CONSTRAINTS ON WINTER HABITAT SELECTION BY THE MOUNTAIN GOAT (*Oreamnos americanus*) IN ALASKA

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1983

Approved by Richard Taber
(Chairperson of Supervisory Committee)

Lawrence C Bliss

Program Authorized
to Offer Degree Forest Resources

Date June 8, 1983

University of Washington

Abstract

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During winter in southeast Alaska food availability, predator avoidance and thermoregulation are potentially important constraints on habitat selection by mountain goats. Hypotheses predicting goat habitat use relative to each constraint were tested with measurements of actual habitat use. Forage biomass was measured in 13 plant communities, ranging from alpine herbfields to dense old-growth forest, which were recognized as important components of goat winter range. Total available forage could be predicted for a plant community under any set of snow conditions through measurement of the pattern of snow accumulation effect on availability of individual forage species. Predictions compared well with actual measurements, and were used in testing the relationship between available forage biomass and use of plant communities by goats. Goat habitat use was positively correlated with available forage biomass where predation risk was constant, and negatively correlated with distance from steep and broken terrain where food availability was constant. Thermoregulatory considerations appear to influence goat habitat use only under the most severe winter conditions. Goats used less windy microsites in the alpine zone during windy conditions when temperatures were below -10° C. A general model of winter habitat selection by goats is constructed based on the costs and benefits of food availability and predation risk. Empirical evidence indicates that a distance limit of 500 m from steep and broken terrain may encompass virtually all of goat habitat use during winter, thus allowing a first approximation of the extent of goat winter habitat in an area. Because of the mild maritime winter conditions, the low elevation, heavily forested areas can provide the most available forage. Where these forested areas are within or in proximity to steep and broken terrain, such sites can provide critical wintering sites for goats.

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ACKNOWLEDGEMENTS

The study was made possible through support and cooperation among the Pacific Northwest Forest and Range Experiment Station in Juneau, the Alaska Department of Fish and Game, the Tongass National Forest, Ketchikan Area and the University of Washington. I would like to express appreciation to the late O. C. Wallmo for providing the opportunity to initiate and develop this project. O. C. Wallmo, John Schoen, Richard Taber, Lawrence Bliss, Charles Driver, Kenneth Raedeke and Thomas Hanley each provided invaluable conceptual input during various phases of the study. The field work was made feasible with able help from Janet Hall, Michael Tehan, and Robert Tanaka. Christian Smith of the Alaska Department of Fish and Game carried out the radio-tracking for the Ketchikan area work. David Murray at the University of Alaska provided help with identification of plant species. Edgar Huizer generously provided the use of his cabin during the study and Stephen and Margaret Jacoby's hospitality made warm many a cold day's return from the mountains.

INTRODUCTION

Habitat selection theory

Habitat selection by ungulates has been the subject of numerous studies and much speculation by wildlife managers and ecologists. The economic and aesthetic value of ungulates has created a need for information on their ecology and consequently much effort has been devoted to this end. While an understanding of the ecological factors that determine the value of habitats to ungulates is important on both theoretical and practical levels, the theoretical underpinnings have been slow to develop in any codified form. Most studies of ungulate habitat selection have been essentially descriptive in nature (e.g., Klebnow 1965, Skoog 1968, Mackie 1970, Peek 1971, Stevens 1974) and reflect a practical orientation to site specific management problems. Meanwhile, the natural history information obtained in such descriptive studies has inevitably led to speculation concerning the causes of observed habitat selection. The desirability of testable habitat selection theory is readily apparent; however, there are some compelling reasons for the paucity of such theoretical development in studies which attempt to explain selection of ungulate habitat.

The value of a particular habitat to an animal lies essentially in the degree to which the use of that habitat enhances the animal's fitness, in an evolutionary sense.

Following from natural selection theory individuals that use available habitat in such a manner as to maximize their own biological fitness will, on average, produce the greatest contribution to the next generation. The animal's selection of habitat reflects an optimization process whereby the costs and benefits of the use of habitat attributes are weighed in terms of biological fitness over the life of the individual. Basically, the information necessary for testing such fitness value accrued to individuals selecting a particular habitat involves measurement of differential survival or reproductive rates related to use of the habitat in question. The gathering of this type of data requires substantial time commitments with the relatively long-lived ungulates and is often very difficult to obtain for such mobile animals. Rigorous collection of such survivorship or reproduction data, as it relates to individual habitat selection, is essentially precluded by logistical constraints. Consequently, studies which have attempted to directly test the evolutionary fitness consequences of habitat selection in ungulates are essentially lacking, save for the current study of red deer on Rhum Island in England (Clutton-Brock et al. 1982).

Some studies have addressed habitat selection in relation to population survivorship or reproduction (Taber and Dasmann 1957, Klein 1965, Wegge 1975). Others have dealt with indirect measures of fitness such as physiological parameters of the animals (Franzmann et al. 1975, 1978) or quality measures of the overall habitat (Wallmo et al. 1978). Though these studies are essentially descriptive and fail to confront the essence of fitness in terms of individual selection, their approaches (indirect measures of fitness and implicit assumptions about individual behavior) are consistent with the bases for more formalized habitat selection theory and provide the substance for subsequent hypothesis testing. Thus, although direct measures of individual fitness may be essentially precluded in studies of ungulates, alternative methods of assessing fitness using indirect measures of animal or habitat quality can be used to evaluate the influence of various potential determinants of habitat selection. Most of the above studies involve implicit formulations of hypotheses concerning habitat selection based on natural selection theory and situations where fitness could be averaged over numerous individuals in a generalized habitat. Since it is apparent that the foundations of habitat selection theory have been integral to many previous studies of habitat selection it is important to be aware of the assumptions and theoretical bases which make such formulations reasonable.

In general, the formulation of testable hypotheses concerning habitat selection is based on natural selection theory and the assumption of optimality in an animal's use of environment (habitat selection). If the rate of long term behavioral adaptation to a changing environment is much greater than the rate of overall environmental change, it follows that current behavior (habitat use), on average, should approximate that which results in maximum fitness. This postulate of optimality in behavior, along with a knowledge of the study animal's natural history, form the bases for hypotheses concerning how the animal should behave in order to maximize fitness (Pyke et al. 1977). While this assumption of optimality in behavior is subject to some debate (May and Gilbert 1972, Wiens 1977, Diamond 1978) it is basic to all current formulations of habitat selection and optimal foraging theory.

Theory of habitat selection has been discussed in some detail (Fretwell and Lucas 1969, Orians 1971, Fretwell 1972, Charnov and Orians 1973). Though not formally developed to a great extent, it can be viewed as a rather straightforward application of natural selection theory, i.e., that habitat which provides the greatest net benefit to survival and reproduction should be selected for use. Where different habitats provide conflicting costs and benefits relative to survival and reproduction needs, optimum use may require selection of different habitats for different needs. Natural history traits of the animal in question provide the framework within which hypotheses are formed concerning which habitats should be selected under a given set of environmental conditions. The most detailed theoretical formulations are restricted to the field of foraging theory, one aspect of habitat selection.

Fretwell and Lucas (1969) have demonstrated an application of the theory of habitat selection (with extensions by Orians 1971, 1980) in terms of bird selection of nesting territory. Their formulation is based on the condition that habitats can be ranked according to fitness value (quality) and a situation where fitness value to the individual decreases as population density increases in the habitat. Thus, all individuals should choose the best habitat until population density decreases individual fitness to that which is available in the next best habitat, at which point that habitat will also be occupied. Alternatively, if habitat selection is a continuing process (unlike selection of nesting territory) and habitats are small relative to the total area utilized, then habitat selection should follow Charnov's (1976) "marginal value theorum" which states that an animal should leave a habitat patch when its fitness value falls to the average for the area utilized.

In formulating hypotheses concerning expected selection of habitat we look for an optimization of behavior under a given set of conditions (constraints) in which something (a currency, e.g., energy or time) is maximized or minimized (Schoener 1971). A currency, appropriate to the question under consideration and the constraints present, is selected which allows a ranking of habitats according to either maximization or minimization of the currency. Hypotheses of optimal behavior then predict that habitat selection should be in some relation to this ranking of habitats according to quality and testing lies in comparisons of observed with predicted habitat use. Habitat quality (rank) in this sense reflects the value of a given habitat in allowing the animal to maximize or minimize the currency under consideration. Fretwell and Lucas' formulation, whereby habitat quality decreases with increasing population density is reasonable where food acquisition is the determinant of habitat selection (as is argued for the bird nesting territories they studied). Under non-territorial conditions, an animal's choice of habitat is a continuing process and previous feeding (rather than strictly population density) will diminish a habitat's quality. Also, for some potential determinants of habitat selection (e.g., mate acquisition or predator avoidance) population density may have a neutral or positive effect on fitness value in some species.

Potential determinants of habitat selection include predator avoidance, thermoregulation, food acquisition and mate acquisition, and are affected by such factors as competition, social organization and weather. Studies of sympatric ungulates have commonly attributed niche separation to differences in habitat selection related to these various determining factors (Flook 1964, Martinka 1968, Telfer 1970, Estes 1974, Jarmen 1974, Anthony and Kearney and Gilbert 1976, Smith 1977, Dunbar 1978), though the effects of the various determinants are often interconnected and confused. With an array of potentially interacting determinants of habitat selection to contend with, it is usually desirable to simplify the interactions and utilize study situations where these factors can be limited in number or isolated.

The more analytical investigations of habitat selection have concentrated on situations where food acquisition could be isolated as the primary determinant of habitat selection, and thus allow the use of optimal foraging hypotheses. A few studies have attempted to predict ungulate diet on the basis of optimal foraging considerations (Westoby 1974, Belovsky 1977, 1978, Hanley 1980), with mixed success (as discussed by Westoby 1978). Other studies have explored the relationship between diet and habitat selection in ungulate communities (Talbot 1962, Lamprey 1963, Gwynne and Bell

1968, Bell 1969, 1971, Hanley 1980). While the most detailed analyses of ungulate habitat selection have concentrated on food acquisition, we must remain cognizant of the overall situation where habitat selection is a function, though not necessarily simultaneously, of all its various determinants.

A notable drawback in dealing with indirect measures (currencies) of fitness is that they are generally different for various determinants of habitat selection, and not directly comparable. Thus, while measures of predation risk and food availability may each be valid means of assessing habitat quality for different aspects of fitness, they are usually measured in different, incompatable units and a combined measure of the trade-off between the two is not easily accomplished. Any assessment of the relative importance of the two factors in determining habitat selection becomes clouded. In a preliminary analysis of goat behavior such as the present study, we are essentially confined to quantitative assessments of the validity of our single factor currencies in measuring habitat quality, with interaction between factors being subject to a more hypothetical evaluation. In developing these assessments of habitat quality, the problem lies in selecting meaningful and measurable currencies (to be maximized or mimimized) and sets of conditions where habitat selection can be directly related to the currency in question.

Mountain goat habitat selection

The mountain goat (*Oreamnos americanus*) has been described as inhabiting relatively rugged mountainous country, typically near or above timberline and with a general seasonal altitudinal migration associated with snow conditions (Anderson 1940, Casebeer et al. 1950, Klein 1953, Brandborg 1955, Rideout 1972, Chadwick 1973, Kuck 1973, Smith 1976, Stevens 1979). The selection of very steep, rugged terrain is thought to be associated with avoidance of predators (Brandborg 1955, McFetridge 1978), though such terrain may also facilitate the availability of food resources under winter snow conditions (Kuck 1973). Goats are said to sometimes seek shelter from wind and rain during storms (Klein 1953, Brandborg 1955, Chadwick 1973) and regularly move to shady, windy or snow covered sites on warm sunny days (Brandborg 1955, Fox 1978, Stevens 1979), indicating that behavioral thermoregulation may affect habitat selection under certain conditions. Habitats used for foraging by goats are typically alpine and subalpine meadows and rock outcrops in summer (Hibbs et al. 1969, Hjeljord 1971, Fox 1978) and timberline rock outcrops, windblown alpine ridges and some shrubby and forested sites during winter (Chadwick 1973, Kuck 1973, Smith 1976, Hebert and Turnbull 1978). Studies of goat food habits (Table 1) generally reflect a preference for grasses and forbs in summer and varied diets in winter related to opportunistic selection of available forage. In some areas goats use mineral licks, primarily in spring, to supplement nutrients and possibly roughage in their diet (Hebert and Cowan 1973, Carbyn 1974, Singer 1978, Stevens 1979). In the fall rutting period male goats search out females for breeding and may travel through habitat not commonly used otherwise (Brandborg 1955, Geist 1966, Smith and Raedeke in press). During the parturition period, female goats tend to isolate themselves in concealing terrain or vegetation (Klein 1953, Brandborg 1955).

There has been some initial work done in the development of a means to identify goat habitat. Shea (1980) derived a habitat suitability index assuming habitat quality rankings based on plant community types (reflecting food abundance) and distance from escape terrain. However, limited substantiation of these assumptions leaves such an index at a still very hypothetical stage. Also, only in a broad sense does it account for seasonal variation in habitat quality. It ignores within season variation in food abundance or quality and is necessarily restricted to the region (southcentral Alaska) where the plant communities it incorporates are present. Even so, such a model represents

Table 1. Food habits studies of mountain goats.

Season and Investigator	Location	Plant classes in diet (percent)						
		Grasses	Forbs	Ferns	Conifers	Shrubs	Lichens	Mosses
Summer								
Anderson (1940)	Washington	12	18	-	-	70	-	-
Cowan (1944)	Alberta	63	14	-	-	23	-	-
Saunders (1955)	Montana	76	18	3	1	2	-	-
Hibbs (1967)	Colorado	82	14	-	t*	4	-	-
Hjeljord (1971)	Alaska	36	64	-	-	-	-	-
Chadwick (1973)	Montana	32	44	-	t	24	-	-
Smith (1976)	Montana	72	26	-	t	2	-	-
Winter								
Anderson (1940)	Washington	90	-	-	1	9	-	-
Casebeer (1950)	Montana	63	2	-	-	35	-	-
Klein (1953)	Alaska	13	-	72	1	14	-	-
Saunders (1955)	Montana	59	10	-	30	1	-	-
Brandborg (1955)	Idaho	54	-	-	-	46	-	-
Hibbs (1967)	Colorado	88	-	-	-	12	-	-
Hjeljord (1971)	Alaska	49	1	45	-	10	-	-
Kuck (1973)	Idaho	36	11	t	6	47	-	-
Chadwick (1973)	Montana	61	18	1	9	12	-	-
This study	Alaska							
alpine-Juneau		15	5	8	51	7	5	9
forest-Juneau		1	3	8	73	8	5	2
forest-Ketchikan		3	10	10	27	7	15	28

* t = trace = less than 0.5%

a useful step in providing a framework for recognizing the type of information needed for further modelling of goat habitat selection.

Various habitat attributes such as food abundance, mineral occurrence, steepness, ruggedness, and shade producing or wind shielding features have all been suggested as being important in providing the necessary requirements for mountain goat survival and reproduction. The present study is basically concerned with the first step of determining whether certain of these suggestions (hypotheses) can be demonstrated as reasonable explanations of goat habitat selection during winter. The development of an acceptable currency to measure potential food acquisition, which includes an accounting for the effects of winter snow conditions, was perceived as critical to an understanding of goat habitat selection in winter and is dealt with in some detail. Several hypotheses dealing with expected goat selection of habitat, derived from various potential determinants of habitat selection and mountain goat natural history traits, are generated and tested against actual habitat use by goats. Secondarily, acknowledging an incompatability of units, an attempt is made to elicit the relative importance of the factors determining habitat selection, and hence, the relative importance of various habitat attributes to goats during winter.

The present study is restricted to the post-rut, pre-parturition period here defined as winter (essentially December through March) and, as such, eliminates the influences of mating activities and parturition behavior on habitat selection. The absence of mineral lick use by goats in the study area further diminishes the number of potential factors affecting habitat selection. This leaves predator avoidance, forage acquisition and thermoregulation as potential determinants of goat habitat selection during winter. Furthermore, field circumstances were sought where these factors could be examined with the others being held constant.

Constraints on mountain goat habitat selection

A. Predator avoidance

When approached by a large mammalian predator a mountain goat will move to, if not already in, steep and broken terrain. If approach by the predator continues, the goat will seek out a vertical face which precludes approach from above, back up against this cliff and, if necessary, face off a predator which pursues the confrontation. The mountain goat, by virtue of its morphology, is more agile than the predator in steep and broken terrain so that, once in such terrain, the risk to the predator usually becomes greater than the benefits of a kill and the attack is suspended. Such predation avoidance behavior is typical of most members of the Bovidae subfamily Caprinae (Schaller 1979) and among ungulates is essentially restricted to this group. This strategy enables a rather straightforward view of habitat quality with respect to predator avoidance. Steep and broken terrain should have an extremely high relative fitness value with other habitats being low and decreasing in value as distance from steep and broken terrain increases. While risk of predation is essentially the factor to be minimized, it can reasonably be measured in terms of the "currency" distance from steep and broken terrain. Thus, if predator avoidance is the overriding determinant of habitat selection, then all goat use should be of steep and broken terrain. If other factors are competing, goat use should still be negatively related to distance from steep and broken terrain. In this context steep and broken terrain is defined as slopes averaging 30° and greater which include numerous breaks in slope, usually caused by rock outcrops, composed of many small or large cliffs and ledges with some cliffs being near vertical and at least 3 m in height. With respect to predator avoidance then, we hypothesize that goat habitat selection should be highly negatively correlated with distance from steep and broken terrain.

B. Food acquisition

Habitat quality with respect to food acquisition can be determined via optimal foraging theory, a derivative of natural selection theory. In optimal foraging theory an animal's diet consists of the mix of available foods which maximize its net rate of nutrient intake (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). Where food acquisition is the determinant of habitat selection, the optimal allocation of time to habitat use must be that which maximizes the net rate of nutrient intake and the use of different habitats should be highly correlated with food availability. Translating this to practical use requires the choice of a reasonable measure (currency) of nutrient value for food resources, and hence, habitat quality. A generalist ruminant such as the mountain goat has a wide array of plant food resources to choose from and these plants vary spatially, temporally and by species in their nutrient quality. Forage nutrient value for ruminants is related to their ability to digest various components of the plant, from highly digestible cellular contents to various less digestible cell wall constituents (Goering and Van Soest 1970, Smith et al. 1971, 1972). Other forage characteristics such as nitrogen content and *in-vitro* digestibility can be used as indices of forage quality since they are frequently correlated with nutrient biomass of available forage per unit area. Forage is defined as current annual growth, the most nutritious part of the plant, and it is available when it is erect or semi-erect (i.e., not incorporated into the duff layer) and present from substrate level to a height of 150 cm. Habitat, in this context, refers to a relatively homogeneous plant community.

The question of forage availability during winter requires further consideration since the effects of frost and snow on the availability of forage can far outweigh any differences in nutrient quality with respect to possible nutrient acquisition from a given habitat. Soil depth, composition and moisture content along with temperature, solar radiation and other environmental factors during the growing season determine the amount of annual growth produced in a particular plant community. Peak annual above-ground net production is a commonly measured parameter which can be related to the amount of food available to herbivores in a plant community. However, disregarding any effects of grazing, the amount of this peak biomass remaining in winter is generally greatly diminished. As much as 30% of the above-ground peak biomass can be transported to roots for overwinter storage (Tieszen 1972, Chapin et al. 1980) and the leaching of soluble compounds by rainfall can also reduce plant biomass and nutrient quality.

For a large herbivore that feeds on erect or semi-erect vegetation, and not on detritus or duff, the dehiscence of flower parts and seeds and the loss of leaves from deciduous species also reduces available food in winter.

The onset of freezing temperatures in early winter has varying effects on plants in the region. Graminoids generally remain intact and semi-erect to erect. Forbs generally have their support structure disintegrated by freezing and quickly become incorporated into the duff layer. Some forest understory forbs are evergreen and maintain an erect posture under the typical freeze-thaw conditions. Shrubs remain erect under freezing conditions, though all are decidous. Most prostrate shrubs or subshrubs, predominantly ericacious, retain their posture and their leaf production, though a few are deciduous. Conifers (krummholz and erect trees) retain their annual needle growth. Lichen stature is not affected by freezing, though they become brittle and subject to breakage.

In habitats exposed to wind, plants may be broken by strong winds or through the abrasive action of wind and snow. Overwinter loss of forage biomass, due to such abrasion, can be as much as 60% in exposed grassland habitats (Hoefs and Brink 1978). Wind action also causes plant breakage in forest communities, which can add to available forage biomass in the form of lichen and conifer litterfall and tree windthrow (Rochelle 1980, Stevenson 1981).

The effects of snow on forage availability, and hence, habitat selection, is a potentially critical factor constraining habitat selection and in the present study is considered in detail. It is probably the paramount determinant of forage availability during winter. Plant posture, flexibility and height determine the effects of snow accumulation on plant availability as forage. The most dramatic loss of forage is due simply to the plants being covered with snow. However, another important factor is the crushing effect of snowpack on flexible plants, most significantly for shrubs and small trees. *Vaccinium alaskaense* and *Menzesia ferruginea* can be crushed by winter snowpack to less than 14% of their snow-free height (Harestad 1979), thus greatly diminishing their availability as forage.

Snow accumulation is related to topographic influences on temperature, wind speed and ground surface area relative to horizontal. It is also significantly influenced by the interception of snowfall by erect plants, especially by coniferous trees (Miller 1964). Precipitation increases and temperature decreases with elevation cause more snow to fall at higher elevations. Mountainous terrain disturbs windflow patterns and orientation to prevailing wind determines the pattern of snow deposition. Relative differences in wind speed determine the degree to which snow accumulation differs on adjacent sites (Perla and Martinelli 1976). Alpine areas experience the greatest wind speeds, with turbulence generally diminishing toward valley floors. Aspect and slope angle determine the potential for solar radiation input and consequently influence the relative amount of snow sublimation and melt at a given latitude and altitude. Slope angle also has a significant effect on the snow cover thickness (measured perpendicular to the slope) and surface area for a given volume of snowfall. Snow cover thickness varies as the cosine of the angle of slope while the snow-air interface surface area varies as the inverse of the cosine of the angle of slope (Perla and Martinelli 1976). For example, on a slope of 60° a given snowfall will be half as thick and expose twice the surface area to sublimation or melt as compared with that which has fallen on a level site. Furthermore, since potential energy of the snowpack increases with slope angle, snowpack redistribution due to gravity (snowslides) is more common on steep slopes. In alpine and timberline habitats wind action and avalanche occurrence are the primary influences on snow accumulation patterns, whereas at lower elevations the effect of tree canopy coverage is paramount (Fitzharris 1975). Slope and aspect exert significant influence in both zones.

