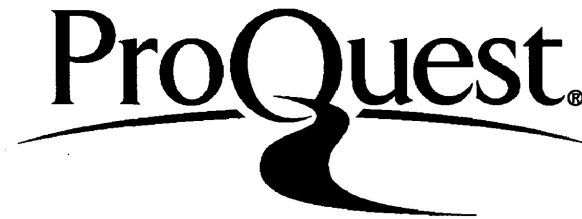
ProQuest Number: 10611698

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 10611698

Published by ProQuest LLC (2017). Copyright of the Dissertation is held by the Author.

All rights reserved.

This work is protected against unauthorized copying under Title 17, United States Code
Microform Edition © ProQuest LLC.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

Dalton, William J. 1984. Beaver central place foraging: literature review, model, and field test. MScF Thesis, Lakehead University, Thunder Bay, Ontario.

ABSTRACT

The spatial distribution of tree cutting activity by beaver (Castor canadensis Kuhl) and tree availability were measured at two beaver colonies near Thunder Bay, Ontario.

Beaver maximize the net rate of energy acquisition (e/t) when they minimize the distance travelled from the lodge, their central place, while obtaining a balanced diet. However, beaver must travel through two mediums to obtain terrestrial forage so minimum distance is a function of the relative costs of swimming and walking. A continuum of relative costs was used to generate two contrasting foraging models: 1) swimming equalled the cost of walking and the foraging path was a straight line from the lodge to a tree; 2) swimming was costless and the foraging path was the shortest distance from water to a tree.

The models were compared for relative goodness of fit with the observed foraging pattern using chi-square and linear regression goodness of fit tests. The water costless model was the best fit model and empirically supported the implicit assumption of most workers that the pond is the effective central place. In practical terms 'water costless' was judged to be indistinguishable from a 5-10 times advantage for swimming over walking. Although experimental confirmation is required, this advantage was considered too large to be explained by energy or time savings and was therefore not an optimization of e/t. It was tentatively concluded that the pond should be viewed as a refuge from predators which probably constrain the relative availability of terrestrial forage to beaver.

A test for optimal foraging, given the predation constraint, showed that beaver were maximizing e/t at Northbranch Pond. At Pinetop Pond, a relatively old site, beaver expanded their refuge to obtain patches of relatively high food quality. They could have realized higher e/t with perfect knowledge of their site, but apparently they maximized e/t with a patch use strategy that minimized search time.

A review of beaver literature discussed optimization processes at four levels: evolution of body form and function, the individual lifespan, yearly, and seasonally. Arguments of particular interest were developed for dispersal (population regulation), central place, and the size-distance relationship.

TABLE OF CONTENTS

	<u>PAGE</u>
ABSTRACT	ii
LIST OF TABLES	iv
LIST OF FIGURES	v
ACKNOWLEDGEMENTS	vi
PREFACE	vii
INTRODUCTION	1
Optimization of Morphology and Physiology.....	6
Optimization of Lifetime Fitness	9
Yearly Optimization	14
Within Season Optimization	21
Optimization Criteria	22
Preference	23
Size - distance	24
Energy - distance	29
The Foraging Models	32
STUDY AREA	41
METHODS	
Field Methods	46
Data Handling	48
Calculating an Expected Cut	49
Testing the Goodness of Fit	51
RESULTS	
Cutting Activity	55
Goodness of Fit Tests	60
Chi-square	65
Linear regression	67
Comparison of tests	71
Pattern of Cut Given A Constraint	72
Species Preference	73
Diameter Preference	81
DISCUSSION	85
LITERATURE CITED	103

LIST OF TABLES

	<u>PAGE</u>
Table 1. Example calculation for the expected cutting of 5 cm aspen in all distance cells.....	50
Table 2a. The tree and shrub tally by species at Northbranch and Pinetop beaver colonies....	55
Table 2b. The diameter distribution for aspen availability and cutting by beaver, at Northbranch and Pinetop Ponds for the 1:1 and 1:0 models.....	57
Table 3. The chi-square statistics for goodness of fit tests of the transformed data for Northbranch and Pinetop ponds.....	66
Table 4. Results of r-test for linear relation between observed and expected stems cut, and t-tests for differences between the equal cost and water costless continuum models.....	67
Table 5. Results of the χ^2 goodness of fit tests, r-tests, and t-tests for the energy optimization, water costless constrained model.....	74

LIST OF FIGURES

	<u>PAGE</u>	
Figure 1.	Theoretical continuum of foraging models based on the potential relative costs of swimming and walking.....	32
Figure 2.	Sensitivity analysis of foraging path models.....	36
Figure 3.	The study area location.....	42
Figure 4.	Cutting activity maps for Northbranch and Pinetop ponds in 1981.....	59
Figure 5.	Graphs of observed cutting versus expected cutting, 1:1 and 1:0 models, for each tree and shrub species by distance at Northbranch Pond.....	61
Figure 6.	Graphs of observed cutting versus expected cutting, 1:1 and 1:0 models, for each tree and shrub species by distance at Pinetop Pond.....	63
Figure 7.	Scatter diagrams for linear regression goodness of fit tests, 1:1 and 1:0 models, at Northbranch Pond.....	68
Figure 8.	Scatter diagrams for linear regression goodness of fit tests, 1:1 and 1:0 models, at Pinetop Pond.....	69
Figure 9.	Species preference histograms, subdivided by distance from the closest shoreline, for Northbranch Pond.....	76
Figure 10.	Species preference histograms, subdivided by distance from the closest shoreline, for Pinetop Pond.....	77
Figure 11.	Mean cutting distance for each tree or shrub species at Northbranch and Pinetop ponds.....	79
Figure 12.	Diameter preference histograms, subdivided by distance from the closest shoreline, for Northbranch Pond..	82
Figure 13.	Diameter preference histograms, subdivided by distance from the closest shoreline, for Pinetop Pond.....	83

ACKNOWLEDGEMENTS

Partial funding for the research was provided by the Lakehead University, University Schools Regional Research Fund and a Canadian Forest Service Fellowship. Lakehead University provided office facilities and computer resources. The dedication of field workers Mike Millard, Steve Dimitroff, and Margaret Morse (nee Manders), exceeded their reimbursement. Margaret also entered the bulk of the data and manipulated much of the same. Her efforts and friendship were greatly appreciated. Typing and subsequent word processing of the drafts was done by Pam Hanna. She greatly eased the burden of manuscript production. H.G. Cumming, W.H. Parker, and S.R. Goldstein sat on the thesis committee. Their comments greatly improved the presentation, documentation, and logic of the research. H.G. Murchison counselled statistical rough spots. Maria Dalton supported the work financially, physically, and with her heart. S.H. Jenkins was the external examiner, his comments were appreciated and have mostly been incorporated in the final draft.

PREFACE

In 1976 my headlong rush to join the professional forester ranks took an abrupt twist.

Hank Hristienko, a friend when he was himself a forestry student, returned as guest lecturer to the wildlife class of Dr. H.G. Cumming. He brought with him a slide show of a caribou study with which he had become involved, and left with a request from myself for an introduction and recommendation to Dr. A. T. Bergerud, University of Victoria. The association that developed focused my attention on foraging behavior, and took me eventually to the University of British Columbia for an upgrading of wildlife and ecological knowledge. While there, under the guidance of Dr. C.J. Krebs, Robert McLenehan and I undertook a study of beaver foraging patterns. The results of that study were the seeds of this thesis project. At the time we had not developed a connection with optimal foraging theory. My introduction to optimal foraging was taking place simultaneously in courses with Dr. F. Bunnell.

Given the suggestive results of that initial foraging pattern study and the little used optimal foraging theory literature, the synthesis that is this thesis was a challenge I could not resist.

BEAVER CENTRAL PLACE FORAGING:
Literature Review, Model, and Field Test

INTRODUCTION

Beavers eat trees. This often used statement has implanted a general misconception of beaver foraging behavior in the public and scientific consciousness. Beaver foraging behavior can be more accurately communicated. For example, beavers eat portions of a large number of woody stems on a seasonal basis. Cumbersome but enlightening, this change leads lay and scientific minds to a functionally different viewpoint.

Many details of tree and shrub useage by beavers (Castor canadensis Kuhl) have received attention in the scientific literature. The beaver literature has passed through two distinct eras and embarked on a third. Bradt (1938) criticized pre-World War II literature because it lacked systematic observation; his work set the standard for papers that followed for 25 years. Beaver studies became more scientific but investigators still concentrated on natural history aspects, usually on a very local basis.

The people involved were of course aware of Darwinian selection and genetic inheritance but did not bring these ideas to bear explicitly on their investigations. The question, why is an observed behavior pattern utilized, was probably not asked because these investigators accepted that natural selection had produced what they observed. Investigations of ultimate causes (see Lack, 1954, for discussion) were avoided because experiments on an evolutionary time scale were unreasonable for wildlife populations. Questions about ultimate causes were shelved because of their tautological nature (Cody 1974). That is, it was considered unscientific to study aspects of biology that were untestable directly.

A body of theory that examines ultimate causes for observed biological phenomena, in spite of the tautology, is known as optimization theory. It has stimulated the third era in beaver biology. Jenkins (1975, 1980b) began integrating the approach with regard to beaver foraging behavior and has explored (Jenkins 1975, 1979, 1980a, 1980b) many of the themes pursued in this thesis. Parallel ideas on life history optimization have been injected by Boyce (1981).

Pyke et al. (1977) reviewed the literature concerning optimal foraging theory; "...this theory assumes that the fitness associated with an animal's foraging behavior has been maximized by natural selection, subject to certain

constraints". Maynard Smith (1978) noted that optimization assumptions and theories are used in biology to understand the diversity of life, not demonstrate that organisms optimize. Someday we may be able to experimentally manipulate genotypes (Gale 1980) such that it could be possible to test whether an extant genotype is optimal. However, in the meantime optimization models test assumptions about constraints, optimization criteria, and heredity, or compare predictions with observations (Maynard Smith 1978).

Lewontin (1977) emphasized that optimality arguments may not have a justifiable genetic basis, and that until that basis is firmly established optimization models may lead to dangerous conclusions. Sih (1982) considered the dichotomy between optimal foraging models and tests of how feeding rate may affect fitness; he concluded that an asymptote in fitness may be reached below the energy maximizing level of foraging. Pearson (1960) found that food quality influences the reproductive rate of beavers. I will proceed on the assumption that foraging behavior can bring to bear sufficient selective pressure to evolve optimal solutions.

Cody (1974) suggested two ways to test for optimal solutions. The first compares two ecosystems with similar selective forces, but genetically or taxonomically different species. Optimality is demonstrated if similar behavioral solutions, or adaptive convergences, are seen. The second

test Cody (1974) suggested "is to contrast what we find in nature to what is predicted a priori on the basis of models designed to mimic the essentials of the natural system".

The modelling approach was adopted for this thesis to examine beaver foraging behavior. The proposed models were limited to beaver foraging on woody plants only; this activity occurs mainly in the fall season. I did not attempt to model across seasons, or years. However, the literature was reviewed from this broader prospective.

Katz (1974) designated the within season and yearly approaches as static and dynamic optimization respectively. The static model optimum is the instantaneous solution of the dynamic optimization model.

Yearly or dynamic optimization develops a useful picture of the relationship between foraging behavior and breeding strategy (see Svendsen 1980b, and Aleksiuik 1970 for the seasonal beaver feeding pattern).

A logical extension of Katz's dynamic approach (yearly optimization) would examine optimization over the lifespan of the animal. Under these even broader criteria questions such as which geographic sites to exploit and for how long (Partridge 1978), what amount of parental investment to make or when to leave the parents (Horn 1978), and whether or not territoriality is appropriate (Davies 1978) are valid.

Consider evolutionary history as one further step in this temporal scenario. Then physical and behavioral

adaptation to changing environments (Darwin 1859) is also a dynamic optimization process (Cody 1974).

For more detail on optimal foraging theory the following reviews should be consulted: Schoener 1971, Pyke et.al. 1977, Maynard Smith 1978, J. Krebs 1978, McCleery 1978. Jenkins (1980b) reviews the implications and potential of the optimal foraging theory for beaver biology.

Eras one and two in the beaver literature have not been synthesized with the third. A review of beaver biology from the standpoint of optimal foraging is warranted for two reasons:

- 1) The implications of optimal foraging theory for a beaver foraging study needed exploring.
- 2) The foraging situation that was studied, and is related herein, is a small portion of the dynamic optimizations that make up what a beaver is. The static model developed and field tested is placed in context by reviewing the overall picture.

The review is presented in the following order, vis-a-vis the time frames suggested in the preceding paragraphs: the optimization of morphology and physiology, the optimization of lifetime fitness, yearly optimization, and within season optimization.

Insights gained in the review process are summarized and then used to develop foraging models.

OPTIMIZATION OF MORPHOLOGY AND PHYSIOLOGY

Morphological and physiological adaptations are primary factors that affect availability of foods to an animal. They constrain the set of possible foraging behaviors a beaver can utilize. The following aspects are considered: beaver morphology, digestive physiology, and detoxifying plant toxins.

Beaver are adapted to swimming and diving. The short, powerful legs, webbed hind feet, streamlined body, furred lips, valvular nostrils and ear flaps, as well as the thick oiled pelage are all adaptive for an aquatic environment (Banfield 1977, Grasse 1951). Also, the beaver's short legs inhibit general agility on land. Given the beaver's aquatic adaptations, a beaver's foraging pattern is probably biased to a greater use of water than land. However, these aquatic adaptations do not necessarily override the possibility that beaver could use terrestrial habitat efficiently in the manner of free ranging or burrowing herbivores.

A beaver's digestive system is capable of processing, physically at least, just about any vegetable matter. The oversized incisors, heavy duty jaw muscles, and grinding molars make a broad diet possible. The wood cutting ability that a beaver's incisor-jaw muscle complex makes possible is a very important adaptation affecting food availability and feeding strategy. Without that basic adaptation an aquatic

placement for the burrow (lodge) would not be possible at latitudes that experience freeze up. The winter food cache must be made up of foods that will not spoil. Herbaceous plants would spoil, and seeds or buds are not available in the quantities a rodent the size of a beaver would require. The only terrestrial food option for a beaver's winter food supply is bark, it will store underwater and is available just before freeze-up. The use of terrestrial woody stems as winter food frees beaver from being restricted to sites with aquatic plants, as are muskrats (Banfield 1977).

What part of the evolution of beavers as aquatic rodents is due to genetic divergence to fill an empty niche and what part due to optimizations for exploiting the niche? I see three scenarios that someone familiar with fossil rodents could pursue.

- 1) The beaver's terrestrial ancestor was a temperate climate animal that evolved tree cutting ability to compete for or make available winter foods, it secondarily became aquatic to optimize this advantage.
- 2) The beaver's terrestrial ancestor was a warm climate animal with small incisors for exploiting mostly herbaceous plants. It became aquatic to obtain foods or avoid predators. It secondarily developed tree cutting ability to move into temperate areas.

- 3) The beaver's terrestrial ancestor was a temperate climate animal with small incisors that burrowed in shores and river banks. Aquatic adaptations and tree cutting ability evolved simultaneously in response to summer use of water habitat and winter use of terrestrial habitat.

A beaver's digestive tract is nearly as capable of digesting plant matter as it is of ingesting it. A large cecum at the anterior of the large intestine is colonized by micro-organisms capable of fermenting fiber (Hoover and Clarke 1972, McBee 1971) to volatile fatty acids which beaver can absorb. The process, however, is inefficient. Less fibrous plant matter yields a greater return on bulk ingested because it does not require processing by micro-organisms before a relatively high energy yield is obtained. The non-fibrous dietary material is unfortunately rare, available only seasonally.

If we reflect once more on Cody's (1974) tests of optimal solutions, convergent adaptation can be readily seen. Cecal adaptations are found in widely separated genera. Horses, elephants, coloboid monkeys, hares, and ptarmigan all share cecal adaptaton with beaver and other rodents (Milton 1979, McBee 1971). The use of a microflora in the gut is not limited to the cecal animals. Most Artiodactyla (the cloven hoofed mammals) are ruminant herbivores; they have a division of the stomach, a rumen,

which performs similar functions as a cecum. Hoover and Clarke (1971) discussed differences in fiber digestion between rumens and cecums (see also Hanley 1982).

A herbivore's diet is also constrained by an evolutionary leg-race between plants and herbivores. Plants have various physical and chemical defences that act to lower the value to a herbivore of a plant's potential energy content (Laycock 1978, Levin 1976). Freeland and Janzen's (1974) discussion of plant chemical defences pointed out that herbivores possess various detoxification mechanisms that are enhanced by natural selection. However, the detoxification systems involve a metabolic cost and have capacity limits. They concluded that herbivores should have broader diets than expected strictly in terms of relative caloric yields of plants. Pulliam (1975) also pointed out that the diet that maximizes caloric intake may, or may not, constitute a balanced diet. A mixed diet is to be expected if the value of a food item is dependent on the nutritional history of the animal (Estabrook and Dunham 1976, Westoby 1978, Milton 1979, Rapport 1980).

OPTIMIZATION OF LIFETIME FITNESS

A beaver must choose, from among numerous possible habitats, a place to live; in other words, the beaver must locate itself optimally with respect to the total resource picture (Orians and Pearson 1976). This basic choice can, and often will, determine the relative fitness of the

individual (Covich 1976). The colloquialism, leaving the parental fold, is not misplaced when studying beaver families. They occupy exclusive territories (Brenner 1967) and an adult pair (the parents) are the only reproductively active beaver (Bradt 1947, Bergerud and Miller 1977). Kits (young of the year) and yearlings remain with the parental pair. Young beaver normally leave the parental territory in the spring of their third year, as two-year-olds (Bradt 1938, Townsend 1953).

It has been suggested that unmated adult beaver are violently intolerant (Bradt 1938) of each other. This may be so but it is an insufficient explanation for dispersal. Many species, for example herding animals, have evolved to radically different solutions. Recent evidence suggests that dispersal of two-year-olds occurs without violent expulsion (Svendsen 1980a), and is delayed when all territory spaces are occupied (Bergerud and Miller 1977). These behaviors reduce sibling-sibling and sibling-parent mortality and are therefore advantageous, but are not ultimate causes for dispersal.

It is easy to understand that kits and yearlings obtain higher fitness by staying with the parents. Throughout lactation and subsequent growth to near adult size parental investment increases the inexperienced young beaver's probability of survival.

Dispersal of two-year-olds, or relocation of a colony is a risky business that often involves loss of life (Harris and Aldous 1946). A vacant site with suitable food and topography (Rutherford 1955, 1964; Slough and Sadlier 1977; Nixon and Ely 1969) must be located and successfully colonized, without incurring death due to predation, accident, or intraspecific strife. There must be some constraint (e.g. predator behavior, starvation) which in the long run, prevents cheaters from taking successful advantage of the apparently higher fitness to be gained by avoiding dispersal.

Why has dispersal evolved in the first place? For this hypothetical discussion ignore that reproduction is suppressed in all but the dominant adult pair (Bergerud and Miller 1977). This is necessary so that alternate life history tactics can be examined; after all, reproductive suppression was also evolved.

Consider first a large concentration of non-dispersing beaver on a small food resource. They would quickly use it up, which in turn would cause mass movements where all individuals risk not locating a suitable site. A small number of individuals, on a small food resource, that send out dispersers probably risk less and end up with high relative fitness; the genetic dispersal event is itself dispersed in time and space and is probably not subject to an all or nothing result. Given selective pressure in the

direction of a small population it would be reduced to its basic unit, the single adult pair and their offspring. This is an evolutionary stable strategy (ESS) (see Maynard Smith 1978, Krebs and Davies 1978) based on individual selection.

Starting from a slightly different perspective a large concentration of beavers on a short or long term food supply, would allow predators to specialize because predation opportunities would be numerous and search time small. For example, territorial wolves could den in close proximity to the beaver concentration and become functional specialists for part of the year (see Cumming 1974 for the effect of clumping when predators can respond by learning). A dispersed population of beavers would lower predator success by increasing predator search time and decreasing the foraging distances that beavers would have to travel for food. The higher the predation pressure becomes the more constrained the safe foraging area will be; this produces a relative food shortage, and a strong selective pressure for a dispersed population.

Next, consider a situation where predator pressure is absent and there is no absolute food shortage. Beaver should avoid dispersal risks if the energetic costs of food gathering do not constrain the relative availability of foods. Smith (1968), studying territorially exclusive squirrels, (one squirrel per territory), calculated that 2 squirrels foraging from a single central nest would expend

1.4 times more energy to gather the necessary food. This is evidence for a constraint on the relative availability of food; even where there are no predators to induce a relative shortage of food, selective pressures would be present to favor dispersal.

Many authors have pointed out that beavers overuse their woody food supplies (Shadel et. al. 1943, Grasse 1951, Harris and Aldous 1946, Aleksasuk 1970, Gese and Shadle 1943, Yeager and Rutherford 1957, Rutherford 1955, 1964, Hall 1960, Bradt 1938, Gibson 1957, Hiner 1938, Patric and Webb 1953, Krefting 1963, Lawrence 1952, Bergerud and Miller 1977, Svendsen 1980a). Brenner (1967) contended, for three colonies he studied, that foods were being produced on a sustained yield basis. However, he chose to ignore the implications of two facts that he presented: first, his colony #1 abandoned a pond in favor of an upstream site; and second, colony #3 fed at an average of 700' further from the pond than colony #1 or #2. The term overuse has been employed in a subjective non-technical sense by most of these authors. Although not explicitly stated in most papers, they documented relative shortages based on a lack of suitable trees within the normal foraging distance from water. Food overuse is not limited to the areas specifically adjacent to active colonies, it extends to the whole beaver territory (Bergerud and Miller 1977).

A test to separate whether the beaver's relative shortage of food is induced by predator pressure on beaver, or energetic limitations of beaver while foraging, is appropriate. This question takes precedence over all others in this thesis, and is the subject of most of the analysis.

YEARLY OPTIMIZATION

Metabolism and reproductive strategy involve the synchronizing of energy demands with seasonal differences in forage quality and availability (i.e. Katz, 1974, dynamic optimization). Only stockpiled woody stems are available in the winter. Aleksasuk and Cowan (1969a) demonstrated that beaver growth is suspended during winter for all age classes, and that a metabolic depression also occurs (see also Potvin and Bovet 1975, Lancia et al. 1982, Novakowski 1967). They concluded that beavers have a metabolic pattern more similar to hibernators than other non-hibernating rodents. Energy intake in the summer equalled energy expenditure, and fat was deposited in the fall but not utilized until the spring when the metabolism is increasing prior to the onset of the spring flush.

