HABITAT USE AND SPATIAL ORGANIZATION OF PINE MARTEN ON SOUTHERN VANCOUVER ISLAND, BRITISH COLUMBIA

by

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Habitat use and spatial organization of pine marten on southern Vancouver Island, British Columbia.

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ABSTRACT

Seasonal food habits of marten (Martes americana) were determined from 126 scats collected in the Nanaimo River Watershed between May 1987 and October 1989. Major prey groups were small mammals and ungulates during winter; birds and ungulates during spring; small mammals, berries and insects during summer; and berries and insects during autumn. Home range and habitat use were investigated using radio telemetry. Densities of marten calculated from trap capture data were between 1.1 and 1.3 marten/km^2. Mean annual home ranges of marten were 2.7 km^2 for females and 4.8 km^2 for males. Seasonal home ranges of marten on Vancouver Island were smaller than those of marten elsewhere in North America. Overlap of home ranges occurred between the sexes as well as among individuals of the same sex. The extent of overlap varied and was confined primarily to the peripheries of home ranges. Core areas of exclusive use were exhibited by males and females. On Vancouver Island, marten use cutovers less than expected based on availability. Their use of second growth forest was greater and use of mature forest and old growth forest was less than that observed elsewhere in North America. Seven natal den sites were located and all were in second growth forest. Most of the dens were in large stumps (> 1.0 m diameter) and in piles of course woody debris (mean piece size > 50 cm diameter).

Large amounts of course woody debris occurred at nearly all marten locations. Because of past logging practices, second growth stands in the Nanaimo River Watershed have frequent canopy openings, abundant understory shrubs and herbaceous vegetation, and high densities of course woody debris. Combined, these habitat characteristics retain some of the structure of old growth forests. Perhaps it is this structure that allows marten to meet their life requisites in younger forest stands on Vancouver Island.

ACKNOWLEDGEMENTS

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I thank MacMillan Bloedel, Cowichan Woodlands Division for allowing me to work on their private land. I would also like to thank all the MB personnel who I met in my travels through the study area, especially Al Dirks, who not only gave me an opportunity to talk to someone other than my two canine companions, but also kept my access routes safe for travel. I thank Bill Shuckel for providing silvicultural information for the study area.

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Completing this project would have been extremely difficult had it not been for Pete. He endured my 'moods' admirably - much better than I probably would have done if our places had been reversed - and was always available when I needed him. Thank you for being so patient.

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GENERAL INTRODUCTION

Marten (Martes americana) are medium sized carnivores in the Family Mustelidae and occur throughout forested regions of British Columbia. In B. C., marten are classified as furbearers and provide the greatest total revenue from trapped species (Blood 1987). The trapping season extends from 15 November to 28 February and is scheduled to protect marten from harvesting during breeding and parturition. Marten are easily trapped and this has led to overharvest in many settled and easily accessible areas. High prices for pelts in the late 1980's and concomitant high harvests elicited concern about management of marten.

In North America, the geographical range of marten coincides with the distribution of coniferous forests (Marshall 1951). Because early seral stages are thought to be poor habitat for marten, harvesting of old growth forests is believed to be detrimental to marten populations (Campbell 1979, Soutiere 1979). The apparent association of marten with climax forests, coupled with their position as secondary consumers, has prompted wildlife managers to tout marten as an old growth dependent species and an indicator of environmental change (Irwin and Cole 1987). The notion that marten are old growth dependent stems mainly from research conducted in the United States (including Alaska) and eastern Canada. Five studies of marten have been conducted in British Columbia. Four of these studies describe food habits in interior forests (Cowan and MacKay 1950, Quick 1955), the Queen Charlotte Islands (Nagorsen et al. 1991) and Vancouver Island (Nagorsen et al. 1989). Only one study, (Kelly 1982), examined habitat relationships in interior forests.

Aside from two food habits studies (Nagorsen et al. 1989, 1991), the biology and habitat relationships of marten have not been examined in coastal ecosystems. Because of climatic, floristic and faunistic differences between coastal and interior B. C., I hypothesized that the ecological relationships of marten in coastal ecosystems may differ from those of marten in interior ecosystems. To facilitate this comparison, I conducted an ecological study of marten in the Nanaimo River Watershed on Vancouver Island. I describe the food habits of marten in Chapter 1. In Chapter 2, I examine home range and spatial organization of marten. In Chapter 3, I examine habitat use of marten in coastal forests.

STUDY AREA

My study area was located in the Nanaimo River Watershed on Vancouver Island, British Columbia. The 65 km^2 study area is on privately owned land (MacMillan Bloedel Limited) centered at $49^o1'$ N, $124^o8'$ W, 20 km southwest of Nanaimo (Fig. 1). The terrain is mountainous with steep U-shaped valleys arranged in an east - west direction. Elevations range from 305 to 1400 m.

The study area is in the Coastal Western Hemlock Biogeoclimatic Zone (Klinka et al. 1984). Approximately 25% of the area is in the wetter subzone (Leeward Montaine Maritime variant, CWHb4) and forest stands are dominated by western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*). The remainder of my study area is in the drier maritime subzone (Vancouver Island variant, CWHa1) and forest stands are dominated by Douglas fir (*Psuedotsuga menziesii*) with some western hemlock and western redcedar (*Thuja plicata*).

Intensive logging, which began in the study area during the 1940's, has resulted in a mosaic of successional stages (Fig. 2). Wildfires during 1965-66 burned approximately 8% of the area and has resulted in stands of mixed pole-sapling and old growth trees. Cutovers (≤ 10-years-old) comprise 41% of the area, second growth stands (> 10 - ≤ 40-years-old) 35%, mature stands

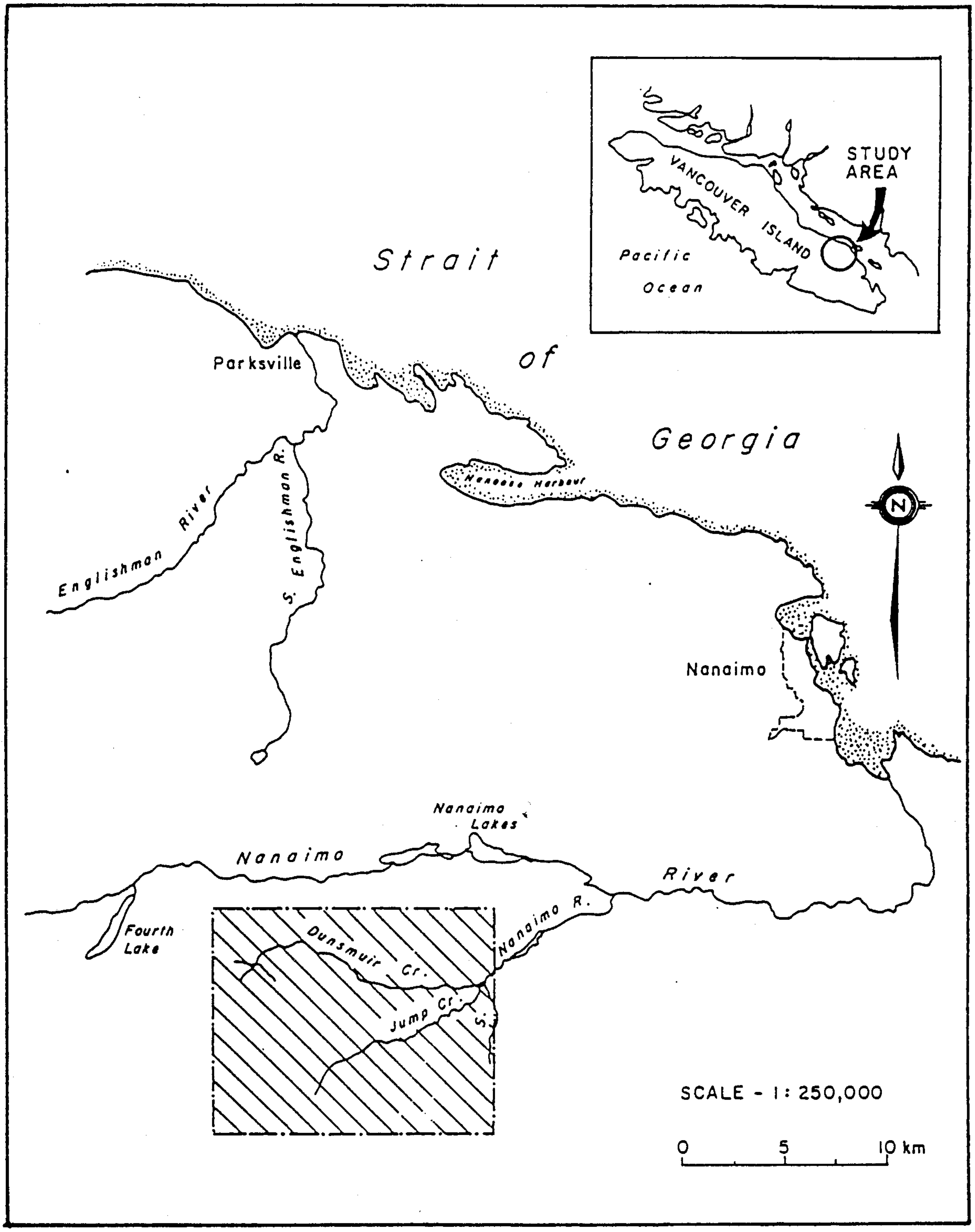

Fig. 1. Study area in Nanaimo River Watershed, British Columbia.

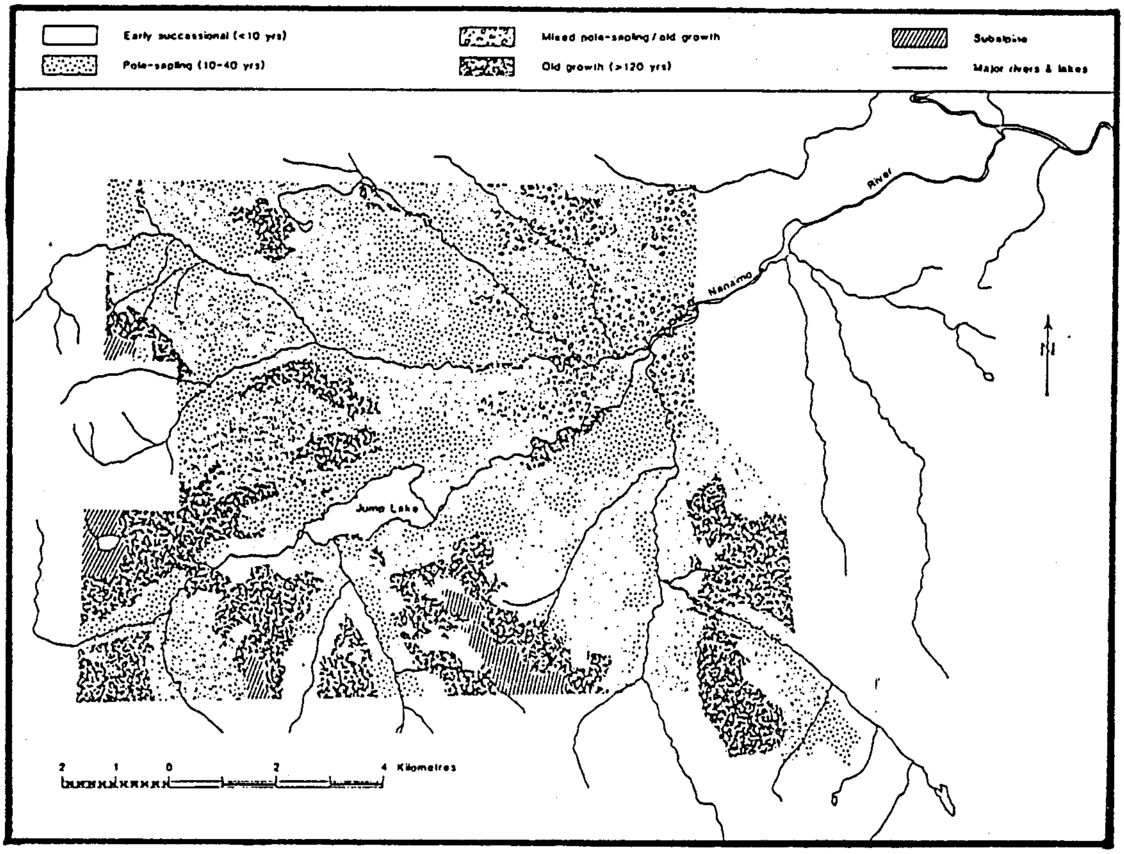

Fig. 2. Successional stage mosaic in the Nanaimo River Watershed that was created by forest harvesting and fire (from McNay and Doyle 1987).

(mixed pole-sapling and old growth trees > 40 - ≤ 120-years-old) 8% and isolated stands of old-growth forest (> 120-years-old) 16% (Fig. 2). Restocking of harvested areas has been exclusively with Douglas fir. A thinning program has been implemented on some pole-sapling stands to reduce stem density. During 1987-1989, logging was limited to the periphery of the study area.

The climate of the area is West Coast Marine and characterized by mild winters. Based on data collected at the Nanaimo Airport from 1902 to 1991, the mean annual precipitation is 945 mm and mean annual snowfall is 245 cm. During my study (1987-1989), snowfall occurred within the Nanaimo River Watershed from November to April and snow depth was recorded weekly. Total annual snowfall for the area was 40.6 cm in 1987-1988 and 321.0 cm in 1988-1989. Snowpacks in the study area were ephemeral. Temperatures were moderate with a mean of 3.2° C in January and a mean of 18° C in July.

Commercial trapping within the study area is conducted by three licensed trappers. To facilitate my study, trapping was voluntarily suspended beginning October 1986.

CHAPTER 1

FOOD HABITS

Several food habits studies of marten have been conducted in western North America. These studies have been largely limited to noncoastal areas of Alaska (Lensink et al. 1955, Buskirk and MacDonald 1984), Northwest Territories (More 1978, Douglass et al. 1983), Yukon (Slough et al. 1989), as well as northeastern British Columbia (Quick 1955), the Rocky Mountains (Cowan and MacKay 1950, Weckwerth and Hawley 1962, Koehler and Hornhocker 1977), the Sierra Nevada of California (Zielinski et al. 1983, Hargis and McCullough 1984) and the eastern Cascades of Washington (Newby 1951). Only Nagorsen et al. (1989, 1991) have published information on marten diets in Pacific Coast habitats and they only reported winter diets.

Marten have been described as being opportunistic as well as selective in their food choice (Buskirk and MacDonald 1984). Studies have shown that marten forage on food items relative to their availability, which results in seasonal shifts in diet. As well, marten select specific prey species as shown by their consuming a higher proportion of some prey groups than their availabilities indicate (Francis and Stephenson 1972, Douglass et al. 1983, Buskirk and Macdonald 1984, Slough et al. 1989).

Information about seasonal variation in diets of marten is required to understand aspects of habitat use and for effective management of marten. Species and diversities of prey along the Pacific Coast are different from interior regions and seasonal availabilities of prey also likely differ. Therefore, diets of marten in interior regions may be quite different from those of marten inhabiting the Pacific Coast. Because little is known of marten diets along the Pacific Coast, my objectives were: to identify types of prey consumed and estimate their relative contribution to seasonal diets of marten; and to examine associations of prey groups within marten scats.

Use of frequency as a measure of prey importance has potential bias. During feeding trials using captive marten, Zielinski (1986) found that the importance of small prey in marten diets, determined from marten scats, is overestimated because small prey have a higher ratio of undigestible matter in their bodies and also because small prey tend to be entirely consumed. In contrast, marten feed selectively upon particular body parts of large prey, resulting in little undigestible matter being consumed. As well, large prey have a lower ratio of undigestible matter in their bodies. The disparity, between what is consumed and what is estimated to be consumed, becomes more exaggerated as prey size differences increase (Zielinski 1986). Therefore, analyses of scats from marten on Vancouver Island, which feed on a wide range of prey groups from insects to ungulates, may yield biased results if based solely on frequency of occurrence. To reduce potential bias resulting from differences in amounts of undigested material among prey, the relative importance of food items identified in my study was expressed as a proportion of total scat weight. Frequency of occurrence was also calculated to facilitate comparison with other studies.

Materials and Methods

A total of 126 scats were collected from May 1987 through October 1989 in the Nanaimo River Watershed on Vancouver Island, British Columbia. Scats were collected from livetraps at marten capture sites and wherever else they were encountered. Standard techniques for studies of carnivore diets (Korschgen 1980) were used to analyze marten scats. Each scat was rehydrated in water. Dishwashing detergent was added to the water to help remove grease from the scats. After soaking overnight, scats were washed and drained using #30 (screen size 0.0059 mm) and #50 (screen size 0.0030 mm) soil sieves.

Scats were then placed in individual petri dishes and dried at 60^{o} C for at least 48 h.

Once dried, scats were examined under a dissecting microscope and the different prey groups were separated and weighed to the nearest 0.001 g. Food items were assigned to the following prey groups: small mammal, ungulate, bird, berry, insect and unidentified matter. Scats were classified by season: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). Food items suspected of being incidentally ingested (leaves, needles), or fish used as bait were generally less than 0.1% of the scat and were disregarded.

Presence and dry weight (to nearest 0.001 g) were recorded for each prey group in each scat. To determine percent frequency of occurrence, each scat containing a food item was expressed as a percentage of the total number of scats in each season as well as a percentage of the total number of scats. Percent weight was determined using both total weight of prey groups for each season and total weight of prey groups on an annual basis. The numbers of prey groups per scat were tabulated disregarding fish (i.e. bait), vegetation and unidentified matter.

Results

Prey Groups

The major prey groups of marten from May 1987 to October 1989 were berries and small mammals, which contributed 35.2% and 26.9% of total scat weight, respectively (Fig. 3). Minor prey groups in their diet were insects (18.1%), followed by birds (8.5%), ungulates (8.2%) and unidentified matter (3.1%).

Variation in food habits was evident among seasons (Fig. 3). During winter, small mammals (65.1%) and ungulates (23.9%) were the major prey groups, which together comprised 89% of scat weight. Birds, berries and insects comprised only 11% of the winter diet. During spring, birds (40.6%) and ungulates (29.4%) were major prey groups with small mammals (19.9%) the next most important prey group. Berries, insects and unidentified matter comprised a total of 10.1% of the spring diet. During summer, there were three major prey groups; small mammals (30.5%), berries (28.9%) and insects (27.4%). The remainder of the diet was comprised of two minor prey groups; birds (7.9%) and ungulates (3.2%). During autumn, berries (68.3%) and insects (20.5%) dominated the diet. Small mammals (6.4%), birds (0.2%) and unidentified matter (< 0.1%) comprised the remainder of the autumn diet.

