Geographic and Sexual Variation of the American Pine Marten (Martes americana) in the Pacific Northwest, with Special Reference to the Queen Charlotte Islands

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ABSTRACT

The American Pine Marten (Martes americana) is among the few native species of mammals on the Queen Charlotte Islands, British Columbia. On these islands marten have evolved distinctive traits. My objectives in the first part of this study were (1) to analyse phenotypic differentiation of marten from the Queen Charlotte Islands and nearby areas, and (2) to determine if the pattern of differentiation among these populations supported the subspecific designations of Swarth (1911) and Hagmeier (1955).

Morphometric analysis suggested that the Queen Charlotte Islands marten form a distinctive group, and marten from other localities should not be included within the same subspecies. I recommend that the trinomial Martes americana nesophila be restricted to marten on the Queen Charlotte Islands.

Marten from Vancouver Island were very similar to those on the nearby mainland. Specimens from Baranof and Chichagof Islands (Alaska) were similar to those from the coastal area. More research, especially genetical analysis, is recommended to clarify certain relationships discussed here.

In the second part of this study, I used multivariate methods of analysis to describe sexual dimorphism and its changes with age, and to estimate whether insular populations are more sexually dimorphic than mainland ones. Sexual dimorphism was greatest in insular samples, and this finding is discussed in rela-

tion to the main hypotheses proposed to explain the strong differences between male and female. There was no clear pattern of variation in sexual dimorphism with age.

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DEDICATION

A mi Madre, quien desperto mi interés por las ciencias naturales

A mi Padre, quien me brindo todo su apoyo desde el comienzo de esta empresa

A María de los Angeles, quien sabe que esto lo hice por los dos

GENERAL INTRODUCTION

The American Pine Marten (Martes americana) is a small carnivore in the family Mustelidae. It was originally associated with mixed and mature coniferous forests throughout North America, but since the beginning of this century has lost much of its southern range due to intensive trapping and habitat destruction. Nonetheless, the American Pine Marten still plays an important role in the North American fur economy, particularly in Canada (Strickland et al., 1982).

Pelage colour of marten varies markedly with locality, season and individual, but the most usual colour is a golden brown with darker legs and tail, and a distinctive orange or yellow patch of variable shape and size on the throat and chest. The face and head are usually lighter in colour. Individuals may vary, however, from almost black to yellow (de Vos, 1952). Marten also vary in size geographically (Hagmeier, 1961). In Ontario male marten average about 60 cm in total length (Strickland et al., 1982), while in the Northwest Territories they are about 80 cm long. Sexual dimorphism is very strong with males larger than females for most morphological characters (Brown, 1983).

The diet of marten is mainly small mammals, birds, insects, and fruits. However, marten are opportunistic feeders, and take a wide variety of items including carrion, especially during the winter months (Soutière, 1978; Koehler et al., 1975; Strickland et al., 1982).

The American Pine Marten was first described by Buffon and d'Aubenton (1758 and 1765). Since then it has variously been considered to belong to the Eurasian species Martes martes, M. zibellina and M. foina (Hagmeier, 1961). Kerr (1792) first used the name americana as the last term of a trinomial. However, Turton in 1802 and 1806 used the term in binomial form, and is usually cited as the authority for the name (Hagmeier, 1955, 1961).

In 1890 Merriam described a new species for the west coast, Martes caurina. This tendency to subdivide the original species continued for many years, and Miller (1924) listed six species and numerous subspecies of North American marten. However, a better understanding of the mechanisms of speciation, population dynamics and evolution led to the development of a more realistic classification. Grinnell and Dixon (1926) were the first to consider two basic types; Allen (1942) classified them as separate species, Martes americana and M. caurina. Wright (1953) provided evidence of the intergradation between them in northern Idaho and Montana, and concluded that they belonged to two major "groups" or "types" of the single species M. americana (Hagmeier, 1955, 1961). Wright's scheme was corroborated by Hagmeier (1955) in his extensive and detailed study of the genus Martes. The americana "type" is distinguished by a relatively high, narrow skull, long and narrow auditory bullae, and small upper molars; the caurina "type" is characterized by a low, broad skull, wide and short rostrum, less inflated and short auditory bullae, and large upper molars (Hagmeier, 1955).

Explanation as to why.

The americana "type" ranges from the boreal forests of Newfoundland to the western mountains of British Columbia, Idaho and Montana, and as far north as Alaska. In contrast, the range of the caurina "type" is restricted to the west coast from the Alaskan panhandle, islands and coastal mountains of British Columbia, south through the Coast and Cascade ranges of Washington and Oregon to Wyoming and the Sierra Nevada of California (Hagmeier 1955, 1956, 1961)

Seven subspecies were described within each of these "groups". Thus, the americana group is made up of the subspecies M. a. americana, brumalis, atrata, abieticola, actuosa, kenaiensis, and abietinoides; the caurina group comprises M.a. caurina, humboldtensis, vancouverensis, vulpina, nesophila, origenes, and sierrae (Hagmeier 1955, 1961). Hagmeier (1958) concluded that the subspecies concept in the americana section is artificial. Geographic variation within this group is moderate, clinal and discordant; thus the different subspecies can be delimited only subjectively.

There was no detailed survey or morphological study performed to evaluate the subdivision of the caurina section into seven subspecies. As for the americana section it is difficult to defend so many subspecies in this group, though some "geographic isolates" are present (Mayr, 1969). These geographical isolates are the subspecies that inhabit the Queen Charlotte Islands and the Alexander Archipelago (M.a. nesophila; Osgood, 1901) and Vancouver Island (M.a. vancouverensis; Grinnell and Dixon, 1926). As Mayr (1969) stated, insular populations present the clearest examples of isolates, and they are frequently of sufficient difference to merit subspecies rank.

The populations of M.a. nesophila that inhabit the Queen Charlotte Islands are the central subject of this study. This large, light-coloured race of marten is one of the most distinctive in North America (Hagmeier, 1955). It was originally described by Osgood (1901), from skulls alone, as a different species Mustela nesophila. Anderson (1946:59) described it as "...larger than Martes caurina caurina and....always light coloured and short haired as compared with the mainland form". Hagmeier (1955) verified that the skins of this "race" can often be identified by its relatively short ears, these being lower and more rounded than in other "races" of the species. The fur would be considered as low grade by a furrier, compared to marten from other regions, due to its thin and coarse hair. The overall coat colour is pale brown with orange or reddish underfur, darker extremities and tail, and a large red-orange spot on the throat and breast. The presence of white hairs mixed with brown ones on the head makes it look grayish. The skull of M.a. nesophila from the Queen Charlotte Islands is also distinguishable in many aspects from mainland forms. It is large and massive with wide zygomatic arches and heavy dentition (Hagmeier 1955, 1961).

Swarth (1911:139) collected a marten on Kuiu Island, Alaska, which he identified as M.a. nesophila, although he observed that it was slightly different from those on the Queen Charlotte Islands "...in slightly greater width, with especially wide spreading zygomata...". In 1912, Swarth collected two more skulls from Admiralty Island, Alaska, which he also referred to as "M. caurina nesophila", although in his earlier paper (1911:140) he had stated that "...should additional specimens show the wide spreading zygomatic arches to be a constant feature, the marten of the Alexander Archipelago should be considered a distinct species".

Hagmeier (1955), after comparing 22 skulls from the Queen Charlotte Islands with 12 skulls from the Alexander Archipelago, concluded that Swarth's designation was correct. He found that skulls from the Queen Charlotte Islands to average slightly larger in most characters, though none reached statistical significance.

Osgood (1901) and Swarth (1911) considered nesophila to be a different species of marten. It was left for Grinnell and Dixon (1926) to determine its similarities with caurina, and hence to classify it as a subspecies, M. caurina nesophila. It was not until Wright (1953) presented strong evidence that all North American marten were one single species, that nesophila changed to its current designation, M. americana nesophila.

The Habitat

The conditions under which marten from the Queen Charlotte Islands live are unusual. These islands are populated by an impoverished flora and fauna, and the distance that separates them from the mainland has led to the evolution of endemic forms. Thirty-four miles (Hecate Strait) separates this archipelago from the closest mainland islands, the distance to the nearest island of the Alexander Archipelago is 31 miles across Dixon Entrance, and it is 49 miles to the nearest mainland (Foster, 1963, 1965).

Foster (1963:6) outlined the main features of the Queen Charlotte Islands when he wrote:

> "The Queen Charlotte Islands form a scimitar shaped group, convex to the Pacific Ocean and with handle towards the south. Graham Island forms the broad northern part of the blade, whereas Moresby and many lesser islands form its tapering southern part. The continental shelf that lies off-shore fringing most continents is absent or very narrow off the Queen Charlotte Islands. Rugged mountains, volcanic in origin, rising to 4,000 feet and forming the westerly back-bone of the islands, drop with little interruption to over 10,000 feet beneath the Pacific Ocean. The eastern side of the islands slopes gently to the shallow basin of Hecate Strait".

There is evidence that glacial refugia existed on the Queen Charlotte Islands, and also that the archipelago may have been connected with the mainland through a temporary bridge (Dahl, 1955; Heusser, 1955, 1960; Foster, 1963, 1965; Fladmark, 1975; Mathewes and Clague, 1982; Warner et al.,1982; Warner, 1984; Mathewes, in press; Heusser, in press).

Objectives

In this study my objectives were the following:

1. To analyse phenotypic relationships between nesophila from the Queen Charlotte Islands and other nearby races within the caurina section (nesophila from the Alexander Archipelago, caurina from the coast of British Columbia and vancouverensis from Vancouver Island). This is the first time that a large sample of these populations has been studied using multivariate statistical methods.

2. To determine if the patterns of differentiation among these populations, with particular emphasis on nesophila, are coincident with the classification of Swarth (1911) and Hagmeier (1955).

3. To compare sexual dimorphism in mainland and islands' populations, and its change with age.

Part 1

GEOGRAPHIC VARIATION OF THE AMERICAN PINE MARTEN (*MARTES AMERICANA*) IN THE PACIFIC NORTHWEST, WITH SPECIAL REFERENCE TO THE QUEEN CHARLOTTE ISLANDS

INTRODUCTION

The Queen Charlotte Islands are among the best places in Canada for studying endemism. This small group of volcanic islands, situated 49 miles off the coast of British Columbia, contains a unique biological community that clearly reflects the effects of geographic isolation and its important role in the origin of new species (Heusser, 1960; Foster, 1963, 1965; Warner, 1984).

The American Pine Marten (*Martes americana*) is among the few species of mammals that occur naturally on these islands (Foster, 1963, 1965). The marten there is a good example of what Mayr (1969) refers to as a "geographical isolate", and has so many distinctive features that Osgood (1901) considered it to be a separate species.

Hagmeier's (1955) review of *Martes* concluded that only a single species of marten occurs in North America, and that the Queen Charlotte Islands form belongs to the subspecies *M.a. nesophila*. He also confirmed Swarth's (1911) observations on the general resemblance between the skulls of marten from the Alexander Archipelago (Alaska) and those from the Queen Charlotte Islands, and considered the range of *nesophila* to extend over the Queen Charlotte Islands, the Alaska panhandle and the adjacent mainland. However, this judgement relied on only a very small sample (34 skulls from both groups and univariate statistical methods) so differences among populations of *nesophila* could easily have been overlooked.

At least since the end of the last glacial period, the marten from the Queen Charlotte Islands have been in a highly isolated environment, feeding on a different prey base, and without many of their competitors and enemies (e.g. Long-tailed Weasel *Mustela frenata*, Fisher *Martes pennati*, and Lynx *Lynx canadensis*). Gene exchange with populations outside this archipelago must be extremely low or nonexistent. It is not clear then, why the marten on the Queen Charlotte Islands should have remained so similar to those in the Alaska panhandle as to be placed in the same subspecies.

Information about past and current distributions of Alaskan marten is scanty and often unreliable (Johnson, 1981). For example, it is not known whether the species occurred naturally in all islands of the Alexander Archipelago. For some of them (Baranof, Chichagof, Prince of Wales and Admiralty Island) it has never been clear whether marten were ever present. To create jobs and revenue from trapping, the Alaska Game Commission transplanted or relocated certain species of fur-bearers to different islands. Marten were among those species. The introductions were as follows (Johnson, 1981): to Prince of Wales Island, ten marten from the subspecies *actuosa* in 1934; to Baranof Island, seven marten from *actuosa* in 1934; to Chichagof Island, six marten from Baranof Island in 1949 (subspecies unknown); to the Pelikan area, 15 animals from different places (Southeast Alaska, Ketchikan, Stikine River, Petersburg, and Anchorage) in 1951 and 1952. The suggestion that islands receiving introductions lacked indigenous marten is contradicted by a specimen from the mammal collection of the U.S. National Museum which was collected on Chichagof Island (Dundas Bay) by Olson in 1923.

It is even more ambiguous when marten were established on Admiralty Island, since published accounts are conflicting. Marten were not mentioned in several earlier mammal surveys of the island, but Johnson (1981) reported five specimens in the U.S. National Museum which had been collected there by A. Hasselborg in 1915. Additional evidence is given by four specimens from that island which I measured and which are included in this study. They are part of the collections of the Museum of Vertebrate Zoology (University of California) and were collected by Swarth, one in 1910 and the others in 1913. The museum specimens indicate that marten were already present on these islands long before the introductions took place, and I do not see any reason to suspect that they were not indigenous.

It is unfortunate that almost all the museum specimens of marten from this archipelago are from only two islands, Baranof and Chichagof. A very small sample from the nearby mainland was also included in my study. The importance of these specimens is that, if the adjacent mainland population is the source of the founder group that colonized the archipelago, the similarity between them and island marten could indicate what effect the marten introductions have had.

The objectives of this study were to analyse and compare the phenotypic characteristics of marten from the Queen Charlotte Islands, the Alaska panhandle, Vancouver Island and the coast of British Columbia, and to review their systematic status.

My working hypothesis was that, in light of the extreme isolation and unusual environment of the Queen Charlotte Islands, the marten there should be more distinctive than other populations of the proposed subspecies.

MATERIALS AND METHODS

Location of Specimens and Study Area

The material for this study consisted of 321 female and 453 male marten skulls. The number of specimens (male/female) from each population was:

(a) Queen Charlotte Islands - 95/63.

(b) Baranof and Chichagof Islands (Alexander Archipelago) - 133/79.

(c) Admiralty Island (Alexander Archipelago) - 1/2.

(d) Kuiu Island (Alexander Archipelago) - 1/0.

(e) Yakutat Island (Alexander Archipelago) - 1/0.

(f) Coast adjacent to Alexander Archipelago - 33/24.

(g) Southern coastal region of British Columbia - 56/40.

(h) Vancouver Island - 93/71.

(i) Mackenzie District (North West Territories) and Road River (Yukon) - 40/42.

Ninety-eight of the specimens examined in this study from the Queen Charlotte Islands were obtained from trappers through the British Columbia Provincial Museum; all the other specimens were from museum collections. The museums and specimen catalogue numbers are listed in Appendix A.

The localities of geographic samples used in this study and the ranges of the different subspecies are shown in Figure 1. For analysis skulls were allocated to five general geographic regions: 1. Queen Charlotte Islands; 2. Alexander Archipelago (all the specimens included in the analyses under Alexander Archipelago are from Baranof and Chichagof Islands; those from Admiralty, Kuiu and Yakutat Islands are usually presented as ungrouped cases); 3. mainland coast adjacent to Alexander Archipelago; 4. Vancouver Island; and 5. southern coast of British Columbia. The specimens of M.a. actuosa from the Mackenzie District (N.W.T.) and the nearby Road River (Yukon), are used only for comparison with specimens from Baranof and Chichagof Islands.

Most animals were aged using the number of cementum annuli in the lower or upper canines (aging was done by Matson's, a commercial firm in Montana). The ages of 53 specimens were not determined because their museums did not allow canines to be removed. The ages, sexes and population distributions of the samples are summarized in Table 1.

Figure 1: **Geographic distribution of 6 samples of North American Pine Marten used in this study..** Locality and specimen data are given in Appendix A.
Shaded areas = sample localities. QCI = Queen Charlotte Islands. G = Graham Island. M = Moresby Island. AA = Alexander Archipelago. B = Baranof Island. C = Chichagof Island. A = Admiralty Island. K = Kuiu Island. AAM = Alaska Panhandle Mainland. VI = Vancouver Island. SC = Southern Coast of British Columbia.

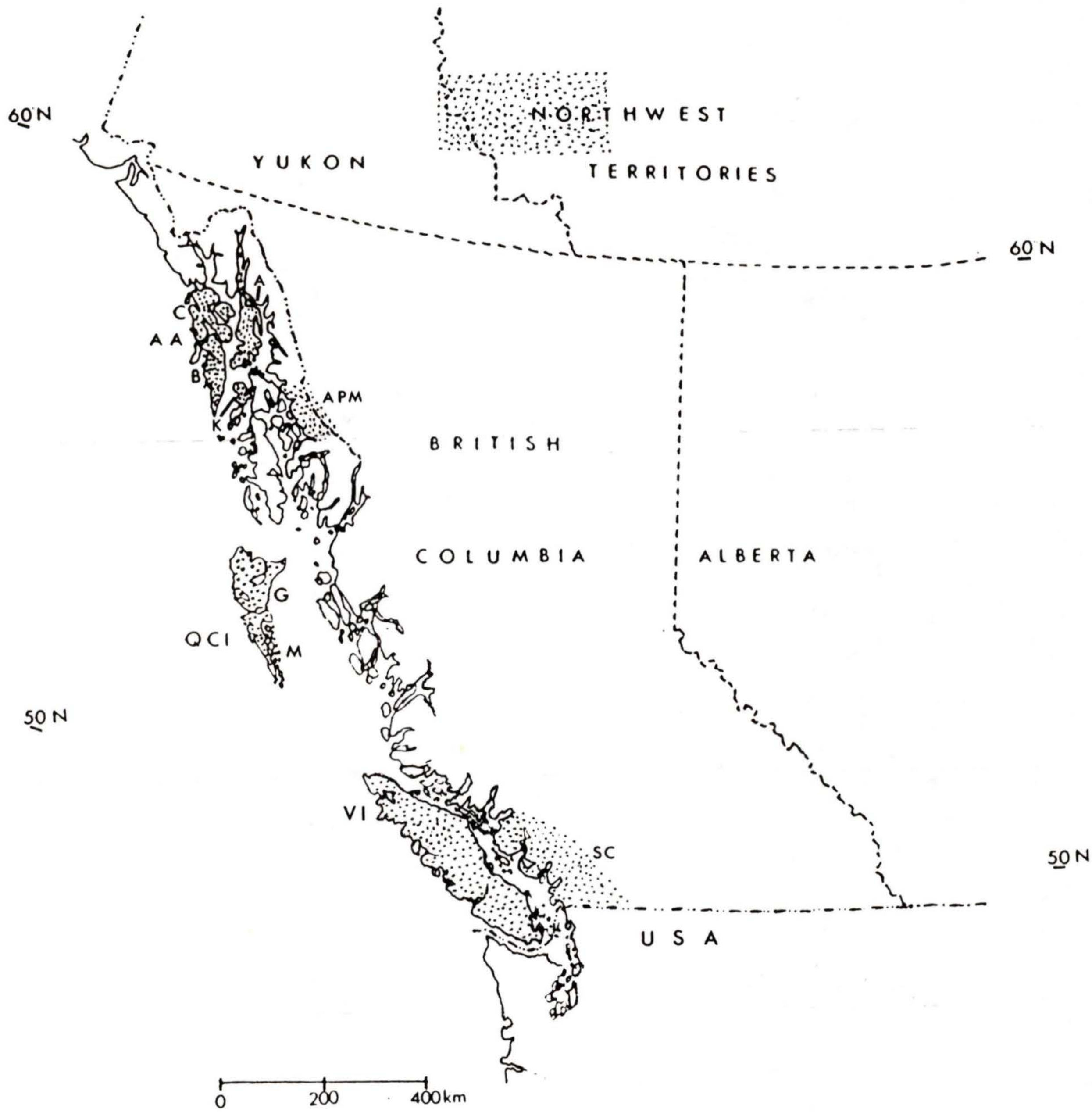

60 N
YUKON
NORTHWEST
TERRITORIES
60 N
C
A
AA
B
APM
K
BRITISH
COLUMBIA
ALBERTA
G
QCI
M
50 N
VI
SC
50 N
USA
0
200
400km

Table 1: Age composition of marten samples from the different localities.

