Geographic Variation in the Cranial Morphology of the Wolf (*Canis lupus*) in Northern Canada.

by

Robert Mulders

Department of Biology

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School of Graduate Studies

Laurentian University

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ABSTRACT

Five hundred and twenty-five adult wolf (*Canis lupus*) skulls from across northern Canada were obtained from Inuit hunters and wildlife biologists in the Northwest Territories, and from curators at 3 Canadian museums. Using univariate and multivariate analysis of 45 cranial, mandibular, and dental measurements, patterns of geographic variation and sexual dimorphism in cranial morphology were assessed for 10 locations in the Northwest Territories, northern Alberta, and central Saskatchewan. Existing subspecific designations for *C. lupus* in north central Canada were evaluated. The relationships between cranial size and (1) latitude, (2) ambient temperature, and (3) primary prey weights were also assessed.

Based on multivariate analysis, 3 primary subspecific designations were identified: High Arctic wolves (*C.l. arctos*), Mainland Tundra wolves, including Baffin Island, (*C.l. occidentalis*), and Central Boreal wolves (*C.l. nubilus*). These subspecific designations do not support the classification used by Goldman (1944), but do tend to support the reduction in designations proposed by Nowak (1983). Wolf subpopulations within these designations likely reflect ecotypes adapted to local conditions. Based on univariate analysis, wolves in northern Canada follow a cline in cranial size with the smallest wolves occurring in the northeast and the largest wolves in the southwest. The observed patterns of cranial size do not support either Bergmann's Rule or Allen's Rule. Wolves are sexually dimorphic and with few exceptions, male cranial parameters are 2 - 9% greater than females'. In northern Canada, the level of sexual dimorphism is clinal, with the lowest levels occuring in the northeast and the highest levels in the southwest.

For wolves of both sexes, there is a significant positive relationship between total skull length (I^1-SagC) and mean annual ambient temperature. There is a significant positive relationship between skull width (Zygom W) and mean annual ambient temperature for males, but not for females.

There is a significant positive relationship between cranial size and mean prey weight in wolves of both sexes. The higher level of significance in the relationship between zygomatic width and mean primary prey weight, for male wolves relative to female wolves, suggests that males may be more specialized for hunting and killing large ungulate prey.

There is a significant positive relationship between annual ambient temperature and mean primary prey weight. A colinear relationship appears to exist between mean annual ambient temperature, mean primary prey weight, and cranial size in *C. lupus*. Mean annual temperature and mean primary prey weight constitute only two environmental parameters which may be influencing the variation in cranial morphology of *C. lupus*.

Future research on the taxonomy of *Canis lupus* would benefit from, (1) additional cranial specimens from specific areas, (2) a standard approach to the number and selection of cranial parameters being used, and (3) genetic analysis of North American wolf populations.

This thesis is dedicated to my parents Anne and Gerard, my wife Donna, and my wonderful daughters Tamika and Ashley. I also dedicate this work to our large carnivorous mammals. Only with a sincere commitment to predator / prey research, public education, and sound wildlife management policies, will Canada be able to maintain the essence of its vast and spectacular wilderness.

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INTRODUCTION

The gray wolf is a member of the family Canidae or dog family, which belongs to the order Carnivora. It is one of the most variable and widely distributed mammal species, occupying nearly the entire land surface of two northern continents. Hybridization appears to occur readily in the genus *Canis* and hybrids have been reported between *C. lupus* and *C. familiaris*, *C. lupus* and *C. latrans*, *C. latrans* and *C. familiaris*, and *C. rufus* and *C. latrans*. All have a diploid chromosome number of 78 and karyological studies have been unable to distinguish among these species (Chiarelli, 1975). At the subspecies level, 24 designations have been described for the gray wolf in North America (Table 1). These subspecific distinctions have been based on morphological, usually cranial differences between geographic areas.

The gray wolf (*Canis lupus*) was historically distributed over most of the Northern Hemisphere. This broad distribution reveals the adaptability of the species to a wide range of habitats and prey species. The extirpation of the wolf throughout most of Europe and the southern portions of North America was due primarily to competition with humans for wild and domestic prey species (Nowak, 1983). The wolf is officially listed as "vulnerable" by the International Union for Conservation of Nature (Anonymous, 1988) and a number of "subspecies" or geographic variations of the wolf in North America have become extinct (Hall, 1981).

Most animal species consist of a number of subpopulations, many of which are visibly different from each other. Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species".

However, the designation of subspecific status by taxonomists can involve subjective criteria. While some taxonomists may distinguish groups along a gradual cline, others require a sharp shift in characters within a small geographical area (Nowak, 1983). The assignment of single individuals to particular subspecies is often problematic, as subspecies are often only represented in the literature by group averages or general non-quantitative descriptions that occur in specific geographic areas (Nowak, 1983). In order to evaluate subspecific status, a "75 percent rule" provides a rough criteria (Mayr *et al.*, 1953). For example, individuals from group A can be considered to be subspecifically distinct from group B, if 75% of the individuals can be distinguished from all individuals of group B. The "subspecies" problem has been discussed by a number of authors, including Mayr *et al.*(1953), Hagmeier (1958), Pimental (1958), Mayr (1963, 1969, 1970), and DeBlase and Martin (1974).

In North America, 24 subspecies of *C. lupus* were listed by Hall (1981); the Canadian subspecies are represented in Figure 1. Twenty-three of those subspecies had been described by Goldman (1944) and another (*C.l. griseoalbus*) was subsequently added by Hall and Kelson (1959). In Canada, 17 subspecies were described of which at least 7 (*C.l. mackenzii, C.l. occidentalis, C.l. griseoalbus, C.l. hudsonicus, C.l. arctos, C.l. bernardi, and C.l. manningi*) were found within the Northwest Territories (Banfield, 1974; Hall, 1981). The validity of the subspecific classification by Goldman (1944) has been continually challenged because of his small sample sizes, the lack of statistical analysis, and the absence of clearly defined taxonomic criteria (Nowak, 1983; Appendix 1). Research in Alaska (R.L. Rausch, 1953; R.A. Rausch, 1967; Pedersen, 1978, 1982) and Canada (Jolicoeur, 1959; Kelsall, 1968; Lawrence and Bossert, 1975; Skeel and Carbyn, 1977; Nowak, 1983; Friis, 1985; Pichette and Voigt, 1985; Brewster and Fritts, 1995; Nowak, 1995) has proposed a consolidation of subspecific classifications for *Canis lupus*. There was insufficient biometric data to determine whether the extirpated Greenland wolf (*C.l. orion*) was distinct from adjacent subspecies or represented immigration from Ellesmere Island (*C.l. arctos*) and/or Baffin Island (*C.l. manningi*) (Dawes *et al.*, 1986).

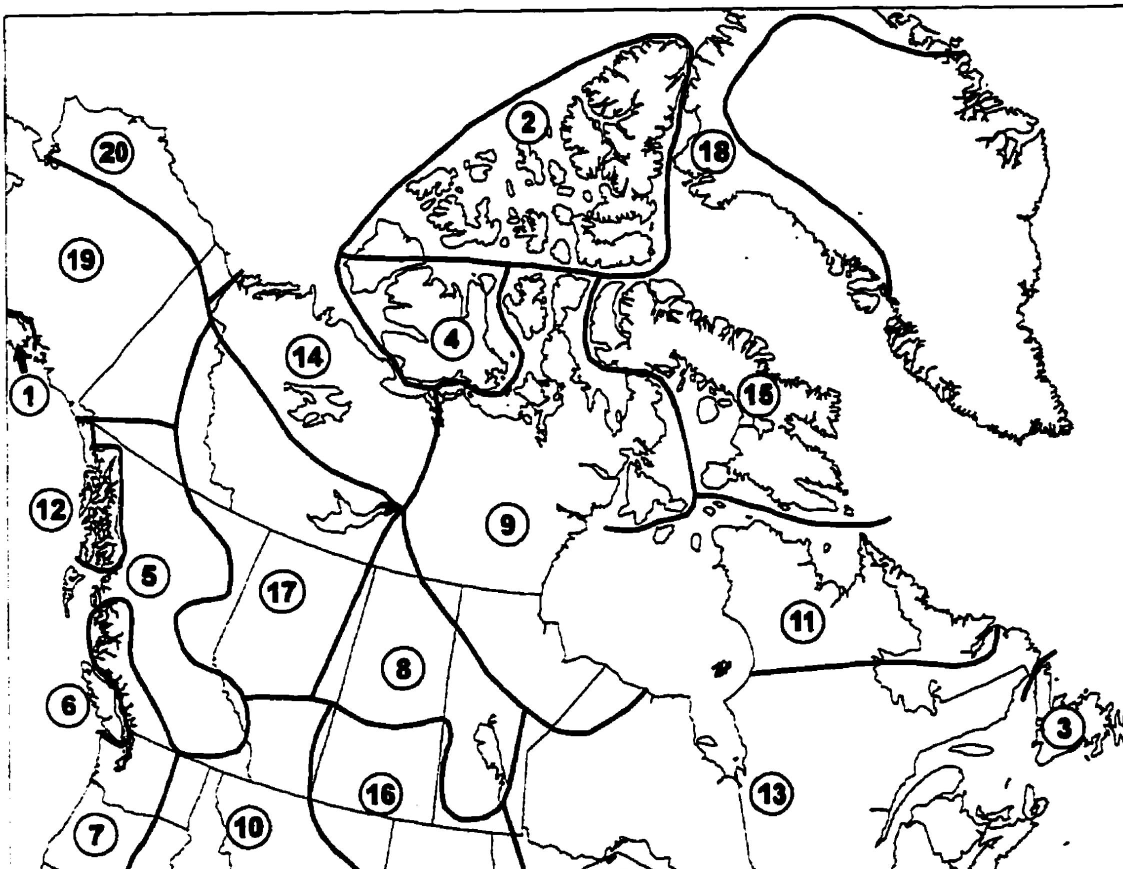
Table 1. Recognized subspecies of *Canis lupus* in North America listed by Hall (1981) and Nowak (1983).

Order Carnivora
Family Canidae
Species *Canis lupus*
Subspecies (North America)

	C.l. alces	Alaska
	C.l. arctos	Arctic Islands
	C.l. baileyi	Mexico
*	*C.l. beothucus*	Newfoundland
	C.l. bernardi	Banks Island
	C.l. columbianus	British Columbia
	C.l. crassodon	Vancouver Island
*	*C.l. fuscus*	S.W. British Columbia
	C.l. hudsonicus	West Coast Hudson Bay
	C.l. griseoalbus	Saskatchewan/Manitoba
*	*C.l. irremotus*	S. Alberta
	C.l. labradorius	N. Quebec/Labrador
	C.l. ligoni	Alaska
	C.l. lycaon	E. North America
	C.l. mackenzii	Mackenzie Delta
	C.l. manningi	Baffin Island
*	*C.l. mogollonensis*	S.W. United States
*	*C.l. monstrabilis*	Texas
*	*C.l. nubilus*	Central United States
	C.l. occidentalis	Alberta/Western N.W.T.
*	*C.l. orion*	Greenland
	C.l. pambasileus	Alaska Interior
	C.l. tundrarum	Alaskan Arctic Coast
*	*C.l. youngi*	S.W. United States

* Believed to be extinct (Adapted from Mech, 1970)

Figure 1. Distribution of currently recognized subspecies of *Canis lupus* in northern North America adapted from Hall (1981) and Nowak (1983).