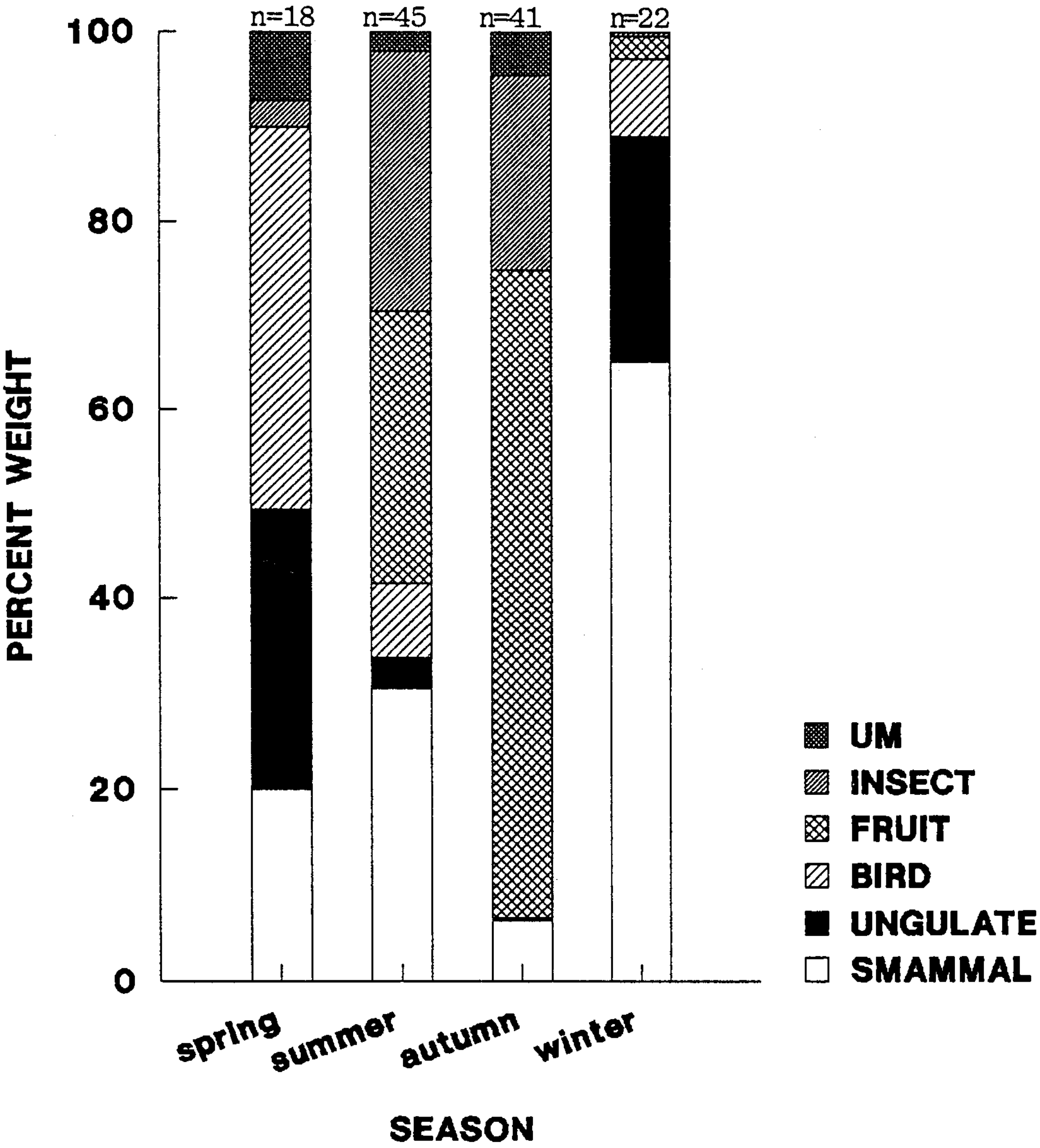

Fig. 3. Percent weight by season of prey groups in 126 marten scats collected between May 1987 and October 1989 from the Nanaimo River Watershed, Vancouver Island, British Columbia. UM=unidentified matter, SMAMMAL=small mammal.

Percent frequency of occurrence was calculated to allow for comparison with other studies. Although limited in its utility, percent frequency of occurrence is broadly consistent with percent by weight of the 126 marten scats that I collected (Fig. 4).

Associations Among Prey Groups

For 126 scats, the mean number of prey groups per scat was 1.6 ± 0.1 (SE) and ranged from 1-3 (Fig. 5). The majority of scats contained only one or two prey groups 49.2% and 39.7%, respectively. Only 11.1% of scats contained remains from three prey groups.

A high level of association between prey groups was detected. Of scats containing berries, 24-44% also contained small mammals or insects. In 34% of scats containing ungulate, no other prey group was found. Both ungulates and birds had low levels of association (< 10%) with berries and insects.

Discussion

Marten have been described as being both arvicolid and microtine specialists (Rosenzweig 1966, Douglass et al. 1983) as well as being dietary opportunists (Simon 1980, Buskirk and MacDonald 1984, Slough et al. 1989).

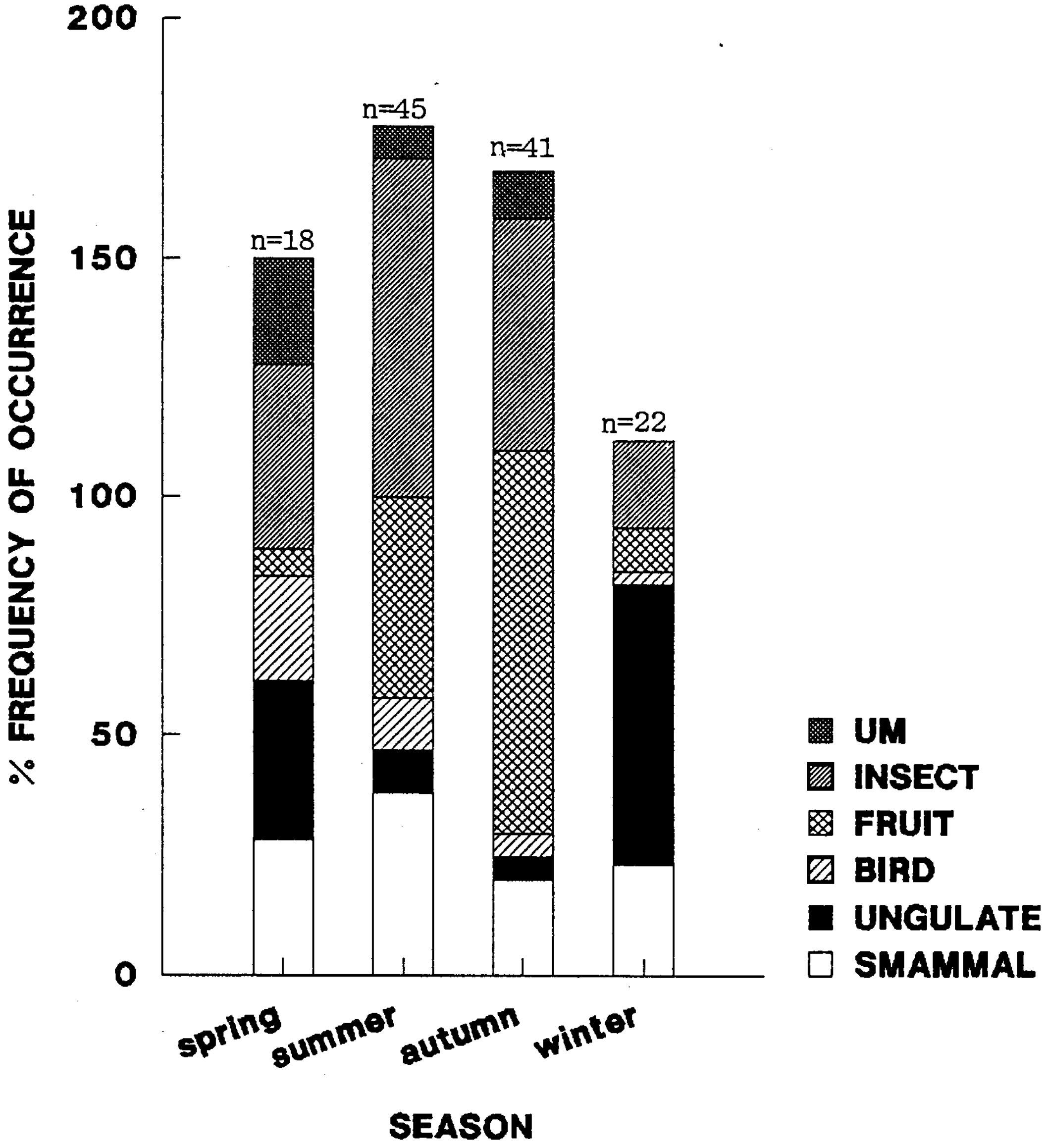

Fig. 4. Percent frequency of occurrence by season of prey groups in 126 marten scats collected between May 1987 and October 1989 from the Nanaimo River Watershed, Vancouver Island, British Columbia. UM=unidentified matter, SMAMMAL=small mammal.

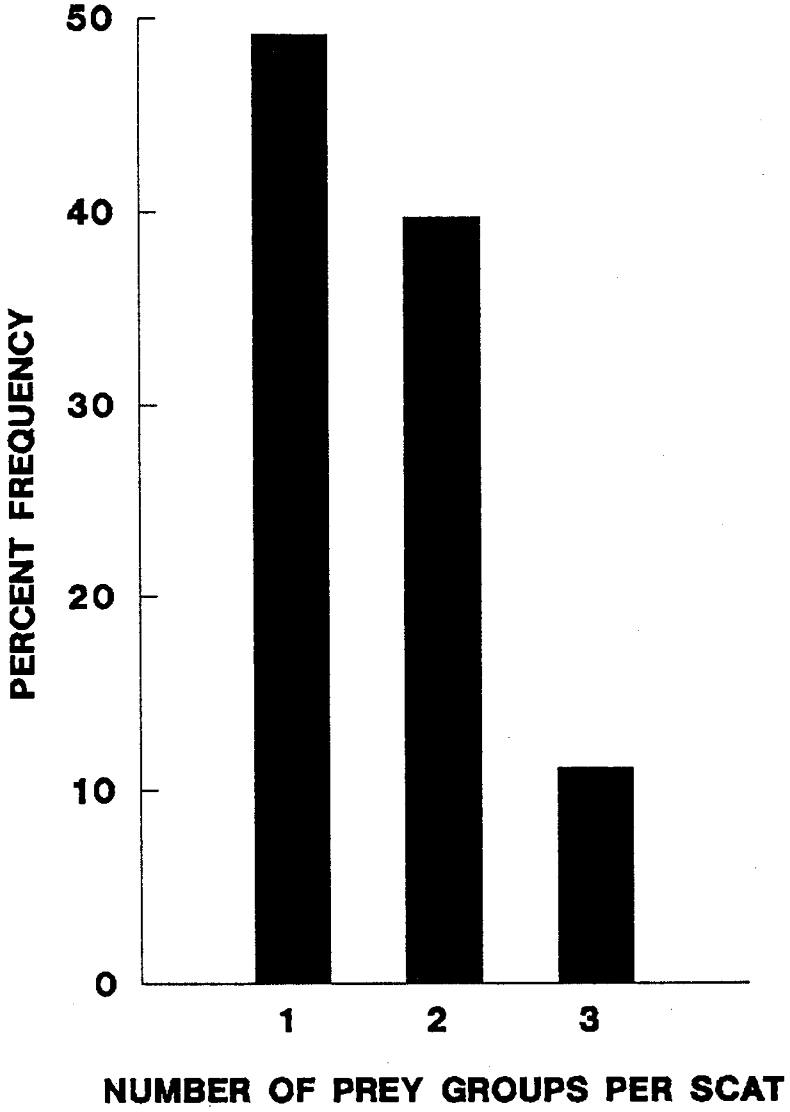

Fig. 5. Frequencies of number of prey groups per marten scat for 126 scats collected between May 1987 and October 1989 from the Nanaimo River Watershed, Vancouver Island, British Columbia.

Studies from most of North America reveal that seasonal shifts in prey occur, but arvicolid species are the dominant prey at all times of the year (Weckwerth and Hawley 1962, Francis and Stephenson 1972, Zielinski et al. 1983, Buskirk and MacDonald 1984, Slough et al. 1989). On Vancouver Island, marten exhibit seasonal changes in prey dominance. These changes indicate that marten have seasonal diets and suggest that marten specialize on seasonally available prey. Marten, on Vancouver Island, prey on different species of small mammals than they do on continental North America. Deer mice, although typically a minor proportion of marten diets on the mainland of British Columbia, are the predominant species of small mammal eaten by marten on Vancouver Island during winter (Nagorsen et al. 1989). My results (Fig. 3) are consistent with other studies of marten diets in that small mammals are the dominant prey group present in winter scats.

Vancouver Island has a depauperate small mammal fauna compared to the mainland of British Columbia and so only deer mouse, house mouse (Mus musculus), black rat (Rattus rattus), Norway rat (Rattus norvegicus), vagrant shrew (Sorex vagrans), dusky shrew (S. monticolus), Townsend's vole (Microtus townsendii) and red squirrel (Tamiasciurus hudsonicus) are potentially available to marten. Forest dwelling voles (e.g. boreal redback vole, Clethrionomys gapperi) are major prey of marten on continental North America, however, Vancouver Island has only one species of vole, Microtus townsendii, which is restricted to pockets of grassy meadow or riparian habitats (Cowan and Guiguet 1960). Other rodents potentially available to marten include muskrat (Ondatra zibethica) and beaver (Castor canadensis), which are common in riparian zones on Vancouver Island. Only one lagomorph species, eastern cottontail (Sylvilagus floridanus) is available on Vancouver Island. It was introduced in the late 1960's near Victoria and has successfully colonized the southern portion of the island (Nagorsen et al. 1989).

Changes to prey dominance in marten diets occurred during each of the four seasons. During autumn, berries were the major prey group and small mammals contributed a minor proportion to the marten's diet, although the deer mouse population was at its greatest seasonal density (D. Carter pers. comm.). During autumn, 33% of the scats with berries, contained only berries, suggesting that berries were selected above other prey groups. Birds and ungulates were major prey groups during spring. The incidence of shell fragments and feather sheaths indicates that marten exploited bird nests. The consumption of birds by marten during spring has also been reported in Ontario (Francis and Stephenson 1972). Prey dominance is shared during summer among small mammal, berry and insect prey groups. At this time, deer mouse populations are high (D. Carter, pers. comm.) and berry and insect abundance is high.

Marten scavenge from ungulate carcasses (Francis and Stephenson 1972). Although this scavenging typically does not constitute a large portion of the diet, it is important in diets of marten in Newfoundland (Bateman 1968). Nagorsen et al. (1989), however, found a greater proportion of ungulate in marten diets on Vancouver Island than had been reported elsewhere and suggested this was due to the abundance of wolves (Canis lupus) and the resulting high availability of ungulate carcasses to marten. In addition to wolves, there are also cougar (Felis concolor) within the Nanaimo River Watershed. Both of these species prey mainly on Columbian blacktail deer (Odocoileus hemionus columbianus). Remains from wolf and cougar kills ensure that marten have deer carcasses readily available. In scat analyses, the importance of small prey tends to be overestimated and that of large prey tends to be underestimated (Zielinski 1986). Because of these biases, ungulate carrion may be more important on Vancouver Island than my data indicate. While never attaining the position of a dominant prey group, ungulates are a distinct codominant in diets of marten on Vancouver Island during both winter and spring.

Consumption of insects by marten has been recorded in diet studies from many places in North America (Quick 1955, Murie 1961, Weckwerth and Hawley 1962, Francis and Stephenson 1972, Douglass et al. 1983, Zielinski et al. 1983, Raine 1987, Nagorsen et al. 1989, Slough et al. 1989). These authors conclude that insect remains occur often but contribute little to the marten's diet. My results support this conclusion in that insects were never a dominant prey group, although during summer and autumn, insects were more important than they were during winter and spring. Typically more than one individual of the same insect species (usually wasps - Family Vespidae), were found in single scats during summer and autumn, indicating that marten were likely feeding on insect nests rather than taking insects incidentally. Only occasional small fragments of insects were present in scats in winter and spring, suggesting that insects were consumed incidentally during these periods.

Associations of prey groups within scats is seldom examined in studies of carnivore diets. Banci (1987) reported associations of prey groups found in wolverine (Gulo gulo) stomach contents and the importance of different prey groups to this primarily scavenging mustelid species. Marten exhibit patterns more consistent with that of an opportunistic or seasonally selective predator. I am led to this conclusion because the majority of marten scats (89%; N=126) contained remains from only one or two prey groups. The presence in a scat of only one prey group could indicate a tendency for marten to select prey, whereas the presence of two prey groups in a scat suggests that marten exploit some prey upon encounter.

Associations among prey groups reveal seasonal patterns. Prey groups that are abundant during a particular season tend to be found together in the scats. The associations between small mammals, berries and insects are likely a function of the high availability of these prey groups to marten during summer. Consumption of berries and insects by marten is associated with low incidence of both ungulate and birds in scats, suggesting that during summer, when berries and insects are abundant, ungulates and birds are unavailable to marten.

Ungulates tended to occur alone in scats and can be explained by the stomach capacity and foraging efficiency of marten. From qualitative observation in the field, it appeared that marten would continue to investigate sources of food (i.e. trap sites) for a number of days after consuming bait. Therefore, if a marten discovered an ungulate carcass, it would be beneficial to continue to exploit it for as long as it lasted rather than expend energy foraging elsewhere. Also, because an ungulate carcass would be larger than one marten meal, I expected scats to contain remains from only ungulates simply due to the stomach capacity of the marten.

My results are consistent with other studies of marten in that marten on Vancouver Island are opportunistic foragers and they consume a variety of prey. Unlike other studies, however, prey dominance changes seasonally, indicating that marten have a series of seasonal diets. I conclude from my results that marten on Vancouver Island specialize on seasonally available prey and are food generalists rather than arvicolid specialists as in other regions of North America (Cowan and MacKay 1950, Newby 1951, Lensink et al. 1955, Quick 1955, Weckwerth and Hawley 1962, Koehler and Hornhocker 1977, More 1978, Douglass et al. 1983, Zielinski et al. 1983, Buskirk and MacDonald 1984, Hargis and McCullough 1984).

CHAPTER 2

HOME RANGE SIZE AND SPATIAL ORGANIZATION

Home range sizes of marten vary among different habitats and between sexes (Weckwerth and Hawley 1962, Bateman 1968, Koehler et al. 1975, Soutiere 1979). Soutiere (1979) and Harestad and Bunnell (1979) noted that the size of a home range depends on an animal's energy requirements and its available food resources, and so, in part, reflects habitat quality. This relationship between home range size and habitat quality is evident for marten. Soutiere (1979) found that the largest home ranges of marten occurred in cutovers, where small mammal densities were lower than those in surrounding forests. Weckwerth and Hawley (1962) found that during winter, as small mammal populations decreased, the home range size of marten increased. In addition, many studies have shown that home ranges of males are larger than those of females (Hawley and Newby 1957, Francis and Stephenson 1972, Clark and Campbell 1976, Buskirk 1983). This variation in home range size, coupled with sexual dimorphism (males are heavier than females), supports Soutiere's (1979) hypothesis that energy requirements, in part, determine home range size.

Home range sizes of marten also differ between the nonreproductive and reproductive seasons. Home ranges of males increased during the breeding period while those of females remained the same size (Steventon 1979). Wynne and Sherburne (1984) found that activity radii of females increased as summer progressed and they suspected that the dependence of kits on their mothers may have influenced the female's activity radii. Support for this hypothesis comes from Davis (1983), who reported that the movements of a female with kits were concentrated in the immediate area around the natal den during the rearing period.

Different states of spatial organization have been observed for marten. Marten exhibit both territorial and non-territorial behaviour. Female home ranges frequently overlap those of both sexes, and sometimes are totally within a male's home range. Male home ranges do not overlap extensively with other males (Hawley and Newby 1957, Francis and Stephenson 1972, Clark and Campbell 1976, Buskirk 1983, Wynne and Sherburne 1984) and where overlap occurs, individuals tend to be separated temporally. The exclusive use of home ranges by males suggest that there is territoriality between males whereas overlap between female home ranges suggests social tolerance between females (Clark and Campbell 1976).

My objectives were: to determine annual and seasonal home ranges, to describe home range overlap and movements, and to estimate density of marten in coastal forests.

Materials and Methods

Live trapping of marten was conducted throughout the year on a monthly basis from May 1987 to May 1989. Havahart live traps (61 x 18 x 18 cm) were placed at 500 m intervals along roads in the study area and checked daily. Monthly trapping sessions lasted 4 to 7 days. To facilitate immobilization, captured marten were moved from the trap into a holding cone, designed by C. Cross (B.C. Ministry of Environment, Victoria).