AGE CLASS	QCI	AA	AAM	SCBC	VI
	Number of specimens from each locality (male - female)				
Unknown	3 - 10	2 - 0	0 - 0	22 - 9	1 - 0
0	15 - 23	87 - 57	21 - 14	18 - 20	49 - 34
1	26 - 17	16 - 9	4 - 6	8 - 7	22 - 23
2	11 - 5	2 - 2	4 - 0	18 - 8	23 - 4
3	11 - 5	5 - 4	0 - 1	1 - 0	8 - 1
4	2 - 1	4 - 1	1 - 1	3 - 0	0 - 2
5	6 - 0	0 - 0	2 - 1	0 - 1	0 - 1
6	4 - 0	0 - 0	0 - 1	1 - 1	1 - 4
7	3 - 3	0 - 0	0 - 0	0 - 0	1 - 0
8	1 - 0	0 - 0	0 - 0	0 - 0	0 - 0
9	1 - 0	0 - 0	1 - 0	0 - 0	0 - 1
12	0 - 0	0 - 0	0 - 0	1 - 0	0 - 0

Age classes are in years. Unknown = not sectioned for cementum analysis. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof-Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

Measurements

Twenty-five cranial and dental characters were recorded; 18 were cranial measurements taken to the nearest 0.1 mm with dial calipers, and 7 were dental characters measured to the nearest unit (0.13 mm) with an ocular micrometer and dissecting microscope. The list of measurements and their abbreviations are given in Appendix B.

Measurements were chosen to reflect skull size and shape, size of auditory bullae, strength of jaws, size of teeth, and breadth of rostrum. They were selected from a variety of sources. Some of them were those used by Hagmeier (1955) to describe differences among marten subspecies, as noted. Others were a selection of measurements used commonly in mammalian studies on geographic variation, growth, and functional morphology (Jolicoeur 1959, Anderson 1970, Radinsky 1981 and 1985, Nagorsen 1982, Brown 1983, Andersen and Wiig 1984, Freeman 1984, Friis 1985). I chose characters that could be reliably measured.

Statistical Methods

Specimens were grouped by sex and age to reduce the undesired effect of sexual and ontogenetic variation on the assessment of similarity between populations. Males are larger than females for most characters (Brown 1983). Independent t-tests were performed for each variable between sexes with all the age groups pooled together. Information about means, standard deviations, ranges and t-test results divided by population and sex are summarized in Appendix C.

I used the PAM program of BMDP (Biomedical Computers Programs) (Dixon, 1983) for data screening and estimating missing values. Specimens with more than four missing measurements were omitted from the study (three males, one female). Of the remaining specimens, one male had four missing values, seven had two and ten had only one; one female had three missing measurements, four had two and ten had one. Missing values were estimated by multiple regression.

Most multivariate statistical techniques make certain assumptions about the data:

1. Random sampling from the universe of interest. The specimens that I used in my study were from different museum collections, and I would not consider them a random sample. Therefore, the results should be treated with some caution.

2. Multivariate normality (Pimentel 1979, Neff and Marcus 1980, Reyment et al. 1984). The frequency distribution plots obtained for each variable showed, in most cases, a bell-shaped curve, but this is not enough to consider the overall multivariate distribution as normal. Unfortunately, multivariate statistical package programs do not include a test for multivariate normality.

3. Homogeneity of variance-covariance matrices among groups (Neff and Marcus 1980, Reyment et al. 1984). A test (Box's M test) is available in the multiple discriminant analysis program of SPSSX (Statistics Programs for Social Sciences), but it is very sensitive to departures from normality.

4. Sample size in multivariate methods. Sample size is one of the most serious limitations. A general rule of thumb is "to have at least 10 specimens per variable used in the analysis" (L. Rosenblood, pers. comm.). My total of 774 animals seems to be adequate for use of all 25 variables, but when the specimens are sorted by sex and age sample sizes become too small (see Table 1).

The violations of the assumptions listed above are usually not critical when multivariate methods of analysis are used, as in my study, to describe patterns of variation (Neff and Marcus, 1980).

I used multivariate statistical techniques which are now widespread in systematics research (e.g., Thorpe, 1976). Specific comments follow:

1. Principal components analysis (PCA) was used in exploratory data analysis to search for relationships among variables and for clustering patterns among samples. Eigenvector coefficients (the loading of each variable on the different axes or eigenvectors) may lead to the recognition of functional complexes. Components with large loadings of variables (0.7 or more) and of the same sign may be interpreted as a size component; when several coefficients have very different values and opposite signs, the component is considered to be summarizing shape (Reyment et al., 1984). BMDP 4M was used for PCA using the correlation matrix.

2. Multiple discriminant analysis (MDA). I used the SPSSX stepwise (MDA) program to identify the best subset of discriminating variables. This method selects the variable that provides the best separation among the groups. After the first variable is entered in the analysis, the next best discriminating variable is selected. At this point, the first variable is reevaluated to determine whether it meets a removal criterion. If it does, it is removed from the model. The method chosen to perform this analysis minimized Wilk's lambda. Thus, at each step the variable that results in the smallest Wilk's lambda for the discriminant function is selected for entry.

It is important to eliminate measurements that do not contribute to discrimination, because they actually may decrease the ability of the analysis to discriminate groups (Van Ness and Simpson, 1976). Furthermore, highly correlated characters make difficult certain transformations that the dispersion matrix undergoes during the analysis (Pimentel, 1979).

In further analyses I reduced the number of variables used retaining those that: (a) contributed substantially to the first three PCA axes ; (b) were considered important in the stepwise MDA; and (c) I could measure accurately.

3. Multivariate analysis of variance (MANOVA). I conducted separate MANOVA analyses for males and females using SPSSx to determine whether the centroids (mean values in the multivariate space) of the five groups were different. I used special contrasts to compare:

A. Queen Charlotte Islands against other localities.

B. Alexander Archipelago (Baranof and Chichagof Islands) against the adjacent mainland (to determine how similar they still were in spite of the introduction of specimens of M.a. actuosa from the Northwest Territories).

C. Vancouver Island against the coast of British Columbia (which Hagmeier (1955) considered to be indistinguishable although they had always been considered as two separate subspecies).

D. Both groups from the Alaska panhandle against both groups from southern British Columbia.

Whenever the hypothesis of no difference was rejected, univariate test results were examined to determine where the differences could be. The univariate F tests were calculated without any correction for the fact that several comparisons were made simultaneously, so had to be used with caution. The actual significance level of those tests was no longer 0.05, since the probability of incorrectly rejecting the null hypothesis at some time during the whole series of tests increases with number of tests (Neff and Marcus, 1980).

I also used MANOVA to investigate the degree of similarity between samples from the Alexander Archipelago and the Northwest Territories, and thus to evaluate the possible effect of the introductions of M.a. actuosa in these islands.

4. Multiple discriminant function analysis (canonical variates analysis, CVA). To investigate how well the different groups could be discriminated from each other, and to determine whether marten belonging to these groups could be correctly identified, I used CVA in SPSSX. This method is affected by violation of the assumption of homogeneity of variance-covariance matrices, and may cause inaccurate group assignments of unknown specimens. However, the results can be accepted with confidence if group separation is clear and correct classification rates are high. Separate analyses were performed for male and female martens.

First, specimens of all ages were lumped, then the sample was divided into three age groups (0, 1-2, 3+ years). Seven specimens from the Alexander Archipelago were included in the analysis as ungrouped cases to determine what group they were assigned to by the discriminant function. These included five males (one from Chichagof Island that had been collected before the introductions, two from Admiralty Island, one from Kuiu Island and another from Yakutat Island) and two females (from Admiralty Island).

Logarithmic transformation of the data is generally used to remove the size factor effect from the analysis, and thus unveil the shape component and its actual contribution to the discrimination among groups (Reist, 1985). However, I refer to the results of the different analyses using the raw data, because equivalent results were obtained from the log-transformed data.

CVA was validated using the "jackknife" or "leave-one-out" method provided in the 7M program of BMDP. This method analyses two random samples from each population, one to calculate the discriminant function, the other to test it.

In comparing specimens from the Alexander Archipelago and the Northwest Territories, I used only specimens of age 0. The specimens from the Northwest Territories were entered in the analysis (a) as ungrouped cases and (b) grouped under their own separate subspecies (actuosa).

5. Other analyses. Phenetic relationships among groups were further evaluated by phenograms derived from cluster analysis of taxonomic distance, using character means of the five groups. The degree of similarity also was investigated using the minimum spanning tree calculated on the taxonomic distances among groups. This method produces a graph in which the different local populations are linked together by a set of lines. A connection between two groups indicates phenetic similarity; the absence of connection is an indicator of lack of phenetic relationship (Nagorsen 1982). These analyses were done with NT-SYS programs (Numerical Taxonomy System for Multivariate Statistical Programs).

RESULTS

Univariate statistics

I treat sexual dimorphism in more detail in part II, but note here that the sexes differed significantly in all variables except PORC (Appendix C). The separate analyses for males and females are clearly justified.

Comparisons of different characters among populations revealed the following significant differences for both males and females: marten from the Queen Charlotte Islands were wider at the zygomatic arches, and had a larger foramen magnum, a broader rostrum, greater width across the postorbital processes and between the ocular orbits, larger distance between infraorbital foramina, wider and higher jaws, larger canines, longer and broader last upper premolars, wider upper molars, larger separation between upper molars and longer first lower molars than the marten from any other group. They also had the shortest bullae in proportion to their condylobasal length and zygomatic width; however, bulla width was not significantly smaller than in the other groups. Some of these differences are displayed in Figures 2 and 3.

In general terms the pattern observed among the other populations was that the Alexander Archipelago was very similar in many characters to the sample from the adjacent mainland, while the Vancouver Island sample was not strongly differentiated from the British Columbia coastal sample.

Figure 2: **Means of selected variables for male and female marten from the sample localities.**

1 = Queen Charlotte Islands.
2 = Alexander Archipelago (Baranof and Chichagof Islands).
3 = Alaska Panhandle Mainland.
4 = Southern Coast of British Columbia.
5 = Vancouver Island.
Means plus and minus two standard deviations.

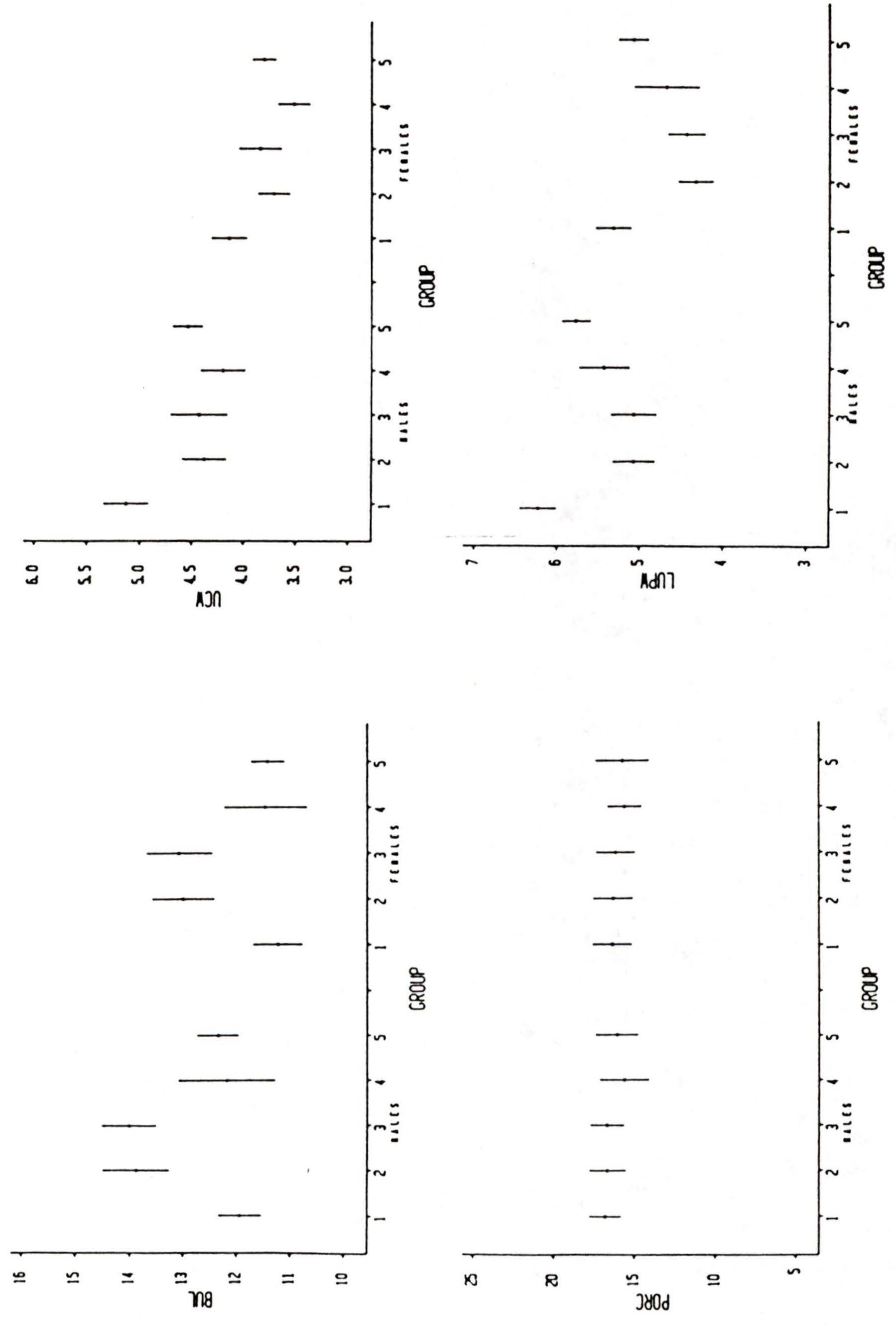
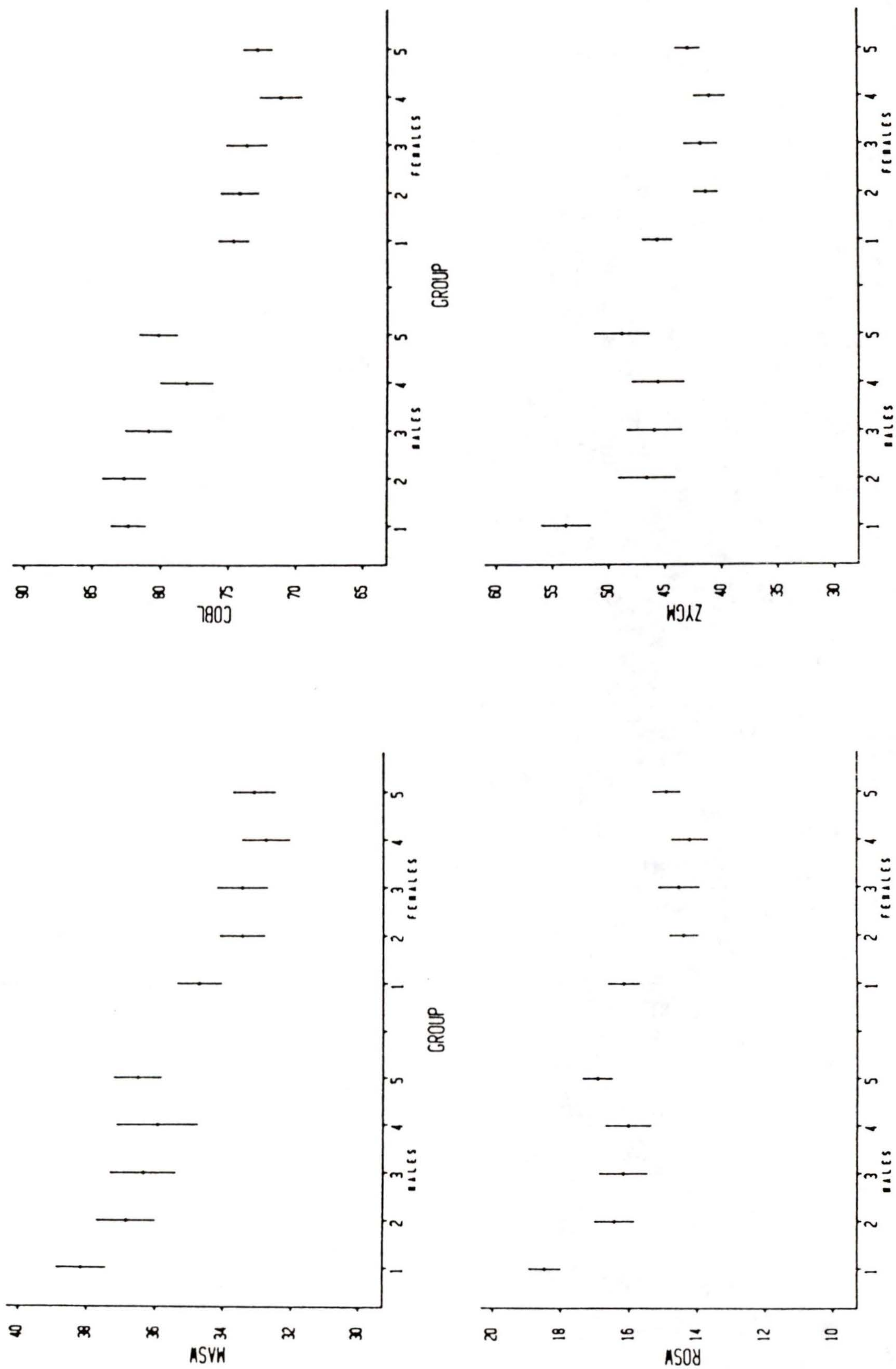

UCW
LUPW
BUL
PORC
GROUP
MALES
FEMALES

Figure 3: **Means of selected variables for male and female marten from the sample localities.**

1 = Queen Charlotte Islands.
2 = Alexander Archipelago (Baranof and Chichagof Islands).
3 = Alaska Panhandle Mainland.
4 = Southern Coast of British Columbia.
5 = Vancouver Island.
Means plus and minus two standard deviations.


COBL
ZYGM
MASW
ROSW
GROUP
MALES
FEMALES

Multivariate Analyses

After combining the information provided by PCA and MDA I reduced the number of variables to nine: JAH, COBL, ZYGM, CHAB, BUL, FOMW, UCW, LUPL and LUPW.

The results of the MANOVA for male Pine Marten were as follows: (a) The first contrast, comparing the Alaska panhandle with Vancouver Island and the southern coast of British Columbia was highly significant (F=118.74, P<0.001). This indicates a sizeable difference among the groups; 73% of the total variance was explained by the group difference (Wilk's lambda=0.269). Univariate analysis revealed that all variables except one (upper canine width, UCWB) differed significantly between the samples. (b) The second contrast compared Vancouver Island marten with marten from the southern coast of British Columbia. This contrast also showed a significant multivariate F value (24.81, P<0.001), thus rejecting the hypothesis of no difference between the two groups. However, only 36% of the total variance was accounted for by the dissimilarities between the groups (Wilk's lambda=0.638). The univariate tests revealed significant differences for all the characters except bulla length (BUL) and last upper premolar length (LUPL). (c) The third contrast was between the two samples from the Alaska panhandle (Baranof plus Chichagof vs. mainland coast). In this case, although again the multivariate F value was significant (8.54, P<0.001), the difference between groups was very slight, with only 16% of the variance explained by the group differences (Wilk's lambda=0.837). The univariate tests accordingly showed significant differences for only two variables: jaw height (JAWH) and condylobasal length (COBL). (d) The final contrast was between the Queen Charlotte Islands and all the other groups. It was the contrast that showed the greatest dissimilarity between groups. Not only was the multivariate test significant ($F=100.00$, $p<0.001$), but the variance explained by the difference between groups was the highest of all: 88% (Wilk's lambda=0.117). All the univariate comparisons were significantly different.

The MANOVA's for females had similar results to those for males, although there were some minor differences in the univariate tests.

Separate PCA's for males and females, using all geographic samples, revealed three groups: Queen Charlotte Islands; Vancouver Island plus the southern coast of British Columbia; and the Alaska panhandle (Figs. 4, 5).

The first three principal components accounted for 50, 19, and 6% of the variance in males, and for 48, 19, and 6% in females. In males most characters loaded heavily on the first component except for condylobasal length, cranial height, bulla length, bulla width and palatal length (all of which fell on the second component), and postorbital constriction (which loaded heavily on the third) (Table 2).

Females followed a similar pattern, though the loading for the distance between upper molars was smaller and foramen magnum width loading on the first component was higher than in males (Table 3).