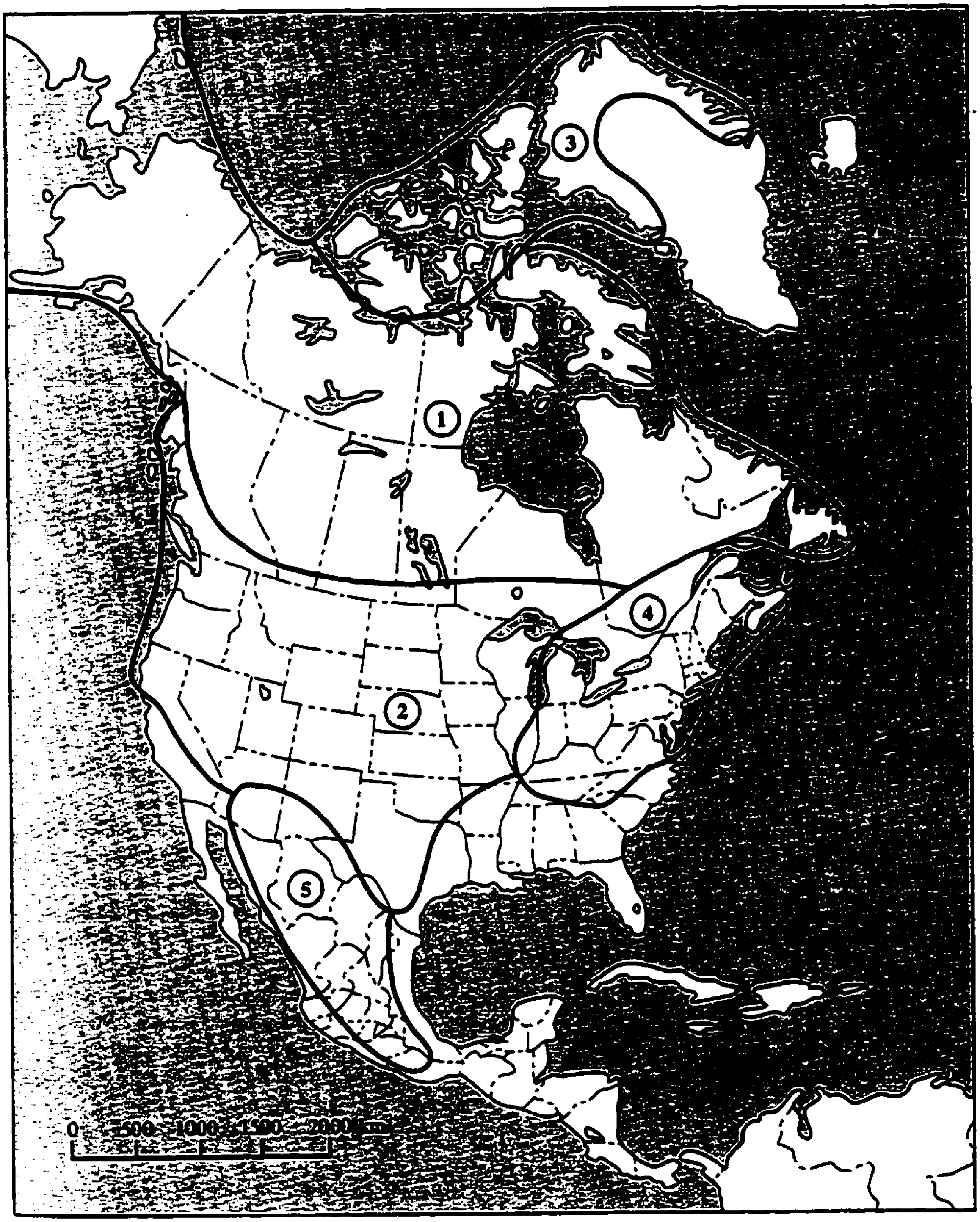


1. *Canis lupus alces*
2. *C.l. arctos*
3. *C.l. beothucus*
4. *C.l. bernardi*
5. *C.l. columbianus*
6. *C.l. crassodon*
7. *C.l. fuscus*
8. *C.l. griseoalbus*
9. *C.l. hudsonicus*
10. *C.l. irremotus*
11. *C.l. labradorius*
12. *C.l. ligoni*
13. *C.l. lycaon*
14. *C.l. mackenzii*
15. *C.l. manningi*
16. *C.l. nubilus*
17. *C.l. occidentalis*
18. *C.l. orion*
19. *C.l. pambasileus*
20. *C.l. tundrarum*

Although most studies have proposed a reduction in the number of subspecies, Kolenosky and Standfield (1975) suggested that *C.l. lycaon* in southern Ontario may be divisible into 2 or 3 subspecies. There has been a general consensus that the existing nomenclature for *Canis lupus* requires formal revision (Nowak, 1995). The results derived from larger sample sizes, multivariate analysis, and molecular genetics suggest that the existing 24 subspecific designations in North America, could be consolidated into 5 subspecies (Brewster and Fritts, 1995; Nowak, 1983) (Fig. 2). Techniques in genetic research using mitochondrial DNA (Kennedy *et al.*, 1991; Lehman *et al.*, 1991, 1992) have indicated relatively little protein variation with low levels of genetic heterozygosity among wolves in northwestern Canada. More recent work with microsatellite sequences of DNA involving the use of "hyperactive microsatellite loci" to examine the genetic relationship of polar bear (*Ursus arctos*) sub-populations, a holarctic species previously deemed to have low levels of heterozygosity (Paetkau *et al.*, 1995), suggests that heterozygosity may be greater than previously thought. Thus, further refinements in genetic analysis may be needed to clarify the taxonomic relationship of North American wolves.

Periods of glaciation in North America are believed to have had a major influence on speciation in northern mammalian species. Late Pleistocene (Wisconsin) glaciation is believed to have caused the genetic isolation of mammalian populations (Coleman, 1941; Rand, 1954; Macpherson, 1965; Nowak,1983; Røed *et al.*, 1991). Wolves which occupied high arctic refugia in eastern Siberia and Alaska (Beringia) and northern Greenland (Pearyland) would have been reproductively isolated from wolf populations along the southern edges of the ice sheet. Subsequent postglacial dispersal and convergence of populations would have contributed to the genetic diversity and morphological variation observed currently in northern populations (Rand, 1954; Macpherson, 1965). Evidence suggests that current subspecific distinctions of Peary caribou (*Rangifer tarandus pearyi*), barren-ground caribou (*R..t. groenlandicus*), and woodland caribou (*R.t. caribou*) may be a direct result of the reproductive isolation during the Wisconsin glaciation (Macpherson, 1965; Banfield, 1962; Røed *et al.*, 1991).

Figure 2. Revised distribution of subspecific boundaries of *Canis lupus* involving 5 subspecies in North America as proposed by Nowak (1983).



1 Northern group
2 Southern group
3 *Canis lupis arctos*
4 Eastern *C. l. lycaon*
5 *C. l. baileyi*

In North America, the historic range of the wolf extended from the Arctic Islands southward into Mexico (Nowak, 1983). By 1900, the wolf was eliminated from the eastern half of the United States and by 1930, after massive wolf control programs, the wolf disappeared from the western half of the United States and much of southwestern Canada. Between 1930 and 1950, a dramatic reversal occurred as wolves began increasing in number and reoccupying vast areas of former range, especially in Alberta, Saskatchewan, and Manitoba. During the 1950's and 1960's, large scale wolf control programs were again organized in Alaska and Canada (Banville, 1983; Gunson, 1983; Heard, 1983; Kolenosky, 1983; Smith, 1983; Stardom, 1983; Tompa, 1983) to curb their increase and expansion. Wolf populations have stabilized since the 1960's and again reported on the prairies throughout Canada and are increasingly reported in areas of the United States, where they have not been seen in decades (Nowak, 1983). Whether the original subspecific designations are valid and whether recent expanding populations are the same subspecies as originally described remain unclear.

A number of authors have examined *C. lupus* crania in northern Canada. Several arctic races of wolf were initially described by Pocock (1935) and Anderson (1943; 1946). The comprehensive taxonomic review of North American wolf subspecies by Goldman (1944) involved small sample sizes (1 to 28) for subspecies described in the Northwest Territories (Appendix 2). Since these initial efforts, additional work has been done studying geographic variation in wolves from the western N.W.T. (Jolicoeur, 1959; Kelsall, 1968; Kuyt, 1972; Jolicoeur, 1975; Clarkson and Liepens, 1989a, 1989b; Williams and Heard, 1989; Williams, 1990; Kennedy *et al.*, 1991; Walker *et al.*, 1993). Research on wolves in the Keewatin Region (Kelsall, 1968; Parker, 1973; Hillis and Mallory, 1989; Hillis, 1990; Lamothe and Parker, 1989; Lamothe, 1991; Hillis and Mallory, 1996) did not address the subspecific status of *C.l. hudsonicus*. Several broadly based morphological studies have incorporated *C.l. hudsonicus* cranial data in their analysis (Jolicoeur, 1959; Skeel and Carbyn 1977; Nowak 1983, 1995).

The existing literature indicates that *C.l. hudsonicus* is broadly distributed from Melville Peninsula down into the James Bay region, along the entire western shore of Hudson Bay (Goldman, 1944; Hall and Kelson, 1959; Hall, 1981). This classification by Goldman (1944), however, was based on a sample of 9 skins and 6 skulls (5 male; 1 female) and limited to the central portion of the Keewatin Region (Appendix 1; Fig. 3). Harper (1955) questioned the extension of the range of *C.l.hudsonicus* into northern Manitoba and northeastern Saskatchewan and suggested that wolves below tree-line may be distinct from wolves on the tundra.

Sexual dimorphism in wolves has been recorded by Anderson (1943), Goldman (1944), Jolicoeur (1959, 1975), Gipson *et al.* (1974), Kolenosky and Standfield (1975), and Hillis and Mallory (1996). It is generally accepted that male skulls are 3 - 8% larger than female skulls (Jolicoeur, 1975; Kolenosky and Stanfield, 1975; Pedersen, 1978; Friis, 1985; Schmitz and Kolenosky, 1985; Schmitz and Lavigne, 1987). This factor further confounds the data of Goldman (1944), as his samples were of both sexes.

Since wolves across the N.W.T. mainland are dispersed over a vast area, there is sufficient opportunity for movement and inter-mixing of populations. The long-range movement (calculated in a straight-line) for wolves has been documented by Kuyt (1962) in the N.W.T (296 km), by Van Camp and Gluckie (1979) in northern Alberta (670 km), and by Fritts (1983) between Minnesota and Saskatchewan (886 km). Between June 1992 and April 1994, a radio-collared male wolf travelled from Bathurst Inlet to Baker Lake, a straight-line distance of 560 km (M. Williams, pers. comm.). Wolves designated as *C.l. hudsonicus* and *C.l. mackenzii* annually invade forested regions occupied by other subspecies (Kelsall, 1968). Since there are no geographic barriers or topographic isolation on the N.W.T. mainland, the proposed convergence of 4 subspecies at the east end of Great Slave Lake (Fig. 4) by Goldman (1944) and subsequently by Hall and Kelson (1959), has been continually challenged (Anderson, 1946; Jolicoeur, 1959; Kelsall, 1968; Skeel and Carbyn, 1977). These authors have contended that tundra wolves on the mainland are relatively wide-ranging and nomadic and that current subspecific boundaries are arbitrary. Jolicoeur (1959) assessed 500 wolves from northwestern Canada and Alaska and concluded that the

Figure 3. Map of the Keewatin Region showing the collection sites for 5 of 6 wolf samples used by Goldman (1944) to classify *C.l. hudsonicus*. The type (a) and topotype (b) specimens were taken at Schultz Lake. The collection site for the sixth sample was only identified as "Hudson Bay".