The relationships of various habitat attributes to snow accumulation have been reviewed in detail because of their potentially profound effects on forage availability, and hence, on the quality of various habitats with respect to food acquisition. Changing snow conditions during winter may substantially alter forage availability in the various habitats so that any assessment of habitat quality must reflect current snow conditions. Thus, we need to be able to rank habitat quality (available forage biomass) for any given set of snow conditions. If forage acquisition is the overriding determinant of habitat selection, then a scenerio similar to that described by Fretwell and Lucas (1969) should apply; all use should be of the highest quality habitat until nutrient intake rate is lowered (through foraging) to that of the next best habitat, when both habitats will be used. However, the goat's generalist feeding habits and the changing forage availability due to constantly changing snowpack conditions confers an advantage to regular sampling of various habitats (Westoby 1974) and suggests a more varied array of habitat use, though still highly correlated with forage availability. Thus, where food acquisition is a primary determinant of habitat selection, we hypothesize goat habitat use to be strongly positively correlated with available forage biomass.

C. Thermoregulation

The third potential determinant of goat habitat selection in the study area during winter is that of thermoregulatory behavior. Lower critical temperature for the mountain goat has been measured at somewhere between -20°C and -30°C (Krog and Monson 1952), which is consistent with that for another Caprinae of similar habits, the bighorn sheep (Chappel and Hudson 1978). Temperatures this low occur only occasionally in the coastal goat ranges of southeast Alaska, where the study took place. However, operational environmental temperatures (Gordon 1968), influenced by wind disturbance of goat hair insulation, may drop below critical more often in the exposed, windy habitats. With respect to quality relative to the need for active thermoregulation, habitats which require the least increase in metabolism to compensate for operational environmental temperatures lower than critical have the highest value and decrease with decreasing values below the critical point. If a situation exists where thermoregulatory behavior is the overriding determinant of habitat selection, then we hypothesize that goat habitat use should be positively related to temperature and negatively related to wind speed in the various habitats.

Study hypotheses

In summary then, the study deals with an evaluation of potential constraints on goat habitat selection imposed by predation risk, food acquisition and thermoregulation under winter conditions. The currencies used to measure habitat quality relative to predation risk (distance from steep and broken terrain) and thermoregulation (temperature and wind speed) are relatively straightforward and are not dealt with in great detail. However, adequate measurement of the currency (available forage biomass) representing habitat quality relative to food acquisition is viewed as more complex and a major portion of the study deals with this problem. Several hypotheses are developed which predict goat habitat use under the special conditions of single factor determinants of habitat selection. These hypotheses are as follows:

1) Where predator avoidance determines habitat selection, goat habitat use should be highly negatively correlated with distance from steep and broken terrain.

2) Where food acquisition determines habitat selection, goat habitat use should be highly positively correlated with biomass of available forage.

3) Where thermoregulation determines habitat selection, goat habitat use should be positively correlated with temperature and negatively correlated

with wind speed.

In the general situation where these various factors are interacting as determinants of habitat selection, overall goat habitat use is likely to be a reflection of their relative importance.

STUDY AREA

The study was located in southeast Alaska. Most of the work took place on a mountain block bounded by the Herbert and Mendenhall Glaciers, 58° 30'N, 134° 40'W, 25 km northwest of Juneau, while a portion of the study (dealing with radio-tracking data) was carried out on the lower Cleveland Peninsula, 55° 30'N, 132° 0'W, 40 km northwest of Ketchikan (Figure 1). Southeast Alaska is a cool temperate region of steep, glaciated mountain ranges, deep fjords and a mosaic of alpine, muskeg and coniferous forest vegetation. Despite its high latitude, southeast Alaska has a cool, wet maritime climate due to the proximity of the North Pacific warm stream (Sverdrup 1940). Mean monthly temperatures at sea-level range from 13°C in July to 1°C in January. The mountainous terrain of the region causes substantial variation in climatic conditions over short distances (Andersen 1955). Annual precipitation (200-600 cm at sea-level) is generally heaviest on the outer coastline, declining to the east as far as the Coast Ranges, where it again increases. Wind patterns, location of water bodies and other factors can dramatically influence local precipitation and temperatures within the region. Probably the most significant climatic differences between southeast Alaska and similar coastal areas of the Pacific Northwest farther south are the somewhat lower temperatures (greater winter snowfall) and the lack of a pronounced summer

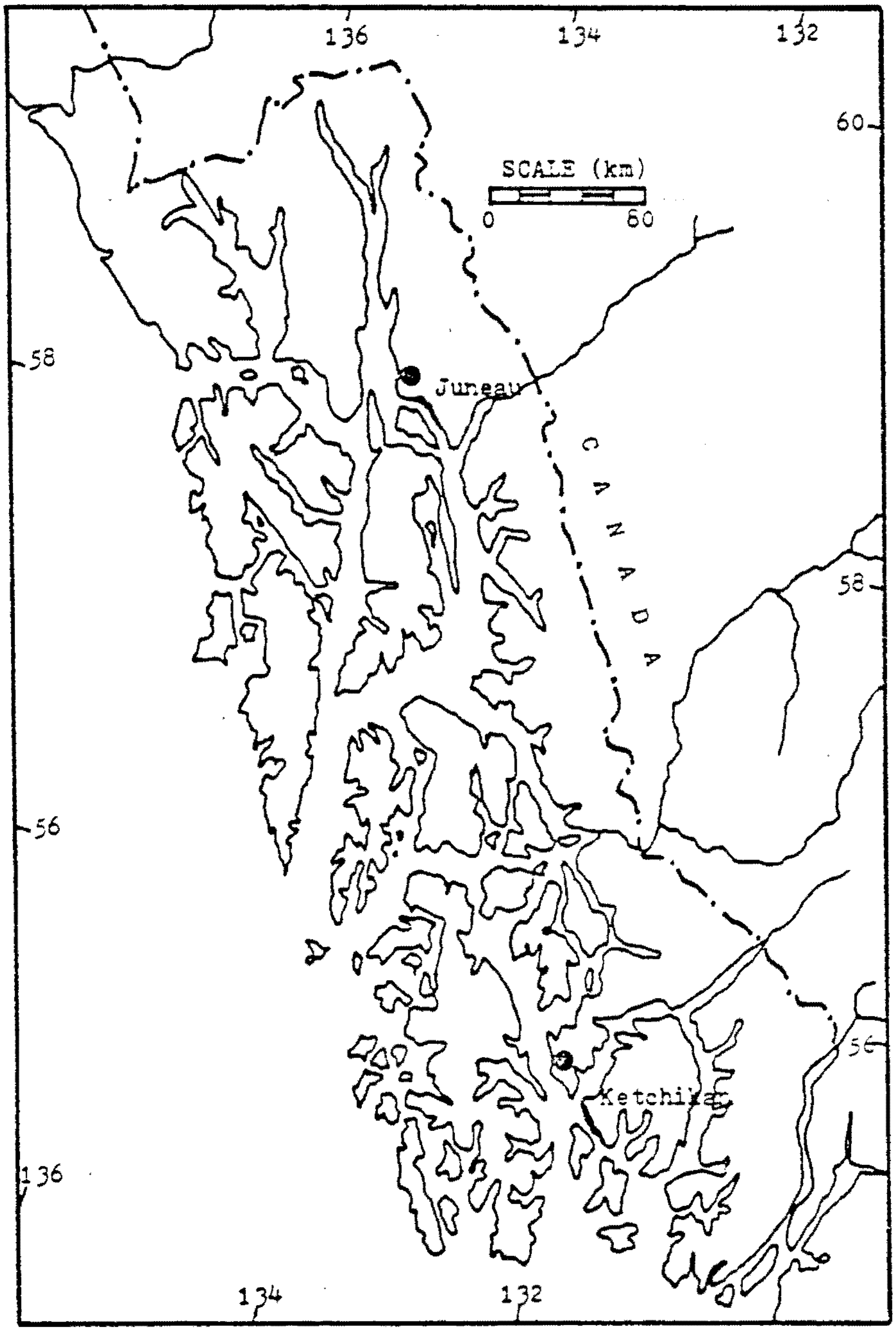

Figure 1. The study areas in southeast Alaska. Study locations are represented by the solid circles.

drought.

Coastal ranges generally vary in height from 2500-3000 m peaks within the huge icefields bordering British Columbia to 1000-2000 m mountains near the coast and on the islands. Physiographically, the features of southeast Alaska result from the northwest orientation of fault systems, bedrock strikes and lineaments. The geological structure is essentially a northwesterly trending eugeosyncline with Paleozoic rocks dominating the central lowlands and more erosion-resistant batholithic rocks of Mesozoic age forming the mainland and outer coastal zones of the mountain systems (Buddington and Chapin 1929, Brew et al. 1966). Soils are generally young (200-10000 yr old), shallow and poorly developed (Crocker and Major 1955, Collins 1974, United States Forest Service 1978).

Bare rock and permanent ice and snow are common at the highest elevations, while some glaciers reach down to sea-level. Alpine plant communities form a significant band of vegetation on the mainland and the larger islands. Treeline in the region, characterized by spruce (Picea sitchensis) and mountain hemlock (Tsuga mertensiana) forest interspersed with thickets of alder (Alnus sinuata), is generally about 800 m (highest in the south). Scrub and krummholz occasionally approach 1000 m. Forests of spruce and western hemlock (Tsuga heterophylla) intermixed with muskegs are predominant on the lower mountain slopes and lowlands.

No comprehensive studies of the structure or composition of forest or alpine vegetation have been made in southeast Alaska. Some qualitative descriptive work is available for both zones (Taylor 1942, Heusser 1954, 1960, Stephens et al. 1969, Neiland 1971, Jacques 1973, United States Forest Service 1978, Alaback 1980) and limited quantitative analyses have been performed at a few sites (Stephens and Billings 1967, Worley 1977, Del Morel 1978). Viereck and Dyrness (1980) have attempted to incorporate most of these varied descriptions into their vegetation classification system for Alaska.

Mountain goats occur naturally only on the mainland in southeast Alaska, though they have been successfully introduced to one of the largest islands, Baranof Island. In this region goats can be found anywhere from 1700 m elevation down to sea-level during winter, but most activity is probably within the range of 300-1200 m in winter.

Large predators present in the region include the wolf (*Canis lupus*), wolverine (*Gulo luscus*), black bear (*Ursus americanus*), brown bear (*Ursus arctos*) and bald eagle (*Haliaeetus leucocephalus*). Bears are not active in winter and are therefore not a factor in predation of goats during this season. Bald eagles are known to kill very young goats

(Brandborg 1955); however, by wintertime goat kids are generally large enough to prevent such predation. Wolverines visit goat habitat during winter, have been known to attack adult goats (Guiguet 1951), but are probably predominantly scavangers on these large mammals. Wolves are common throughout most of southeast Alaska, are known to prey on goats (Fox and Streveler, in prep.) and are present in both study areas. Near Juneau, groups of wolves visited the study area (including the alpine zone) approximately every two weeks through the winter.

The study area near Juneau was within a mountain block (highest elevation, 1753 m) of about 80 km^2 bounded to the north and east by glaciers and icefields and to the south and west by lowland forests on level terrain. This area supported a pre-parturition population of about 60 goats. The ground sampling work for this study was carried out in a small (approx. 20 km^2) portion of this mountain block. Approximately one-third of the goat population could be found within this portion at any one time during winter. During this study most goats were adult females or subadults of both sexes. The portion of the study carried out near Juneau took place during the winters of 1978-1979 and 1979-1980.

Most of the study deals with the area near Juneau; however the portion dealing with data from radio-tracked goats was carried out in the area near Ketchikan. This study area on the lower Cleveland Peninsula northwest of Ketchikan consists of some 250 km^2 of relatively low elevation and predominantly forested land (highest elevation, 960 m). While the area has very little alpine habitat it supports about 40 mountain goats (Raedeke 1980) which make substantial use of the forested habitats, especially in winter. The portion of the study carried out near Ketchikan took place during the winters of 1980-1981 and 1981-1982. The study area near Juneau included substantial alpine and forest habitat while that near Ketchikan was predominantly forested.

METHODS

Plant Communities

Plant communities present in the Juneau study area, recognized by dominant species and plant structure, were identified from previous work in the area (Fox 1978) and during reconnaissance for this study. Identification of plant communities includes alpine and forest habitat since goat winter range encompasses both of these vegetation zones. In the forest, plant communities were distinguished primarily on the basis of understory composition since this portion is most important in terms of forage for goats. Only those plant communities with significant areal extent within winter range of goats were considered. Thus, several distinct but very minor communities associated with certain types of snowbanks, streamsides or ponds were not described or sampled for plant biomass.

Relatively homogeneous stands (identified on the basis of species composition and plant structure) representing each of the various plant communities identified were chosen for limited sampling to floristically describe each community. The sampling was carried out during summer and therefore reflects differences apparent during this period of peak annual production. In representative stands, plant cover (%) was estimated for each species within three 5 m diameter circular plots for each of the plant communities identified. From these samples species composition lists were compiled and general estimates of cover (%) were derived for plant classes and important species in each community. Nomenclature throughout is according to Hulten (1968).

Forage biomass determinations

A. Ground-rooted forage

Relatively homogeneous stands representing each of the 13 plant communities were selected for sampling of plant biomass. Stands chosen for each plant community were large enough (minimum size, 250 m^2) to accommodate several destructive samples taken during the winter. Each sample consisted of 30-50 .1-m^2 rectangular quadrats (Daubenmire 1959) set out in a restricted random fashion (Bliss 1963) within each of the selected stands. During the winter of 1979-1980 an initial sample was taken in November just before winter snow accumulation began, then two more samples were taken in late January and early March with snow on the ground.

For low growing species (forbs, grasses, subshrubs) a double sampling technique was used to derive linear regressions to predict the dry weight biomass of species from estimates of cover. In all of the quadrats, canopy coverage for each species was estimated while a subsample (10-25 quadrats for each species) was also clipped, dried and weighed, thus yielding a relationship between dry weight and percentage cover (Table 2). Several of the regression equations for forb species (e.g., *Cornus*, *Rubus*, *Coptis*, *Tiarella*) can be compared with those derived by Alaback (1980) for the same species in the same region, though his are from summer measurements. In each case the regression slope is slightly less for our samples, which indicates lower biomass per unit percentage cover during winter. This difference can be expected considering the loss of reproductive plant parts and possible translocation of carbohydrates and nutrients to underground parts during winter.

Double-sampling procedures did not prove feasible for shrubs and small trees so that for these plants current annual growth was clipped, dried and weighed for all quadrats. For the samples taken after snow covered the ground, biomass measurements were divided into 2 zones; above the snow surface and within 25 cm below the snow surface, to account for the fact that goats dig or push away snow to get at plants below the snow surface. These measurements, taken after the development of snowpack, are then compared with predicted available forage biomass (see following section) as a test of prediction accuracy.

Table 2. Biomass prediction equations. Least squares estimates were used to calculate regression parameters to predict biomass (g/.1m^2) from plant percent cover.

Class and species	B_o	B_1	r^2	S^2Y/X	n	Range X_i*
Graminoids						
Calamagrostis canadensis	.1066	.0802	.95	.106	15	2-55
Carex circinnata	-.0301	.0620	.90	.019	15	2-22
Carex macrochaeta	.0265	.0518	.97	.025	15	5-60
Carex nigricans	-.0097	.0545	.97	.015	15	20-70
Luzula arcuata	-.0575	.0520	.96	.008	15	2-34
Forbs						
Coptis asplenifolia	.0057	.0230	.98	.001	15	1-25
Cornus canadensis	.0405	.0181	.94	.003	15	1-40
Pyrola secunda	.0569	.0270	.92	.002	10	1-17
Rubus pedatus	.0755	.0128	.87	.003	25	1-40
Tiarella spp.**	.0300	.0291	.92	.003	15	4-26
Subshrubs						
Andromeda polifolia	-.0584	.0375	.90	.006	15	1-20
Cassiope mertensiana	.0094	.0238	.97	.012	10	1-70
Cassiope stelleriana	-.0012	.0274	.89	.014	10	1-35
Empetrum nigrum	-.1552	.0273	.93	.012	10	2-45
Loiseleuria procumbens	-.0239	.0076	.88	.001	10	5-35
Luetkea pectinata	-.1646	.0639	.84	.040	10	4-25
Phyllodoce aleutica	-.1744	.0964	.94	.031	15	2-25
Vaccinium spp.***	-.0219	.0238	.89	.031	10	1-10
Ground-lichens (alpine)	-.0116	.0250	.95	.003	10	1-25

* X_i = percent cover

** *T. trifoliata* and *T. unifoliata*

*** *V. uliginosum* and *V. caespitosm*

B. Lichens on tree trunks

A double-sampling technique was used to estimate lichen biomass on tree trunks. Line-intercept transects were run up each the north and south sides of 52 tree-trunks to measure percentage interception for lichen in 25 cm intervals to a height of 250 cm. Then, forty 50-cm^2 surface area samples of lichens were collected, dried and weighed to determine a relationship between surface area coverage and dry weight. Lichens formed 100% cover in each of these samples, though only those thalli easily scraped off of the tree-trunk surface were collected to simulate potential forage.

Lichen biomass on tree trunks and forest litterfall biomass were calculated based on relative tree-trunk area and overstory canopy coverage, respectively. Canopy coverage was estimated in each forest community using a 10 cm long, 2.5 cm diameter plastic tube with a 90° angle and cross-haired mirror embedded at 45° in the bend. With this device the overhead sky was viewed in a quartered circle while looking horizontally and canopy coverage was estimated within the circle. In each forest commmunity 120 point estimates of canopy coverage were made at 1 m intervals along transects within the sample stands.

Estimates of timber volume and associated average DBH (diameter at breast height) and number of trees per unit area were made in each forest community stand using variable plot crusing (Dilworth 1974) with a sample of 30 plots (10 fully measured) in each stand. The timber volume estimates were based on standard volume tables (Girard and Bruce 1963) and a scaledown for unusable wood of 26%, typical for southeast Alaska.

C. Forest litterfall

Forest litterfall was collected in 8 pairs of litter traps (fenced and open) constructed with an 87 cm diameter circle of muslin cloth staked to the ground. Five pairs of traps were placed in the Tsuga-Picea-Vaccinium Forest community where goat presence was expected, while 3 pairs were placed 1.6 km away in the same type of forest, but with low expectation of goat use. All litter traps were at an elevation of approximately 325 m in old-growth Tsuga-Picea-Vaccinium forest with overstory canopy coverage of about 80%. Litterfall accumulation in the muslin traps was collected, separated into forage classes, dried and weighed.

Factors affecting forage availability

A. Snow conditions

Snow depth measurements, made with a meter stick or a 2.2 cm diameter snow pole, were taken at 1 m intervals along transects through each plant community stand. The samples consisted of 50-80 measurements and were conducted on at least monthly intervals in each plant community. Snow density measurements (n=10-20) were made by collecting and weighing snow cores from a hollow 3 cm diameter plastic tube and using known snow depth to calculate grams per cubic centimeter.

Estimates of the depth to which goats sink into the snowpack were made using a 20 oz lead ball dropped from a height of 150 cm. Comparisons of lead ball sinking-depth and adult goat sinking-depth made under various snow conditions showed no significant difference (n=124, $p<.05$). Measurements of 20-30 sinking-depths of the lead ball comprised a sample for each plant community and were conducted on at least monthly intervals with the snow depth measurements or whenever biomass predictions were needed.

In making the predictions of available forage biomass an "effective" snow depth is used to account for the fact that goats dig through snow for food. In general, goats do not dig below about 25 cm into the snow for food and this figure is used in determining effective snow depth.

However, if the snow is hard enough that goats do not sink as far as 25 cm, then sinking-depth is used to determine effective snow depth. For example, if the sinking-depth in a 50 cm snowpack is 10 cm then the effective snow depth is 40 cm, and if the sinking-depth is 32 cm (i.e., >25 cm) the effective snow depth is 25 cm.

B. Plant stature

Plant height was measured for each of the species encountered in the various plant communities. Height measurements of 15 to 70 plants comprised a sample for each species. Distribution of current annual growth over plant height was measured for shrubs using *Vaccinium ovalifolium* and *V. parvifolium* as typical examples. Thirty-five individual *Vaccinium* spp. shrubs were each divided into 6 equal sections by height. Current annual growth was clipped and weighed for each section, and a regression analysis was performed to portray the height distribution of current annual growth.

The compression of flexible shrubs by snowpack accumulation was measured for *Vaccinium ovalifolium* and *V. parvifolium*, *Oploparax horridus*, and *Alnus sinuata*. Randomly chosen branch tips, either protruding above the snow surface or found after excavation of snow, were tagged and their respective heights above ground were measured. Snow was then removed from around the tagged plants so they regained their snow-free height. Each tagged branch height was then remeasured, along with the total height of the shrub. Snow depth and density were measured at each site, and a relationship between snowpack water-equivalent and relative compression of the shrubs from their original height could then be derived. Snow depths ranged from 6 to 134 cm, snow densities from .113 to .389 g/cm^3 and water-equivalents from 2.9 to 38.3 cm for all the samples.

The measurements of potential forage biomass made prior to snowpack development provide a baseline upon which to relate changes in available forage biomass due to snowfall accumulation. With knowledge of plant heights, distribution of forage over plant height, interaction of plant height with snowpack accumulation, and snow depth, density and goat sinking-depth we can make predictions as to how much of the potential forage biomass will be available to a goat under a given set of snow conditions. The measurements of available forage biomass made with snowpacks present in late January and early March provide tests of the accuracy of these predictions, made using snow conditions present when the biomass measurements were taken.

Goat habitat utilization

A. Visual observations

Goats were easily visible in the various alpine and timberline habitats and relative goat use was measured in these areas using visual point-in-time observations (Altmann 1974). At 15 minute intervals data were recorded on activity and location within categories of plant community, slope, aspect, terrain type, elevation, distance from cliffs and estimated snow depth for each goat under observation. Temperature, wind speed, cloud conditions and precipitation type were recorded at the observer position, a permanent site at an elevation of 950 m. Observation distance was approximately 1 km and sightings were made with the aid of a 25 power spotting scope. The observations were conducted during two winters and include the dates 8-11 and 23-31 Jan., 12-14 Feb., 7-8 and 24-30 March in the winter of 1978-1979 and 2-6 Dec., 25 Jan.-9 Feb., 3-10 March in the winter of 1979-1980.

The visual observations were used for measuring relative goat feeding activity in various plant communities within a constant distance from cliffs (predation risk), providing data to test whether goat use was correlated with available forage biomass. They were used in measuring goat use relative to wind speed (using snow depth as a surrogate measure of relative wind speed for alpine habitats) and temperature (using elevation as a surrogate measure), providing data to compare actual goat habitat use with that expected if thermoregulation were determining habitat selection. Finally, the visual observations were also used in determining overall goat habitat use which was used in assessing relative importance of the various habitat attributes in the alpine study site.