The reproductive strategy of beavers is also closely synchronized with seasonal food availability. The most nutritious foods a beaver eats are new growth of herbaceous plants (Aleksasuk 1970, Koslowski and Keller 1966). Pre-

sumedly aquatic plants are also highly nutritious. The reproducing female's highest energy demands are when lactation occurs; parturition occurs in mid-to-late May (Bergerund and Miller 1977) when spring flush is at its height through most of the beaver's range.

Females that are in poor condition should limit the bodily resources allocated to reproduction. Mechanisms for reproduction deferral should be observable when habitats of relatively good and bad quality are compared. Three mechanisms for avoiding reproductive investments have been noted: reduced ovulation (Henry and Bookhout 1969, Rutherford 1964), lack of implantation (op. cit.), and resorption of embryos (Hammond 1943, Osborn 1953, Brenner 1964, Henry and Bookhout 1969, VandenBerg and Vohs 1977). These papers invoked one or both of the following reasons to explain the observations: females had not reached adult size (demands of growth reduced the energy available for reproduction therefore reproduction is deferred), and (or) habitat conditions were poor. Supporting evidence is found in the several studies that examine the relationship between relative habitat quality and growth or reproductive rate (Rutherford 1964, Gibson 1957, Yeager and Rutherford 1957, Northcott 1964). These suggest a genetic basis for optimal

foraging models but do not constitute a sufficient test (Lewontin 1977), experimental work is necessary and should be pursued as soon as possible.

The broad diet of beaver could indicate an insensitivity of resultant fitness to variations in the available foods. The studies just cited suggest that this is not the case, but the question is not fully resolved. Jenkins (1979) asserted that beaver "thrive" in the absence of aspen, the most highly preferred species, and that they will prefer one or more of several other species, depending on availability. "Thrive" was not defined. Shadle et.al. (1943), among others, was cited in support of his preference argument. However, Shadle et. al. (1943) make the important observation (their summary point #6) that "as the depletion of the preferred genera progresses the gradual shift to the less desirable genera is evident".

The generalist habit that allows exploitation of less than optimal foods may be a compromise that allows survival and reproduction, albeit probably reduced, in geographic areas where it would otherwise be eliminated due to forest succession, depletion of the best food, or simply an absence in the flora of the best possible food. Estabrook and Dunham's (1976) model has varied diets that fall on isoclines of equal fitness and is probably realistic in that it allows some variation in diet to result in equal fitness states.

Beaver are constrained in their foraging behavior by the fact that they are central place foragers. That is, beaver forage to and from a fixed point, rather than moving at random through the total habitat.

Jenkins (1980a) considered the central place to be the pond, as have most investigators concerned with the distance from water that a beaver forages (see Northcott 1964 for review). The true central place that a beaver forages from is the lodge, the lodge being the point of embarkation on all foraging excursions (Gillespie 1977). Fixing the lodge as a central place is necessary for eventual consideration of beaver optimal foraging behavior in all seasons. Beaver remain within the bounds of their pond while foraging for aquatic vegetation, or while consuming the food cache.

It is possible that, for terrestrial foraging, the functional central place is the pond, but this has not been tested quantitatively. Contrasting the lodge and the pond as central places may serve as a test for what induces the relative shortage of trees for cutting, energy limitations while foraging or predator pressure on beaver.

Beaver respond to seasonal availability of foods by varying their diet (Svendsen 1980b, Aleksasuk 1970). Westoby (1978) identified four situations where a varied diet would optimize the rate of energy captured while foraging:

- 1) a saving in search costs can be made by taking several foods,
- 2) the optimal food changes because of shifts in relative search costs (relative abundance) or relative nutritional properties,
- 3) the optimal diet cannot be deduced from past experience,
- 4) different foods are the best sources of different important nutrients; conversely, the food may minimize intake of deleterious compounds (negative nutrients).

Before freeze-up in the fall, and after thaw before the spring flush of new leaves and herbs, beavers eat bark from freshly cut trees (Green 1936, Aleksiuik 1970, Jenkins 1979). Beavers switch to herbaceous and aquatic plants as soon as they are available in the spring (point #2 above) and continue to eat these foods, with the exception of the odd woody stem cut, until they are unavailable in the fall (Brenner 1962, Svendsen 1980b, Gillespie 1977, Northcott 1971, Aleksiuik 1970, Green 1936, Townsend 1953, Chabreck 1958). The central place aspect of a foraging trip probably plays a role in the switch to aquatic and herbaceous plants, the latter materialize in a zone interposed between the lodge and trees.

Aleksiuk (1970) calculated protein:calorie ratios of leaves, twigs and bark. His findings show that beavers eat

the most highly nutritious foods available within season (point #4 above). Svendsen (1980b), looking at proportions of food types in the diet over all seasons, concluded that beavers "maximize use of the available food resources". His use of "maximize" corresponds to maximizing the use of the most nutritious foods, given that aquatic and herbaceous vegetation is more valuable than woody vegetation as food.

In the fall, beavers cache a large volume of twigs, branches, and stems of trees. A "raft" of non-food and low preference foods is used to sink preferred foods low in the cache profile (Slough 1978). This interesting use of materials seems to be an optimal 'fix' for the otherwise wasteful loss of foods frozen into surface ice.

The food cache is an integral part of the beavers foraging strategy. The cache allows beaver to obtain energy while foraging in the winter, without inducing a possible net loss of energy for the foraging trip. In addition, Aleksuk (1970) pointed out that beaver that can stay under the ice all winter have a selective advantage over those that must emerge in midwinter. Beaver thus avoid predation risk since they are poorly adapted for locomotion in the snow. They also use less energy to maintain a positive heat balance; beaver are not fully adapted for sub zero temperatures, their feet and tail are hairless.

When utilizing the food cache, beavers use only the bark of stems, branches and twigs (except for the very smal-

lest twigs which are consumed whole) (Aleksiuk 1970). While the beaver's cecum microflora are capable of extracting nourishment from wood fibre, presumedly the most nutritious food available is bark (Aleksiuk, 1970, assumed the relative nutritional properties of wood fiber and bark would be constant while stored; Brenner, 1967, was of the opinion that leaching could decrease nutrient value of bark).

Possible corroboration of the hypothesis that beavers optimize their diet by using the most nutritious foods available to them is found in beavers living in habitats that experience short or no periods of freeze-up. Hay (1958) notes that plains beaver infrequently cache food while the nearby mountain beaver do. Chabreck (1958), working in Louisiana where the streams did not freeze, found beaver did not store food, that they fed on trees in place more often than northern beavers, barked standing trees to obtain food, and built few dams. Svendsen (1980b), and Brenner (1962) found that while food was cached, fresh terrestrial food was used if the water remained open. In the same vein Aleksiuk (1970) and Jenkins (1980b) cited papers and presented data to show that food caching of woody stems is forestalled at ponds where abundant water lilies with thick rhizomes are present. Leaching of nutrients (Brenner 1967), by the solvent action of water, probably reduces the value of cached food. This reasoning is necessary to explain the apparently non-optimal behavior

where beaver bypass their closest available energy supply, the food cache.

WITHIN SEASON OPTIMIZATION

(OPTIMIZATION OF TREE CUTTING BEHAVIOR)

The balance of this thesis is a consideration of tree and shrub foraging only; an activity concentrated in the fall. If the model developed here proves to be a useful investigative tool, there may be application in multi-season studies such as Svendsen's (1980b).

Jenkins' (1975) stepwise linear model testing (using the variables genus, choice, diameter, site and their interactions), produced conflicting results. He cited the paucity of "data on relative nutritional value of different tree species for beavers and time and energy costs of cutting trees of different species and sizes" as reasons to avoid discussion of the preferences shown.

There is probably an additive model that would best describe beaver foraging behavior. For example, foraging may be a function (net energy gain per unit of time = $f(A,B,C\dots)$) of tree species, tree diameter, tree quality, beaver digestive capabilities, topography, distance, predator pressure, etc. Unfortunately descriptions of beaver energetics (Aleksiuk and Cowan 1969b, Novakowski 1967), the nutritional properties of beaver foods (Aleksiuk 1970, Novakowski 1967), the efficiency of conversion of foods to nutrients, and beaver nutrient requirements (Aleksiuk and

Cowan 1969a) require more work for a full understanding (as noted by Gibson, 1957). Until the individual components of a linear additive model and their interactions are better understood, this methodology will not be satisfactory.

Although Jenkins' (1975) modelling was inconclusive, he demonstrated clearly that beavers are selective tree cutters; there are inter- and intra-species differences in preference.

Intra-species differences suggest (Jenkins 1975) that nutritional properties vary within a species group. Intra-species preference might be explained by subtle differences in relative availability (ie. spatial considerations). Central place foraging ideas (a special case in optimal foraging theory) are applicable to the definition of relative availabilities.

The optimal foraging methodology, as opposed to additive model building, first seeks a workable optimization criterion, a function that will be minimized or maximized. Criterion selection is complicated by diverse attributes of the foraging resource; plant species preference, intra-species plant variability, and relative availability of foods are possible optimization criteria.

Optimization Criteria

The first optimal foraging models, developed for predators seeking discrete prey items, mostly used maximization of the net energy gain per unit time function (e/t) as

their optimization criterion (Schoener 1971).

For most predators this proved a workable criterion. However, for herbivores many authors have found it inadequate (Freeland and Janzen 1974, Pulliman 1975, Westoby 1978, Rapport 1980). Plant nutrient properties, including plant chemical defences, can alter the herbivore optimal diet away from a strict e/t optimal solution.

The following discussions culminate in the choice of an optimization criterion.

Food Preference

A review of food habit studies produces the consistent observation that beavers have a varied diet involving ordered preference (Shadle et al. 1943, Hazeltine 1950, Chabreck 1958, Krefting 1963, Aleksasuk 1970, Henry and Bookhout 1970, Northcott 1971, Svendsen 1980b), and also show diameter preferences (Aldous 1938, Gibson 1957, Chabreck 1958, Hall 1960, Nixon and Ely 1969, Henry and Bookhout 1970). Jenkins (1980b) compared studies that have presented preference data, he concluded there was no overall ordering of genus preferences to be deduced.

Jenkins (1980b) noted that this conclusion may be incorrect because distance to cutting was not controlled for adequately in most studies. That is, use and availability are functions of distance from refugia for a central place forager (Covich 1976; Jenkins, 1980b, but in another context). Preference indices assume constant availability.

This assumption is violated in most studies, but its importance is generally negligible for mobile animals. However, central place foragers start each foraging trip from the same location, so violation of the constant availability assumption does obscure the measurement of preference and availability.

For independent expected results, based on species preference optimization criteria, the nutrient properties of the trees available and the energetics of beaver while foraging would have to be quantified. This is an area that deserves attention but it is beyond the scope of this study.

Size-Distance

A prediction from optimal foraging theory that is testable (Schoener 1979) is paraphrased here as follows: 'the range of food sizes with positive e/t decreases with distance travelled', in other words, selectivity by size class of prey (trees in this case) increases with the distance travelled. Jenkins (1980a) confirmed the prediction and found that, for beavers tree diameter and genus act jointly on selection, not independently.

The choice of a food size is intimately connected with capture costs in optimal foraging theory. Jenkins developed the argument, possibly fostered by the utilization studies of Aldous (1938) and Stegeman (1954), that beaver provisioning time (the time taken to move a tree from the cutting site to the food cache) is greater for a large tree, than a

small tree, because it requires more trips to the pond. Schoener (1979) accepted this line of reasoning. I do not dispute the logic inherent in Jenkins viewpoint, however the above plus Jenkins' assumption that "branches or logs of approximately equal mass are carried to the pond in each trip" may be biologically inadequate. That is, the thinking engendered by these points of logic do not lead to the most useful overview of beaver foraging behavior. Consider the following discussion.

First it is implicit in the assumption that these packages of equal mass have equal net food value. This has not been documented and may be unlikely since wood fiber is an "antiquality component" and should affect food selection (Green 1936, Novakowski 1967, Aleksiuik & Cowan 1969, Milton 1979). The ratio of bark to wood fiber in packages of equal mass could vary dramatically from bole to crown in relatively large trees. Stegeman (1954) concluded that there was only a 2.4 percent difference in ratios of bark to wood in young (1") trees and old trees (2"-9"). Stegeman's result does not address the food package question, and his paper, although not clearly stated, hints that these numbers were calculated for branches and twigs only, whereas tree boles should have been included. I am persuing this line of inquiry in a separate study. The tentative finding of the pilot study is that for packages of equal mass, the bark volume captured in small diameter loads is considerably

greater than in large diameter loads (within the range of stick lengths and weights that beaver can practically manipulate).

Secondly, the provisioning behavior of beaver may be better understood in the context of a single trip rather than multiple trips for large trees. Orians and Pearson (1979) defined the basic unit in central place foraging as the round trip. The round trip takes a beaver from lodge to tree to lodge, and presumably is the unit upon which decisions to revisit a downed tree or select another are based. In this framework, the food package provisioned on a single trip is the prey item. As such the prey item is not a large or small tree per se, it is a quantity of wood fiber, cambium, bark, and buds with discrete e/t.

A tree in this view is a patch of variable quality. If there is any validity to the optimal foraging hypothesis, beaver should stop removing food packages from the tree when e/t drops below the average rate for the entire habitat (see Sih 1980 for discussion). Waddington (1982) points out that a "simultaneous encounter model," where many potential food items are being encountered, frequently predicts partial preferences (usually in the context of whether more than one food species is included in the diet) because the time spent moving to the next item is employed in the decision process. Schoener's (1979) model has a simultaneous encounter mathematical form; however his treatment of beaver foraging

assumes multiple trips to a single tree in a sequential encounter manner, that is, with no simultaneous encounter decision making. This is not a realistic formulation of beaver behavior because beavers can re-evaluate the foraging opportunities after each round trip (Orians and Pearson 1979).

Wastage of downed trees, a frequently noted problem with beaver foraging behavior (Aldous 1938, Shadle and Austin 1939, Gese and Shadle 1943, Gibson 1957, Hall 1960, Rutherford 1964, Northcott 1971), is usually partial wastage and may be explained by the unequal energy yield of various tree portions.

Also, abandoned lodged trees, which have been considered wasted by biologists, should be abandoned because their chance of falling when cut a second time is less than that of an unfelled tree. In other words, there is an energetic advantage to abandoning a lodged tree.

Maximum e/t for a given quantity of food is realized when the energy expended and time used for capture are minimized.

The top 3 m of a 10 m tree are more expensive to capture than a tree that is in total 3 m high, because the latter requires less cutting. For packages with the same gross energy, the net energy yield is lower from a large tree. However, the total energy available in a large tree will exceed that of a small tree (Aldous 1938). Do the

extra cutting costs in securing packages (prey items) from a large tree exceed the extra search costs for securing an equal amount of energy from small trees? I don't know. Jenkin's (1980a) demonstration that beaver are more selective at long distance is satisfactory, but the reasons behind beaver selectivity have not been thoroughly researched. Increased selectivity for small trees may be an anti-predator strategy; by scattering the cutting effort in time and space beaver may be less predictable and therefore less vulnerable to predation.

At the other end of the scale, trees smaller than the largest that can be provisioned intact reduce overall e/t if chosen, but may still be a larger net energy package than a similar portion from a large tree. Very small trees are not efficient packages unless two or more can be handled at once (see Orians and Pearson's, 1979, selection of prey during a trip discussion). In addition, very small trees, which have a high ratio of bark to wood, may be inefficient food packages when compared to slightly larger stems, because beaver cannot separate bark from wood on very small stems (Aldous 1938)(i.e. stems < 1 cm may involve digestive inefficiency). These last points about small trees are important. They provide a coherent basis for an optimal tree size choice, based on a continuum, the optima being neither a minimum or maximum. The general conclusion of papers examining diameter preference is that small trees are

preferred (Aldous 1938, Gibson 1957, Chabreck 1958, Hall 1960, Nixon & Ely 1969, Henry & Bookhout 1970, Jenkins 1980a). The conclusion may be technically incorrect from an optimal foraging standpoint, because investigators only measured trees down to a stated minimum diameter (ie. 1 or 2 inches).

The size-distance relationship is not a practical optimization criterion for my purposes because selection is jointly dependent on genus [probably species] and diameter (Jenkins 1980a). I chose to factor these effects out of the analysis using another criterion and type of analysis.

Energy-Distance Relationships

Hiner (1938) observed that beavers forage food closest to the lodge first and the next closest food thereafter (see also Gillespie 1977). However, Hiner noted that maximum land distances were shorter than maximum water distances. Hiner's observations implicitly assumed a functional relationship between the cost of using land versus water. He did not demonstrate that beavers maximize e/t . Hazeltine (1950) was cognizant of the effect of distance on availability when he ordered species preferences; he noted that the most available stems were taken first. Covich's (1976) discussion of central place emphasizes that the energy-distance relationship is probably constrained by predator avoidance behavior. Hiner (1938) stated that after the shore nearest the lodge was cleared beaver worked laterally

along the shore. Hall (1960) showed a trend for the heaviest cutting to be as close to shore as availability permitted.

A foraging trip must secure an energy surplus for other activities: growth, sleep, grooming, social interaction, predator avoidance, and reproduction (Schoener 1971). Energy expenditure is a positive linear function of the distance travelled, when the medium being travelled in, the load being moved, and the velocity of travel are constants. This means that beaver have a lower rate of energy delivery to the central place as distance increases (Orians and Pearson 1976), and this translates into the following optimization criterion: beaver should choose, in the choice between two identical food packages, the package that minimizes the distance travelled along a foraging path. I define identical food items as those of the same species and size class. I have assumed that intra-species nutrient variability is negligible.

The distance-energy relationship may be a primary element of an additive equation describing beaver foraging behavior. An optimization model based on a minimum distance criterion for deriving expected values would evaluate its importance. The design must control for species, and diameter (Jenkins 1975) as these have already been shown to be important parameters.

Jenkins' (1975, 1980a) data set should not be used as a test of the hypothesis that beavers minimize the foraging distance from their central place; he evaluated availability at beaver cutting sites only (instead of over the whole area where trees were available), and did not define the overwintering lodge at which a food cache was constructed. It may be possible to reject the hypothesis if the food cache location is a matter of record and there was only one overwintering lodge per pond. To complete the test, individual foraging sites would have to be at varied distances from the central place, or the site records for cutting and availability would have to be subdivisible by distance within the sites. Availability was apparently sampled irrespective of distance (Jenkins pers. comm., distance and overwintering lodges were noted with respect to Jenkins 1980a). Testing of the hypothesis will require a data set that randomly samples cutting and availability over the whole potential cutting area.

In summary, a realistic beaver foraging model should incorporate the following points:

- 1) In general, maximum energy yield from any particular food package is realized when the distance travelled is minimized.
- 2) The relative cost of movement in water and on land are important.
- 3) Diameter affects choice of tree.

- 4) Species affects choice of tree.
- 5) Beaver tree cutting activity and tree availability must be sampled over the whole foraging area and should be divisible by distance.
- 6) Beaver forage from a central place.

THE FORAGING MODELS

The beaver caches a winter food supply in close proximity to its central foraging point, the lodge. The food cache is situated in a body of water, while woody foods must be collected at terrestrial locations. The relative costs of swimming and walking are not known, but by generalizing the foraging path situation a continuum of relative costs can be examined (Figure 1). At one end of

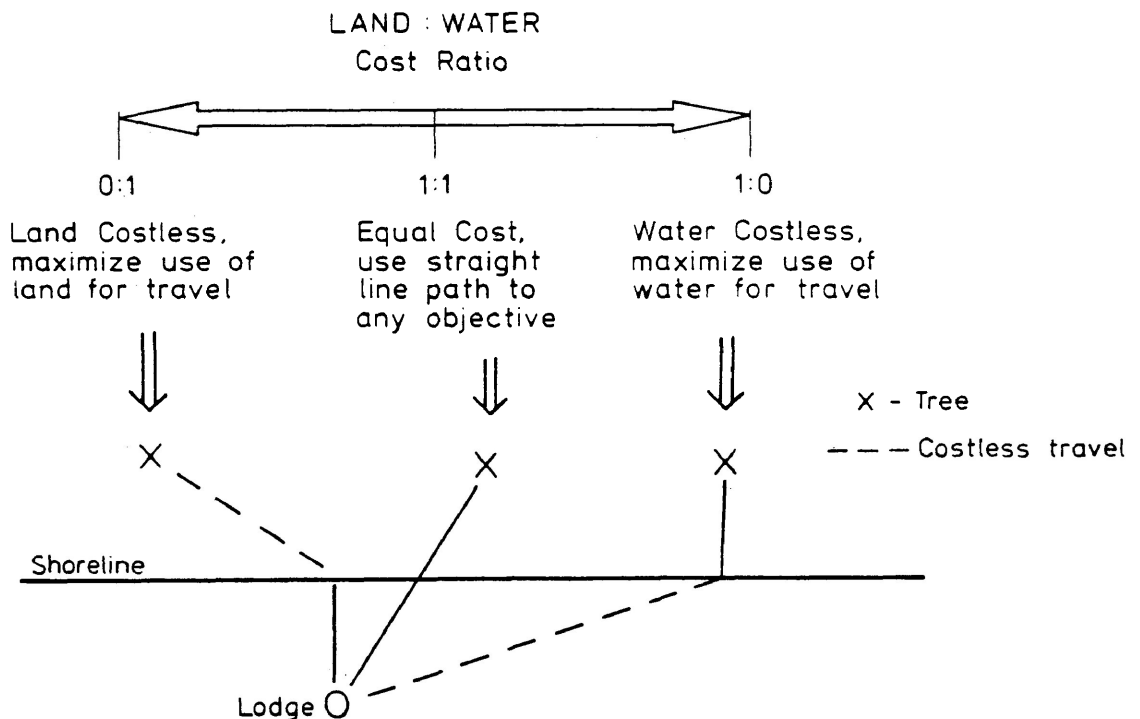


Figure 1: Theoretical continuum of foraging models based on the potential relative costs of swimming and walking. Diagram of foraging paths to an individual tree given the 0:1, 1:1, and 1:0 foraging models.

the continuum swimming is costless relative to walking, at the other end walking is costless relative to swimming.

Any given cost ratio can be translated into a foraging path that represents minimum travel cost to the beaver. However, path definition at non-integer ratios (given that all ratios are in terms of decimal fractions) requires an iterative determination based on the actual spatial relationships at a pond. The foraging path is easily defined at the following points (Figure 1, foraging path diagrams):

- 1) When the cost of walking equals the cost of swimming, 1:1, the foraging path is a straight line from lodge to tree.
- 2) When the cost of swimming is zero, 1:0, the foraging path should maximize the water distance, and minimize the land distance.
- 3) When the cost of walking is zero, 0:1, the path should maximize the land distance, and minimize the water distance.