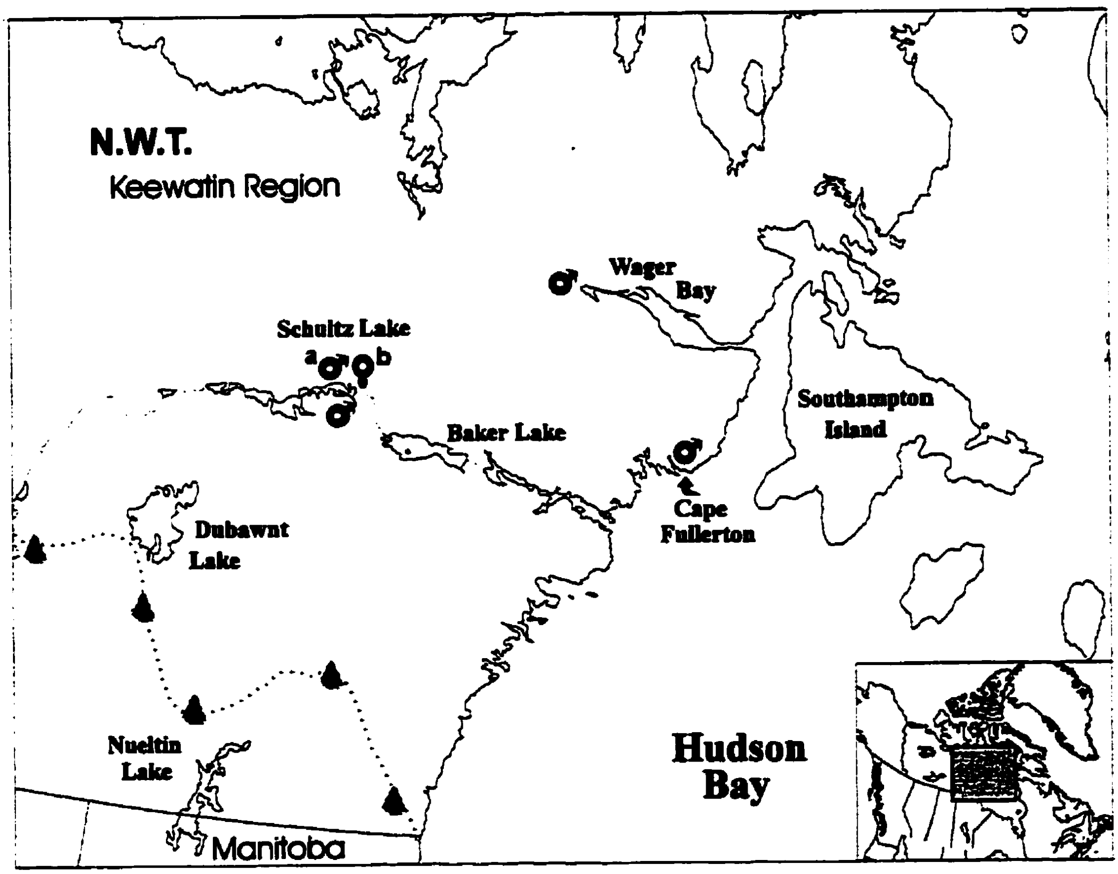
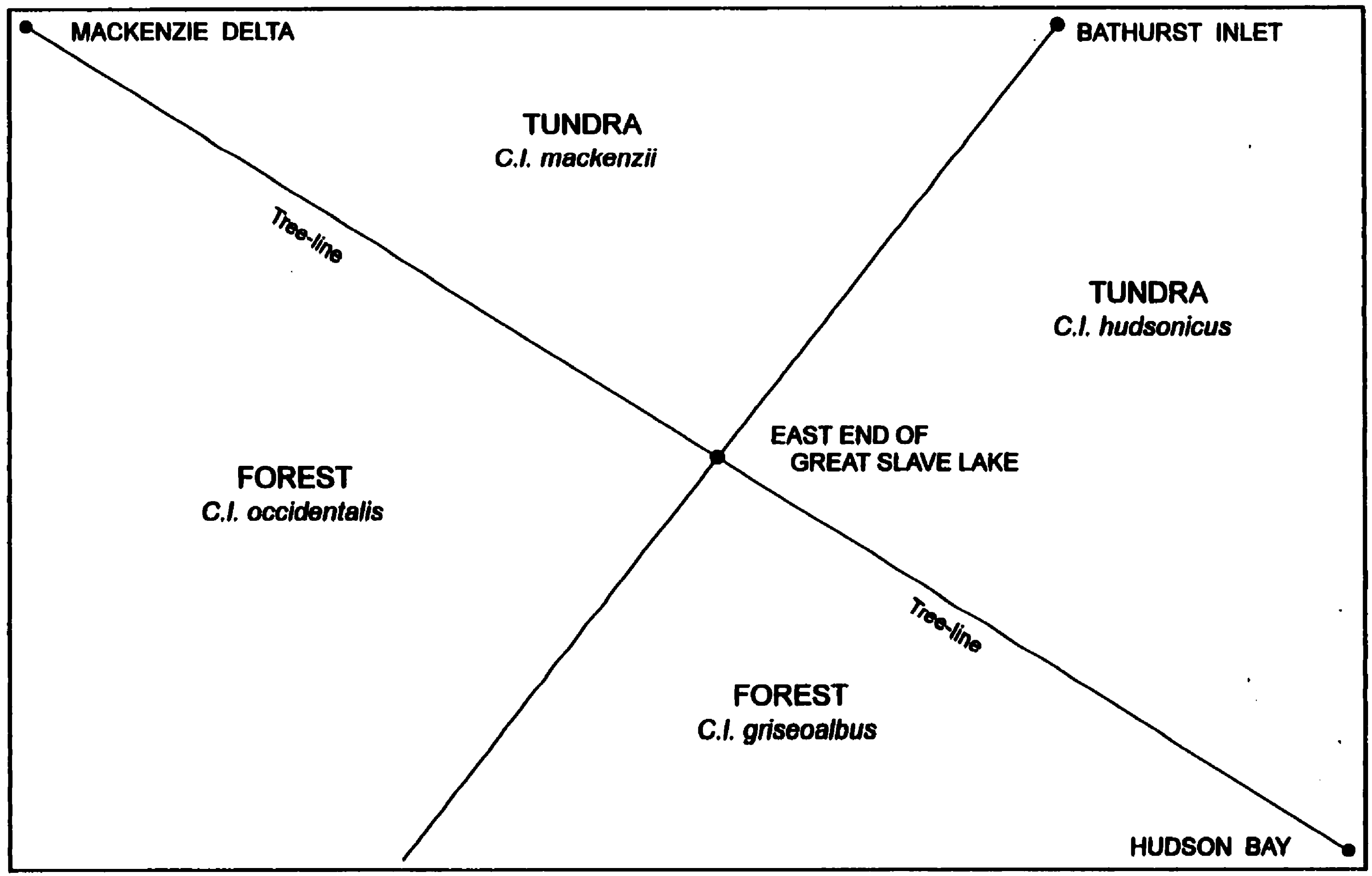

N.W.T.
Keewatin Region
Wager
Bay
Schultz Lake
a
b
Baker Lake
Southampton
Island
Dubawnt
Lake
Cape
Fullerton
Nueltin
Lake
Hudson
Bay
Manitoba

Figure 4. Relative distribution of *Canis lupus* subspecies in the western Northwest Territories proposed by Hall and Kelson (1959) as presented by Kelsall (1968).


MACKENZIE DELTA
BATHURST INLET
TUNDRA
C.l. mackenzii
Tree-line
TUNDRA
C.l. hudsonicus
EAST END OF
GREAT SLAVE LAKE
FOREST
C.l. occidentalis
Tree-line
FOREST
C.l. griseoalbus
HUDSON BAY

pattern of variation "was more suggestive of an incomplete panmictic continuum than of distinct subspecific units ". Ice formations aid in the distribution of mammals and counteract the isolating effect of water barriers (Banfield, 1954). The inter-island movement of caribou in the Canadian arctic archipelago has been recorded on numerous occasions (Preble, 1908; Miller *et al.*, 1977; Miller and Gunn, 1978; Miller, 1995). Although polynia and extensive leads in the sea-ice may restrict movement in certain areas, high arctic wolves similarly encounter few geographic barriers. Two biogeographic rules based on patterns of adaptation in homeothermic vertebrates will also be considered in this study. Bergmann's Rule states that in homeotherms body size varies inversely with ambient temperature so that body size increases latitudinally (Bergmann, 1847; Remmert, 1980; Pianka, 1988). Although this pattern may exist in the lower United States and southern Canada, the pattern reverses between 53° and 65° N. latitude (Geist, 1987), resulting in small body sizes at the lowest and highest latitudes. An exception to Bergmann's Rule is seen in the smaller skull and body size of wolves in the high arctic (Jolicoeur, 1975; Skeel and Carbyn, 1977). The long arctic winter may reduce food intake (Mayr, 1970) or cause a "metabolic and/or hormonal imbalance" (Jolicoeur, 1959), which could account for these smaller phenotypes. The low body weights found in several Greenlandic wolves may also reflect winter malnutrition as opposed to a distinct morphological difference (Dawes *et al.*, 1986).

Allen's Rule states that protruding parts of the body, such as ears, rostrum and other extremities are relatively shorter in cooler geographic regions (Remmert, 1980; Pianka, 1988). According to Jolicoeur (1959, 1975), the short rostrum relative to skull width found in high arctic wolves conforms to Allen's Rule.

Geographic variation in the diet of predators often reflects regional variation in available prey species (Rosenzweig, 1968). This view has been subsequently supported with more recent studies of *C. lupus* (Fuller and Keith, 1980; Holleman and Stephenson, 1981; Schmitz and Lavigne, 1987). This pattern presupposes that wolves prey primarily upon the largest mammalian prey species present in their environment (Mech, 1970) and that "ecotype" boundaries are in fact gradients reflecting the gradual shift in prey-types. Wolves on the N.W.T. mainland feed primarily on caribou with occasional use of moose or muskox

(Kelsall, 1968; Kuyt, 1972; Heard and Williams, 1988; Lamothe and Parker, 1989; Lamothe, 1991). On the high arctic islands, wolves prey on caribou and on muskox (Tener, 1965; Miller, 1975; Mech 1988b; Miller, 1995b). On Baffin Island the only available ungulate species is caribou (Clark, 1971). In Prince Albert National Park in central Saskatchewan, wolves prey primarily on moose and elk (Banfield, 1951; E. Kowal, pers. comm.). Wolves in the vicinity of Wood Buffalo National Park feed primarily on bison and secondarily on moose (Oosenbrug and Carbyn, 1982; Van Camp, 1987; Carbyn *et al.*, 1993; Larter *et al.*, 1994). Wolves in northern Alberta, south of Wood Buffalo National Park, rely primarily on moose and to a lesser extent on woodland caribou (Fuller and Keith, 1980). While winter feeding habits of wolves focus on available large ungulate species, summer diet may be more varied and include a higher proportion of smaller mammals (Kuyt, 1972; Voigt *et al.*, 1976; Fuller and Keith, 1980; Gauthier and Theberge, 1987).

Although determination of subspecific status may appear academic, there are practical aspects. A marked reduction or loss of unique wolf types could take place unless local variation is considered in wolf management efforts. In the high arctic, for example, the relatively unique *C.l. arctos* may be threatened due to a decline in Peary caribou abundance (Miller, 1995b). In order to address the growing concern over loss of biodiversity, it is necessary to first describe the morphological variation among and between wolf populations.

In 1986, the Government of the N.W.T.'s Department of Renewable Resources initiated a study of wolves within the Keewatin Region. In co-operation with Laurentian University, three students undertook research to cover independent aspects of this study:

a) body morphometry, condition, reproduction, population age structure, and temporal and spatial ecology of wolves in association with the caribou herds of the region (Hillis, 1990),

b) winter feeding habits of wolves in the Keewatin Region, determination of tissue burdens of certain toxic metals (cadmium, lead, nickel, zinc, copper, and iron) and assessment of the transfer of these metals through key items within the food chain - (soil-vegetation-caribou-wolf) (Lamothe, 1991), and

c) cranial morphology of wolves across northern Canada to consider geographical variation and subspecific designations (this study).

The objective of this study was to examine the geographic variation in the cranial morphology of *Canis lupus* in northern Canada, with the goal of assessing existing subspecific designations. The initial focus on *C.l. hudsonicus* was broadened to consider all subspecific designations in the Northwest Territories, as well as adjacent subspecific designations in central Saskatchewan and northern Alberta. Geographic patterns of sexual dimorphism in cranial morphology were also examined. Potential relationships between (a) cranial size and mean latitudinal temperature and between (b) cranial size and primary prey weight were also evaluated. More specifically, the following questions were addressed:

1) Do the existing subspecific designations and boundaries proposed by Goldman (1944) and Nowak (1983) for *Canis lupus* in northern Canada appear warranted?

2) Is the subspecific designation used by Goldman (1944) for *C.l. hudsonicus* valid and can Keewatin samples be distinguished from adjacent populations using his criteria?

3) Do wolves in the southern Keewatin have a greater morphometric affinity to wolves in the central and northern Keewatin (*C.l. hudsonicus*) than to wolves from central Saskatchewan (*C.l. griseoalbus)* ?

4) What patterns of sexual dimorphism occur spatially within *C. lupus* across northern Canada?

5) For *C. lupus* in northern Canada, is there a significant relationship between (a) cranial size and ambient air temperature and between (b) cranial size and primary prey weight?

MATERIALS AND METHODS

Collection of Keewatin Cranial Specimens

Four hundred and thirty three wolf (*Canis lupus*) carcasses were collected from hunters in the Keewatin Region between February 1987 and December 1989. The Government of the Northwest Territories, Department of Renewable Resources, purchased skinned wolf carcasses from Inuit hunters in five communities: Arviat, Rankin Inlet, Chesterfield Inlet, Baker Lake, and Repulse Bay (Fig. 5). Hunting methods employed by native hunters on snow-machine in open tundra were believed to provide a representative sample of the wolf population since whole packs were killed whenever possible. For each specimen, hunter name, kill date, and kill location, were recorded. The carcasses remained frozen at ambient temperatures until May, when they were thawed and necropsied. Individuals eventually identified as pups (< 12 months; n=208) or where the sex or kill location could not be confirmed (n=12) were excluded from analysis. Within the Keewatin Region, specimens were assigned to one of three areas (northern, central, and southern) extending over a range of 1000 km (Fig. 6). Considering the close proximity of wolf specimens collected from Baker Lake, Rankin Inlet, and Chesterfield Inlet, samples were combined and classified as part of the central Keewatin group.

Skull Preparation

Skulls were cleaned by gently boiling in water for several hours and scrubbing with a soft brush. Water pressure was used to remove soft tissues within the nasal cavity, foramina, and brain case. Once clean, skulls and jaws were placed in a paper bag and stored under cool, dry conditions for at least two months to permit shrinkage prior to taking any measurements.

Figure 5. Map of the Keewatin Region showing the five communities which provided wolf carcasses in 1987, 1988, and 1989.