Figure 6 shows the ordination of male groups on the first two canonical discriminant functions. The first function accounted for 76% of the variance and clearly separated the Queen Charlotte Islands, Vancouver Island and the Alaska panhandle groups. The second discriminant function accounted for 22% of the variance, and separated Vancouver Island plus the southern coast of British Columbia from Queen Charlotte Islands plus Alaska panhandle. The groups from the Alaska panhandle (Baranof and Chichagof Islands and adjacent mainland coast) overlapped almost entirely.

Figure 4: **Plot of first two principal components for male marten from the sample localities. These components accounted for 50 and 19% of the variance respectively.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
APM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.

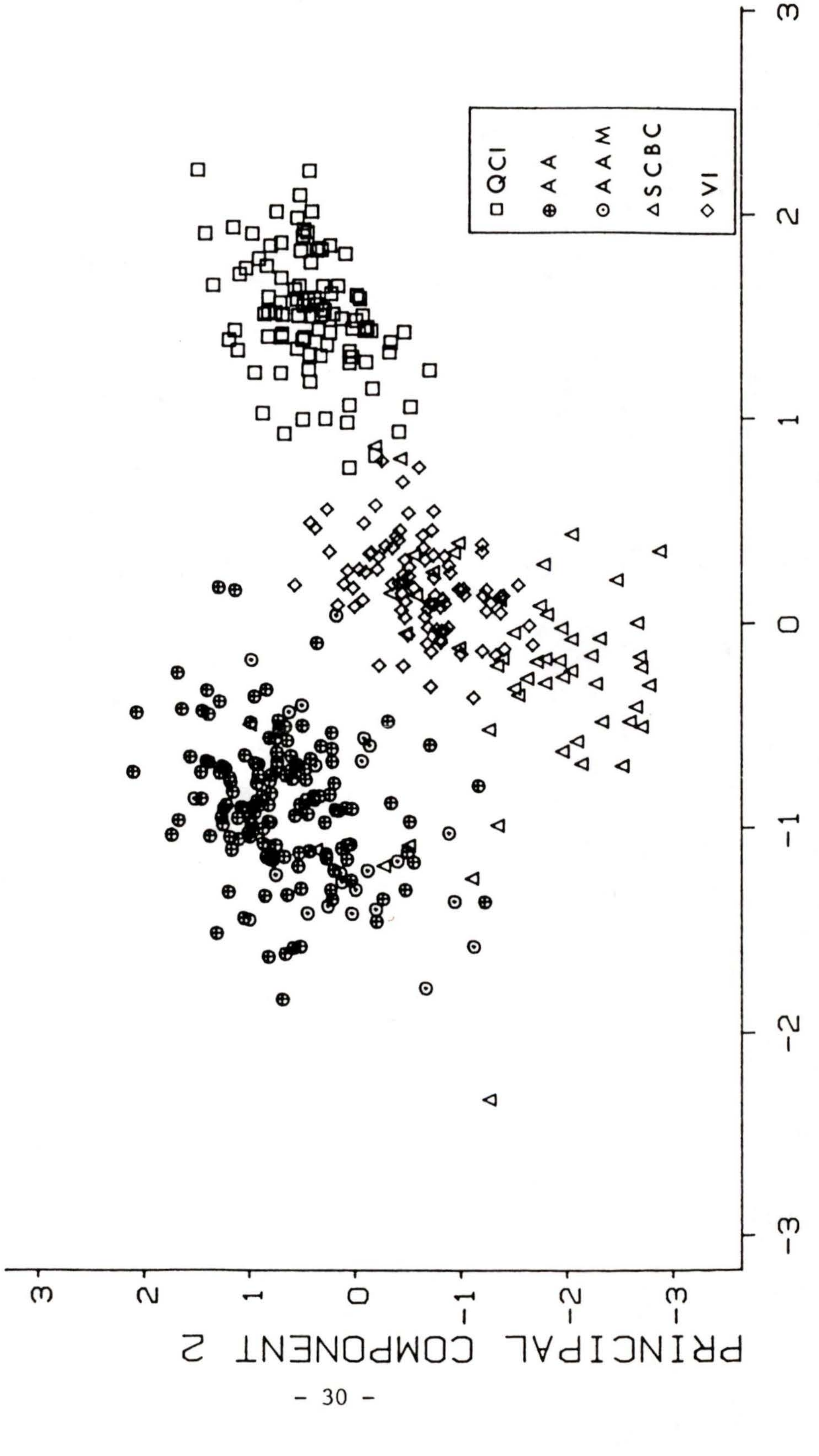

QCI
A A
A A M
S C B C
VI
PRINCIPAL COMPONENT 1
PRINCIPAL COMPONENT 2
-3
-2
-1
0
1
2
3

Figure 5: **Plot of first two principal components for female marten from the sample localities. These components accounted for 48 and 19% of the variance respectively.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
APM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.

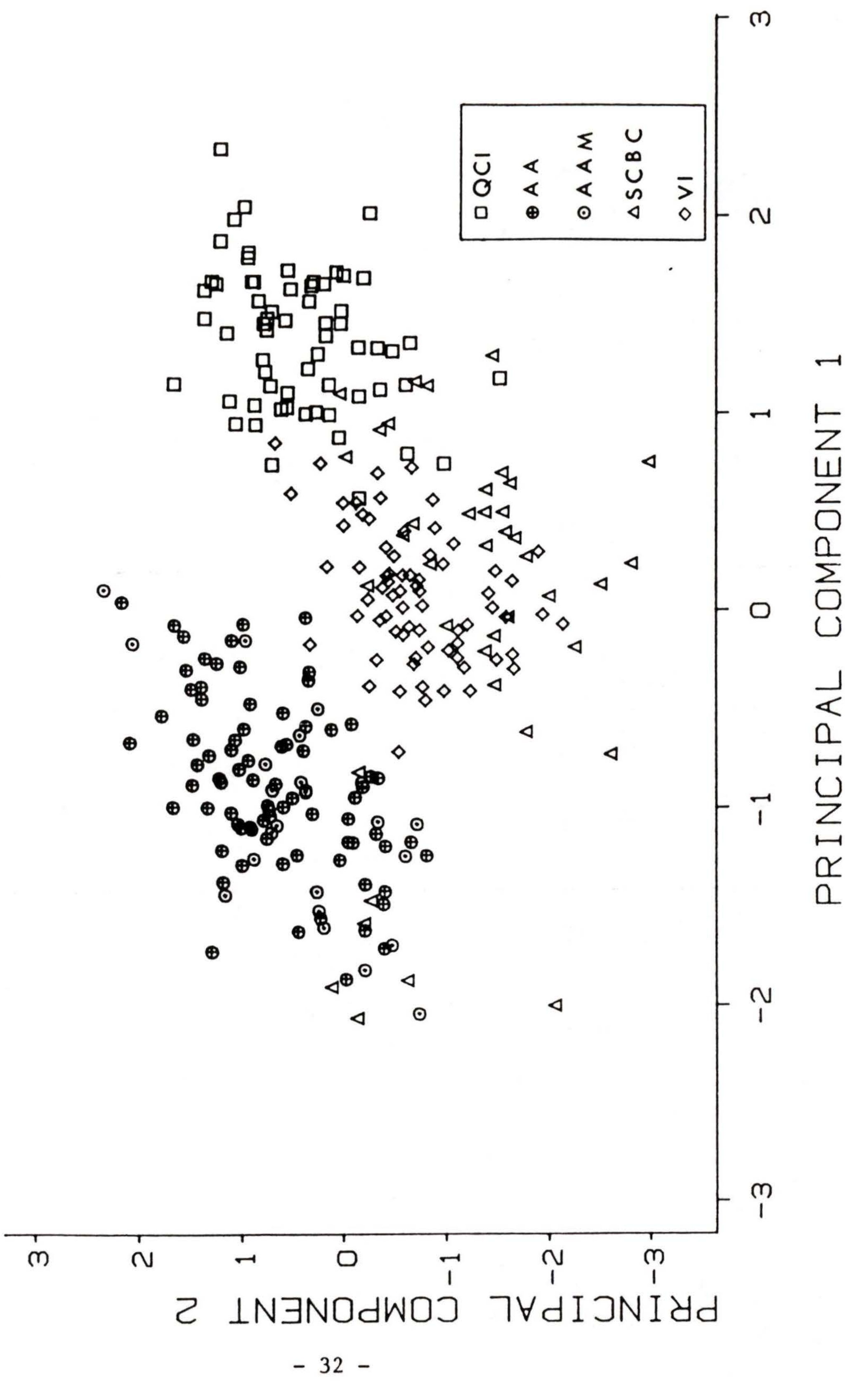

PRINCIPAL COMPONENT 1
PRINCIPAL COMPONENT 2
QCI
AA
AAM
SCBC
VI
-3
-2
-1
0
1
2
3

Table 2: **Factor loadings and eigenvalues for first three components from principal components analysis on male marten**

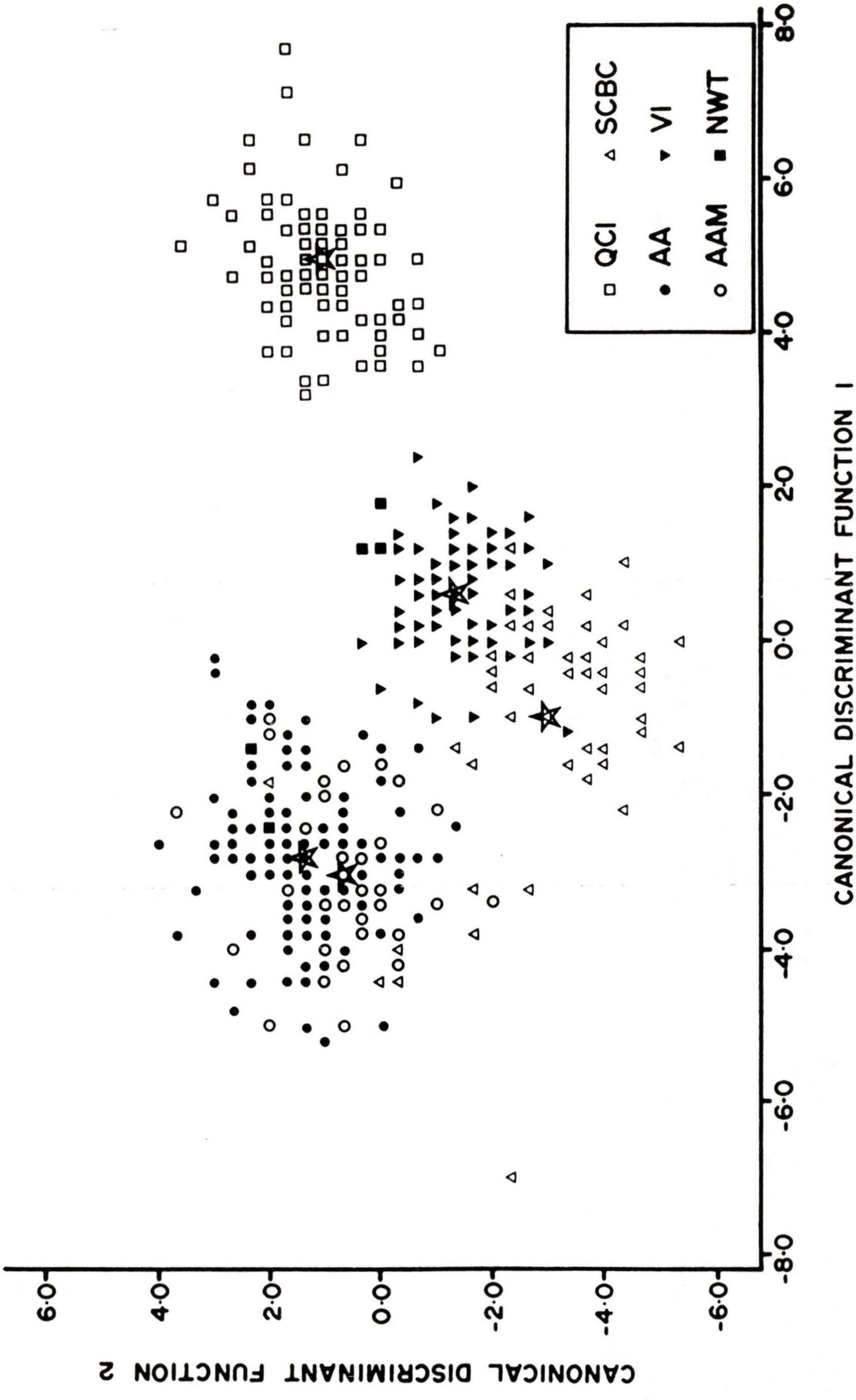
VARIABLE	PC1	PC2	PC3
ROSW	0.938	0.000	-0.044
IFOW	0.908	-0.139	-0.064
JAH	0.903	0.048	-0.106
ZYGM	0.890	-0.058	-0.304
IORW	0.882	0.072	-0.098
UCW	0.867	0.006	-0.025
WPOP	0.857	-0.202	-0.166
FLML	0.831	-0.307	0.153
LUPL	0.805	-0.315	0.119
LUPW	0.798	-0.428	0.106
JAW	0.773	0.061	-0.067
MASW	0.771	0.348	-0.033
UMW	0.758	-0.319	0.241
TRL	0.734	0.468	-0.002
JAL	0.728	0.491	-0.086
FOMW	0.695	0.191	0.211
DBUM	0.671	0.127	-0.236
UMIL	0.599	-0.484	0.243
FOMH	0.580	-0.226	0.291
BUW	0.085	0.825	0.029
COBL	0.453	0.808	-0.091
PALL	0.400	0.788	-0.078
BUL	-0.451	0.783	-0.075
CHAB	0.137	0.765	0.417
PORC	0.052	0.291	0.827
eigenvalue	12.615	4.711	1.390
% of variance	50.0	19.0	6.0

Table 3: **Factor loadings and eigenvalues for first three components from principal components analysis on female marten**

VARIABLE	PC1	PC2	PC3
ROSW	0.937	-0.016	-0.048
ZYGM	0.905	-0.020	-0.157
JAH	0.859	0.116	-0.050
IFOW	0.854	-0.253	-0.062
FLML	0.851	-0.284	0.031
JAL	0.830	0.362	-0.168
LUPL	0.823	-0.293	-0.032
UCW	0.812	0.159	-0.091
UMW	0.787	-0.346	0.096
MASW	0.781	0.390	0.027
WPOP	0.779	-0.220	-0.011
TRL	0.753	0.422	-0.187
JAW	0.745	0.085	0.219
LUPW	0.744	-0.473	-0.038
FOMW	0.723	0.204	0.318
IORW	0.701	0.082	0.014
FOMH	0.692	-0.196	0.352
UMIL	0.630	-0.396	0.093
DBUM	0.443	0.271	-0.136
BUW	0.024	0.857	0.047
PALL	0.317	0.797	-0.186
BUL	-0.435	0.792	-0.125
CHAB	0.051	0.769	0.452
COBL	0.548	0.723	-0.217
PORC	0.036	0.253	0.851
eigenvalue	12.104	4.625	1.446
% of variance	48.0	19.0	6.0

Figure 6: **Plot of the male marten samples on the first two canonical discriminant functions. These functions accounted for 76 and 22% of the variance respectively. Stars indicate group centroids.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.


QCI
SCBC
AA
VI
AAM
NWT
CANONICAL DISCRIMINANT FUNCTION I
CANONICAL DISCRIMINANT FUNCTION 2
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0

The standardized canonical discriminant function coefficients for males indicate the contribution of the variables to the overall discriminant function (Table 4). The variables which contributed most to the first function were jaw height, bulla length and last upper premolar width (their signs suggested that jaw height and premolar width would increase towards the right, while bulla length would decrease in that same direction along the first canonical function axis). Upper canine width, cranial height, and last upper premolar length showed high discriminant coefficients on the second function (the first two characters increased in value towards the positive side of the second canonical axis, and premolar length seemed to increase in the opposite direction, Figure 6).

The classification table for this discriminant analysis is shown in Table 5. Marten from the Queen Charlotte Island had the best classification rate (100%). Classification rates for the other groups ranged from 73% (southern coastal British Columbia) to 95% (Vancouver Island). The most frequent misclassifications occurred between the two samples from the Alaska panhandle, and between the southern coast of British Columbia and Vancouver Island.

The five male specimens that were included later in the analysis as "ungrouped cases" were classified as follows: the marten from Baranof (before introductions) and the one from Yakutat Island were classified with the Baranof-Chichagof martens; the two specimens from Admiralty Island and the one from Kuiu were assigned to the Vancouver Island group.

The MDA results for females were similar to those for males (Fig. 7). However, samples from the Alaska panhandle overlapped less. The smaller sample size for females could be one reason for differences from the male patterns.

Table 4: Variables used during canonical variates analysis of the male marten samples, with standardized canonical discriminant coefficients for four significant functions

VARIABLE	FUNCTION 1	FUNCTION 2	FUNCTION 3	FUNCTION 4
JAH	0.5032	0.2386	0.3463	-0.6184
COBL	0.3866	0.4109	-1.0409	-0.4836
ZYGM	0.0449	-0.0652	-0.1697	0.3781
CHAB	0.2336	0.5108	0.1543	-0.0352
BUL	-0.4714	0.0275	0.3158	0.6032
FOMW	0.2377	0.2620	0.6359	0.0243
UCW	0.3200	0.4512	0.0868	0.5291
LUPL	0.1824	-0.4617	0.4524	-0.1906
LUPW	0.4032	-0.2373	-0.5323	0.3885

Table 5: **Classification table from canonical variates analysis of the male marten samples**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(95)	95 100%	0	0	0	0
AA(131)	0	108 82.4%	22 16.8%	1 0.8%	0
AAM(33)	0	6 18.2%	27 81.8%	0	0
SCBC(56)	0	1 1.8%	6 10.7%	41 73.2%	8 14.3%
VI(93)	0	0	0	5 5.4%	88 94.6%
Ungrouped cases(5)	0	2 40.0%	0	0	3 60.0%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 88.0%

The first discriminant function accounted for 72% of the variance and again showed the same three distinctive groups -Queen Charlotte Islands, Vancouver Island and the Alaska panhandle. The second discriminant function accounted for 24% of the total variance and, as for males, it divided Vancouver Island plus the southern coast of British Columbia from the Queen Charlotte Islands plus the Alaska panhandle. Female martens from the southern coast of British Columbia presented a broad distribution, as for males.

Table 6 shows the standardized canonical discriminant function coefficients for females. The variables that made major contributions to the first two functions were bulla length (first function), and cranial height and upper canine width (second function). Jaw height showed an almost equal contribution on both functions.

The classification table for females (Table 7), showed that 100% of the females from the Queen Charlotte Islands were reassigned to their own group. The correct classification rates for the other groups ranged from 68% for the animals from the southern coast of British Columbia, to 97% for Vancouver Island. As for males, misclassification occurred most often between the two groups from the Alaska panhandle and between the southern coast of British Columbia and Vancouver Island.

The two female specimens from Admiralty Island, included in this analysis as ungrouped cases, were classified with the Vancouver Island marten.

The classification tables which resulted from the use of the jackknifing to validate the canonical discriminant functions are shown in Tables 8 and 9. For males all the randomly selected marten from Queen Charlotte Islands and Van-

Figure 7: **Plot of the female marten samples on the first two canonical discriminant functions. These functions accounted for 72 and 24% of the variance respectively.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.