Feasible energetic solutions in the half of the continuum where walking is less costly than swimming are unlikely (however, see pg. 37); beaver are adapted to the aquatic environment and water provides neutral buoyancy for body weight and tree parts. The actual foraging path employed by beaver, from a strictly energetic standpoint, should lie between the 1:1 and 1:0 cost ratios. The 1:1

ratio does not take sufficient advantage of the beavers' aquatic adaptations, while the 1:0 ratio is unattainable because swimming does have an energetic cost.

The predicted distance to individual trees selected for cutting should be different for the two models. In the first, the cost of travel is equal in water or on land (1:1), and the distance of interest is from lodge to plot. In the other, water is costless for travel (1:0), and the appropriate distance is the shortest distance from the shoreline to the plot.

Can the 1:1 and 1:0 foraging patterns be distinguished on the ground? Consider a data set of observed cutting with known spatial distribution. Expected data sets can be generated, given the distance minimization rule discussed earlier, for each ratio. The ratios (1:1, 1:0) can be viewed as models of beaver foraging behavior, chosen from the continuum of potential foraging models (paths). Goodness of fit can then be examined, and a decision made about which expected data set fits better with the observed data. However an analysis of what the models can actually tell us (sensitivity analysis) is necessary for an understanding of decision quality.

The distance minimization criteria, used to choose between trees of equal food value, is a robust delimiter of which tree to cut under a given model. The goodness of fit tests which will be used in the analysis to chose the best

fit model should therefore be equally robust. The pattern for site usage given the 1:1 model is concentric enlargement of the cutting area centered on the lodge. The pattern of site use for the 1:0 model is isoclinal enlargement of the cutting area based on the shape of the water body.

More subtle, and essential to understanding what the continuum can reveal, is the question of whether or not the foraging path to individual trees is significantly different between models. There is a physical area where the paths are essentially the same (i.e. very close to shore at any distance from the lodge, and at any distance from shore where the lodge-tree path is the same for both models, e.g. at the four points of the compass in an oblong pond running east-west, or in any direction in a round pond with the lodge at its center). This does not influence goodness of fit, because choice between trees is more important. What it does suggest is that the scaling of energetics on the continuum should be understood. For a number of lodge and tree locations, I determined, using an iterative procedure, the paths of least cost given a set of possible foraging paths and a set of cost ratios from the possible ranges (eg. Figure 2). The cost ratios represented equal cost (1:1), 1.25 times advantage for swimming (1:0.8), 2 times advantage for swimming (1:0.5), 5 times (1:0.2), 10 times (1:0.1), and water costless (1:0).

1:1.0- equal cost walking:swimming
 1:0.8 - 1.25 times advantage to swim
 1:0.5 - 2.0 times advantage to swim
 1:0.2 - 5.0 times advantage to swim
 1:0.1 - 10.0 times advantage to swim
 1:0.0 - swimming costless

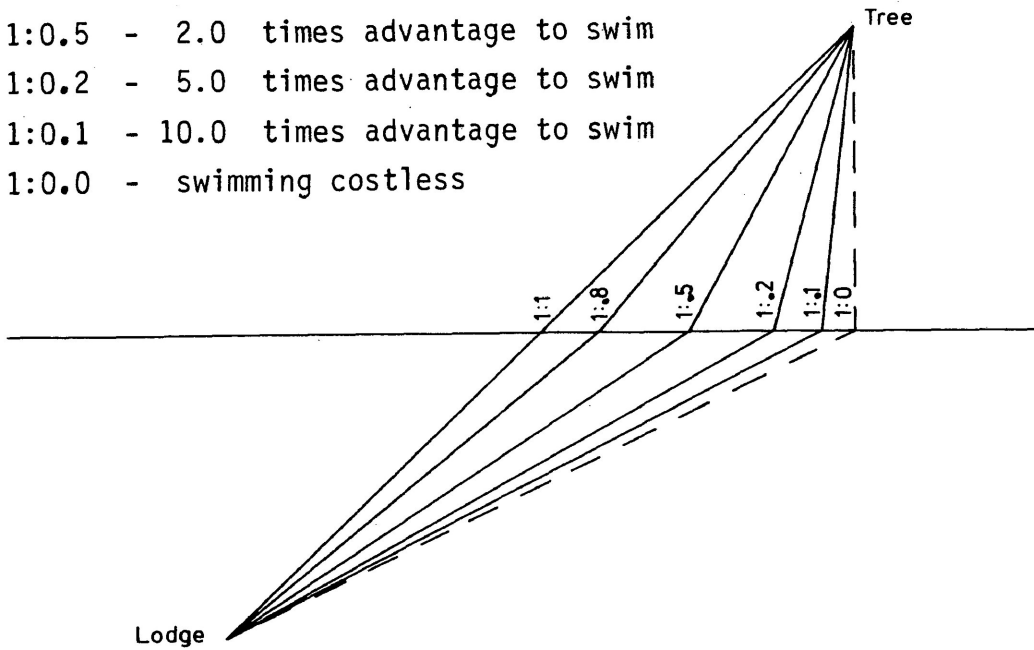


Figure 2: The minimum cost foraging paths given a range of relative costs of walking:swimming, a sensitivity analysis.

The sensitivity analysis above suggested that the foraging path for a 10 times advantage to swimming is for practical purposes indistinguishable from the water costless path (Figure 2). A conclusion of good fit with the 1:0 model should probably be interpreted as an advantage to swimming in the range of 5 to 10 or greater times that of walking. A less than 1 time advantage of swimming over walking will apparently be indicated if there is a good fit of observed cutting with the 1:1 model (Figure 2) and would be interpreted as energy relationships limiting the relative availability of foods. A finding of a poor fit for both

models may indicate a 1-5 times advantage for swimming (Figure 2), however, it would be technically incorrect to define the alternate hypothesis in terms of this poor fit.

What does a 5 or 10 times advantage to swimming mean? Is this in the realm of possible energetic advantage for swimming over walking? If not, we would conclude that there is a constraint on the free ranging behavior of beaver. There is no good answer in the beaver literature as no metabolic chamber measurements are available for beaver. The same can be said with respect to land:water velocities or land:water load capabilities.

Schmidt-Nielsen (1972) discusses the energy costs of swimming, flying, and running (where running refers to quadrupedal or bipedal movement and includes walking speeds). Although the data are not substantial, the mallard duck, which propels itself by paddling as beaver do, had a cost of swimming greater than the cost of running for similar sized mammals. A beaver may be a more efficient swimmer than the duck because it would not set up as much wake; but this cannot be said for a beaver towing a log home where wake and turbulence would seriously impede swimming efficiency. Bouyancy in water is counteracted by large energy losses due to moving through the medium; negligible air resistance on land is counteracted by losses to drag and physically supporting a portion of the log mass. At this point there is no reason to believe that there is any

energetic advantage for a beaver to swim rather than walk. The possibility of an energetic disadvantage while towing foods should be considered and tested.

Time is also a component of the function e/t being maximized. It would seem unlikely that swimming could increase the rate of energy acquisition in the order of 5 to 10 times. Beavers travel at about the same rate on land or in water (personal observation). That is not to say that water travel could not effectively speed the rate of energy acquisition. Water bodies are natural highways, with few obstructions, while terrestrial travel is hampered by terrain and vegetation. However, beaver improve their freedom of movement on land by clearing trails. In the end any conclusion drawn from accepting the water costless model (1:0) would have to be tentative. Experimental confirmation of the possible range for the advantage of swimming over walking is necessary.

To test which model better represents the foraging strategy that beaver use, spatial distribution data for beaver foraging of trees and shrubs were collected. The data collection included locations of observed beaver-felled trees and the locations of trees available for cutting. The data were also classified by species and diameter so that these two factors could be controlled in the analysis.

The data were collected at two separate beaver colonies in the fall of 1981. The respective data sets were

analysed separately and compared for consistent results. Northbranch pond is relatively unexploited when compared with Pinetop pond. This contrast was deliberately included so that differences in foraging behavior on new vs old sites would be revealed.

The main question addressed in the analysis was the following.

- 1) Is the relative shortage of food at beaver ponds induced by energetic limitations or predator pressure? Jenkins S.H., pers. comm., notes that I imply that an energy maximizing foraging strategy means that food limits population growth. He does not believe this to be true. I agree, but add that it is grounds to suspect a case of food limitation. In the same vein, constrained foraging behavior is grounds to suspect population limitation by whatever is causing the non-optimal foraging behavior. (i.e. Do beaver maximize e/t , or forage in a constrained manner?) That is, does the water costless model or the equal cost model better fit the observed data?

A number of secondary questions were also asked.

- 2) Is tree species preference demonstrated and is it a function of distance from the central place?
- 3) Is diameter selectivity demonstrated and does it increase with distance from the central place?

- 4) Can intra-(tree)species anomalies in food selection by beavers be explained by differences in relative availability, rather than invoking nutritional properties?
- 5) What differences in beaver foraging behavior are there between relatively old and new beaver colony sites? (Is there evidence for a relative shortage of food in this study?)

STUDY AREA

The study area was located (Figure 3) close to the city of Thunder Bay, Ontario, on the Savigny Creek flowage. Two beaver colonies were selected for study. Northbranch Pond is 6.5 km, and Pinetop Pond is 9 km by road from the city. They are at approximately 48°32' N latitude, and 89°08' W longitude, in Zone 16UCJ of the Universal Transverse Mercator Grid System; Northbranch Pond at 411749, and Pinetop Pond at 425782.

Pinetop pond had a large cutting area with a number of accessory dams built above and below the main dam. The colony is relatively older than the Northbranch colony. Northbranch pond is a single water body, similar in area to Pinetop's main pond. (See Figure 4 in the results). Aerial photography from 1975 shows Northbranch Pond flooded to the same degree as 1981. Pinetop Pond had the same configuration of dams below the main pond in 1975 as was present in 1981; dams above the main pond were built in the interval 1975-81.

A primary consideration in the selection of these beaver colonies was their convenient location relative to Thunder Bay. However, they were required to meet certain basic criteria that would eliminate complicating phenomena, or provide an enlightening contrast. In respect to the latter, the ponds were chosen so that a relatively old

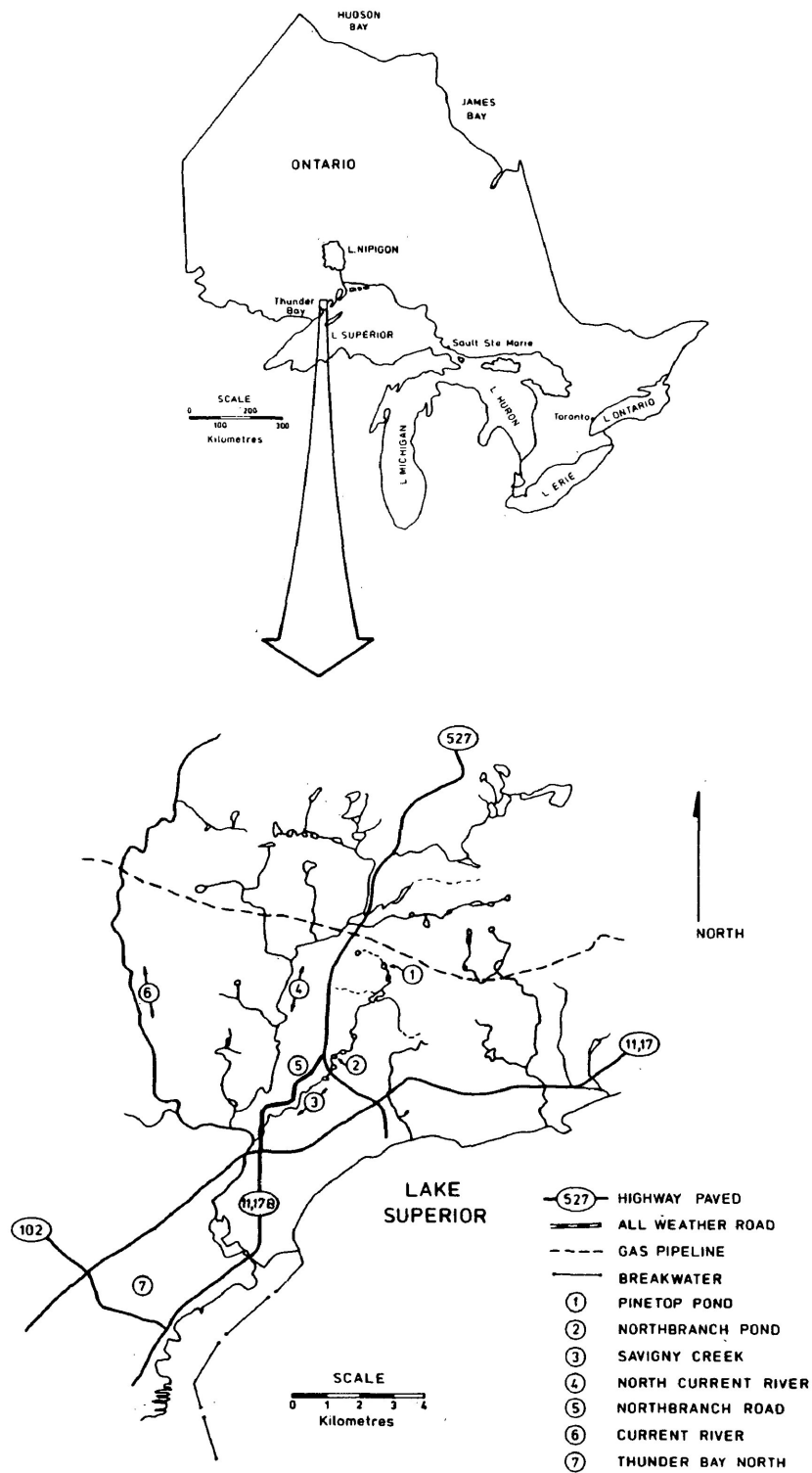


Figure 3: The locations of Northbranch and Pinetop Ponds, the two beaver colonies studied.

colony would be contrasted with a relatively young colony. As nearly as possible, identical composition of tree species was sought to facilitate comparing beaver foraging behavior between colonies. It was especially important that aspen be present. Aspen is generally acknowledged to be the most preferred food; foraging behaviors that altered the use of aspen between ponds would then be more easily interpreted. The forest surrounding each pond (i.e. prior to beaver impacts) was to be as homogeneous as possible in the valley bottom situation to avoid subtle differences in availability that might interfere with interpretation of results. Stable site conditions were sought; colonies were sought that would not be subject to flood or drought. The colonies were to have only one lodge, at present and historically, so that all consequences of cutting activity at the sites could be attributed to a single central place.

The ponds are on the northernmost edge of the Great Lakes - St. Lawrence forest region, in Rowe's (1972) Quetico forest section. In the immediate locality of the study area Rowe's observation that logging and fire have favored the prominence of boreal tree species is apt. The colonies have identical tree species composition: white and black spruce (*Picea glauca* (Moench) Voss. and *P. mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), Larch (*Larix laricina* (DuRoi)K.Koch.), cedar (*Thuja occidentalis* L.), aspen and balsam poplar (*Populus tremuloides* Michx. and *P.*

balsamifera L.), white birch (Betula papyrifera Marsh.), and mountain ash (Sorbus decora (Sarg.)C.K.Schneid,) are the arboreal species present. Shrubs found at the ponds are alder (Alnus rugosa (DuRoi)Spreng. and A. crispa (Ait.) Putsh.), red osier dogwood (Cornus stolonifera Michx.), willow (Salix L. spp.), pin cherry and choke cherry (Prunus pensylvanica L.f. and P. virginiana L.), serviceberry (Amelanchier sanguinea (Pursh)DC.), broken hazel (Corylus cornuta Marsh.), cranberry (Viburnum L.), and mountain maple (Acer spicatum Lam.).

The broad valley of the Savigny Creek flowage has a gradient of 1.6% in the head water area (1:50,000 topographic map sheet 52A/11). Pinetop pond appears to have dependable subterranean flow in what would otherwise be an intermittent location. Northbranch Pond, lower in the valley, is fed by a well defined creek with year round flow. Forest cover on the watershed above the ponds is essentially continuous and soils are well drained.

Topographic relief is rather shallow at both colonies. In one respect this minimizes the effects of slope on foraging behavior, but it also induces moisture related stand changes in low areas at both sites. Consequently stand homogeneity was somewhat compromised.

At Pinetop Pond a large area adjacent to the main pond was a black spruce swamp, while the forest above (north of) the pond complex was low lying and contained few aspen. At

Northbranch Pond a partially inundated balsam poplar stand was present although its location minimized its effect on the observed foraging pattern.

The occupation history of the ponds is not known in detail. Northbranch Pond was more accessible to the registered trapper. Since 1973 the pond had been occupied almost continuously (Don Barnes, pers. comm.). In 1980 personal observation at the pond determined that 3-6 beaver were actively constructing the food cache (night scope observations). A dead diseased (Dr. M. Lankester pers. comm.) beaver was found in late November 1981 after the measurements were completed. No more than one beaver at a time was observed in the fall of 1981 although observations were not attempted. The trapper judged that there were no live beaver in the pond that winter. My impression from the food pile constructed, and activity on the lodge (mudding), was that the family observed the previous fall still occupied the lodge. The results of the tree tally (pg. 54) indicated that 2-3 beaver were responsible for the observed cutting (Nixon & Ely 1969, Bradt 1938, Shadle & Austin 1938). Pinetop Pond has been trapped twice since 1973, in 1978 and 1979. It was occupied each time the trapper visited the colony, and had a minimum of 4 beavers in the fall of 1981 (personal observations).

METHODS

FIELD METHODS

Using a surveyors transit and rod for bearings, the intersections of a grid with 5 m spacing were staked. The grid was oriented N-S and E-W with a co-ordinate point corresponding to the lodge. Triangulation was used to obtain starting points on land and to check the additive error of the grid layout as it became progressively larger. This error never exceeded 2 m and adjustments were not made to the grid.

A 30 m tape, stretched between transit and rod, was used to locate the 5 m intervals on a preliminary 30 m grid. Stake locations for the 25 square meter quadrates, or plots, within the 30 m grid were obtained by taping between the 5 m intervals on the 30 m grid to minimize transit setups. Each plot was numbered as an (X,Y) ordinate, with the lodge at the X,Y axial intersection.

Beaver harvest a limited number of trees in a season. Even when all cut stems are tallied (Nixon and Ely 1969, Hazeltine 1950, Shadle and Austin 1938, Gibson 1957, Jenkins 1975) the species diameter cell frequency counts are small. The chi-square goodness of fit test, one of two tests to be used, is a large sample test. It was desirable to tally all cut stems. This was especially important in this study where spatial subdivisions also depleted cell (species-

diameter-distance) sample sizes. At Northbranch Pond all plots, to a distance of 10 meters past a furthest beaver felled tree, were tallied. The Pinetop Pond cutting area was much larger; it was sampled to 50 percent with a checkerboard pattern (random in that the sample was defined by the flip of a coin). All available stems were tallied on all plots that were sampled.

This method differed from Nixon and Ely (1969) and Jenkins (1975) who sampled availability within areas of intensive cutting activity using random circular plots. Areas of intensive cutting were defined by recording the locations of all stems cut. This method leaves unsampled areas that preclude model testing with a distance minimization criteria. Hall's (1960) "spoke samples" (transects perpendicular to the pond 10 m wide, 100 m deep, subdivided by 10 m intervals) of tree cutting and availability could be an adequate sampling methodology.

A two person crew measured and tallied all woody stems and stumps on the plot. These were dot tallied under three cut status sub-headings: old cutting, not cut, and new cutting. A new cutting was defined as a tree cut in 1981. The tally was further subdivided by tree or shrub species, and diameter at stump height (DSH). Diameters were recorded by 2 cm classes (1, 3, 5, 7...). The "true class limits" (Snedecor and Cochran 1980) for diameter were 0-2.0 cm, 2.1-4 cm, 4.1-6 cm, ... to the upper limit of tree sizes.

All stumps were spray painted during the tally. Old stumps were not painted prior to the cutting season so the decision, old versus new cut, was based on stump weathering (discoloration or mould) and disposition of cutting chips if available (relative to leaf litter). The final check of the ponds was after freeze-up, when beaver could not break ice.

DATA HANDLING

Data for each pond were entered into sequential files on Lakehead University's DEC 2020 computer. An interactive BASIC program, with control and error routines, was written to facilitate data entry.

A record in the file was specific to a species-diameter-cut status cell on the tally sheet (e.g. 4 mountain maple - 3 cm DSH - not-cut). A record contained the plot co-ordinates, straight line distance from the lodge (axial intersection point) to the plot center (calculated trigonometrically by the entry routine), shortest distance to the shoreline from the plot center (hand measured from scale diagrams because the pond and shoreline were not digitized), cut status (old-cut, not-cut, new-cut), species, diameter, and the number of stems recorded in the cell.

I chose distance classes so that the data would be spread across the same number of distance classes regardless of the model or pond being examined. At Northbranch the 1:1 model used 20 m distance classes, the 1:0 model 10 m classes; at Pinetop - 1:1, 30 m - 1:0, 15 m.

For each pond, two tables (1981 stems available, and newcut stems) of three dimensions (species, diameter, distance) were compiled for both models (1:1, 1:0). In addition corresponding summation tables of species-diameter (distance ignored) were compiled for new-cut stems. These were used for calculating expected cutting. Two expected cuts were calculated, one for each model.

CALCULATING AN EXPECTED CUT

When testing a model it is preferable that a priori expected results are used. In this case an optimal set of trees that should be cut would be generated to test against. A simulation model could generate a priori expected results but there is insufficient knowledge of the criteria that beaver use for tree selection. At this point in time a simulation model would contain many shaky assumptions and oversimplifications.

The aim in this thesis is to examine the role of the distance parameter and not to build an all encompassing foraging simulation. Consequently the summation of the observed trees cut, using species and diameter information, is used to generate the expected cut. The set of trees in the expected cut is identical to what the beaver actually cut. Only the spatial distribution of the cutting activity is tested. In doing so I run the risk of criticism for ignoring possible spatial differences in food quality (Jenkins 1978) or relative availability (due to physical

aspects of the landscape). However, the colony sites studied are reasonably homogeneous, and were selected to minimize these effects so that this test could be carried out.