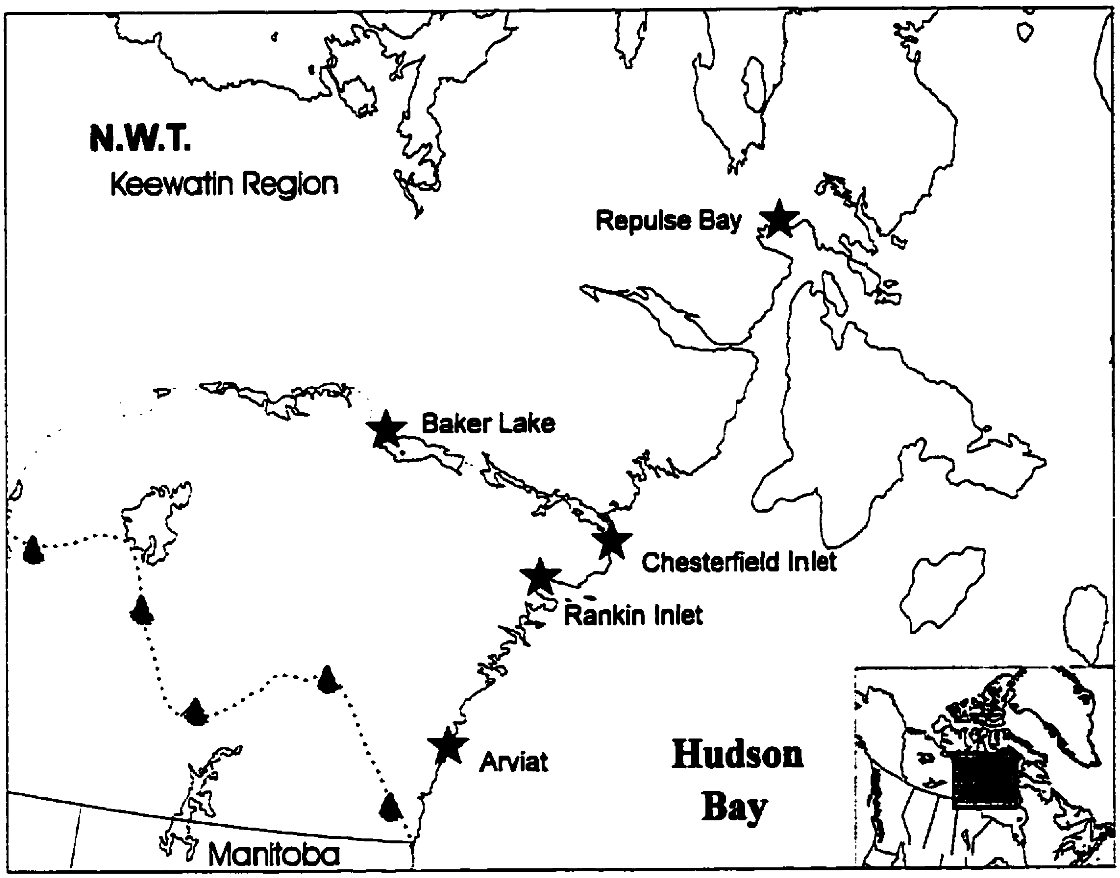
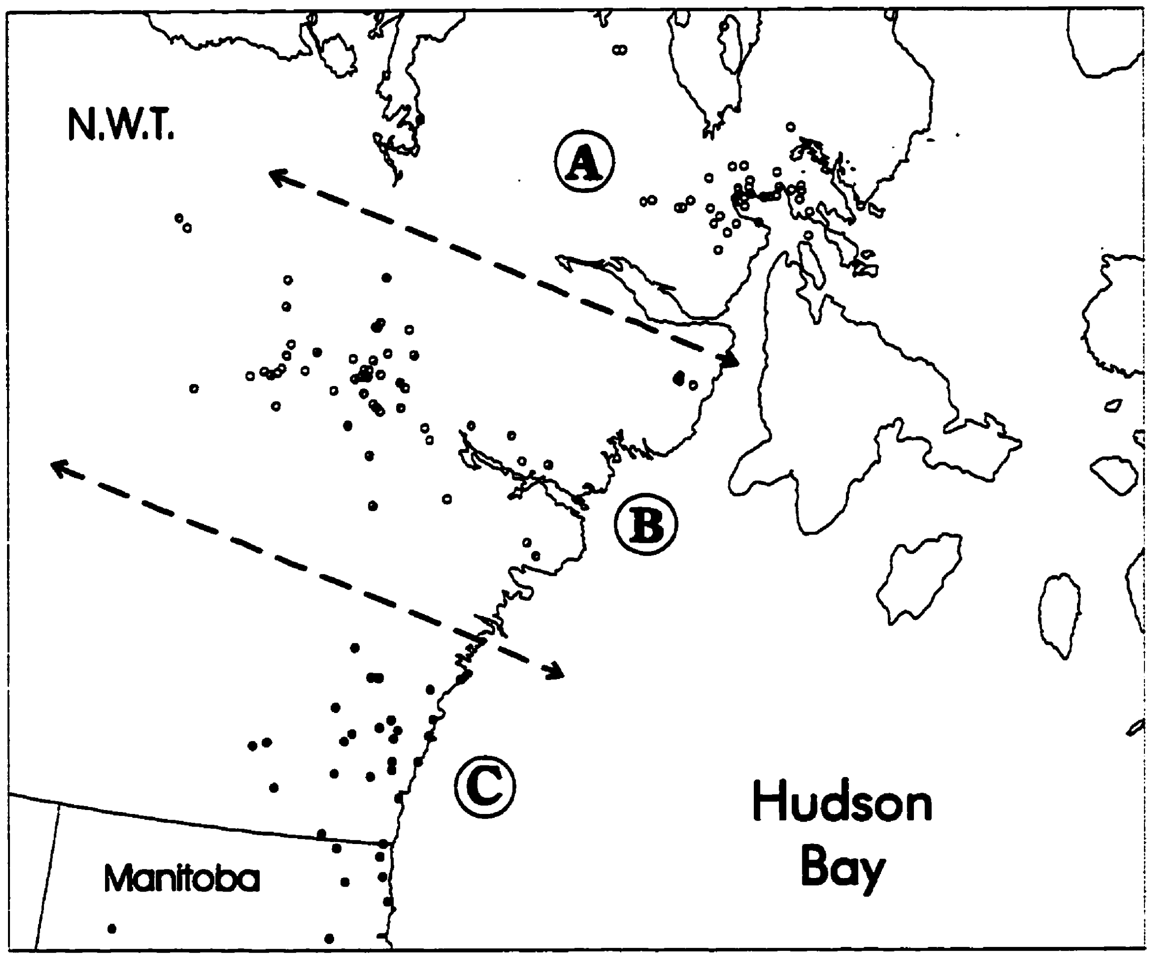

N.W.T.
Keewatin Region
Repulse Bay
Baker Lake
Chesterfield Inlet
Rankin Inlet
Arviat
Hudson Bay
Manitoba

Figure 6. Harvest locations of adult *C.l. hudsonicus* specimens in the northern (A), central (B), and southern (C) portions of the Keewatin Region.


N.W.T.
A
B
C
Manitoba
Hudson
Bay

Additional Cranial Specimens

In order to broaden the study and consider cranial variation for wolves beyond the Keewatin Region, additional adult skulls were sought out and measured from across northern Canada. In addition to the Keewatin samples, specimens provided by several wildlife biologists in the Northwest Territories and curators at two Canadian museums were examined. All adult crania used in this study are identified in Table 2. The harvest locations for all adult wolf samples examined in this study are presented in Figure 7.

Ageing of Specimens

In comparing cranial features, pups were excluded from analysis since it is not until the adult stage (> 20 months) that the maximum size of all major dimensions of the skull is attained (Young and Goldman, 1944; Skeel and Carbyn, 1977). Ages of field sampled wolves were determined by examining the number of cementum annuli present in the root of the lower, left premolar (P_1). This premolar was either removed during the necropsy or removed later, after the jaw had been placed in water and gently boiled to facilitate the breakdown of the periodontal membrane. Premolars were sent to Matson's Laboratory (Milltown, Montana) for preparation and scoring of cementum annuli. Each premolar was decalcified as described by Goodwin and Ballard (1985) and 14 μm sections were removed along the sagittal plane of the root and stained with Harris's haematoxylin. In addition to examining cementum annuli, pups were distinguished from adults on the basis of closure of the presphenoid-basisphenoid suture (Skeel and Carbyn, 1977). Discrepancy between these two techniques was rare; closure of the presphenoid-basisphenoid suture took precedence in distinguishing pups from adults.

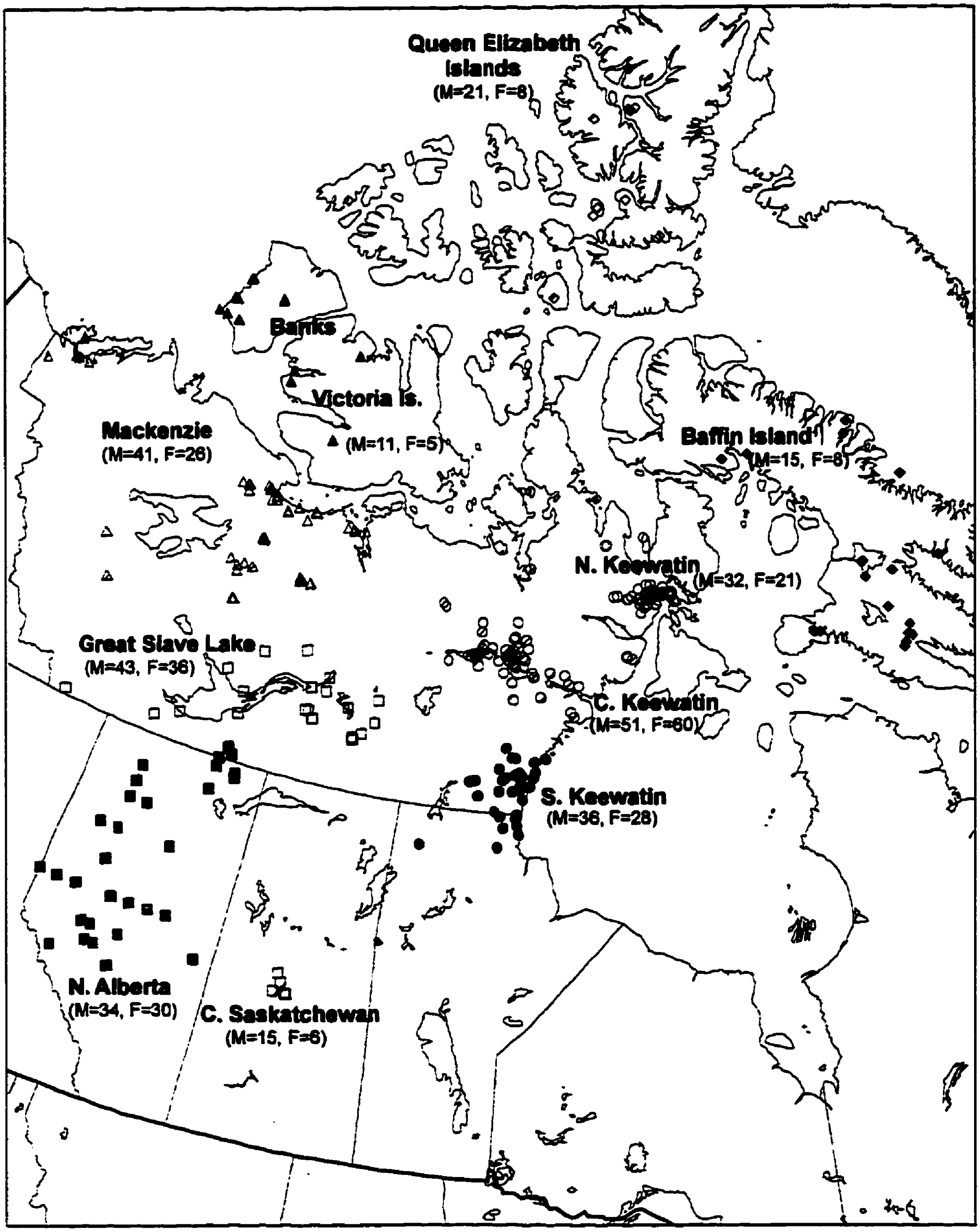
Since most wolf pups within the N.W.T. are born in May (Kuyt, 1972; Heard and Williams, 1988), the date of birth was set to May 15. As wolves shot between February and April had survived approximately 3/4 of an annual cycle, age classes were set at 0.75 years for pups, and ≥ 1.75 years of age for older individuals.

Table 2. List of locations, origins, subspecific designations, period of harvest, and numbers of all adult (>20 months) wolf cranial specimens examined in this study. Specimens were provided by Inuit hunters, wildlife biologists, and museum curators.