B. Pellet-group counts and goat tracks in snow

In the forest zone, where consistent visual observation of goats was not possible, both fecal pellet-group counts and the presence of goat tracks in snow were used as measures of relative goat abundance in the various habitats. In both of these techniques the data were gathered using 1 X 10-m plots oriented consecutively to form belt transects (Wallmo and Schoen 1980) which were run parallel to the slope.

Pellet-group presence (frequency) was measured along 25 transects (33 to 142 plots per transect) each of which intersected steep and broken terrain. This allowed a measure of goat distribution in relation to distance from steep and broken terrain and within the confines of one plant community (_Tsuga_-_Picea_-_Vaccinium_ forest), thus enabling a test of correlation between goat use and predation risk. Sampling sites encompassed elevations from sea-level to 400 m and were located in _Tsuga_-_Picea_-_Vaccinium_ forest and the steep and broken terrain of *Tsuga*-*Picea*-*Vaccinium* forest outcrop plant communities. The transects were run in spring just after snow-melt (14 May - 1 June) and represent evidence of goat distribution over the entire winter of 1978-1979.

Transects to measure presence of goat tracks in snow were run on 16-18 Feb. 1979, 13-14 Feb. 1980, and 21-22 Dec. 1980. The transects were located in a portion of the area used for pellet-group sampling and in several other plant communities adjacent to steep and broken terrain. In each case there was complete snow cover in all plant communities sampled and no precipitation for a period of 3-4 days prior to sampling. Goat densities were estimated to be comparable during each of the sampling periods. Plot transects were set within the steep and broken terrain of the *Tsuga*-*Picea*-*Vaccinium* forest outcrop plant community and were oriented away from such terrain in adjacent stands of several other plant communities. This procedure allowed a measure of goat distribution in several plant communities within a constant distance from steep and broken terrain, and hence another test of correlation between goat use and available forage biomass.

C. Radio-tracking data

This portion was carried out on the Cleveland Peninsula study area, near Ketchikan. A 100 mile^2 (260 km^2) area on the lower Cleveland Peninsula was sectioned on a 1:31680 scale map into approximately 10,200 grid squares, each representing an area of 0.01 mile^2 . Since all maps were scaled in feet and miles these units are used in the present analysis. Each grid intersection (or point) identified the grid square of which it formed the southwest corner and was used as a sample point from which habitat data were taken from maps to represent that grid square. Elevation, slope, aspect and distance from cliffs were taken from USGS 1:63360 scale maps which had been blown up to a scale of 1:31680. Slope was measured by taking the shortest distance between the two 100 ft contour lines adjacent to the grid point in question. Distance from cliffs was obtained by identifying all areas with greater than than 50° slope as "cliff" area. From USFS 1:31680 scale timber-type maps timber volume was identified at each sample point.

Radio-tracking techniques for the study have been described by Smith (1982). One hundred and eight re-locations of 6 radioed goats were obtained between 1 November and 31 March during the winters of 1980-1981 (48 locations, 6 goats) and 1981-1982 (60 locations, 4 goats). Each data point represents the location of a goat within one of the 0.01 $mile^2$ grid squares. Frequency distribution of the goat locations using univariate habitat data were used to test for differences in habitat use between the light snowfall winter of 1980-1981 and the heavy snowfall winter of 1981-1982.

This radio-tracking data provides an independent, though slightly different type of test regarding our hypothesis of habitat selection due to food acquisition. A natural experiment presented itself in that the two years encompassing this portion of the study produced greatly different amounts of winter snowfall. The temperatures during these winters were moderate enough that thermoregulatory behavior can reasonably be disregarded as an important determinant of habitat selection. Nor is it likely that relative risk of predation is substantially influenced by differences in snowdepth. If no substantial differences in risk of predation or thermoregulation are apparent between the two winters, then food acquisition should drive any changes in habitat selection by goats between winters. Unfortunately, the accuracy of the radio-tracking technique did not permit identification of goat locations to plant community types, which would have allowed prediction of available forage biomass. However, since the habitat is predominantly forested and terrain characteristics will have similar effects on snow depth throughout the area, we mayy assume that the areas of lower elevation, steeper slope, more southerly aspect and greater timber volume (representing greater snow interception) will have relatively less snow accumulation, and hence, more forage available. If food acquisition is driving habitat selection in this situation, as is suggested, then during the winter with relatively heavy snowfall (1981-1982) goats on the lower Cleveland Peninsula should select areas of lower elevation, steeper slope, more southerly aspect and greater timber volume than they did in the winter with less snowfall (1980-1981).

RESULTS

Plant communities

Thirteen plant communities were recognized as forming significant components of vegetation in the Juneau study area. Brief floristic and habitat descriptions follow for these various communities. For each community an accompaning table provides a species list along with estimates of cover (%) for plant groups and constituent species. Percent cover for plant groups is rounded to the nearest 5%. Unmarked species had less than 5% cover while more abundant ones are so designated in the tables. Plant communities are named after the dominant species and plant growth forms.

a) Forb-*Cassiope*.

This is an alpine herb and subshrub community occurring from timberline to near the upper limits of vegetation. It is typical of steep well-drained rock outcrops and is occasionally found on stable scree or old moraines. Most sites are relatively wind exposed or steep so that snow does not accumulate. The forb-subshrub vegetation is characterized by *Cassiope mertensiana*, *C. stelleriana*, *Phyllodoce aleutica* and a mixture of numerous graminoids and forbs, including several spceies of *Saxifraga* (Table 3). Due to the presence of surface rock its plant cover is variable and relatively low, ranging from about 25 to 75% cover. This is a common alpine community type and covers

Table 3. Forb-*Cassiope* community. An alpine community characteristic of rock outcrops and with little snow accumulation in winter. Cover estimates assume a total plant cover of 50%.

Class and species

Subshrubs 15%

*Cassiope mertensiana**
Cassiope stelleriana
Luetkea pectinata
Phyllodoce aleutica
Salix arctica
Salix reticulata
Vaccinium uliginosum

Forbs 15%

Antennaria pallida
Arabis lyrata
Artemisia arctica
Campanula rotundifolia
Cerastium fontana
Epilobium Hornemannii
Epilobium latifolia
Erigeron humilis
Gentiana glauca
Hedysarum alpinum
Hieracium triste
Lycopodium alpinum
Oxyria digyna
Parnassia palustrius
Pedicularis oederi
Polygonum viviparum
Potentilla hyparctica
Primula cuenifolia
Ranunculus cooleyae
Ranunculus pacificus

Class and species

Forbs (continued)

Sagina intermedia
Saxifraga bronchialis
Saxifraga ferruginea
Saxifraga oppositifolia
Saxifraga punctata
Sedum rosea
Silene acaulis
Tofieldia coccinea
Veronica Wormskjoldii

Ferns < 5%

Cryptogramma crispa

Graminoids 10%

Carex circinnata
Carex macrochaeta
Juncus sp.
Hierochloe alpina
Luzula arcuata
Poa alpina
Trisetum spicatum

Lichens 5%

Bryophytes 15%

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* 5-10% cover

about 15% of goat winter range in the study area.

b) Empetrum subshrub.

This community is typical of relatively dry windswept and smooth alpine ridgetops and other fellfield conditions on well-drained rises in the alpine zone. The presence of surface rock keeps plant cover generally between 25 and 75% cover. Snow accumulation is very low, especially in the more wind-exposed sites. Characteristic species include Empetrum nigrum, Vaccinium uliginosum, Salix arctica and S. reticulata (Table 4). Loiseleuria procumbens is not abundant but appears to be restricted to this community. The community comprises about 5% of goat winter range.

c) Cassiope heath.

A subshrub community which occurs above and below timberline under moderately moist conditions, often in slight but well drained depressions and more commonly on northerly aspects. These are sites which develop substantial snow accumulation during winter. This community is characterized by dense mats of Cassiope mertensiana, C. stelleriana, Phyllodoce aleutica and Luetkea pectinata with minor components of forbs, graminoids and cryptograms (Table 5). It occupies about 5% of goat winter range.

d) Calamagrostis meadow.

A sedge-forb community occuring on well drained, moderately wind-exposed slopes near timberline. It is usually

Table 4. *Empetrum* subshrub. An alpine community characteristic of stony fellfield conditions on wind exposed and well-drained rises and ridgetops. Cover estimates below assume a total plant cover of 50%.

Class and species	Class and species
Subshrubs 30%	Graminoids 5%
Cassiope mertensiana	*Carex circinnata*
Cassiope stelleriana	*Hierochloe alpina*
*Empetrum nigrum***	*Luzula arcuata*
Loiseleuria procumbens	
Phyllodoce aleutica	Lichens 5%
*Salix arctica**	
Salix reticulata	
*Vaccinium uliginosum**	Bryophytes 10%
Forbs 10%	
Artemisia arctica	
Campanula lasiocarpa	
Geum calthifolium	
Lloydia serotina	
Polygonum viviparum	
Ranunculus cooleyae	
Tofieldia coccinea	
Trientalis europaea	

* 5-10% cover

** >10% cover

Table 5. _Cassiope_ heath. An alpine or subalpine community dominated by dense mats of ericaceous subshrubs and occurring commonly in wind-protected depressions.

Class and species
Subshrubs 100%
Cassiope mertensiana**
Cassiope stelleriana**
Empetrum nigrum
Luetkea pectinata**
_Phyllodoce aleutica_*
Vaccinium caespitosum
Vaccinium uliginosum
Forbs 5%
Hieracium triste
Lycopodium sp.
Polygonum viviparum
Trientalis europaea
Graminoids < 5%
Carex macrochaeta
Carex sp.
Luzula arcuata
Lichens 5%
Bryophytes < 5%

* 5-10% cover

** >10% cover

dominated by *Carex macrochaeta* but characterized by a substantial presence of *Calamagrostis canadensis*. Numerous forbs, most characteristic being *Anemone narcissiflora*, are also present along with a few ferns and substantial bryophyte ground cover (Table 6). Snow accumulation is generally light. This community occupies about 5% of the goat winter range.

e) *Veratrum* meadow.

A lush sedge-forb community occupying relatively well-drained but moist subalpine slopes, most commonly on southern aspects. Snow accumulation is relatively deep. This community is physically dominated by the large forbs *Veratrum viride* and *Heracleum lanatum* but is essentially a dense mixture of numerous forbs and the sedge, *Carex macrochaeta* (Table 7). These subalpine meadows are fairly common and occupy about 15% of the area within goat winter range.

f) *Fauria* meadow.

A sedge-forb community occurring typically below timberline in slight depressions under moist to wet conditions and more commonly on northerly aspects. It is commonly protected from strong wind by surrounding subalpine forest and develops deep snow accumulations. This community is dominated by *Fauria crista-galli*, with a lesser but substantial component of sedges (*Carex* spp.) along with

Table 6. *Calamagrostis* meadow. A sedge-forb community characteristic of moderately wind-exposed slopes near timberline.

Class and species
Subshrubs 5%
Luetkea pectinata
Phyllodoce aleutica
Vaccinium uliginosum
Forbs 50%
*Aconitum delphinifolium**
Achillea borealis
*Anemone narcissiflora**
*Arnica latifolia**
Castilleja parviflora
Erigeron humilis
*Erigeron peregrinus**
Fritillaria camchatcensis
Gentiana platypetala
*Geranium erianthum**
Geum calthifolium
Hieracium triste
*Lupinus nootkatensis**
Pedicularis verticillata
Rubus pedatus
*Sanguisorba stipulata**
Solidago lepida
Trientalis europaea
Ferns 5%
Cryptogramma crispa
Gymnocarpium dryopteris
Thelypteris phegopteris
Graminoids 50%
*Calamagrostis canadensis***
*Carex macrochaeta***
Elymus sp.
Juncus sp.
Luzula arcuata
Lichens 5%
Bryophytes 25%

* 5-10% cover
** >10% cover

Table 7. *Veratrum* meadow. A lush sedge-forb community of moist subalpine slopes.

Class and species	Class and species
Forbs 65%	Graminoids 40%
Achillea borealis	*Carex macrochaeta***
*Arnica amplexicaulis**	*Carex* sp.
Claytonia sibirica	*Elymus* sp.
Conioselinum chinense	*Juncus drummondii*
Epilobium Hornemannii	*Luzula* sp.
Equisetum sp.	
Gentiana platypetala	Lichens < 5%
*Heracleum lanatum***	
Hieracium triste	
Lupinus nootkatensis	Bryophytes 35%
Osmorhiza chilensis	
Ranunculus pacificus	
*Sanguisorba stipulata**	
*Saussurea americana**	
*Senecio triangularis**	
*Valeriana sitchensis**	
*Veratrum viride***	
Viola langsdorffii	
Ferns 5%	
Athyrium filix-femina	
Dryopteris dilatata	
Thelypteris limbosperma	
Thelypteris phegopteris	

* 5-10% cover

** >10% cover

several other mesophytic forb species such as *Caltha leptosepala* and *Petasites frigidus* (Table 8). It covers about 5% of goat winter range.

g) *Carex* muskeg.

A wet sedge meadow or peatland community occuring on poorly drained level or gently sloping sites below timberline. These sites are openings in the coniferous forest and accumulate relatively deep snowpack. This community is characterized by a dense cover of *Carex* spp., some ericaceous subshrubs such as *Andromeda polifolia* and *Vaccinium oxycoccus* and a high coverage of bryophytes (Table 9). This particular floristic assemblage is probably more typical of higher elevation muskeg vegetation, with greater species diversity at lower elevations. The community occupies only about 1% of the winter goat range.

h) *Tsuga*-*Picea* krummholz.

This community is the highest elevation representative of coniferous vegetation and is characterized by stunted and wind-flagged trees. It occurs in slightly protected and well drained sites along windswept ridges and slopes at the upper limits of treeline. Its overstory is dominated by *Tsuga mertensiana* and *Picea sitchensis* with an understory of *Vaccinium* spp. shrubs, *Cassiope* spp. subshrubs and various forbs typical of the transition zone between alpine and forest vegetation (Table 10). Relatively deep snow

Table 8. *Fauria* meadow. A sedge-forb community occurring in moist to wet lightly sloping concavities in the subalpine zone.

Class and species

Subshrubs 5%

Cassiope mertensiana
Cassiope stelleriana
Luetkea pectinata

Forbs 70%

Caltha leptosepala
Epilobium latifolia
*Fauria crista-galli***
Parnassia fimbriata
Petasites frigidus
Sanguisorba stipulata
Saxifraga ferruginea
Tiarella sp.
Veratrum viride

Class and species

Graminoids 30%

Carex macrochaeta
*Carex nigricans**
Carex spp.**
Elymus sp.
Juncus drummondii
Juncus sp.
Luzula sp.

Lichens <5%

Bryophytes 25%

* 5-10% cover

** >10% cover

Table 9. _Carex_ muskeg. A wet sedge meadow or peatland occurring on poorly drained gently sloping sites below timberline.

Class and species	Class and species
Subshrubs 25%	Graminoids 60%
_Andromeda polifolia_*	_Carex nigricans_**
_Empetrum nigrum_*	_Carex_ spp.**
Kalmia polifolia	_Eriophorum angustifolium_
Ledum groenlandicum	_Festuca_ sp.
Rubus chamaemorus	_Juncus drummondii_
Vaccinium caespitosum	_Juncus_ sp.
_Vaccinium oxycoccus_*	_Trichophorum caespitosum_*
Forbs 15%	Lichens <5%
Coptis trifolia	
Cornus suecica	Bryophytes 60%
Dodecatheon jeffreyii	
Drosera sp.	
Fauria crista-galli	
Lycopodium sp.	
Petasites frigidus	
Rubus pedatus	
Sanguisorba stipulata	
Tofieldia glutinosa	
Trientalis europaea	
Platanthera sp.	

* 5-10% cover

** >10% cover

Table 10. *Tsuga-Picea* krummholz. A community dominated by stunted conifers in slightly protected and well-drained slopes at the upper limits of tree-growth.

Class and species

Trees 70%

*Picea sitchensis***
*Tsuga mertensiana***

Shrubs 20%

Cladothamnus pyrolaeflorus
Menziesia ferruginea
Rubus spectabilis
*Vaccinium caespitosum**
*Vaccinium ovalifolium**
Vaccinium parvifolium

Subshrubs 15%

*Cassiope mertensiana**
Cassiope stelleriana
Phyllodoce aleutica

Forbs 15%

Achillea borealis
Claytonia sibirica
Cornus canadensis
Epilobium sp.
Fauria crista-galli
*Rubus pedatus**
Trientalis europaea
Viola langsdorfii

Class and species

Ferns < 5%

Gymnocarpium dryopteris
Thelypteris phegopteris

Graminoids < 5%

Carex macrochaeta
Luzula arcuata
Poa alpina

Lichens 5%

Bryophytes 15%

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* 5-10% cover

** >10% cover

accumulats in the wind-protected understory. This community occupies about 2% of winter goat range.

i) *Alnus* shrubland.

A tall shrub community commonly occurinng in sites of recent land slippage, recently glaciated terrain and in avalanche tracks at or below timberline. These sites are moist to wet, usually relatively steep and generally accumulate deep snow. The community is dominated by an overstory of *Alnus sinuata* with a predominantly herbaceous understory typically including a substantial component of the fern, *Athyrium filix-femina* (Table 11). It covers about 5% of goat winter range.

j) *Tsuga*-*Vaccinium* subalpine forest.

This is an open canopy coniferous forest community, typical of the higher forested elevations and occurs on relatively well drained slopes. The overstory is predominantly *Tsuga mertensiana* and the understory is characterized by a dense shrub layer dominated usually by *Vaccinium ovalifolium* and *V. parvifolium* and occasionally by *Cladothamnus pyrolaeflorus*. A relatively dense herb layer also occurs, comprised predominantly of *Rubus pedatus*, *Cornus canadensis* and *Coptis asplenifolia* (Table 12). The open overstory canopy results in relatively deep snow accumulation for forest vegetation in the area. This community occupies about 10% of goat winter range.

Table 11. *Alnus* shrubland. A tall shrub community occurring on relatively steep moist to wet sites from timberline to low elevations.

Class and species

Shrubs 85%

*Alnus sinuata***
Oplopanax horridus
Salix sp.
Sambucus racemosa
Spiraea Beauverdiana
Ribes bracteosum
Rubus spectabilis
Viburnum edule

Forbs 45%

*Achillea borealis**
Actaea rubra
Epilobium sp.
*Geum macrophyllum**
*Heuchera glabra**
*Tiarella trifoliata**
Tiarella unifoliata
Viola langsdorfii

Class and species

Ferns 20%

*Athyrium filix-femina***
*Dryopteris dilatata**

Graminoids 5%

Bromus sitchensis
Calamagrostis canadensis
Carex sp.
Elymus hirsutus
Juncus sp.

Lichens < 5%

Bryophytes 15%

* 5-10% cover

** >10% cover

Table 12. *Tsuga*-*Vaccinium* subalpine forest. An open canopy coniferous forest occurring on well-drained slopes at the higher elevations of forest vegetation.

Class and species

Trees 45%

*Tsuga mertensiana***
Picea sitchensis

Shrubs 80%

Cladothamnus pyrolaeflorus
Menziesia ferruginea
Vaccinium alaskensis
*Vaccinium ovalifolium***
*Vaccinium parvifolium**

Forbs 60%

Claytonia sibirica
*Coptis asplenifolia***
*Cornus canadensis***
Lycopodium sp.
Pyrola asarifolia
Pyrola secunda
*Rubus pedatus***
Streptopus sp.*
Tiarella trifoliata
Trientalis europaea
Viola glabella

Class and species

Ferns < 5%

Dryopteris dilatata
Gymnocarpium dryopteris

Graminoids < 5%

Carex sp.

Lichens < 5%

Bryophytes 30%

* 5-10% cover

** >10% cover

k) *Tsuga*-*Picea*-*Oplopanax* forest.

A moderately open canopy coniferous forest community occuring on moist, moderately drained and relatively gently sloping terrain. The overstory is characterized by *Tsuga heterophylla* (*T. mertensiana* at higher elevations) and *Picea sitchensis* with a shrub understory dominated by *Oplopanax horridus*. An open herbaceous layer below the *Oplopanax* commonly includes *Tiarella* spp., *Coptis asplenifolia* and *Athyrium filix-femina* (Table 13). Snow accumulation is moderately deep, reflecting the moderately open overstory canopy cover. This community covers about 2% of the goat winter range.

l) *Tsuga*-*Picea*-*Vaccinium* forest.

A closed canopy coniferous forest community occuring on relatively well-drained sites. The overstory is dominated by *Tsuga heterophylla* with a lesser but substantial component of *Picea sitchensis*. The understory is composed of a well-developed shrub layer of *Vaccinium ovalifolium*, *V. parvifolium*, *Menziesia ferruginea*, and herbaceous cover dominated by *Cornus canadensis* and *Rubus pedatus* (Table 14). Snow accumulation is relatively low due to the snow interception by the relatively closed coniferous canopy. This is the most common forest community and occupies about 15% of goat winter range.

Table 13. Tsuga-Picea-Oplopanax forest. A moderately open canopy coniferous forest community characteristic of moist, moderately drained slopes.

Class and species	Class and species
Trees 60%	Ferns 10%
Picea sitchensis**	Athyrium filix-femina*
Tsuga heterophylla**	Blechnum spicant
Tsuga mertensiana	Polypodium vulgare
	Polystichum Braunii
Shrubs 60%	Graminoids 5%
Aruncus sylvester	Luzula parviflora
Menziesia ferruginea	Elymus sp.
Oplopanax horridus**	
Sambucus racemosa	
Ribes bracteosum	Lichens < 5%
Vaccinium ovalifolium	
Vaccinium parvifolium	Bryophytes 25%
Forbs 40%	
Coptis asplenifolia*	
Corallorhiza sp.	
Lysichiton americanum	
Moneses uniflora	
Pyrola secunda	
Rubus pedatus	
Streptopus sp.	
Tiarella trifoliata**	
Tiarella unifoliata*	

* 5-10% cover

** >10% cover

Table 14. *Tsuga*-*Picea*-*Vaccinium* forest. A closed canopy coniferous forest community characteristic of well-drained sites and the most common forest type.