For each model tested distance to cutting is recalculated. Therefore, the observed cut and expected cut are also recalculated. Given the test between two models from the continuum, there are two sets of observed and expected cutting.

The optimization criterion, discussed previously, was that distance to cutting be minimized. This criterion was used in a deterministic way. With probability equal to one, the expected new-cut tree was the closest available. For example (Table 1), given 4 available 5 cm aspen stems in the 0-10m distance cell and a total of 12 observed 5 cm aspen stems cut by beaver in all distance cells, the expected cut was allocated as all 4-5 cm stems available in the cell.

Table 1: Example calculation for the expected cutting of 5 cm aspen in all distance cells.

	Distance (meters)				Sum
	0-10	10-20	20-30	30-40	
5cm Aspen Avail	4	6	12	12	34
Observed Cut	2	5	5	0	12
Expected Cut	4	6	2	0	12

However, the observed cut was 2-5 cm aspen in the 0-10 m distance cell. The expected cutting calculations were done by hand.

TESTING THE GOODNESS OF FIT

Two methods were used to test the goodness of fit of the observed cutting pattern with the expected cutting pattern. These were the chi-square goodness of fit test (Snedecor and Cochran 1980), and simple linear regression (Goulding 1979). These analyses were carried out on an Apple II plus computer using S.P.S. Version 4.2 (Buhyoff and Hull 1983), supplemented by a personal adaptation for chi-square goodness of fit summations.

The chi-square goodness of fit test uses the following statistic.

$$\chi^2 = \sum_{i=1}^k \left[\frac{(\text{observed} - \text{expected})^2}{\text{expected}} \right]$$

where K = total number of cells

The significance of the statistic was obtained from tables of cumulative distribution of chi-square (Snedecor and Cochran 1980). A non-significant result would indicate there was no significant difference between observed and expected, in other words, a good fit.

The chi-square test is a large sample test and is conditional on a working rule (Snedecor and Cochran 1980) that no expectation (expected cell value) should be below 1, and two extreme expectations may be close to 1 provided that

most of the other expected values exceed 5. With data that violates this rule a transformation can correct the deficiency.

The Northbranch and Pinetop data contain a large number of cells with expectations lower than 5, and there were also zero values among the expected.

Transformation by adding 1 corrected for division by zero errors but did not solve the basic bias to small frequencies in the data. However, the minimum chi-square is the best fit model (pers. comm. Dr. Carl Walters, U.B.C.) when we wish to choose between models (i.e. 1:1 and 1:0), because the relative goodness of fit is revealed as long as the statistic can be calculated. Even though the significance tests are not valid, the best fit model can be selected.

The bias to small frequencies can be alleviated by adding a large constant, and even though it is not necessary, we can gain information by doing so. I added progressively larger constants until there was no statistical difference between observed and expected. The conclusion of best fit was considered justified when the transformations that placed opposed models in the area of non-significance were different

The second goodness of fit test, simple linear regression (Goulding 1979), asked that the regression of predicted cut on observed cut be significant, the slope coefficient

not significantly different from 1, and the intercept not significantly different from zero. The latter two points set the goodness of fit test apart from the standard useage of linear regression that seeks a best-fit line. The analysis does not seek the equation of a line, only the satisfaction of criteria as stated above.

My useage of this method may more correctly be called correlation analysis since neither observed or expected values can be considered independent, and the change in Y with change in X is not of concern. However, the conditions for slope, y-intercept, and the ability to examine data biases blur whether correlation or regression is the appropriate terminology. Goulding's (1979) terminology will be used here, a more substantial treatment of the test would be a useful addition to the literature.

When the correlation coeffecient (r) is significant in a test of the hypothesis that the population value (ρ) of the correlation coefficient is zero, the regression is significant (Snedecor and Cochran 1980, test of r). This test is equivalent to the F-test of r . When the confidence interval for the slope coefficient (b in the equation $Y=a+bX$) encompasses 1, the slope is not significantly different from 1.

A test for whether or not one model was a significantly better fit than the other was done; correlation coefficients were tested against the hypothesis

that they were estimates of the same population correlation coefficient (Snedecor and Cochran 1980, t-test of r's converted to z's - Table A12). The comparison of models was not suggested by Goulding (1979) but is my own extension of the method.

Biases in the data can be examined by analysing the residuals (Edwards 1979). Regression analysis is conditional on an assumption of normally distributed, independent, data sets. The residual analysis examined whether these assumptions (possible sources of bias for conclusions drawn) were met.

RESULTS

CUTTING ACTIVITY

In the fall of 1981 a total of 70,215 trees, shrubs, and stumps was tallied at Northbranch and Pinetop beaver colonies. Stems were classified by species, diameter, location on the site, and by whether or not they had been cut by beavers in, or prior to, 1981 (i.e. cut status).

In overview, woody species availability and cutting activity by beavers can be quickly summarized (Table 2a). With the exception of seven white spruce trees cut prior to 1981 at Pinetop Pond, the conifers were not cut. Of 23,421 trees and shrubs available in 1981 at Northbranch 2,832 were deciduous trees; 1,284 of 38,215 stems at (Pinetop) were deciduous trees: of these aspen comprised 55% (37%), balsam

Table 2a: The tree tally^a by species at Northbranch and Pinetop beaver colonies.

Species	Northbranch				Pinetop			
	Pre ^b 1981	Old Cuts	1981 ^c	New Cuts	Pre 1981	Old Cuts	1981	New Cuts
Aspen	2,109	536	1,573	71	868	397	471	6
Balsam Poplar	738	95	643	18	379	127	252	40
White Birch	263	16	247	18	462	66	396	22
Mtn. Ash	415	46	369	7	231	66	165	3
Spruce	173	-	173	-	641	7	634	-
Balsam Fir	12	-	12	-	186	-	186	-
Larch	9	-	9	-	161	-	161	-
Cedar	-	-	-	-	2	-	2	-
Alder	12,410	970	11,440	184	20,840	1,753	19,087	159
Mtn. Maple	2,747	396	2,351	50	7,181	1,120	6,051	223
Willow	3,265	523	2,742	172	2,423	775	1,648	172
Hazel	2,046	118	1,928	10	8,963	1,035	7,928	103
Serviceberry	913	105	808	17	887	159	728	20
Choke Cherry	747	82	665	17	104	16	88	-
Pin Cherry	316	70	246	7	513	105	408	2
Cranberry	215	-	215	-	-	-	-	-

^a 100% tally at Northbranch, 50% of area tally at Pinetop.

^b Pre-1981 availability; the sum of old cut, not cut, and new cut trees.

^c 1981 availability; the sum of not cut, and new cut trees.

poplar 23% (20%), white birch 9% (30%), and mountain ash 13% (13%). There were 20,395 and 35,948 shrub stems tallied at Northbranch and Pinetop respectively. Alder dominated shrubs tallied at Northbranch and (Pinetop): alder 56% (53%), maple 12% (17%), willow 13% (5%), hazel 9% (22%), serviceberry 4% (2%), chokecherry 3% (0.2%), pincherry 1% (1%), and cranberry 1% (nil).

There were 571 new cut stems (1981 cutting activity) at Northbranch Pond and 750 new cut stems tallied on the 50% area sample at Pinetop Pond (Table 2a). Similarly there were 2,957 old cut stems (trees cut prior to 1981) at Northbranch, and 5,626 old cuts at Pinetop (Table 2a).

New cutting activity at Northbranch (and Pinetop) was comprised of 12% (1%) aspen, 3% (5%) poplar, 3% (3%) birch, 1% (0.4%) ash, 32% (21%) alder, 9% (30%) maple, 30% (23%) willow, 2% (14%) hazel, 3% (3%) serviceberry, 3% (nil) chokecherry, and 1% (0.2%) pincherry, while cranberry was not cut anywhere.

The pre-1981 availability and old cut records (Table 2a) have experimental error due to stump decomposition, regeneration, and site invasion or expansion by trees or shrubs. These data were not used in the goodness of fit statistical analysis. They were included in the species and diameter preference graphics to examine two assumptions: first, that distance to present cutting is a consequence of past cutting patterns, and second, that past preferences mirror present preferences.

Table 2b is presented as an example of the tree and shrub data summarized in Table 2a. Aspen is the tree species presented. The data was limited to 1981 availability and new-cut stems by diameter class and distance from the central point. Distance is a function of the foraging model (1:1 or 1:0) being considered so two diameter-distance sub-tables are required for each pond.

Table 2b: An example of the data summarized in Table 2a. The diameter and distance distribution for aspen availability and cutting by beaver, at Northbranch and Pinetop Ponds. The models, 1:1 and 1:0, redistribute the same data base (i.e. have different observed and expect cutting).

Northbranch Pond - Aspen - 1:1 Model - [# stems cut (# stems available)]							
Diameter (cm)	1	3	5	7	9	11-15	17+
Distance (m) From lodge							
20-40	9 (68)	2 (7)	1 (4)	0 (1)	0 (0)	0 (0)	0 (0)
40-60	11 (357)	15 (69)	3 (36)	6 (42)	1 (25)	4 (54)	1 (29)
60-80	1 (144)	1 (113)	6 (96)	2 (89)	3 (78)	1 (111)	1 (54)
80-100	0 (15)	0 (31)	2 (13)	0 (7)	0 (6)	0 (9)	0 (2)

Pinetop Pond - Aspen - 1:1 Model - [# stems cut (# stems available)]							
Diameter (cm)	1	3	5	7	9	11-15	17+
Distance (m) From lodge							
20-50	0 (4)	(-)	0 (1)	(-)	(-)	(-)	(-)
50-80	0 (127)	4 (12)	(-)	0 (2)	0 (4)	0 (24)	0 (12)
80-110	1 (71)	1 (4)	(-)	(-)	0 (3)	0 (23)	0 (44)
110-140	0 (63)	0 (5)	(-)	(-)	(-)	0 (3)	0 (7)

Northbranch Pond - Aspen - 1:0 Model - [# stems cut (# stems available)]							
Diameter (cm)	1	3	5	7	9	11-15	17+
Distance (m) From shore							
1-10	15 (157)	8 (55)	4 (17)	1 (3)	0 (1)	0 (1)	0 (0)
10-20	6 (308)	10 (105)	4 (48)	5 (34)	2 (27)	5 (42)	2 (25)
20-30	0 (95)	0 (91)	5 (72)	2 (70)	2 (65)	0 (80)	0 (33)
30-40	0 (50)	0 (21)	0 (31)	0 (32)	0 (18)	0 (56)	0 (27)

Pinetop Pond - Aspen - 1:0 Model - [# stems cut (# stems available)]							
Diameter (cm)	1	3	5	7	9	11-15	17+
Distance (m) From shore							
1-15	0 (6)	0 (2)	0 (1)	(-)	(-)	(-)	(-)
15-30	1 (44)	1 (6)	(-)	(-)	(-)	(-)	(-)
30-45	0 (104)	0 (4)	(-)	0 (1)	0 (3)	0 (19)	0 (17)
45-60	0 (113)	4 (10)	(-)	0 (3)	0 (27)	0 (26)	0 (2)

The relative ages of the ponds in the Pinetop pond complex are indicated in Figure 4. Ponds 1-4 were constructed prior to 1975 (pond #1 is the oldest), ponds 5-7 since 1975 (aerial photography).

Cutting activity (Figure 4) at the Pinetop site in 1981 fell into three categories: close to the shore of the older ponds (i.e. ponds 1-4), in the proximity of the newest ponds (i.e. ponds 5-7 northwest of the lodge), and in a corridor reaching to the limit of old cutting activity adjacent to the oldest pond (i.e. pond 1). With the exception of one important plot in the latter area, plots that recorded 1981 cutting activity, without cutting prior to 1981, were chiefly found around the new ponds (5-7 northwest of the lodge). Thirty-three percent of the 483 plots with cutting prior to 1981 were revisited by beavers in 1981. Fifteen plots with no previous cutting activity had one or more stems taken in 1981. However two of these plots are within the general bounds of the old cutting area, for a net increase in cutting area of 2.7%, or 13 plots.

At the Northbranch site in 1981 (Figure 4) beaver cut trees at 46% of the 255 plots that had one or more trees cut prior to 1981. The cutting area was expanded 5%, 13 plots, during the season; the few plots with new cutting alone are found on the outer margins of cutting activity east and west of the lodge, and along the stream course at the north end of the pond.

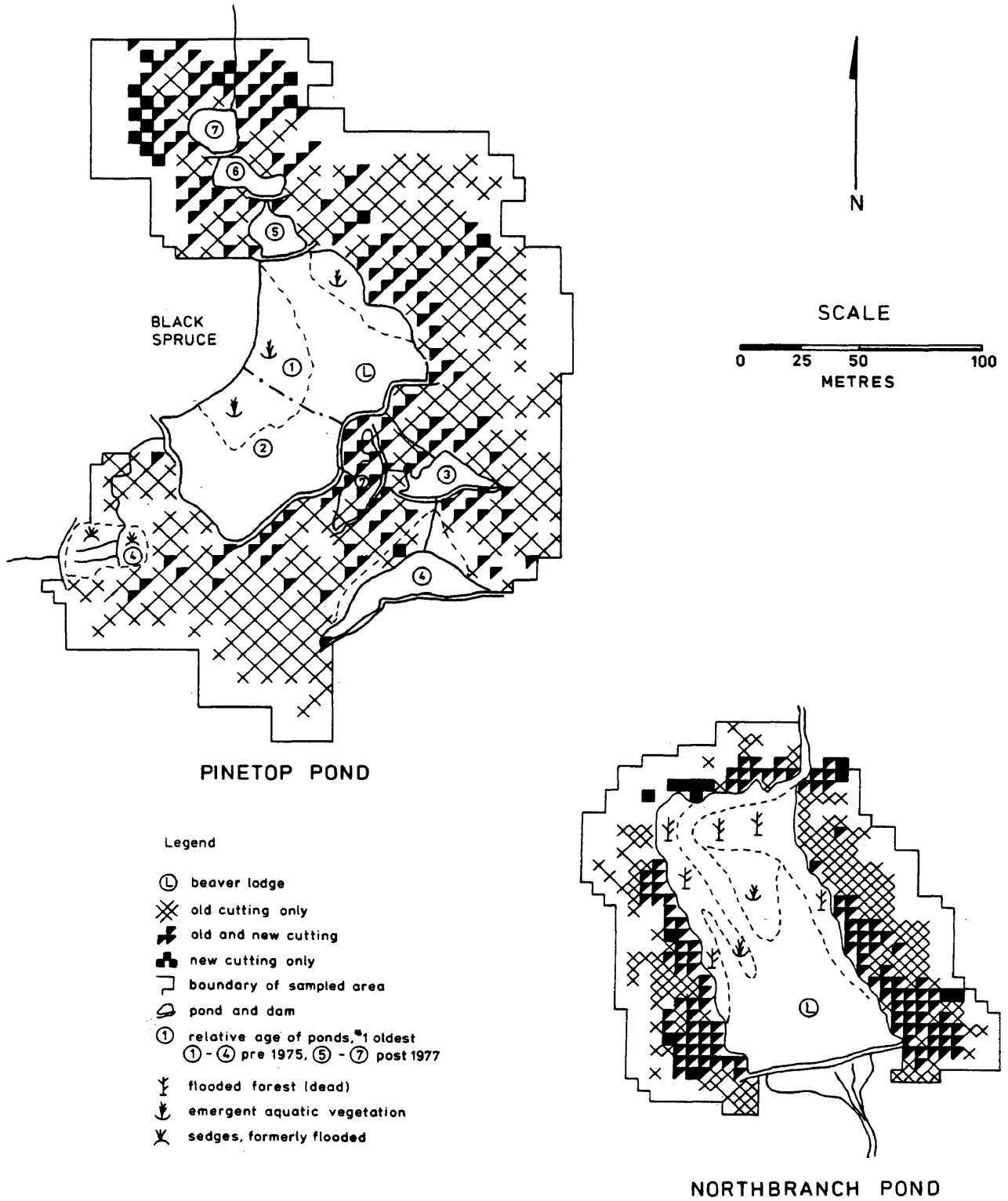


Figure 4: Cutting activity maps for Northbranch and Pinetop Ponds in 1981.

GOODNESS OF FIT TESTS

The data used in the goodness of fit tests are three-dimensional: species-diameter-distance. To simplify graphic contrasting of the observed foraging patterns and the expected foraging patterns for each model, the number of stems cut in each distance class was plotted by species only (i.e. species-distance) (Figures 5 and 6). The data points in Figures 5 & 6 represent summations across diameter classes. They are not the observed-expected data pairs used in the statistical analysis where diameter-species-distance was used.

Except where perfect fit is indicated (eg. balsam poplar at Northbranch model 1:0, Figure 5), the plots of expected pattern were left skewed. This is the effect of the minimum distance foraging criterion.

By inspection, the observed foraging pattern is a good fit with the expected 1:0 (water costless) model of foraging pattern for all species but one. Aspen may have been cut according to a 1:1 pattern. The chi-square test was used on the aspen species-distance data (used in Figure 5 and 6) to clarify which way the pattern for aspen was tending. At Northbranch the beaver cutting pattern for aspen favoured the 1:0 model (1:1 $\chi^2=242$, 1:0 $\chi^2=57$), while at Pinetop the pattern favoured the 1:1 model (1:1 $\chi^2=5$, 1:0 $\chi^2=19$).

Two statistical analyses for goodness of fit, all trees and shrubs included, were carried out on the species-

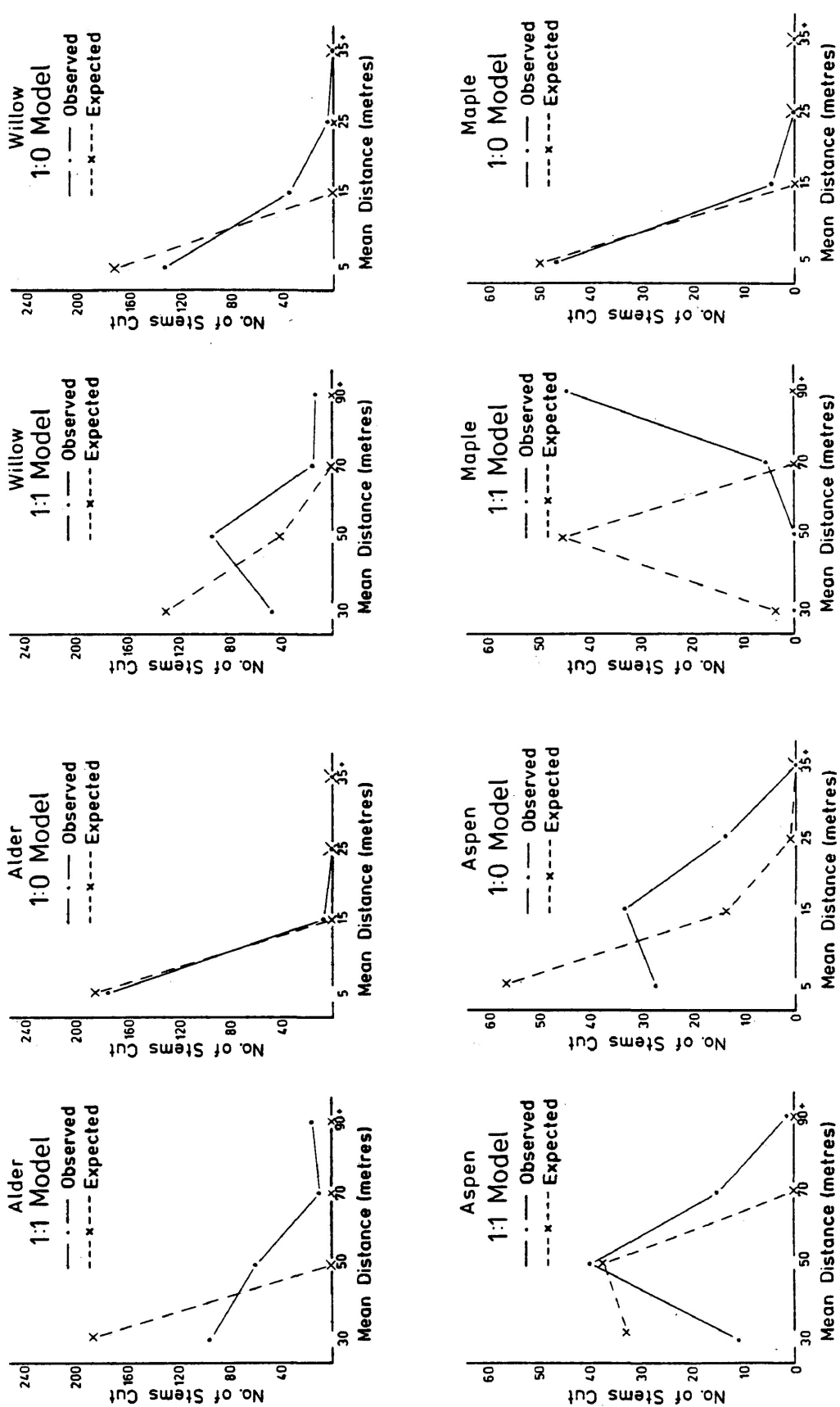


Figure 5: Graphs of observed and expected cutting for the 1:1 and 1:0 models at Northbranch Pond. Diameters were grouped to simplify the figure.