Region	Specific Location	Designated Subspecies of *C. lupus*	Period of Harvest	*n* Male	*n* Female	*n* Total
Northern Keewatin [1]	Repulse Bay	*hudsonicus*	1987-90	31	21	52
Central Keewatin [1]	B.L., RI., & C.I.	*hudsonicus*	1987-90	46	57	103
Southern Keewatin [1]	Arviat	*hudsonicus*	1987-90	32	26	58
S.W. Arctic [2]	Banks /Victoria Is.	*bernardii*	1986-88	3	1	4
Mackenzie Region [2]	Coppermine	*mackenzii*	1986-87	13	4	17
Great Slave Lake [3]	Reliance	*hudsonicus*	1988-89	31	27	58
High Arctic [4]	Queen Elizabeth Is.	*arctos*	1951-69	21	8	29
S.W. Arctic [4]	Banks /Victoria Is.	*bernardii*	1915-71	8	4	12
Eastern Arctic [4]	Baffin Island	*manningi*	1966-71	15	8	23
Mackenzie Region [4]	Delta - Great Bear	*mackenzii*	1960-70	28	22	50
Great Slave Lake [4]	Great Slave Lake	*hudsonicus*	1924-64	12	9	21
Keewatin Region [4]	Central Keewatin	*hudsonicus*	1964-70	8	5	13
C. Saskatchewan [4]	Prince Albert N. P.	*griseoalbus*	1950-58	15	6	21
Alberta / WBNP [4]	Northern Alberta	*occidentalis*	1926-49	5	3	8
Alberta [5]	Northern Alberta	*occidentalis*	1975	0	8	8
Alberta / WBNP [6]	Northern Alberta	*occidentalis*	1966-82	19	15	34
Alberta [7]	Northern Alberta	*occidentalis*	1953-74	10	4	14
				297	228	525

1. Samples provided by Inuit hunters (Keewatin Region)
2. Courtesy of Anne Gunn (DRR, G.N.W.T)
3. Courtesy of Doug Heard & Mark Williams (DRR, G.N.W.T.)
4. Courtesy of Stan van Zyll de Jong (National Museum of Canada)
5. Courtesy of John Gunson (Alberta Fish & Wildlife)
6. Courtesy of Hugh Smith (Alberta Provincial Museum)
7. Courtesy of Wayne Roberts (University of Alberta, Zoology)

Figure 7. Harvest locations of all *C. lupus* specimens from across northern Canada considered in this study.



Queen Elizabeth
Islands
(M=21, F=8)
Banks
Victoria Is.
(M=11, F=5)
Mackenzie
(M=41, F=26)
Baffin Island
(M=15, F=8)
N. Keewatin
(M=32, F=21)
Great Slave Lake
(M=43, F=36)
C. Keewatin
(M=51, F=60)
S. Keewatin
(M=36, F=28)
N. Alberta
(M=34, F=30)
C. Saskatchewan
(M=15, F=6)

Most of the museum specimens were not aged. However, older wolves were distinguished from pups primarily on the basis of closure of the presphenoid-basisphenoid suture and secondarily on the basis of canine eruption, degree of tooth wear, degree of ossification, and development of postorbital processes (Kolenosky & Standfield, 1975; Skeel and Carbyn, 1977). Only adult specimens with complete information on kill date, kill location, and sex were used. Full reliance was placed on the museums' and biologists' kill date and location data.

Cranial Measurements

All measurements were recorded with 30 cm long digimatic calipers (Mitutoyo Model 500-323) to an accuracy of 0.01 mm. A digimatic mini-processor (Mitutoyo Model DP-1AT 264-502) was connected to the calipers. This arrangement eliminated recording error by allowing measurements to be recorded directly into a hard copy format. Measurements were entered onto a software spreadsheet and proofread, in preparation for analysis. In order to minimize sampling bias, all measurements were taken by the same individual (RM). After a one month delay, a sub-sample of 19 skulls were remeasured to examine measurement precision (Appendix 4). One would expect that smaller measurements would have a higher relative measurement error since the lower limit of absolute error is set by caliper accuracy. As well, some measurements may be poorly defined and may be difficult to measure consistently (Bailey and Byrnes, 1990). None of the parameters were excluded from analysis. Thorpe (1985) suggests that with a set of significant characters, the addition of insignificant characters to multivariate analysis has little effect on representing the same geographic pattern.

The selection of cranial characters used in this study was important as these formed the basis for interpreting the results and classification assessments. Based on the parameters used for *C. lupus* by a number of authors (Goldman, 1944; Jolicoeur, 1959; Lawrence and Bossert, 1967; Kolenosky and Standfield, 1975; Skeel and Carbyn, 1977; Pedersen, 1978; Pichette and

Voigt, 1985; Schmitz and Kolenosky, 1985; and Friis, 1985), a total of 45 cranial, mandibular, and dental measurements were recorded (Table 3; Fig. 8). These parameters offer a comprehensive representation of the dimensions and proportions of the skull and reflect basic differences in skull size, breadth of rostrum, massiveness of teeth, as well as the size and strength of the jaw. The 10 cranial parameters used by Nowak (1995) are described in Appendix 5. Although non-metrical cranial traits are less sensitive to size selective bias (Taylor, 1986) and may avoid the influence of environmental or dietary conditions (Friis, 1985), only metrical analysis was undertaken in this study.

Statistical Analysis

Statistical analysis of cranial morphometrics has proven useful in taxonomic studies of *Canis lupus* (Jolicoeur, 1959; Lawrence and Bossert, 1967; Gipson *et al.*, 1974; Jolicoeur, 1975; Kolenosky and Standfield, 1975; Pedersen 1978, 1982; Nowak, 1983; Friis 1985; Pichette and Voigt, 1985; Nowak, 1995). However, the limited *C. lupus* cranial measurement data in the literature for individual specimens, precluded any direct statistical analysis or comparison with specimens examined in this study. For example, Goldman's (1944) small sample size (n=6) for *C.l. hudsonicus* (Appendix 2) offered little opportunity for in-depth statistical analysis or quantitative comparison. However, a review of published mean values for several cranial parameters for subspecific designations of C. *lupus* in northern Canada (Appendix 6) did provide an opportunity to compare patterns of geographic variation. Statistical analysis described in this thesis was performed only on the adult cranial specimens (n=525) measured in this study (Table 2).

Descriptive statistics were calculated with the (DESCRIPTIVE) program of SPSS-PC+ V5.0.1 (Norusis, 1988a). Probabilities of less than 5% were considered to have biological significance. Student's *t*-tests were performed to compare the degree of sexual dimorphism

Figure 8. Cranial, mandibular, and dental parameters (n=45) measured from *C. lupus* specimens. Corresponding descriptions are listed in Table 3.

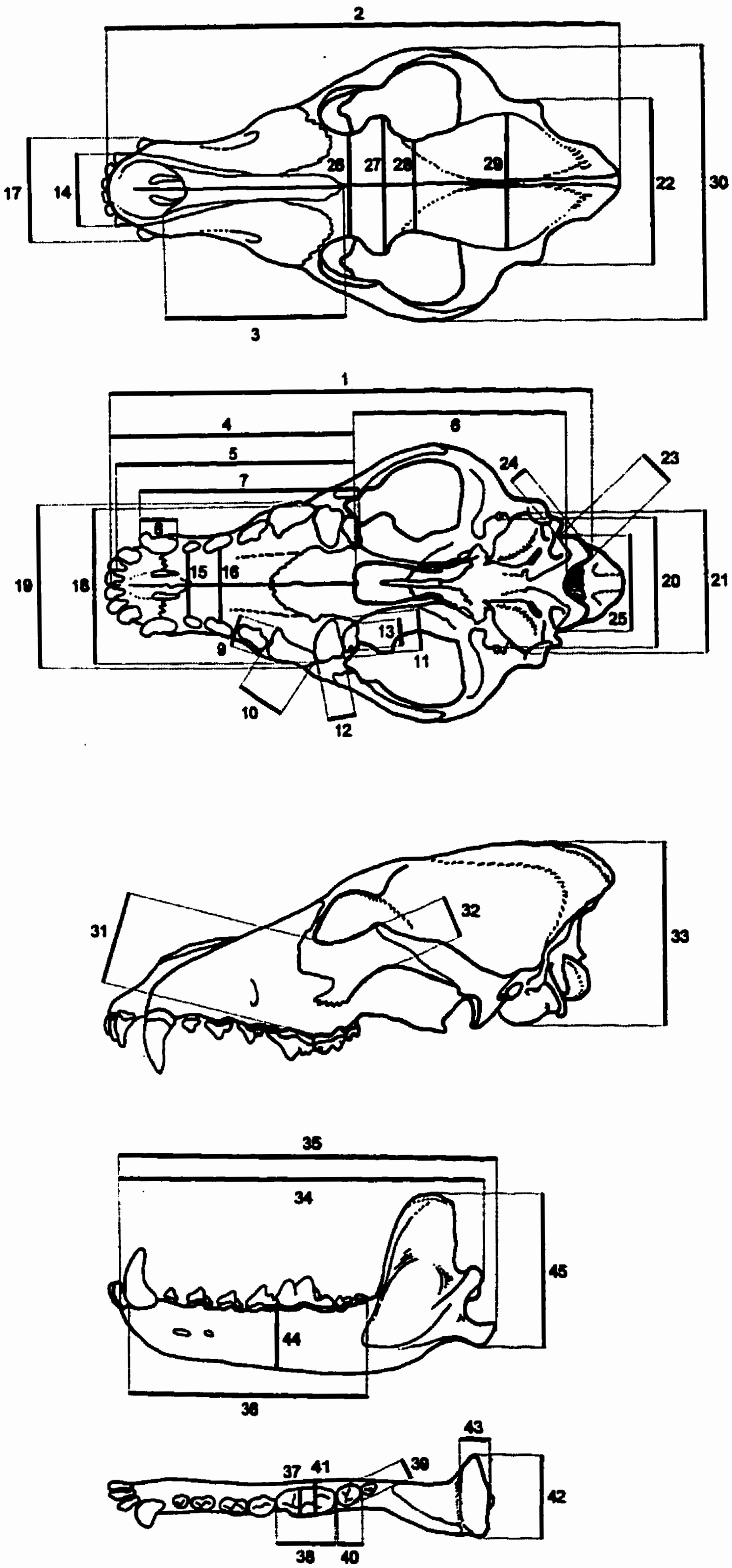


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Table 3. Cranial, mandibular and dental measurements (n=45) taken from *C. lupus* samples, as depicted on the cranium and mandible diagrammed in Figure 8.

No.	Abbrev.	Description
1	Condy L	Condylobasal length (from premaxilla to occipital condyle)
2	I^1- SagC	Maximum length from premaxilla to posterior of sagittal crest
3	Nasal L	Maximum length of nasals
4	I^1- Palat	Palatal length from alveolar of I^1
5	I^2- Palat	Palatal length from alveolar of I^2
6	PosPal L	Post palatal length
7	C^1 to M^2	Crown length of upper cheek teeth from C to M^2
8	W of C^1	Maximum anterior-posterior width of upper canine at base
9	W of P^4	Maximum buccolingual width of P^4 at enamel line
10	L of P^4	Maximum anterior-poster length of P^4 at enamel line
11	W of M^1	Buccolingual width of M^1 at enamel line (at major cusp)
12	L of M^1	Maximum anterior-posterior length of M^1 an enamel line
13	W of M^2	Crown width of M^2
14	I^3 to I^3	Crown width across upper incisors
15	P^1 to P^1	Minimum width between alveoli of P^1
16	P^2 to P^2	Palatal width inside the second upper premolars (at hollow)
17	C^1 to C^1	Width of skull across outside of upper canines
18	M^1 to M^1	Palatal width outside the first upper molars
19	Cheek T W	Maximum crown width across upper cheek teeth
20	Pos For W	Width between the postglenoid foramina
21	Aud Bul W	Width between the auditory bullae
22	Occ Cre W	Maximum width of skull at lateral borders of occipital crest
23	Condyle W	Maximum width of long axis of left condyle
24	Condyle L	Maximum width of short axis of left condyle
25	Occ Con W	Total width across both occipital condyles
26	InterOr W	Minimum interorbital width
27	Postorb W	Width at postorbital processes
28	Tem Fos W	Minimum cranial width at temporal fossa
29	Pari - Temp	Maximum breadth of brain case at parietotemporal suture
30	Zygom W	Maximum zygomatic width
31	M^1 to Orb	Minimum distance from alveolar margin of M^1 to orbit
32	Jugal H	Minimum height of jugal at right angles to axis of bone
33	SagC - AudB	Height of skull from auditory bulla to sagittal crest
34	Sym - AngPr	Maximum length from symphysis to angular process
35	Sym - Condy	Maximum length from symphysis to condyle
36	C_1 to M_3	Maximum crown length of tooth row from anterior of C to M_3
37	W of P_4	Buccolingual width of P_4
38	L of P_4	Anterior-posterior length of P_4
39	W of M_1	Buccolingual width of M_1
40	L of M_1	Anterior-posterior length of M_1
41	Mandib W	Width of mandible at P_4
42	Art Con W	Maximum width of long axis of articular condyle
43	Art Con L	Maximum width of short axis of articular condyle
44	H of Ramus	Maximum height of ramus between P_4 and M_1
45	AngP - CorP	Distance from angular process to top of coronoid process

present for each parameter. For each *t*-test, Levene's test (Norusis, 1988a) was performed to identify unequal variances. A one-way Analysis of Variance (ANOVA) was used to determine significant differences among mean factor scores for wolf populations on each principal component.