Class and species
Trees 85%
*Picea sitchensis***
*Tsuga heterophylla***
Shrubs 60%
*Menziesia ferruginea***
Rubus spectabilis
Vaccinium alaskensis
*Vaccinium ovalifolium***
*Vaccinium parvifolium***
Forbs 70%
Clintonia uniflora
*Coptis asplenifolia**
*Cornus canadensis***
Goodyera oblongifolia
Linnaea borealis
Listeria sp.
Lycopodium sp.
Maianthemum dilatatum
Moneses uniflora
Osmorhiza chilensis
Pyrola asarifolia
*Pyrola secunda**
*Rubus pedatus***
Streptopus spp.*
Tiarella trifoliata
Viola glabella

Class and species
Ferns 10%
Blechnum spicant
Dryopteris dilatata
Gymnocarpium dryopteris
Polypodium vulgare
Polystichum Braunii
Thelypteris phaegopteris
Lichens < 5%
Bryophytes 35%

* 5-10% cover

** >10% cover

m) Tsuga-Picea-Vaccinium forest outcrop. This is a special case of the previous forest community and is characterized by a relatively sparse understory of vascular plants. It is characteristic of steep and broken, but fully forested, terrain (rock outcrops) which are often extensively used by mountain goats. The overstory, as in the similar Tsuga-Picea-Vaccinium forest community outside of rock outcrops, is a closed canopy of primarily Tsuga heterophylla with some Picea sitchensis. The understory is similarily composed of Vaccinium spp. and Menziesia ferruginea shrubs and an herbaceous layer, but in much less abundance. However, bryophytes are relatively abundant as a ground cover in this community (Table 15). Snow accumulation is the least for forest communities due to the high overstory canopy cover and the steep slopes. This community type ocurs on about 5% of the goat winter range.

Suggested placement of these plant communities within Viereck and Dyrness' (1980) classification of Alaska vegetation is shown in Appendix I. Reconnaissance of plant communities in the Ketchikan study area indicated that comparable plant communities are present in both study areas, although in different relative abundances. Alpine communities are essentially non-existent in the Ketchikan study area.

Table 15. *Tsuga-Picea-Vaccinium* forest outcrop. A special case of the previous community (Table 14) which occurs on steep and broken terrain and which is characterised by a sparse understory of vascular plants.

Class and species	Class and species
Trees 75%	Ferns 5%
*Picea sitchensis*** *Tsuga heterophylla***	*Dryopteris dilatata* *Polypodium vulgare* *Thelypteris phaegopteris*
Shrubs 15%	Lichens < 5%
Alnus sinuata *Menziesia ferruginea* *Rubus spectabilis* *Vaccinium alaskensis* *Vaccinium ovalifolium** *Vaccinium parvifolium*	Bryophytes 45%
Forbs 20%	
Coptis asplenifolia *Cornus canadensis** *Heuchera glabra* *Lycopodium* sp. *Pyrola secunda* *Rubus pedatus** *Streptopus* sp. *Tiarella trifoliata**	

* 5-10% cover

** >10% cover

Forage biomass determinations

A. Ground-rooted forage

Ground-rooted forage biomass, measured in November just prior to the onset of winter snow accumulation, ranged from 25 kg/ha in the *Tsuga-Picea-Vaccinium* forest outcrop community to 389 kg/ha in the *Alnus* shrubland community (Table 16, Figure 2, see Appendix II for a breakdown of biomass by plant species). The subalpine communities of *Calamagrostis* meadow and *Veratrum* meadow were comparable in forage biomass to the *Alnus* shrubland community, while other meadow and muskeg communities had less, though still substantial amounts of forage. While the alpine and subalpine *Cassiope* heath community had a relatively large amount of available forage at the onset of winter, the other alpine communities (Forb-*Cassiope* and *Empetrum* subshrub) had some of the smallest amounts of forage. *Tsuga-Picea* krummholz had substantial available forage, largely in the form of conifer branch tips. The forest communities had moderate amounts of available forage with the exception of the small amount in the *Tsuga-Picea-Vaccinium* forest outcrop community.

Table 16. Ground-rooted forage biomass (kg/ha) available in November, immediately prior to the onset of winter snow accumulation.

Plant community	Forage class biomass Graminoids	Forbs	Shrubs	Conifers	Lichens	Total
Forb-Cassiope	40	1	12	-	3	57
Empetrum subshrub	7	-	21	-	3	31
Cassiope heath	2	-	310	-	9	321
Calamagrostis meadow	313	40	5	-	7	366
Veratrum meadow	164	163	-	-	-	327
Fauria meadow	78	74	2	-	-	154
Carex muskeg	232	1	18	-	-	250
Tsuga-Picea krummholz	15	17	16	188	-	236
Alnus shrubland	t*	294	95	-	1	389
Tsuga-Vaccinium subalpine forest	-	28	167	29	t	224
Tsuga-Picea-Oplopanax forest	-	85	60	12	1	158
Tsuga-Picea-Vaccinium forest	-	42	60	22	t	124
Tsuga-Picea-Vaccinium forest outcrop	-	14	5	5	t	25

* t = trace = less than 0.5 kg/ha

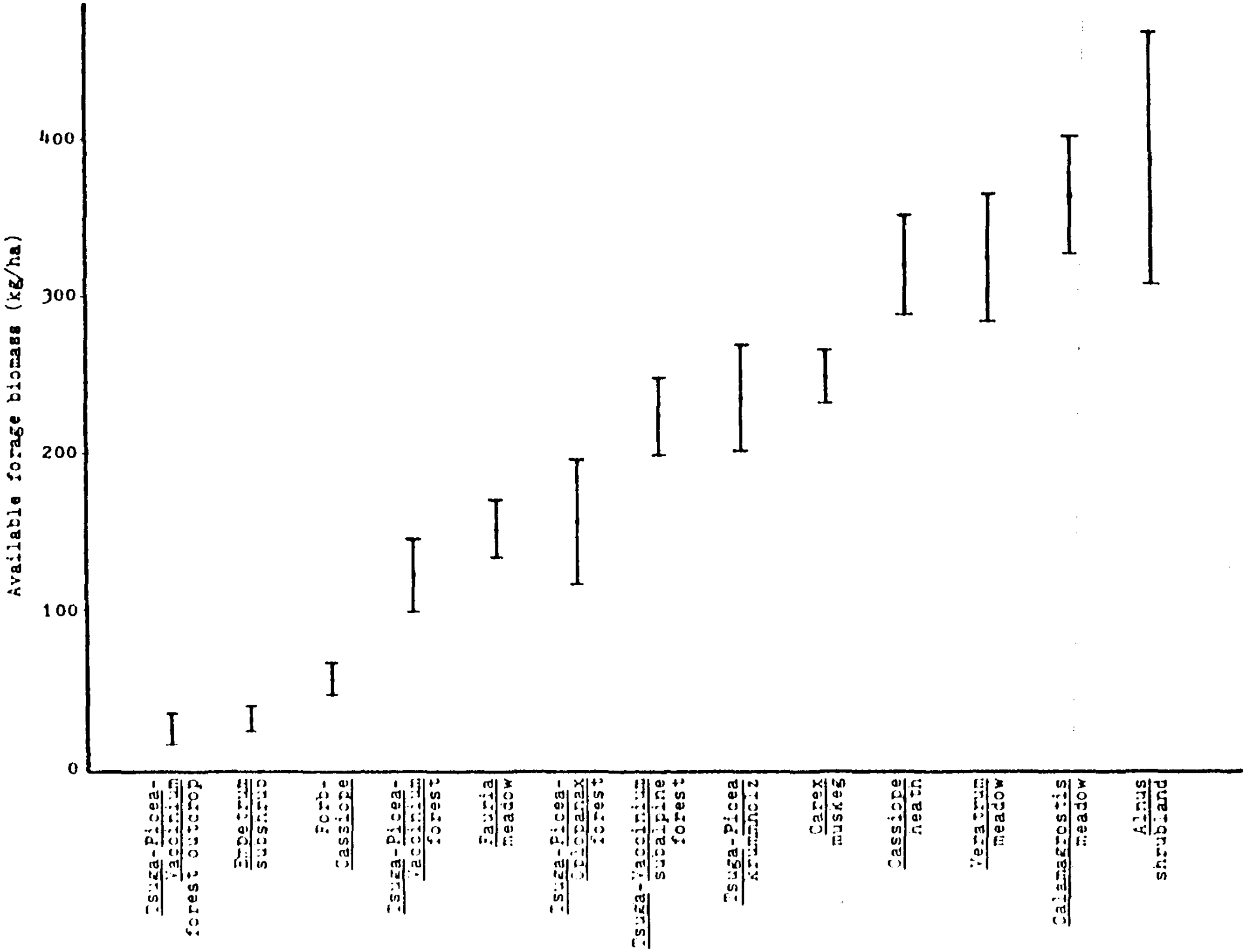

Figure 2. Ground-rooted forage biomass prior to winter snow accumulation. Bars represent 95% confidence limits.

B. Lichen on tree trunks

For all types of lichen found on tree trunks the mean biomass of potential lichen forage was 0.14 kg/m^2 (SD=0.03, n=32) measured on tree surfaces with 100% lichen cover. The mean percentage cover of lichen on tree trunks was 11.6% (SD=5.3, n=640). Using the timber statistics of average DBH and number of trees per unit area (Table 17) for each forest community, we can estimate the contribution of lichen to total forage biomass per unit ground area in each case. Biomass from lichen on tree trunks varied from 5.8 kg per hectare of ground surface in *Tsuga-Picea-Vaccinium* forest to 1.2 kg per hectare of ground surface in *Tsuga-Vaccinium* subalpine forest (Table 18).

C. Forest litterfall

The forage component of forest litterfall was not different in the fenced and unfenced plots (paired t-test, $p>.05$) in either the supposed goat-present or goat-free sites. This is reasonable since very little evidence of goat activity was noted in the vicinity of the traps during the winter of litter collection 1979-1980. There were some differences in litter composition between the goat-present and goat-free sites, due primarily to differences in local forest overstory (Table 19). However, on the basis of forage litterfall per day during winter there was no difference between the two sites ($p>.10$), thus giving

Table 17. Timber measurements for the forest communities.

Forest community	Timber* volume	Trees per acre	Average** DBH	Canopy*** coverage
Tsuga-*Vaccinium* subalpine forest	7,800	83	17	37
Tsuga-*Picea*-*Oplopanax* forest	27,500	97	20	60
Tsuga-*Picea*-*Vaccinium* forest	39,400	123	21	79
Tsuga-*Picea*-*Vaccinium* forest outcrop	36,700	107	22	77

* board feet per acre

** diameter at breast height (inches)

*** percent

Table 19. Litterfall biomass (kg/ha) accumulated during winter in two sites within *Tsuga-Picea-Vaccinium* forest.

Collection site and period	Non-forage debris	Forage litterfall				Total forage	Forage litterfall per day
		Usnea	Foliose lichen	*Tsuga*	*Picea*		
Tsuga dominated site (1 Dec.-3 April)	812	10	7	135	15	167	1.36
Picea dominated site (1 Dec.-20 May)	1851	-	21	6	242	269	1.58

1.4 kg/ha/day as the average litterfall rate. For purposes of determining available forage, with consideration that litterfall is periodically buried by snowfall, available litterfall forage was estimated by taking one week's accumulation (10.10 kg/ha/week) as typical of that available at any given time. Estimates of litterfall available in other forest communities are calculated from proportions of canopy coverage relative to that present in the *Tsuga*-*Picea*-*Vaccinium* forest sites where litterfall was measured (Table 20).

D. Total forage

Total forage, including ground rooted forage, lichen on tree trunks and litterfall ranged from 31 kg/ha in the *Empetrum* subshrub community to 389 kg/ha in *Alnus* shrubland. Potential forage in the forest communities was increased from between 7 and 15 kg/ha by the contributions of tree-trunk lichen and litterfall (Table 21). These biomass totals, with the constituent species breakdown for ground-rooted forage (Appendix II), form the baseline from which predictive estimates of available forage biomass under different snow conditions during winter are made.

Table 20. Weekly litterfall forage accumulation in the forest communities. Litterfall was measured in the *Tsuga*-*Picea*-*Vaccinium* forest community, while that for the other communities is estimated on the basis of relative canopy coverage.

Forest community	Percent canopy coverage	Litterfall kg/ha/week
Tsuga-*Vaccinium* subalpine forest	37	4.7
Tsuga-*Picea*-*Oplopanax* forest	60	7.7
Tsuga-*Picea*-*Vaccinium* forest	79	10.1
Tsuga-*Picea*-*Vaccinium* forest outcrop	77	9.8

Table 21. Total potential forage biomass (kg/ha).

Plant community	Ground-rooted forage	Lichen on tree trunks	Forage litterfall	Total
Forb-*Cassiope*	57	-	-	57
Empetrum subshrub	31	-	-	31
Cassiope heath	321	-	-	321
Calamagrostis meadow	366	-	-	366
Veratrum meadow	327	-	-	327
Fauria meadow	154	-	-	154
Carex muskeg	250	-	-	250
Tsuga-*Picea* krummholz	236	t*	-	236
Alnus shrubland	389	t	-	389
Tsuga-*Vaccinium* subalpine forest	224	2	5	231
Tsuga-*Picea*-*Oplopanax* forest	158	4	8	169
Tsuga-*Picea*-*Vaccinium* forest	124	5	10	139
Tsuga-*Picea*-*Vaccinium* forest outcrop	25	5	10	40

* t = trace = less than 0.5 kg/ha

Factors affecting forage availability

A. Snow conditions

Winter snow accumulation in the various plant communities sampled demonstrated a wide variety of patterns in both the alpine and the lower elevation forested sites (Figure 3). The samples are somewhat site restrictive and some variation in snow accumulation should be expected within plant communities due, for example, to elevation, slope, aspect and forest canopy cover. However, the patterns do show strong relationships between plant community and winter snowpack.

The winter of 1979-1980 was somewhat below average in terms of precipitation and snowpack in the Juneau area (Nat. Weather Serv. 1980, Soil Cons. Serv., unpub. data). Snowpack densities varied from .113 to .387 g/cm^3 and generally increased as winter progressed. During the periods when measurements were taken, the depth to which goats would sink in snow ranged from 1 cm on dense crusted snow in the *Empetrum* subshrub community to 44 cm in *Carex* muskeg after a fresh snowfall.

B. Plant stature and snowpack

Plant height means for shrubs and smaller plant species encountered in the study plots are outlined in Table 22. The distribution of current annual growth over the height of

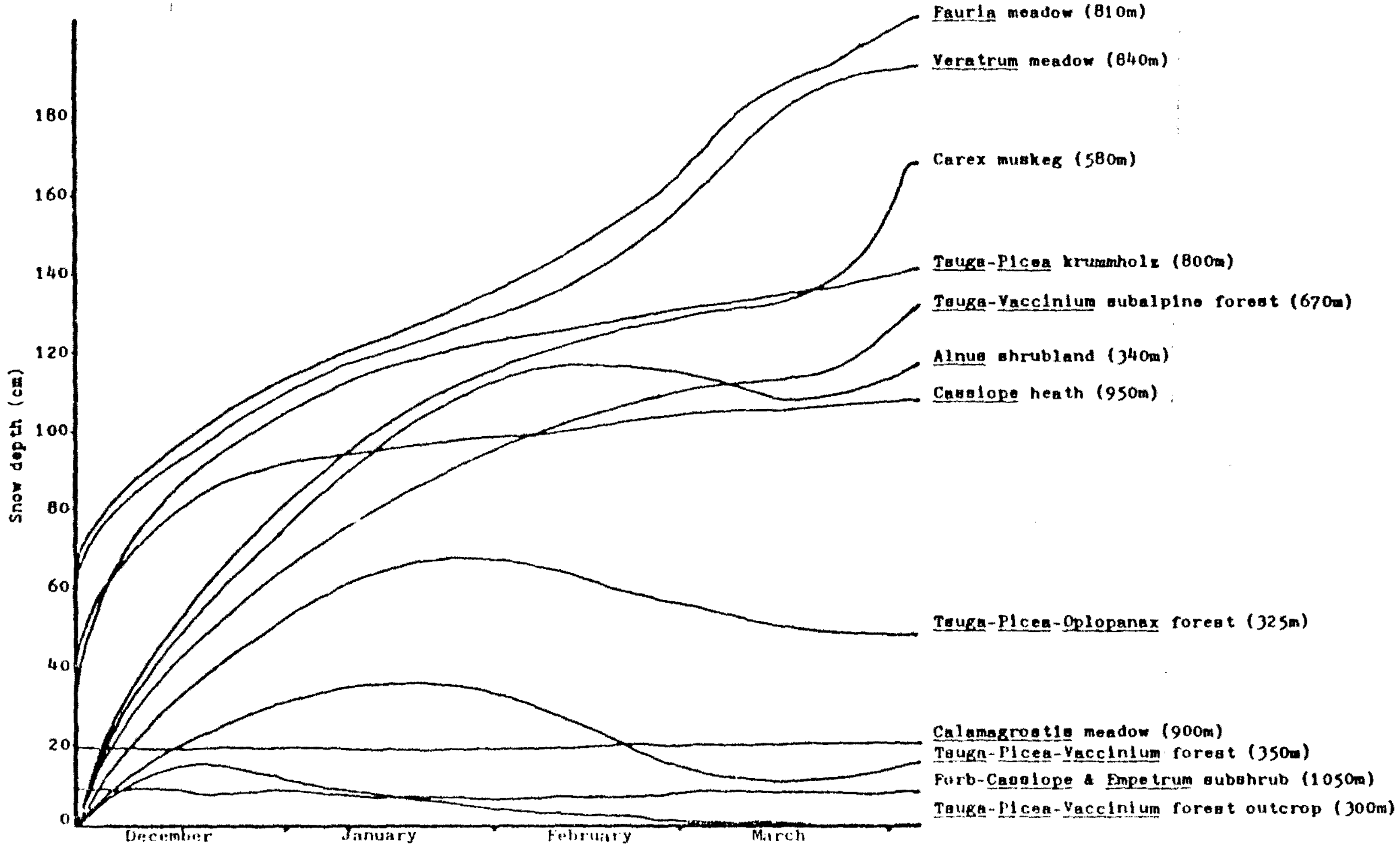

Figure 3. Snow accumulation in the plant communities during the winter of 1979-1980. Elevation of the sampled stand is given in parenthesis.

Table 22. Plant heights prior to snow accumulation.

Class and species	Mean height (cm)	SD	n
Graminoids			
Calamagrostis canadensis	12.5	7.5	41
Carex circinnata	7.7	2.3	20
Carex macrochaeta	9.2	3.8	30
Carex nigricans	7.6	1.8	20
Elymus sp.	11.8	6.2	20
Hierochloe alpina	6.3	1.8	20
Juncus sp.	9.3	4.3	20
Luzula arcuata	9.8	3.6	30
Poa alpina	6.3	1.9	20
Forbs			
Claytonia sibirica	4.2	0.8	15
Coptis asplenifolia	6.2	2.0	30
Cornus canadensis	8.5	1.4	30
Fauria crista-galli	7.9	2.2	30
Heracleum lanatum	23.4	11.8	20
Lupinus nootkatensis	17.2	9.8	20
Lycopodium sp.	8.0	3.2	15
Petasites frigidus	8.4	4.0	15
Pyrola secunda	7.3	2.5	30
Rubus pedatus	5.3	1.5	30
Sanguisorba stipulata	8.4	4.1	15
Saxifraga oppositifolia	forms ground surface		
Silene acaulis	forms ground surface		
Tiarella spp.	6.0	2.1	30
Veratrum viride	18.3	6.3	20

Table 22. (continued)

Class and species	Mean height (cm)	SD	n
Subshrubs			
Andromeda polifolia	13.4	2.4	30
Cassiope mertensiana	7.8	2.5	20
Cassiope stelleriana	7.8	2.4	20
Empetrum nigrum	7.7	2.7	30
Loiseleuria procumbens	4.3	1.0	20
Luetkea pectinata	12.5	3.2	25
Phyllodoce aleutica	7.3	2.0	20
Salix spp.**	4.8	1.3	20
Vaccinium spp.***	4.9	1.4	20
Shrubs			
Alnus sinuata	266.2	93.4	31
Menziesia ferruginea	126.9	45.6	46
Oplopanax horridus	83.3	34.6	54
Vaccinium spp.****	51.7	22.7	70
Ferns			
Athyrium filix-femina			
(old fronds)	19.2	9.6	25
(rhizomes-new shoots)	4.7	1.6	20
Dryopteris dilatata	8.7	3.7	20
Lichens			
ground lichens (alpine)	2.1	0.9	25

* *T. trifoliata* and *T. unifoliata*

** *S. arctica* and *S. reticulata*

*** *V. uliginosum* and *V. caespitosum*

**** *V. ovalifolium* and *V. parvifolium* a shrub, using Vaccinium ovalifolium and V. parvifolium as data sources, can be approximated by the cubic relationship $Y = 0.03 + 1.00X^3$ (Y=cummulative percent of current annual growth, X=fraction of shrub height, $r^2 = .82$, $n=35$, $p<.001$).

In the case of shrubs, the crushing effects of snow can be a significant determinant of forage availability within the range of winter snow conditions present in some of the plant communities. The compression of flexible shrubs by snowpack appears to be an approximately linear relationship with snowpack water-equivalent. Multiple regression analysis using the Vaccinium ovalifolium and V. parvifolium data showed that, within the range of plant heights present in the study plots, neither branch height relative to total plant height nor total plant height were important in explaining the degree to which the branch was crushed by snowpack. The linear regression equations for Vaccinium ovalifolium and V. parvifolium, Oplopanax horridus and Alnus sinuata (Table 23) show significant relationships in all cases, though they do include a good deal of variation, as indicated by the r^2 values. It is likely that natural variation in the sequence of precipitation events which form the snowpack causes substantial variance in the degree of plant compression relative to snowpack water-equivalent.

Table 23. Compression of shrubs as a function of snowpack water-equivalent. Least squares estimates were used to calculate regression parameters to predict percent compression from water-equivalent (cm).

Species	B_0	B_1	r^2	S^2Y/X	n	Range X_i
Vaccinium spp.*	1.04	.061	.56	295.1	370	3-16
Oplopanax horridus	1.08	.044	.63	225.4	40	5-17
Alnus sinuata	1.13	.042	.61	317.4	40	6-21

* *V. ovalifolium* and *V. parvifolium*

A small sample for *Menziesia ferruginea* (n=20) showed no significant difference from the regression for the *Vaccinium* spp. (p>.10), so the *Vaccinium* spp. relationship is used for both genera. Other shrubs rarely encountered in the study plots (e.g., *Salix* spp., *Ribes bracteosum*, *Sambucus racemosa*, *Rubus spectabilis*) were similar in form to the *Menziesia* and *Vaccinium* spp. shrubs and are also represented with the *Vaccinium* spp. compression relationship. The distribution of forage biomass over the height of the plant as determined for the *Vaccinium* spp. was used for all shrubs.