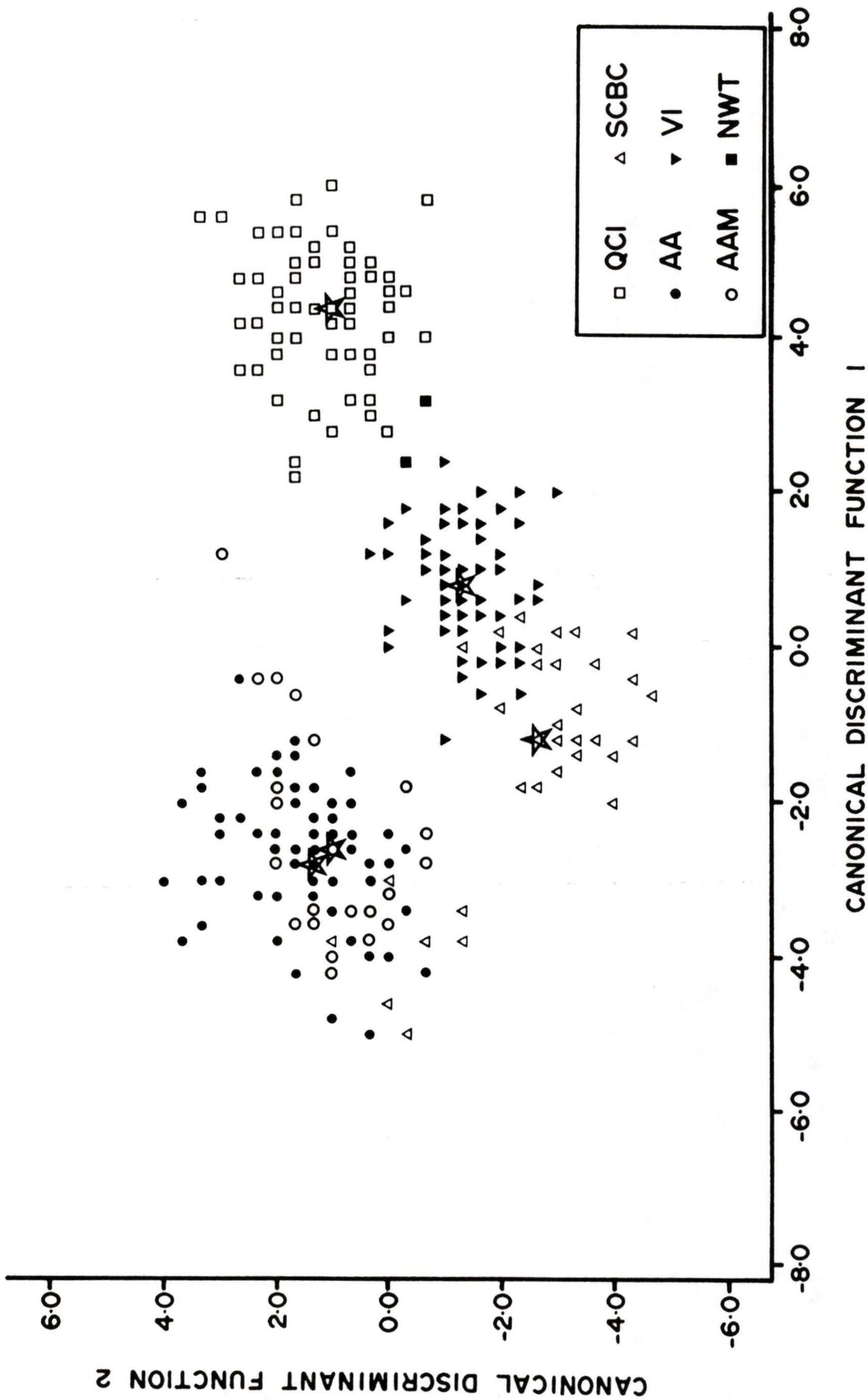

QCI
SCBC
AA
VI
AAM
NWT
CANONICAL DISCRIMINANT FUNCTION I
CANONICAL DISCRIMINANT FUNCTION 2
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0
6·0
4·0
2·0
0·0
-2·0
-4·0
-6·0

Table 6: **Variables used during canonical variates analysis of the female marten samples, with standardized canonical discriminant coefficients for four significant functions**

VARIABLE	FUNCTION 1	FUNCTION 2	FUNCTION 3	FUNCTION 4
JAH	0.3472	0.3527	-0.4496	-0.5036
COBL	-0.1981	0.2329	0.3017	-0.7038
ZYGM	0.3245	-0.1187	0.1789	0.2804
CHAB	0.1070	0.4662	0.1576	-0.3233
BUL	-0.5261	0.1712	-0.0167	0.5428
FOMW	0.2556	0.2844	-0.4104	0.4073
UCW	0.1840	0.4041	0.4642	0.5515
LUPL	0.1397	-0.1927	-0.5875	0.1885
LUPW	0.3930	-0.2936	0.5785	-0.0999

Table 7: **Classification table produced by canonical variates analysis of the female marten samples.**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(63)	63 100%	0	0	0	0
AA(79)	0	61 77.2%	18 22.8%	0	0
AAM(24)	0	4 16.7%	20 83.3%	0	0
SCBC(40)	0	2 5%	4 10%	27 67.5%	7 17.5%
VI(71)	0	0	0	2 2.8%	69 97.2%
Ungrouped cases(2)	0	0	0	0	2 100%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 86.6%

couver Island were classified correctly by the discriminant function. Most of the specimens from the Baranof-Chichagof Islands, the Alaska panhandle mainland and the southern coast of British Columbia also were recognized and correctly reassigned. The results observed for female martens from the jackknifed discriminant analysis also reflected the same trend.

When I used MDA on the data set subdivided into three age groups results were very similar to those from previous analyses, for both sexes. One limitation was that the sample sizes for the old age groups (especially females) were very small, and this made it almost impossible to correctly interpret any differences with the previous analyses (Figs. 8 to 13).

The rate of misclassification among different groups was smaller when older specimens were considered in the analysis. The degree of overlap among groups seemed to decrease with age (Tables 10 to 15).

Cluster analysis showed clear separation of the Queen Charlotte Islands sample from all others (Fig. 14). Two other groups also were evident, one included the southern coast of British Columbia and Vancouver Island, and the other consisted of both samples from the Alaska panhandle.

The minimum spanning tree analysis showed what was already suggested in MDA. The groups from the Alaska panhandle were the most phenetically similar to each other. Vancouver Island and the southern coastal area of British Columbia were also alike, though the degree of phenetic similarity here was smaller. Once more the sample from the Queen Charlotte Islands was the most distinctive, and its closest group in this study (in terms of taxonomic distance) was from Vancouver Island (see Fig. 15).

Table 8: Classification table produced by jackknifed canonical variates analysis of the male marten samples

ACTUAL GROUP(N)	New QCI	New AA	New AAM	New SCBC	New VI
	PREDICTED GROUP MEMBERSHIP				
NewQCI(18)	18 100%	0	0	0	0
NewAA(22)	0	19 86.4%	2 9.1%	1 4.5%	0
NewAAM(5)	0	1 20.0%	4 80.0%	0	0
NewSCBC(9)	0	1 11.1%	1 11.1%	6 66.6%	1 11.1%
NewVI(16)	0	0	0	0	16 100%

1. All "New" groups are formed by specimens selected at random from their original samples. NewQCI = Queen Charlotte Islands, NewAA = Alexander Archipelago (Baranof and Chichagof Islands), NewAAM = Alaska Panhandle Mainland, NewSCBC = Southern Coast of British Columbia, NewVI = Vancouver Island.

Table 9: **Classification table produced by jackknifed canonical variates analysis of the female marten samples.**

	PREDICTED GROUP MEMBERSHIP				
ACTUAL GROUP(N)	New QCI	New AA	New AAM	New SCBC	New VI
NewQCI(12)	12 100%	0	0	0	0
NewAA(11)	0	8 72.7%	3 27.3%	0 0	0
NewAAM(5)	1 20.0%	1 20.0%	3 60.0%	0	0
NewSCBC(6)	0	0	1 16.6%	4 66.6%	1 16.6%
NewVI(15)	0	0	0	0	15 100%

1. All "New" groups are formed by specimens selected at random from their original samples. NewQCI = Queen Charlotte Islands, NewAA = Alexander Archipelago (Baranof and Chichagof Islands), NewAAM = Alaska Panhandle Mainland, NewSCBC = Southern Coast of British Columbia, NewVI = Vancouver Island.

Figure 8: **Plot of the male marten samples (age = 0) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.

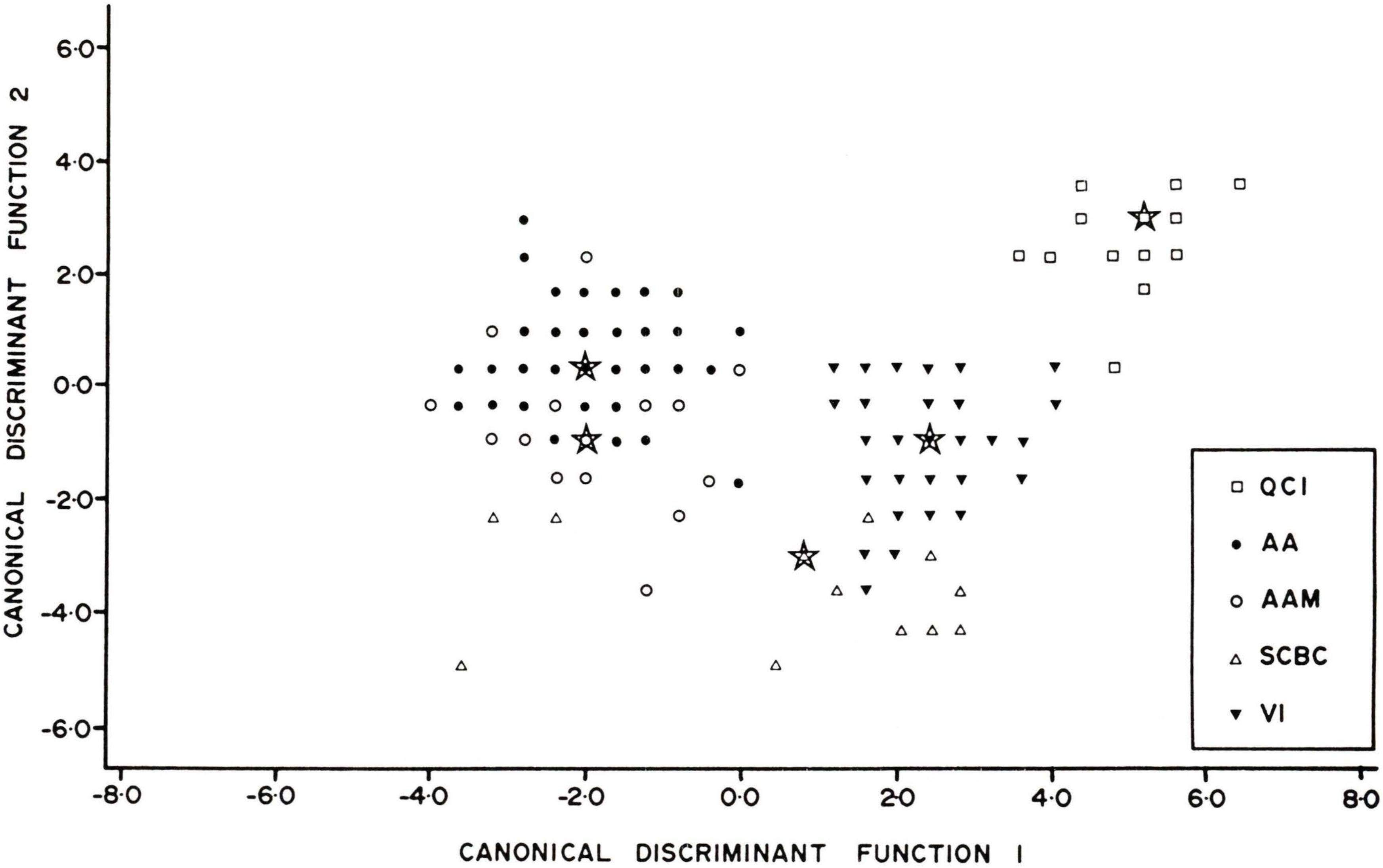
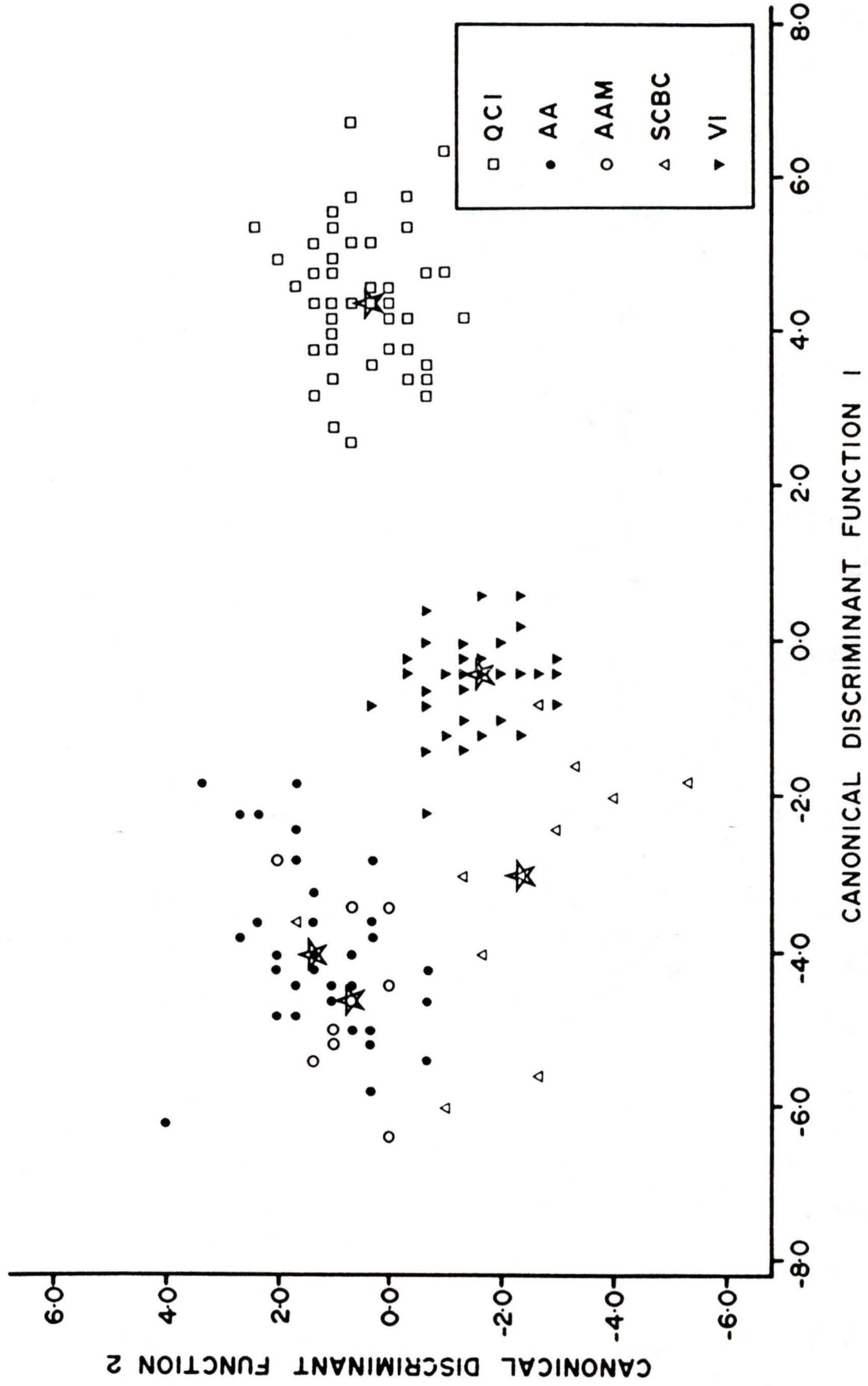

QCI
AA
AAM
SCBC
VI
CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0

Figure 9: **Plot of the male marten samples (age = 1-2) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.



QCI
AA
AAM
SCBC
VI
CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0

Figure 10: **Plot of the male marten samples (age = 3+) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.

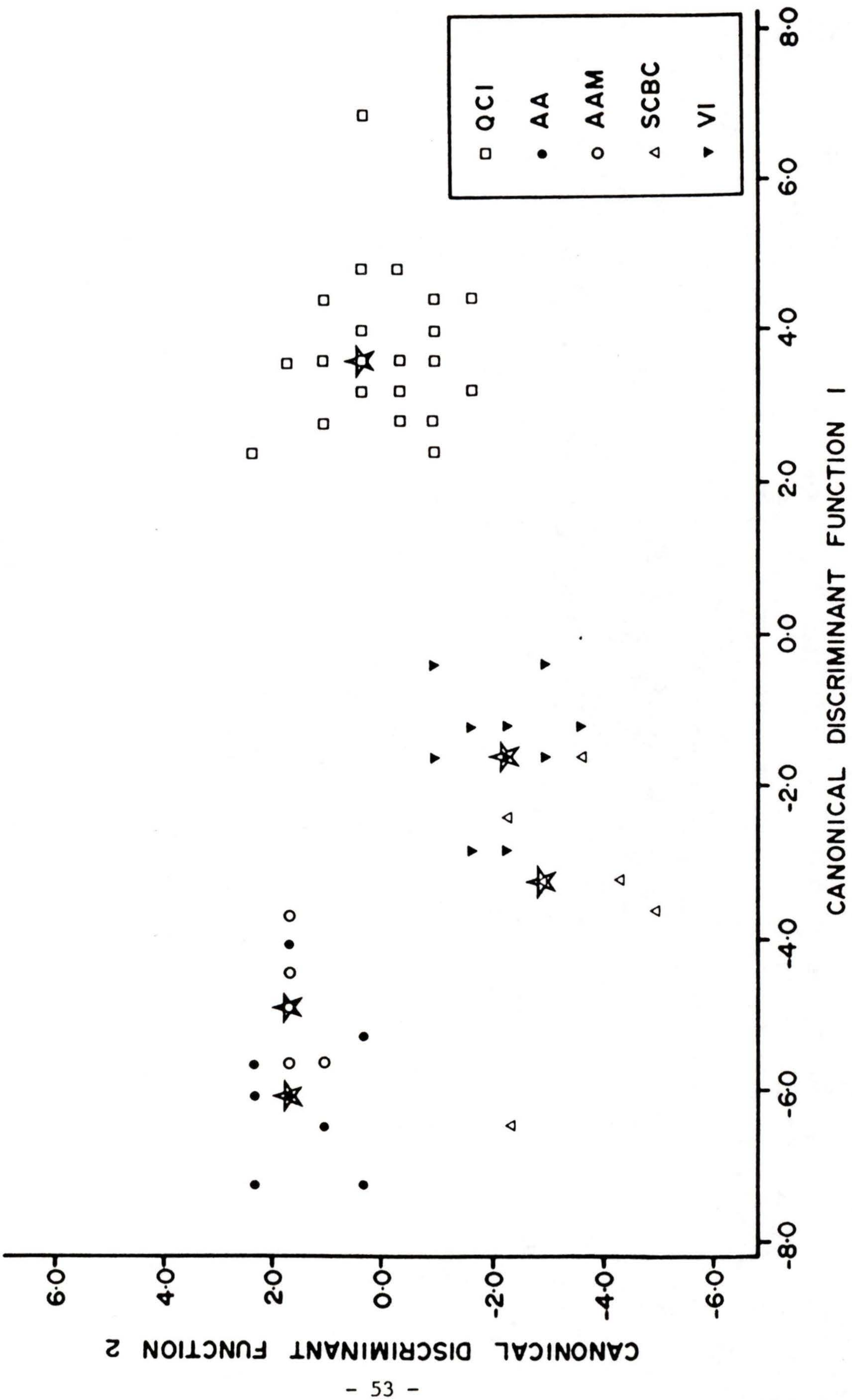
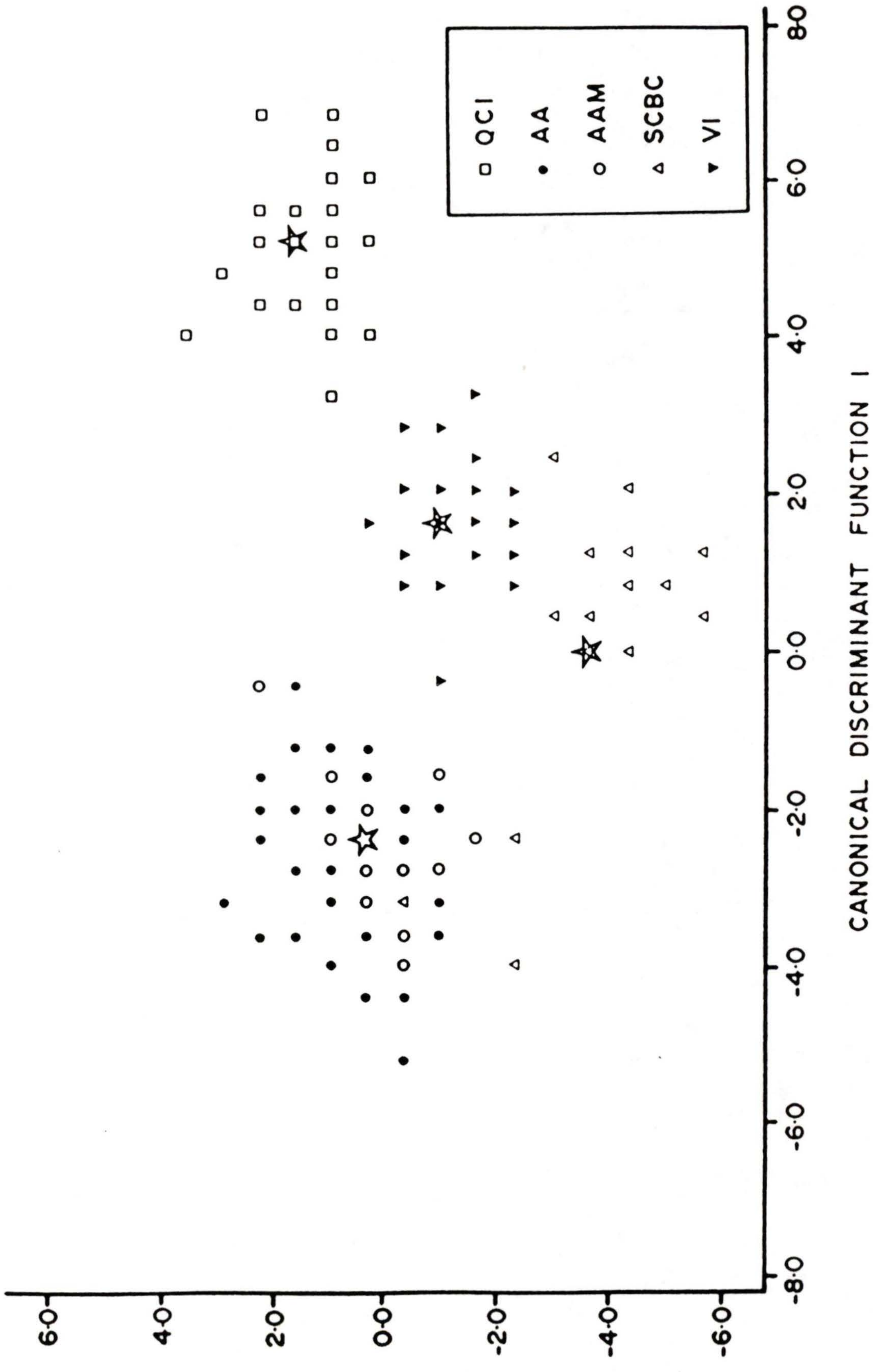

QCI
AA
AAM
SCBC
VI
CANONICAL DISCRIMINANT FUNCTION I
CANONICAL DISCRIMINANT FUNCTION 2
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0

Figure 11: **Plot of the female marten samples (age = 0) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.


CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
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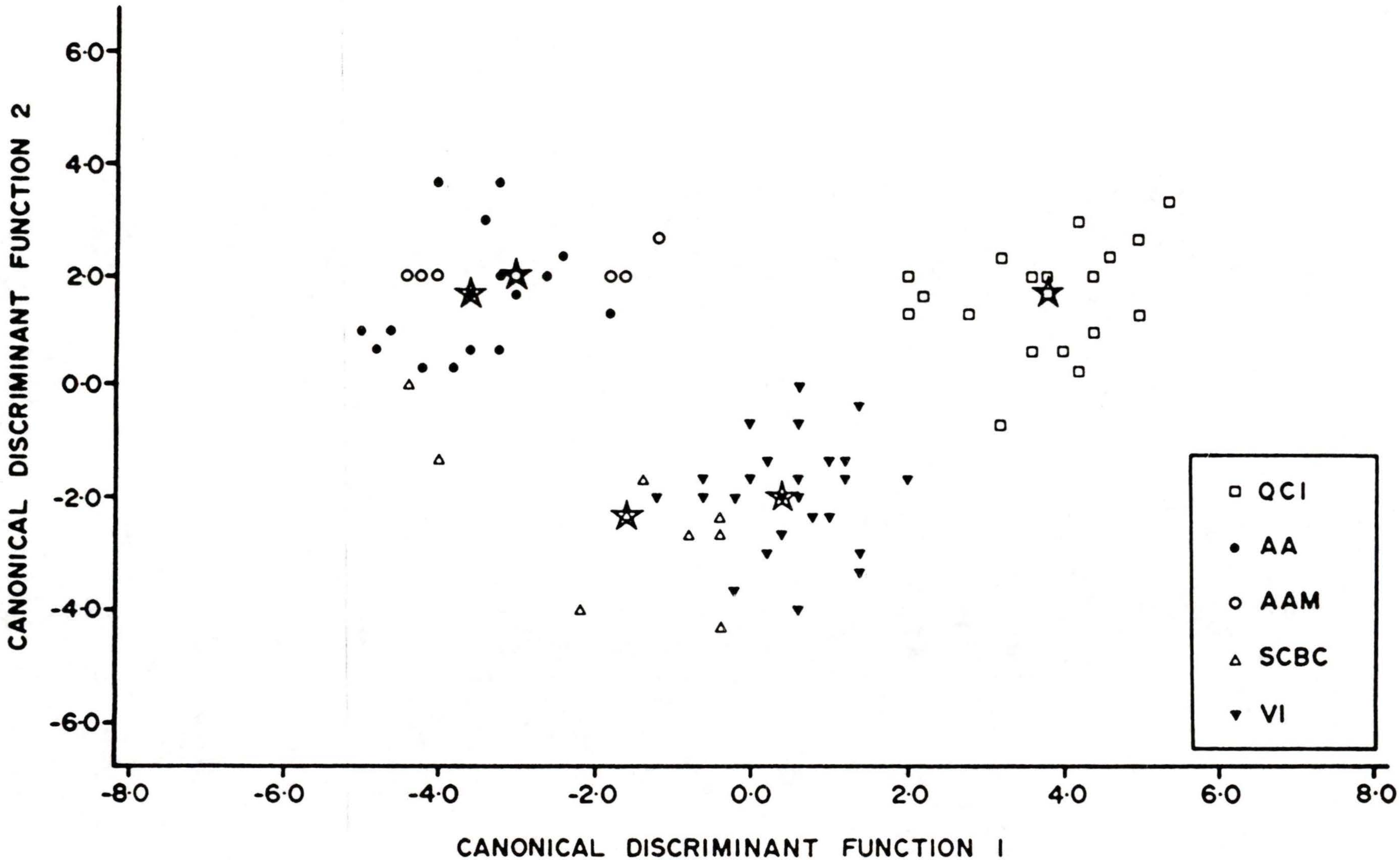
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
QCI
AA
AAM
SCBC
VI

Figure 12: **Plot of the female marten samples (age = 1-2) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.


CANONICAL DISCRIMINANT FUNCTION 2
6·0
4·0
2·0
0·0
-2·0
-4·0
-6·0
-8·0
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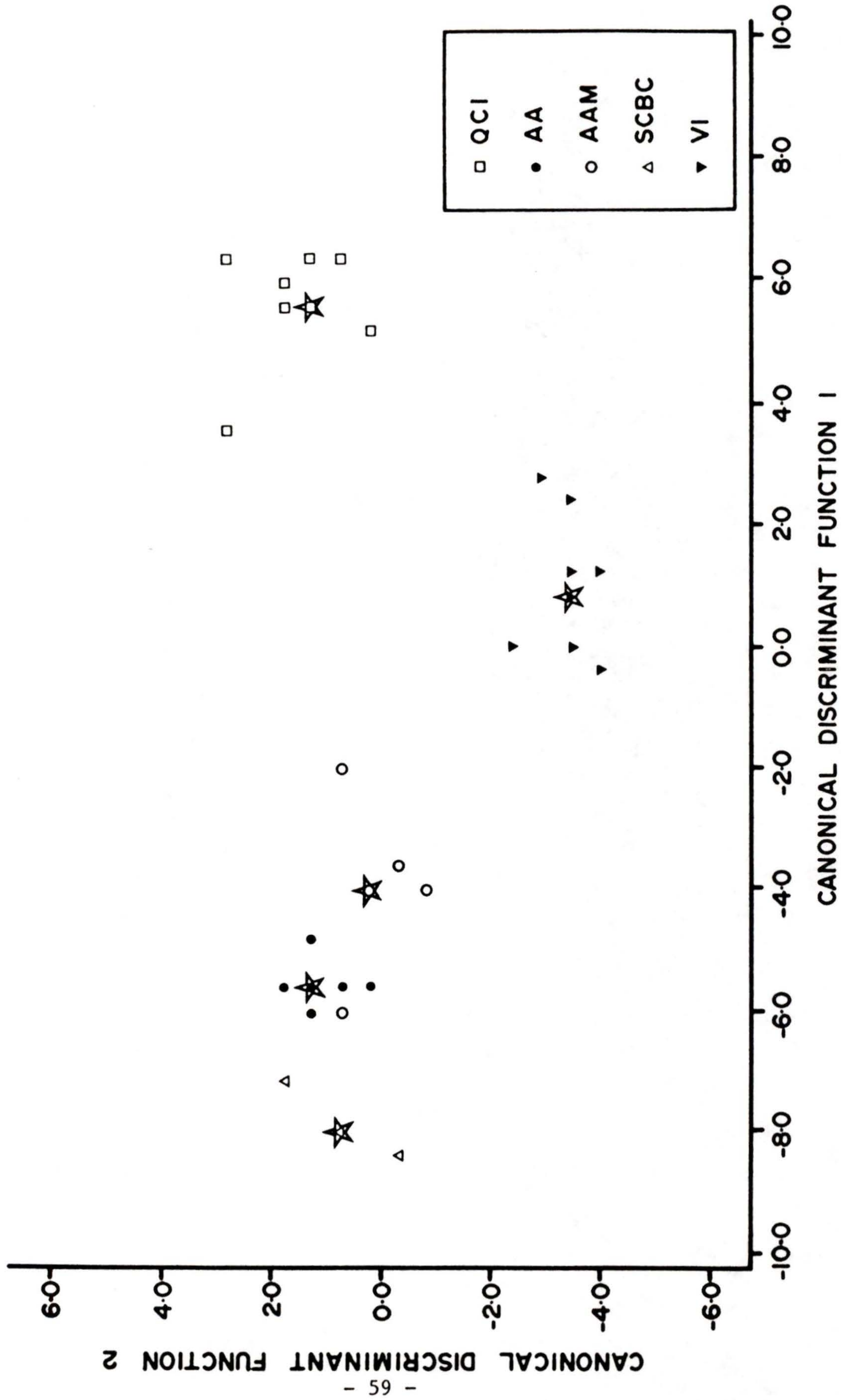
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0
CANONICAL DISCRIMINANT FUNCTION I
QCI
AA
AAM
SCBC
VI

Figure 13: **Plot of the female marten samples (age 3+) on the first two canonical discriminant functions.**

QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.
Stars indicate group centroids.


CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
QCI
AA
AAM
SCBC
VI
-10·0
-8·0
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-2·0
0·0
2·0
4·0
6·0
8·0
10·0
6·0
4·0
2·0
0·0
-2·0
-4·0
-6·0

Table 10: **Classification table from canonical variates analysis of the male marten samples (age class 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(15)	15 100%	0	0	0	0
AA(87)	0	74 85.1%	12 13.8%	1 1.1%	0
AAM(21)	0	2 9.5%	18 85.7%	1 4.8%	0
SCBC(18)	0	0	4 22.2%	12 66.7%	2 11.1%
VI(49)	0	0	0	3 6.1%	46 93.9%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 86.8%

Table 11: **Classification table from canonical variates analysis of the male marten samples (age class 1-2).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(49)	49 100%	0	0	0	0
AA(34)	0	30 88.2%	4 11.8%	0	0
AAM(8)	0	2 25.0%	6 75.0%	0	0
SCBC(10)	0	1 10.0%	1 10.0%	7 70.0%	1 10.0%
VI(33)	0	0	0	0	33 100%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island,

2. Overall classification rate= 93.3%

Table 12: **Classification table from canonical variates analysis of the male marten samples (age class 3+).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(28)	28 100%	0	0	0	0
AA(9)	0	7 77.8%	2 22.2%	0	0
AAM(4)	0	1 25.0%	3 73.0%	0	0
SCBC(6)	0	0	0	5 83.3%	1 16.7%
VI(10)	0	0	0	0	10 100%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island,

2. Overall classification rate= 93.0%

Table 13: **Classification table from canonical variates analysis of the female marten samples (age class 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(23)	23 100%	0	0	0	0
AA(57)	0	48 84.2%	9 15.8%	0	0
AAM(14)	0	3 21.4%	11 78.6%	0	0
SCBC(20)	0	1 5.0%	1 5.0%	16 80.0%	2 10.0%
VI(34)	0	0	0	2 5.9%	32 94.1%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 87.8%

Table 14: **Classification table from canonical variates analysis of the female marten samples (age class 1-2).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(21)	21 100%	0	0	0	0
AA(17)	0	13 76.5%	4 23.5%	0	0
AAM(6)	0	1 16.7%	5 83.3%	0	0
SCBC(9)	0	1 11.1%	0	7 77.8%	1 11.1%
VI(28)	0	0	0	1 3.6%	27 96.4%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 90.1%

Table 15: **Classification table from canonical variates analysis of the female marten samples (age class 3+).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(9)	9 100%	0	0	0	0
AA(5)	0	5 100%	0	0	0
AAM(4)	0	0	4 100%	0	0
SCBC(2)	0	0	0	2 100%	0
VI(9)	0	0	0	0	9 100%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island.

2. Overall classification rate= 100%

Figure 14: **Phenograms of male (A) and female (B) marten samples. Scale indicates the taxonomic distance.**

Cophenetic correlation coefficient: males = 0.94 and females = 0.93.
QCI = Queen Charlotte Islands.
AA = Alexander Archipelago (Baranof and Chichagof Islands).
AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelago).
SCBC = Southern Coast of British Columbia.
VI = Vancouver Island.

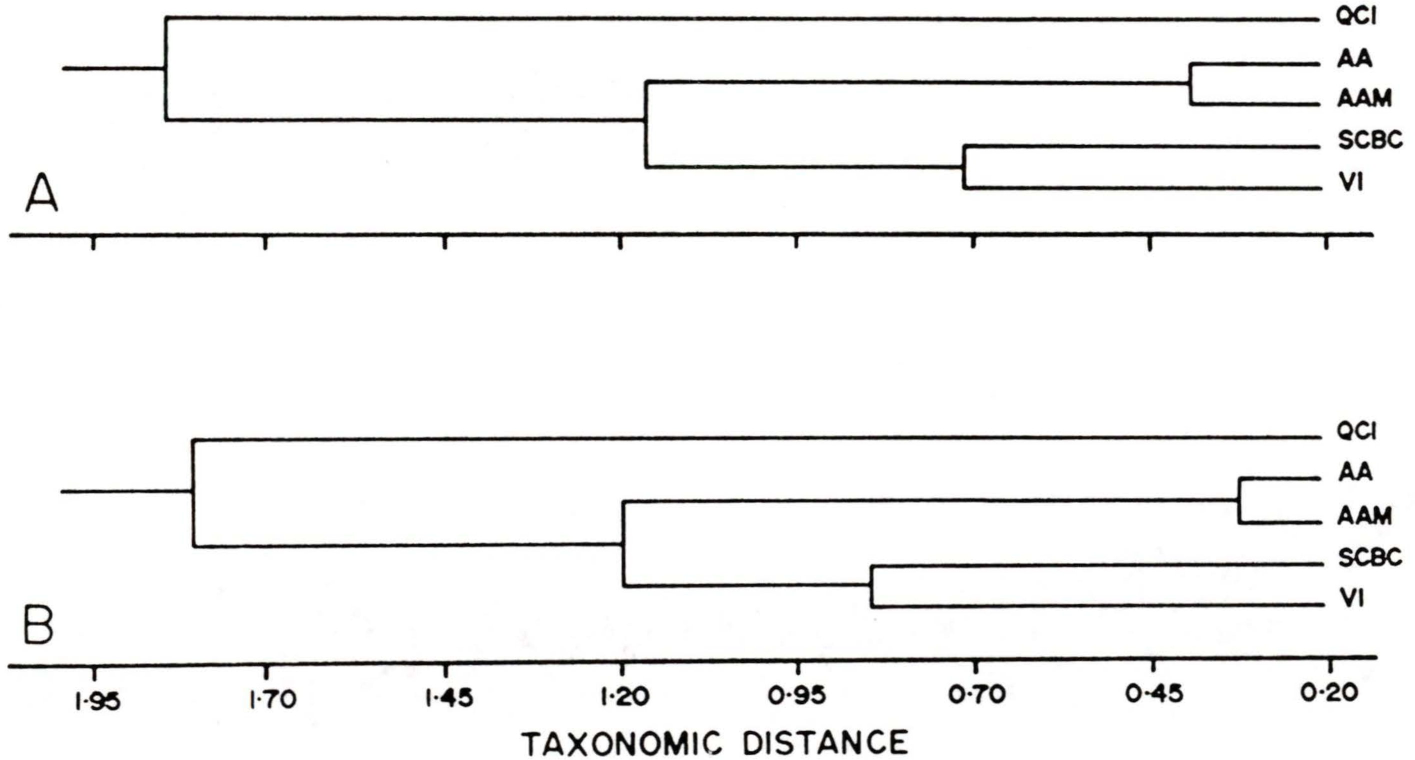
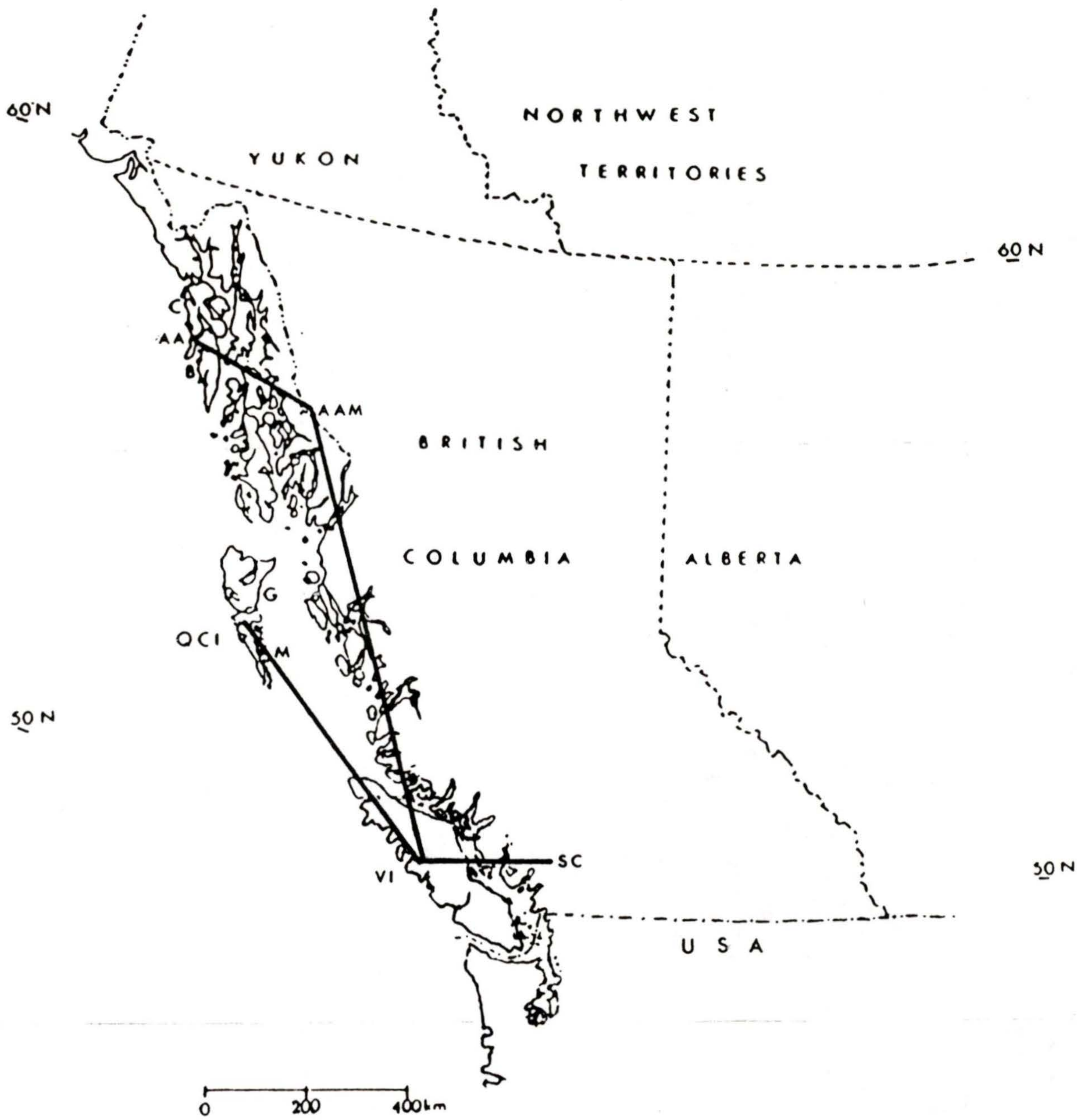

QCI
AA
AAM
SCBC
VI
A
QCI
AA
AAM
SCBC
VI
B
1·95
1·70
1·45
1·20
0·95
0·70
0·45
0·20
TAXONOMIC DISTANCE

Figure 15: **Map showing the localities considered in this study joined by lines that represent the results of the minimum spanning tree analysis.**

QCI = Queen Charlotte Islands. AA = Alexander Archipelago (Baranof and Chichagof Islands). C = Chichagof Island. B = Baranof Island. AAM = Alaska Panhandle Mainland (adjacent to Alexander Archipelgo). SCBC = Southern Coast of British Columbia. VI = Vancouver Island.
Taxonomic distances between samples.
QCI - VI = 1.42 (males) and 1.38 (females)
VI - SCBC = 0.73 (males) and 0.86 (females)
VI - AAM = 1.04 (males) and 1.02 (females)
AAM - AA = 0.39 (males) and 0.32 (females)


60 N
NORTHWEST
YUKON
TERRITORIES
60 N
C
AA
B
AAM
BRITISH
COLUMBIA
ALBERTA
G
QCI
M
50 N
SC
VI
50 N
USA
0
200
400 km

Effects of the introduction of M. a. actuosa

The MANOVA analysis to test the hypothesis of no difference between the juvenile specimens from Baranof-Chichagof Islands and the juveniles from the Mackenzie District-Road River area (Northwest Territories and Yukon respectively), produced a significant multivariate F value for both males (12.62, $P<0.001$) and females (22.21, $P<0.001$). Thus, the hypothesis was rejected.