Considering the high level of variability within wolf populations and the extensive overlap of univariate parameters, a multivariate approach was invaluable for exploring differences among groups and considering group relatedness. Relationships of populations may be more accurately interpreted when characters are considered as an integrated whole, which in life they are, than when each is considered separately (Skeel and Carbyn, 1977).

The technique of principal component analysis (PCA) was first described by Pearson (1901). The initial step in multivariate analysis involves measuring inter-correlations among the original variables and creating new axes from combinations of variables by finding the eigenvalues of the sample covariance matrix (Manly, 1986). The four steps in this analysis include computation of a correlation matrix, factor extraction, rotation, and computation of factor scores. The basic assumption of PCA analysis is that underlying dimensions or factors which are not directly obvious, can be identified and used to explain a large or complex set of variables (Norusis, 1988b). These components are ordered so that the first component displays the largest amount of variation and subsequent components reflect decreasing levels of variation until all of the variation is represented (Ludwig and Reynolds, 1988). The first component is generally viewed as representing overall size, which is verified when characters are positively correlated with this component (Manly 1986; Somers, 1986). Subsequent components are believed to reflect differences in shape, although there has been some discussion on whether or not subsequent components are truly free of the influence of size (Bookstein, 1989; Somers, 1989; Sundberg, 1989). Attention is generally focused on the first few components with higher eigenvalues (≥ 1.0), which contribute to 5.0 % or more of the variance. In order to ensure that variables have equal weight in the analysis, the data are standardized to have a mean of zero and unit standard deviations by transforming with either Z scores or natural logarithms. Unlike other multivariate tests, PCA requires no prior assumptions about the data. The use of PCA has been employed by numerous researchers to study cranial morphology and cranial subspeciation in *C. lupus* (Jolicoeur 1959, 1975; Kolenosky and Standfield, 1975; Skeel and Carbyn, 1977; Pedersen, 1978; Nowak, 1983; Pichette and Voigt, 1985; Schmitz and Kolenosky, 1985; Friis, 1985; Nowak, 1995).

Using a set of variables for cases where group membership is known, discriminant analysis seeks to identify the variables that are important for distinguishing among groups. Introduced by Sir Ronald Fisher, discriminant analysis employs linear combinations of predictor variables to predict group membership for new cases (Norusis, 1988b). Considering the high level of variability within many species and the extensive overlap of univariate parameters among populations, this multivariate approach is invaluable for exploring differences among populations and assessing taxonomic and genetic relatedness. Discriminant analysis has been employed by numerous researchers to study cranial morphology and subspeciation in *C. lupus* (Jolicoeur 1959, 1975; Kolenosky and Standfield, 1975; Skeel and Carbyn, 1977; Pedersen, 1978; Nowak, 1983; Friis, 1985; Pichette and Voigt, 1985; Schmitz and Kolenosky, 1985; Nowak, 1995).

Discriminant analysis requires that a number of assumptions be met (Krzanowski, 1977; Neff and Marcus, 1980; Williams, 1983). Essentially, multivariate normality and homogeneity of variance - covariance matrices are required in order to draw statistical conclusions. Although data can be analysed for normality on a univariate basis, SPSS-PC does not provide a test for multivariate normality. The test for homogeneity of variance (Box's M) assumes multivariate normality. Violation of either of these assumptions may result in inaccurate group assignments. High classification rates and clear group separation can, however, offer a measure of confidence. There is a suggestion that violations of these assumptions may not be critical (Manly, 1986), particularly if the analysis is exploratory in nature.

If possible, multivariate analysis should be validated by comparing two random subsamples from the same population or by deriving a discriminant function on one sample and using it to classify another sample. There were an insufficient number of specimens to use this approach. Male and female specimens were analysed and compared separately. Although these two groups do not constitute a legitimately split sample, each sex should reveal similar patterns of variation when multivariate analysis is applied. Since some of the skulls and mandibles were slightly damaged, the complete set of measurements could not be taken. Multivariate analysis, however, requires complete cases. Rather than substitute with group means or utilize regressions for the multivariate analysis, it was decided to exclude all cases with missing data.

Principal component analysis and discriminant analysis were conducted using SPSS-PC sub-programs (FACTOR) and (DISCRIMINANT). These methods and their applications have been explained by Sokal and Sneath (1963), Seal (1964), Morrison (1967), Sokal and Rohlf (1969), Child (1970), Blackith and Reyment (1971), Zar (1974), Krzanowski (1977), Neff and Marcus (1980), Williams (1983), Romesburg (1984), and Manly (1986).

Ambient Temperature

In order to examine the relationship between the variation in cranial size and geographic variation in ambient air temperatures, isotherms reflecting mean annual air temperature (°C), mean July air temperature (°C), and mean February air temperature (°C) were utilized (Anonymous, 1979). Mean annual ambient air temperatures were considered to be the primary and broadest measure of this environmental parameter. The total skull length (I^1-SagC) and width (Zygom W) were used as a measure of cranium size. As well, length of the rostrum (Palat L) was used in order to evaluate Allen's Rule. These relationships were examined using regression analysis.

Ungulate Prey Weight

In order to consider the relationship between variation in wolf cranial size and ungulate prey size, a number of whole body weights for northern ungulates were extracted from the literature. Except for Baffin Island and the northern Keewatin, where only *R.t. groenlandicus* is available, most wolf populations have access to two or more large ungulate species. A synopsis of the largest ungulate prey species available to wolves across northern Canada was described earlier in the Introduction. In order to arrive at a representative ungulate prey size for each geographic location, a mean pooled weight was derived by taking the mean value of the largest male and female ungulate species as well as the second largest male and female ungulate species. Considering the limited available data on wolf hunting strategies, such as the specific prey cohorts actually being targeted, a pooling of these four weights provided an estimate of the mean ungulate prey size, which wolves typically encounter in the various geographic locations. Two cranial parameters, total skull length (I^1-SagC) and skull width (Zygom W) were used to represent cranial size. A third parameter, Palat L was also used as a comparison to the temperature analysis. These relationships were examined using regression analysis.

Since ungulate prey weight may also be influenced by ambient temperature, and would consequently have a bearing on the above analysis, regression analysis was also used to assess the relationship between mean pooled ungulate weight and mean annual temperature.

RESULTS

Principal Component Analysis of Cranial Parameters

All 45 cranial parameters (Table 3) were processed for PCA. A summary of the derived dimensions or components is outlined in Table 4, followed by a brief description of the more significant parameters influencing each component. A detailed breakdown of eigenvalues and factor loadings for all components is summarized in Table 5 (males) and Table 6 (females). Six components accounted for 73.3% of the cumulated variance for males (Table 5), while 7 components accounted for 73.0% of the cumulated variance for females (Table 6). The first principal component accounted for 48.2% of the total variance in males and 46.9% in females; the second for 11.5% and 9.5%; the third for 4.8% and 4.3%, respectively. The first principal component had an eigenvalue of 21.7 for males and 21.1 for females. The second component had an eigenvalue of 5.2 for males and 4.2 for females. Transformation of the data with either Z scores or natural logarithms had no affect on the outcome of the analysis.

Table 4. Description of parameter associations found on principal components for male and female wolves.

Component	Male	Female
I	length & height	length & height
II	tooth size	tooth size
III	rostrum width	rostrum width
IV	condyle size	brain case & orbital width
V	brain case & orbital width	condyle size
VI	unspecified	tooth width
VII	(no component)	auditory bulla width

Table 5. Component loadings of 45 cranial measurements with the first 6 principal components for 304 adult male wolves. All 45 parameters were processed; variables with scores > 0.7 are highlighted in bold and enclosed in boxes. Standardized data (Z scores) provided identical results to the untreated data.

	Component					
Measurement	I	II	III	IV	V	VI
I^1-Sag C	***0.90148***	0.14644	0.18259	0.19863	0.16542	0.07149
Condy L	***0.89135***	0.16453	0.18373	0.27728	0.16160	0.04026
Sym-Condy	***0.87962***	0.17745	0.21488	0.24367	0.20593	0.00638
I^1-Palat	***0.87630***	0.15366	0.10449	0.19865	0.10667	0.14273
I^2-Palat	***0.87616***	0.13718	0.09636	0.19778	0.11890	0.13076
Sym-AngPr	***0.86263***	0.18640	0.25643	0.21841	0.18834	-0.02271
C^1-M^2	***0.84325***	0.32591	0.06307	0.16198	0.16967	-0.03609
Nasal L	***0.80376***	0.10572	0.19025	0.11538	0.06166	0.09937
C_1-M_3	***0.78510***	0.30437	0.06050	0.09230	0.20877	-0.04033
PosPal L	***0.76540***	0.14352	0.21714	0.23366	0.14690	-0.05230
M^1 to Orb	***0.72404***	0.19769	0.42953	0.05031	0.12982	-0.02241
H of Ramus	0.65799	0.10473	0.40712	0.14914	0.10226	-0.05251
AngP-CorP	0.65525	0.18109	0.43825	0.26489	0.12622	-0.00143
Occ Cre W	0.58177	0.14469	0.29896	0.42949	0.28288	-0.15078
Art Con L	0.55641	0.09437	0.46522	0.28003	0.13549	-0.07221
Zygom W	0.54748	0.05040	0.53752	0.24830	0.37547	-0.11988
Jugal H	0.54563	0.09218	0.47798	0.18700	0.23948	0.07299
SagC-AudB	0.54224	0.03512	0.39683	0.22421	0.24708	-0.25476
W of M_1	0.16638	***0.84589***	0.06413	0.17956	-0.04715	0.07734
L of M_1	0.16709	***0.81259***	0.24493	0.08812	0.01575	-0.15415
W of P_4	-0.05585	***0.79717***	-0.02862	0.20339	0.03891	0.06304
L of M^1	0.17235	***0.79130***	0.07119	0.05043	-0.05575	0.05672
L of P_4	-0.00705	***0.78500***	0.18696	0.06997	-0.04883	-0.26647
W of P^4	0.11985	***0.75753***	-0.03557	0.13335	0.08665	0.21265
L of P^4	0.32549	***0.75616***	0.24197	0.02253	-0.00726	-0.12263
W of M^1	0.16695	***0.75142***	0.24803	0.04715	0.16672	0.02130
W of C^1	0.18799	***0.73801***	0.09929	0.18009	0.05775	-0.11644
W of M^2	0.14488	0.62469	0.24371	0.01403	0.13443	0.10866
I^3 to I^3	0.28236	0.56555	0.17707	-0.00908	0.07500	0.32344
P^2 to P^2	0.19826	0.30739	***0.77717***	0.11017	0.06969	-0.00930
P^1 to P^1	0.26776	0.27610	***0.76440***	0.10185	0.09864	0.20275
Cheek T W	0.45660	0.31752	0.55944	0.26363	0.23548	-0.16348
C^1 to C^1	0.52899	0.34997	0.55821	0.18471	0.26745	0.07178
Mandib W	0.36311	0.40300	0.55128	0.08634	0.13803	-0.04121
M^1 to M^1	0.34131	0.36876	0.50801	0.19801	0.32854	-0.21797
Occ Con W	0.45934	0.22750	0.08464	0.69340	0.09906	-0.03553
Condyle L	0.42362	0.21507	0.19500	0.65113	0.08956	0.11122
Aud Bul W	0.31766	0.18622	0.08958	0.61377	0.16123	-0.08703
Condyle W	0.34324	0.15278	0.19713	0.57120	0.13013	0.38841
Pos For W	0.32852	0.23177	0.33665	0.52941	0.26096	-0.35799
Art Con W	0.40662	0.14402	0.32991	0.45901	-0.00768	0.19755
Tem Fos W	0.19258	0.08206	0.08887	0.01774	***0.83780***	0.13935
InterOr W	0.39525	0.03697	0.26061	0.16153	***0.72465***	-0.12409
Postorb W	0.29689	-0.08283	0.30859	0.16095	***0.70045***	-0.17154
Pari-Temp W	0.20497	0.11415	-0.00938	0.22195	0.52947	0.40826
Eigenvalue	21.71	5.16	2.17	1.56	1.34	1.03
% Variance	48.2	11.5	4.8	3.5	3.0	2.3
Cum. %	48.2	59.7	64.5	68.0	71.0	73.3

Table 6. Component loadings of 45 cranial measurements with the first 7 principal components for 230 adult female wolves. All 45 parameters were processed; variables with scores > 0.7 are highlighted in bold and enclosed in boxes. Standardized data (Z scores) provided identical results to the untreated data.