There are undoubtedly interactions between snowpack and the height of low-growing subshrubs and forbs. However, due to the small absolute shift in their heights relative to goat foraging height, the effect is small and is ignored in calculating available forage for subshrubs, forbs, graminoids and ferns. In addition, the simplifying assumption that forage is distributed evenly over the height of the plant is used in calculating available forage for these small plants. Thus, we would predict that a forb of 7 cm average height would have 3/7 of its forage available to goats if the effective snow depth was 4 cm.

C. Prediction of forage biomass

With data on potential forage, its distribution over plants, height of species and compressability by snowpack (derived or assumed as outlined above) we can make predictions of available forage under different snow conditions. The changes in availlable forage with varying snow conditions for each plant community can be illustrated by graphing the relationship under a given set of snow conditions (Figure 4). In these illustrations a constant snow density (.250 g/cm^3) is used, and available forage includes that 125 cm above and 25 cm below the snowpack surface. While the only snow condition variable considered here is effective snow depth, clear differences in the disappearance of available forage biomass among the various plant communities are apparent, reflecting differences in plant physiognomy in the various communities. For example, with the low stature plants in alpine communities, available forage quickly disappears with a relatively small snow accumulation while, even with large snow accumulation in the forest communities significant forage remaines available in the form of conifers, lichen on tree trunks and litterfall.

Actual snow conditions were quite variable among the various plant communities (Figure 3) and effected important differences in forage availability among the plant communities. As an illustration, the relationship of snow

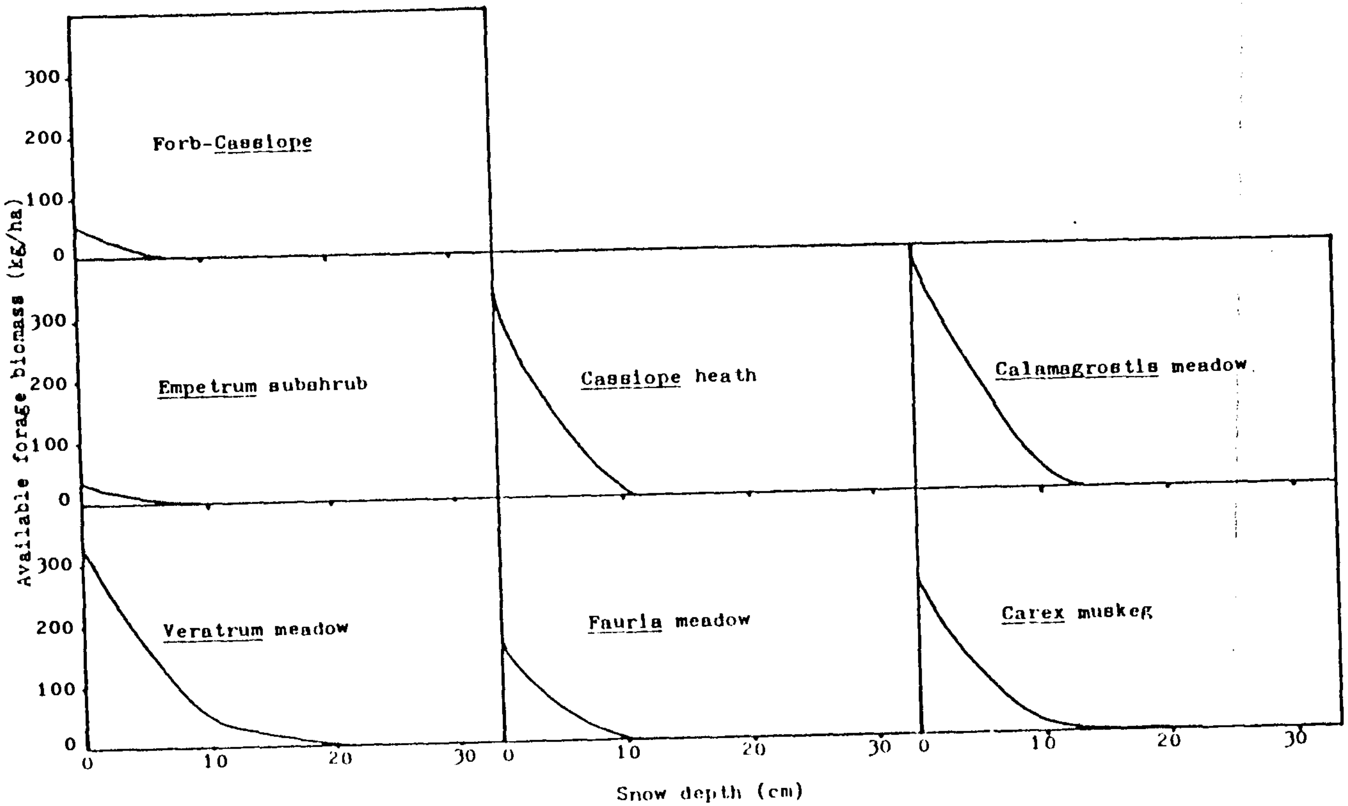

Figure 4. Available forage as related to snow depth in the various plant communities.

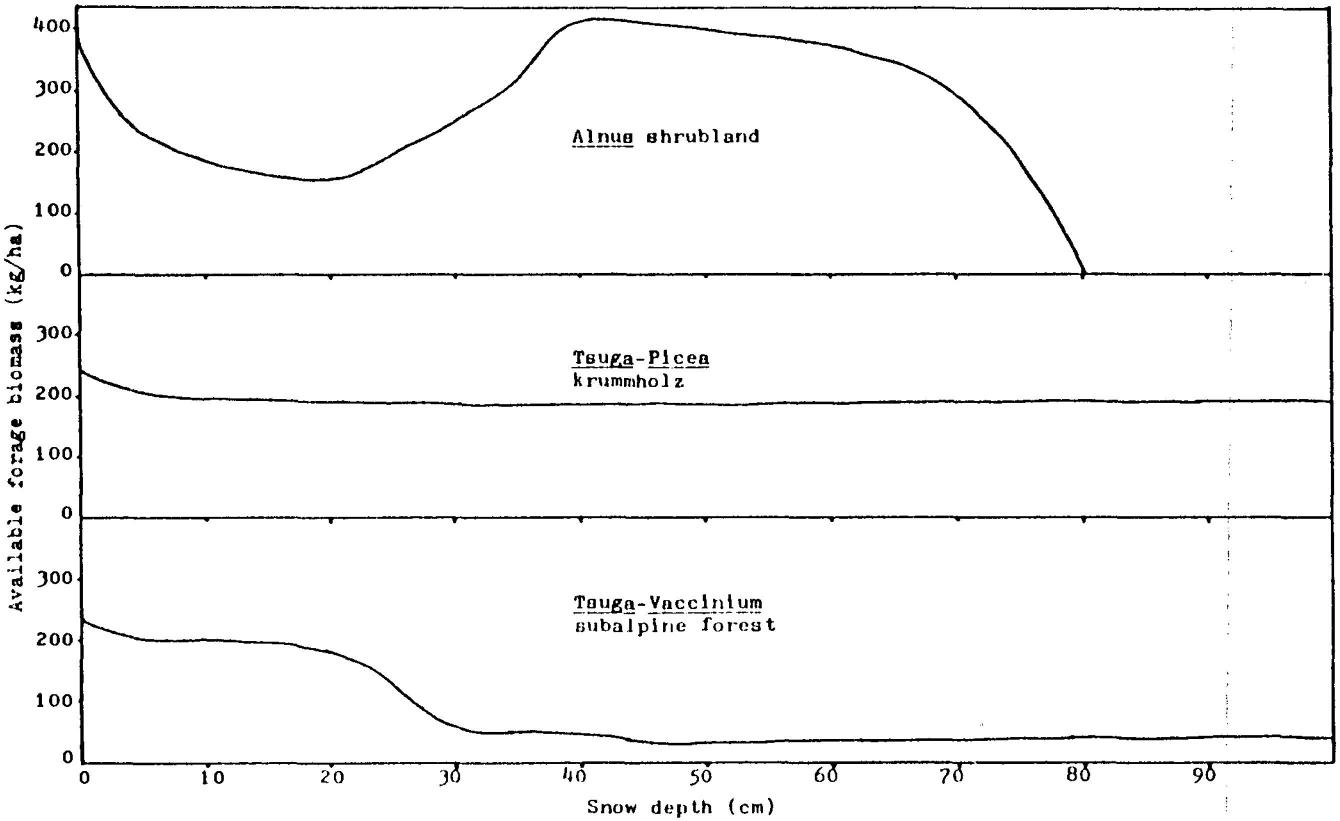

Figure 4. (continued)

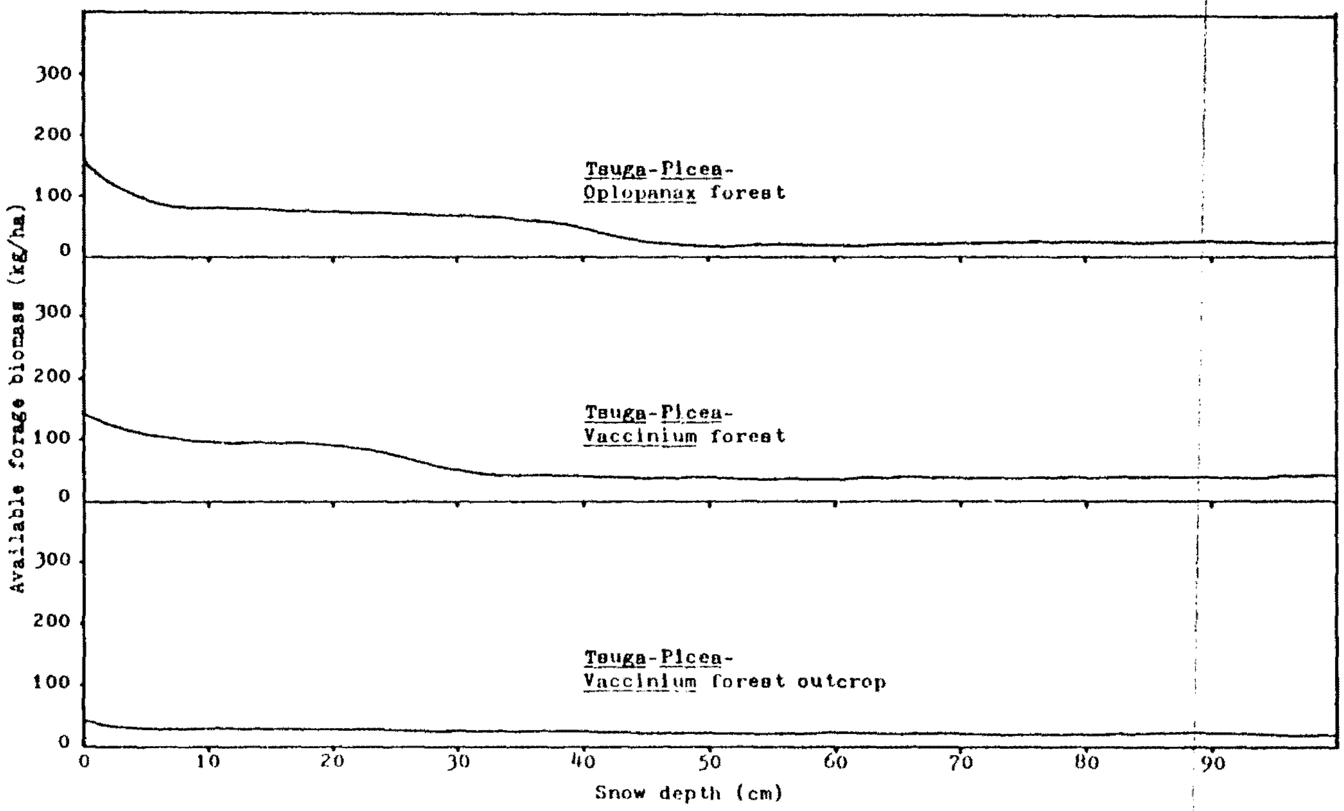

Figure 4. (continued)

depth effect on forage availability, actual winter snow depths, and the consequent amount of available forage biomass is shown for two plant communities, *Calamagrostis* meadow and *Tsuga*-*Picea*-*Vaccinium* forest, over the winter of 1979-1980 (Figure 5). *Calamagrostis* meadow, with a large amount of low-growing forage and a realtively constant but small snow accumulation, provided a large amount of available forage over the winter. The *Tsuga*-*Picea*-*Vaccinium* forest, with a moderate amount of forage from plants of a variety of sizes and variable but moderate snow accumulation, provided a moderate amount of forage over the same winter.

Relatively windswept alpine plant communities (i.e., Forb-*Cassiope*, *Empetrum* subshrub, *Calamagrostis* meadow) did
not accumulate deep snow and their forage remained at lea
partially available through much of the winter. Alpine
subalpine communities which experienced less wind (i.e
Cassiope heath, *Veratrum* meadow, *Fauria* meadow, *Care*
muskeg) tended to accumulate deep snow and forage w
unavailable through the entire winter. *Alnus* shr
accumulated deep snow and although forage became
by mid-winter, there was a period in early win
forage (upper branches of the alder shrubs) a
remained high. *Tsuga*-*Picea* krummholz conti
substantial forage in the form of conifer

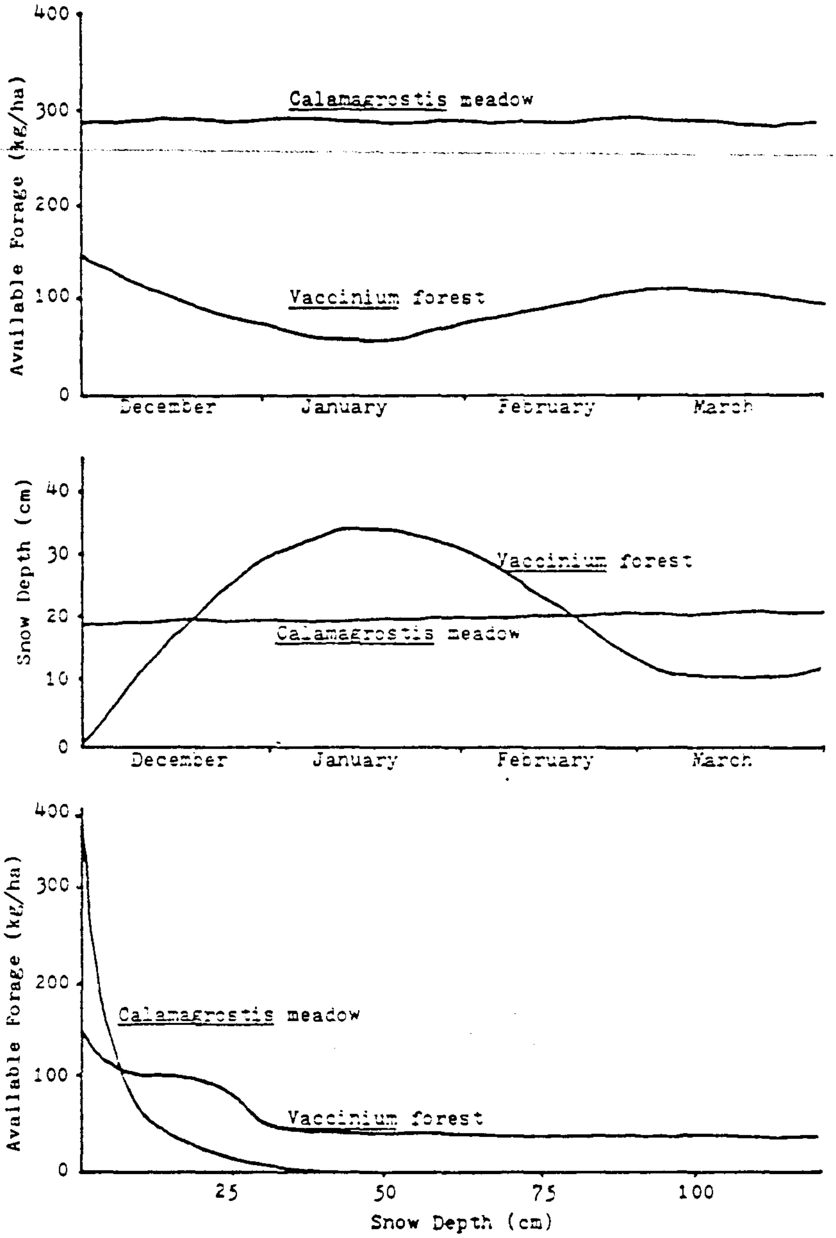

Figure 5. Snow depth - available forage relationships for two plant communities during the winter of 1979-1980.

throughout the winter. The forest communities were different in snow accumulation, due primarily to slope angle and snow interception by the forest canopy, effecting differences in the proportion of understory forage available. However, conifer forage, lichen on tree trunks and litterfall were available in the forest communities even under the deepest snow conditions.

D. Test of biomass predictions

In order to test the accuracy of the biomass predictions, measurements of available forage were made during two periods, late January and early March, in each of the plant communities. Comparisons were made between the measurements and the predictions which were based on snow conditions present at the time of measurement (Table 24). In seven cases (* in Table 24) the additional samples were, in effect, remeasurements of potential forage since the effective snow depths were zero. In all of these cases potential biomass measurements were not significantly different ($p>.05$), demonstrating the reproducibility of the potential biomass measures. In all the other cases, with variance assumed to be proportional to the available forage for the prediction figures, there were no significant differences ($p>.05$) between predicted and measured forage biomass in the plant communities under various snow conditions. Though variances are substantial in most cases,

Table 24. Ground-rooted forage biomass: prediction versus measurement.

Plant community	Date	Snow** depth	Snow*** density	Forage biomass (kg/ha) Measurement	Forage biomass (kg/ha) Prediction
Forb-*Cassiope*	29-1-80*	4		45	57
	11-3-80*	10		53	57
Empetrum subshrub	31-1-80*	4		38	31
	13-3-80*	14		34	31
Cassiope heath	1-2-80	121		-	-
	5-3-80	109		-	-
Calamagrostis meadow	28-1-80*	24		381	366
	11-3-80	28		242	244
Veratrum meadow	1-2-80	128		-	-
	10-3-80	176		-	-
Fauria meadow	10-2-80	126		-	-
	14-3-80	189		-	-
Carex muskeg	23-1-80	108		-	-
	14-3-80	132		-	-
Tsuga-*Picea* krummholz	30-1-80	74		168	188
	13-3-80	105		145	186
Alnus shrubland	22-1-80	122	.188	5	-
	16-3-80	106	.247	-	-
Tsuga-*Vaccinium* subalpine forest	23-1-80	94	.155	18	29
	12-3-80	111	.276	37	29
Tsuga-*Picea*-*Oplopanax* forest	20-1-80	66	.185	38	18
	16-3-80	50	.287	32	22
Tsuga-*Picea*-*Vaccinium* forest	22-1-80	37	.230	53	79
	18-3-80*	13	.323	104	124
Tsuga-*Picea*-*Vaccinium* forest outcrop	22-1-80*	7	.230	22	25

* the effective snow depth was zero on these dates

** cm

*** g/cm^3

we appear to have a satisfactory procedure for estimating expected available forage biomass under different snow conditions. When compared with the potential forage available before winter snows, forage biomass measurements taken in late January demonstrate the profound effects of winter snow accumulation on available forage (Figure 6).

Goat habitat selection

A. Predator avoidance

From the analysis of the manner in which goats use steep and broken terrain to avoid predators, we have hypothesized a negative relationship between goat use of habitat and distance from steep and broken terrain. This was tested using frequency of pellet-group presence as a measure of goat use and restricting the sampling to one plant community (*Tsuga*-*Picea*-*Vaccinium* forest) in order to minimize the effects of differential forage abundance and thermoregulatory factors on goat distribution. The relationship demonstrated (Figure 7) is strongly negative ($p<.001$) and appears to be exponential in form. The negative relationship is as expected, showing diminished use by goats of areas farther from escape terrain.

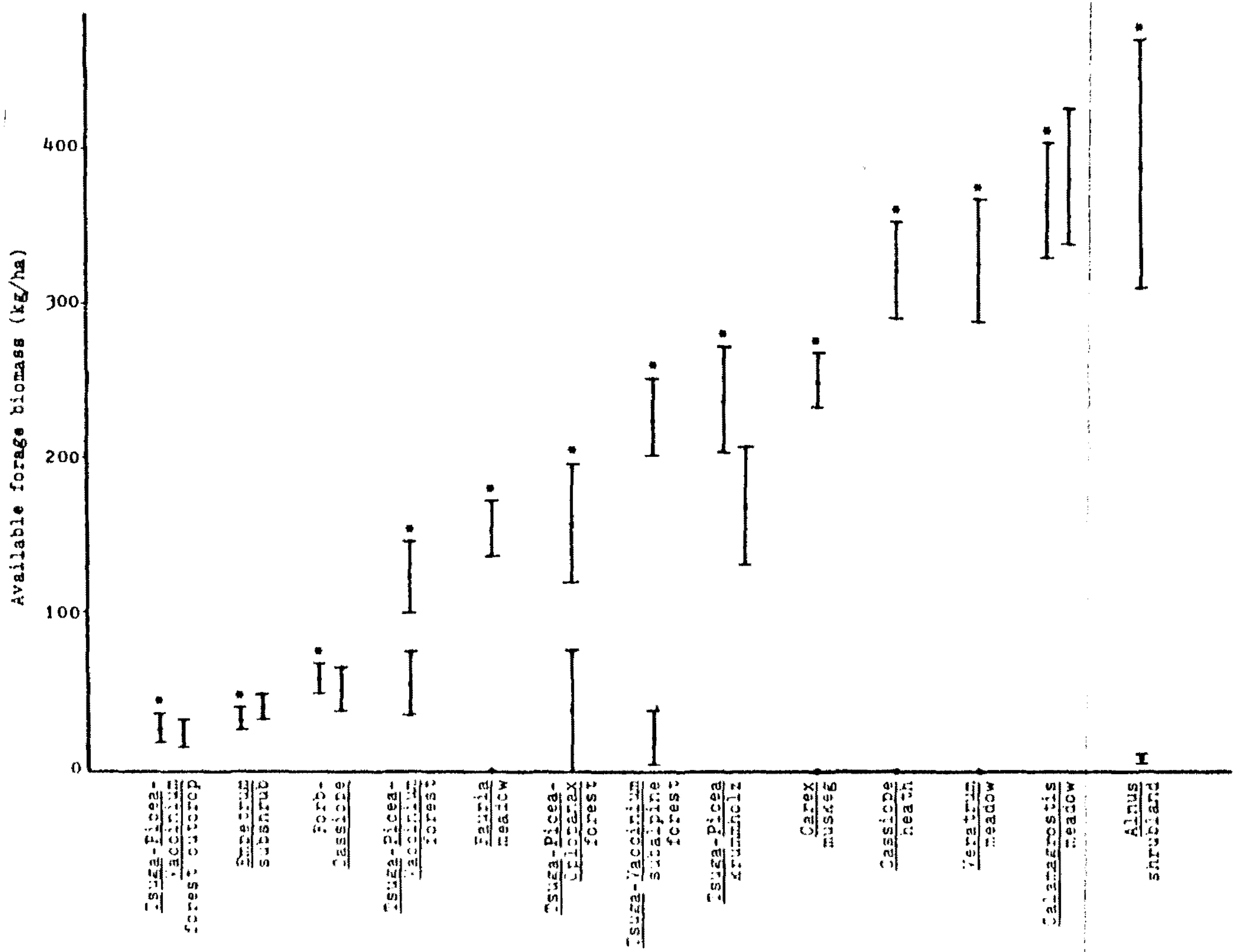

Figure 6. Available ground-rooted forage biomass: pre-snow accumulation versus midwinter 1980. Pre-snow accumulation measurements are indicated by asterisks, while the midwinter measurements are unmarked. Bars represent 95% confidence limits.