Marten were weighed while in the trap to estimate appropriate dosages of anesthetic. Aqueous ketamine hydrochloride ("Rogarsetic", Rogar/STB Ltd.) was administered at concentrations of 15 - 20 mg/kg body weight plus 0.1 cc Atropine. Marten were injected intramuscularly in the back using 1.0 cc syringes and 25 gauge stainless steel needles. Immobilized marten were weighed, measured, ear tagged and tattooed. An upper premolar (PM1) was extracted for aging prior to release. Age class, to be confirmed from cementum analysis of the extracted premolar, was estimated (young of year, juvenile, or adult) based on weight, tooth wear, pelage and condition of testes or mammary glands.

At the onset of the study, radio collars (Lotek Engineering Inc., Aurora Ont.), weighing approximately 32 g were fitted only on 'resident' animals - those marten which had been recaptured within the study area over a 3-month period. It soon became apparent that some marten were more prone to return to traps than others, so from then on radio collars were fitted onto any marten captured, regardless of its 'residency' period.

Monitoring occurred year-round from July 1987 to May 1989. Ground tracking of marten was done using a hand-held null antenna (Telonics Inc., Mesa, AZ). Radio locations were obtained twice a week, except during times of limited access due to fire hazard restrictions or heavy snowfall. If a marten could not be located during a scheduled monitoring time, due to poor access or mountainous terrain, attempts were made to locate it on the following day.

Permanent telemetry stations were established within my study area by McNay and Doyle (1987). I used the same stations and UTM grid system in my study. During field monitoring, compass bearings were taken at 3 to 5 different stations for each marten and the marten's location estimated by triangulation. Date, weather conditions, temperature, the animal's activity and comments were recorded for each location.

A home range is an area normally traversed by an animal over a specific time interval (Burt 1943). It follows that there can be daily, seasonal and lifetime home ranges. The 100% home range contains all the known locations of an individual. Home ranges containing 90% and 50% of the individual's closest locations are useful in identifying areas of intensive use and eliminating unusual movements, whose inclusion could bias estimates of home range parameters. Home ranges can be presented in a number of ways. The minimum home range method (Dalke and Sime 1938) provides a simple spatial description. I used a version of the minimum home range method, modified by Harestad (1979), to identify cores of intensive use.

Logistics of capturing and monitoring of marten, equipment failure and losses of study animals determined the number of marten monitored. Of the 19 marten radio-collared, 2 were lost through transmitter failure shortly after attachment. Three were lost through predation after 1.5 to 3 months of data collection and 1 male died after entangling his collar on a branch in a clearcut 1 month after collar attachment. Problems encountered in recapturing previously collared marten, to renew nonfunctioning collars, resulted in gaps of data collection or, in the case of 1 male, termination of data collection because he was not recaptured for the duration of the study.

Marten lost after a short period of data collection resulted in few locations and so were not used in home range analyses. Marten that were monitored for portions of the year were included for the appropriate seasons.

Therefore, this study consists of complete seasonal home range patterns for 6 marten (3 males; 3 females), and partial patterns for 6 marten (5 males; 1 female). Sufficient locations (> 30 locations obtained over a 6-month period or longer) were obtained for 8 marten (4 males; 4 females) to calculate annual home range sizes.

Seasonal home ranges were determined from relocations collected during periods biologically important to marten. The denning season can be variable but from published information and my field observations, I estimated it to be between February and May. This period likely spans the time from implantation to the end of lactation. The breeding season was estimated to occur between June through September. The winter season (October-January) is a time of dispersal for young of the year.

The Wilcoxon signed-ranks test (Siegel 1956) was used to compare seasonal home range sizes. Home ranges from the breeding season were compared to those from the denning season for both males and females. Breeding and winter season home ranges were also compared.

The Jolly-Seber method of population estimation is fully stochastic and as such accounts for both loss (death and emigration) and dilution (births and immigration) (Jolly and Dickson 1983). Reliability of the method depends on the assumption that the probability of an animal surviving to the next trapping period is independent of its age at first capture. This assumption creates some problems with short-lived animals, such as insects (Manly and Parr 1968), however, this assumption should be valid for long lived species like marten.

Home range overlap between marten were calculated using proportional home ranges from 100% to 10% at intervals of 10%. Proportional home ranges were overlaid on neighbouring marten ranges and the area of overlap measured by planimeter.

Based on annual home ranges, mean areas of overlap were calculated for 4 types of interaction. Female x female interactions refer to the percent of overlap when females overlap with other females and male x male interactions refer to when male ranges overlap. Female x male interactions exist when female ranges overlap with males and the calculated percent of overlap refers to overlap of the female home range by the male's home range. Male x female interactions are also an interaction between the sexes and the percent of overlap refers to the overlap of the male's home range by the female's home range. Overlap was also examined for seasonal home ranges.

Results

Annual Home Range Size

Sufficient data (> 30 locations obtained over a minimum 6-month period) were collected on 1 juvenile female, 3 adult females and 4 adult males to calculate annual 100%, 90% and 50% home ranges (Tables 1, 2 and 3 respectively). The mean 100% home ranges of adult males was 4.8 km^2 and that of adult females was 2.7 km^2. The mean 90% home ranges for adult males was 2.8 km^2 and that of adult females was 1.7 km^2. The mean 50% home range for adult males was 0.9 km^2 and that of adult females was 0.7 km^2. There was a large degree of variation between home ranges of individuals (Tables 1, 2 and 3), however mean male home ranges were between 1.3 - 1.8 times larger than those of females.

Seasonal Home Range

Individual marten did not occupy the same area from season to season. With the exception of 1 adult male, however, all seasonal home ranges of 9 marten (5 males; 4 females) overlapped with their other two seasonal home ranges (Figs. 6-14).

TABLE 1. Seasonal and annual home ranges containing 100% of observations for 12 marten radio-collared in the Nanaimo River Watershed, Vancouver Island, British Columbia, 1987-1989.

SIZE OF HOME RANGE (km^2)

ANIMAL	DENNING Feb-May	BREEDING Jun-Sep	WINTER Oct-Jan	ANNUAL Jan-Dec
Young of Year Males				
Yogi	2.13(n=17)	-	-	2.13(n=17)*
Victor	5.86(n=20)	-	-	5.91(n=21)*
Adult Males				
Skippy	-	3.13(n=16)	-	3.13(n=16)*
Harry	2.10(n=25)	1.27(n=11)	3.51(n=20)	3.76(n=56)
Yogi2	1.87(n= 8)	1.25(n=18)	1.16(n=19)	2.52(n=45)
Vic2	6.35(n= 7)	5.80(n=10)	4.40(n=17)	7.80(n=34)
Larry	0.97(n=27)	0.51(n= 6)	-	1.04(n=33)*
Kermit	1.04(n= 6)	2.27(n=14)	1.97(n=11)	5.09(n=31)
MEAN (SE)	2.47(0.89)	2.37(0.71)	2.76(0.64)	4.79(0.98)
n	5	6	4	4
Young of Year Females				
Janey	0.61(n=28)	0.71(n=17)	0.90(n=41)	1.11(n=86)
Adult Females				
Amy	1.85(n=100)	0.44(n= 5)	1.21(n=36)	2.36(n=141)
Winny	1.22(n=102)	0.17(n= 9)	0.23(n=19)	1.34(n=130)
Noreen	4.02(n=116)	2.41(n=13)	-	4.48(n=129)
MEAN (SE)	2.36(0.69)	1.01(0.58)	0.72(0.35)	2.73(0.76)
n	3	3	2	3

* not used in annual home range calculation

TABLE 2. Seasonal and annual home ranges containing 90% of observations for 12 marten radio-collared in the Nanaimo River Watershed, Vancouver Island, British Columbia, 1987-1989.

SIZE OF HOME RANGE (km^2)

ANIMAL	DENNING Feb-May	BREEDING Jun-Sep	WINTER Oct-Jan	ANNUAL Jan-Dec
Young of Year Males				
Yogi	0.74(n=15)	-	-	0.74(n=15)*
Victor	2.09(n=18)	-	-	2.09(n=18)*
Adult Males				
Skippy	-	1.61(n=13)	-	1.63(n=15)*
Harry	1.31(n=22)	0.70(n=9)	2.27(n=18)	2.39(n=50)
Yogi2	1.44(n= 7)	0.67(n=16)	0.73(n=17)	1.36(n=40)
Vic2	1.41(n= 6)	3.63(n= 9)	3.81(n=16)	3.90(n=27)
Larry	0.64(n=24)	0.14(n= 5)	-	0.69(n=29)*
Kermit	0.80(n= 5)	1.62(n=12)	1.02(n= 9)	3.71(n=26)
MEAN (SE)	1.12(0.15)	1.39(0.51)	1.96(0.61)	2.84(0.42)
n	5	6	4	4
Young of Year Females				
Janey	0.45(n=25)	0.64(n=15)	0.56(n=36)	0.94(n=76)
Adult Females				
Amy	1.28(n=90)	0.17(n= 4)	0.97(n=32)	1.49(n=126)
Winny	0.49(n=91)	0.14(n= 8)	0.15(n=17)	0.57(n=116)
Noreen	2.87(n=104)	0.58(n=11)	-	2.92(n=117)
MEAN (SE)	1.55(0.57)	0.30(0.12)	0.56(0.29)	1.66(0.56)
n	3	3	2	3

*not used in annual home range calculation

TABLE 3. Seasonal and annual home ranges containing 50% of observations for 12 marten radio-collared in the Nanaimo River Watershed, Vancouver Island, British Columbia, 1987-1989.

SIZE OF 50% HOME RANGE (km^2)

ANIMAL	DENNING Feb-May	BREEDING Jun-Sep	WINTER Oct-Jan	ANNUAL Jan-Dec
Young of Year Males				
Yogi	0.10(n= 9)	-	-	0.10(n= 9)*
Victor	0.55(n=11)	-	-	0.55(n=11)*
Adult Males				
Skippy	-	0.18(n= 8)	-	0.23(n= 9)*
Harry	0.36(n=13)	0.36(n=13)	0.22(n= 6)	0.68(n=32)
Yogi2	0.02(n= 4)	0.22(n= 9)	0.19(n=10)	0.41(n=23)
Vic2	0.10(n= 4)	0.03(n= 5)	0.70(n= 9)	1.48(n=18)
Larry	0.11(n=14)	0.01(n= 3)	-	0.18(n=17)*
Kermit	0.04(n= 3)	0.52(n= 7)	0.03(n= 6)	0.83(n=16)
MEAN(SE)	0.13(0.05)	0.22(0.07)	0.29(0.13)	0.85(0.17)
n	5	6	4	4
Young of Year Females				
Janey	0.13(n=14)	0.16(n= 9)	0.14(n=21)	0.24(n=44)
Adult Females				
Amy	0.53(n=50)	0.07(n= 3)	0.36(n=18)	0.64(n= 71)
Winny	0.10(n=51)	0.02(n= 5)	0.03(n=10)	0.12(n= 66)
Noreen	1.21(n= 58)	0.05(n= 7)	-	1.37(n= 66)
MEAN(SE)	0.61(0.27)	0.05(0.01)	0.20(0.12)	0.71(0.29)
n	3	3	2	3

* not used for annual home range calculation

During the breeding and denning seasons, 100% home ranges were examined for 8 adult marten (5 males; 3 females) (Tables 1, 2 and 3). The mean male home range during these periods was not significantly different from that of females (Wilcoxon signed-ranks test; $P > 0.10$). Home ranges of females during the denning period were not significantly different from those during the breeding season (Wilcoxon signed-ranks test; $P = 0.11$). Despite these statistical tests, in all cases female home ranges during the denning period were larger than those during the breeding season. With the exception of 1 male with a small sample size for the denning season, all male 100% home ranges during the denning season were larger than male home ranges during the breeding season, however these differences were not significant (Wilcoxon signed-ranks test; $P > 0.10$).

Home ranges during the breeding and winter seasons were compared for 7 marten (4 males; 3 females). Breeding home ranges of females were not significantly different from winter home ranges (Wilcoxon signed-ranks test; $P = 0.11$). Male home ranges for these seasons did not differ significantly. With the exception of 1 male, where only a few locations were obtained for the winter season, all male home ranges during the breeding seasons were larger than their home ranges during the winter season, however, these differences were not significant (Wilcoxon signed-

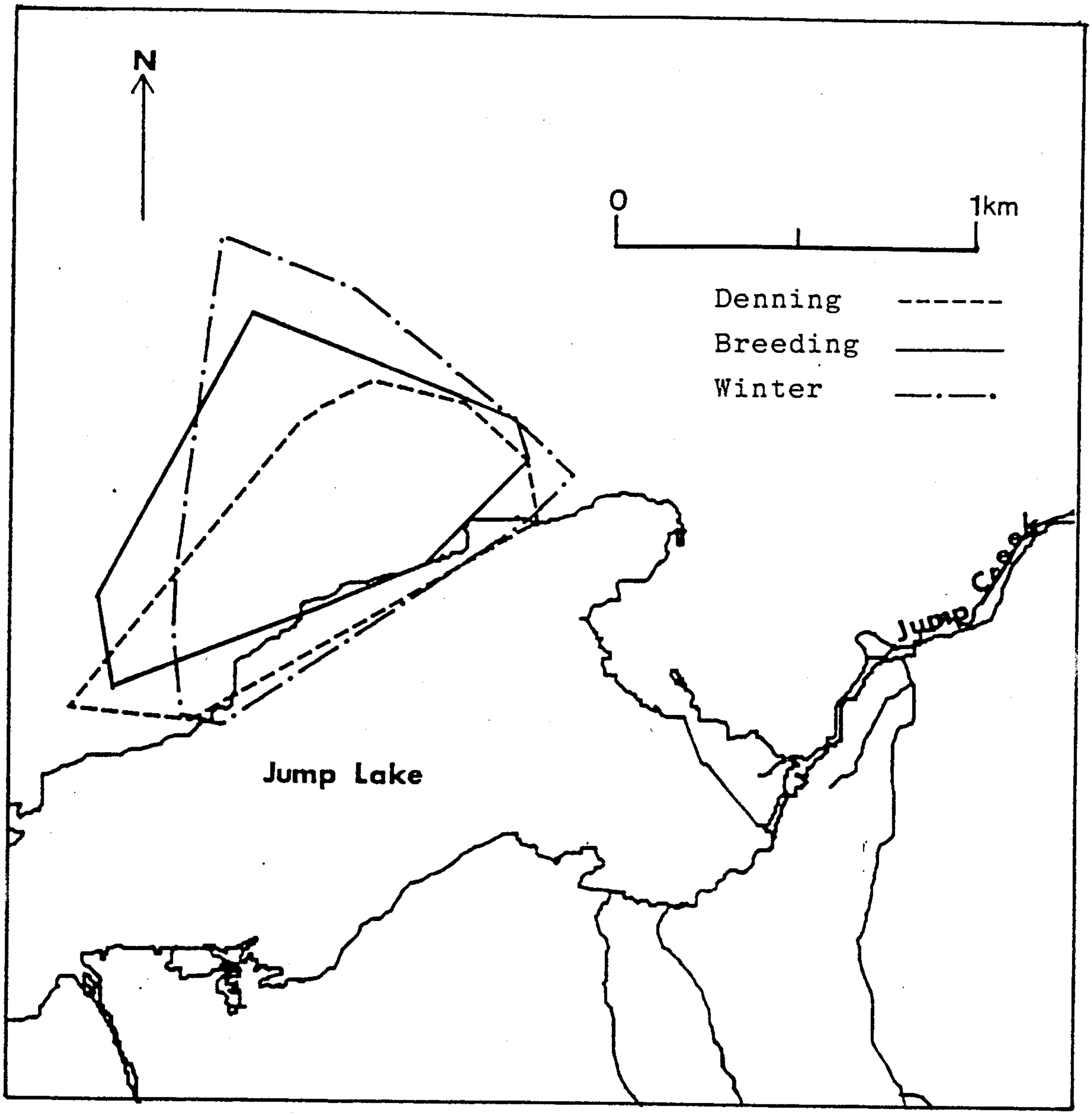

Fig. 6. Seasonal 100% home ranges for radio-collared juvenile female, Janey, Nanaimo River Watershed. 1987-1989.

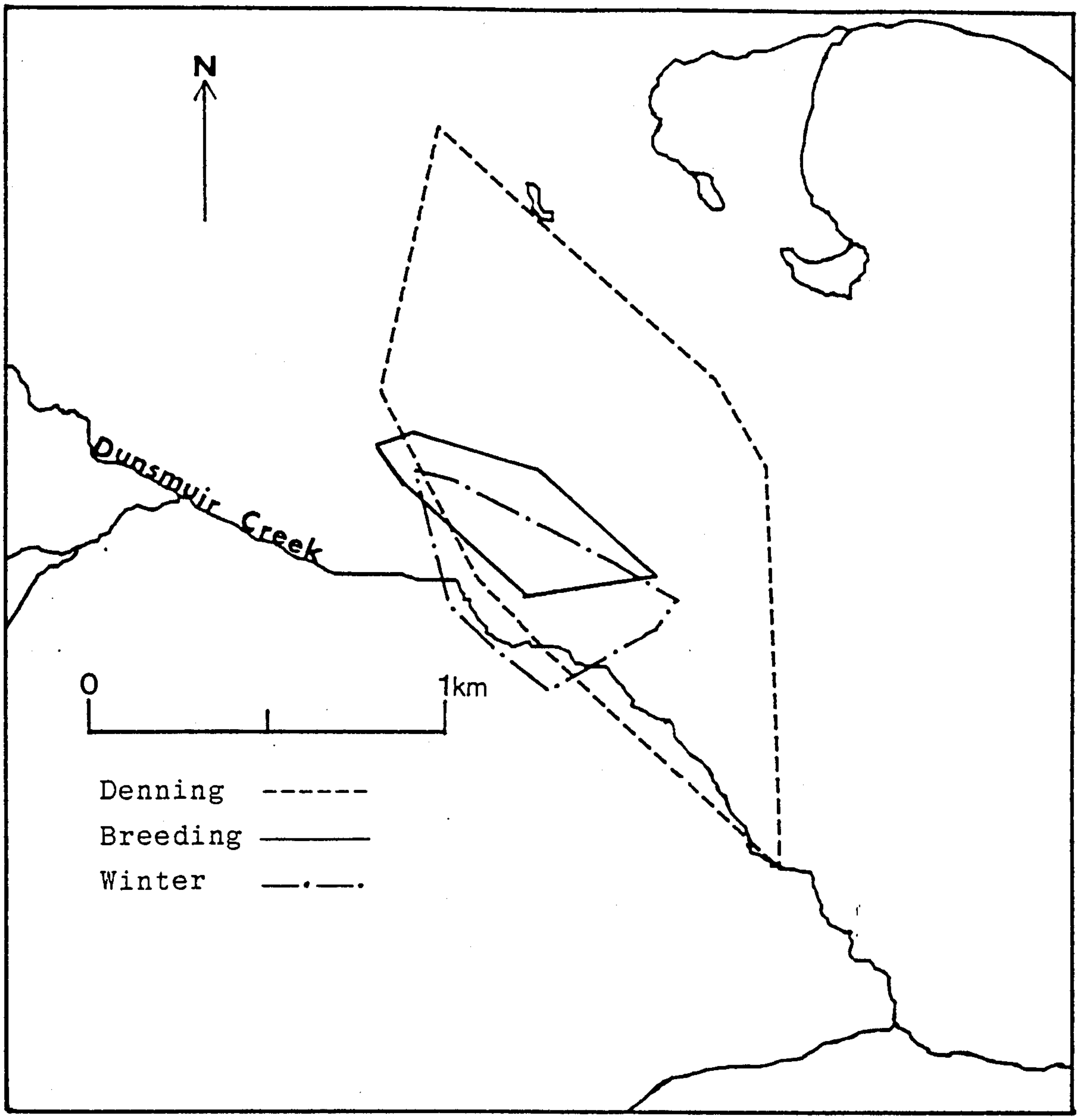

Fig. 7. Seasonal 100% home ranges for radio-collared adult female, Winny, Nanaimo River Watershed. 1987-1989.