	Component						
Measurement	I	II	III	IV	V	VI	VII
Sym-Condy	***0.90632***	0.10939	0.17521	0.14732	0.14487	0.10844	0.12567
Sym-AngPr	***0.89624***	0.12727	0.18126	0.14993	0.13570	0.13462	0.10892
Condy L	***0.88929***	0.11552	0.17439	0.13146	0.27541	0.06770	0.18200
I^2-Palat	***0.87977***	0.14913	0.09524	0.11415	0.24799	0.08762	0.04695
I^1-Sag C	***0.87951***	0.13816	0.17981	0.14669	0.17765	0.08490	0.21881
I^1-Palat	***0.87926***	0.15909	0.10273	0.11026	0.25659	0.09346	0.04574
C_1-M_3	***0.81572***	0.33568	0.07310	0.14950	0.10138	0.16492	0.09372
PosPal L	***0.80922***	0.04234	0.23640	0.13887	0.13754	-0.00668	0.23556
C^1-M^2	***0.80318***	0.28441	0.09185	0.16685	0.13881	0.10782	0.22082
Nasal L	***0.80157***	0.00707	0.18062	0.08717	0.10518	0.16568	0.11561
AngP-CorP	***0.77294***	0.06298	0.28092	0.10075	0.03780	0.10287	0.12160
H of Ramus	***0.76439***	0.04816	0.31062	0.23789	0.07155	0.15717	0.00446
M^1 to Orb	***0.73326***	0.23610	0.39800	0.09845	0.11302	-0.02508	0.07419
Zygom W	0.60249	0.15927	0.42035	0.28782	0.03472	-0.04492	0.36768
Occ Cre W	0.57549	0.05388	0.26825	0.18637	0.28919	-0.01851	0.45588
Jugal H	0.56245	0.13133	0.37372	0.04499	0.21440	0.01057	0.06010
SagC-AudB	0.54957	0.08868	0.35607	0.25579	0.06541	0.11156	0.26357
Art Con L	0.48723	0.12461	0.25068	0.17799	0.10735	0.09803	0.33750
Art Con W	0.48386	-0.01546	0.12527	0.08862	0.24877	0.10347	0.11732
Mandib W	0.44794	0.35144	0.41098	0.13186	0.14120	0.12619	-0.03627
L of M_1	0.18502	***0.82999***	0.23614	0.01937	0.07089	0.25086	0.01918
L of M^1	0.14793	***0.82105***	-0.10417	0.10764	0.03505	-0.00885	0.01954
L of P^4	0.09810	***0.77217***	0.30053	-0.01388	0.08114	0.23463	0.13152
L of P_4	-0.00829	***0.73963***	0.14434	0.11507	0.00563	0.25464	0.11697
W of M^2	0.39538	0.51005	0.14136	0.18904	0.06906	0.04105	0.03974
W of C^1	0.09438	0.45056	0.32270	-0.00295	0.07827	0.33174	0.20344
P^2 to P^2	0.25795	0.14610	***0.81592***	0.13768	0.03091	0.09370	0.22982
P^1 to P^1	0.41979	0.13576	***0.77282***	0.19058	0.04230	-0.02828	0.11239
C^1 to C^1	0.39722	0.21889	0.57672	0.07469	0.17019	0.12568	0.00482
M^1 to M^1	0.37286	0.25440	0.55807	0.27641	0.07520	0.31528	0.29698
Cheek T W	0.52193	0.24360	0.54373	0.12856	0.15123	0.23519	0.22183
I^3 to I^3	0.17715	0.35362	0.44224	0.19200	0.24459	0.39590	-0.03107
Tem Fos W	0.21919	0.01926	0.11091	***0.79790***	0.08205	0.17325	-0.09598
InterOr W	0.40971	0.21876	0.16976	0.67164	-0.05713	0.04335	0.19908
Pari-Temp W	0.08670	0.00111	0.11145	0.65972	0.33791	0.07857	0.03176
Postorb W	0.34855	0.25346	0.19090	0.59776	-0.05734	-0.16540	0.11217
Condyle W	0.34745	0.05677	0.02266	0.18513	***0.74342***	0.06047	0.10795
Occ Con W	0.35904	0.21117	0.13933	0.07185	0.69410	-0.00116	0.29807
Condyle L	0.43531	0.06538	0.16163	0.03635	0.68176	-0.04504	0.17814
W of P_4	0.02756	0.29476	0.09740	0.01253	-0.09646	***0.78093***	0.05308
W of P^4	0.29299	0.25589	0.03988	0.11637	-0.00403	0.69742	0.02401
W of M_1	0.21422	0.54381	0.16105	0.05274	0.18997	0.60805	-0.10265
Pos For W	0.37562	0.11520	0.19941	0.07775	0.11651	0.04437	***0.77608***
Aud Bul W	0.27116	0.06677	0.11147	-0.04608	0.31997	-0.00735	***0.71113***
Eigenvalue	21.10	4.21	1.92	1.78	1.52	1.20	1.12
% Variance	46.9	9.3	4.3	3.9	3.4	2.7	2.2
Cum. %	46.9	56.2	60.2	64.5	67.8	70.5	73.0

Component I Skull length and height represented by I^1- SagC, Condy L, Sym - Condy, I^1 - Palat, I^2 - Palat, Sym - AngPr, C^1 - M^2, Nasal L, C_1 - M_3, PosPal L, and M^1 - Orb recorded high (absolute value of ≥ 0.7) loadings for both males and females on this component. While H of Ramus and AngP-AudB recorded > 0.7 for females, these variables were considered minor (absolute value of loadings between 0.50 and .69) for males. Occ Cre W, Zygom W, Jugal H, and SagC- AudB had minor positions for both males and females on Component I.

Component II Tooth size represented by L of M_1, L of M^1, L of P^4, and L of P_4 recorded high loadings for both males and females. W of M_1, W of P_4, W of P_4, W of M^1, and W of C^1 recorded high loadings for males, but were not represented by females on Component II. W of M^2 recorded a minor loading for both males and females. I^3 to I^3 had a minor loading for males on Component II.

Component III Rostrum width represented by P^2 to P^2 and P^1 to P^1 recorded high loadings for both males and females. C^1 to C^1, M^1 to M^1, and Cheek T W recorded minor loadings for both males and females. I^3 to I^3 had a minor loading for females on Component III.

Component IV For males, condyle size represented by Occ Con W, Condyle L, Aud Bul W, Condyle W, and Pos For W, recorded minor loadings for males on Component IV. For females, brain case and orbital width represented by Tem Fos W recorded highly on this component, while InterOr W, Pari-Temp W, and Postorb W recorded minor loadings.

Component V For males, orbital width represented by Temp Fos W, InterOr W, and Postorb W recorded highly on this component, while Pari-Temp W recorded a minor loading. For females, condyle size represented by Condyle W recorded highly on this component, while Occ Con W and Condyle L recorded minor loadings.

Component VI For males, no specific parameters had high loadings on this component. Twenty-four of the 45 parameters involved negative loadings in contrast to the predominantly positive loadings on the first 5 components. For females, tooth size represented by W of P_4 recorded a higher loading on this component, while W of P^4 and W of M_1 recorded minor loadings.

Component VII For females, auditory bulla width represented by Pos For W and Aud Bul W were the only two variables on this component, and both recorded higher loadings.

Factor analysis was used to reduce the large number of variables into a smaller number of new factor scores. Mean factor scores were determined for each geographic location for male (Table 7) and female (Table 8) wolves. Mean values for each cranial measurement are included on these tables. For each component, higher positive and negative factor scores were able to distinguish some wolf populations.

Factor Scores for Component I Given the importance of overall size for this component, male and female wolves from central Saskatchewan and northern Alberta had high positive loadings, while wolves from Baffin Island and the Banks / Victoria Island sample had a high negative loading.

Factor Scores for Component II The importance of tooth size for this component reflected relatively high positive loadings for male and female wolves from Banks /Victoria Island and the Queen Elizabeth Islands. Female wolves from Great Slave Lake had a high positive loading in contrast to males for this location which had a high negative loading.

Factor Scores for Component III Rostrum width reflected high positive loadings for males from northern Alberta, Banks /Victoria Island, and the Queen Elizabeth Islands, and for females from the Queen Elizabeth Islands and central Saskatchewan. Males from the northern Keewatin and Baffin Island, and females from the northern Keewatin and the Mackenzie had higher negative loadings.

Factor Scores for Component IV For males, condyle size reflected modestly positive loadings for males in the central Keewatin, while Baffin Island, Great Slave Lake, and Mackenzie males had modestly negative loadings. For females, Tem Fos W and similar measures of orbital width had a high positive loading for Baffin Island females, but a negative loading for the Queen Elizabeth Islands.

Table 7. Means of factor scores and cranial measurements (mm) for male wolves from 10 geographic locations from across northern Canada. Sample sizes identified in brackets.

	Queen Eliz. (21)	Baffin (15)	Victoria (11)	Mackenzie (41)	G. Slave (43)	N. Keew. (31)	C. Keew. (50)	S. Keew. (36)	C. Sask. (15)	N. Alberta (34)
Factor Scores										
Component I	-0.7441	-1.0154	-1.0945	-0.3839	-0.3815	-0.2628	-0.2554	0.4156	1.2778	1.2286
Component II	0.5366	-0.1834	0.8384	-0.1100	-0.7838	0.0900	-0.1204	0.2246	0.2210	-0.3088
Component III	0.6667	-0.6045	0.7361	-0.1016	0.2856	-0.6106	-0.2807	-0.2222	0.1819	0.8713
Component IV	-0.2749	-0.6706	0.0131	-0.4079	-0.4497	0.1541	0.4251	-0.3101	0.2667	0.2897
Component V	-0.5245	0.1175	-0.3266	0.3279	-0.4446	-0.0448	-0.0239	-0.2264	-0.0067	0.4710
Component VI	-1.2507	0.5275	-1.3560	0.3698	-0.1353	0.2602	0.0077	-0.1735	0.2368	0.3654
Variable										
Condy L	236.7	231.1	233.0	238.4	239.6	238.2	239.4	243.8	256.1	255.6
I^1- Sag C	256.4	252.7	252.1	259.2	261.9	259.8	259.2	265.8	275.3	278.0
Nasal L	95.7	94.3	96.3	96.4	98.3	95.7	95.4	100.1	102.7	105.3
I^1- Palat	116.1	115.5	115.4	119.2	120.2	119.5	119.6	122.7	127.6	126.5
I^2- Palat	113.9	112.7	113.1	116.7	117.9	117.2	117.3	120.2	125.1	124.0
Pos Pal L	101.1	96.5	98.5	100.5	100.9	99.3	100.7	102.4	108.5	107.9
C^1- M^2	108.1	105.0	105.8	108.0	109.2	109.6	109.1	111.0	114.5	114.1
W of C^1	15.9	14.4	15.9	14.8	14.8	15.1	14.9	15.3	15.7	15.3
W of P^4	10.9	11.0	11.1	10.9	10.9	11.1	11.0	11.1	10.8	11.0
L of P^4	27.1	25.7	27.2	26.4	26.2	26.1	26.0	26.8	27.1	26.8
W of M^1	20.9	20.4	21.8	20.9	20.7	20.6	20.7	21.0	21.5	21.5
L of M^1	16.9	16.1	16.9	16.6	16.6	16.7	16.8	17.0	17.2	16.7
W of M^2	13.7	13.1	14.3	13.6	13.5	13.9	13.6	13.5	14.2	14.2
I^3 to I^3	38.2	38.0	37.4	38.2	37.4	37.6	37.3	38.5	39.0	38.3
P^1 to P^1	32.7	30.7	31.8	31.9	32.0	31.4	31.7	32.1	33.4	33.7
P^2 to P^2	36.9	34.0	36.8	35.6	35.4	35.1	35.5	36.0	36.5	37.3
C^1 to C^1	48.4	46.8	47.7	48.1	48.4	47.9	47.8	49.4	51.7	51.7
M^1 to M^1	81.7	79.3	83.5	82.0	81.3	80.6	81.4	82.5	81.8	84.8
Cheek T W	82.8	77.9	84.6	80.7	80.9	80.7	81.3	82.4	85.0	86.1
Pos For W	66.2	62.5	65.6	64.4	64.7	64.6	65.3	65.3	66.0	67.0
Aud Bul W	18.6	17.5	19.3	19.0	19.3	19.4	19.3	18.8	21.1	21.1
Occ Cre W	80.8	79.6	83.0	82.0	82.1	80.6	82.4	83.3	85.6	86.2
Condyle W	11.9	12.4	11.9	12.2	12.1	12.2	12.4	12.3	13.1	13.6
Condyle L	25.3	24.8	24.8	25.8	25.8	25.7	26.4	26.4	28.0	27.4
Occ Con W	50.1	49.0	50.4	50.0	50.5	50.3	50.8	50.8	53.7	52.4
InterOr W	46.3	44.9	45.2	47.1	47.1	46.3	47.3	47.7	48.2	50.1
Postorb W	63.9	60.9	63.7	63.4	64.2	63.9	63.2	64.0	66.3	68.9
Tem Fos W	40.0	41.5	40.8	42.3	42.2	41.5	41.3	41.8	43.0	43.9
Pari-Temp W	64.8	67.9	65.8	67.3	67.0	67.6	67.2	66.5	67.4	68.9
Zygom W	142.4	136.4	140.2	141.1	140.9	138.0	141.1	142.6	146.2	150.5
M^1 to Orb	41.8	40.4	42.5	41.5	42.4	41.1	41.9	43.4	46.3	46.8
Jugal H	19.0	18.9	19.5	18.9	19.3	18.6	19.1	19.4	20.4	21.8
SagC-AudB	86.6	83.2	85.6	84.7	85.4	83.1	84.5	86.2	89.2	90.1
Sym-AngPr	189.2	184.3	189.6	190.7	190.6	191.0	191.5	195.5	203.0	204.0
Sym-Condy	186.0	181.8	186.1	188.6	187.5	188.7	189.5	192.8	203.8	202.7
C_1 - M_3	119.7	118.0	119.6	122.0	121.8	122.7	122.6	124.7	128.1	127.3
W of P_4	8.3	8.1	8.9	8.2	8.2	8.5	8.4	8.4	8.4	8.1
L of P_4	17.5	16.2	17.7	16.2	16.1	16.5	16.4	16.5	16.6	16.3
W of M_1	12.1	11.8	12.1	11.7	11.8	12.0	11.9	12.1	12.2	11.9
L of M_1	30.4	28.5	31.1	29.4	29.3	29.5	29.6	29.9	29.8	30.0
Mandib W	14.3	14.2	14.3	14.0	14.6	14.0	13.9	14.3	14.9	15.4
Art Con W	12.3	11.3	11.8	12.0	12.3	12.7	12.4	12.5	13.2	13.7
Art Con L	33.2	31.0	32.5	32.7	32.7	32.8	32.6	33.9	35.0	35.1
H of Ramus	31.3	31.0	30.4	30.5	31.6	31.0	30.8	32.4	33.8	34.4
AngP - CorP	76.9	73.0	77.0	78.5	78.0	76.9	77.7	80.2	81.9	84.6