For males, about 43% of the variance was explained by the difference between groups (Wilk's lambda=0.568). The univariate tests for COBL, CHAB, BUL, UCWB, LUPL, LUPW were significant, whereas those for ZYGM, and FOMW were non-significant. For females, 61% of the variance was accounted for by the difference between groups (Wilk's lambda=0.388), and only the univariate-F values for ZYGM, FOMW, and LUPW were non-significant.

For MDA, as well as for MANOVA, only eight variables were used because none of the Northwest Territories-Yukon specimens had complete jaws (they had been broken to extract the canines for aging purposes). The absence of the jaw height character resulted in a slightly worse discrimination among the groups than before (Tables 16 to 19).

Two different MDA's were performed (for both males and females), the first with actuosa specimens entered in the analysis as ungrouped cases. Most of them were assigned to the Baranof-Chichagof group and very few to the group from the adjacent mainland (Tables 16, 17). The second analysis had the actuosa specimens included as a separate group. In that case the great majority were reassigned to their own group, and very few to the sample from Baranof-Chichagof Islands. The correct classification rate for actuosa was smaller for males than for females (see Tables 18,19).

Table 16: **Classification table from canonical variates analysis of the male marten samples, with NWT specimens as ungrouped cases (age class 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(15)	15 100%	0	0	0	0
AA(87)	0	67 77.0%	18 20.7%	2 2.3%	0
AAM(21)	0	2 9.5%	18 85.7%	1 4.8%	0
SCBC(18)	0	0	4 22.2%	12 66.7%	2 11.1%
VI(49)	1 2.0%	0	0	4 8.2%	44 89.8%
Ungrouped cases: NWT (40)	0	37 92.5%	3 7.5%	0	0

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island, NWT = Northwest Territories.

2. Overall classification rate= 82.1%

Table 17: **Classification table from canonical variates analysis of the female marten samples, with NWT specimens as ungrouped cases (age class 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI
QCI(23)	23 100%	0	0	0	0
AA(57)	0	46 80.7%	11 19.3%	0	0
AAM(14)	0	4 28.6%	10 71.4%	0	0
SCBC(20)	0	2 10.0%	0	16 80.0%	2 10.0%
VI(34)	0	0	0	2 5.9%	32 94.1%
Ungrouped cases: NWT (40)	0	30 71.4%	12 28.6%	0	0

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island, NWT = Northwest Territories.

2. Overall classification rate= 85.8%

Table 18: **Classification table from canonical variates analysis of the male marten samples, with NWT specimens as a group (age class 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI	NWT
QCI(15)	15 100%	0	0	0	0	0
AA(87)	0	56 64.4%	18 20.7	2 2.3%	0	11 12.6%
AAM(21)	0	4 19.0%	15 71.4%	1 4.8%	0	1 4.8%
SCBC(18)	0	0	4 22.2%	12 66.7%	2 11.1%	0
VI(49)	1 2.0%	0	0	3 6.1%	45 91.8%	0
NWT(40)	0	5 12.5%	2 5.0%	0	0	33 82.5%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island, NWT = Northwest Territories.

2. Overall classification rate= 76.5%

Table 19: **Classification table from canonical variates analysis of the female marten samples, with NWT specimens as a group (age class = 0).**

ACTUAL GROUP(N)	PREDICTED GROUP MEMBERSHIP QCI	AA	AAM	SCBC	VI	NWT
QCI(23)	21 91.3%	0	0	0	2 8.7%	0
AA(57)	0	41 71.9%	12 21.1	0	0	4 7.0%
AAM(14)	0	3	11 21.4%	0 78.6%	0	0
SCBC(20)	0	2 10.0%	1 5.0%	15 75.0%	2 10.0%	0
VI(34)	0	0	0	1 2.9%	33 97.1%	0
NWT(42)	0	2 4.8%	1 2.4%	0	0	39 92.9%

1. Sample Localities: QCI = Queen Charlotte Islands, AA = Alexander Archipelago (Baranof and Chichagof Islands), AAM = Alaska Panhandle Mainland, SCBC = Southern Coast of British Columbia, VI = Vancouver Island, NWT = Northwest Territories.

2. Overall classification rate= 84.2%

DISCUSSION

My results demonstrate the strong differentiation of the Queen Charlotte Islands Pine Marten, and suggest that marten on the Queen Charlotte Islands and the Alexander Archipelago should not remain together in the subspecies nesophila. This name should refer only to the former population.

Almost all the specimens from the Alexander Archipelago used in this study come from islands where introductions took effect. However, I do not believe that the information used by the Alaska Bureau of the U.S. Biological Survey when planning the introductions was correct. First, a specimen was collected at Dundas Bay, Chichagof Island, by Olson in 1923 (USNM 349526). This specimen was classified with the Baranof-Chichagof sample when it was included in the analysis with the ungrouped cases. If marten were originally present on Chichagof Island, as this specimen indicates, there is no reason why they could not have been present on Baranof Island as well, since the islands come very close together at Peril Strait.

Information about Admiralty Island is incomplete and conflicting. Johnson (1981) reported that there was no mention of marten in accounts of the mammals and trapping records on this island. However, Swarth (1912) obtained two marten skulls from Admiralty Island in 1912, and five specimens from that island were collected in 1910 and 1913 (M.V.Z. 19178, 19179, 12674, 12675, and 19177; the last specimen was not included in my study because it was damaged).

The high success of the introductions is also suspicious. Johnson (1981) found this fact "particularly striking" considering the small number of animals released on each island, and the relatively low reproductive potential of the species. Finally, there is no clear reason why marten could not have reached those particular islands naturally since they were present on all of the other islands of the Alexander Archipelago. Therefore, I conclude that marten were indigenous throughout the Alexander Archipelago before these introductions.

Were the marten populations already present on Baranof, Chichagof and Admiralty Islands affected phenetically by the introductions? My data suggest that effects of the introductions were negligible, since the Baranof-Chichagof sample is very similar to that from the adjacent mainland.

It is surprising that five of the seven specimens from the Alexander Archipelago which were included in the analysis as ungrouped cases grouped with the Vancouver Island marten. This, and the fact that those five animals were from islands other than Baranof and Chichagof, suggests some heterogeneity among populations of the Alexander Archipelago. However, marten from the Alaska panhandle were also phenetically more similar to marten from Vancouver Island than to marten from the Queen Charlotte Islands.

When specimens from the Northwest Territories were compared with marten from the Alaska panhandle, both insular and coastal, they showed remarkable similarity. This could indicate that they are possibly more related to the subspecies actuosa than to other populations south of the Alexander Archipelago, but further research and comparison with other northern subspecies (e.g. kenaiensis) are necessary.

I conclude that the marten from the Queen Charlotte Islands form a distinctive group , and that marten from other localities should not be included within the same subspecies. Osgood (1901) originally used the species name nesophila for the Queen Charlotte Island marten, and the type specimen was collected on Graham Island. Therefore, I suggest that the trinomial Martes americana nesophila be used to designate marten only from the Queen Charlotte Islands. Genetical research, such as electrophoretic or mitochondrial DNA analysis, would be useful in determining the relationships discussed here. It would be important to include in this study specimens from southern islands of the Alexander Archipelago and from the northern coast of British Columbia.

Foster (1963, 1965) rejected the hypothesis that Queen Charlotte Islands marten are a relict population of a race that was present in the Pacific Northwest before the last glacial period, and concluded that nesophila's traits evolved under the unique environmental conditions of the Queen Charlotte Islands.

Some recent studies (Mathewes and Clague, 1982; Warner et al., 1982; Warner,1984; Heusser, in press; and Mathewes, in press) strengthen, but do not confirm, the possibility that full biotic refugia existed on the Queen Charlotte Islands. Warner (1984,p.151) wrote that "...data in support of a refugium are encouraging in so far as late Wisconsinan Queen Charlotte ice was in recession by 16,000 years B.P., presumably during the height of late Wisconsinan glaciation in southern British Columbia". Warner et al. (1982) and Heusser (in press) state that late Wisconsinan refugia, consisting of coastal tundra with colonies of trees, were centres for biotic dispersal in the Queen Charlotte Islands, at least as early as 16,000 years ago.

If refugia existed on the islands, marten could have survived in them as Foster (1963, 1965) suggested. Under these circumstances, persistent genetic drift could have played a very important role in the evolution of nesophila's distinctive characteristics (see Berry, 1983). However, even if marten reached these islands only by the late Wisconsin, the time elapsed since then (10,000 to 12,000 years) may have been enough for the derivation of this form through genetic drift, or natural selection (Patton et al., 1975; Berry et al., 1978; Berry ,1983).

Foster (1963, 1965) found crab parts in five of eighteen marten stomachs examined and suggested that the heavier dentition and associated areas of the skull of nesophila are adaptations to a change in diet from small birds and mammals to intertidal animals. However, I found no evidence of crab or other littoral invertebrates in the stomachs of the ninety-eight carcasses examined in this study. It is possible, though, that marine invertebrates are used during periods of scarcity of small vertebrates (which might well have been the case if they survived in a refugium) or were used until squirrels were introduced, in the early 1960's (L. Hakki and K. Newton, pers. comm.). A more complete study of nesophila's diet, is necessary to understand better the evolution of their strong masticatory apparatus.

There was an unusually small proportion of juvenile specimens in the sample from the Queen Charlotte Islands (see Table 1). Possible reasons for this are: sampling error; overtrapping to such an extent that removal rate exceeds replacement; or high adult survivorship due to favorable conditions on these islands. The distinct age distribution exhibited in this sample may have important ecological consequences, and possible management implications. Detailed ecological studies, focusing on the demography of the Queen Charlotte Islands marten should be performed to shed light on this problem.

I agree with Hagmeier (1961) that the marten from Vancouver Island, subspecies vancouverensis, are "indistinguishable" from caurina on the nearby mainland. I suspect that the difference shown in MDA is because some specimens of caurina were collected in Manning Park, where this subspecies may intergrade with the americana type (Hagmeier, 1955). If so, the marten from Vancouver Island should be assigned to the subspecies caurina. However, this remains to be confirmed through genetical analyses of specimens from the mainland coast and Vancouver Island.

Part 2

SEXUAL VARIATION OF THE AMERICAN PINE MARTEN (MARTES AMERICANA) IN THE PACIFIC NORTHWEST, WITH SPECIAL REFERENCE TO THE QUEEN CHARLOTTE ISLANDS

INTRODUCTION

Sexual dimorphism, developmental changes, and temporal variation are the most common sources of variation in a local population, and their assessment is a prerequisite for systematic studies (Thorpe, 1976; Baker, 1985). Sexual dimorphism is of particular interest because it can be influenced greatly by feeding ecology, interspecific competition, energetics, and sexual selection.

Male mustelids are typically larger than females, and this also applies to American Pine Marten, Martes americana (Wright and Coulter, 1967; Petrov, 1975; Erlinge, 1979; Moors, 1980; Brown, 1983; Clutton-Brock and Harvey, 1983; Ralls and Harvey, 1985). The evolution of extreme sexual dimorphism in mustelids has been explained by two main hypotheses:

1. Reduction of intersexual competition for food (Brown and Lasiewski, 1972).

2. Selection for increased male size through reproductive competition among males (Erlinge, 1979; Moors, 1980).

The study of sexual dimorphism in M. americana has been based mainly on external traits (de Vos, 1952), and the postcranial skeleton (Dagg et al., 1975; Leach and Dagg, 1976; Leach, 1977; Leach and de Kleer, 1978). Studies on cranial characters include Grinnell et al. (1937), who reported significant sexual differences in ten cranial measurements in the subspecies sierrae, and Marshall (1951), who observed that the sagittal crest was sexually dimorphic. In addition, Brown (1983) recently completed an extensive quantitative study of sexual and age variation in marten from south central Ontario.

The Queen Charlotte Islands marten, *M. a. nesophila*, as demonstrated in the previous section, is a distinctive subspecies. In this chapter I analyze and compare sexual dimorphism and age-related variation in this subspecies with other populations.

My working hypotheses were:

1. Island populations should be more sexually dimorphic than on the mainland, due to the special ecological conditions found on islands (e.g. less diverse prey base and lack of many competing species of carnivores) (Case, 1978).

2. Sexual dimorphism should increase with age (Rossolino and Plavinov, 1974; Brown, 1983; King, 1984).

MATERIALS AND METHODS

The specimens used in Part 1 served as material for these analyses, and the same measurements and measurement procedures were used.

Statistical Methods

Differences in character means between sexes were tested by Student's t-tests, and differences in character variances were tested with F tests of the variance ratio (Zar, 1984). Both tests were performed using BMDP 3D. When sample variances were significantly different ($\alpha=0.05$), an adjusted t-test was used (separate variance estimate of BMDP 3D; Biomedical Computer Programs; Dixon, 1983). This information is summarized in Appendix C.

I conducted multivariate analysis of variance (MANOVA) using SAS, to determine whether the centroids of male and female marten for each population were different. The significance of the interaction effects (sex x population) was assessed to determine if the absolute difference between sexes differed across populations. This was done in ten separate MANOVA's, comparing all possible pairs of populations (Queen Charlotte Islands vs. Baranof and Chichagof Islands; Queen Charlotte Islands vs. Vancouver Island; etc.). Whenever the interaction term (sex x population) gave a significant multivariate-F value , univariate test results were examined to determine which variables exhibited significantly different sexual dimorphism between populations.

Sexual dimorphism can be expressed in both absolute and relative terms. Even when the absolute differences between the sexes in two populations are equal, the relative degree of sexual dimorphism may differ, depending on the size of individuals in each population. For those variables that did not differ significantly in absolute sexual dimorphism between populations, a coefficient was computed using the ratio of male mean to female mean for each variable (modified from Williams and Findley, 1979). If the coefficients of two populations being compared were distinct, this indicated that relative sexual dimorphism differed between them. These ratios were tested for significant difference using Student's t-test (Zar, 1984). To perform these tests the variances of the coefficients were calculated using formula 2.34 from Cochran (1963:31, modified by P. Konkin, pers. comm.):

$$V\frac{\bar{Y}}{\bar{X}} = \frac{1}{n\,\bar{X}^2}\left[\frac{\Sigma Y^2 + \left(\left(\bar{Y}/\bar{X}\right)^2 \Sigma X^2\right)}{n-1}\right]$$

where $\bar{y}$ is the mean for males and $\bar{x}$ is the mean for females, y and x are the raw scores for males and females respectively. The sample size was represented by n, and was always the smaller of male or female sample size, to provide a conservative estimate of the variance.

The multiple discriminant function analysis (canonical variate analysis, CVA) program of SAS was used to obtain D^2, the Mahalanobis distance, between male and female group centroids for each population. D^2 is a good estimator of the distance between male and female groups in multivariate space (Johnston and Selander, 1973; Johnston and Fleischer, 1981). CVA was performed first with specimens of all ages lumped, then the samples were divided into three age groups (0, 1, 2+ years). Sorting by sex and age critically affected the sample sizes, which ideally should have ten specimens for each variable used in CVA (L. Rosenblood, pers. comm.), so I reduced the number of variables in CVA to ten in a first run (COBL, ZYGM, MASW, ROSW, PORC, IFOW, PALL, RTRL, JAL, UCW), and to four in a second one (COBL, ZYGM, JAL, UCW) in an attempt to reduce the effect of small sample size. I retained those variables that I was able to measure more accurately, and were not extremely correlated with each other.

Large D^2 values could be the consequence of large body size. To remove the size effect from the determination of sexual dimorphism, I performed an additional CVA on the logarithms of ratios (obtained by dividing each variable by COBL) (Mosimann and James, 1979; Reist, 1985). Some authors consider that if ratios are used, the logarithmic transformations alleviate the problems that result from nonlinear relationships between the ratios and the original variables (Reist, 1985). However, it is important to consider that ratios should be used with caution in this type of study. Their ability to remove the effect of size is still a matter of debate, and some authors advise against using them in multivariate analysis (Atchley et al., 1976; Albrecht, 1978; Atchley, 1978; Atchley and Anderson, 1978; Dodson, 1978; Lemen, 1983).

RESULTS

Sexual dimorphism is pronounced, and the sexes differ in most characters (Appendix C). Queen Charlotte Islands marten were clearly dimorphic for all variables except FOMH. Animals from Vancouver Island, the Alaska panhandle coast, and the southern coast of British Columbia showed divergence between the sexes for all traits except PORC, whereas sexes differed signifientl y on all variables in the Baranof and Chichagof Islands sample. Each population exhibited significant sexual dimorphism, as assessed by MANOVA's (Queen Charlotte Islands F=152.46, P<0.0001; Baranof and Chichagof Islands F=134.70, P<0.0001; Alaska panhandle coast F=15.99, P<0.0001; southern coast of British Columbia F=29.97, P<0.0001; Vancouver Island F=121.54, P<0.0001).

MANOVA's on different pairs of samples indicated that sexual dimorphism varies between populations. Multivariate F values for the interaction terms (population x sex) were highly significant (P<0.001) for each pair of populations compared except Alaska panhandle coast vs. southern coast of British Columbia (P>0.80). Univariate test results revealed which variables contributed to the differences (Table 20). Figure 16 illustrates some intersample comparisons for selected variables. For ZYGM the difference between sexes was larger on the Queen Charlotte Islands than on Baranof and Chichagof Islands, as indicated by a significant univariate F value for the interaction term and lack of parallelism between lines (Fig. 16A). For MASW sexual dimorphism was similar on both the

Table 20: **Variables with a significant difference (P<0.05) for the interaction term (population x sex) in MANOVA**

CONTRASTS

QCI vs. AA	QCI vs. AAM	QCI vs. SCBC	QCI vs. VI
CHAB	DBUM	DBUM	BUL
COBL	FLML	IFOW	DBUM
DBUM	IFOW	IORW	FLML
FLML	IORW	JAH	IORW
IORW	JAH	JAL	JAH
JAH	JAW	LUPW	JAW
JAL	LUPL	PALL	LUPW
JAW	LUPW	ROSW	PALL
LUPW	MASW	TRL	ROSW
ROSW	PALL	UCW	UCW
TRL	ROSW	WPOP	WPOP
UCW	TRL	ZYGM	ZYGM
WPOP	UCW		
ZYGM	WPOP		
	ZYGM		

AA vs. AAM	AA vs. SCBC	AA vs. VI	AAM vs. VI	SCBC vs. VI
COBL	COBL	JAL	IFOW	IFOW
IFOW	FLML	UMIL	IORW	IORW
JAH	IFOW	UCW	JAH	JAL
MASW	JAL		MASW	ZYGM
PALL	TRL		ROSW	
ROSW	UMIL		TRL	
TRL			UCW	
ZYGM			UMW	
			WPOP	
			ZYGM	

Queen Charlotte Islands and the southern coast of British Columbia, the F value is insignificant and lines are parallel (Fig. 16B).