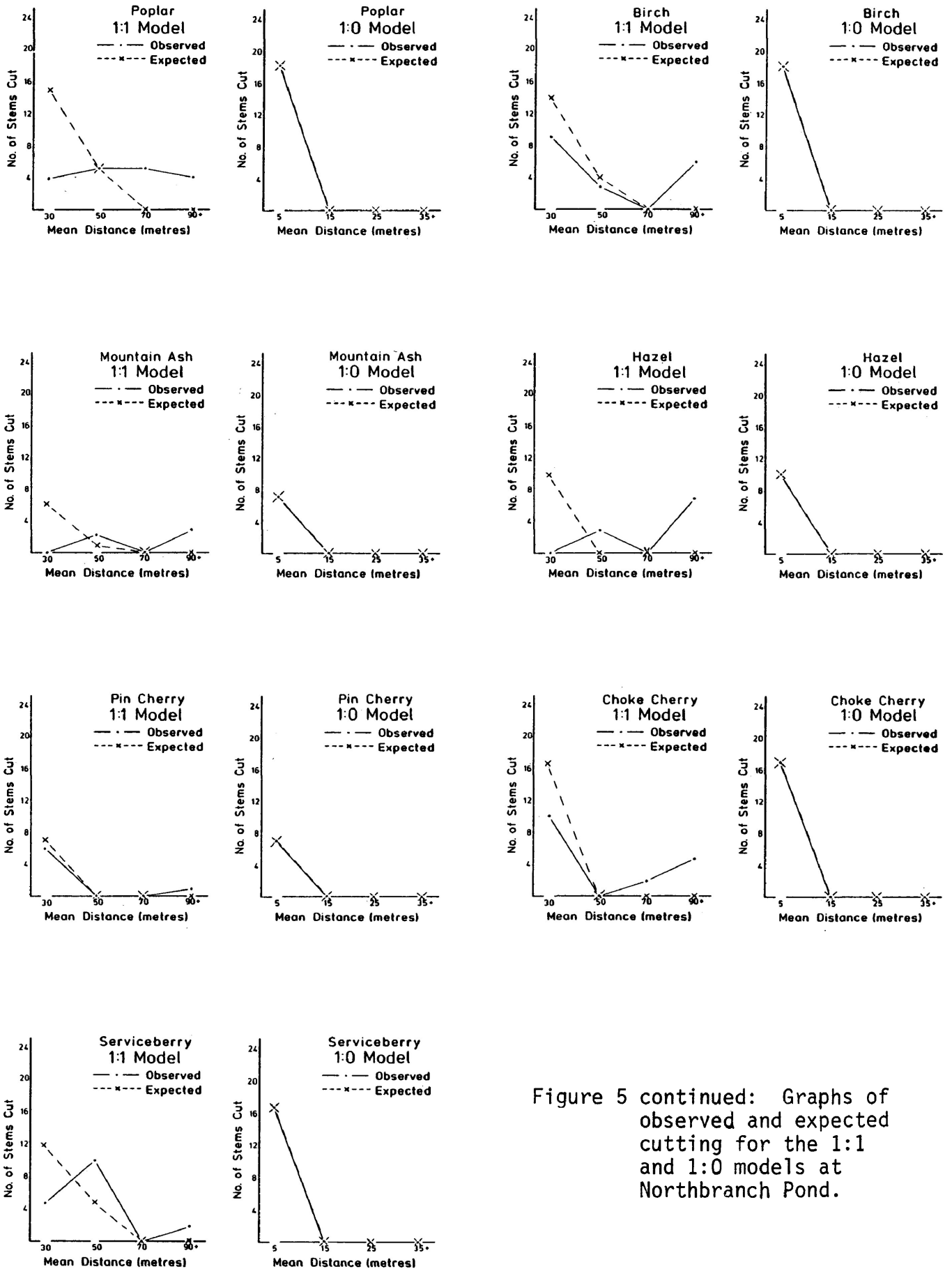


Figure 5 continued: Graphs of observed and expected cutting for the 1:1 and 1:0 models at Northbranch Pond.

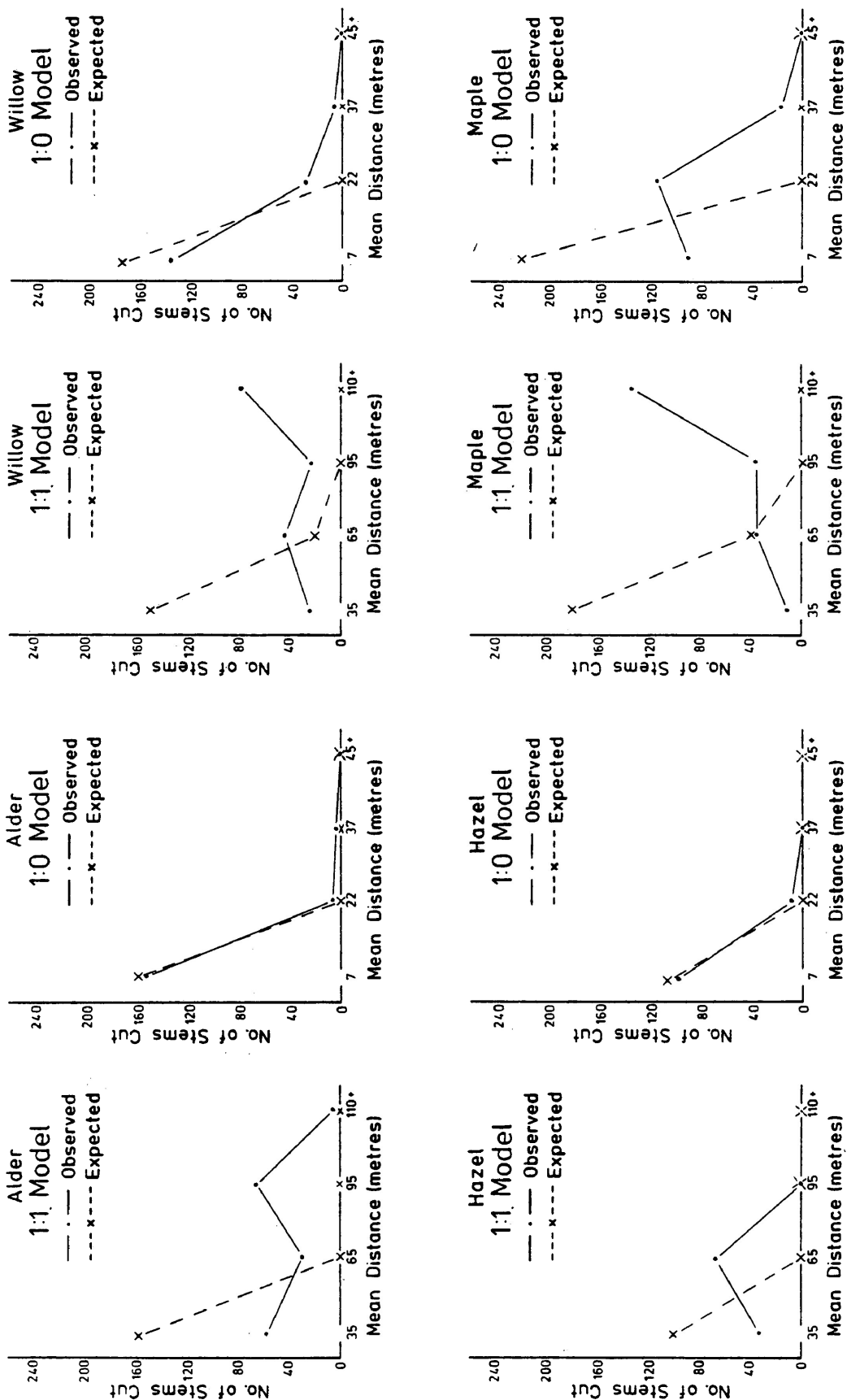


Figure 6: Graphs of observed and expected cutting for the 1:1 and 1:0 models at Pinetop Pond. Diameters were grouped to simplify the figure.

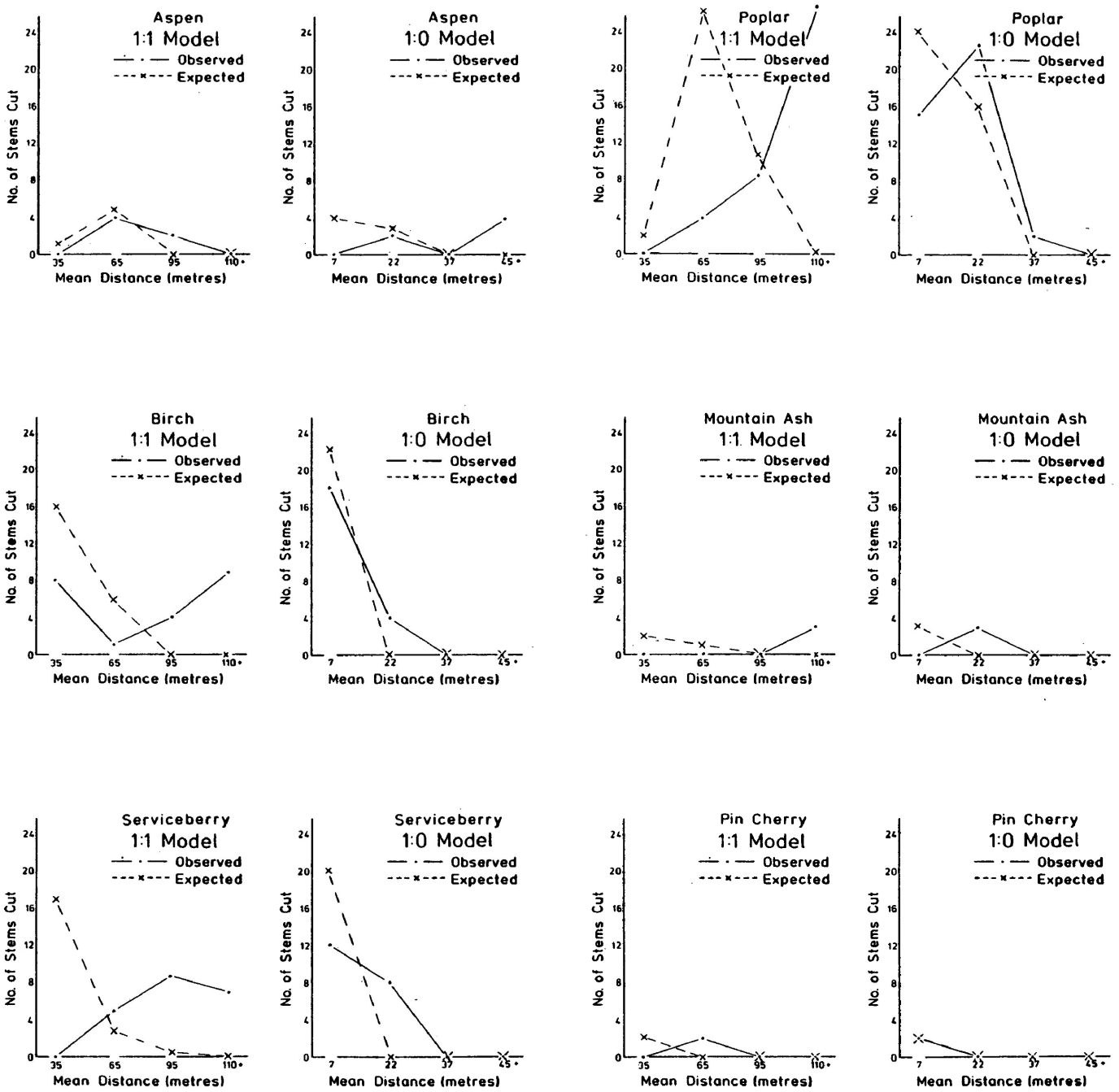


Figure 6 continued: Graphs of observed and expected cutting for the 1:1 and 1:0 models at Pinetop Pond.

diameter-distance data pairs: chi-square and simple linear regression. They are presented separately and then compared in a summary paragraph. Data from the two ponds were never combined, instead the separate results were examined for consistency of conclusions.

Chi-square Goodness of Fit Test

The chi-square goodness of fit null hypothesis is the following:

H_0 : There is no significant difference between observed and expected observations.

The test is valid for large samples only. Transformation by adding a constant can allow small sample data sets to be tested. However there are no rules for choosing a transformation, and for almost any data a large enough transformation can be chosen such that H_0 is satisfied. The observed beaver cutting data had extremely small sample sizes. Chi-square should be abandoned in this case. However, the real question in this analysis is not H_0 as above, but rather does one model (1:1 or 1:0) better describe the data.

i.e. H_0 : The 1:1 model chi-square statistic is less than the 1:0 model chi-square statistic.

H_1 : The 1:0 model is the minimum chi-square.

A supplementary condition that should help in drawing a correct conclusion is that the transformations that reduce each model to the area of non-significance should be different.

For both ponds the 1:0 model (water is costless for travel) produced (Table 3) the minimum chi-square (Northbranch 1:1=4,729, 1:0=967; Pinetop 1:1=18,369, 1:0=8,144). The chi-square sums were larger at Pinetop pond which indicates that the fit was better at Northbranch pond.

The additive transformation that reduces chi-square to the region of non-significance is distinct in each case (Table 3; for Northbranch plus 60 at 1:1, plus 20 at 1:0; for Pinetop plus >150 at 1:1, plus 100 at 1:0). The difference between the models is apparently sufficient to warrant a conclusion that the water costless (1:0) model is a better fit than the model for equal cost of travel in water or on land (1:1).

Table 3: The Chi-square statistics for foraging model goodness of fit tests of the addition transformed data for Northbranch and Pinetop ponds.

Model ²	Chi-square sums ¹			
	Northbranch		Pinetop	
	1:1 (123)	1:0 (56)	1:1 (102)	1:0 (69)
Transformation				
+ 1	4,729**	967**	18,369**	8,144**
+ 10	342**	112**	1,238**	445**
+ 20	249**	44	909**	354**
+ 40	168**	29	626**	222**
+ 60	116	19	447**	151**
+ 80	97	16	380**	126**
+ 100	69	11	282**	91*
+ 150	54	9	226**	71

1 * 5% significance level, ** 1% significance level.

Chi²=Sum ((obs-exp)²/exp).

2 Cost of travel on land : cost of travel in water.

Linear Regression Goodness of Fit Test

The species-diameter-distance scatterplots and the calculated regression lines are shown in Figures 7 and 8. Tests of the goodness of fit criteria follow.

The r-tests for linear relation were significant (i.e. significant regressions) for both models, at both ponds (Table 4). However, the correlation coefficient (r) was relatively small for the 1:1 model (1:1 r=.68 versus 1:0 r=.96 at Northbranch, and 1:1 r=.38 versus 1:0 r=.86 at Pinetop). The r's were significantly different between models, 1:1 vs 1:0 (Northbranch t=7.02, P<.01; Pinetop t=5.67, P<.01). In other words, the 1:0 model is correlated significantly better than the 1:1 model.

Table 4: The results of r-tests^a for linear relation between observed and expected stems cut, and t-tests^b for differences between the equal cost and water costless models.

Pond	Cost Land:Water	N	H ₀ :p=0			H ₀ :p ₁ =p ₂		
			r	df	r.01	t	df	t.01
Northbranch	1:1	124	0.69**	100	.25	7.02**	55	2.67
	1:0	58	0.96**	50	.35			
Pinetop	1:1	104	0.38**	100	.25	5.67**	60	2.66
	1:0	70	0.86**	60	.32			

^a The regression correlation coefficient (r) is tested against the hypothesis that the population correlation coefficient (p) equals zero (Snedecor and Cochran 1980, p. 184).

^b Two regression correlation coefficients are converted to z's and tested against the hypothesis that they are estimates of the same population correlation coefficient (Snedecor and Cochran 1980, p. 186).

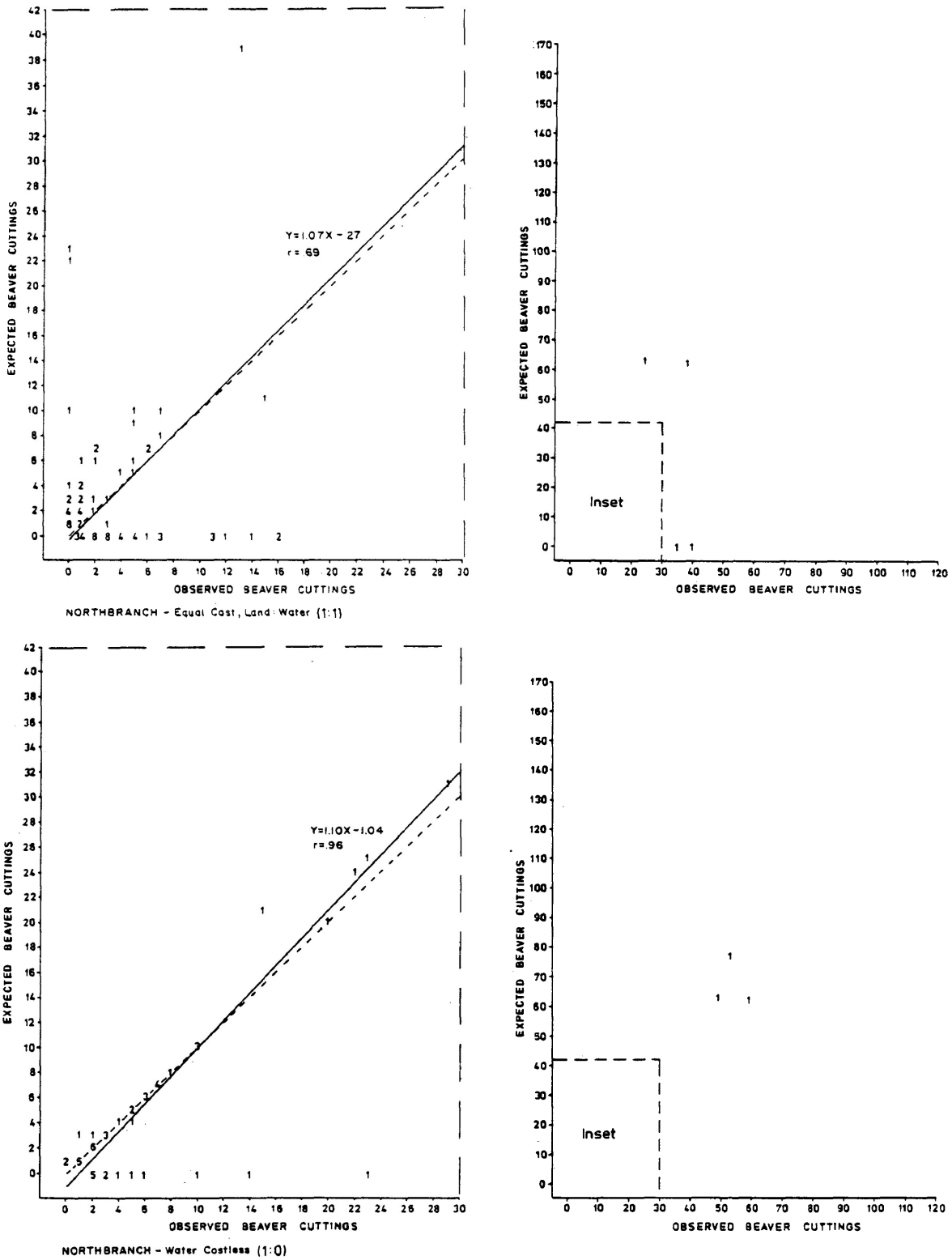


Figure 7: Scatterdiagrams for linear regression goodness of fit tests, the 1:1 and 1:0 models all species combined, at Northbranch Pond. Numbers in the figures represent the number of cells with the indicated expected-observed cuttings.

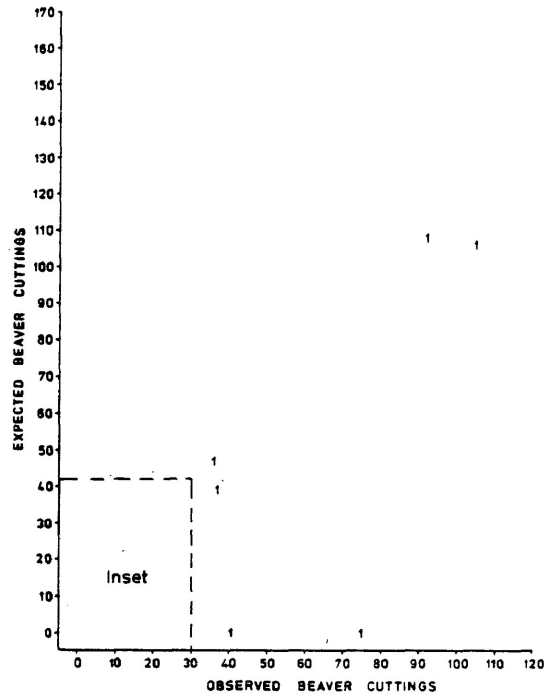
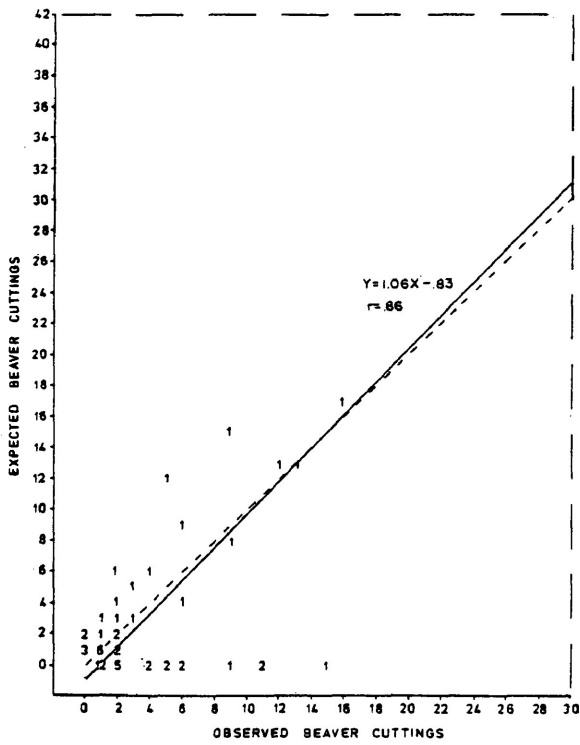
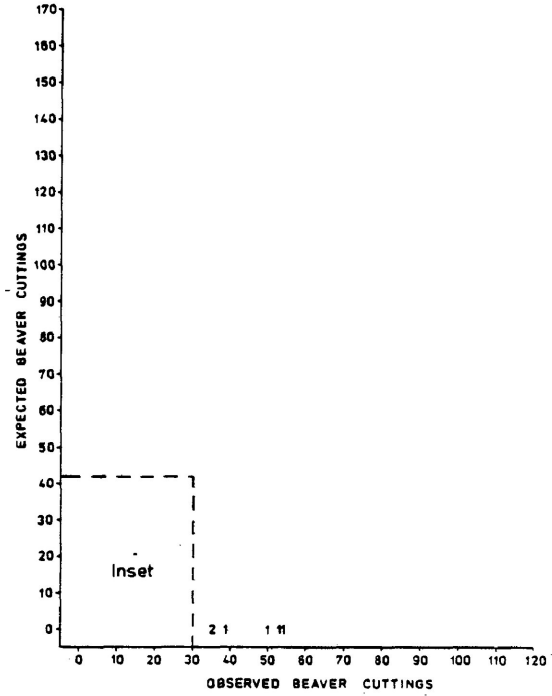
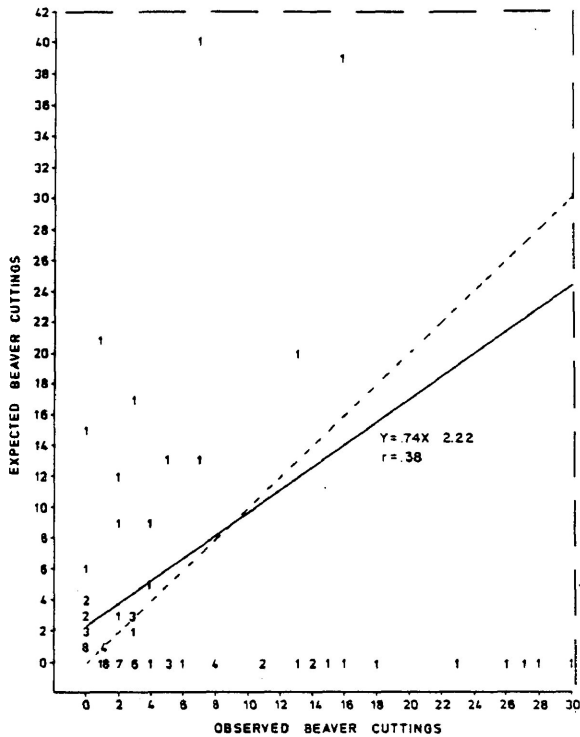


Figure 8: Scatterdiagrams for linear regression goodness of fit tests, the 1:1 and 1:0 models all species combined, at Pinetop Pond. Numbers in the figures represent the number of cells with the indicated expected-observed cuttings.