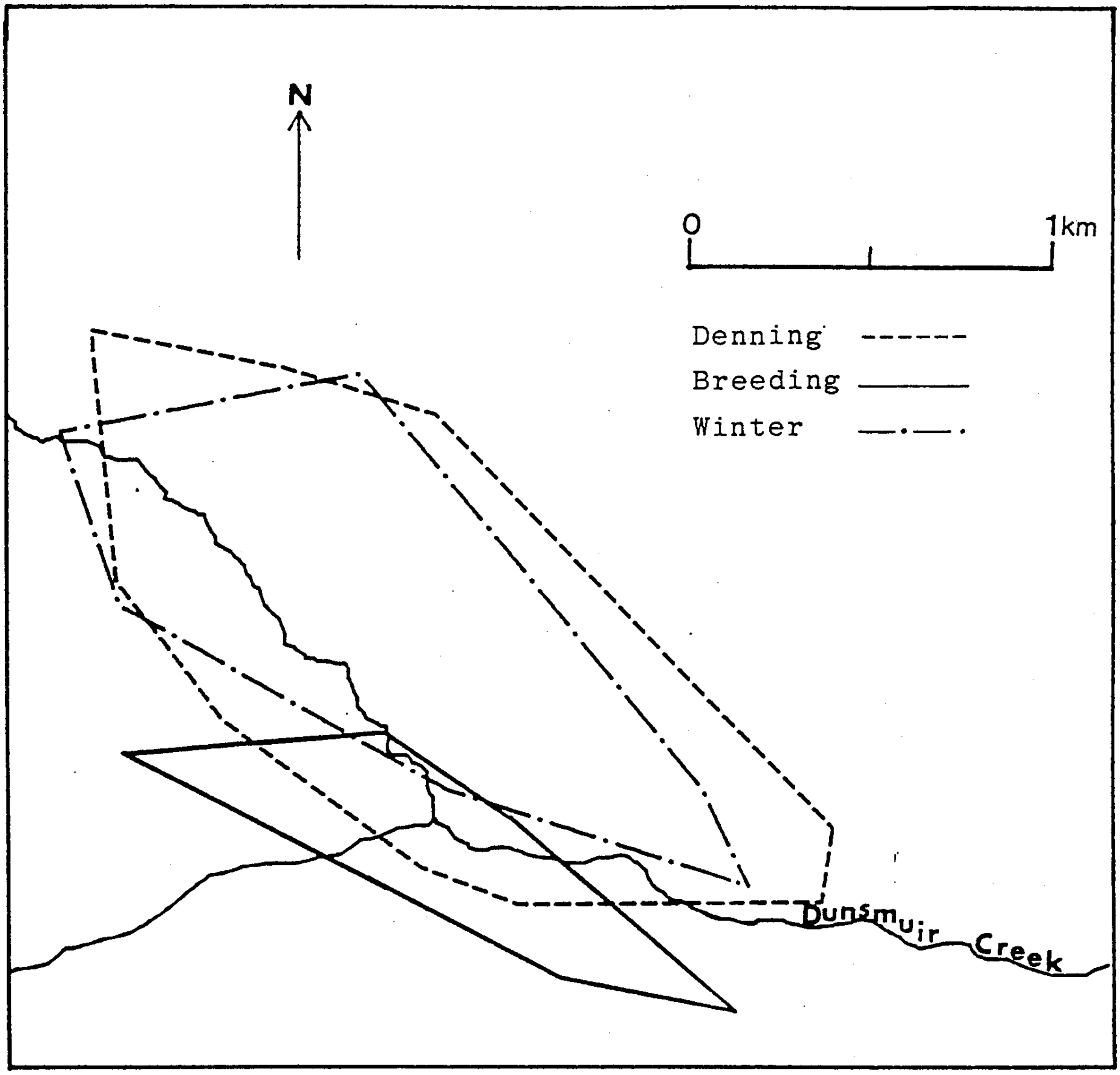

Fig. 8. Seasonal 100% home ranges for radio-collared adult female, Amy, Nanaimo River Watershed. 1987-1989.

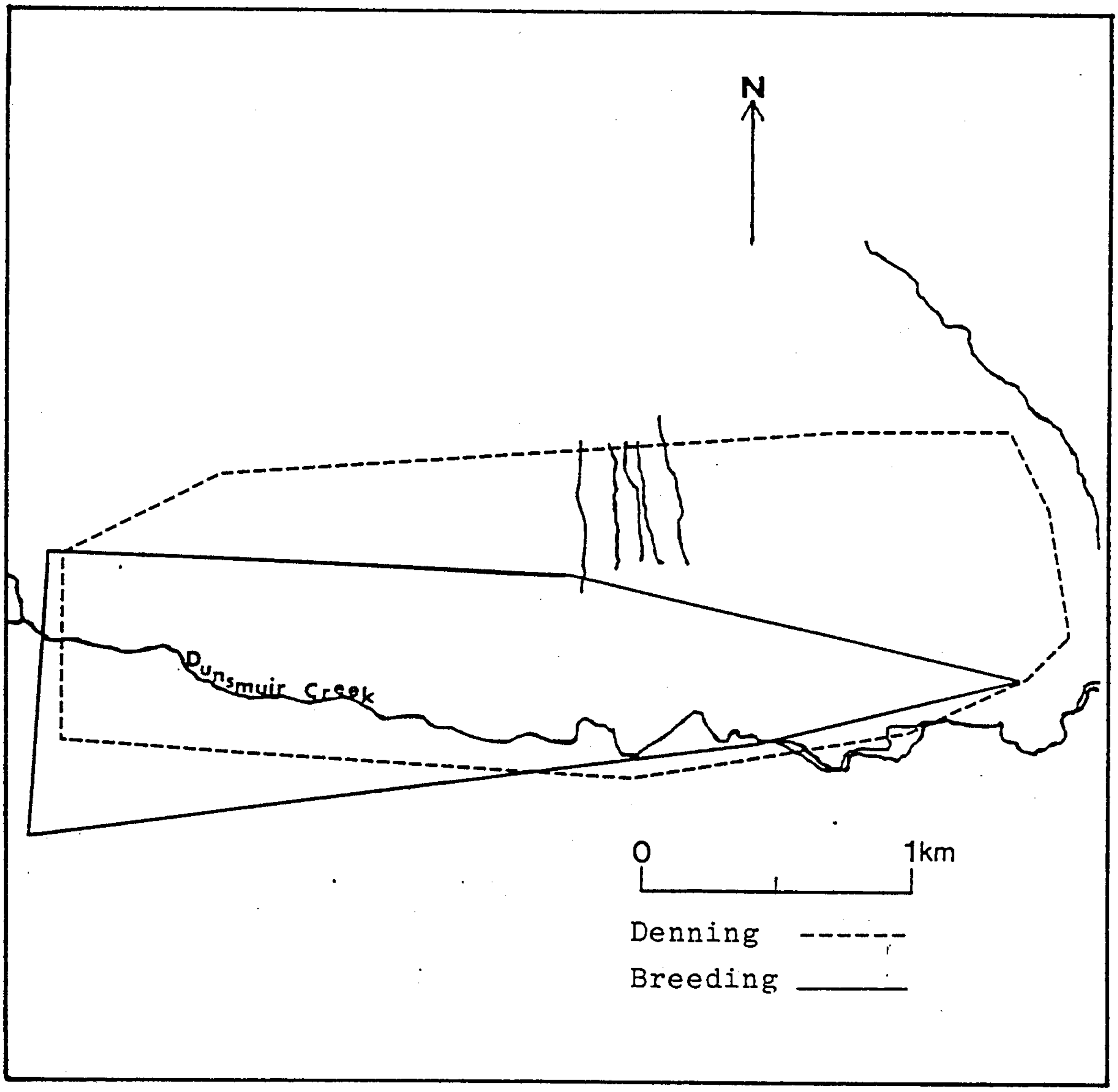

Fig. 9. Seasonal 100% home ranges for radio-collared adult female, Noreen, Nanaimo River Watershed. 1987-1989.

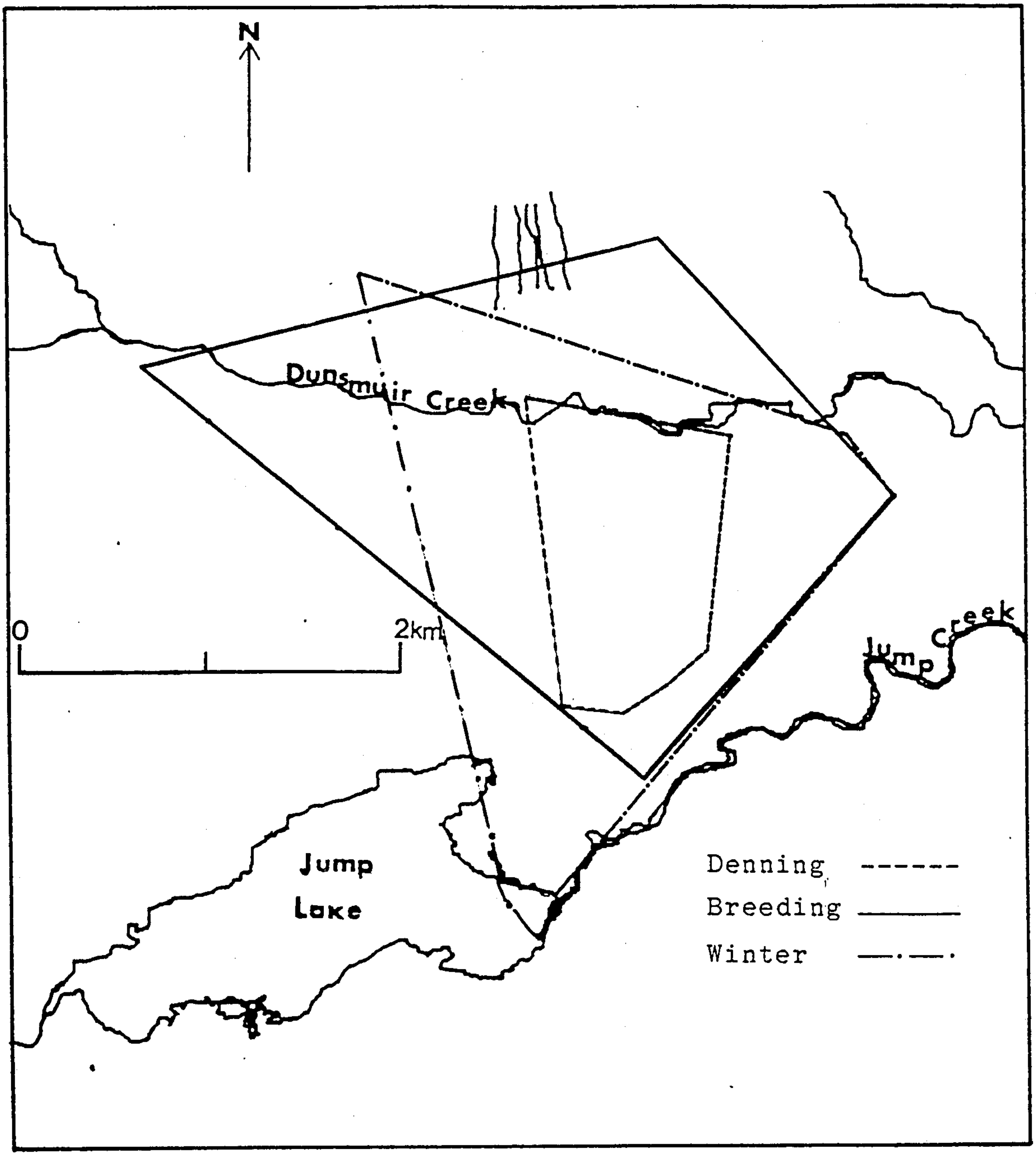

Fig. 10. Seasonal 100% home ranges for radio-collared adult male, Vic2, Nanaimo River Watershed. 1987-1989.

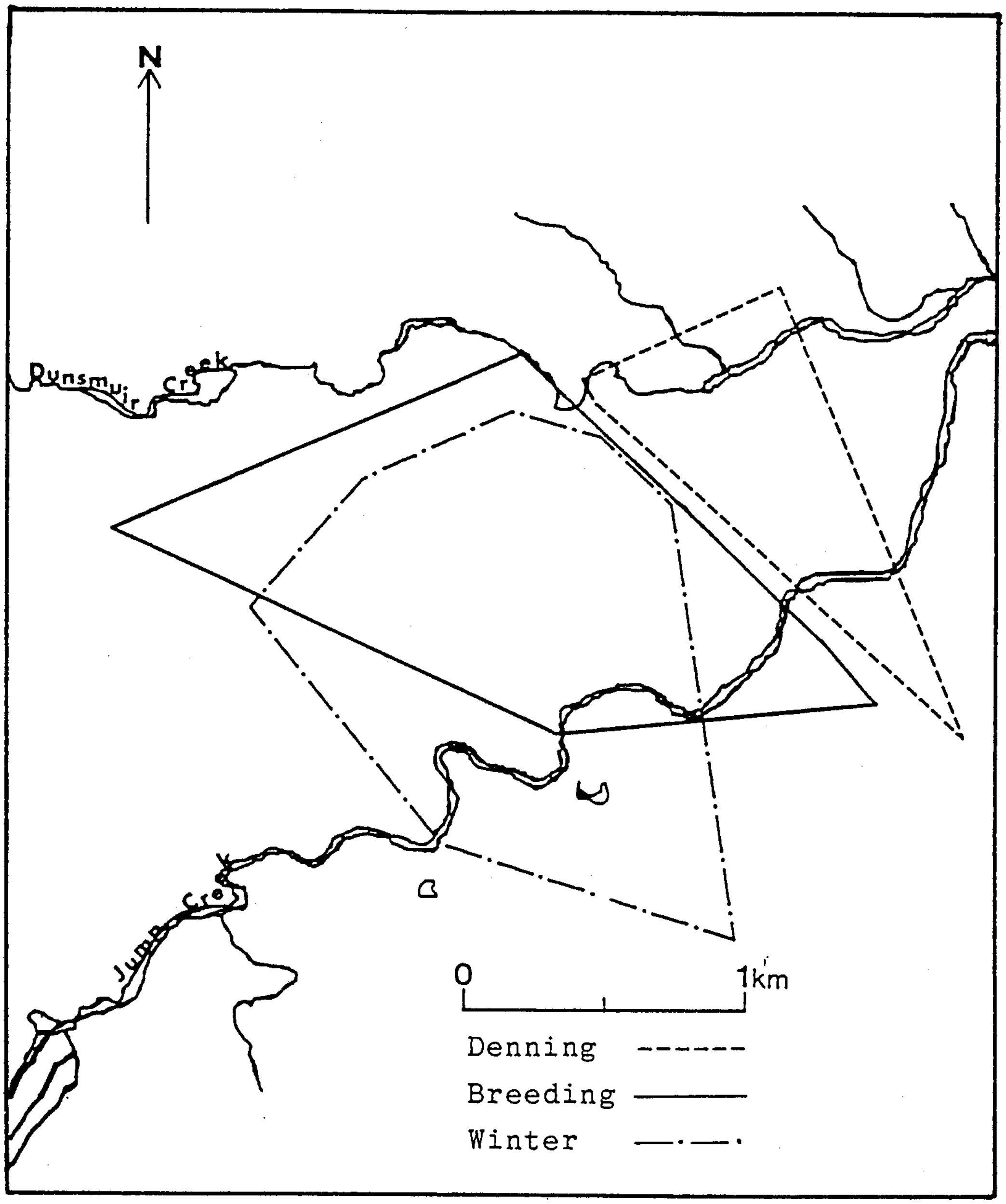

Fig. 11. Seasonal 100% home ranges for radio-collared adult male, Kermit, Nanaimo River Watershed. 1987-1989.

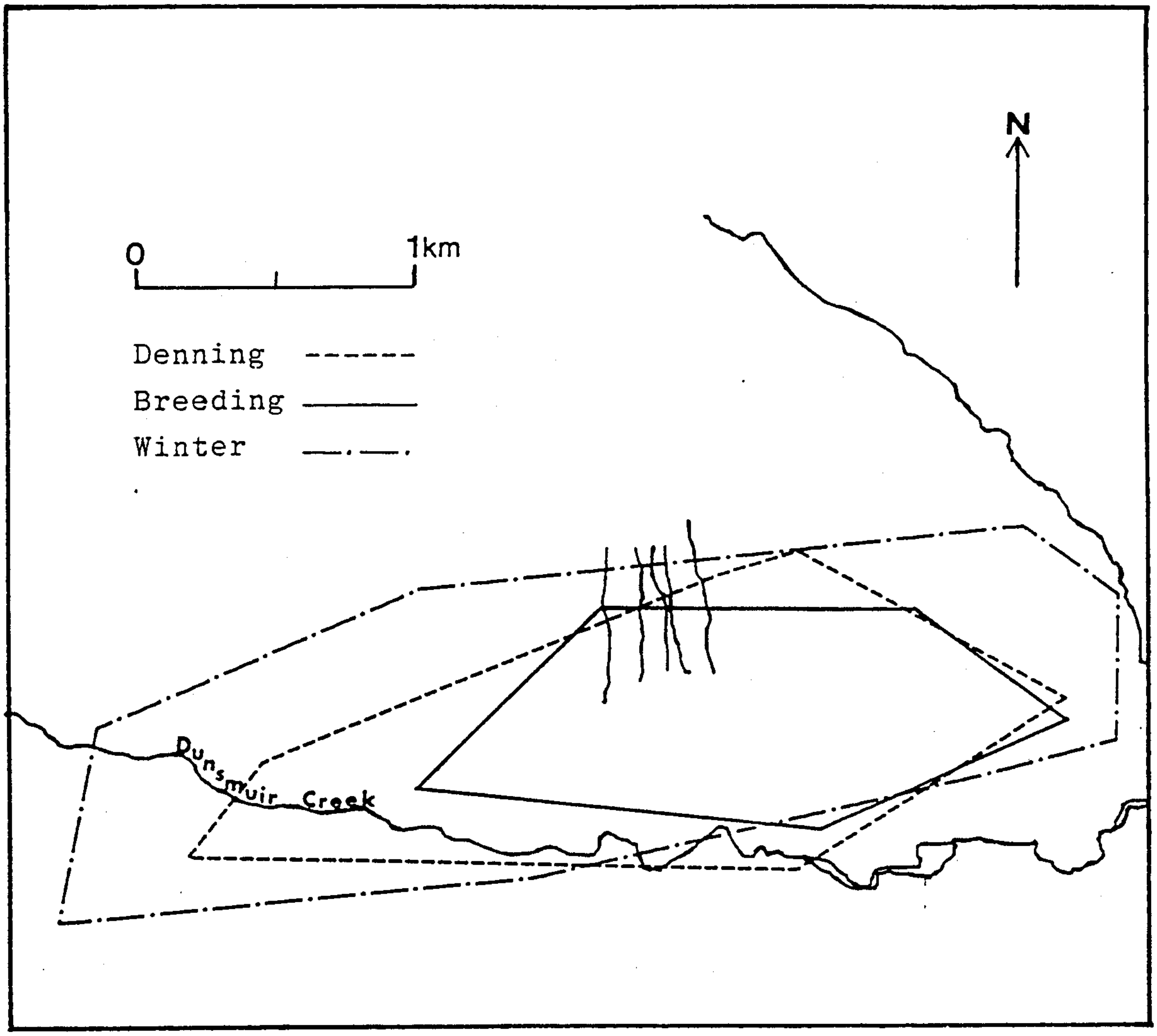

Fig. 12. Seasonal 100% home ranges for radio-collared adult male, Harry, Nanaimo River Watershed. 1987-1989.