Absolute sexual dimorphism varied greatly among populations, but relative dimorphism showed no significant differences. Thus sexual differences among populations simply reflected absolute size differences.

Multivariate sexual dimorphism was estimated by D^2 between male and female centroids. Results depended slightly on whether untransformed data or logarithmic transformations were used, but not on the number of variables (ten or four). However, in spite of this difference, marten from the Queen Charlotte Islands and Vancouver Island had the largest D^2 values, Baranof and Chichagof Islands had intermediate values, and both coastal samples (Alaska panhandle and southern British Columbia) had the lowest (Table 21). Histograms of discriminant scores for the five local populations, derived from two-group CVA's on ten of the original variables, are shown in Figure 17.

Figure 16: **Comparison of sexual dimorphism between localities for selected variables**

Parallel lines indicate a non-significant interaction term, and non-parallel lines indicate a significant interaction term (sex x population).
M = males, F = females.
1 = Queen Charlotte Islands.
2 = Alexander Archipelago (Baranof and Chichagof Islands).
3 = Alaska Panhandle Mainland.
4 = Southern Coast of British Columbia.
5 = Vancouver Island.
Interaction terms were significant for parts A, C, and E.

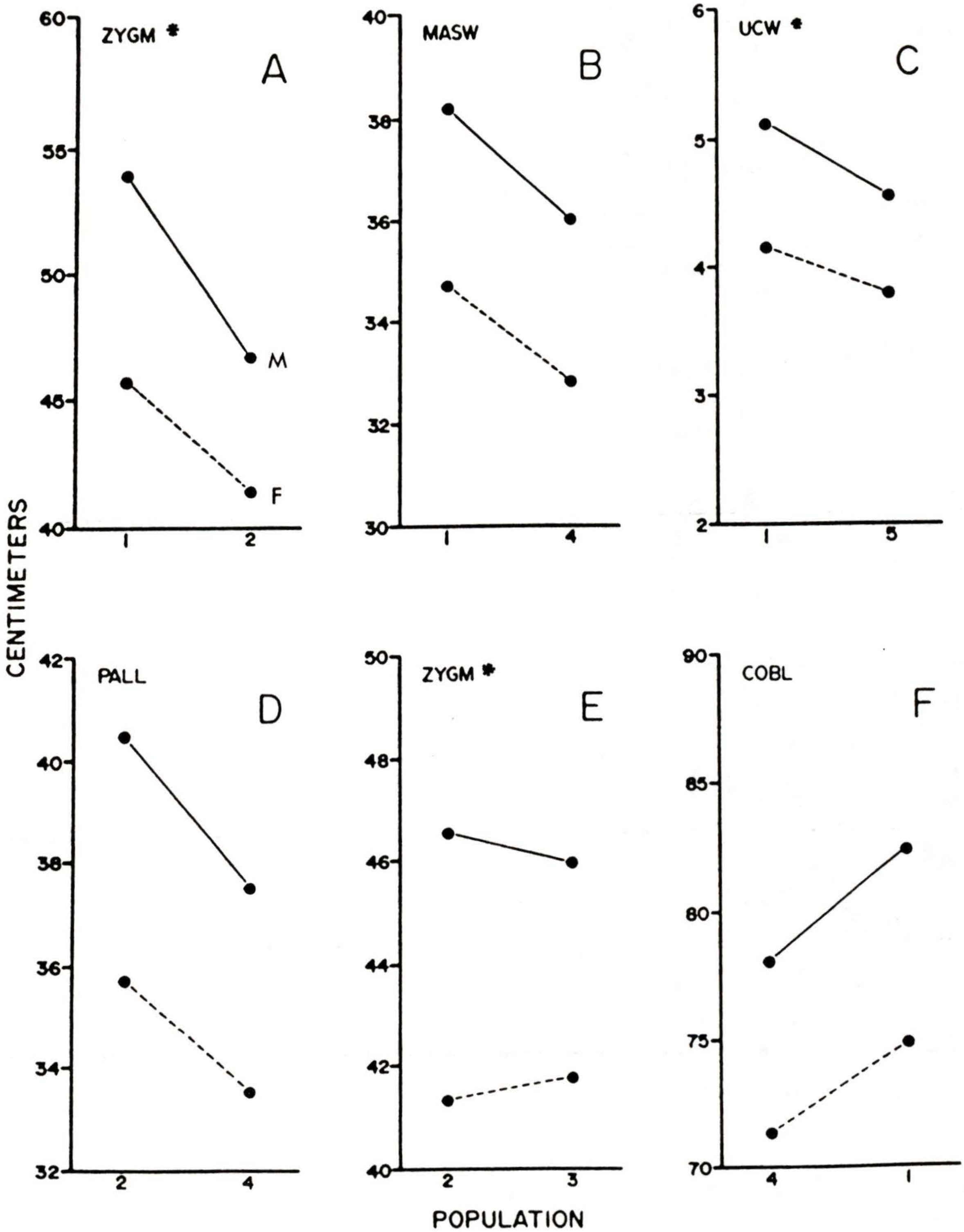

ZYGM *
A
M
F
MASW
B
UCW *
C
PALL
D
ZYGM *
E
COBL
F
CENTIMETERS
POPULATION

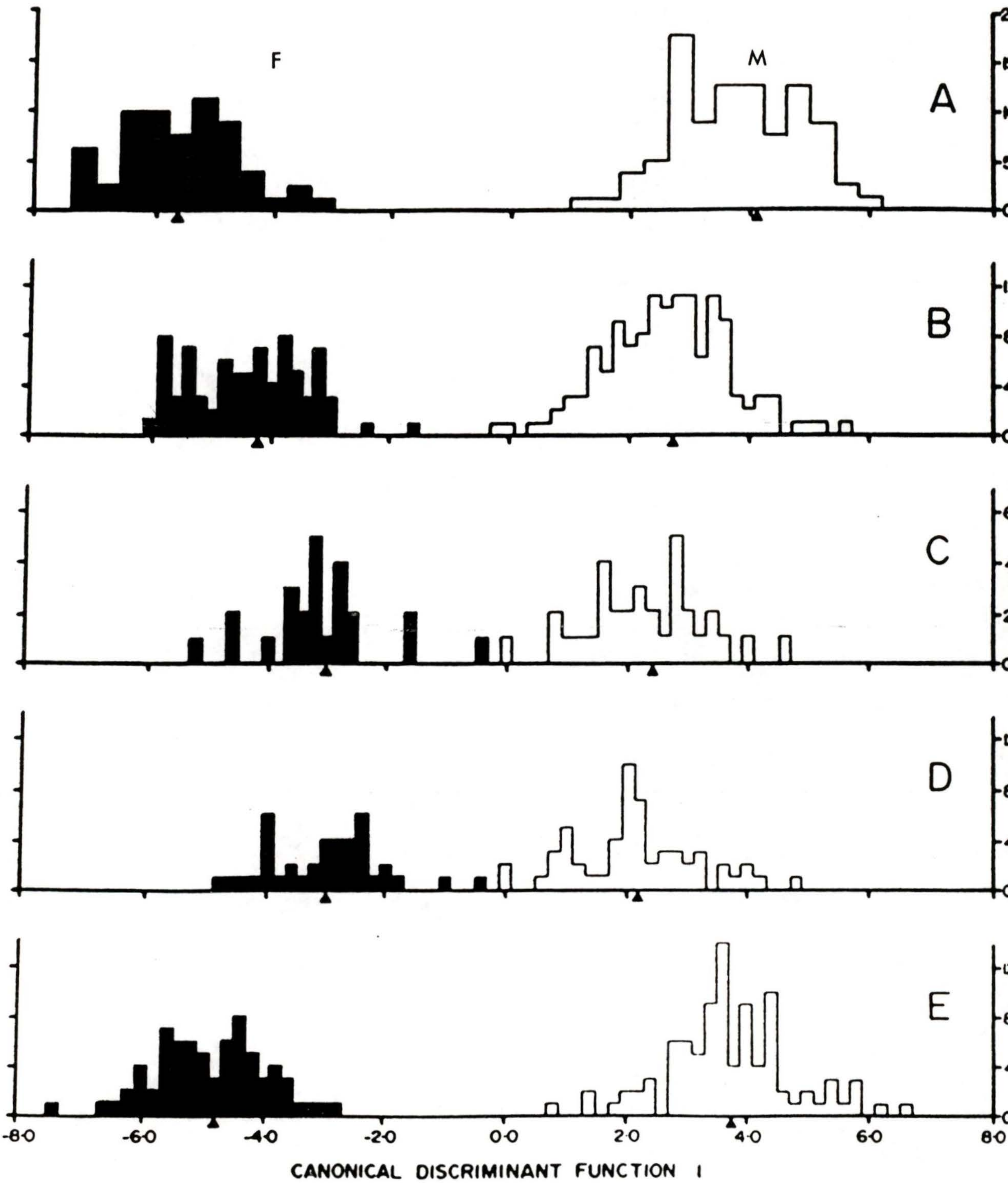
Table 21: **Mahalanobis distances (D^2) between sexes from canonical variates analysis on the geographic samples**

SAMPLE (No. of Variables)	Transformation: Log X/COBL (9)	Log X/COBL (4)	None (10)	None (4)
QCI	4.3	3.9	9.3	8.3
VI	4.9	4.0	8.6	7.8
AA	3.3	2.5	7.0	6.6
SCBC	2.7	1.9	5.2	4.8
AAM	2.7	1.8	5.4	5.1

1. QCI = Queen Charlotte Islands, VI = Vancouver Island, AA = Alexander Archipelago (Baranof and Chichagof Islands), SCBC = Southern Coast of British Columbia, AAM = Alaska Panhandle Mainland.

Figure 17: **Histograms of discriminant scores for male and female marten samples.**

Distances between histograms indicate degree of sexual dimorphism in each sample. Triangles indicate centroids.
A = Queen Charlotte Islands
B = Alexander Archipelago (Baranof and Chichagof Islands)
C = Alaska Panhandle Mainland
D = Southern Coast of British Columbia
C = Vancouver Island



F
M
A
B
C
D
E
FREQUENCY
-8·0
-6·0
-4·0
-2·0
0·0
2·0
4·0
6·0
8·0
CANONICAL DISCRIMINANT FUNCTION I

Change in Sexual Dimorphism with Age

Trends in D^2 values with age differed according to whether transformed (logs. of ratios) or untransformed data were used, and also depended on the number of variables used. There were no clear trends of increasing or decreasing sexual dimorphism with age overall, or in any single analysis.

DISCUSSION

Any analytical approach to sexual dimorphism suffers from oversimplification because there are many variables that must be considered and they vary in importance among populations. The advantages of multivariate methods are clear in such cases. Thus, a combination of MANOVA and CVA may reveal important aspects of sexual dimorphism. MANOVA may indicate the existence of strong dissimilarities between sexes, and also which populations differ in the degree of sexual dimorphism. Additionally, the univariate F tests produced by most MANOVA programs are useful to determine which individual variables contribute most to total dimorphism. CVA provides a measurement of the intensity of sexual dimorphism: the larger the value of D^2 between sexes the more different males are from females in that sample. However, caution is necessary, because as separate CVA's are performed on individual samples (in some cases of unequal size, and each of them with a different variance), the results obtained (D^2 values in this case) are not always easy to compare.

Male and female marten are very different, and the strong sexual dimorphism was apparent from both univariate and multivariate analyses. The results of t-tests on character means between sexes were in agreement with Brown's (1983) observation that males averaged larger than females in most skull measurements (see Appendix C). In both studies the only exception was postorbital constriction. Brown, using t-tests on various ratios of cranial variables, concluded that size was the main difference between the skulls of male and female marten. To confirm this finding he performed ordination by PCA of males and females. However, this method is not always useful for this purpose, because the first principal component not only includes size but also some shape-related information, while the other principal components account for some size information as well (Neff and Marcus, 1980). The plot of variable means (see Figures 2 and 3) depicted the same pattern across populations for both males and females, suggesting that size was indeed the most important difference between sexes as Brown (1983) observed. The relative position of means in the plot would have been dissimilar for males and for females across samples if shape was also an important factor. Nonetheless, the absence of difference between sexes in size of postorbital constriction indicated that, though minor, there was some shape-related dimorphism. This also was observed by Brown (1983).

The results of the MANOVA's contrasting ten pairs of samples revealed unequal levels of dimorphism in nine of them. For those nine, the univariate F tests were used to estimate how many and which variables contributed to the total sexual dimorphism. The only exception to this was the contrast between the Alaska panhandle coast and the southern coast of British Columbia. This suggested that there was not an important difference in the degree of sexual dimorphism between these two populations, which was also indicated by the similar D^2 values between sexes. This finding, and the fact that sexual dimorphism was greatest for the insular samples (Figure 18), are probably the most important outcomes and deserve further consideration.

I have already mentioned the two main hypotheses for sexual dimorphism in mustelids. These hypotheses have received attention from different authors. Brown and Lasiewski (1972) in their study on weasels suggested that the energy needs of weasels are high because of their elongated body shape, which enables them to exploit a wider range of prey. They propose that a more intense intersexual competition for food, due to this higher energy requirement, led to the evolution of sexual size dimorphism.

This hypothesis is criticized by Erlinge (1979), Moors (1980), and Ralls and Harvey (1985). Erlinge points out that, if sexual dimorphism was primarily the result of selection for differences in food exploitation by the sexes, one would expect marked sexual dissimilarities in the structures associated with feeding. He agreed that weasels show a marked difference in their masticatory apparatus. However, he pointed out that sexual dimorphism becomes especially marked as old male skulls gradually acquire a different shape. Therefore, the main differences in skull shape do not occur early in life as one would expect if they were a result of selection for different food exploitation. Erlinge (1979) also mentions that sexual dimorphism is well developed in mustelids without elongated body shape such as marten (Martes martes) or polecat (Mustela putorius), so dimorphism is not especially linked to elongated body shape. Ralls and Harvey (1985) analyzed data for a variety of mustelid species, and concluded that sexual dimorphism was not correlated with the degree of body elongation as Brown and Lasiewski had indicated.

Moors's (1980) main criticisms are that Brown and Lasiewski's hypothesis does not predict which sex should be the larger one, and they do not consider that large mustelids can also exploit the same food resource as smaller ones.

In his discussion supporting sexual selection, Erlinge (1979) concluded that small females are selected for because of their greater efficiency in reproduction, and large males because of intersexual competition.

How well these theories explain sexual dimorphism in body size of moderately dimorphic mustelids such as otter (Lutra lutra) and badger (Meles meles) is unclear (Wiig, 1986). Mating systems do not explain the differences between sexes in a monogamous species like badger. Selection for exploitation of different food resources in male and female otters and badgers, which prey upon organisms much smaller than themselves, does not account for the dimorphism in their masticatory apparatus (Wiig, 1986).

I consider that my results, showing more intense sexual dimorphism for the insular populations of the same species, support the hypothesis that natural selection affecting niche width may play a very important role in the evolution of sexual differences. Colonizing species have the opportunity to expand their ecological niche in an island environment beyond that utilized in their "source habitat" (MacArthur and Wilson, 1967; Case, 1978). It is clear that islands offer marten different conditions from the mainland, because the competitive interaction with other small carnivores is much less intense.

On the Queen Charlotte Islands, the only carnivores that occur naturally are Ermine (Mustela erminea haidarum), Marten (M. a. nesophila), River Otter (Lutra canadensis pericylzomae), and Black Bear (Ursus americanus carlottae). These species differ greatly ecologically. The absence of Fisher (M. pennati) and Long-tailed Weasel (Mustela frenata), as well as Bobcat (Lynx rufus) and other possible competitors must certainly reduce competitive pressure on marten.

We may assume that any of the islands included in this study have at least the same environmental productivity as the mainland (as is suggested by the excellent nutritional state of marten carcasses used in this study). Productivity on the islands may even be higher, particularly for the Queen Charlotte Islands, because insular environments are often more productive due to their more moderate climate (Case, 1978). This possibility, plus the decreased competition on islands, may account for the high sexual dimorphism observed, which is in agreement with Roughgarden's (1974) prediction of a broader niche and a larger "between-phenotype component" under these circumstances. A larger "between-phenotype component" characterizes a more polymorphic population with many kinds of specialists that, as a group, use the entire niche width.

In the present study the strong sexual dimorphism observed in some of the samples, may decrease intersexual competition and optimize the use of available resources by each sex. This more intense dimorphism is translated into a broader niche. Food habits that decrease intersexual competition, as well as reproductive strategies that increase reproductive efficiency, must interact in a complex manner reinforcing each others effect and selection for dimorphism.

Unfortunately, little information is available on sexual dimorphism of mammals on islands. Most studies have been oriented to understand body-size modification and its relationship with the island's area, distance from mainland, and particular environmental conditions (Case, 1978; Heaney, 1978; Lawlor, 1982; Angerbjörn, 1985; Lomolino, 1985). Foster (1963, 1965) noted reduced sexual dimorphism in ermine from the Queen Charlotte Islands compared to mainland populations, but he did not discuss this finding.

More studies on sexual dimorphism on islands have been conducted on birds. An interesting example is the increased dimorphism relative to mainland, especially in bill length, observed in three species of woodpeckers endemic to the islands of Hispaniola (Centurus striatus), Guadeloupe (C. herminieri), and Puerto Rico (Melanerpes portoricensis) (Selander, 1966, 1971). These studies considered the reduction of interspecific competition as the main cause of the dissimilarity between sexes.

It is clear that the evolution of sexual dimorphism is far more complex than it has been considered to be in most studies. More comparative research on sexual dimorphism between islands and mainlands could provide an important insight into the nature of this interesting phenomenon. Multivariate analysis would be a very useful tool for this purpose, and its use is recommended, but it is important to be aware of its basic assumptions and its limitations, sample size being one of the most important ones.

Change in Sexual Dimorphism with Age

There was no clear pattern of variation in sexual dimorphism with age. Increase in sexual dimorphism during the first two years has been reported for European Marten (Martes martes) by Rossolino and Plavinov (1974), and for Ermine (Mustela erminea) by King and Moody (1982). A similar trend was expected in the populations studied here. However, the crude aging of juvenile specimens to year class only, plus the very small sample sizes in older age groups, probably contributed to the ambiguous results. A larger number of young specimens obtained over the whole year and for every month, would be a much more suitable sample for this kind of study.

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APPENDIX A

SPECIMENS EXAMINED

Information on specimen localities was taken from specimen labels. This information was often imprecise, but was sufficient to locate specimens within study areas given. Place name are often of the nearest recognizable geographic feature; marten may have been collected several km distant. Sex is indicated by M (male) and F (female).

Abbreviations for institutions in which this material is held:

BCPM British Columbia Provincial Museum, Victoria.

MVZ Museum of Vertebrate Zoology, University of California, Berkeley.

UAM University of Alaska Museum, Fairbanks.

UBC Cowan Vertebrate Museum, University of British Columbia, Vancouver.

USNM National Museum of Natural History, Washington D.C.

Queen Charlotte Islands

Moresby Island 12M 1F (BCPM); Sandspit 17M 11F (BCPM) 8M 8F (UBC); Alford Main 4M 4F (BCPM); Mosquito Lake 1M (BCPM); Tasu 2M 2F (UBC); Skidegate 1M (BCPM) 2M 1F (UBC); Louise Inlet 7M 7F (BCPM); Morsekly Lake 4M 3F (BCPM); Peel Inlet 2M 3F (BCPM); Braverman Creek 1M 1F (BCPM); George Bay 1M (UBC); Juskatla 1F (UBC); Deana River 4M 2F (UBC); Skedans 1F (UBC); Alliford Bay 1M

(UBC); Graham Island 5M (BCPM) 3M 10F (USNM); Virago Sound 2M 1F (BCPM); Copper River 12M 7F (BCPM) 6M (UBC).

Alexander Archipelago

Chichagof Island 32M 20F (UAM); Suloia Bay 2M (UAM); Pelican Area 6M 7F (UAM); Rose Channel 1M (UAM); Whitestone Harbour 3M 4F (UAM); Hoonas 16M 7F (UAM) 1M (USNM); Idaho Inlet 9M 2F (UAM).