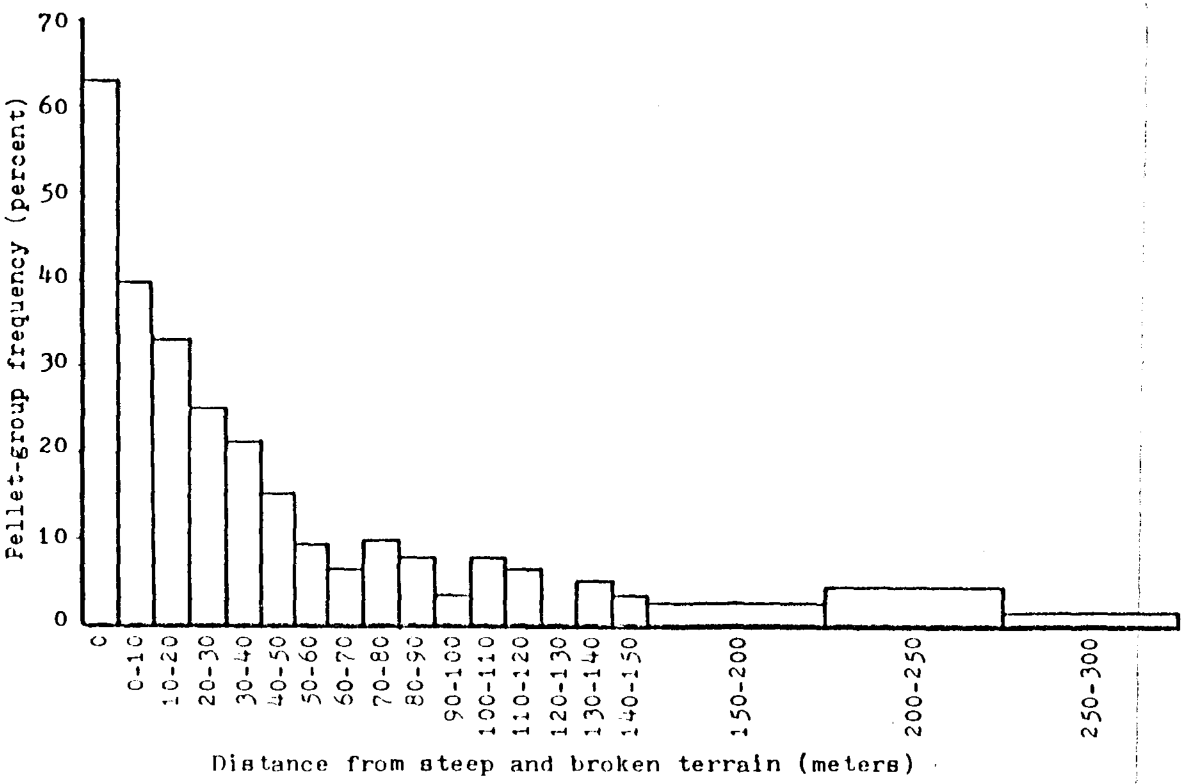

Figure 7. Use of distance from steep and broken terrain.

B. Food acquisition

From optimal foraging considerations we hypothesized a positive relationship between potential food acquisition in a habitat (here measured as available forage biomass in a plant community) and goat use of that habitat, other factors being equal. In order to eliminate the influence of predator avoidance on habitat selection, goat abundance was measured within a fixed distance (50 m) from the steep and broken terrain of *Tsuga-Picea-Vaccinium* forest outcrop in several plant communities adjacent to such terrain. Under three sets of snow conditions, and consequently different amounts of available forage in the various plant communities, relative goat use (track presence in snow) was measured in each of the plant communities (Table 25). A composite test using all three sets of data indicates a strong positive correlation (Spearman rank correlation, p<.001) between available forage biomass and relative goat use.

Relative goat use of habitat was also measured (visual point-in-time observations) in plant communities adjacent to steep and broken terrain in the alpine zone. Snow conditions and hence, available forage in the various plant communities, was relatively stable over much of the winter. Thus, visual observations of goat use made over a period of weeks in midwinter were compared with a constant figure for

Table 25. Available forage biomass and goat use in plant communities adjacent to and equidistant from escape terrain in the forest study site. Three sets of measurements were made, as indicated by the dates given for each sample.

Plant community	22-12-80		22-1-79		23-2-79	
	Forage* biomass	Percent track presence	Forage biomass	Percent track presence	Forage biomass	Percent track presence
Tsuga-_Picea_-_Vaccinium_ forest	126	73	126	71	70	64
Open _Tsuga_-_Picea_-_Vaccinium_ forest	112	40	36	8	36	9
Tsuga-_Picea_-_Oplopanax_ forest	100	21	37	8	23	5
Alnus shrubland	81	8	0	3	0	2
Carex muskeg	1	1	0	0	0	3

* kg/ha

available forage biomass in each plant community (Table 26). Goat habitat use was again strongly positively correlated (Spearman rank correlation, p<.001) with available forage biomass in plant communities where risk of predation is considered comparable.

Measurements of goat habitat use (radio-tracking locations) within the generally forested region of the lower Cleveland Peninsula provided an additional, independent, but somewhat different assessment of the relationship between potential food acquisition and goat habitat selection. It was earlier proposed that the differences in amount of snowfall between the two winters of study should have little effect on thermoregulatory needs or risk of predation. Supporting the contention that risk of predation was not affected by the differences in snow depth, there was no significant difference (p>.10) in the distribution of goat habitat use relative to distance from steep and broken terrain between the two winters of study. (In all cas
chi-square analysis was used as the test for diff
the frequency distribution of goat use of th
habitat attributes between winters.)

The hypothesis was that in th
1981-1982 goats should find grea
using steeper slopes, more souther
timber volume than in the light snow.

Table 26. Available forage biomass and goat use in plant communities adjacent to alpine escape terrain.

Plant community	Forage biomass (kg/ha)	Number of goat observations
Calamagrostis meadow	254	347
Tsuga-*Picea* krummholz	188	126
Empetrum subshrub	24	62
Alnus shrubland	5	26
Cassiope heath	0	16
Forb-*Cassiope* scree	0	15
Veratrum meadow	0	0
Fauria meadow	0	0

1980-1981. For each habitat characteristic taken separately, there were no significant differences ($p>.10$) in the distribution of goat use between winters. However, as median values for goat use of these habitat characteristics indicate (Table 27), all variables differed numerically in the expected directions between winters. With all differences taken as a combined trend, there was a significant shift ($p<.05$) in the distribution of goat habitat use toward sites with characteristics related to relatively lower snow depth (probable greater available forage) in the winter with heavy snow, as was expected. The trend is not extremely strong, but considering the limitations in location accuracy for the radio-tracking data, its existence is noteworthy and lends further support to the acceptability of our model of forage availability as a reasonable explanation of goat habitat selection in winter.

C. Thermoregulation

In the study region environmental conditions were such that thermoregulation was probably an important determinant of habitat selection only under the most cold and/or windy conditions present during the study. We hypothesized that if thermoregulation was a significant determinant of habitat selection, goat habitat use should be negatively correlated

Table 27. Median values for goat use of selected habitat characteristics on the Cleveland Peninsula during the winters of 1980-1981 and 1981-1982.

	Median value	
Habitat variable	1980-1981	1981-1982
Elevation	1730 ft	1680 ft
Slope	39°	43°
Aspect*	3	4
Timber volume**	7450	9800

* North-South continuum (N=1)(NE,NW=2)(E,W=3)(SE,SW=4)(S=5)

** net board feet per acre

with wind speed and positively correlated with temperature in the available micro-habitats. Environmental conditions could not be measured at the sites of goat locations during the visual observations and indirect measures of relative wind speed (snow depth), and relative temperature (elevation) are used in the present analysis. Snow depth is an acceptable measure of relative wind speed in this case due to the dominant effect of wind speed on snow distribution in alpine habitats (i.e., the greater the relative wind speed in a site, the less the snow depth). Temperature generally decreases about 1°C for every 180 m increase in elevation (Perla and Martinelli 1975).

Goats did not use lower elevations (higher relative temperatures) during colder weather (chi-square=874, $p>.05$), indicating that either ambient temperatures alone did not produce critically low operational environmental temperatures for goats or other factors were more important in determining habitat selection. Acknowledging some variation in temperature during the observation of goats in alpine habitats, we still expect a negative correlation between wind speed and goat use in alpine micro-habitats if thermoregulatory behavior is present. Goat use (visual point-in-time observations) in cold weather conditions (<-10°C) was tabulated with respect to snow depth at sites used by goats under different general wind conditions, measured as wind speed at the fixed observer location (Table 28). These cold temperatures occurred about 20% of the time during the winter, with about 6% associated with the light winds, 12% with the moderate winds and 2% with the strong winds indicated in Table 28. It is clear that goats used sites with deeper snow (lower relative wind speed) to a greater extent during windy conditions than they did under calmer conditions (chi-square=593, p<.001). This result is consistent with our hypothesis and indicates that under the more severe (windy) weather conditions present during the study, thermoregulation provides an explanation for goat habitat selection.

D. Overall habitat selection

Seventy-seven percent of all goat observations (n=4001) recorded in the alpine study site were in steep and broken terrain. This proportion of use represents highly significant selection (chi-squared=2175, p<.001) of such habitat relative to its availability in the study area (availability from Fox 1978), and suggests the primacy of predator avoidance in determining goat habitat selection in winter. While it is apparent from results above that goat habitat selection is positively correlated with the availability of food, it is noteworthy that in the alpine site 74% of all feeding observations were in the

Table 28. Snow depths used by goats in an alpine habitat as related to general wind conditions (measured at a fixed observation point). These data are restricted to periods when temperatures were less than -10°C.

	Wind speed (km/hr)		
Snow depth (cm)	0 - 8	9 - 25	26 - 50
0 - 10	132*	87	-
11 - 50	53	182	122
> 50	59	44	-

* number of visual point-in-time observations of individual goats

Forb-*Cassiope* plant community characteristic of rock outcrops (alpine escape terrain) where available forage biomass was relatively low. *Calamagrostis* meadow and *Tsuga-Picea* krummholz communities had substantially more available forage, but only 20% of all feeding observations occurred there. The indication is that, although goat habitat selection is related to forage availability as predicted, the importance of forage availability is subordinate to predator avoidance in determining habitat selection, at least under the conditions of the present study. Only 6% of all goat observations in the alpine study site were in habitats expected to be consistently the warmest and least windy (subalpine Forest and krummholz). The indication here is that thermoregulatory behavior was not an overriding determinant of goat habitat selection during the winter period.

DISCUSSION

Habitat selection by mountain goats during winter is potentially constrained by requirements for predator avoidance, food acquisition and thermoregulation. The results of the present study indicate that these constraints can be acceptably represented by distance ffrom steep and broken terrain, available forage and, to some extent, relative wind speed, respectively. Essentially, the results have demonstrated that these currencies chosen to measure habitat quality with respect to the potential determinants of habitat selection vary consistently with hypothesized expectations, and thus provide reasonable explanations for observed habitat selection by goats. Having demonstrated their association with the respective determinants of habitat selection, these variables provide a basis for understanding and forming practical models of goat habitat selection in winter.

Predator avoidance

Habitat selection is constrained by the need to maintain a minimum possible risk of predation. This is effectively accomplished by remaining in or near to the habitat within which goats can best fend off direct confrontation by predators. The study results demonstrate that distance from steep and broken terrain provides a measurement of goat habitat use that is consistent with theoretical expectations relative to risk of predation in the absence of other competing constraints. We can therefore reasonably view risk of predation in terms of distance from steep and broken (escape) terrain. The contribution of predator avoidance in the determination of habitat use should be reflected in the degree to which distance from steep and broken terrain constrains overall selection of habitat by goats.

While the risk of predation appears highly correlated with distance from steep and broken terrain, the form of this relationship (linear or otherwise) is somewhat unclear, and it seems that slope angle affects the relationship to some extent. The pellet-group data show that, away from escape terrain, there was less use by goats of slopes less than 35° than of slopes greater than or equal to 35° (Mann-Whitney test, $p<.025$). While this difference may in part be associated with decreased snow thickness (hence, increased available forage) on steeper slopes, it is probably related to decreased risk of predation on steeper slopes. If the goat's agility in rugged terrain provides its advantage against predators, then it is reasonable that goats are relatively safer on steeper slopes. Even so, the steepest slopes probably diminish in value due to their sheer rather than broken nature which is unsuitable and perhaps non-negotiable in the avoidance of predators.

However, regardless of the presence of steep slopes, broken terrain (including cliffs) is apparently a prerequisite to goat habitation. The best evidence for this is the existence far from cliffs of otherwise suitable habitat on expanses of steep, unbroken (smooth) slopes which invariably show little or no use by goats, indicating the essential nature of terrain broken into cliffs.

In most situations steep slopes are associated with the presence of broken terrain and cliffs so that slope angle used by goats provides a useful index of habitat use relative to predation risk. It is useful basically because most previous studies of goat habitat use have recorded slope angle use and not distance from escape terrain. From studies that have documented use of slope steepness (Kuck 1973, Smith 1976, McFetridge 1977, Fox 1978, Schoen et al. 1982), the range of average slope angles used by goats in both summer and winter was 35° to 50°, suggesting a consistent and very substantial component of predator avoidance in the determination of goat habitat selection.

Results from the pellet-group data indicate that most goat use is within 200-300 m of steep and broken terrain (Figure 7). This corroborates other evidence from western Alberta where McFetridge (1977) reported that 95% of goa observations were within 300 m of escape terrain duri months of October and November. He also reported t during summer the distance encompassing 95% of goat observations increased to 600 m, presumably in response to increased food acquisition benefits away from escape terrain. On Kodiak Island and the Kenai Mountains in Alaska, Hjeljord (1971) estimated that goats there spent most of their time within 275 m of escape terrain during summer. Limits on distance from steep and broken terrain vary from one site to another due to differences in food distribution and predator pressure. However, the increase in distances used during summer noted above is probably a general pattern within a site because of the increased mobility of goats due to lack of snow and to the abundant food sources outside of rock outcrops in summer.

Distance from steep and broken terrain appears to provide a practical (measurable) constraint on goat habitat use which is conceptually associated with risk of predation. As such, it should provide a very useful component in theoretical models of goat habitat selection. And if limits on use relative to distance from escape terrain within the overall range of 300-600 m are further corroborated, we have an excellent constraint with which to develop an empirical model of goat habitat selection.

Food acquisition

The procurement of sufficient food to sustain life is unquestionably a survival requirement constraining the selection of habitat by goats. Abundant escape terrain, for example, is available at high elevations amid the icefields bordering British Columbia, but the sparseness or absence of plants there precludes any sustained habitation by goats. Evaluation of a minimum food density necessary to sustain viable goat populations is beyond the scope of this study, for it requires additional information on goat nutrient requirements and nutrient density. However, goats in the alpine study site near Juneau remained fairly consistently throughout the winter within areas with an average of about 70-100 kg/ha of available forage. Our study results demonstrate that the biomass of available forage provides a measure of habitat quality which has a relationship to goat habitat use consistent with that expected from habitat selection theory relative to food acquisition. Food acquisition may therefore be viewed in terms of available forage biomass and its contribution as a determinant of habitat selection should be reflected in the degree to which this factor constrains the selection of feeding sites by goats.

Our measurement of available forage is presumed to represent differences in potential food acquisition. As defined here, it is the dry weight of plant current annual growth available to a goat, and takes into account the effects on forage availability of the snow conditions present at the time in question. A major part of the study has involved the development of a method allowing prediction of available forage biomass under any set of snow conditions. This was accomplished by measuring the initial forage biomass in plant communities immediately prior to winter snow accumulation and determining the effect of snowpack depth and density on the availability of forage biomass for all constituent plant species. Additionally, the contribution of litterfall in the forest communities was measured and included in the predictions of available forage biomass. Although the process involved in making the biomass measurements and the snowpack related biomass predictions was somewhat time consuming and complex, the result is a very useful variable with respect to food acquisition. Available forage essentially integrates numerous physical habitat variables into one variable can be considered as directly associated with poten’ acquisition in any area under winter conditions.

Available forage does not account for differences in nutrient concentrations and digestibilities (factors affecting net nutrient intake) among plant species. Although it is here implicitly assumed that nutrient values are comparable among available forages in winter, there is undoubtedly some variation. The next step in developing the best currency to measure potential food acquisition should include nutrient and digestibility variation among plants. Meanwhile, recognizing the overwhelming influence of snow accumulation on the amount of forage obtainable under winter conditions typical of the study, available forage appears to provide an acceptable measure of habitat quality relative to potential food acquisition. Extension of the use of this currency (forage biomass) as a measure of habitat quality to the summer season is probably not acceptable due to the great variation in forage quality at that time of year.

Within an area of sufficient forage abundance to sustain a goat population, and in the absence of other competing constraints, the choice of which habitat patches (plant communities) to use is seen to be correlated with potential food acquisition. In both the alpine and forest study sites near Juneau, different measures of goat habitat use each showed positive correlation between available forage biomass and goat utilization. In the forested area near Ketchikan, goat use was also positively correlated with physical habitat attributes associated with increased available forage. Since habitat quality with respect to potential food acquisition can be reasonably and feasibly assessed in terms of available forage, we have an additional measurable constraint which can be incorporated in the modelling of goat habitat selection.

Thermoregulation

The need to maintain constant body temperature, most desirably without resort to increased metabolic rate, represents a significant potential constraint on goat habitat selection during winter. Through behavioral thermoregulation, both in posture and in selection of habitat, goats may act to minimize their net heat loss in winter. The selection by goats of micro-sites with characteristics which maximize their operative environmental temperature (e.g., sites with higher temperatures, lower wind speeds, greater solar influx) can lessen the need to expend energy in metabolic heat production. The results showed that in weather below -10 C, under windy conditions there was increased use by goats of sites with relatively lower wind speeds, which is expected if thermoregulation is affecting habitat selection. There was no indication that goats used sites with lower ambient temperatures (lower elevations) during colder weather in the study area. The overall implication is that the thermal benefits of moving to lower and warmer elevations did not sufficiently outweigh other benefits associated with remaining. Alternatively, it was energetically worthwhile to make use of local micro-sites with relatively low wind speeds to ameliorate conditions during especially windy weather.

Since the measurements of site specific temperature and wind speed were, in fact, inferred from terrain or snow characteristics, their accuracy is open to question and undoubtedly there was some failure in assessing the variety of microhabitat environments. For instance, these currencies do not provide universal representations of habitat quality over the complete array of possible habitats and, as such, leave something to be desired as useful associates of thermoregulation requirements. Snow depth, for example, is only applicable as a surrogate measure of relative wind speed in the alpine habitats where wind determines snow accumulation. Furthermore, even with measures of wind speed, temperature and solar input, intercorrelations will tend to obscure single variable assessments of habitat quality relative to thermoregulation. However, the present approximation of wind speed must serve here until it is possible to measure a single currency, such as operative environmental temperature, which integrates the effects of these different factors.

Climate-space models of thermal flux across the surface of a mountain goat may be helpful in determining thermoregulatory needs, and in developing such an integrated currency with which to assess potential thermal stress. Such data, ideally, would be correlated with measurements of environmental variables at the micro-site being used by the goat. However, a satisfactory and practical currency with which to measure habitat quality with respect to thermoregulatory needs under any array of habitats remains to be developed. At the same time, our results indicate that there is probably some influence of thermoregulatory behavior on habitat selection in the study area. Thus, we are left with the suggestion that, while thermoregulation does appear to be a determinant of habitat selection in the study region, the environmental conditions are such that it will likely create selective pressure only under the most severe weather conditions which occur in the area.

Overall habitat selection

The overall selection of habitat reflects trade-offs in costs and benefits of habitat attributes related to risk of predation, food acquisition and thermoregulation, and is presumably adjusted to maxiimize overall fitness value to the individual. We can imagine various habitat configurations which demand different solutions to the trade-offs among these constraints. For instance, in a situation where prime escape terrain supports no food resources, the maintenance of lowest possible predation risk would incur death by starvation. Low risk of predation must be sacrificed for the necessity of food acquisition. The presence of sufficient food within acceptable limits of predation risk (distance from steep and broken terrain) would probably result in a situation where goats move out of escape terrain long enough to fill their rumens, then retreat to the unvegetated escape terrain to ruminate and sleep. Conceivably, a situation might also exist where the most abundant forage occurs within escape terrain and goats could remain within such habitat, venturing out only to move to a different patch.

Real goat habitats, varying both temporally and spatially, probably encompass the full spectrum between these extremes. Predator avoidance and food acquisition are both essential and consistent daily determinants of habitat selection. Active thermoregulation requiring significant habitat shifts under extreme cold and windy conditions will not be a consistent determinant of habitat selection except when weather conditions are extreme.

Results from the visual observations of goat habitat use in the alpine study site show that, during daylight hours, 77% of goat use was in the best predator avoidance habitat, 18% in the best food acquisition habitats and 6% in the best habitats for thermoregulatory purposes. The inclination is to conclude that, in this study site during winter, predator avoidance was by far the most important determinant of habitat selection, with food acquisition secondary and thermoregulation of minor importance. However, since the constraints are ultimately of equal importance, relative importance is more meaningfully applied to habitat types as measured by their utilization by goats, for this may change temporally or spatially. The relative amount of time goats spend in a habitat type associated with a particular constraint may differ from one area to another in response to variation in its quality with respect to each constraint and its juxtaposition relative to other available habitats. It is this variation in use for a given type of habitat which is of practical interest in assessing the relative importance of these various habitats to goats in a particular area and can have significant implications for variation in management approaches from one area to another.