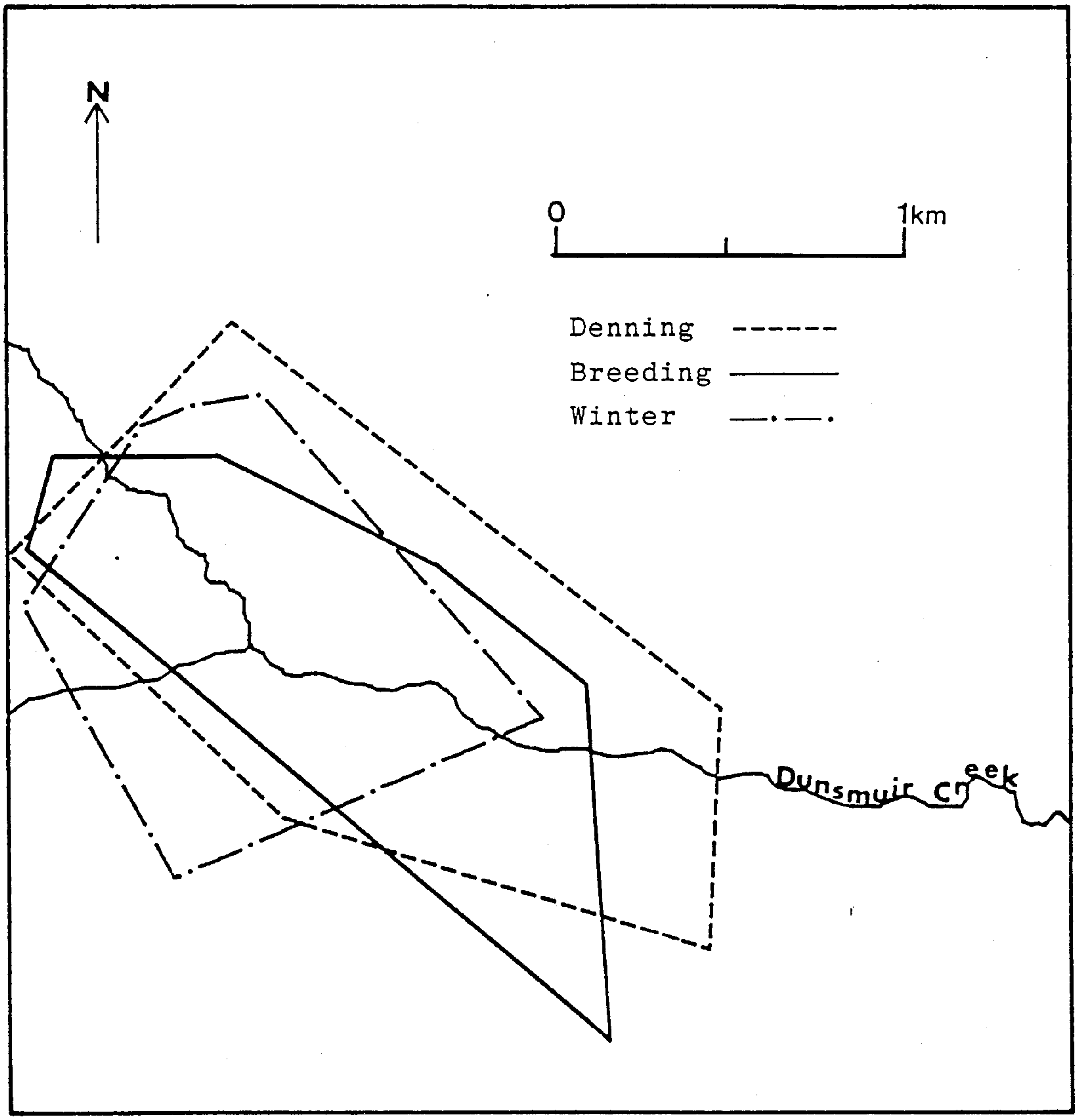

Fig. 13. Seasonal 100% home ranges for radio-collared adult male, Yogi2, Nanaimo River Watershed. 1987-1989.

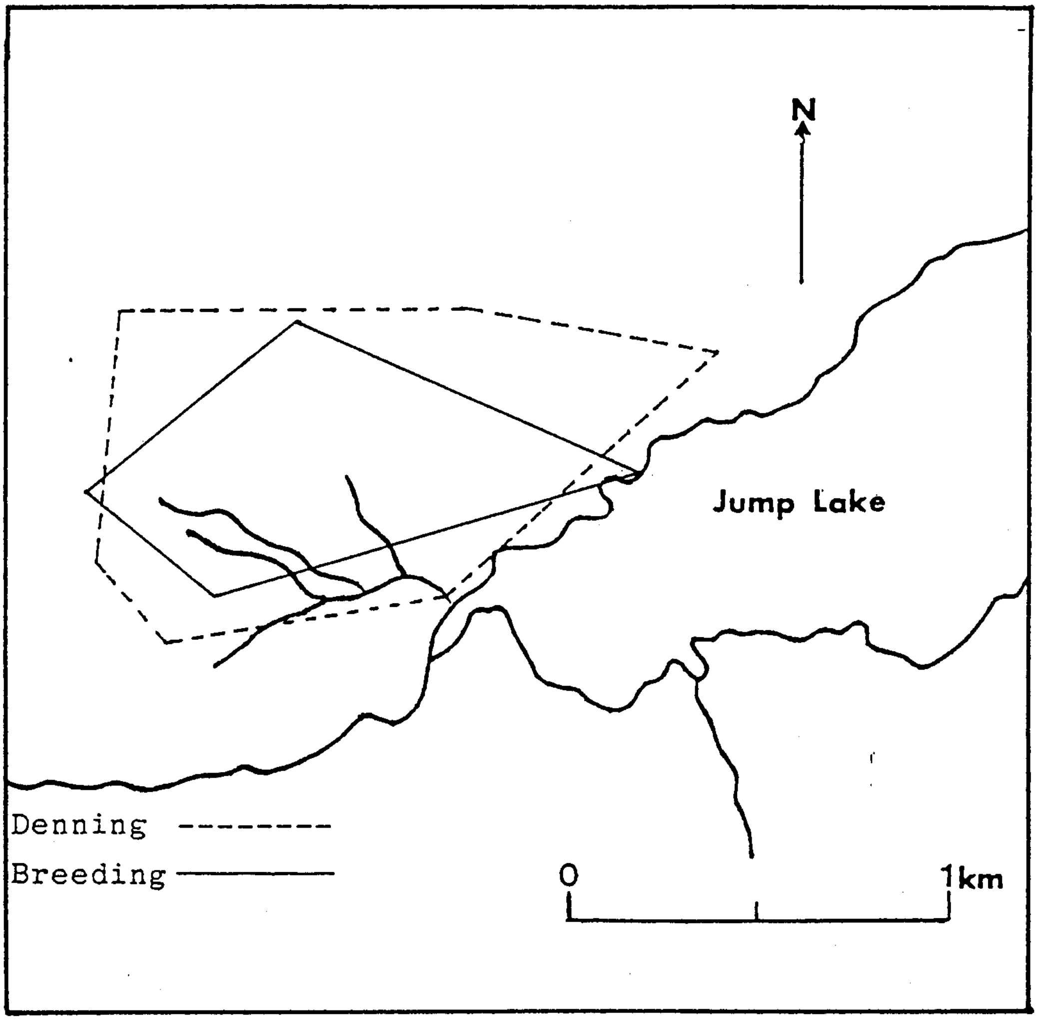

Fig. 14. Seasonal 100% home ranges for radio-collared adult male, Larry, Nanaimo River Watershed. 1987-1989.

ranks test; $P > 0.10$).

Density

When based on data from trapping an open population with unequal catchability, the Jolly-Seber method gives somewhat negatively biased estimates of population size. I estimated marten population sizes for each trapping period using the Jolly-Seber method for trap capture data (Fig. 15). Mean population estimates, calculated from monthly population estimates, were calculated for the denning, breeding and winter seasons of 1986-1988 to illustrate the timing of seasonal population changes (Fig. 16). Marten densities were estimated using these mean population sizes in combination with size of study area. The minimum and maximum sizes of the study area were calculated to bound the range of seasonal population densities.

To estimate the minimum area of the study area, all known home ranges were plotted on a 1:20,000 map. The outermost points of these home ranges were then connected to create a minimum convex polygon surrounding areas of known marten habitation. This polygon of 30 km^2 represents only a portion of the whole study area and coincides with areas of trapping success. A maximum area estimate of 40 km^2 was calculated by including all areas where traps were placed regardless of trapping success.

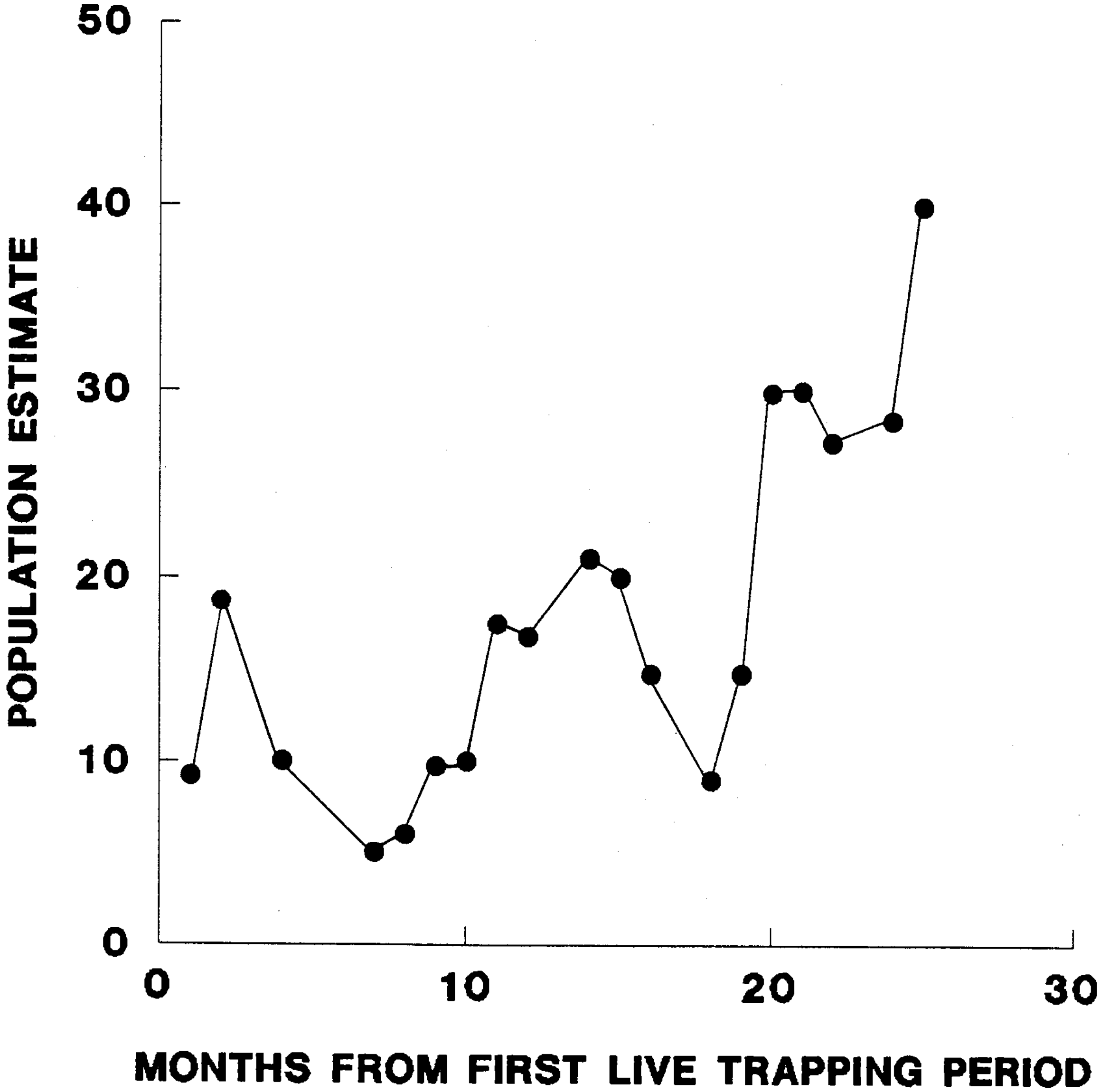

Fig. 15. Population estimates for each trapping period from November 1986-January 1989 in the Nanaimo River Watershed.

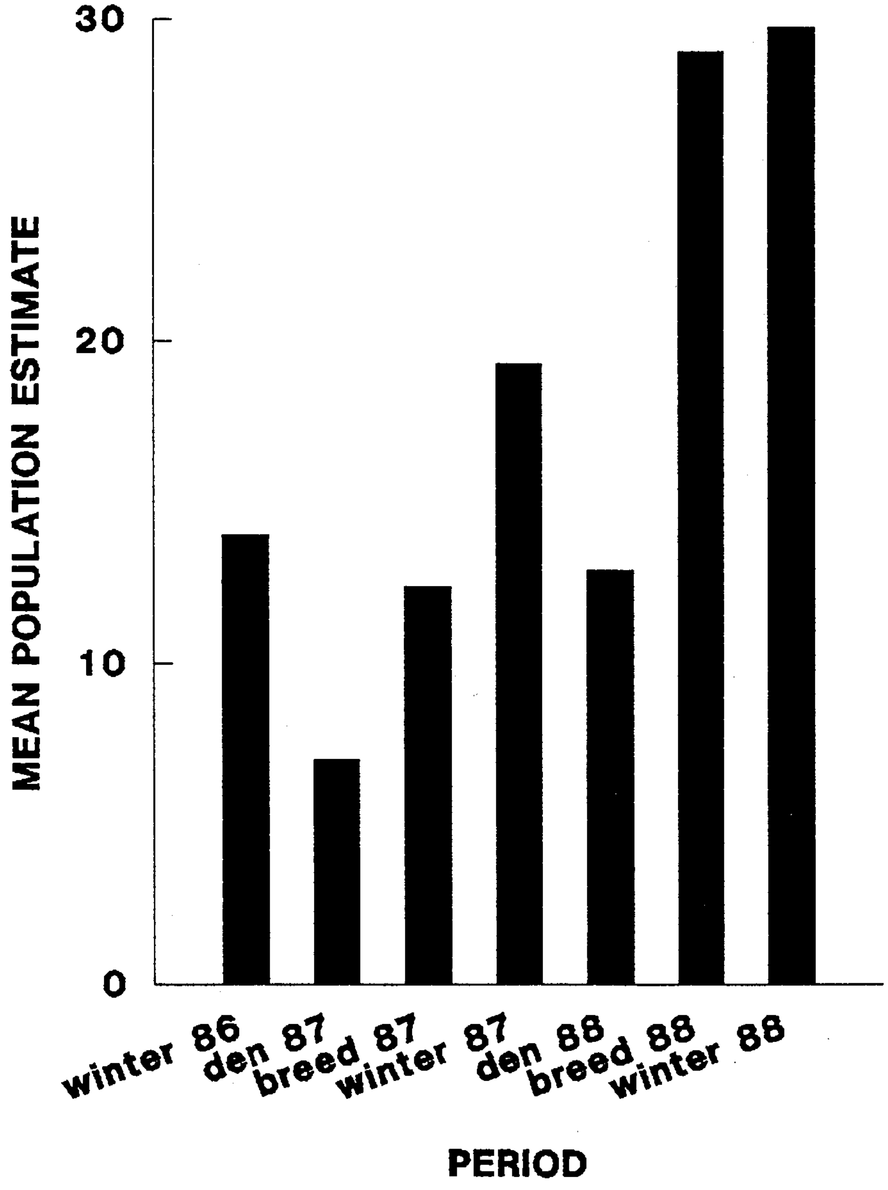

Fig. 16. Mean population estimates for the Nanaimo River Watershed from November 1986-January 1989. (den=denning, breed=breeding).

Commercial trapping in the study area was voluntarily suspended in October 1986 and did not recommence until November 1991. Because of heavy trapping prior to 1986, the marten population in my study area could have been in a rebounding state. Figure 15 suggests that the population had not reached an asymptote by the end of my study. Therefore, population densities were calculated only for 1988 thus allowing approximately one year (1987) for the marten population to stabilize. Densities were calculated for the following three seasons: denning (February-May); breeding (June-September); and winter (October-January). In addition, the highest and lowest densities for 1988 were calculated.

Densities of marten within the study area were calculated using areas of trapping success as well as the entire study area, regardless of trapping success (Table 4). A maximum density of 1.1 - 1.3 marten/km^2 occurred in November 1988. Trapping effort beyond this time was reduced and further trapping records were unsuitable for calculating density. A minimum density of 0.23 - 0.30 marten/km^2 occurred in April 1988. Density ranges for denning, breeding and winter seasons were 0.32 - 0.43 marten/km^2, 0.73 - 0.97 marten/km^2 and 0.75 - 0.99 marten/km^2, respectively.

Table 4. Population density range of marten in the Nanaimo River Watershed, January 1988-December 1988.

PERIOD	DENSITY RANGE (marten/km^2)		
1988 Minimum	0.23	-	0.30
1988 Maximum	1.00	-	1.30
Denning	0.32	-	0.43
Breeding	0.73	-	0.97
Winter	0.75	-	0.99

Overlap

Annual patterns of home range overlap occurred between the sexes as well as among individuals of the same sex, however, the degree of overlap varied (Fig. 17). Overlap was greatest between sexes. There was less overlap between males. Overlap between females was lowest of the 4 types of interactions.

Seasonal patterns of home range overlap were similar to annual patterns but were more pronounced during particular seasons. Overlap between the sexes was greatest during the denning season whereas overlap between males only occurs at the 100% home range level during this period. Overlap between females was also low during the denning season with exclusive use of space by 1 female occurring below the 70% home range level.

During the breeding and winter seasons, overlap between the sexes was greatest while overlap between males decreases during these periods. During the breeding season, females exhibited overlap only at the 100% home range level.