None of the slopes was significantly different from 1: (the confidence interval and calculated slope are given below)

Northbranch 1:1 - $.9 < b < 1.3$ - slope 1.074,
 Northbranch 1:0 - $1.0 < b < 1.2$ - slope 1.1005,
 Pinetop 1:1 - $.4 < b < 1.1$ - slope 0.7379,
 Pinetop 1:0 - $.9 < b < 1.2$ - slope 1.065.

Slope in this case could be an artifact of the way the expected cut was distributed; with $P=1$ the expected tree cut was the closest. When fit is poor in a near distance class the point of no fit is counteracted by a point(s) of no fit of opposite weight in a far distance class. When I regressed only the points from the first distance band the slopes (b's) were more indicative of the true nature of the data: Northbranch 1:1, $b=2.0$; 1:0, $b=1.1$; Pinetop 1:1, $b=2.2$; 1:0, $b=1.2$. As each distance class was added the slope approached 1 for the 1:1 model, while it stayed close to 1 for the 1:0 model. This indicates that the calculated slopes for the 1:1 model were in fact an artifact and this indicates poor fit with the observed data.

Snedecor and Cochran (1980; pg. 173) provide a t-test for the null hypothesis that the y-intercept is not significantly different from zero. None of the calculated y-intercepts were significantly different from zero:

Northbranch	1:1	y-int.=	-.27	t=	-.32 _{ns.05,}
Northbranch	1:0	y-int.=	-1.04	t=	-1.218 _{ns.05,}
Pinetop	1:1	y-int.=	+2.22	t=	.785 _{ns.05,}
Pinetop	1:0	y-int.=	-.83	t=	-.406 _{ns.05.}

Examination of residuals showed two departures from normality, a basic assumption of the linear regression analysis. The first was a concentration of points with low frequency; the second was a linear trend for residuals of points with zero expected results. Both of these trends were anticipated and will not alter conclusions: small total sample sizes resulted in low cell frequencies when sorted by species-diameter-distance; and due to the deterministic optimization criteria, numerous zero expected values were generated when the model fit was poor.

Residuals for the 1:0 models were scattered more in the fashion expected from normal data than were the residuals of the 1:1 model. Low frequency data points were minimized by the 1:0 model. The linear trend for points with zero expected results was present in the 1:0 models but was less pronounced than in the 1:1 model.

Comparison of Chi-square and Linear Regression Tests

The chi-square goodness of fit test and the linear regression goodness of fit test both select water costless for travel (1:0) as the better model of beaver foraging behavior. Although only two ponds have been examined the

choice was clear in both cases. The pattern of cutting was isoclinal enlargement of the cutting area based on the shape of the pond.

One must remember that this is a result that can only be valid in a local sense. There are time and energy costs associated with swimming, and we do not observe extremely long distances for foraging even where they are possible on large lakes or rivers. Having arrived at a decision in favor of the 1:0 model, this decision should be viewed as a 5 to 10 times or greater advantage to swimming over walking (see pg. 35). This large an advantage could not be attributed to energy or time conservation. Terrestrial foraging by beavers must therefore be constrained by a factor more important to beaver fitness than e/t .

PATTERN OF CUTTING GIVEN A CONSTRAINT

Acceptance of the water costless model (1:0) on the energy for travel continuum, and the derived constraint on foraging behavior, does not rule out a possible energy optimization within the constraint bounds. The water costless solution has meant only that trees are sequentially harvested in increasing isoclinal bands around the occupied water body. An energy optimization within this constraint would mean that the trees harvested in a band would be those closest to the lodge.

Only the trees cut in a band were used to generate the expected values in the particular band. It had

already been shown that cutting from isoclinal bands produced a good fit between observed and expected results so this was not re-tested.

In this analysis the stems available by species were summed in the bands parallel to shore. The geographic centre of availability was then determined and this are designated as the bisector of two areas referred to as close and far, that is, close to and far from the lodge. I based the areas on availability, rather than distance, so that energy radii from the lodge would still be used to classify the data. Availability overcomes an anomaly that occurs when imposing radial bands on restricted parallel bands; more land area is included in the arc at moderate radii than long radii.

For each band and species, observed new-cut stems were individually summed for the two species-dependent areas. Three sets of expected observations were calculated. The sum of newcut stems in a band was distributed to the close and far energy areas; in model one 25% of summed new cut stems were assigned as the expected cut in the close area, 75% to the far area; model two was 50:50, and model three 75:25. These correspond to beaver cutting far from the lodge, cutting 50% from the close and 50% from the far available stems (randomness is dependent on equal stem densities, if stem densities are not equal then beaver are cutting more frequently in the area of concentrated

density), and cutting close to the lodge respectively.

At Northbranch pond the chi-square and regression tests of goodness of fit (Table 5) both indicated that the best fit was associated with a 75% probability that beaver cut close to the lodge (minimum $\chi^2=135$; regression coefficient =.89, correlation coefficient =.93, y intercept =1.7).

The outcome for the goodness of fit analysis (Table 5) for Pinetop rejects the hypothesis that beaver were cutting close to the lodge. Minimum chi-square (135) and the highest correlation coefficient (.93) were calculated for the 50% cut close, 50% far model. The best fit regression

Table 5: Results of the χ^2 goodness of fit tests, r-tests, and t-tests for the energy optimization, water costless constrained model. Distance increments were based on the available stems cast as the close 50% versus the far 50%.

Pond	Stems Cut	N	p ^a close	p far	χ^2	b ^b	y-int	r H ₀ :p=0 ^c	t H ₀ :p ₁ =p ₂	
N.Branch	571	32	.25	.75	658**	.43	9.5	.45**		
			.50	.50	143**	.66	5.6	.81**	2.537*	4.636**
			.75	.25	135**	.89	1.7	.93**	2.099ns	
Pinetop	750	60	.25	.75	258**	.97	0.3	.89**		
			.50	.50	135**	.88	1.4	.93**	1.26ns	2.747**
			.75	.25	613**	.79	2.6	.72**	4.00**	

a. Distribution of the expected cuts according to the probability (P) of cutting close to or far from the lodge.

b. Slope of the regression line.

c. Where p is the population correlation coefficient, and the null hypotheses are rejected if the test is significant.

coefficient (.97) and Y intercept (0.3) were associated with a 75% probability that beaver cut far from the lodge. A random cut is not indicated in this case because stem densities were higher in the vicinity of the newest and least exploited pond at Pinetop (i.e. pond 7, Figure 3).

The pattern of cutting within bands parallel to shore was reversed from Northbranch to Pinetop ponds (Table 5). The beaver at Northbranch biased cutting to trees from the close half of available stems; Pinetop beaver biased cutting to the far half of the available stems.

SPECIES PREFERENCE

Jenkins (Figure 3 1975,) cast his data of uncut stems versus cut stems in histograms to illustrate preference. I utilized (Figure 9 and 10) his format to facilitate comparisons but made the following changes: stems cut prior to 1981 (oldcuts) are included and sum to 100% (old cuts not included in Jenkins figure), coniferous species (included in the computations) were omitted from the figure because they were not cut and their low availability had a negligible effect on computations, stems available are the sum of uncut and newcut stems (Jenkins available stems based on a sample), and diameter information has been omitted in favor of an alternate figure.

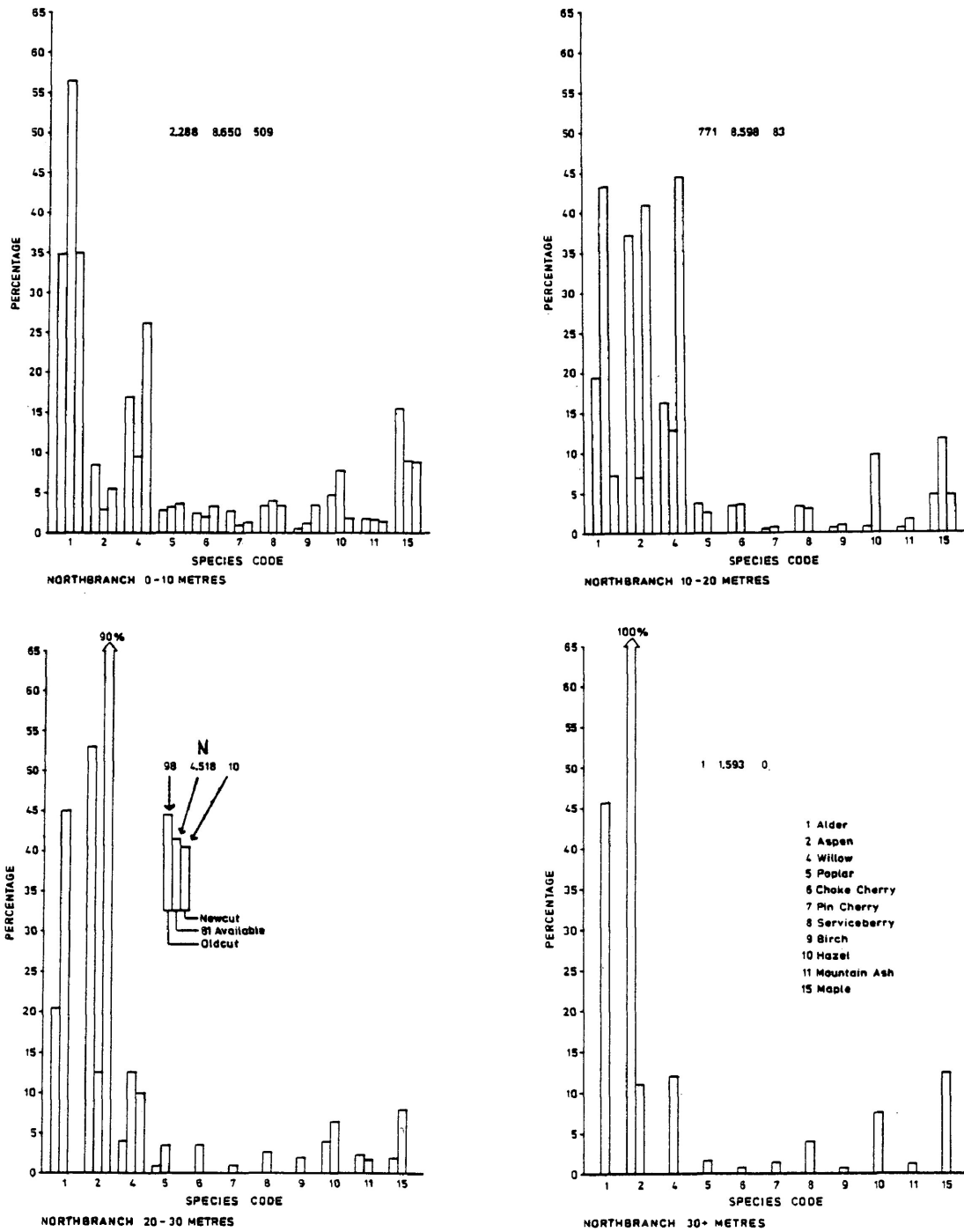


Figure 9: Species preference histograms subdivided by distance from the closest shoreline for Northbranch Pond, showing the percentage of total stems(N) for each classification(oldcut, 1981 stems available, and newcut).

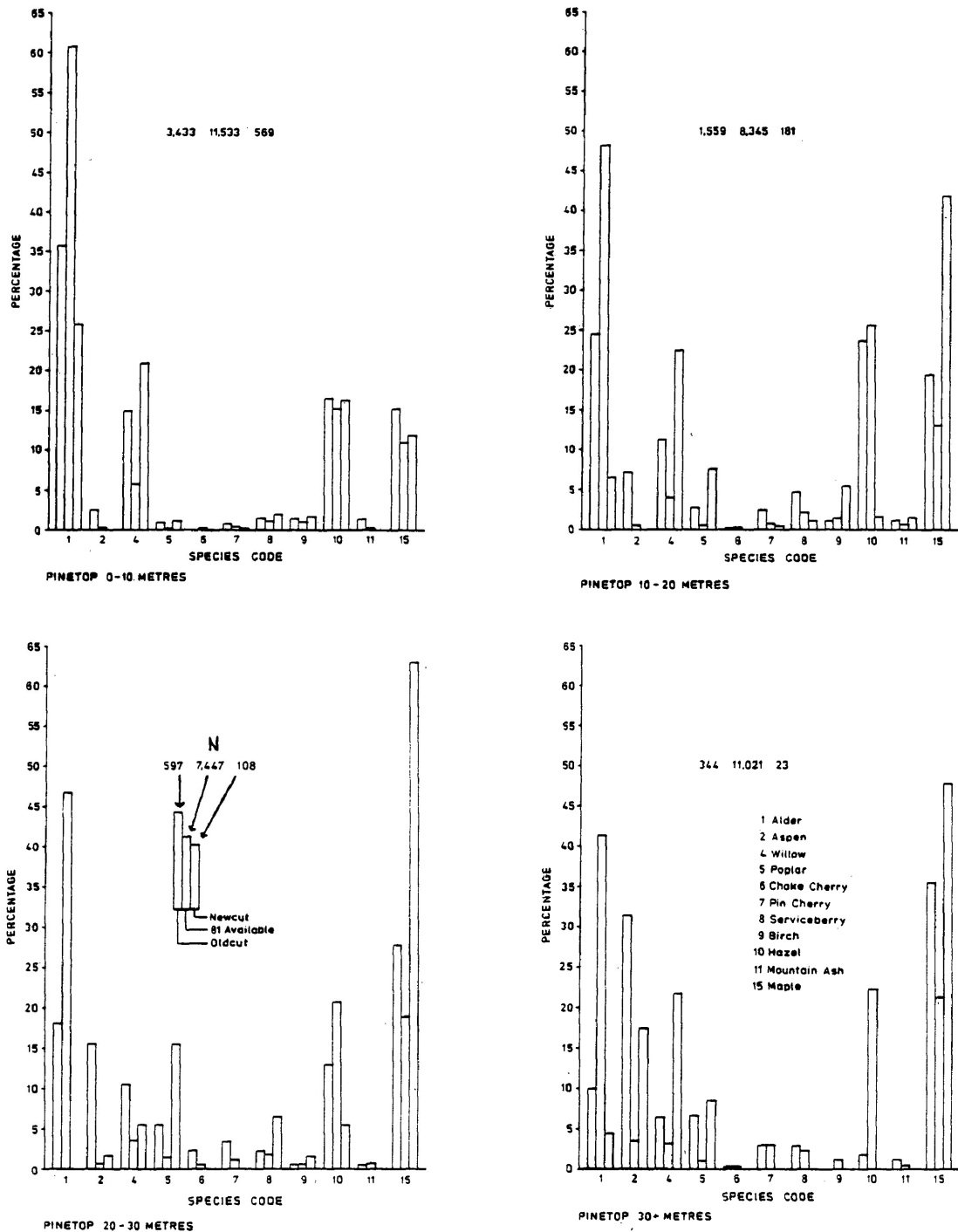


Figure 10: Species preference histograms subdivided by distance from the closest shoreline for Pinetop Pond, showing the percentage of total stems (N) for each classification (oldcut, 1981 stems available, and newcut).

The extremely large numbers of alder available at each pond (an order of magnitude larger availability than any other species) (Figure 9 and 10), and the lack of preference for the same, exaggerates the preference for all other species. Selection of less stems than the proportion available is therefore strong evidence of negative selection. Moderate selection for a species should not be construed as good evidence for preference. Also because the proportions are based solely on numbers of stems, and do not consider biomass or nutrient value captured, the preference histograms may be misleading.

Species preferences were exhibited in each distance class, and selectivity by species increased as distance from water increased. Examination of the old cut information (Figure 9 and 10) indicated that distance to stems being cut was a consequence of prior removal of close stems.

Balsam poplar, mountain ash, serviceberry, and white birch were dropped from the diet past 10 m from water at Northbranch Pond, where availability of, and selection for, aspen increased with distance from water (Figure 9). At Pinetop where availability of aspen was reduced at all (actively used) distances due to past cutting the species listed above were retained in the diet, and were selected for, to the limits of cutting activity (Figure 10).

Beaver removed preferred trees from an area first and less preferred trees next. It follows that beaver, in their

efforts to obtain preferred species, will travel farther (from water since the 1:0 model was the best fit model) for stems of preferred species than those of less preferred species.

An index of preference is therefore the rank order of species when sorted by their mean distances to cutting activity (Figure 11). When species composition is the same at two beaver ponds in the same area (such as Pinetop and

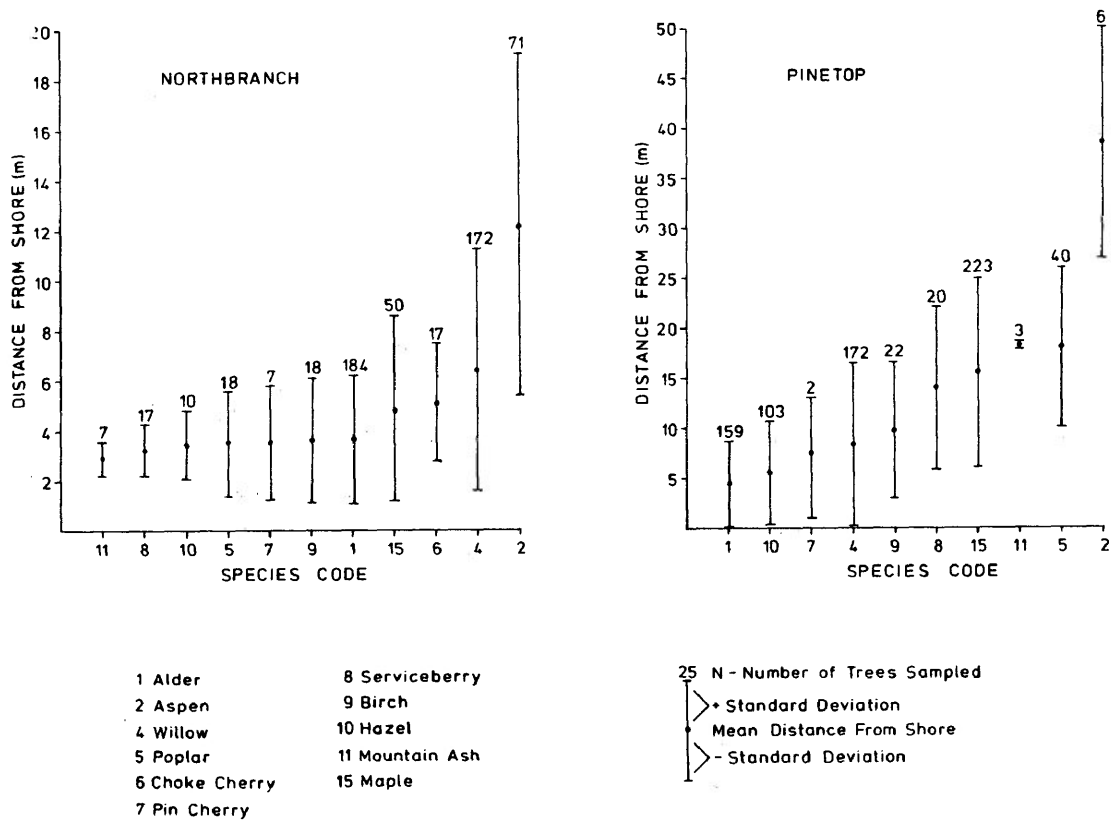


Figure 11: Mean distance from shore to stems cut by beavers at Northbranch and Pinetop Ponds. Chokecherry occurred with low frequency at Pinetop and none was recorded cut.

Northbranch ponds), and other things being equal or unimportant, the rank of species should be identical.

i.e. H_0 : Species ranking by distance to cutting was the same at Northbranch and Pinetop Ponds.

H_1 : The ranks were different.

The tree and shrub species present and consumed at both ponds were ranked according to their respective mean distances (Figure 11) from the pond (i.e. furthest =1. closest=10). Chokecherry was scarce at Pinetop and was not eaten; it was not included in the rank tests.

Spearman's rank correlation coefficient (r_s) was calculated for absolute ranks (i.e. 1, 2, 3,...10) and for grouped ranks (e.g. 1, 2, 3.5, 3.5, 5,...10). Absolute ranked species exhibited no correlation ($r_s=0.02$; $r_{s.05}=0.648$). For the grouped test, I considered alder, balsam poplar, pincherry, serviceberry, birch, hazel, and mountain ash as one rank for Northbranch pond, while aspen, willow, and maple remained discrete. For Pinetop I grouped alder with hazel, willow with pincherry, serviceberry with mountain maple, and balsam poplar with mountain ash, again aspen remained discrete. As in the case of the absolute ranking, the grouped ranking showed no significant correlation ($r_s=.47$; $r_{s.05}=0.648$). The rank order of the trees based on mean distance is different between ponds.

DIAMETER PREFERENCE

Aspen alone, at Northbranch, had sufficient diameter range and cutting activity over the three distance subdivisions (Figure 12) to warrant examining diameter preference. Diameter preference is indicated where the percentage of stems cut exceeds the percentage of stems available (Figures 12 and 13).

Aspen less than 4 cm DSH was not preferred at any distance. Diameter selection at 10-20 m from the pond favored all the larger classes, however the 4-10 cm class was most preferred. At 20-30 m from the pond only the 4-10 cm class was selected. Size selectivity increased with increasing distance from the pond refuge, and an intermediate class was preferred.