We need to consider more fully, however, the meaning in this context of relative importance (as measured by utilization) of the various habitats as they relate to the various determinants of habitat selection. An important caveat in such evaluations of importance based on measures of habitat use lies in the fact that habitats associated with the least time consuming survival concern tend to be biased against in assignments of importance. Avoiding predation is ultimately no more important than getting enough food, but if one is limited in the amount of time possible for feeding (e.g., due to limited stomach size and digestion rate, or to darkness), then those habitats used when not feeding will be predominant and the constraints for which they hold the highest value will appear as more important in determining overall habitat selection. Thus, predator avoidance (distance from steep and broken terrain) will usually explain most goat habitat use, for it is a paramount concern during periods spent sleeping and ruminating, by far the bulk of a goat's life.

A further caution is necessary in assessing the relative importance of habitats as they relate to food acquisition. The amount of time spent feeding is not necessarily an indication of the amount of food procured, since intake rate is probably highly correlated with forage abundance (Hanley 1980). Even though some habitats are used only a small portion of the time for feeding, they may contribute substantially to total food intake.

Comparisons of relative habitat use and activity also require some further interpretationn because the various techniques used to measure goat abundance reflect somewhat different components of daily activity. Pellet group counts may produce results somewhat biased toward overestimation of the relative use of those habitats selected when animals are active (Collins and Urness 1979), though this is certainly less so than for track counts. Tracks in snow reflect active time only, which is predominantly feeding and predominantly associated with daylight. Visual observations cover only the daylight period, a variable interval but one which includes some bedding time and virtually all feeding activity. In making comparisons of goat habitat use, and hence, importance of the various habitats to goats, one must be aware of these variations in time period, activity type and food intake rate.

The trade-offs between predator avoidance and food acquisition in determining habitat selection can be illuminated with measures of goat utilization in habitats of high quality with respect to each constraint. In the region outside of steep and broken (escape) terrain, food acquisition appears to be a major determinant of habitat selection. Visual observation data in the alpine study site showed that the habitat with the most dense available forage (Calamagrostis meadow) received about 80% of its use in the form of feeding activity, as compared to 55% feeding within the steep and broken terrain, which had substantially less forage density. A further look at this comparison, on the basis of a full 24 hr day, would probably still show 80%

feeding in Calamagrostis meadow and only about 13% feeding within escape terrain, indicating even more strongly that escape terrain is forsaken for feeding purposes.

The difference between relative presence of tracks in snow and relative presence of pellet-groups should allow a relative comparison of feeding activity to total use within a habitat. Within the first 50 m away from steep and broken terrain in the forested habitats, presence of tracks in snow (active time, predominantly feeding) in the Tsuga-Picea-Vaccinium forest community was 81% of that in escape terrain, while pellet group presence (active and resting time) was only 44% of that in escape terrain, suggesting again that food acquisition is probably a primary stimulus to leave steep and broken terrain. Evidence from a study in western Alberta also indicates that feeding by goats becomes an increasingly more important component of their activity as distance from escape terrain increases (McFetridge 1977). Also, in southeast Alaska occasional winter observations by local persons indicate that during periods of unusually deep snow goats are sometimes seen far outside their usual winter ranges, apparently seeking food.

Time spent feeding and searching for food constituted 57% of daylight hours (the only time visual observations can be made) but only 15% of the total 24 hr day (assuming no feeding at night) during midwinter in the alpine study area.

Forage availability is a primary concern only during this relatively small period of the day. While 70% of activity within the abundant forage habitats of Calamagrostis meadow and Tsuga-Picea krummholz was feeding activity, only 20% of total feeding time was spent in these two communities. Thus, even considering that feeding time is a small proportion of 24 hr daily activity, the preponderance of feeding in habitats other than those best for forage procurement indicates a strong contribution of factors other than forge abundance (i.e., predator avoidance) in determining habitat selection.

We must also consider differences, however, in food intake rate among the plant communities. Seventy-four percent of feeding activity in the alpine study site took place within escape terrain, suggesting that there was sufficiently dense forage there (approx. 60 kg/ha) to accomodate a substantial portion of goat forage needs. But, the intake of forage per unit time in a Calamagrostis meadow (250-360 kg/ha) will probably be much higher, so that the actual contribution of such meadows to total forage consumption may be greater than in the escape terrain, even though more time is spent feeding in the escape terrain. Such considerations illustrate the potential value of a single unit with which to evaluate the trade-offs involved in habitat selection. However, since such a unit (e.g., survival rate) is currently impractical in most study situations, we can best evaluate habitat quality (importance) separately in terms of each constraint.

Overall, winter habitat selection in the study area appears essentially to reflect trade-offs between food acquisition and predator avoidance. If the animals are behaving optimally in selecting habitats, as we assume, they are simply balancing costs and benefits relative to these equally important constraints on survival. Thus, even though dense forage exists away from escape terrain, it is not smart (in an evolutionary sense) to increase predation risk by doing all feeding in such habitats (even though feeding time might be substantially lessened), if a portion of the daily forage requirement can be acquired while being at the lowest possible risk of predation. While such trade-offs reflect the specific array of habitat types present in a site, and may be rather complex, the advantage here is that we have shown they can reasonably be viewed in terms of available forage and distance from steep and broken terrain.

Goat habitat selection models

A. General model for winter

Mountain goats can only exist in areas where food is sufficient, predation pressure is low enough and environmental conditions are benign enough to allow survival in winter. Each factor represents limits which can potentially preclude the establishment of a viable goat population, and in this sense each is an equally important constraint on habitat selection. Within the context of an existing goat population in a particular area, an evaluation of the relative contribution of each constraint to the total quality (fitness value) of different habitats is basic to an understanding of the overall distribution of habitat use at that site. For practical management purposes, it may be sufficient simply to know which habitat characteristics are important to a particular population at a particular time. However, for theoretical purposes, and where practical needs require extrapolation of information to new conditions (as is usually the case), an understanding (in essence, a model) of the causes for selection of habitat, and for temporal or spatial differences in such selection, is essential.

The framework for such a model has been developed in the present study. As the basis for this study, a general theoretical model was presented arguing for the presence of three constraints (predator avoidance, food acquisition and, possibly, thermoregulation) which determine the selection of habitat by goats during winter (Figure 8). The model is essentially restricted to winter for the following reasons: 1) it does not account for behavior related to breeding in autumn or parturition in spring, 2) forage biomass does not adequately represent habitat quality relative to food acquisition during summer when there is wide variation in nutrient quality among plants, and 3) thermoregulation concerns under heat stresses of summer demand minimization rather than maximization of operational environmental temperature. Measurable currencies which represent the above constraints were proposed and their validity tested, resulting in acceptable variables for predation risk and food acquisition and a tenuous one for thermoregulation need. On a practical basis, then, the interaction of these constraints can be represented in a model using 1) distance from steep and broken terrain, 2) forage biomass, and 3) relative wind speed (under severe weather conditions).

Hypotheses derived from this model are based on the premise that knowledge of relative values for these parameters provides sufficient information to explain or predict variation in goat selection of habitat. Thus, for example, variation in available forage due to changing snow conditions will effect predictable changes in goat selection of habitat types. Alternatively, variation in predation

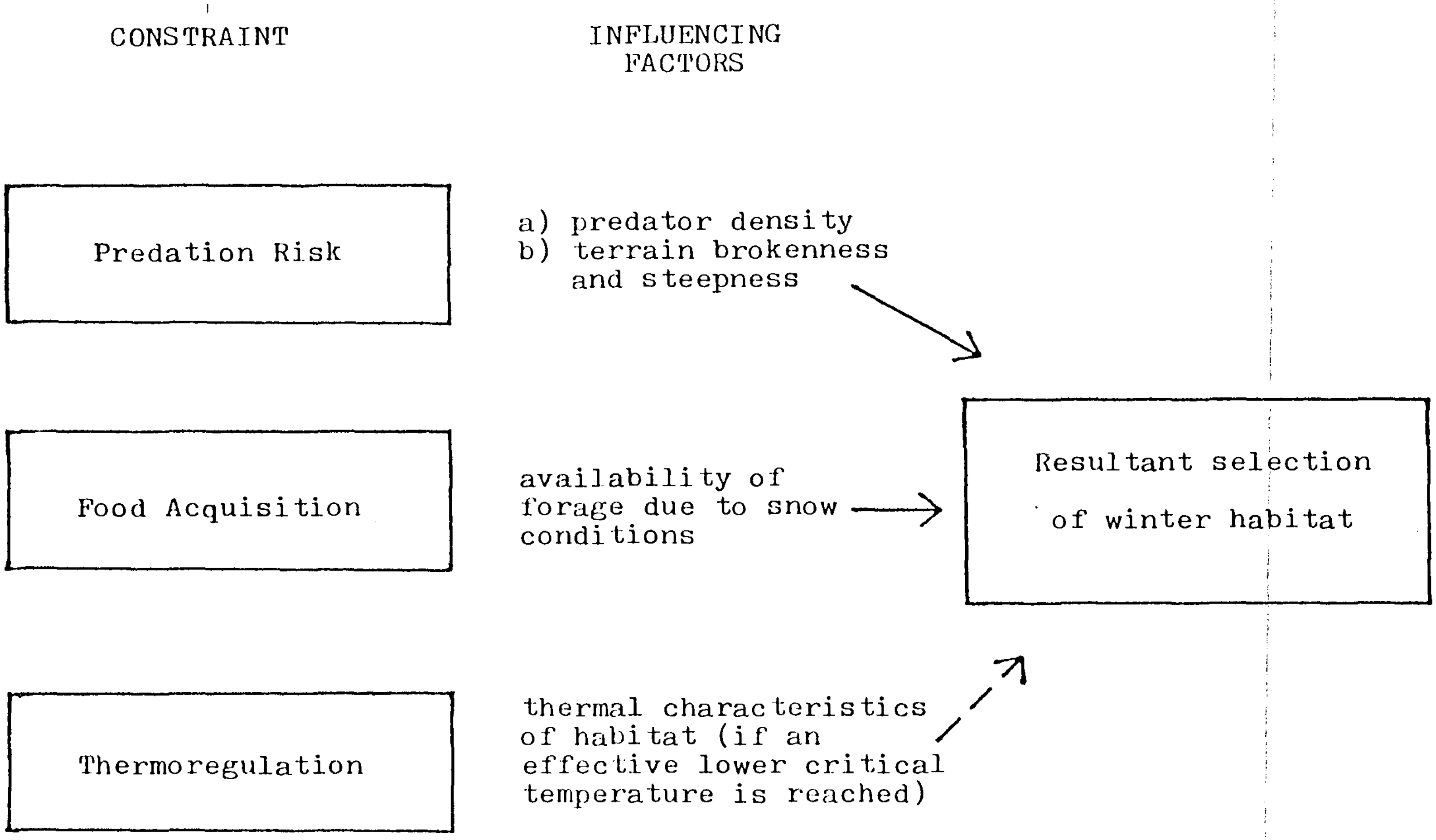

Figure 8. Model of constraints on goat habitat selection in winter. The dotted arrow reflects possible lack of, or intermittent effect of thermoregulation.

risk at a given distance from steep and broken terrain due to changes in predation pressure should also result in predictable trends in habitat selection.

The model has several consequences for which natural experiments may exist. Some of these have already been indicated in the examples of expected goat use in habitats with all available forage either within or outside of escape terrain. Habitat use will be more restricted to escape terrain in areas where such terrain also provides substantial food resources.

Wherever they have been studied, goats have been shown to be closely associated with the presence of steep and broken terrain, even in areas where predation is considered minimal. Goat response to threatening situations (retreat to steep and broken terrain) probably has a strong genetic component; but, to the degree that it is learned behavior, there should be resultant variation in habitat selection in response to differences in predation pressure. If goat response to actual predation pressure is fairly plastic, then, other constraints being equal, we would expect greater use of areas farther from escape terrain in regions where large predators are scarce or absent. Thus, it is conceivable that mountain goats in the contiguous United States (where large predators are scarce) should have somewhat larger ranges surrounding escape terrain than those in Canada and Alaska (where large predators, especially wolves, are common). Such a difference is necessarily contingent on other factors in the regions being comparable and is a general prediction, for mosaics of habitat quality vary from site to site.

Unfortunately, good comparable measurements of goat distribution relative to distance from steep and broken terrain are not presently available for testing the above prediction. However, the response of goats to human presence is certainly different in areas with and without substantial predator pressence. Where possible influences on goat behavior due to human hunting are not a factor (e.g., National Park lands), it is apparent (pers. observation) that goats retreat toward escape terrain at a much greater distance from humans in an area with abundant large predators (Glacier Bay National Monument, Alaska) than in an area with few predators (Olympic National Park, Washington).

Other predictions of relative differences in goat habitat use are possible, based on differences in the juxtaposition of habitat types and their quality relative to food acquisition and predation risk. The value of such a general model lies in the ability to envision situations where clearcut predictions are possible and in its provisions for measurement of these predicted differences in habitat use. Ultimately, it also provides some of the foundations for further proposal and development of better currencies for measuring the potential constraints on habitat selection.

B. A simple empirical model

The evidence that goats are essentially restricted to areas within a certain distance from steep and broken terrain suggests some practical limits to goat habitat. We have reviewed evidence for the restriction of almost all goat activity to within 300-600 m from escape terrain. Recognizing that such a restriction varies in response to spatial and temporal differences in habitat quality relative to competing constraints on habitat selection, a limit of 500 m from escape terrain may provide an initial, conservative, but useful rough approximation for defining goat habitat in winter. Within such a constraint, variations in forage abundance or weather severity will be reflected in differences in the distribution of goat habitat use, but within the 500 m limit from escape terrain.

This is, in effect, a very simple empirical model of the suitability of an area for goat habitation. Such a model ignores all the interactions which bring about variation in the distribution of habitats used, but predicts that all such variation will occur within 500 m of escape terrain. Recognizing the danger in promoting a specific distance from escape terrain as effectively all-inclusive of goat habitat use, it usefulness as a first approximation for delineating important goat habitat is readily apparent. If, in further studies, 500 m from escape terrain proves to be a consistent limit to goat habitation, its immediate practical value is apparent in its facilitation of the identification of important goat habitat, essential for management purposes.

Application of the models to southeast Alaska

A. Climate and habitat quality in southeast Alaska

In southeast Alaska, where the wet summers and vast alpine summer ranges provide superabundant nutritious forage for growth and fat accumulation, the severity of winter conditions probably provides the most important limits to goat survival. The range of winter storm conditions in southeast Alaska creates a situation where, depending on the weather, quite different habitats can provide the best winter range at different times. Changing storm characteristics (predominantly temperature and wind speed) create shifting snowline elevations through the winter and influence the overall snowfall patterns and snowpack accumulation. As discussed earlier, site specific influences on snow accumulation in alpine and low elevation forest sites are very different, with relative depths in the alpine zone being essentially wind determined, while those at lower elevations are affected primarily by tree canopy cover, slope and aspect. Since the mechanisims providing limited snow accumulation in each site are quite different, it is possible for a single storm to have opposite effects on snow accumulation in the two zones.

Basic determinants of goat habitat selection are the same in both alpine and low forested sites, resulting in the selection of habitats with relatively limited snow accumulation that provide for both low predation risk and food acquisition. But the location of those habitats with the most available forage may change dramatically depending on storm conditions. A succession of cold, windy storms would drop a large amount of snow on low elevations while keeping alpine sites blown free of snow. Goats would be better off in the alpine zone where forage is available. Conversely, relatively warm and calm snowfalls would accumulate in all alpine habitats (quickly rendering the low-growing forage unavailable) while producing rainy and melting conditions at the lower elevations. In this case, available forage is essentially restricted to the lower elevation forested zone. Goat populations that have a range from alpine to low elevation wintering sites are probably in a better position to survive such extremes of winter weather than those whose wintering sites are more restricted. Such differences in the range of available wintering sites could result in very different overwinter survival rates even for adjacent populations.

The coastal goat ranges of southern Alaska, British Columbia and Washington are unique in the effects of their maritime climates on winter habitat quality for goats. Only recently have we begun to recognize and appreciate the quality of heavily forested areas in providing suitable winter habitat for goats and the degree to which goats make use of these sites. Hebert and Turnbull (1977) first discussed the importance of forested areas as wintering sites for goats in coastal British Columbia. In conjunction with the present study a limited search turned up numerous forested goat wintering sites across southeast Alaska. I have also observed similar forested wintering sites in both the Olympic Mountains and the North Cascades of Washington.

Previous studies of goat winter habitat selection have not indicated the degree of forest use which is apparent in the coastal region. This is probably related to the location of these studies in interior regions where the colder continental climate produces a different regime of snowfall, and hence forage availability in forest habitats. Within the elevational range of goat habitat, the colder interior climate consistently produces snow (as opposed to frequent rains on the coast) at the lower elevations, thus producing a continually increasing snowpack. In addition, the more open canopy forests of these drier climates allow greater through-fall of snow and hence deeper snowpack. The end result is a relatively low availability of forage in the forests of interior goat ranges and a greater reliance by goats in these areas on higher elevation wind-blown sites (Hebert and Turnbull 1977).

B. Management implications in southeast Alaska, especially with respect to logging

The foregoing discussion, along with a knowledge of the range of winter snow conditions, provides some basis for assessing the effect of habitat alteration on goat habitat selection. Since the predominant form of habitat manipulation in southeast Alaska is timber removal and regeneration, reference is made specifically to potential conflicts between timber harvest and goat habitat use.

Assuming the validity of the simple empirical model which restricts goat habitat use to within about 500 m of escape terrain, the region of direct effects becomes apparent. Forested areas which are more than about 500 m from steep and broken terrain probably are essentially unused or used primarily for travel if they occur between wintering sites. Direct effects of logging in these areas beyond the 500 m radius are basically restricted to factors which may change energy expenditures required for travel between preferred wintering sites. Such factors include large amounts of slash which may hinder ease of movement and add to energy expenditure (Lyon and Jensen 1980, Wallmo and Schoen 1980). The inverse relationship between forest canopy cover and snow depth (Harestad and Bunnell 1980) indicates that, before canopy closure in the regeneration phase, increased snow depth in logged areas will increase the energy costs of movement through such areas.

For timbered areas less than about 500 m from steep and broken terrain, which have been shown to be important for feeding, logging will affect not only ease of movement but also the amount of forage available to goats. Even though more potential forage may become available soon after logging, the loss of canopy cover will result in increased snow depth, thus rendering forage unavailable in winter. Furthermore, during a substantial period after canopy closure (and decreased snowdepth) potential understory forage is greatly diminished, thus keeping the logged site less attractive than 'old-growth' forest for foraging (Wallmo and Schoen 1980, Alaback 1982). On balance, logging will tend to diminish foraging resources for goats during winter in southeast Alaska.

An initial reconnaissance of goat wintering sites in southeast Alaska, performed in conjunction with this study, suggests that, under current logging practices, most goat wintering sites would not logged. However, there are undoubtedly some sites which have already been logged, and others (some already identified) that are scheduled for logging. Given the relatively small distances (approx. 500 m) surrounding escape terrain which are used for foraging by goats, it is reasonable to recommend protection of such sites. Where logging would affect travel routes between wintering sites (i.e., areas between, but greater than 500 m from escape terrain) an initial recommendation would be to leave pathways of 'old-growth' between such wintering sites. Such pathways should be at least wide enough to prevent increased snowdepths due to snow being blown in from adjacent open clear-cut areas.

In one area about 50 km northwest of Juneau there are several heavily forested goat wintering sites within 2 km of tideline, including one small site adjacent to the beach. The location and juxtaposition of these sites makes them easily susceptible to direct effects of logging, both within 500 m of steep and broken terrain and on travel routes between the sites. Such a winter range merits protection of these precisely defined areas in the event of logging or other land use activities in the area. The importance to goat populations of such low elevation forested wintering sites, as explained above, is related to their provision of suitable habitat during certain extreme winters. The tideline site, for example, may not be used every winter, but under conditions of deep snow at higher elevations it could provide a crucial refuge.

Such a scenario illustrates the practical advantage of an understanding of the factors which determine goat habitat selection. The ability to forsee which habitats will be crucial under the extreme conditions which limit goat populations is essential to the responsible management of these animals and their habitat.

LITERATURE CITED

Alaback, P. B. 1980a. Biomass and production of understory vegetation in seral Sitka spruce - Western hemlock forests of southeast Alaska. Ph.D. diss. Oregon State Univ., Corvallis. 79p.

_______. 1980b. Provisional plant community types of southeast Alaska. Unpuplished rep. on file at USDA For. Serv., Inst. North. For., Fairbanks, Alaska. 15p.

_______. 1982. Dynamics of understory biomass in Sitka spruce - western hemlock forests of southeast Alaska. Ecology 63:1932-1948.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-265.

Andersen, H. E. 1955. Climate in southeast Alaska in relation to tree growth. Alaska Forest Research Center Paper 3. U.S. Forest Service, Juneau, Alaska.

Anderson, N. W. 1940. Mountain goat study. Washington Dept. of Game, Biol. Bull. 2. 21p. Anthony, R. G. and N. S. Smith. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. Ecol. Monogr. 47:255-277.

Bell, R. H. V. 1969. The use of the herb layer by grazing ungulates in the Serengeti. Pages 111-123 in A. Watson, editor. Animal populations in relation to their food resources. Symp. of the British Ecol. Soc. (Aberdeen). Blackwell Scientific Publ., Oxford and Edinburg.

_______. 1971. A grazing ecosystem in the Serengeti. Scientific American 225:86-93.

Belovsky, G. E. 1977. Optimal behavior of a generalist herbivore. Ph.D. diss. Harvard Univ., Cambridge, Mass.

_______. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14:76-104.

Bliss, L. C. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44:678-697.

Brandborg, S. M. 1955. Life history and management of the mountain goat in Idaho. Idaho Dept. of Fish and Game, Wildl. Bull. No. 2. 142p.

Brew, D. A., R. A. Loney and L. J. P. Muffler. 1966. Tectonic history of southeast Alaska. Pages 149-170 *in* Tectonic history and mineral deposits of the western cordillera. Canadian Inst. of Minerals and Metallurgy Special 8. Montreal, Quebec.

Buddington, A. F. and T. Chapin. 1929. Geology and mineral deposit of southeastern Alaska. U.S. Geological Survey Bull. 800.

Carbyn, L. N. 1974. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey density. Canadian Wildlife Service. 220p.

Casebeer, R., M. Rognrud and S. Brandborg. 1950. The Rocky Mountain goat in Montana. Montana Fish and Game Dept., P-R Project I-R, Bull. 5. 107p.

Chadwick, D. N. 1973. Mountain goat ecology--logging relationships in the Bunker Creek drainage of western Montana. M.S. thesis. Univ. Montana, Missoula. 260p.

Chapin, F. S. III, D. A. Johnson and J. D. McKendrick. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. J. Ecol. 68:189-209.