Baranof Island 13M 9F (UAM); Fish Bay 16M 15F (UAM); Deep Inlet 2M 1F (UAM); Herring Cove 1F (UAM); Nakwesina 7M 3F (UAM); Olga Strait 1M (UAM); Peril Strait 18M 10F (UAM); Neka Bay 2M (UAM).

Admiralty Island 2M 1F (MVZ); Kuiu Island 1F (MVZ); Yakutat Island 1M (MVZ).

Alaska Panhandle Mainland

Bradfield Canal 15M 11F (UAM); Bradfield River 3M 4F (UAM); Aaron Creek 15M 9F (UAM).

Southern Coast of British Columbia

Port Moody 24M 9F (USNM); Manning Park 14M 18F (UBC); Alta Lake 2M 3F (UBC); London Mount 1F (UBC); Mount Whistler 1F (UBC); Cheakamus Lake (Garibaldi Park) 3M 1F (UBC); Pemberton 1M (UBC); Kynoch Inlet 1M (UBC); Skeena River 1M (UBC); Wistaria 6M 4F (BCPM); Atnarka 1F (BCPM); Bella Coola 2M (BCPM); Texas Creek 2M 2F (BCPM); Mount Seymour 1F (BCPM).

Vancouver Island

Vancouver Island 8M 17F (BCPM); Zeballos 5M 2F (BCPM); West Coast 1M 2F (BCPM); Mahatta River 5M 3F (BCPM); Cowichan Lake 3M 3F (BCPM); Quatsino 3M (BCPM); Jeune Landing 1M (BCPM); Sooke Lake 2M 3F (BCPM); Victoria 1M (BCPM); Tofino Inlet 2M 3F (BCPM); Cameron River 1M (BCPM); Whiskey Creek 1F (BCPM); Little Qualicum Drainage 1F (BCPM); Qualicum 1F (BCPM) Klanawa River 20M 10F (BCPM); Englishman River 1M 2F (BCPM); Jordan River Meadows 14M 17F (BCPM); Nanaimo 1M 3F (BCPM); Little Nitinat River 2M (BCPM); Coombs (NW Bay) 2M 1F (BCPM); French Creek Drainage 2F (BCPM); Nanaimo River Camp 2M 3F (BCPM); Fleet Creek Watershed 2M 1F (BCPM); Mohun (Brewster Lakes) 1F (BCPM); Bowser Forest Road 16M 7F (BCPM).

APPENDIX B

LIST OF SKULL MEASUREMENTS.

Bulla length (BUL): Length of the right auditory bulla measured from osseous auditory canal to jugular foramen.

Bulla width (BUW): Width of right auditory bulla from stylomastoid foramen to carotid canal.

Condylobasal length (COBL): Linear antero-posterior distance from most anterior point of premaxillae to midpoint of a line connecting most posterior surface of occipital condyles.

Cranial height at bullae (CHAB): Greatest dorso-ventral height of cranium, taken at and including deepest part of the bullae. Not including sagittal crest if present.

Distance between upper molars (DBUM): Smallest distance separating lingual borders of upper molars.

First lower molar length (FLML): Length of first right lower molar, taken at base.

Foramen magnum height(FOMH): Greatest dorso-ventral height separating inner superior and inferior edges of foramen magnum.

Foramen magnum width (FOMW): Greatest width across foramen magnum.

Infraorbital foramen width (IFOW): Width between medial surfaces of infraorbital foramina.

Interorbital width (IORW): Least width between orbits.

Jaw height (JAH): Straight distance between upper and the lower edges of mandible, taken at anterior extreme of first molar.

Jaw length (JAL): Distance from anterior edge of median incisor alveolus to angular notch.

Jaw width (JAW): Width of dentary bone beneath anterior part of first molar.

Last upper premolar length (LUPL): Greatest distance along last right premolar.

Last upper premolar width (LUPW): Greatest width of last right upper premolar, measured at lobe.

Mastoid width (MASW): Greatest width separating outer surfaces of mastoid processes.

Palatal length (PALL): Medial distance from posterior surface of incisors to posterior edge of palate.

Postorbital constriction (PORC): Least width of the skull at postorbital constriction.

Rostral width (ROSW): Greatest width of rostrum at canines.

Toothrow length (TRL): Medial distance from anterior surface of incisors to posterior surface of right molar.

Upper canine width (UCW): Width of canine base, taken along imaginary antero-posterior line.

Upper molar inner lobe (UMIL): Greatest antero-posterior length of right upper molar inner lobe.

Upper molar width (UMW): Greatest mesial-labial width of right upper molar.

Width across postorbital processes (WPOP): Greatest width across postorbital processes.

Zygomatic width (ZYGM): Greatest width across zygomatic arches.

APPENDIX C

Sample Statistics and Univariate Tests of

Differences Between Male and Female *Martes americana*

Sample statistics and univariate tests of differences between male and female *Martes americana* (Queen Charlotte Islands)

Character	Males (N=95) $\bar{X}$	Range	SD	Females (N=63) $\bar{X}$	Range	SD	P_t	P_F
COBL	82.4	85.1-79.2	1.27	74.7	76.7-71.3	1.14	<0.000	0.4282
ZYGM	53.8	59.4-47.8	2.20	45.7	48.1-42.9	1.33	<0.000	0.0012
CHAB	31.2	32.9-29.6	0.68	28.8	30.2-27.7	0.63	<0.000	0.7767
BUL	11.9	13.0-11.1	0.40	11.2	12.1-10.3	0.45	<0.000	0.1236
BUW	9.5	10.7- 8.4	0.43	8.8	9.5- 8.1	0.35	<0.000	0.1551
MASW	38.2	39.7-36.4	0.73	34.7	36.0-33.2	0.66	<0.000	0.3651
FOMH	8.9	10.0- 7.5	0.62	8.7	9.8- 7.9	0.49	<0.096	0.0477
FOMW	12.2	13.4-10.8	0.65	11.4	12.4-10.1	0.61	<0.000	0.3783
ROSW	18.5	19.5-17.0	0.47	16.2	17.1-15.2	0.46	<0.000	0.8862
WPOP	26.9	20.1-23.3	1.14	23.1	25.4-20.6	0.97	<0.000	0.2479
PORC	16.8	19.4-14.5	0.98	15.3	19.3-13.9	1.18	<0.010	0.0417
IORW	20.5	22.0-19.2	0.59	17.8	19.6-13.1	0.84	<0.000	0.5164
IFOW	22.0	23.0-20.8	0.55	19.9	20.9-18.8	0.50	<0.000	0.2931
PALL	40.1	42.1-37-6	0.85	35.3	37.0-33.5	0.82	<0.000	0.4719
TRL	34.8	36.6-31.7	0.70	31.2	32.2-29.6	0.56	<0.000	0.1997
JAL	53.6	55.6-51.0	0.90	47.5	48.9-45.5	0.74	<0.000	0.0821
JAW	5.0	6.1- 4.5	0.31	4.2	5.2- 3.5	0.27	<0.000	0.6158
JAH	4.3	10.2- 8.5	0.34	7.9	8.4- 7.2	0.28	<0.000	0.0957
UCW	5.1	5.6- 4.6	0.21	4.1	4.5- 3.7	0.17	<0.000	0.0284
LUPL	8.4	9.3- 7.7	0.30	7.5	8.0- 6.8	0.24	<0.000	0.3163
LUPW	6.2	7.1- 5.8	0.22	5.3	5.7- 4.8	0.21	<0.000	0.6165
UMW	8.9	9.3- 8.3	0.26	7.9	8.5- 7.5	0.21	<0.000	0.0497
UMIL	5.5	5.9- 4.9	0.22	4.8	5.2- 4.0	0.18	<0.000	0.1232
DBUM	11.1	12.3-10.3	0.40	10.2	11.0- 9.0	0.42	<0.000	0.9910
FLML	10.2	10.7- 9.6	0.25	9.1	10.0- 8.5	0.21	<0.000	0.6480

Sample statistics and univariate tests of differences between male and female *Martes americana* (Baranof and Chichagof Islands)

	Males (N=132)			Females (N=79)				
Character	$\bar{X}$	Range	SD	$\bar{X}$	Range	SD	P_t	P_F
COBL	82.7	86.4-77.9	1.58	74.2	76.7-71.3	1.42	0.000	0.7847
ZYGM	46.6	52.6-42.0	2.53	41.3	43.8-38.4	1.06	0.000	0.0000
CHAB	31.6	33.7-28.9	0.90	29.5	32.0-27.3	0.97	0.000	0.4880
BUL	13.9	15.2-12.7	0.61	13.0	14.5-11.9	0.58	0.000	0.4781
BUW	9.9	10.9- 8.3	0.47	9.3	9.9- 8.5	0.32	0.000	0.0003
MASW	36.9	39.0-34.6	0.86	33.5	34.9-32.0	0.66	0.000	0.0185
FOMH	7.9	8.9- 6.0	0.46	7.6	8.6- 6.8	0.41	0.000	0.1976
FOMW	11.2	12.3- 9.9	0.51	10.4	11.5- 9.4	0.43	0.000	0.1303
ROSW	16.4	18.2-15.1	0.58	14.4	15.6-13.5	0.43	0.000	0.0138
WPOP	22.3	26.8-19.9	1.26	20.1	22.1-17.7	0.96	0.000	0.0171
PORC	16.6	19.0-14.1	1.10	16.3	18.8-11.8	1.22	0.033	0.9618
IORW	18.7	20.8-17.0	0.68	16.8	18.3-15.4	0.59	0.000	0.1224
IFOW	19.9	21.6-18.3	0.61	18.0	19.1-16.4	0.58	0.000	0.8275
PALL	40.4	42.7-35.6	1.13	35.7	37.5-33.8	0.82	0.000	0.0078
TRL	33.8	35.8-31.4	0.83	30.3	31.6-28.5	0.65	0.000	0.0236
JAL	52.2	54.6-49.4	1.05	45.6	48.0-43.6	1.00	0.000	0.7452
JAW	4.3	4.9- 3.7	0.29	3.7	4.2- 3.1	0.21	0.000	0.0002
JAH	7.9	9.1- 7.0	0.42	6.8	7.7- 6.0	0.38	0.000	0.4071
UCW	4.4	5.0- 4.0	0.21	3.7	4.0- 3.5	0.15	0.000	0.0504
LUPL	7.3	8.1- 6.5	0.33	6.5	7.1- 5.8	0.28	0.000	0.1507
UMW	8.0	8.8- 7.2	0.28	7.1	7.7- 6.5	0.24	0.000	0.1748
UMIL	4.8	5.6- 4.1	0.27	4.1	4.8- 3.6	0.25	0.000	0.6979
LUPW	5.1	5.6- 4.3	0.25	4.3	4.8- 3.7	0.21	0.000	0.2670
DUBM	10.2	11.9- 8.0	0.64	9.8	11.4- 9.0	0.41	0.000	0.0006
FLML	8.8	9.9- 8.0	0.36	7.8	8.8- 7.1	0.29	0.000	0.1405

Sample statistics and univariate tests of differences between male and female *Martes americana* (Alaska Panhandle Mainland)

Character	Males (N=33) $\bar{X}$	Range	SD	Females (N=24) $\bar{X}$	Range	SD	P_t	P_F
COBL	80.9	83.7-77.4	1.72	73.7	77.0-71.1	1.52	0.000	0.3446
ZYGM	45.9	50.7-41.5	2.45	41.8	46.4-39.0	1.50	0.000	0.0019
CHAB	31.4	33.0-29.8	0.80	29.2	31.0-27.0	1.12	0.000	0.0445
BUL	14.0	15.0-13.0	0.50	13.1	14.2-12.1	0.62	0.000	0.1604
BUW	9.7	10.5- 8.8	0.42	9.1	9.9- 8.3	0.38	0.000	0.4872
MASW	36.4	38.2-34.0	0.96	33.5	35.3-32.4	0.75	0.000	0.4873
FOMH	7.9	8.0- 7.0	0.44	7.5	8.4- 6.7	0.43	0.000	0.8698
FOMW	11.1	11.8-10.4	0.41	10.4	11.4- 9.6	0.49	0.000	0.3677
ROSW	16.2	18.2-15.2	0.70	14.5	16.2-13.0	0.61	0.000	0.2390
WPOP	21.8	24.1-20.1	1.21	20.4	24.6-18.0	1.35	0.000	0.8879
PORC	16.7	18.9-14.4	1.03	16.1	18.4-14.2	1.18	0.071	0.3164
IORW	18.4	19.8-17.4	0.64	16.9	18.7-15.4	0.76	0.000	0.5422
IFOW	19.8	21.1-18.5	0.68	18.4	19.4-17.6	0.50	0.000	0.0917
PALL	39.2	41.3-36.9	1.22	35.3	37.9-32.0	1.20	0.000	0.4790
TRL	33.2	35.7-31.1	0.88	30.3	32.2-29.0	0.73	0.000	0.2387
RJAL	51.5	53.5-48.9	1.13	45.6	49.0-43.6	1.08	0.000	0.2937
RJAW	3.9	4.6- 3.4	0.29	3.4	4.0- 3.2	0.20	0.000	0.1221
RJAH	7.5	8.5- 6.6	0.47	6.6	7.2- 5.8	0.39	0.000	0.4623
UCW	4.4	4.9- 4.0	0.27	3.8	4.4- 3.5	0.20	0.000	0.0405
LUPL	7.3	8.3- 6.5	0.47	6.5	7.5- 5.8	0.37	0.000	0.1180
UMW	7.9	8.6- 7.2	0.35	7.7	7.5- 6.6	0.27	0.000	0.1762
UMIL	4.6	5.2- 3.9	0.28	4.0	4.4- 3.2	0.29	0.000	0.8058
LUPW	5.7	5.8- 4.7	0.27	4.4	5.0- 3.9	0.22	0.000	0.2134
DBUM	10.5	11.7- 9.4	0.55	70.0	10.5- 9.3	0.28	0.000	0.0248
FLML	8.7	9.8- 7.7	0.44	7.9	9.0- 7.5	0.39	0.000	0.4795

Sample statistics and univariate tests of differences between male and female *Martes americana* (Southern Coast of British Columbia)

	Males (N=56)			Females (N=40)				
Character	$\bar{X}$	Range	SD	$\bar{X}$	Range	SD	P_t	P_F
COBL	78.1	82.8-72.6	1.97	71.1	74.6-67.7	1.59	0.000	0.2253
ZYGM	45.6	52.0-41.7	2.31	41.0	44.6-38.9	1.41	0.000	0.0024
CHAB	29.4	32.8-27.7	1.17	27.1	29.7-25.3	1.01	0.000	0.4949
BUL	12.2	14.8-10.5	0.90	11.5	13.6-10.3	0.77	0.000	0.2844
BUW	8.8	10.0- 7.8	0.56	8.2	9.2- 7.4	0.50	0.000	0.3358
MASW	36.0	38.8-33.8	1.19	32.8	34.3-31.4	0.71	0.000	0.0039
FOMH	8.1	9.1- 7.4	0.43	7.8	8.9- 6.9	0.49	0.000	0.5019
FOMW	10.8	11.9-10.0	0.46	10.0	10.6- 9.4	0.30	0.000	0.0035
ROSW	16.0	17.8-13.5	0.67	14.2	15.3-13.3	0.53	0.000	0.2327
WPOP	22.3	25.4-19.5	1.38	20.2	23.4-18.3	1.21	0.000	0.1633
PORC	15.6	18.5-11.8	1.51	15.6	17.5-13.5	1.04	0.899	0.0118
IORW	18.1	19.8-16.3	0.85	16.5	17.9-15.3	0.71	0.000	0.3815
IFOW	20.1	22.0-18.3	0.71	18.5	20.0-17.2	0.68	0.000	0.8136
PALL	37.4	40.2-34.8	1.38	33.5	35.9-30.6	1.15	0.000	0.1164
TRL	32.5	34.4-31.0	0.90	29.3	31.3-27.6	0.79	0.000	0.3341
JAL	49.4	52.8-1.95	1.95	44.0	46.4-40.6	1.26	0.000	0.3535
JAW	4.1	5.0- 3.4	0.38	3.5	4.1- 3.0	0.25	0.000	0.0156
JAH	7.6	8.6- 5.7	0.47	6.4	7.2- 5.5	0.39	0.000	0.5654
UCW	4.2	4.5- 3.5	0.21	3.5	3.9- 3.2	0.15	0.000	0.0847
LUPL	7.7	8.4- 6.6	0.30	6.8	7.5- 5.9	0.33	0.000	0.2606
UMW	8.2	9.0- 7.2	0.39	7.4	8.0- 6.5	0.39	0.000	0.8543
UMIL	5.3	5.8- 4.3	0.33	4.5	5.2- 3.7	0.37	0.000	0.2921
LUPW	5.4	6.1- 4.5	0.30	4.7	5.3- 3.9	0.39	0.000	0.0270
DBUW	9.9	11.2- 8.8	0.55	9.5	10.7- 8.6	0.57	0.000	0.3794
PLML	9.3	10.5- 8.0	0.43	8.1	8.9- 7.2	0.43	0.000	0.9532

Sample statistics and univariate tests of differences between male and female *Martes americana* (Vancouver Island)

Character	Males (N=93) $\bar{X}$	Males Range	Males SD	Females (N=71) $\bar{X}$	Females Range	Females SD	P_t	P_F
COBL	80.2	83.3-76.9	1.41	72.9	74.8-69.8	1.08	0.000	0.3190
ZYGM	48.8	53.0-43.4	1.47	42.9	45.7-40.7	1.11	0.000	0.0000
CHAB	30.0	31.7-28.6	0.66	27.9	29.9-26.0	0.65	0.000	0.7959
BUL	12.4	13.2-11.5	0.39	11.4	12.1-10.7	0.30	0.000	0.0209
BUW	8.9	9.7- 8.3	0.31	8.2	9.0- 7.3	0.30	0.000	0.4538
MASW	36.5	37.9-34.5	0.70	33.1	34.6-31.4	0.62	0.000	0.2801
FOMH	8.3	9.1- 7.5	0.32	8.0	8.6- 7.0	0.38	0.000	0.0514
FOMW	11.0	11.9-10.0	0.38	10.2	11.1- 9.3	0.35	0.000	0.2892
ROSW	16.9	18.1-15.9	0.43	14.9	15.8-14.1	0.40	0.000	0.7367
WPOP	24.5	23.3-20.6	1.27	22.1	24.1-20.0	0.82	0.000	0.0003
PORC	16.0	20.0-13.1	1.29	15.7	18.0-12.1	1.63	0.098	0.7021
IORW	19.0	20.8-17.5	0.65	17.0	18.7-15.9	0.46	0.000	0.0029
IFOW	20.9	22.2-19.6	0.48	19.0	19.9-18.0	0.45	0.000	0.7216
PALL	38.7	41.7-63.2	0.97	34.3	36.0-32.7	0.75	0.000	0.0870
TRL	33.4	34.9-32.2	0.63	30.0	31.4-28.7	0.59	0.000	0.2267
JAL	52.7	54.5-49.3	1.03	45.9	47.2-43.7	0.82	0.000	0.0139
JAW	4.1	4.6- 3.4	0.25	3.6	4.1- 3.2	0.20	0.000	0.0521
JAH	8.1	8.8- 7.1	0.37	6.9	7.7- 6.3	0.28	0.000	0.0024
UCW	4.5	4.9- 4.1	0.14	3.8	4.0- 3.5	0.11	0.000	0.2875
LUPL	7.8	8.5- 7.2	0.24	6.9	7.4- 6.5	0.20	0.000	0.1787
UMW	8.6	9.0- 8.0	0.24	7.6	8.1- 7.1	0.22	0.000	0.1207
UMIL	5.0	5.9- 4.5	0.22	4.3	4.6- 4.0	0.16	0.000	0.0265
LUPW	5.8	6.2- 5.4	0.17	5.7	5.7- 4.8	0.18	0.000	0.8871
DBUM	10.5	11.5- 9.4	0.43	9.9	10.7- 9.0	0.36	0.000	0.1098
FLML	9.2	10.1- 6.7	0.27	8.2	8.5- 7.7	0.19	0.000	0.0048

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Title of Thesis

Geographic and Sexual Variation of the American Pine Marten

(*Martes americana*) in the Pacific Northwest, with Special

Reference to the Queen Charlotte Islands

Author [redacted]

Signature

Guillermo Roberto Giannico

Name

December 5, 1986

Date