At Pinetop Pond (Figure 13) only balsam poplar and white birch were suitable for diameter preference study. At 0-10 m balsam poplar were taken in proportion to availability. At 10-20 m, beaver preferred trees larger than 4 cm and especially those 4-10 cm. At 20-30 m all diameters were still taken but preference was for 4-10 cm trees. At 30-40 meters trees > 10 cm were excluded, trees < 4 cm were taken more or less in proportion to availability, and trees 4-10 cm were preferred. Again selectivity increased with distance and an intermediate class was preferred.

White birch > 17 cm were excluded from the diet at all

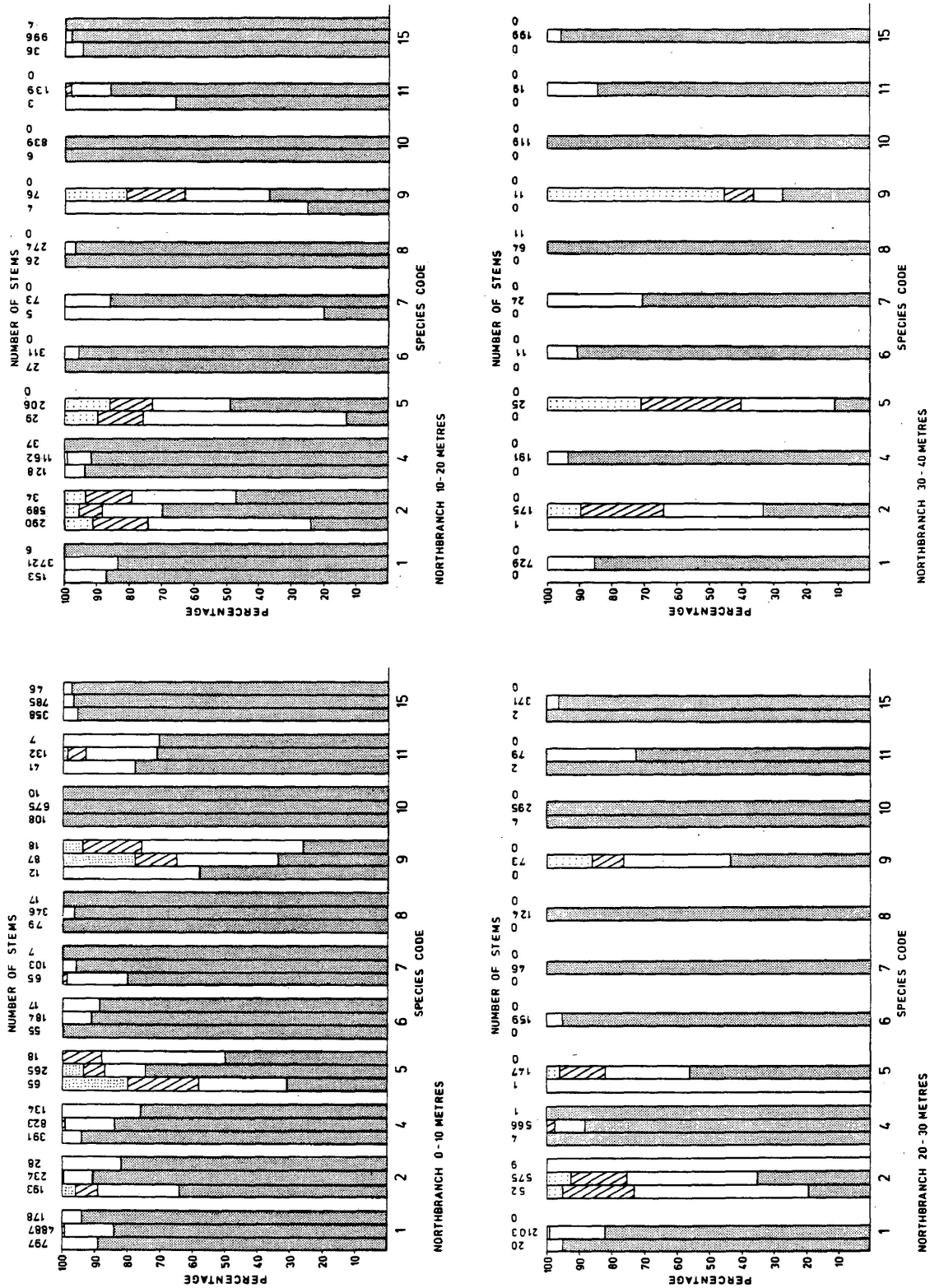


Figure 12: Diameter preference histograms, subdivided by distance from the closest shoreline, for Northbranch Pond.

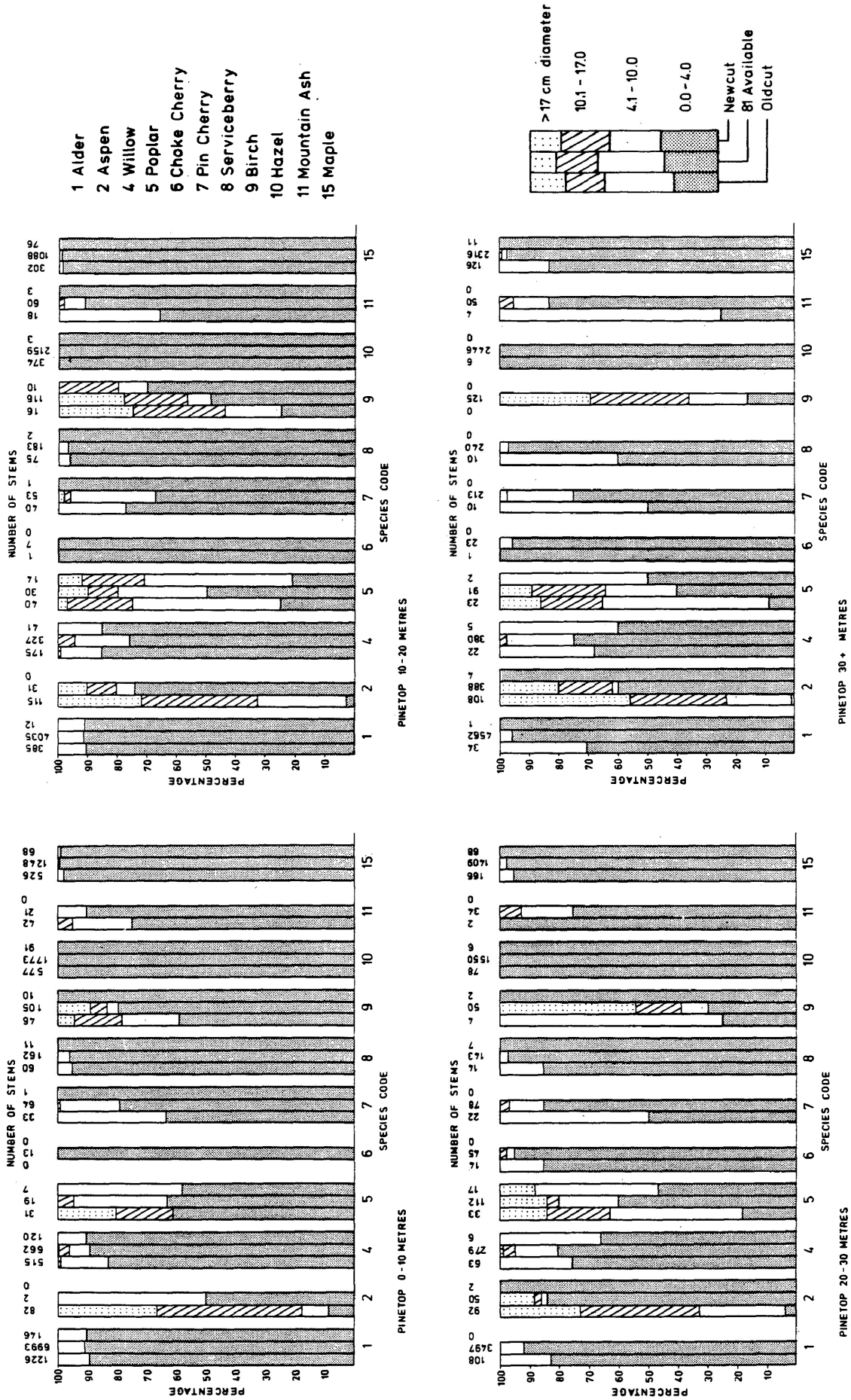


Figure 13: Diameter preference histograms, subdivided by distance from the closest shoreline, for Pinetop Pond.

distances. Birch < 4 cm were preferred at all distances, and from 0-20 m the intermediate classes were taken in proportion to abundance. Again size selection increased with distance, however here we see specialization on the smallest diameter class delineated.

DISCUSSION

One major question and four secondary questions were posed (pg. 38) and addressed in this study.

Question 1) Is the relative shortage of food at beaver ponds induced by energetic limitations or predator pressure? (i.e. do beaver maximize e/t , or is foraging constrained to the area adjacent to water by predators?)

The answer in its simplest form is that predators probably induce the relative shortage of food at beaver ponds. In review, the test between concentric enlargement of the foraging pattern centered on the lodge or isoclinal enlargement of the foraging pattern based on the shape of the pond favored the latter. That is, the water costless for travel model was the best fit model; e/t was not maximized because swimming would not enhance e/t to the 5-10 or greater times advantage (pg. 36) that the sensitivity analysis indicated (pg. 34). This conclusion is empirical confirmation of the implicit assumption of most past studies that beaver harvest trees from the closest water available. However, it would be wise to confirm experimentally, with metabolic chamber measurements, that beaver do not realize a 5-10 times energetic advantage while swimming over walking.

"The extent to which risk influences choice of central place can be estimated by the nature of deviation of the central place from the location predicted on purely

energetic criteria" (Orians and Pearson 1978). The conclusion of this study was that the central place is effectively the pond or system of ponds, while the optimal central place for maximum e/t is the lodge. Wolf predation on beaver has been documented at Algonquin Provincial Park (Pimlott et.al. 1969) and Isle Royal National Park (Allen 1979). However, studies of the rate of predator visitation to beaver ponds, and their effectiveness in limiting beaver foraging behavior should be carried out to confirm that predation is in fact the cause of relative shortages of food to beaver.

The above is consistent with Covich's (1976) predictions that herbivores exposed to predation risk may starve, reduce activity, or create more refugia (see also Osborn and Allan 1949): i.e. expansion of refuge size, and reduced aspen consumption at Pinetop should be interpreted as 'starvation' relative to the beavers at Northbranch.

If and when the predation risk function is defined it can be tested against two presently available models of foraging behavior with predation risk. Covich's (1976) graphical analysis determines the optimal distance a consumer is expected to travel, given a risk function and a resource yield function. Rosenzweig (1974) uses profit after metabolic cost curves as functions of time out of a burrow; optimal foraging bout length (time) is determined where the slope of the profit curve is equal to the slope of

a predation risk curve. The Rosenzweig analysis does not explicitly include distance and may only be satisfactory for cases where distance from refuge plays a relatively minor role in whether or not a predator detects and captures its prey.

Beaver did not optimize e/t in a strict sense, but the question of whether beaver optimize e/t within the predation constraint is answered with a qualified yes. Beaver minimized the distance travelled, and therefore optimized e/t within the constraint, so long as the foraging area was small enough that beaver could meet an assumption of perfect knowledge (Schoener 1979) of their site (i.e. Northbranch Pond). That beaver do not have perfect knowledge of the resources available is evidenced by the foraging tactics of beaver at Pinetop. They apparently minimized search time, instead of distance travelled, by foraging distant patches of high relative food quality as predicted by Orians and Pearson (1976) (around the newest sub-ponds). In doing so the beavers likely optimized e/t so far as they were capable. However, the energetic efficiency of beaver at Pinetop was measureably lower than the Northbranch beaver.

The absolute count and 50% sample, at Northbranch and Pinetop respectively, only sampled availability under the foraging model that beaver actually employed. Availability was tallied on plots to 10 m past the margin of the past or present beaver cutting. A better method would have been to

locate the farthest cut tree from the lodge and sample plots within the area encompassed by the radius to that tree plus 10 meters (i.e. to independantly sample availability for all models) but I did not realize this when the field work was carried out. Tests of foraging models may lead to incorrect conclusions in some situations where availability is not measured completely. Replication of this work should use the modified method, but there was no effect on the calculation of expected values in this case; tree and shrub availability in the undersampled distance-cells was sufficient for expected value calculation because at any distance there was at least a small fraction of unimpacted forest included (i.e. sampled to furthest cut tree plus 10 m), and species composition was homogeneous enough to ensure that the trees included were representative of all trees that would have been included.

One might question whether all woody stems cut in 1981 regardless of the date or time of cutting should be included in the same analysis of woody plant foraging pattern. For example, Hall (1960) thought that relative availability of aspen might be a function of darkness as well as distance, and that closer species would be taken in daylight or twilight as opposed to darkness. Also, Hazeltine (1950) cited Tevis' [1950] observation of beaver feeding extensively on alder leaves during the summer months (bark

ignored). Leaf foraging of the shrubs on my study areas could have been a major use of cut stems. However, the important question is does temporal variation in either relative availability or usage affect the distance minimization analysis I used? The answer is no because each species (and diameter) is treated independently for the classification and calculation of observed and expected results. The foraging models represent different limitations on relative availability, and partial usage of the tree harvested (bark or leaves) should not alter the distance minimization principle.

Two factors worked against each other when the arbitrary distance classes for each model at each pond were chosen: when the distance criterion is removed completely the observed cutting will match the expected exactly, but if the distance classes are too fine, minor variation in stand composition and topography may lead to an incorrect conclusion of poor fit. In addition, increasing the number of distance classes decreases the sample sizes per species-diameter-distance cell. I chose distance classes so that the data would be spread across the same number of distance classes regardless of the model or pond being examined; for practical intents this meant four distance classes. At Northbranch the 1:1 model used 20 m distance classes, the 1:0 model 10 m classes; at Pinetop - 1:1, 30 m - 1:0, 15 m. This manipulation did not reduce the number of cells with

data in the 1:1 model (Northbranch 124, Pinetop 104) to the same number of cells with data in the 1:0 model (Northbranch 58, Pinetop 70). This is a reflection of the poor fit of the 1:1 model since the data were distributed across the same potential number of cells; that is, rather than as a cause of poor fit in the chi-square or linear regression tests.

Question 2) Was tree species preference demonstrated and was it a function of distance from the central place?

There were two major differences between Pinetop and Northbranch in the species preference analysis: at Pinetop pond the mean distance to cutting of any particular species and all in general was greater, also the frequency that aspen was cut relative to other species was reduced to almost nil. These points were not independent; beaver constrained their foraging behavior in order to forage a minimum distance from water. The reduced frequency of aspen cutting at Pinetop was a direct consequence of the long distances that were travelled to it. There was no absolute shortage of aspen, it was a relative shortage associated with long distances.

The maximum distance to beaver cuttings from water at Northbranch was 45 m (150 ft) while at Pinetop beaver had travelled as far as 70 m (225 ft) from water. Many authors (see Gibson 1957) have emphasized an extreme cutting distance when it has been observed; however, Hall (1960)

limited his measures of cutting and availability to < 100 ft from stream edges since 90% of cutting occurred within that distance. He further discussed 'normal' maximum distances that authors had noted: i.e. MacDonald [1956], 150 ft; Bradt (1938), 200 ft; Hodgdon and Hunt [1953], 300 ft. Green (1936) stated that beaver would abandon their lodges if they had to travel more than 75 yds (225 ft) for aspen trees. Pinetop beaver, the 'old' pond of this study, appeared to be quickly approaching, or may have reached, these maximum foraging distances (70 m). I do not want to imply that a generalization should be derived from normal maximum foraging distances. Fitness is relative to ones neighbours in a given region and I would expect beaver to be sensitive to relative habitat quality in their local region. Foraging distance maximums should therefore vary with the relative quality of presently unexploited habitat. The maximum distances to cutting were discussed here to emphasize that Pinetop and Northbranch beaver exhibit reasonably normal foraging behavior.

Species preferences were demonstrated but the assumptions of the preference analysis may well prove false: i.e. that the observed cutting occurred concurrently, that accumulation of bark in a food cache was the primary useage (rather than leaf useage or building materials), and that regeneration rates of the various species were constant (most unlikely given shrub versus tree forms and the varied

regeneration requirements). Species preferences are further discussed under Question #4.

The set of foods at Northbranch and Pinetop are identical. A prediction from foraging theory (Estabrook and Dunham 1976) is that for foods that have changing absolute and relative abundance the set of foods eaten should vary. For beaver central place foraging we should observe a broadening of diet as relative abundance of aspen decreases. With respect to the set of foods eaten this was not the case; however, the proportions of the foods in the diet did change as predicted by Estabrook and Dunham's (1976) model, and the inclusion of at least a small quantity of each food type is consistent with the simulations they presented.

Question 3) Is diameter selectivity demonstrated and does it increase with distance from the central place?

There is a very real possibility that tree diameter selection by beaver was not important to an analysis of foraging pattern with the distance minimization criteria. An early test of the data (not presented) showed that the inclusion of diameter information would improve goodness of fit. Whether it improved the goodness of fit significantly was not addressed. The graphic presentation (Figure 5) showed qualitatively that tree diameter could probably have been eliminated without altering the conclusions of the subsequent quantitative goodness of fit tests. However, the

findings of the diameter preference analysis agree with the predictions of Schoener's (1979) size-distance model and with Jenkins' (1980a) test of the model. Beavers were more selective for diameter at long foraging distances. I argued (pg. 26-28) that each tree is a patch and that an intermediate sized stem would be the most energetically favorable. Intermediate sized aspen were cut in preference to very small or large trees (i.e. 4-10 cm) at Northbranch Pond. Aspen was not cut in sufficient quantity at Pinetop for analysis. Selection for balsam poplar at Pinetop was most intense for intermediate sizes (i.e. 4-10 cm). White birch selection at Pinetop favored the smallest trees available (i.e. < 4 cm), but this may be because the bark of white birch becomes markedly more fibrous as tree size/age increases.

The above is not a divergence from past studies (Aldous 1938, Hodgdon and Hunt 1953), but it redefines the arguments in terms of optimal foraging theory and a tree tally with no lower limit on stem diameters. The most intense work on diameter preference (Hall 1960) showed preference for 2 inch aspen over larger aspen, and 1 inch aspen. Hall (1960) struggled with an explanation for the use of 2 inch trees over larger trees and ignored completely that 1 inch trees were not similarly preferred.

Question 4) Could intra-(tree)species anomalies in food selection by beavers be explained by differences in

relative availability rather than invoking nutritional properties?

Changes in rank order of cutting between Northbranch and Pinetop Ponds may reflect adjustments in diet that were necessary to compensate for the reduced availability of aspen at Pinetop; energy constraints were an unlikely explanation for the relative shortage of aspen at the distances it was available (i.e. e/t not optimized). Also, if beaver ranked food preferences solely on energy content, the loss of availability of aspen should not alter the ranking of the species still available. The result of the Spearman rank correlation test suggests strongly that this was not the case.

It appears that preference for balsam poplar, mountain ash, serviceberry, and white birch was dependent on the effective exclusion of aspen from the beaver diet. Willow was cut heavily at both ponds but its rank was depressed at Pinetop to below that of maple. Willow may be complementary to aspen, but not to the balsam poplar, mountain ash, serviceberry, and white birch group. This study can be added to the growing number of papers that challenge the realism of energy maximizing models from a nutritional standpoint (Pullian 1975, Westoby 1974, 1978, Freeland & Janzen 1974, Shi 1980, Lacher et.al. 1982, Hegner 1982, Stamps & Tanaka 1981).

Henry and Bookhout (1970) found species preference order switching very similar to what was found here; that is, the switching was keyed to the relative abundance of aspen. Hall (1960) found that willow use increased as aspen availability diminished. This is not contradictory to my result where aspen was replaced by a complex of other species because willow use may have increased as aspen use decreased. My single season study could not detect the pattern even if it were present.

Jenkins (1975, 1979) found inconsistent selection between cutting sites, between years at the same cutting sites, and between seasons. He suggested that intra-species nutritional variation may explain the observed inconsistencies. I agree with Jenkins' view that nutritional properties can change between sites, seasons, and years and therefore must play a role in food selection. However, inter-species nutritional properties may account for the observed inconsistencies. A nutritionally balanced diet is a mix of foods with at least a minimum of all basic requirements of the animal (Westoby 1978, Freeland and Janzen 1974, Pulliman 1975, Rapport 1980). An optimally balanced diet is the best nutrient mix possible, chosen from the available foods. At Pinetop where reduced relative availability of aspen effectively excluded it from the diet, beaver adjusted the proportions of other trees cut. Nutritional variability within species (i.e. between sites) need not be involved in

this case, although it does remain as a possible explanation.

Question 5) Were there differences in foraging behavior between relatively old and new beaver colony sites?

As discussed under question #1 beaver at Pinetop, the old site, foraged with a patch use strategy as opposed to beaver at Northbranch, the new site, that foraged with what appeared to be a perfect knowledge strategy. In fact, Northbranch beaver probably also foraged with a patch use strategy but there was no opportunity there to distinguish it from the perfect knowledge strategy.

When aspen availability is considerably reduced, as at Pinetop, beaver take greater risks to harvest it; that is, the aspen cut at Pinetop are cut to maximize e/t rather than minimize distance from shore as the beaver at Northbranch did.

One striking similarity between the old and new sites is that both colonies were expanding their foraging area. Given the long period of occupation at Pinetop, I can only conclude that the site was being overused and that beaver were depleting their food resources. Gese and Shadle (1943) observed that beaver were "making serious inroads among the aspens, their chief food supply. Areas around colonies [were] cleared of aspen, thus forcing the animals to use less desirable species and finally to move elsewhere due to food depletion". This type of statement (Hall 1960,

Aleksiuk 1970, Hazeltine 1950) has prompted authors who study beaver without aspen (Jenkins 1979), or where alternate sites with aspen are not available (Hall 1960), to counter that beaver thrive in the absence of aspen on alternate species. Both groups are probably approaching the problem in the wrong light. Beaver colony site abandonment is probably less a function of depletion of one or more tree or shrub species, or the capability of the site to produce some or all foods on a sustained yield basis, (Henry and Bookhout 1970) than it is a function of the relative quality of the site compared with other unoccupied sites. It is relative reproductive fitness within sub-populations that will determine the foraging behaviors exhibited in a certain geographic area. Estabrook and Dunham's (1976) foraging model is valid within a single colony of beavers, but because it implicitly assumes that the population is exposed to constant environment, it cannot be used for the whole population. That is, the model operationally defines the optimal feeding strategy as the best available foods under given conditions. This is not valid for a central place forager where a shift in central place can change the animal's relative fitness.