Chappell, R. W. and R. J. Hudson. 1978. Winter bioenergetics of Rocky Mountain bighorn sheep. Can. J. Zool. 56:2388-2393.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorum. Theor. Pop. Biol. 9:129-136.

Charnov, E. L. and G. H. Orians. 1973. Optimal foraging: some theoretical explorations. unpub. manuscript. Dept. Zoology, Univ. Washington, Seattle. 160p.

Clutton-Brock, T. H., F. E. Guinness and S. D. Albon. 1982. Red deer: Behavior and ecology of two sexes. The Univ. of Chicago Press, Chicago. 378p.

Collins, T. M. 1974. Soils and soil development. Pages 20-23 *in* The Forest ecosystem of southeast Alaska. I. The setting. Forest Serv. General Tech. Rep. PNW-12.

Collins, W. B. and P. J. Urness. 1979. Elk pellet group distributions and rates of deposition in aspen and lodgepole pine habitats. Pages 140-144 in M. S. Boyce and L. D. Hayden-Wing, eds. North American elk: ecology, behavior and management. Univ. Wyoming Press, Laramie. 294p.

Cowan, I. McT. 1944. Report of wildlife studies in Jasper, Banff and Yoho National Parks in 1944 and parasites, diseases, and injuries of game animals in the Rocky Mountain National Parks, 1942-1944. unpub. report. Wildlife Serv., Dept. of Mines and Res., Ottawa. 83p.

Crocker, R. L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. of Ecology 43:427-448.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Sci. 33:43-64.

Del Morel, R. and A. F. Watson. 1978. Vegetation on the Stikine Flats, southeast Alaska. Northwest Sci. 52:137-150.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. Amer. Scientist 66:322-331.

Dilworth, J. R. 1974. Log scaling and timber crusing. O.S.U. Book Stores Inc. Corvallis, Ore. 471p.

Dunbar, R. I. M. 1978. Competition and niche separation in a high altitude herbivore community in Ethiopia. East African Wildl. Journal 16:183-199.

Emlen, J. M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.

Estes, R. D. 1974. Social organization of the African bovidae. Pages 166-205 in V. Geist and F. Walther, editors. The behavior of ungulates and its relation to management. Volume 1. International Union for the Conservation of Nature Publication No. 24. I. U. C. N., Morges, Switzerland.

Fitzharris, B. B. 1975. Snow accumulation and deposition on a west coast midlatitude mountain. Ph.D. diss. Univ. British Columbia, Vancouver. 272p.

Flook, D. R. 1964. Range relationships of some ungulates native to Banff and Jasper National Parks, Alberta. Pages 119-128 in D. J. Crisp, editor. Grazing in terrestrial and marine environments. A Symp. of the British Ecol. Soc. (Bangor). Blackwell Scientific Publ., Oxford.

Fox, J. L. 1978. Weather as a determinant factor in summer mountain goat activity and habitat use. M.S. thesis. Univ. Alaska, Fairbanks. 64p.

Franzmann, A. W., A. Flynn and P. D. Arneson. 1975. Levels of some mineral elements in Alaskan moose hair. J. Wildl. Manage. 39:374-378.

Franzmann, A. W. and R. E. LeResche. 1978. Alaskan moose blood studies with emphasis on condition evaluation. J. Wildl. Manage. 42:334-351.

Freeland, W. J. and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Nat. 108:269-289.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, N. J.

Fretwell, W. J. and H. L. Lucas. 1969. On territorial behavior and other factors in influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Geist, V. 1964. On the rutting behavior of the mountain goat. J. Mammal. 45:551-568.

Girard, J. W. and D. Bruce. 1963. Tables for estimating board foot volume of trees in 32 foot logs. Mason, Bruce & Girard, Portland, Oregon. 40p.

Goering, H. R. and P. J. van Soest. 1970. Forage fiber analysis. USDA Agr. Res. Ser., Agriculture Handbook No. 379. 20p.

Gordon, M. S. 1968. Animal function: Principles and adaptations. New York, Macmillan.

Guiguet, C. J. 1951. An account of wolverine attacking mountain goat. Can. Field Nat. 65:187.

Gwynne, M. D. and R. H. V. Bell. 1968. Selection of vegetation components by grazing ungulates in Serengeti National Park. Nature, London 220:390-393.

Hanley, T. A. 1980. Nutritional constraints on food and habitat selection by sympatric ungulates. Ph.D. diss. Univ. Washington, Seattle. 176p.

Harestad, A. S. 1979. Seasonal movements of black-tailed deer on northern Vancouver Island. Ph.D. diss. Univ. British Columbia, Vancouver. 197p.

Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. diss. Univ. British Columbia, Vancouver. 357p.

Hebert, D. M. and I. McT. Cowan. 1971. Natural salt licks as a part of the ecology of the mountain goat. Can. J. Zool. 49:605:610.

Hebert, D. M. and W. G. Turnbull. 1978. A description of southern interior and coastal mountain goat ecotypes in British Columbia. Pages 126-146 in W. M. Samuel and W. G. Macgregor, eds., Proc. First Intl. Mtn. Goat Symp. Queen's Printer, Victoria, B.C. 243p.

Hulten, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, California. 1008p.

Heusser, C. J. 1954. Nunatak flora of the Juneau Ice Field, Alaska. Bull. Torrey Bot. Club 81:236-250.

Hibbs, D. L. 1967. Food habits of the mountain goat in Colorado. J. Mammal. 48:242-248.

Hibbs, L. D., F. A. Glover and D. L. Gilbert. 1969. The mountain goat in Colorado. Transactions N. Amer. Wildl. Nat. Res. Conf. 34:409-418.

Hjeljord, O. G. 1971. Feeding ecology and habitat preference of the mountain goat in Alaska. M.S. thesis, Univ. Alaska, Fairbanks. 126p.

_______. 1973. Mountain goat forage and habitat preference in Alaska. J. Wildl. Manage. 37:353-362.

Hobbs, N. T., D. L. Baker, J. E. Ellis and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45:156-171.

Hoefs, M. and V. C. Brink. 1978. Forage production and utilization of a Dall sheep winter range, southwest Yukon Territory. Pages 87-105 in Proc. 1978 Northern Wild Sheep and Goat Conference. Penticton, B.C. 412p.

Jacques, D. R. 1973. Reconnaissance botany of alpine ecosystems on Prince of Wales Island, southeast Alaska. M.S. thesis. Oregon State Univ., Corvallis. 133p.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

Johnston, A. L., L. M. Bezeau and S. Smoliak. 1968. Chemical composition and in-vitro digestibility of alpine tundra plants. J. Wildl. Manage. 45:156-171.

Kearney, S. R. and F. F. Gilbert. 1976. Habitat use by white-tailed deer and moose on sympatric range. J. Wildl. Manage. 40:645-657.

Klebnow, D. A. 1965. A montane forest winter deer habitat in western Montana. J. Wildl. Manage. 29:27-33.

Klein, D. R. 1953. A reconnaissance study of the mountain goat in Alaska. M.S. thesis, Univ. Alaska, Fairbanks. 121p.

_______. 1965. Ecology of deer range in Alaska. Ecological Monogr. 35:259:284.

Krog, H. and M. Monson. 1954. Notes on the metabolism of a mountain goat. Amer. J. Physiol. 178:515-516.

Kuck, L. 1973. Rocky Mountain goat ecology. Idaho Fish and Game Dept., P-R Proj. Rept. W-114-R-3.

Lamprey, H. F. 1963. Ecological separation of large mammal species in the Tarangire Game Reserve, Tanganyika. East African Wildl. Journal 1:1-30.

Lyon, L. J. and C. E. Jensen. 1980. Management implications of elk and deer use of clearcuts in Montana. J. Wildl. Manage. 32:597-614.

MacArthur, R. H. and E. R. Pianka. 1966. On the optimal use of a patchy habitat. Amer. Nat. 100:603-609.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildlife Monogr. 20. 79p.

Martinka, C. J. 1968. Habitat relationships of white-tailed and mule deer in northern Montana. J. Wildl. Manage. 32:558-565.

McFetridge, R. J. 1977. Strategy of resource use by mountain goat nursery groups. Pages 169-173 in W. M. Samuel and W. G. Macgregor, eds., Proc. First Intl. Mtn. Goat Symp. Queen's Printer, Victoria, B.C. 243p.

Miller, D. H. 1964. Interception processes during snowstorms. United States Forest Service Research Paper PSW-18. 24p.

National Weather Service. 1980. Local climatological data: Juneau, Alaska. U. S. Dept. of Commerce, National Climate Center, Ashville, N.C.

Neiland, B. J. 1971. The forest bog complex of southeast Alaska. Vegetatio, Acta Geobot. 22:1-64.

Orians, G. H. 1971. Ecological aspects of behavior. Pages 513-546 in Farner, D. S. and J. R. King, editors. Avian biology, Vol. 1. Academic Press.

_______. 1980. Some adaptations of marsh-nesting blackbirds. Monog. in Pop. Biol., No. 14. Princeton Univ. Press, Princeton, N.J. 295p.

Palmer, L. J. 1942. Major vegetation types of southeastern Alaska. Unpublished report prepared by U.S. Fish and Wildl. Serv., Juneau, Alaska. 16p.

Peek, J. M. 1971. Moose habitat selection and relationships of forest management in northeastern Minnesota. Ph.D. diss., Univ. Minnesota, St. Paul. 250p.

Perla, R. I. and M. Martinelli, Jr. 1975. Avalanche Handbook. U.S.D.A., Agric. Handbook No. 489. 238p.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology 52:137-154.

Raedeke, K. J. 1980. USFS Administrative study progress report, Cleveland Peninsula mountain goats. College of Forest Resources, Univ. of Washington. 16p.

Rideout, C. B. 1974. A radio telemetry study of the ecology of the Rocky Mountain goat in western Montana. Ph.D. diss., Univ. Kansas, Lawrence. 146p.

Rochelle, J. A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Ph.D. diss. Univ. British Columbia, Vancouver. 295p.

Saunders, J. K., Jr. 1955. Food habits and range use of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Manage. 19:429-437.

Schaller, G. B. 1979. Mountain Monarchs. Univ. Chicago Press, Chicago, Ill. 425p.

Schoen, J. W., M. D. Kirchoff, O. C. Wallmo, J. L. Fox and R. D. Taber. 1982. Habitat use by mountain goats in southeast Alaska. P-R Project Rept. W-17-10,11 and W-21-1,2. Alaska Dept. Fish and Game, Juneau.

Schoener, T. W. 1971. Theory of feeding strategies. An. Rev. of Ecol. and Syst. 2:277-313.

Shea, L. C. 1981. Habitat suitability index model for mountain goats (<u>Oreamnos kennedyi</u> Elliot) in coastal southcentral Alaska. unpub. report. U.S. Fish and Wildlife Service, Anchorage, Alaska. 21p.

Short, H. L., R. M. Blair and C. A. Segelquist. 1974. Fiber composition and forage digestibility by small ruminants. J. Wildl. Manage. 38:197-209.

Singer, F. J. 1975. Behavior of mountain goats, elk and other wildlife in relation to U. S. Highway 2, Glacier Natl. Park, Montana. Natl. Park Serv., West Glacier, Montana. 98p.

Skoog, R. O. 1968. Ecology of the caribou (<u>Rangifer tarandus granti</u>) in Alaska. Ph.D. diss., Univ. California, Berkeley. 699p.

Smith, B. L. 1976. Ecology of Rocky Mountain goats in the Bitterroot Mountains, Montana. M.S. thesis. Univ. Montana, Missoula. 203p.

Smith, C. A. 1982. Habitat use by mountain goats. P-R Project Rept. W-21-2. Alaska Dept. Fish and Game, Juneau. 23p.

Smith, C. A. and K. J. Raedeke. in press. Group size and movements of a dispersed, low density goat population with comments on interbreeding and human impacts. Proc. 1982 N. Amer. Wild Sheep and Goat Conf., Fort Collins, Colorado.

Smith, L. W., H. K. Goering and C. H. Gordon. 1972. Relationships of forage compositions with rates of cell wall digestion and indigestibility of cell walls. J. Dairy Sci. 55:1140-1147.

Smith, L. W., H. K. Goering, D. R. Waldo and C. H. Gordon. 1971. In-vitro digestion rate of forage cell wall components. J. Dairy Sci. 54:71-76.

Stephens, F. R. and R. F. Billings. 1967. Plant communities of a tide-influenced meadow on Chichagof Island, Alaska. Northwest Sci. 41:178-183.

Stephens, F. R., C. R. Gass, R. F. Billings, and D. E. Paulson. 1969. Soils and associated ecosystems of the Tongass. Ecol. Soc. of Amer. Supplementary Publication Service Doc. No. ESPS-8107. 67p.

Stevens, D. R. 1974. Rocky Mountain elk - Shiras moose range relationships. Le Naturaliste Canadien 101:505-516.

Stevens, V. 1979. Mountain goat (Oreamnos americanus) habitat selection in Olympic National Park. M.S. thesis, Univ. Washington, Seattle. 106p.

Stevenson, S. K. 1978. Distribution and abundance of arboreal lichens and their use as forage by black-tailed deer. M.S. thesis, Univ. British Columbia, Vancouver. 48p.

Sverdrup, H. U. 1940. Currents of the Pacific Ocean and their bearing on the climates of the coast. Science 91:273:282.

Taber, R. D. and R. F. Dasmann. 1957. The dynamics of three natural populations of the deer Odocoileus hemionus columbianus. Ecology 38:233-246.

Talbot, L. M. 1962. Food preferences of some East African wild ungulates. East African Agriculture and Forestry Journal 27:131-138.

Telfer, E. S. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34:533-559.

Tieszen, L. L. 1972. The seasonal course of aboveground production and chlorophyll distribution in a wet arctic tundra at Barrow, Alaska. Arct. Alp. Res. 4:307-324.

United States Forest Service. 1974. Forest ecosystems of southeast Alaska. I. The setting. Forest Serv. General Tech. Rep. PNW-12.

_______. 1978. Tongass land management plan. U.S. Forest Service, Alaska Region, Juneau, Alaska.

Viereck, L. A. and C. T. Dyrness. 1980. A preliminary classification system for the vegetation of Alaska. Forest Serv. General Tech. Rep. PNW-106. 38p.

Wallmo, O. C. and J. W. Schoen. 1980. Response of deer to secondary forest succession in southeast Alaska. Forest Sci. 26:448-462.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R.B. Gill and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122-127.

Wegge, P. 1975. Reproduction and early calf mortality in Norwegian red deer. J. Wildl. Manage. 39:92-100.

Welch, B. L. and J. C. Pederson. 1981. *In vitro* digestibility among accessions of big sagebrush by wild mule deer and its relationship to monoterpenoid content. J. Range Mgmt. 34:497-500.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Nat. 108:290-304.

_______. 1978. What are the biological bases of varied diets? Amer. Nat. 112:627-631.

Wiens, J. A. 1977. On competition and variable environments. Amer. Scientist 65:590-597.

Appendix I. Identification of important plant communities recognized in the study area within Viereck and Dyrness' (1980) vegetation classification system for Alaska.

Plant communities in this study	Viereck and Dyrness' classification
Forb-*Cassiope*	2B(2b) Alpine herbs (Alpine herbaceous tundra)
Empetrum subshrub	2D(2d) Crowberry shrub tundra, or 2E(1f) Ericaceous shrub tundra
Cassiope heath	2D(2e) Ericaceous shrub tundra
Calamagrostis meadow	4A(2b) Bluejoint mixed herbs, or 2A(2b) Mesic sedge-herb meadow
Veratrum meadow	4A(4c) Cow parsnip (Tall grass-herbs)
Fauria meadow	2A(1c) Wet sedge-herb meadow (Sedge-grass tundra), or 2B(2b) Alpine herbaceous tundra
Carex muskeg	4C(1a-b) Sedge or moss-sedge, wet sedge-grass marsh
Tsuga-*Picea* krummholz	1A(2c) Mountain hemlock open conifer forest
Alnus shrubland	3A(1b) Alder closed tall shrubland
Tsuga-*Vaccinium* subalpine forest	1A(1e) Mountain hemlock closed conifer forest
Tsuga-*Picea*-*Oplopanax* forest	1A(1a-b) Sitka spruce-western hemlock closed conifer forest
Tsuga-*Picea*-*Vaccinium* forest	1A(1b-c)
Tsuga-*Picea*-*Vaccinium* forest outcrop	1A(1b-c)

Appendix II. Results of biomass sampling by species for current annual growth (kg/ha) of ground-rooted forage in each plant community in November 1979. Elevation, aspect and slope angle are given for each plant community stand sampled. t = trace (less than 0.5 kg/ha)

Plant species	Forb-*Cassiope* 1050m S-SW,40°	*Empetrum* subshrub 1050m NW,20°	*Cassiope* heath 950m NW,5°	*Calamagrostis* meadow 900m W,30°	*Veratrum* meadow 840m S,30°	*Fauria* meadow 810m NW,15°	*Carex* muskeg 580m level	*Tsuga*-*Picea* krummholz 800m SW,30°	*Alnus* shrubland 340m W,15°	*Tsuga*-*Vaccinium* subalpine forest 670m NW,25°	*Tsuga*-*Picea*-*Oplopanax* forest 325m NW,20°	*Tsuga*-*Picea*-*Vaccinium* forest 350m W,25°	*Tsuga-Picea-Vaccinium* forest outcrop 300m W,45°
TREES													
Picea sitchensis	-	-	-	-	-	-	-	19	-	-	2	2	t
Tsuga heterophylla	-	-	-	-	-	-	-	-	-	t	9	19	5
Tsuga mertensiana	-	-	-	-	-	-	-	168	-	29	t	t	-
SHRUBS & SUBSHRUBS													
Alnus sinuata	-	-	-	-	-	-	-	-	59	-	-	-	-
Andromeda polifolia	-	-	-	-	-	-	13	-	-	-	-	-	-
Cassiope mertensiana	2	t	116	-	-	1	-	2	-	-	-	-	-
Cassiope stelleriana	t	t	43	-	-	t	-	t	-	-	-	-	-
Empetrum nigrum	t	13	-	-	-	-	t	-	-	-	-	-	-
Loiseleuria procumbens	-	1	-	-	-	-	-	-	-	-	-	-	-
Luetkea pectinata	-	-	60	1	-	1	-	-	-	-	-	-	-
Menziesia ferruginea	-	-	-	-	-	-	-	2	-	17	4	5	3
Oplopanax horridus	-	-	-	-	-	-	-	-	32	-	53	-	t
Phyllodoce aleutica	7	-	92	3	-	-	-	1	-	-	-	-	-

Appendix II. (continued)

Plant species	Forb-*Cassiope*	*Empetrum* subshrub	*Cassiope* heath	*Calamagrostis* meadow	*Veratrum* meadow	*Fauria* meadow	*Carex* muskeg	*Tsuga*-*Picea* krummholz	*Alnus* shrubland	*Tsuga*-*Vaccinium* subalpine forest	*Tsuga*-*Picea*-*Oplopanax* forest	*Tsuga*-*Picea*-*Vaccinium* forest	*Tsuga*-*Picea*-*Vaccinium* forest outcrop
Ribes bracteosum	-	-	-	-	-	-	-	-	t	-	-	-	-
Rubus spectabilis	-	-	-	-	-	-	-	-	t	-	-	-	-
Salix spp. (shrub)	t	-	-	-	-	-	-	-	1	-	-	-	-
Salix spp. (subshrub)	1	3	-	1	-	-	-	-	-	-	-	-	-
Sambucus racemosa	-	-	-	-	-	-	-	-	2	-	-	-	-
Saxifraga oppositifolia	t	-	-	-	-	-	-	-	-	-	-	-	-
Silene acaulis	t	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium spp. (shrub)	-	-	-	-	-	-	4	10	-	150	2	54	3
Vaccinium spp. (subshrub)	2	4	-	1	-	-	-	-	-	-	-	-	-
FORBS & FERNS													
Athyrium filix-femina (fronds)	-	-	-	-	-	-	-	-	171	-	24	-	-
(new shoots)	-	-	-	-	-	-	-	-	113	-	19	-	-
Coptis asplenifolia	-	-	-	-	-	-	-	-	-	10	-	6	t
Cornus canadensis	-	-	-	-	-	-	-	-	-	1	-	11	4
Claytonia sibirica	-	-	-	-	7	-	-	2	-	-	-	-	-
Dryopteris dilatata	-	-	-	-	1	-	-	-	-	-	-	-	-
Fauria crista-galli	-	-	-	-	-	63	t	-	-	-	-	-	-

Appendix II. (continued)

Plant species	Forb-Cassiope	*Empetrum* subshrub	*Cassiope* heath	*Calamagrostis* meadow	*Veratrum* meadow	*Fauria* meadow	*Carex* muskeg	*Tsuga-Picea* krummholz	*Alnus* shrubland	*Tsuga-Vaccinium* subalpine forest	*Tsuga-Picea-Oplopanax* forest	*Tsuga-Picea-Vaccinium* forest	*Tsuga-Picea-Vaccinium* forest outcrop
Heracleum lanatum	-	-	-	-	29	-	-	-	-	-	-	-	-
Lupinus nootkatensis	-	-	-	-	12	-	-	-	-	-	-	-	-
Lycopodium spp.	t	-	-	-	-	-	-	-	-	-	-	5	t
Petasites frigidus	-	-	-	-	-	1	t	-	-	-	-	-	-
Pyrola secunda	-	-	-	-	-	-	-	-	-	-	12	2	1
Rubus pedatus	-	-	-	5	-	-	-	15	-	15	13	17	6
Sanguisorba stipulata	-	-	-	-	t	1	-	-	-	-	-	-	-
Tiarella spp.	-	-	-	-	-	8	-	-	10	1	28	-	3
Veratrum viride	-	-	-	-	63	1	-	-	-	-	-	-	-
unidentified	-	-	-	35	41	t	t	-	-	-	-	-	-
GRAMINOIDS													
Calamagrostis canadensis	t	-	-	181	9	-	-	-	-	-	-	-	-
Carex circinnata	12	3	-	-	-	-	-	-	-	-	-	-	-
Carex macrochaeta	4	-	-	132	152	24	-	9	-	-	-	-	-
Carex spp.	-	-	-	-	-	48	226	-	-	-	-	-	-
Elymus spp.	-	-	-	t	2	t	-	-	t	-	-	-	-
Hierochloe alpina	11	2	-	-	-	-	-	-	-	-	-	-	-
Juncus spp.	-	-	-	-	-	2	6	-	-	-	-	-	-
Luzula arcuata	13	2	2	-	1	3	-	7	-	-	-	-	-
Poa alpina	t	t	-	-	-	-	-	t	-	-	-	-	-
LICHENS	3	3	9	7	-	-	-	-	1	t	1	t	t

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