Discussion

It is difficult to compare studies in which different

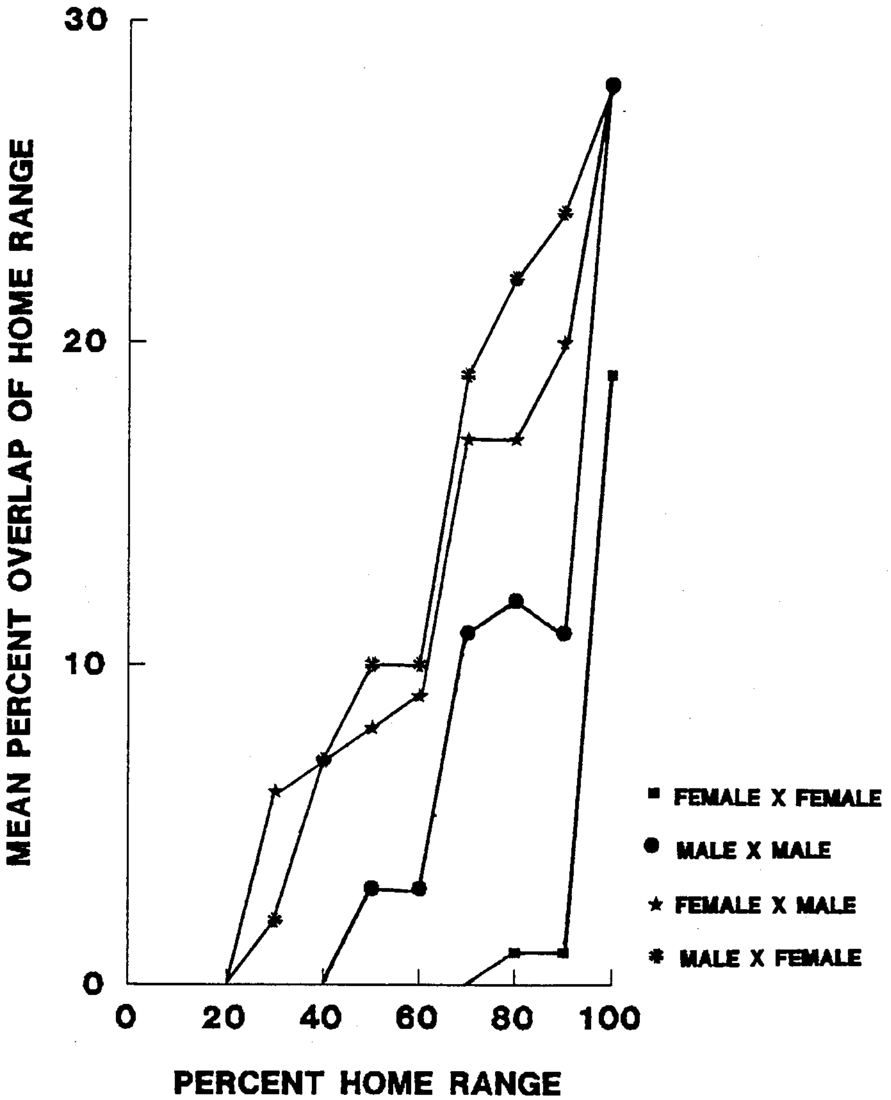

Fig. 17. Mean percent overlap between annual home ranges for 4 interaction types between marten: female x female; male x male; female x male; male x female.

techniques were used to obtain locations and analyze data. Estimates of home range size are influenced by sample size, sampling interval (Jennrich and Turner 1969, Swihart and Slade 1985 and Clark et al. 1989) and location of study and season (McNab 1963). Habitat quality may also affect home range size (Harestad and Bunnell 1979, Lindstedt et al. 1986). However, one trend evident from previous radio-telemetry studies of marten is that male home ranges are 2 - 3 times larger than those occupied by females in the same area (Clark and Campbell 1976, Mech and Rogers 1977, Steventon and Major 1982, Buskirk 1983, Davis 1983, Raine 1983, Wynne and Sherburne 1984, Clark et al. 1989). Differences between annual home range sizes in my study are consistent with those of previous studies in that males home ranges are 2 times larger than those of females.

Sample size becomes more crucial when comparing seasonal home ranges from different studies. Seasonal home ranges calculated from home range estimates based on annual data are difficult to use for detailed comparisons with those obtained where intensive monitoring was done during a specific season. Intensive monitoring will usually result in a larger number of locations and as such home range estimates from the increased sample size could possibly be larger due to the positive relationship between home range size and number of observations (Clark et al. 1989). Therefore, studies employing two different sampling intensities are likely to exhibit differences in home range estimates as a result of sampling technique rather than reflecting different strategies of marten. Archibald and Jessup (1984) studied marten in Yukon during the breeding season. Based on 248 observations from 8 marten (4 males; 4 females) male home ranges were only 1.3 times larger than female home ranges. In the Nanaimo River Watershed, during the breeding season, based on 97 observations from 8 marten (5 males; 3 females), male home ranges were 2.6 times larger than those of females.

Initially, my results appear to conflict with those obtained in Yukon, however, this may be due to differences in sample size. Due to equipment malfunction, I obtained few observations for females during the breeding season. Because there is a positive relationship between home range size and number of observations (Clark et al. 1989), I believe that larger numbers of observations of females would have resulted in home range sizes closer to those of male marten during this period, thereby reducing differences in home range size between the sexes.

Estimates of winter home range sizes from interior regions of North America may differ from mine because of differences in climatic factors (Mech and Rogers 1977, Steventon 1979, Raine 1983). Interior regions have more extreme winters than does Vancouver Island. In interior regions, the snowpack is deeper, occurs for a longer duration and ambient temperatures are lower than those experienced by marten in the Nanaimo River Watershed. Assuming that home range size increases with the energy requirements of an animal, then home range size may vary accordingly to the direct and indirect influences of weather and climate and their effects on habitat quality (McNab 1963, Harestad and Bunnell 1979).

Large differences exist between winter home range sizes of marten on Vancouver Island and those of marten from other areas. The mean home range estimates of marten during winter in Michigan and Maine were 12.5 km^2 for male marten (N=5) and 3.2 km^2 for females (N=3). Mean home ranges on Vancouver Island were 2.8 km^2 for males (N=4) and 0.7 km^2 for females (N=2). As mentioned earlier, the number of locations used to determine home ranges may partially affect the estimate of home range size, however, I believe the mild climatic conditions within my study area result in lower energy demands and greater relative habitat quality. This hypothesis is supported by examining the ratio of male and female home range areas for Michigan-Maine and Vancouver Island. For both locations, mean female home ranges are 0.26 times smaller than those of male home ranges. This suggests that in regions where extreme climatic conditions prevail, absolute home range sizes are greater but these sizes, relative to the opposite sex at the same location, are similar to those in areas having mild winters. Lowered energy requirements, coupled with high habitat quality in terms of prey availability, could explain the small home ranges of marten on Vancouver Island during winter.

Core areas of intensive use within marten home ranges are seldom examined. Hawley and Newby (1957), although not identifying core areas, recognized that some portions of home ranges were used to a greater intensity than others and Clark et al. (1989) reported home ranges containing 95% of the closest observations surrounding the geometric centre of the home range. Consideration of 95% of the observed locations is useful in eliminating unusual movements, which, if included, could yield erroneous home range estimates. Examination of only 50% of the closest locations identify cores of intensive use where marten were most often located.

Examining core areas of intensive use within marten home ranges could provide new insight into marten spatial patterns and minimum home range requirements. My analysis of overlap among different percent home ranges (Fig. 17) suggests core areas of intensive use exist in which there is exclusive use by only one sex. Because of these patterns, I propose that home range cores are defended from potential competitors and represent a critical portion of the home range.

Identification of minimum home range size requirements are useful for managing marten populations where habitat capability can be determined. Knowledge of these minimum requirements, coupled with specific habitat needs, would allow managers to better assess trapline placement and the ability of marten to shift home ranges in response to habitat alteration (e.g. logging). Minimum home range requirements also have utility for estimating the size of refugia needed to sustain harvested populations.

Each marten's seasonal home range exhibited a high degree of overlap with its other seasonal home ranges, with the exception of 1 adult male marten whose winter range did not overlap with his denning or breeding home range. In Montana, resident marten exhibited no seasonal deviations from their home ranges for up to 819 days (Hawley and Newby 1957). On the other hand, Buskirk (1983) reported altitudinal movements by marten in Alaska during spring and autumn. Assuming that an animal's home range reflects habitat quality, it follows that if a change in habitat quality occurs, as during winter at high elevations, a resultant shift in home range could be due to changing prey availability. Alternatively, fidelity to the same area between seasons could indicate continuous prey availability. Perhaps interhabitat differences in prey availability on Vancouver Island are not great enough to invoke seasonal shifts in home ranges.

Seasonal home ranges have been calculated in different studies using data from portions of a 12 month period. Consecutive seasonal home ranges, however, have seldom been examined for an entire year from the same study area. Examination of three seasonal home ranges - denning (February-May), breeding (June-September) and winter (October-January) - indicate home range sizes vary between consecutive seasons.

Wynne and Sherburne (1984) found female activity radii around the denning home range centre were shorter than those during the breeding season. They suggested there was a relationship between this retraction of home range and the birth and rearing of kits. Contrary to the observations of Wynne and Sherburne (1984), my data indicate that sizes of home ranges during the denning season are not significantly different from those during the breeding season. This difference in results is likely due to different methods of analysis rather than to spatial strategies by marten. From my field observations, it appears that although the female home ranges were not compressed during the denning-kit rearing period, there were few forays by the female to the outer home range boundary. One female, after occupying her den and moving less than 200 m from the den site for 19 h, travelled

5500 m in 4 h. Under these conditions, home range size was not compressed, however, intensity of use of the outer boundaries of the home range had decreased.

Hawley and Newby (1957) observed that male home ranges were larger during the breeding season than during the non-breeding season. My findings, on the other hand, are similar to those of Wynne and Sherburne (1984) in that sizes of male home ranges during the breeding season are not significantly different from those during the denning season. Given that adult males have two basic requirements, food and access to females, it follows that home ranges should shift seasonally to meet these requirements. Therefore, if home ranges are not seasonally altered, it suggests that the basic requirements of marten are being met. My observations of collared marten are consistent with this hypothesis, in that all collared males had at least 1 mature collared female within their range and 1 male's home range overlapped with the home ranges of 3 mature females (Fig. 18).

Sites of breeding and winter home ranges for both males and females within the Nanaimo River Watershed were not significantly different. Archibald and Jessup (1984) found female home ranges increased during estrus, suggesting that females increased their home ranges to ensure contact with males. Given that population density

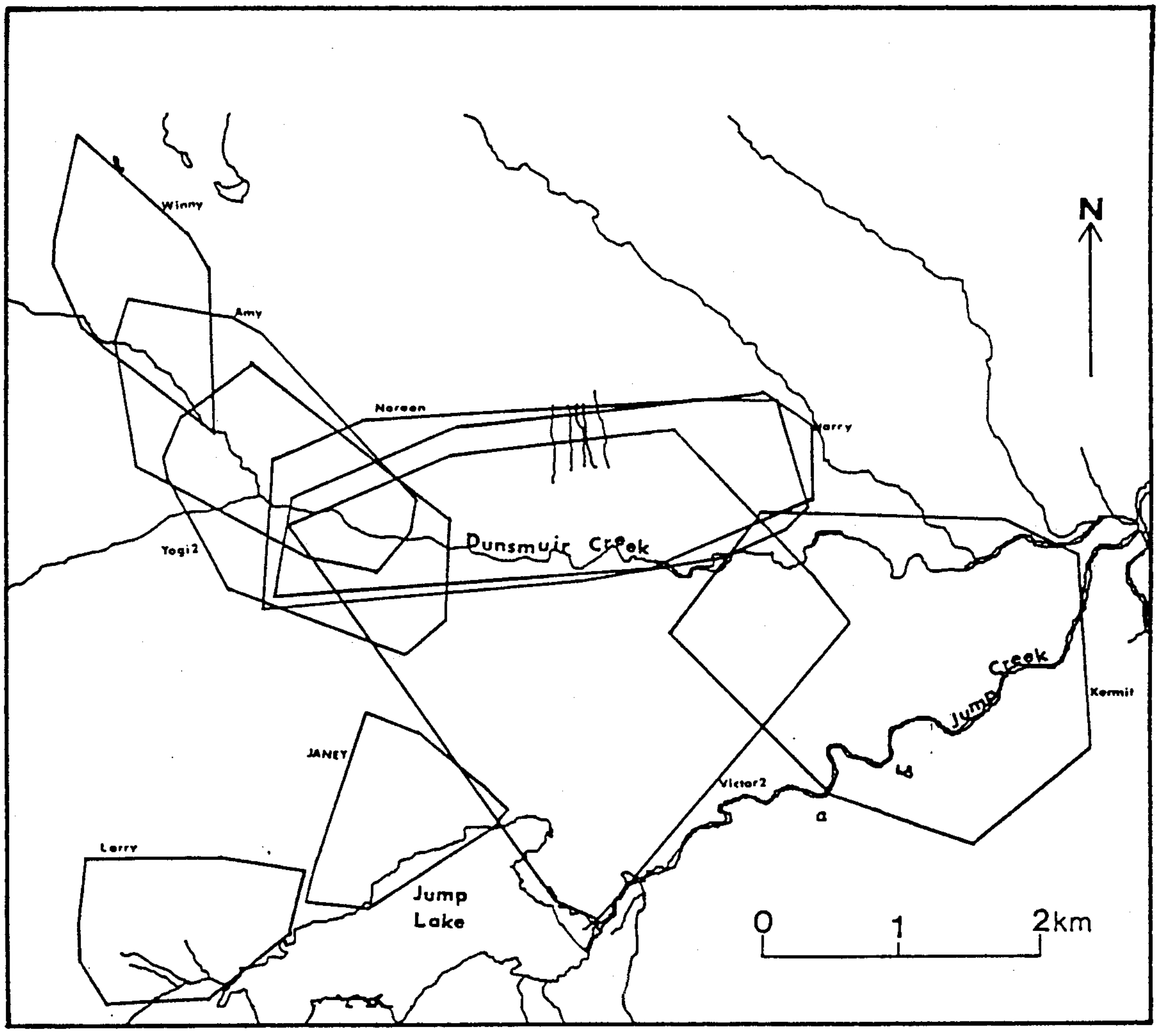

Fig. 18. Home ranges of radio-collared marten resident in the Nanaimo River Watershed, 1987-1989.

can affect home range size and that accessibility to mates is a function of density, it follows that if home range size is not increased, it could be a result of having adequate mating opportunities within the present home range. A competing hypothesis is that there may not be suitable adjoining areas into which home ranges could be expanded.

Population densities have been reported from several areas of interior North America, however, different techniques used to calculate densities create problems when comparisons are attempted. Minimum densities of marten in the Nanaimo River Watershed occurred during the denning season (April 1988) and maximum densities occurred during winter (November 1988). The winter season, as defined in this study, is a time of juvenile dispersal, a time when other researchers report increased densities (Francis and Stephenson 1972, Soutiere 1979, Archibald and Jessup 1984). Densities in mixed forests in Ontario (Francis and Stephenson 1972) are greater than those in the Nanaimo River Watershed. However my estimates of densities are similar, taking into account different techniques used to obtain estimates, to those reported by Soutiere (1979) for conifer-hardwood forests in Maine. Soutiere (1979) concluded that regenerating clearcuts sustained lower population densities than did partially cut or undisturbed stands. Habitat modification in my study area may be influencing density of marten. Large blocks of regenerating cutovers, representing the high level of habitat alteration through timber harvesting in my study area, may be contributing to densities of marten which are lower than those found elsewhere in North America.

I found extensive home range overlap between sexes, in my study which is consistent with spatial behaviour of marten in other areas (Hawley and Newby 1957, Francis and Stephenson 1972, Clark and Campbell 1976, Major 1979, Buskirk 1983, Clark et al. 1989). However, my analyses indicate that this apparent tolerance between sexes has limits. No overlap occurred below the 30% home range core and little overlap (< 10%) existed up to the 50% home range core. This minor overlap suggests that in both male and female home ranges a core area of exclusive use occurs and may even be defended.

Furthermore, overlap between the sexes below the 60% home range level only occurred during the denning season. Because I defined the denning season as the period from February to May inclusive, this period can also be thought of as the denning and kit-rearing season. A male could enhance his fitness if he tolerated females and young in his home range, because such behaviour would maximize his likelihood for reproductive encounters and provide an area of reduced competition for the growth and development of his offspring.

During the denning season home range overlap between males is limited to the 100% home range. This pattern supports the hypothesis that I proposed which considers home range overlap in terms of fitness. By excluding other males, the home range ensures reduced competition for food both for the females and their offspring. Benefits from this behaviour are that females are able to feed both themselves and their kits, which aids kit survival and thereby increases the male's fitness, and it encourages the female to remain in their present range, thereby increasing the chance for reproductive encounters in the future.

Intrasexual home range overlap occurred but was less extensive than intersexual overlap. Similar to other studies, when intrasexual overlap occurred it was less than in cases of intersexual overlap and temporal separation of marten occurred in the shared area. Unlike other studies (Clark and Campbell 1976, Burnett 1977), intrasexual overlap between females in the Nanaimo River Watershed was less than that found between males. This anomaly may be a result of the problems encountered when attempting to trap mature female marten. I had low trapping success, and I am certain that all adult females were not radio-collared, therefore, it is possible that overlap between females may be greater than that between males as has been found elsewhere. Nevertheless, in all cases a larger core area of exclusive use occurred than was found with intersexual interactions.

Identifying core areas of exclusive use is important, both in terms of interpreting spatial distribution patterns and minimum home range requirements of marten, but also, and perhaps more importantly, for the management of the species. Management agencies are continually being asked to set sustainable harvest levels but they often have little information to base their decisions on.

In summary, my results are generally in agreement with other studies, however, some variations do exist. Home range estimates from my study are broadly similar to those of other studies employing similar methods, with male marten home ranges being roughly 2 - 3 times larger than female home ranges. Marten spatial distribution in my study area is also similar to that reported in other studies in that intersexual overlap of home ranges exceeds the level of overlap from intrasexual encounters. I also show that marten do not share a core area representing 30% to 50% of their home range.

Estimates of marten density in the Nanaimo River Watershed were slightly lower than those found in areas where both the biogeoclimatic zone was different and timber harvesting was less extensive. However, although in a different biogeoclimatic zone, marten densities in my study were similar to those found by Soutiere (1979) in an area affected by timber harvesting to a similar extent.

Examining core areas of intensive use within home ranges has important management implications for wildlife agencies regarding trapline placement and timber harvesting plans. Traplines should be placed in a way to ensure an adequate and suitable area capable of sustaining a breeding source population from which to harvest dispersing juveniles. Marten are likely capable of shifting their home ranges into adjacent stands of forest if timber harvesting activities affect them, however the degree of home range compression is finite and will be influenced by the size of the home range core.

Patterns of spatial organization of marten in my study are similar to previous findings in that females demonstrate social tolerance towards other females and males. However, overlap between males was greater than that reported in other areas.

CHAPTER 3

HABITAT USE

Marten are associated with dense, mature and old growth coniferous forests throughout their range (Marshall 1951, Francis and Stephenson 1972, Koehler et al. 1975, Campbell 1979, Soutiere 1979, Taylor and Abrey 1982, Wynne and Sherburne 1984). In old growth forests, habitat structures, such as snags, stumps and coarse woody debris provide marten with denning sites for females and their kits, winter resting sites and hunting sites in areas where snowpacks exceed 1.0 m (Bateman 1968, Davis 1983, Buskirk 1984). Because early seral stages normally lack these habitat structures, marten are thought to require old growth coniferous forest. This old growth dependency make marten vulnerable to habitat alterations induced by forest harvesting.

My objectives were: to examine habitat characteristics and determine their relationships to habitat use; to describe habitats used by marten for hunting and resting; to identify features of natal den sites; and to compare habitat use by marten among seasons.

Materials and Methods

Habitat Use

Radio collared marten were relocated within the study area between August 1987 and April 1989. At the time of location, activity of the animal (resting or active) and weather conditions were recorded. Radio collar attachment and subsequent monitoring techniques were the same as those used to estimate home range size (Chapter 2). Habitat use by marten was determined by overlaying telemetry locations on an ecosystem association map of the study area produced by the B.C. Ministry of Forests.

I tested whether use of a habitat was equal to its availability by chi-square goodness of fit tests. If significantly different ($P < 0.05$), I determined if the habitat type was preferred or avoided (Neu et al. 1974). Habitat was considered available at 2 levels: habitat available within each marten's home range and habitat available within the entire study area. Analyses of habitat use based on habitat availability within home ranges may be biased because the location of home ranges may implicitly reflect a degree of selection (Johnson 1980). Consideration of habitat availability within the study area helps avoid these biases. However, due to the patchy distribution of older forest stands my study area, some marten may not have had older forest stands available for use. This distribution of older forest stands could yield erroneous estimates of selection or avoidance of these habitat types when availability within the study area is used.

During the summer of 1989, I visited each telemetry location and measured 6 habitat characteristics: canopy cover, aspect, habitat type, percent herbaceous ground cover, debris volumes and mean dbh (diameter at breast height) of nearby trees. I treated each telemetry location as a plot centre. I established 4, 25-m transects, radiating out from the plot centre. At 5 m intervals along the transects, I measured canopy cover, percent herbaceous ground cover and dbh of the closest tree. Coarse woody debris was measured continuously along each 25 m transect. Debris volumes were calculated using methods for forest fuel sampling (Van Wagner 1968).