The foregoing has a bearing on arguments of population regulation. Bergerud and Miller (1977) observed that

"food overuse is at odds with the two most prominent theories of population self-regulation that of Chitty [see Krebs 1978] and Wynne-Edwards

(1962). Both authorities argue that territorial behavior is a means of self-regulation of numbers below the level where food is overused. Lack (1966) argues to the contrary, that the primary function of territorial behavior is dispersal rather than to regulate numbers below food resources".

The self regulation theories argue that ultimately animals will evolve self-regulatory bio-feedback mechanisms to overcome the paradox of high reproductive potential while there are only limited food resources. This is supposedly accomplished by changes in individual quality (C. Krebs 1978) due to physiology, behavior, or genetics. The argument is hard to formulate in terms of individual selection; group selection, and its association with the self regulation theories (C. Krebs 1978, Wynne Edwards 1962), has been debunked (Davies and Krebs 1978, C. Krebs 1978). A pair of cheating parents (i.e. they use their food supply at a high rate thereby overusing it) can produce more young than their self regulating neighbours; the cheaters genotype will disperse at a higher rate, and they will come to dominate the population (Davies and Krebs 1978). Wynne-Edwards (1962) ignored the evidence before him with respect to beavers overusing their food supplies. He referred to beavers four times in his landmark book, but never with regard to their foraging behavior even though a number of good feeding studies were available (see pg. 13).

Beaver apparently have a pure evolutionary stable strategy (ESS) which, in Lack's (1954) sense, has only one genotype, the disperser. Maximum reproductive output of an

adult pair of beaver is attained when they breed on a site with unimpaired food resources. By definition, a site occupied by adults (i.e. parents) is impaired to some degree so the better site for raising young is someplace else. Given that, if there is space available elsewhere for occupation.

A mixed ESS (Maynard Smith 1978) would probably evolve if space were easily limited. A mixed strategy, with low and high potential reproductive rates for a polymorphic population (C. Krebs 1978), could have an ESS that is a repeating fluctuating function (i.e. cyclic animals, where cycles may or may not result in overused food resources). There is no evidence that beaver are cyclic.

The reason beaver have not evolved a mixed ESS is probably that their habitat quality (or space) is variable, spatially and temporally, in two respects (Slough and Sadleir 1977, Lawrence 1954): plant community succession changes site quality with time, and fire resets the successional clock in random areas at random times. In general dispersing beaver will settle sites of better average quality than those that are occupied.

Data from Bergerud and Miller (1977) and Payne (1982) indicate that a significant percentage of dispersal-age beaver fail to disperse when population density is high. This is not evidence for a mixed ESS because the non-dispersing females do not breed. The social fence

hypothesis (Hestbeck 1982) argues that as density increases social interactions increase to the point of inhibiting dispersal. This seems to be at least partly correct for beaver. However, the fate of the majority of dispersing beaver in the 'fenced' situations studied was not known. The second contention of the social fence hypothesis is that once the population is fenced the population will be regulated by resource depletion. I suspect this is not the case for beaver. The available resources on a territory are probably reduced to the point where reproductive output is depressed irrespective of whether the social fence is in place. The possible advantage for an adult pair that stays on a territory longer than strict food optimization would allow is that lifetime fitness is probably maximized. I would expect a tendency to expand a territory, or stay on a stagnating territory, rather than disperse for two reasons: adults are encumbered by two generations of young and a mate, and they have an intimate knowledge of the site they presently occupy.

A study of dispersing beaver in fenced and unfenced populations is possibly the most potentially fruitful area for future research.

The facts and implications of this study suggest the following pattern of habitat exploitation by beaver. In the early stages of site occupation, as at Northbranch pond, beaver constrain their foraging to trees close to water and

at the same time optimize e/t by taking the trees that are also close to the lodge. At a pre-Northbranch site, a simple energy optimization foraging pattern may not differ significantly from the predator constrained, pattern (Hiner 1938). However, the predation constraint is operative in relatively early stages of site occupation. At Northbranch pond the water costless model fit the observed cutting pattern, in spite of the fact that the maximum foraging distance was only half that at Pinetop.

The next stage in site occupation is apparently exhaustion of the supply of most preferred foods in the vicinity of the pond containing the lodge (i.e. depressed aspen availability at Pinetop). This is followed by the addition of new dams (Krefting 1963, Sevendsen 1980, Hay 1958) and, therefore, an expanded refuge. A new dam represents an abrupt increment in foraging territory. At this advanced stage the measurement of optimization becomes more complicated.

It is almost assured that the new unexploited forest made available is of better quality than the exploited forest that was available. Increasing the refuge size introduces a patch of habitat with high relative quality. This is the situation at Pinetop pond and beaver biased their cutting to this new patch. However, based on the actual stems available, and the distance minimization criterion, this was not the optimal foraging strategy. It

would be seen as an optimization of foraging behavior if e/t were improved by patch foraging. My data are not sufficient to determine if this was the case. Direct observation of foraging beaver would be needed to document whether beaver take longer to locate and harvest a stem from the low quality patch (previously exploited area). We can assume (until shown otherwise), in the spirit of the optimal foraging literature, that the observed behavior is the optimal solution.

The last logical step in the development of the foraging pattern occurs when beaver build a new lodge in one of the newly added ponds (Krefting 1963, Hay 1958, Bergerud and Miller 1977). In fact, Bergerud and Miller (1977) found a positive correlation between mean territory length and the number of lodges. At this point beaver remind us that water is not costless for travel, it just looks that way in the local sense. There is indeed an energetic advantage to changing one's central place. On the other side of the same coin, predators induce energy expenditures by beavers for foraging area expansion. For beavers, expending energy on dam building is a better life-history tactic than taking risks with predators.

LITERATURE CITED

- Aleksiuk, M. 1968. Scent - mound communication, territoriality, and population regulation in beaver. *J. of Mamm.* 49(4): 759-761.
- Aleksiuk, M. 1970. The seasonal food regime of arctic beavers. *Ecology* 51(2): 264-270.
- Aleksiuk, M. and I. Mct.Cowan. 1969a. Aspects of the seasonal energy expenditures in the beaver at the northern limits of its distribution. *Can. J. Zool.*, 74: 471-481.
- Aleksiuk, M., and I.Mct. Cowan. 1969b. The winter metabolic depression in Arctic beavers (Castor canadensis Kuhl) with comparisons to California beavers. *Can. J. Zool.*, 47: 965-979.
- Allen, Durward L. 1979. *The wolves of Minong*. Houghton Mifflin Co., Boston.
- Andersson, M. 1981. Central place foraging in the Whinchat, Saxicola rubetra. *Ecology* 62(3): 538-544.
- Banfield, A.W.F. 1977. *The Mammals of Canada*. Toronto: National Museums of Canada by University of Toronto Press.
- Bergerud, A.T. and D.R. Miller. 1977. Population dynamics of Newfoundland beaver. *Can. J. Zool.* 55: 1480-1492.
- Boyce, M.S. 1974. Beaver population ecology in interior Alaska. M.Sc. Thesis. University of Alaska, College.
- Boyce, M.S. 1981. Beaver life-history responses to exploitation. *Jour. of Applied Ecology* 18: 749-753.
- Bradt, G.W. 1938. A study of beaver colonies in Michigan. *J. of Mamm.* 19(2): 139-162.
- Brenner, F.J. 1962. Foods consumed by beavers in Crawford County, Pennsylvania. *J. of Wildl. Mgmt.* 26: 104-107.
- Brenner, F.J. 1964. Reproduction of the beaver in Crawford County, Pennsylvania. *J. of Wildl. Mgmt.* 28(4): 743-747.
- Brenner, F.J. 1967. Spatial and energy requirements of beaver. *Ohio J. Sci.* 67: 242-246.

- Buhyoff, G.J. and R.B. Hull IV. 1983. Users manual: Statistical processing system version 4.2. Unpublished Draft, Virginia Tech.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology* 61(1): 119-128.
- Chabreck, R.H. 1958. Beaver - forest relationships in St. Tammany Parish, Louisiana. *J. of Wildl. Mgmt.* 22: 179-183.
- Cody, M.L. 1974. Optimization in ecology. *J. of Sci.* 183: 1156-1164.
- Cumming, H.G. 1974. Clumping behavior and predation with special reference to caribou. First International Reindeer and Caribou symposium. Biological papers, University of Alaska, Special Report No. 1.
- Covich, A.P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. *Ann. Rev. Ecology Syst.* 7: 235-257.
- Cumming, H.G. 1974. Clumping behavior and predation with special reference to caribou. First International Reindeer and Caribou Symposium. Biological papers, University of Alaska, Special Report No. 1.
- Darwin, C. 1859. The origin of species. New York: The New American Library, Inc.
- Davies, N.B. 1978. Ecological questions about territorial behavior. Ch. 11 in J.R. Krebs and N.B. Davies. Behavioral ecology: an evolutionary approach. Oxford, Blackwell Sci.Pub.
- Davies, N.B. and J.R. Krebs. 1978. Introduction: Ecology, natural selection, and social behavior. Ch. 1 in J.R. Krebs and N.B. Davies Behavioral ecology: an evolutionary approach. Oxford, Blackwell Sci.Pub.
- Dixon, K.R. and M.C. Swift. 1980. The optimal harvesting concept in furbearer management. Worldwide Furbearer Conference Proceedings, Frostburg, Maryland. Vol.II: 1524-1551.
- Edwards, Allen L. 1979. Multiple Regression and the analysis of variance and covariance. W.H. Freeman and Company, San Francisco.

- Estabrook, G.F. and A.E. Dunham. 1976. Optimal diet as a function of absolute abundance, relative abundance and relative value of available prey. *Amer. Nat.* 110: 401-413.
- Farrow, E.P. 1917. On the ecology of the vegetation of Breckland. *J. of Ecology* 5: 1-18.
- Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *Amer. Nat.* 108: 269-289.
- Gale, J.S. 1980. Population genetics, Blackie, Glasgow.
- Gese, E.C. and A.R. Shadle. 1943. Reforestration of Aspen after complete cutting by beavers. *J. of Wildl. Mgmt.* 7(2): 223-228.
- Gibson, G.G. 1957. A study of beaver colonies in southern Algonquin Park, Ontario, with particular reference to the available food. M. Sc. Thesis, Univ. of Toronto.
- Gillespie, P.S. 1977. Summer activities, home range and habitat use of beavers. M. Sc. Thesis, Univ. of Toronto.
- Goulding, C.J. 1979. Validation of growth models used in forest management. *N.Z. J. of Forestry* 24(1): 108-124.
- Grasse, J.E. 1951. Beaver ecology and management in the Rockies. *J. of For.* 49(1): 3-6.
- Green, H.U. 1936. The beaver of the Riding Mountain, Manitoba: an ecological study and commentary. *Can. Field. Nat.* Vol.50: 1-8, 21-23, 36-50, 61-67, 85-92.
- Hall, J.G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. *Ecology*, 41(3): 484-494.
- Hammond, M.C. 1943. Beaver on the Lower Souris Refuge. *J. of Wildl. Mgmt.* 7(3): 316-321.
- Hanley, T.A. 1982. The nutritional basis for food selection by ungulates. *J. Range. Manage.* 35: 146-151.
- Harris, D. and S.E. Aldous. 1946. Beaver management in the northern Black Hills of South Dakota. *J. of Wildl. Mgmt.* 10(4): 348-353.
- Hazeltine, F.T. 1950. A study of beaver colony composition and woody plant utilization on two streams in Penobscot County, Maine. M. Sc. Thesis. Univ. of Maine.

- Hay, K.G. 1958. Beaver census methods in the Rocky Mountain region. *J. of Wildl. Mgmt.* 22: 395-402.
- Hegner, R.E. 1982. Central place foraging in the white-fronted bee-eater. *Anim. Behav.* 30: 953-963.
- Henry, D.B. and T.A. Bookhout. 1969. Productivity of beavers in northeastern Ohio. *J. of Wildl. Mgmt.* 33(4): 927-932.
- Henry, D.B. and T.A. Bookhout. 1970. Utilization of woody plants by beavers in northeastern Ohio. *J. of Sci.* 70: 123-127.
- Hestbeck, J.B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. *Oikos* 39: 157-163.
- Hiner, L.E. 1938. Observations of the foraging habits of beavers. *J. of Mamm.* 19: 317-319.
- Hoover, W.H. and S.D. Clarke. 1972. Fibre digestion in beaver. *J. of Nat.* 102: 9.
- Horn, H.S. 1978. Optimal tactics of reproduction and life history. Ch. 14 in J.R. Krebs and N.B. Davies. *Behavioral ecology: an evolutionary approach.* Oxford, Blackwell Sci.Pub.
- Jenkins, S.H. 1975. Food selection by beavers: a multi-dimensional contingency table analysis. *Oecologia (Berl)* 21: 157-173.
- Jenkins, S.H. 1978. Food selection by beavers: sampling behavior. *Breviora* 447: 1-6.
- Jenkins, S.H. 1979. Seasonal and year to year differences in food selection by beavers. *Oecologia (Berl.)* 44: 112-116.
- Jenkins, S.H. 1980a. A size distance relation in food selection by beavers. *Ecology*, 61(4): 740-746.
- Jenkins, S.H. 1980b. Problems, prospects and progress in studies of food selection by beavers. First Worldwide Furbearer Conference, Aug. 3-11. Frostburg, Maryland.
- Katz, P.L. 1974. A long-term approach to foraging optimization. *Amer. Nat.* 108: 758-782.
- Koslowski, T.T., and T. Keller. 1966. Food relations of woody plants. *Bot. Rev.* 32: 293-382.

- Krebs, C.J. 1978. A review of the Chitty Hypothesis of population regulation. *Can. J. Zool.* 56: 2463-2480.
- Krebs, J.R. 1978. Optimal Foraging: Decision Rules for Predators. Ch. 2 in J.R. Krebs and N.B. Davies. *Behavioral ecology: an evolutionary approach.* Oxford, Blackwell Sci.Pub.
- Krebs, J.R. and N.B. Davies. 1978. *Behavioral Ecology: an evolutionary approach.* Oxford, Blackwell Sci.Pub.
- Krefting, L.W. 1963. The beaver of Isle Royale, Lake Superior. *Nat. (Minn)* 14(2): 1-11.
- Lacher, T.E. Jr., M.R. Willig, and M.A. Mares. 1982. Food preference as a function of resource abundance with multiple prey types; an experimental analysis of optimal foraging theory. *Am. Nat.* 120: 297-316.
- Lack, D.L. 1954. *The natural regulation of animal numbers.* Oxford, Clarendon Press. Reprinted 1967 by University Microfilms, Ann Arbor.
- Lancia, R.A., W.E. Dodge, and J.S. Larson. 1982. Winter activity patterns of two radio-marked beaver colonies. *J. Mamm.*, 63(4): 598-606.
- Lawrence, W.H. 1952. Evidence of the age of beaver ponds. *J. of Wildl. Mgmt.* 16(1): 69-78.
- Lawrence, W.H. 1954. Michigan beaver populations as influenced by fire and logging. Ph.D. Thesis. Pub #8329 University of Michigan, Ann Arbor. 232 p. Dis.Abstr. MICH 14/07/1011, MICA54-1484.
- Laycock, W.A. 1978. Coevolution of poisonous plants and large herbivores on rangelands. *J. Range. Manage.* 31: 335-352.
- Levin, D.A. 1976. The chemical defenses of plants to pathogens and herbivores. *Ann. Rev. Ecol. syst.* 7: 121-59.
- Lewontin, R.C. 1977. Fitness, survival, and optimality. in D. Horn ed. *Analysis of Ecological Systems*, Ohio State Univ. Press, Columbus.
- Maynard Smith, J. 1978. Optimization theory in evolution. *Ann. Rev. Ecology Syst.* 9: 31-56.
- McBee, R.H. 1971. Significance of intestinal microflora in herbivory. *Annu. Rev. Ecology Syst.* 2: 165-176.

- McCleery, R.H. 1978. Optimal behavior sequences and decision making. Ch. 13 in J.R. Krebs and N.B. Davies. Behavioral ecology: an evolutionary approach. Oxford, Blackwell Sci. Pub.
- Merriam, H.G. and A. Merriam. 1965. Vegetation zones around woodchuck burrows. Can.Field.Nat. 79: 177-180.
- Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Amer. Nat. 144: 362-378.
- Monk, C.E. 1980. History and present status of fur management in Ontario. Worldwide Furbearer Conference Proceedings, Frostburg, Maryland. Vol.II: 1501-1523.
- Nixon, C.M. and J. Ely. 1969. Foods eaten by a beaver colony in Southeast Ohio. Ohio J. of Sci. 69: 313-319.
- Northcott, T.H.A. 1964. An investigation of the factors affecting carrying capacity of selected areas in Newfoundland for the beaver. Castor canadensis caccator (Bangs 1913). M. Sc. Thesis, Memorial University, St. John's.
- Northcott, T.H. 1971. Feeding habits of beaver in Newfoundland. Oikos 22: 407-410.
- Novakowski, N.S. 1967. The winter bioenergetics of a beaver population in northern latitudes. Can. J. Zool. 45: 1107-1118.
- Orians, G.H., and N.E. Pearson. 1976. On the theory of central place foraging. In D. Horn; ed. Analysis of ecological systems. Ohio State Univ. Press, Columbus.
- Osborn, B. and P.F. Allan. 1949. Vegetation of an abandoned prairie-dog town in tall grass prairie. Ecology 30: 322-332.
- Osborn, D.J. 1953. Age classes, reproduction and sex ratios of Wyoming beaver. J. of Mamm. 34(1): 27-44.
- Patric, E.F. and W.L. Webb. 1953. A preliminary report on intensive beaver management. 18th N. Amer. Wildl. Conf. pp. 533-537.
- Partridge, L. 1978. Habitat selection. Ch. 12 in J.R. Krebs and N.B. Davies. Behavioral ecology: an evolutionary approach. Oxford, Blackwell Sci.Pub.

- Payne, N.F. 1982. Colony size, age, and sex structure of Newfoundland beaver. *J. Wildl. Manage.* 46 (3): 655-661.
- Pearson, A.M. 1960. A study of growth and reproduction of the beaver (*Castor canadensis* kuhl) correlated with the quality and quantity of some habitat factors. M.S. Thesis, Univ. of British Columbia, Vancouver.
- Pimlott, Douglas H., J.A. Shannon and G.B. Kolenosky. 1969. The ecology of the timber wolf in algonquin Provincial Park. Ont. Dept. Lands and Forests, Res. Rept. (Wildl.) 87.
- Potvin, C.L. and J. Bovet. 1975. Annual cycle patterns of activity rhythms in beaver colonies. *J. Comp. Physiol.* 98: 243-256.
- Pulliman, H. Ronald. 1975. Diet optimization with nutrient constraints. *Amer. Nat.* 109: 765-768.
- Pyke, G.H., H.R. Pulliman and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 52: 137-154.
- Rapport, D.J. 1980. Optimal foraging for complimentary resources. *Amer. Nat.* 116: 324-346.
- Rosenzweig, M.L. 1974. On the optimal above ground activity of Bannertail Kangaroo Rats. *J. of Mamm.* 55(1): 193-199.
- Rowe, J.S. 1972. Forest Regions of Canada. Dept. of the Environ., Can. For. Serv. Pub. No. 1300.
- Rutherford, W.H. 1955. Wildlife and environmental relationships of beavers in colorado forests. *J. of For.* 53(11):803-806.
- Rutherford, W.H. 1964. The beaver in Colorado: its' biology, ecology, management and economics. Tech. Publ. No. 17. Game Res. Div. Col. Game, Fish & Parks Dept.
- Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecology Syst.* 2: 369-404.
- Schoener, T.W. 1979. Generality of the size-distance relation in models of optimal feeding. *Amer. Nat.* 114: 902-914.
- Schmidt-Nielsen, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science* 177: 222-227.

- Shadle, R.A. and T.S. Austin. 1939. Fifteen months of beaver work at Allegany State Park, New York. *J. of Mamm.* 20(30): 299-303.
- Shadle, A.R., A.M. North, E.C. Gese, and T.S. Austin. 1943. Comparison of tree cuttings by six beaver colonies in Allegany State Park, New York. *J. of Mamm.* 24(1): 32-39.
- Sih, A. 1980. Optimal foraging: partial consumption of prey. *Am. Nat.* 116: 281-290.
- Shi, A. 1982. Optimal Patch Use: Variation in selective pressure for efficient foraging. *Am. Nat.* 120: 666-685.
- Slough, B.G. 1978. Beaver food cache construction and utilization. *J. of Wildl. Mgmt.* 42(3): 644-646.
- Slough, B.G. and R.M.F.S. Sadleir. 1977. A land capability classification system for beaver. *Can. J. Zool.* 55: 1324-1335.
- Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. *Ecol. Monogr.* 38: 31-63.
- Snedecor, G.W. and W.G. Cochran. 1980. *Statistical Methods*. The Iowa State Univ. Press, Ames.
- Stamps, J., and S. Tanaka. 1981. The relationship between selectivity and food abundance in a juvenile lizard. *Ecology* 62(4): 1079-1092.
- Svendsen, G.E. 1980a. Population parameters and colony composition of beaver Castor canadensis in southeastern Ohio. *Amer. Midland Nat.* 104(1): 47-56.
- Svendsen, G.E. 1980b. Change in feeding patterns of beaver in southeastern Ohio. *J. of Wildl. Mgmt.* 44(1): 285-290.
- Townsend, J.E. 1953. Beaver ecology in western Montana with special reference to movements. *J. of Mamm.* 34(4): 459-479.
- VandenBerge, R.J. and P.A. Vohs, Jr. 1977. Population status of beaver on the free running Missouri River, southeastern South Dakota. *Proc. South Dakota Acad. Sci.* 56: 230-236.
- Waddington, K.D. 1982. Optimal diet theory: sequential and simultaneous encounter models. *Oikos* 39(2): 278-280.

- Weigl, P.D. and E.V. Hanson. 1980. Observational learning and the feeding behavior of the red squirrel Tamiasciurus hudsonicus: The otogeny of optimization. Ecology 61(2): 213-218.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108: 290-304.
- Westoby, M. 1978. What are the biological bases of varied diets? Amer. Nat. 112: 627-631.
- Wynne-Edwards, V.C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh & London.
- Yeager, L.E. and W.H. Rutherford. 1957. An ecological basis for beaver management in the Rocky Mountain region. 22nd N. Amer. Wildl. Conf.: 269-300.