Habitat characteristics and Habitat Use

I used simple linear regressions to examine relationships between habitat characteristics and seasonal marten habitat use. I conducted simple linear regressions for habitat use data stratified by activity (active and resting locations) and season [winter (October-January), denning (February-May) and breeding (June-September)]. For my analyses, I defined winter as being the time between the first and last snowfall in the study area.

Using the best predictors determined from simple linear regressions, I then conducted multiple linear regressions to estimate how much of the variation in marten habitat use could be accounted for by habitat characteristics. Pearson correlation coefficients were calculated on all pairs of variables. For significantly correlated variables ($P < 0.05$; $r \geq 0.50$ or $r \leq -0.50$), only one of the pair of correlated variables was used in the multiple regression analysis.

Natal Den Sites

Because of the frequent lack of snow in the study area, I had to rely on telemetry locations to locate natal den sites. To facilitate location of den sites, intensive monitoring was conducted during a portion of the denning period (March-April). Telemetry locations were obtained hourly for each mature female over at least a 24 hr period. During these intensive monitoring periods, I determined when marten were resting from differences in signal strength. Areas where marten rested were then visited the next day to locate the den. Habitat characteristics at the den sites were determined by assessing habitat type and measuring percent canopy cover, diameter of stump (if applicable), dbh of tree (if den was situated within the rootball) and mean diameter of coarse woody debris (if the den was located within a debris pile).

Coarse Woody Debris

Research in the interior of the continental United States suggests coarse woody debris is an important habitat characteristic for marten during winter foraging, to gain access to subnivean zones and during resting or denning periods (Marshall 1951, Newby 1951, Burnett 1977, Mech and Rogers 1977, Campbell 1979, Steventon and Major 1982, Hargis and McCullough 1984, Buskirk et al. 1987, Spencer 1987). To ascertain the importance of coarse woody debris, I used ANOVAs to compare debris volumes at male and female locations for different seasons and activities (resting or active).

Results

Habitat Use

Of 50 (29 males; 21 females) marten captured in the study area, 12 (8 males; 4 females) were radio collared and monitored for sufficient lengths of time to provide habitat use data. Three adult females were intensively monitored during denning (February-May).

Although all 4 habitat types were available within the study area, not all marten chose to occupy all habitat types within their home range (Tables 5 and 6). Individual variation in habitat use was evident for all seasons. On an annual basis, all (4 of 4) collared females exhibited significant habitat selection ($P < 0.05$) while only 4 of the 8 collared males exhibited habitat selection (Tables 7 and 8).

Seasonal habitat use

Broad patterns of seasonal habitat use show that females used regenerating cutovers ($\leq$ 10 yrs) less than expected and used second growth forests (> 10 - $\leq$ 40-years) more than expected ($P < 0.05$) (Fig. 19). Use of mature (> 40 - $\leq$ 120-years) and old growth forest stands (> 120-years) was less than or equal to that expected ($P < 0.05$).

Male marten were more variable in their habitat use. Males used cutovers less than expected in all seasons except during breeding when their habitat use was equal to the proportion of habitat available within their home ranges ($P < 0.05$). However, if habitat availability was based on that available within the study area, males used cutovers less than expected during each season ($P < 0.05$).

Use of second growth by males was greater than expected during winter and the denning season ($P < 0.05$).

TABLE 5. Annual habitat use of 4 different habitat types as shown by proportional home ranges of female marten.

ANIMAL	PROPORTIONAL HOME RANGE	CUTOVERS < 10 YRS	SECOND GROWTH	MATURE FOREST	OLD GROWTH
Winny	100	0.39	0.30	0.0	0.31
	90	0.52	0.26	0.0	0.22
	50	0.41	0.57	0.0	0.02
Amy	100	0.53	0.46	0.0	0.01
	90	0.54	0.46	0.0	0.00
	50	0.46	0.54	0.0	0.00
Noreen	100	0.28	0.64	0.05	0.03
	90	0.30	0.69	0.01	0.00
	50	0.08	0.92	0.00	0.00
Janey	100	0.10	0.63	0.00	0.27
	90	0.05	0.75	0.00	0.20
	50	0.01	0.86	0.00	0.13
MEAN	100	0.32	0.51	0.01	0.16
	90	0.35	0.54	0.00	0.11
	50	0.24	0.72	0.00	0.04

TABLE 6. Annual habitat use of 4 different habitat types as shown by proportional home ranges of male marten.

ANIMAL	PROPORTIONAL HOME RANGE	CUTOVERS < 10 YRS	SECOND GROWTH	MATURE FOREST	OLD GROWTH
Vic2	100	0.50	0.44	0.03	0.03
	90	0.61	0.32	0.07	0.00
	50	0.51	0.42	0.07	0.00
Harry	100	0.28	0.64	0.07	0.01
	90	0.17	0.76	0.07	0.00
	50	0.14	0.86	0.00	0.00
Yogi	100	0.63	0.33	0.00	0.04
	90	0.64	0.36	0.00	0.00
	50	0.38	0.62	0.00	0.00
Yogi2	100	0.51	0.35	0.00	0.14
	90	0.53	0.40	0.00	0.07
	50	0.65	0.35	0.00	0.00
Victor	100	0.53	0.32	0.14	0.01
	90	0.67	0.28	0.05	0.00
	50	0.29	0.70	0.01	0.00
Larry	100	0.40	0.53	0.00	0.07
	90	0.37	0.42	0.00	0.21
	50	0.91	0.06	0.00	0.03
Skippy	100	0.42	0.31	0.00	0.27
	90	0.64	0.36	0.00	0.00
	50	0.74	0.26	0.00	0.00
Kermit	100	0.27	0.32	0.29	0.12
	90	0.29	0.21	0.35	0.15
	50	0.25	0.11	0.59	0.05
MEAN	100	0.44	0.40	0.07	0.09
	90	0.49	0.39	0.07	0.05
	50	0.48	0.42	0.08	0.02

Table 7. Annual habitat selection by 4 female marten in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a] I	Availability[a] II
Amy	141			
cutover		0.35	0.53[b]	0.41[d]
second growth		0.65	0.47[c]	0.35[c]
mature		0.00	0.00[b]	0.08[b]
old growth		0.00	0.01[b]	0.16[b]
Winny	130			
cutover		0.06	0.39[b]	0.41[b]
second growth		0.79	0.30[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.15	0.31[b]	0.16[d]
Noreen	129			
cutover		0.05	0.28[b]	0.41[b]
second growth		0.89	0.64[c]	0.35[c]
mature		0.06	0.05[d]	0.08[d]
old growth		0.00	0.03[b]	0.16[b]
Janey	86			
cutover		0.16	0.10[d]	0.41[b]
second growth		0.66	0.63[d]	0.35[c]
mature		0.00	0.00[b]	0.08[b]
old growth		0.18	0.27[d]	0.16[d]

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Table 8. Annual habitat selection by 6 male marten in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a] I	Availability[a] II
Harry	56			
cutover		0.02	0.28[b]	0.41[b]
second growth		0.96	0.64[c]	0.35[c]
mature		0.02	0.07[d]	0.08[b]
old growth		0.00	0.01[d]	0.16[b]
Yogi2	45			
cutover		0.28	0.51[b]	0.41[d]
second growth		0.70	0.35[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.02	0.14[d]	0.16[d]
Kermit	31			
cutover		0.11	0.27[b]	0.41[b]
second growth		0.39	0.32[d]	0.35[d]
mature		0.23	0.29[d]	0.08[d]
old growth		0.27	0.12[d]	0.16[d]
Vic2	34			
cutover		0.46	0.50	0.41
second growth		0.50	0.44	0.35
mature		0.04	0.03	0.08
old growth		0.00	0.03	0.16
Yogi	17			
cutover		0.24	0.63[b]	0.41[d]
second growth		0.76	0.33[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.04[b]	0.16[b]
Victor	21			
cutover		0.50	0.53	0.41
second growth		0.50	0.32	0.35
mature		0.00	0.14	0.08
old growth		0.00	0.01	0.16

Larry	33			
cutover		0.55	0.40	0.41
second growth		0.35	0.53	0.35
mature		0.00	0.00	0.08
old growth		0.10	0.07	0.16
Skippy	16			
cutover		0.50	0.42	0.41
second growth		0.50	0.31	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.27	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

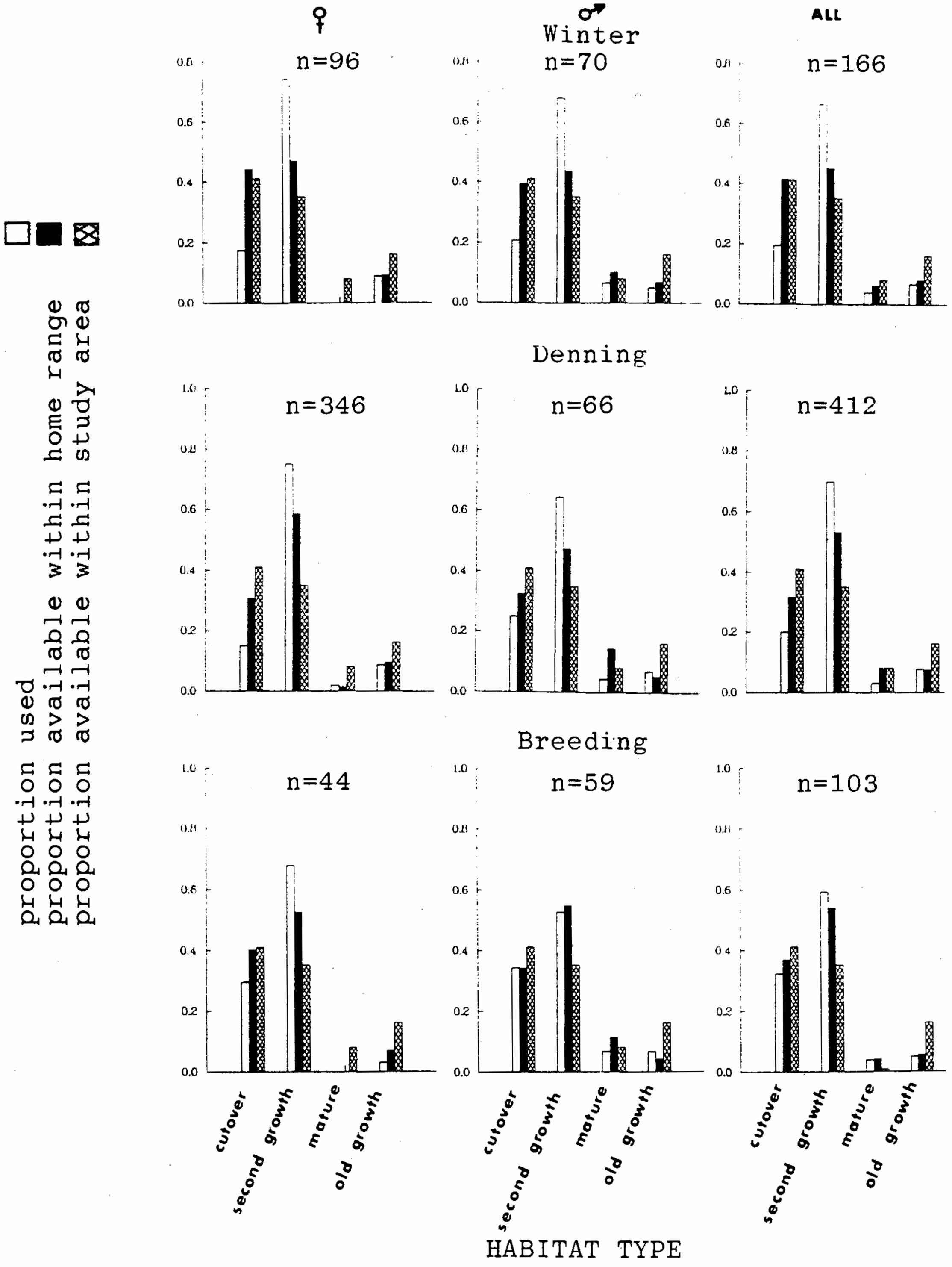

Fig. 19. Seasonal habitat use by marten within the Nanaimo River Watershed, 1987-1989, (Winter=Oct-Jan, Denning=Feb-May, Breeding=Jun-Sep).

During the breeding season, second growth was used more than expected if availability was based on percent available within the study area, but use was less than expected when habitat availability was calculated on availability within their home ranges ($P < 0.05$).

Males used mature and old growth forest stands less than expected for all seasons except during denning when old growth stands were used greater than that expected from habitat availability within their home ranges ($P < 0.05$).

Cutovers ($\leq$ 10 yrs)

Marten used cutovers less frequently than second growth stands even though cutovers and second growth were roughly equal in availability. The avoidance of clearcuts was especially pronounced during denning (February-May), when 3 females and 1 male marten had significantly fewer radio locations within this habitat type than expected ($P < 0.05$) (Tables 9 and 10). Four marten (3 males; 1 female) showed no habitat selection during the denning season ($P > 0.05$).

Cutovers continued to be underused (i.e avoided) by marten during winter (Tables 11 and 12). During this season, 2 adult females used cutovers less than expected ($P < 0.05$) and 5 marten (4 males; 1 female) exhibited no significant habitat selection ($P > 0.05$).

Table 9. Habitat selection by 4 female marten during the denning period (February-May) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a]	
			I	II
Amy	100			
cutover		0.38	0.56[b]	0.41[d]
second growth		0.62	0.44[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.00[d]	0.16[b]
Winny	102			
cutover		0.03	0.29[b]	0.41[b]
second growth		0.73	0.36[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.24	0.35[d]	0.16[d]
Janey	28			
cutover		0.14	0.10	0.41
second growth		0.76	0.87	0.35
mature		0.00	0.00	0.08
old growth		0.10	0.03	0.16
Noreen	116			
cutover		0.04	0.28[b]	0.41[b]
second growth		0.89	0.67[c]	0.35[c]
mature		0.07	0.05[d]	0.08[d]
old growth		0.00	0.00[d]	0.16[b]

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Table 10. Habitat selection by 5 male marten during the denning period (February-May) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a]	
			I	II
Harry	25			
cutover		0.00	0.31[b]	0.41[b]
second growth		1.00	0.69[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.00[d]	0.16[b]
Yogi2	8			
cutover		0.14	0.51	0.41
second growth		0.86	0.49	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.00	0.16
Larry	29			
cutover		0.52	0.34	0.41
second growth		0.38	0.50	0.35
mature		0.00	0.00	0.08
old growth		0.10	0.16	0.16
Kermit	6			
cutover		0.33	0.14	0.41
second growth		0.33	0.22	0.35
mature		0.17	0.58	0.08
old growth		0.17	0.05	0.16
Victor	21			
cutover		0.50	0.53	0.41
second growth		0.50	0.32	0.35
mature		0.00	0.14	0.08
old growth		0.00	0.01	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Table 11. Habitat selection by 3 female marten during winter (October-January) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a] I	Availability[a] II
Amy	36			
cutover		0.27	0.55[b]	0.41[d]
second growth		0.73	0.45[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.00[d]	0.16[b]
Winny	19			
cutover		0.13	0.70[b]	0.41[b]
second growth		0.87	0.30[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.00[d]	0.16[b]
Janey	41			
cutover		0.12	0.07	0.41
second growth		0.62	0.66	0.35
mature		0.00	0.00	0.08
old growth		0.26	0.27	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Table 12. Habitat selection by 4 male marten during winter (October-January) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a] I	Availability[a] II
Harry	20			
cutover		0.06	0.25	0.41
second growth		0.88	0.66	0.35
mature		0.06	0.07	0.08
old growth		0.00	0.02	0.16
Yogi2	19			
cutover		0.25	0.47	0.41
second growth		0.69	0.44	0.35
mature		0.00	0.00	0.08
old growth		0.06	0.09	0.16
Kermit	14			
cutover		0.14	0.29[d]	0.41[b]
second growth		0.58	0.25[d]	0.35[d]
mature		0.14	0.29[d]	0.08[c]
old growth		0.14	0.17[d]	0.16[d]
Vic2	16			
cutover		0.38	0.56	0.41
second growth		0.56	0.39	0.35
mature		0.06	0.05	0.08
old growth		0.00	0.00	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Avoidance of cutovers was less pronounced during breeding (June-September) (Tables 13 and 14). During breeding, 1 female and 1 male avoided cutovers, 1 juvenile female used cutovers more frequently than expected ($P < 0.05$) and 6 marten showed no habitat selection ($P > 0.05$). Two of the male marten, who did not exhibit habitat selection, were found dead in regenerating cutovers. Wounds on the carcasses appeared to have been inflicted by great horned owls (Bubo virginianus) (R. W. Campbell, pers. comm.).

Second Growth (> 10 - ≤ 40 yrs)

During denning, marten used second growth stands heavily (Tables 9 and 10). Three adult females used this habitat more than expected. One adult male used second growth exclusively, however his home range contained only regenerating cutovers and second growth stands. During denning, 4 other marten (3 males; 1 female) showed no significant habitat selection.

Second growth stands continued to be preferred during winter (Tables 11 and 12). Second growth stands in winter were used more than expected by 2 adult females ($P < 0.05$). One male used second growth more than that expected from availability, however, there were insufficient data to infer preference or avoidance. Three

Table 13. Habitat selection by 4 female marten during the breeding period (June-September) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a]	
			I	II
Amy	5			
cutover		0.60	0.39	0.41
second growth		0.40	0.61	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.00	0.16
Winny	9			
cutover		0.14	0.79[b]	0.41[d]
second growth		0.86	0.21[c]	0.35[c]
mature		0.00	0.00[d]	0.08[b]
old growth		0.00	0.00[d]	0.16[b]
Janey	17			
cutover		0.35	0.04[c]	0.41[d]
second growth		0.53	0.75[d]	0.35[d]
mature		0.00	0.00[d]	0.08[b]
old growth		0.12	0.21[d]	0.16[d]
Noreen	13			
cutover		0.08	0.39	0.41
second growth		0.92	0.54	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.07	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

Table 14. Habitat selection by 5 male marten during the breeding period (June-September) in the Nanaimo River Watershed. Proportions of habitat use were compared to habitat availability.

	N	Use	Availability[a] I	Availability[a] II
Harry	11			
cutover		0.00	0.09	0.41
second growth		1.00	0.91	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.00	0.16
Yogi2	18			
cutover		0.35	0.36	0.41
second growth		0.65	0.56	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.08	0.16
Larry	7			
cutover		0.70	0.41	0.41
second growth		0.30	0.55	0.35
mature		0.00	0.00	0.08
old growth		0.00	0.04	0.16
Kermit	14			
cutover		0.00	0.35[b]	0.41[b]
second growth		0.34	0.25[d]	0.35[d]
mature		0.33	0.31[d]	0.08[d]
old growth		0.33	0.09[d]	0.16[d]
Vic2	10			
cutover		0.67	0.49	0.41
second growth		0.33	0.46	0.35
mature		0.00	0.05	0.08
old growth		0.00	0.00	0.16

[a] I-within home range, II-within study area
[b] Use less than expected ($P < 0.05$)
[c] Use more than expected ($P < 0.05$)
[d] insufficient data to reject H0

males and 1 female exhibited no habitat selection during winter.

Results are less clear for the breeding season when only 1 mature female used second growth stands more than expected ($P < 0.05$) (Tables 13 and 14). Four males and 2 females showed no habitat selection during the breeding season.

Mature (> 40 - ≤ 120 yrs)

Mature forest stands were typically not selected for nor avoided during any season. This lack of selection is in part due to the relative scarcity of this habitat type within the study area. Mature forest existed in only 1 male marten's home range. This male showed significant habitat selection ($P < 0.05$) during winter and breeding, however, there were insufficient data to infer preference or avoidance of habitat types (Tables 12 and 14).

Old Growth (> 120 yrs)

Significant habitat selection was exhibited ($P < 0.05$) by 1 adult female during denning, however, there were insufficient data to infer preference or avoidance of old growth forest stands (Tables 9 and 10).

Marten showed little habitat selection for old growth forest stands during winter (Tables 11 and 12). One male marten exhibited significant habitat selection for old growth forest stands during winter ($P < 0.05$), however, there were insufficient data to infer preference or avoidance.

During breeding, marten continued to show little habitat selection for old growth stands (Tables 13 and 14). One male exhibited habitat selection ($P < 0.05$), but there were insufficient data to infer preference or avoidance for old growth forest stands.

Habitat Characteristics and Habitat Use

Regression analyses were used to examine relationships between habitat characteristics and seasonal habitat use by marten. Four habitat variables were chosen: percent ground cover (GC), percent canopy closure (CC), mean diameter at breast height of trees (DBH) and debris volume (DVOL). Pearson correlation coefficients among these variables are shown in Tables 15 to 26.

Results of linear regressions (R^2 values) from marten habitat use and habitat characteristics are presented in Table 27. During denning and winter, percent canopy closure (CC) was significant for active and resting females and males ($R^2 = 0.11 - 0.39$, $r = 0.33 - 0.63$, $P < 0.05$). During breeding, percent canopy closure (CC) was significant for active males ($R^2 = 0.29$, $r = 0.54$, $P < 0.05$). When I included debris volume (DVOL) in this regression model, (marten habitat use = constant + DVOL +

Table 15. Pearson correlation coefficients between habitat characteristics for resting male marten during breeding (June-September) in the Nanaimo River Watershed. CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.11		
DBH	0.04	0.75*	
DVOL	-0.66*	-0.11	-0.20

* significant at $P < 0.05$

Table 16. Pearson correlation coefficients between habitat characteristics for active male marten during breeding (June-September) in the Nanaimo River Watershed. CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.56*		
DBH	-0.02	0.58*	
DVOL	-0.28*	0.08	0.01

* significant at $P < 0.05$

Table 17. Pearson correlation coefficients between habitat characteristics for resting male marten during winter (October-January) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.66*		
DBH	-0.07	-0.38*	
DVOL	-0.15	-0.01	-0.18

* significant at P < 0.05

Table 18. Pearson correlation coefficients between habitat characteristics for active male marten during winter (October-January) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.63*		
DBH	-0.24	0.74*	
DVOL	-0.47*	0.22	0.11

* significant at $P < 0.05$

Table 19. Pearson correlation coefficients between habitat characteristics for resting male marten during denning (February-May) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.48*		
DBH	-0.34	0.63*	
DVOL	-0.08	-0.32	-0.39*

* significant at P < 0.05

Table 20. Pearson correlation coefficients between habitat characteristics for active male marten during denning (February-May) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.57*		
DBH	-0.22	0.57*	
DVOL	-0.12	-0.05	0.04

* significant at $P < 0.05$

Table 21. Pearson correlation coefficients between habitat characteristics for resting female marten during breeding (June-September) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.86*		
DBH	0.89	-0.98*	
DVOL	0.23	-0.61	0.55

* significant at $P < 0.05$

Table 22. Pearson correlation coefficients between habitat characteristics for active female marten during breeding (June-September) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.83*		
DBH	-0.12	0.21	
DVOL	0.10	-0.11	-0.09

* significant at $P < 0.05$

Table 23. Pearson correlation coefficients between for habitat characteristics for resting female marten during winter (October-January) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.70*		
DBH	0.31	-0.37	
DVOL	-0.10	0.04	0.56

* significant at P < 0.05

Table 24. Pearson correlation coefficients between habitat characteristics for active female marten during winter (October-January) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.74*		
DBH	-0.04	-0.19	
DVOL	-0.07	-0.12	0.33*

* significant at $P < 0.05$

Table 25. Pearson correlation coefficients between habitat characteristics for resting female marten during denning (February-May) in the Nanaimo River Watershed.
CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.68*		
DBH	-0.30*	0.13	
DVOL	-0.07	0.03	0.16

* significant at $P < 0.05$

Table 26. Pearson correlation coefficients between habitat characteristics for active female marten during denning (February-May) in the Nanaimo River Watershed. CC = percent overstory canopy closure, GC = percent herbaceous ground cover, DBH = mean tree diameter at breast height, DVOL = debris volume (m^3/ha).

	Habitat variables		
	GC	CC	DBH
CC	-0.69*		
DBH	-0.28*	0.20*	
DVOL	-0.05	-0.05	0.03

* significant at $P < 0.05$

Table 27. Results of linear regressions (R^2 values) of seasonal marten habitat use index (habitat use-habitat available) against selected habitat characteristic variables in the Nanaimo River Watershed.
MWREST=male winter resting locations,
MWACT=male winter active locations,
MBREST=male breeding resting locations,
MBACT=male breeding active locations,
MDREST=male denning resting locations,
MDACT= male denning active locations,
FWREST=female winter resting locations,
FWACT=female winter active locations,
FBREST=female breeding resting locations,
FBACT=female breeding active locations,
FDREST=female denning resting locations,
FDACT=female denning active locations.
Beneath significant R^2 values, r values are shown in parentheses.

Habitat Use Index	Habitat Characteristic Variables				
	N	DVOL[a]	DBH	CC	GC
MWREST	22	0.16	0.02	0.39** (0.63)	0.18** (0.43)
MWACT	75	0.00	0.32** (0.57)	0.38** (0.61)	0.02
MDREST	30	0.03	0.12* (0.34)	0.00	0.16** (0.40)
MDACT	33	0.06	0.02	0.11* (0.33)	0.03
MBREST	11	0.00	0.00	0.01	0.26
MBACT	32	0.03	0.23** (0.48)	0.29** (0.54)	0.00
FWREST	17	0.10	0.02	0.15	0.07
FWACT	76	0.02	0.02	0.13** (0.36)	0.03
FDREST	82	0.00	0.04	0.17** (0.41)	0.02
FDACT	126	0.00	0.01	0.18** (0.42)	0.01
FBREST	6	0.01	0.00	0.01	0.02
FBACT	38	0.00	0.05	0.03	0.00

* significant at $P < 0.10$
** significant at $P < 0.05$
[a] refer to Table 15 and text for description and mnemonics of variables

CC), it accounted for an additional 6% ($P < 0.01$) of the variation in active male denning habitat use ($R^2 = 0.17$, $r = 0.41$); and 15% ($P < 0.01$) of the variation in resting male winter habitat use ($R^2 = 0.54$, $r = 0.74$). Herbaceous ground cover (GC) was significant for resting males ($R^2 = 0.16 - 0.18$, $r = 0.40 - 0.43$, $P < 0.05$). When I included tree diameter at breast height (DBH) in this regression model, (marten habitat use = constant + GC + DBH) it accounted for an additional 5% ($P < 0.05$) of the variation in denning resting male habitat use ($R^2 = 0.21$, $r = 0.45$).

Natal Den Sites

Seven natal den sites were located in 30-40 year old second growth forest stands. Two dens were beneath stumps greater than 1.0 m in diameter. Three dens were in piles of debris in which the average piece size ranged from 51 cm to 57 cm in diameter. One den was in the rootball of a windthrown tree. One den was beneath a large stump (> 1.0 m in diameter) within a small copse of trees (mean dbh = 20 cm). This stump was surrounded by a pile of woody debris in which the average piece size was 52 cm in diameter.

Coarse Woody Debris

Except for active and resting male locations during winter when debris volumes were significantly different

(ANOVA, $P < 0.05$), I did not detect any significant differences ($P > 0.10$) between debris volumes at locations used by females and those used by males either during resting or active periods during breeding, winter, denning, or on an annual basis (Table 28).

Discussion

Broad patterns of habitat use by marten on Vancouver Island reveal some differences between males and females. On an annual basis, all collared females (4 of 4) exhibited habitat selection, while only 50% of males (4 of 8) showed habitat selection. These findings suggest that females have more stringent demands on their life requisites, possibly due to their denning requirements. However, unlike other regions in North America where mature or old growth forests are preferred, on Vancouver Island, all marten do not choose to have old growth in their home ranges, they generally prefer second growth forest stands throughout the year, and they use mature and old growth forests proportionately less than available. Similar to marten in other areas, marten in the Nanaimo River Watershed generally avoid cutovers, (i.e. use it less than expected based on availability). However,

Table 28. Mean debris volumes (m^3/ha) at, active and resting marten radio locations within the Nanaimo River Watershed during different seasons. Standard errors are given in parentheses beneath means.

	Active				Resting			
	N	female	N	male	N	female	N	male
Breeding (June-Sept)	38	644.7 (92.8)	52	492.7 (48.1)	6	637.5 (198.7)	16	444.8 (87.0)
Winter (Oct-Jan)	76	531.2 (49.8)	37	478.3 (40.3)	17	553.0 (129.0)	22	690.4 (97.5)
Denning (Feb-May)	126	430.9 (26.3)	76	450.2 (40.0)	85	473.6 (30.6)	30	453.7 (66.8)
Annual	240	496.5 (25.9)	164	469.9 (25.4)	108	472.9 (32.2)	67	527.4 (49.8)

marten do use cutovers and this habitat type comprises substantial proportions of their home ranges.

Different patterns of habitat use between male and female marten may be due to the natal denning requirements of females. Natal dens in my study area (coarse woody debris piles, stumps or rootballs), are similar to those reported from softwood-dominated stands in other regions of North America (Spencer et al. 1983, Buskirk 1984, Buskirk et al. 1987, Spencer 1987). Unlike interior regions, where denning requirements tend to be fulfilled in mature or old growth forests, on Vancouver Island these den sites are found in second growth forests approximately 23-35 years of age. Furthermore, these stands had average seedling survival rates of 75-85% from planting programs done approximately 10 years post harvest, were fill planted approximately 10-15 years post harvest, had some residual western hemlock and amabilis fir, and were either lightly burned or unburned (W. Shuckel, pers. comm.). These stands also had frequent canopy openings and aspects between 135^{o} to 270^{o}. Buskirk (1984) documented high use of south-facing slopes by marten and he hypothesized that aspect preferences of marten for resting sites probably reflected site preferences for vegetation structures, which were common on south-facing slopes. Similarly, marten in my study may exhibit aspect preferences as a result of site preferences for vegetation structures used both in hunting and denning activities. The high level of debris on the ground is a result of logging residue left from the first cut of an old growth coastal forest. This condition may not persist in future forests. Successive cuts with shorter rotation times (< 80 years) may result in insufficient large diameter debris for denning requirements in 35 year old stands. Den sites would then only occur in older stands where coarse woody debris volumes had accumulated over time as is the case in studies from interior regions of North America. Perhaps it is this accumulation of coarse woody debris in interior forests that determines preferential use of older seral stages.

Low preference by marten for mature and old growth stands on Vancouver Island is contrary to that found elsewhere in North America (Campbell 1979, Major 1979, Soutiere 1979, Kelly 1982, Steventon and Major 1982, Snyder 1984, Koehler et al. 1990). Reasons for this apparent discrepancy may be that Vancouver Island marten exploit a prey base which reaches high densities in different habitat types than those exploited by mainland populations of marten (Chapter 1). Support for this hypothesis comes from More (1978), who found that marten activity was greater in habitats with greater numbers of prey and from Douglass et al. (1983), who suggested that marten select habitat on the basis of prey abundance and availability. Red-backed voles, the main prey for mainland marten populations (Strickland and Douglas 1987) typically attain high densities in older seral stages whereas deer mice, the main mammalian prey of Vancouver Island marten, are most abundant in younger seral stages. Therefore, low use of older seral stages by marten on Vancouver Island could be partly due to low prey abundance and availability in these habitat types.

Individual variation in habitat use is apparent, especially during the breeding season when habitat selection decreases. This decrease in habitat selection may be in response to high prey abundance and availability in all habitat types in my study area, especially cutovers. This factor has been reported elsewhere in North America (Koehler and Hornhocker 1977, Major 1979, Soutiere 1979, Steventon and Major 1982). However, the relative value of regenerating cutovers to marten may be lower than prey abundance and availability indicates. Two males within the Nanaimo River Watershed were killed in cutovers by great horned owls during the breeding season. Because of risk of predation, although prey is plentiful in all habitats during the breeding season, not all habitat types are suitable for marten.

Selection of habitats by marten increases during winter and I hypothesize that this selectivity is due to abundance and availability of prey. Within the study area, deer mice are the principal prey of marten during winter (Chapter 1). This reliance on deer mice suggests that it is important to manage for prey species while managing marten populations.

Coarse woody debris has been identified as being important to marten for hunting, denning and resting activities (Spencer et al. 1983, Buskirk 1984, Buskirk et al. 1987, Spencer 1987). Because debris volumes are seldom quantified, I cannot make comparisons between volumes found in my study with those of other regions. However, debris volumes in sites used by male marten within my study area during different seasons were not significantly different from those sites used by females. This lack of difference could be due to high debris volumes throughout the area, which are a result of logging practices at the time of harvest. Perhaps the volumes of coarse woody debris were well above the requirements of marten. Also, because I did not sample randomly for debris volumes, but rather only sampled at known marten locations, it is possible I was sampling at areas already selected by marten for specific debris volumes. However, from casual field observations of logging residue, it appeared that debris volumes were high throughout the study area.

Restrictions on logging residue were not in place when much of my study area was logged and therefore there were large amounts of debris left everywhere. However, current restrictions (0 m^3/ha avoidable waste allowed), are more severe and they could result in much less coarse woody debris in newly logged areas. This low waste practice could lead to a decrease in availability of den sites for marten. However, because many den sites are comprised of residue outside of the utilization specifications (i.e. rotten wood, short logs, wood that cannot be retrieved safely), it is possible that the zero waste tolerance, initiated in 1989 by the Ministry of Forests, will have a negligible effect on the abundance of potential marten den sites. Lofroth and Banci (1991) recommend a minimum of 300 m^3/ha of coarse woody debris be left post-logging for den sites. To ensure suitable habitat for marten in the Nanaimo River Watershed, this recommendation should be addressed by habitat management agencies.

In summary, habitat use by marten on Vancouver Island is similar to other regions of North America in that marten generally avoid cutovers although due to the high availability of this habitat, overall use is high. However, use of second growth stands on Vancouver Island is greater than that observed elsewhere, and use of mature and old growth forest stands is lower than that in interior regions of the continent. Habitat structures, such as coarse woody debris suitable for denning, resting and hunting are found in much younger seral stages on Vancouver Island than in interior regions. Perhaps it is this large amount of coarse woody debris that enhances suitability of younger stands for marten on Vancouver Island. I conclude from my results that marten in low elevation coastal forests can successfully exploit younger forest stands because of the high densities of deer mice, as well as the abundance of habitat structures (i.e. coarse woody debris) found within coastal second growth forest stands, at least during the first rotation.

CHAPTER 4

SUMMARY AND MANAGEMENT RECOMMENDATIONS

My study was initiated in 1987 on southern Vancouver Island, British Columbia. My broad objectives were: to describe and explain patterns of seasonal habitat use by marten in a coastal forest; to assess seasonal habitat productivity; to identify attributes of marten habitat; and to propose recommendations for management of marten in coastal habitats.

Chapter 1

Seasonal food habits were determined from 126 scats collected during 1987-1989 in the study area. Major prey groups found within scats were berries and small mammals. Minor prey groups were insects, birds and ungulates. Food habits varied seasonally. During winter, small mammals and ungulates had the greatest representation in scats. During spring, birds and ungulates were dominant. During summer, small mammals, berries and insects shared dominance and during autumn berries and insects were dominant. The number of prey groups per scat showed some variation, however, the majority of scats contained only one or two prey groups. A high level of association between prey groups was detected. Scats containing berries, often contained small mammals or insects. Scats containing ungulate seldom contained any other prey group.

Chapter 2

Home range use and spatial organization patterns were examined for marten in a study area located on southern Vancouver Island, British Columbia. Annual home range sizes were calculated for 8 marten: 1 juvenile female, 3 adult females and 4 adult males. Seasonal home ranges were obtained for 9 marten (5 males; 4 females). Annual home range sizes of marten on Vancouver Island are similar to those from other regions of North America, however, winter home ranges of marten on continental North America tend to be larger than those of marten on Vancouver Island.

Live-trapping data were used to calculate densities of marten in the study area. Densities of marten in the study area were lower than estimates from other regions of North America where timber harvesting had not been as extensive. This difference in density suggests timber harvesting results in lower marten densities for a period of time after timber harvest.

Overlap of home ranges occurred between the sexes as well as among individuals of the same sex. Overlap was greatest between the sexes, suggesting social tolerance.

Overlap between individuals of the same sex was less extensive and exhibited characteristics of territorial behaviour. Overlap of home ranges, both between the sexes as well as among individuals of the same sex, showed that marten avoid overlap of core areas of intensive use.

Chapter 3

Radio telemetry was used to determine habitat use of marten within the study area. Twelve marten (8 males; 4 females) were monitored for sufficient lengths of time to provide habitat use data. Four habitat types were available within the study area, however, some marten did not use all habitat types. All marten had cutovers and second growth forest in their home ranges, whereas not all marten had mature or old growth forest within their home ranges.

Use of habitat types varied seasonally. Regenerating cutovers were used less than expected during the denning and winter season but this avoidance was less pronounced during the breeding season. Risk of predation may also be a factor in avoidance of cutovers by marten in that 2 male martens were killed in cutovers by great horned owls. During winter, selection of habitats by marten tended to increase possibly due to changes in the abundance and availability of prey.

Habitat selection was exhibited by all female marten whereas only half of the males demonstrated habitat selection. Second growth forest stands were generally preferred and cutovers avoided. Mature and old growth forest stands tended to be used less than expected based on availability. High use of second growth stands was likely due to the unique characteristics of coastal, first rotation, second growth forests. Frequent canopy openings, abundant understory and large diameter trees in my study area create suitable marten habitat at a much earlier seral stage than that observed elsewhere in North America.

Coarse woody debris is important to marten as denning, resting and hunting sites. Amounts of coarse woody debris in first rotation, coastal second growth forest stands tends to be high and may contribute to use of younger forest stands by marten in coastal ecosystems.

Management Recommendations

Home range and habitat use by marten are functions of 1) distribution and availability of prey and 2) availability of suitable den sites. These factors likely vary throughout different coastal ecosystems. High use of second growth forest stands by marten on Vancouver Island suggests they can use younger seral stages when conditions within these stands are adequate for hunting and denning. My results suggest denning requirements of marten in the Nanaimo River Watershed were met through use of coarse woody debris, left over from logging of old growth forest stands (i.e. large diameter stumps, debris piles with piece size > 50 cm in diameter) as well as "natural" den sites created from windthrown trees. Hunting requirements were met through use of areas which had frequent canopy openings, dense understory shrubs and herbaceous vegetation and abundant coarse woody debris suitable as cover for prey.

Suitable denning, resting and hunting sites for marten in newly logged areas is an important structural attribute which should be maintained or created in forest harvesting plans. Through careful yarding, all large diameter stumps should be left as intact as possible post-logging to provide denning and resting sites. Debris, which is commonly yarded to roadsides and then burned, could be left or at least only lightly burned to create potential denning and resting sites in newly logged blocks. Intense broadcast burns should be discouraged in an attempt to maintain overhead cover for marten and protect them from avian predators in newly logged blocks. Buffer strips or travel corridors between cut blocks should be planned to allow for adequate security and thermal cover close to these productive hunting sites. To maintain marten habitat, silvicultural treatments should be modified. Non-uniformly stocked stands are desirable to provide a mosaic of canopy openings and trees. The small patches these openings create provide good hunting habitat for marten.

Marten have relatively small home ranges which, suggests that population management on a registered trapline basis is possible. Trapping pressure on marten populations can be increased through enhanced access provided by newly constructed logging roads. There are several ways to counteract this potential for overharvest. Blocking of logging roads which are no longer required for timber harvesting or silvicultural activities could be used to reduce access to portions of traplines. However, management of marten will probably be best achieved by informing trappers of the need to retain unharvested source populations of marten within their traplines.

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