Table 8. Means of factor scores and cranial measurements (mm) for female wolves from 10 geographic locations from across northern Canada. Sample sizes identified in brackets

	Queen Eliz. (8)	Baffin (8)	Victoria (5)	Mackenzie (26)	G. Slave (36)	N. Keew. (21)	C. Keew. (60)	S. Keew. (28)	C. Sask. (6)	N. Alberta (30)
Factor Scores										
Component I	-0.3247	-0.8418	-0.4691	0.0933	0.0768	-0.6238	-0.5308	-0.2535	0.8538	1.4192
Component II	0.6125	-0.6102	1.0264	0.1651	0.7593	0.1678	-0.0854	-0.1779	-0.1033	-0.0123
Component III	1.1404	0.2176	0.6993	-0.3813	0.6982	-0.4799	-0.1631	-0.1159	0.8883	0.2366
Component IV	-1.2720	1.2087	0.0546	0.1397	0.1731	0.5007	-0.1338	-0.1449	-0.3951	0.0302
Component V	-1.4637	0.5227	-1.5602	-0.0817	0.6887	0.0135	-0.0241	-0.2995	0.7845	0.2703
Component VI	0.6609	1.0877	-0.4313	-0.0261	1.1471	0.2196	-0.0277	-0.1515	-0.8621	-0.1211
Component VII	1.5074	-1.1575	-0.1706	-0.1755	0.1524	-0.1695	0.2477	-0.3585	-0.7523	0.2050
Variable										
Condy L	228.1	222.6	226.0	230.0	229.1	226.2	226.8	227.5	240.3	243.7
I^1- Sag C	246.8	240.3	243.0	247.8	249.0	244.0	245.4	245.7	258.0	263.6
Nasal L	89.7	89.4	91.4	90.5	92.0	88.5	89.6	90.4	95.3	99.6
I^1- Palat	113.3	111.7	112.2	116.2	116.0	112.9	113.8	114.5	120.6	121.4
I^2- Palat	111.0	109.5	109.2	113.6	113.6	110.5	111.5	112.1	118.2	118.9
Pos Pal L	97.7	93.3	95.4	96.7	95.9	94.5	95.1	95.6	101.6	103.3
C^1- M^2	105.0	100.6	103.4	105.2	104.9	104.0	104.4	103.5	108.2	109.6
W of C^1	14.6	13.6	14.3	13.9	13.8	14.0	13.9	13.6	14.1	13.9
W of P^4	10.3	10.7	10.4	10.4	10.4	10.5	10.4	10.3	9.9	10.7
L of P^4	25.8	24.8	25.6	25.0	25.0	24.8	25.0	24.7	25.2	25.2
W of M^1	19.9	19.6	20.2	19.8	20.1	20.0	19.8	19.5	20.0	20.3
L of M^1	16.3	15.8	16.3	16.1	16.2	16.3	16.3	16.0	16.1	16.4
W of M^2	13.4	12.6	13.5	13.2	13.2	13.4	13.0	12.7	13.4	13.6
I^3 to I^3	36.4	36.4	35.0	35.8	35.5	35.7	35.8	35.2	36.7	36.5
P^1 to P^1	31.8	29.2	31.0	30.3	30.7	29.8	29.9	30.4	32.2	32.2
P^2 to P^2	35.2	33.1	35.3	33.6	34.0	33.6	33.7	33.7	35.4	35.2
C^1 to C^1	46.0	44.2	45.7	45.7	45.5	45.2	44.9	45.4	48.0	47.3
M^1 to M^1	79.0	78.4	80.7	76.5	77.8	76.6	77.4	76.9	79.1	80.0
Cheek T W	79.4	76.4	81.5	76.2	77.1	76.6	77.5	76.8	81.3	81.3
Pos For W	64.2	59.2	63.4	62.4	62.8	62.0	62.7	62.6	62.6	65.0
Aud Bul W	19.2	16.5	18.1	18.0	17.9	18.1	18.6	18.1	19.1	19.9
Occ Cre W	79.3	76.9	79.2	77.9	79.3	77.8	78.4	78.1	80.5	82.5
Condyle W	11.3	11.7	10.8	11.3	11.3	11.6	11.4	11.4	12.3	12.3
Condyle L	23.9	24.0	24.0	24.5	24.5	24.3	24.6	24.6	26.1	25.9
Occ Con W	47.0	46.6	46.6	47.7	47.9	48.0	47.9	47.6	49.7	49.9
InterOr W	44.3	43.6	46.0	44.9	44.7	44.1	43.9	44.7	45.6	46.4
Postorb W	61.5	61.8	64.7	61.2	59.8	59.5	59.5	60.4	61.9	63.7
Tem Fos W	39.0	42.9	40.9	41.4	40.0	41.2	39.9	40.7	41.5	42.3
Pari-Temp W	63.6	67.1	64.0	66.0	65.5	66.7	66.1	65.9	65.5	66.9
Zygom W	136.6	130.0	138.0	134.0	134.2	130.2	133.0	133.7	137.9	140.3
M^1 to Orb	40.8	37.4	41.4	40.2	39.5	38.0	38.9	39.6	42.6	43.7
Jugal H	18.7	18.4	18.8	18.3	18.1	17.3	17.7	18.0	19.1	20.0
SagC-AudB	85.2	82.3	82.8	81.4	81.7	80.0	80.5	81.0	82.5	85.1
Sym-AngPr	183.8	177.8	182.1	184.1	184.9	179.2	181.0	181.7	190.9	195.4
Sym-Condy	180.4	175.4	180.0	181.3	183.4	177.3	178.4	179.3	190.0	193.5
C_1 - M_3	118.0	113.2	116.7	118.9	119.4	116.2	116.4	116.8	121.1	122.6
W of P_4	8.1	7.8	8.3	7.8	7.8	8.0	7.9	7.8	7.7	7.9
L of P_4	16.8	15.5	16.7	15.5	15.6	16.0	15.6	15.4	15.5	15.6
W of M_1	11.3	11.2	11.4	11.0	11.2	11.2	11.1	11.2	11.4	11.3
L of M_1	28.9	27.9	29.4	27.9	28.3	28.3	28.2	28.0	28.3	28.7
Mandib W	13.6	13.0	13.9	13.7	13.6	13.0	12.9	13.4	13.9	14.3
Art Con W	12.0	11.2	10.9	11.1	11.7	11.6	11.4	11.6	11.8	12.6
Art Con L	31.2	29.8	31.8	31.0	31.4	30.0	30.7	31.4	31.2	32.4
H of Ramus	30.5	28.8	29.3	29.5	29.6	28.5	28.6	29.0	32.0	32.0
AngP - CorP	72.0	70.0	71.6	73.8	72.9	71.7	72.3	72.3	76.1	80.3

Factor Scores for Component V For males, Pari-Temp W and measures of orbital width reflected modestly positive loadings for northern Alberta and Mackenzie males, and moderately negative loadings for Queen Elizabeth Island, Great Slave Lake, and Banks / Victoria Island males. For females, condyle size reflected modestly positive loadings for females from central Saskatchewan and Great Slave Lake, and strong negative loadings for females from Banks / Victoria Island and the Queen Elizabeth Islands.

Factor Scores for Component VI For males, no specific parameter appeared to dominate this component, but in sum this component had a strong negative loading for males from Banks / Victoria Is. and Queen Elizabeth Islands. For females, premolar width (W of P^4 and W of P_4) contributed positive loadings for Great Slave Lake and Baffin Island females, and negative loadings for females from central Saskatchewan.

Factor Scores for Component VII For females, width of the auditory bulla region contributed strong positive loadings for Queen Elizabeth Island females, and negative loadings for females from Baffin Island and central Saskatchewan.

Mean regression factor scores ± 2 standard deviations were compiled for each principal component, by location and sex (Table 9). Analysis of Variance was employed on the factor scores in order to assess between group variance of the principal components and summarized as F-ratio, F-probability, and Eta^2 values. As indicated in Table 9, factor scores for PC I contributed a large portion of the variance as indicated by the F- ratio values for males (19.99) and females (22.05). The second PC was a component dealing with tooth measurements, and the relatively lower F-ratio values for males (2.48) and females (1.15) may be attributed, in part, to the higher levels of measurement error associated with the dental parameters (Appendix 4). The F-probability values for the remaining components indicated that their mean factor scores were representing significant differences in the cranial dimensions for wolves from the 10 geographic locations.

Table 9. Mean factor scores ± 2. S.D. for each principal component, by sampling location and by sex. F-ratio, F-probability, and Eta^2 values derived by ANOVA. Visual representation of mean factor scores ± 2 S.D. presented in Appendix 7.

MALES

		(PC I)		(PC II)		(PC III)		(PC IV)		(PC V)		(PC VI)	
	Location	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.
1	Queen Eliz. Is.	-0.744	1.262	0.537	1.530	0.667	1.804	-0.275	1.717	-0.524	1.459	-1.251	1.864
2	Banks / Victoria	-1.094	0.798	0.838	1.245	0.736	1.061	0.013	2.141	-0.327	2.578	-1.356	1.520
3	Baffin Island	-1.015	1.197	-0.183	2.173	-0.605	1.505	-0.671	1.584	0.117	1.369	0.528	1.949
4	Mackenzie	-0.384	1.380	-0.110	2.136	-0.102	1.958	-0.408	1.769	0.328	1.850	0.370	1.456
5	Great Slave Lake	-0.381	1.559	-0.784	1.718	0.286	1.545	-0.450	2.769	-0.445	2.278	-0.135	1.753
6	N. Keewatin	-0.263	1.216	0.096	1.619	-0.611	1.891	0.154	1.671	-0.045	2.108	0.260	1.568
7	C. Keewatin	-0.255	1.425	-0.120	1.239	-0.281	1.705	0.425	1.668	-0.024	1.588	0.008	1.681
8	S. Keewatin	0.416	1.286	0.225	1.462	-0.222	1.681	-0.310	2.192	-0.226	2.152	-0.173	1.765
9	C. Saskatchewan	1.278	1.645	0.221	1.362	0.182	1.203	0.267	1.630	-0.007	1.885	0.236	1.786
10	N. Alberta	1.229	2.111	-0.309	3.373	0.871	2.104	0.290	2.170	0.471	2.281	0.365	2.370
	F- Ratio	19.997		2.482		6.937		3.075		1.949		6.684	
	F- Prob.	< 0.000		0.0106		< 0.000		0.002		0.047		< 0.000	
	Eta ^{2}	0.484		0.104		0.246		0.126		0.084		0.239	

FEMALES

			(PC I)		(PC II)		(PC III)		(PC IV)		(PC V)		(PC VI)		(PC VII)	
	Location		Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.	Factor Score	2 S.D.
1	Queen Eliz. Is.	1	-0.325	0.306	0.612	1.112	1.140	1.975	-1.272	1.941	-1.463	1.292	0.661	2.693	1.507	1.331
2	Banks / Victoria	2	-0.469	2.537	1.026	1.231	0.699	1.425	0.055	1.242	-1.560	2.557	-0.431	0.630	-0.171	1.949
3	Baffin Island	3	-0.842	0.595	-0.610	2.759	0.218	1.248	1.209	2.692	0.523	2.104	1.088	2.764	-1.158	2.288
4	Mackenzie	4	0.093	1.532	0.165	1.641	-0.381	1.899	0.140	2.860	-0.082	1.623	-0.026	1.380	-0.175	2.280
5	Great Slave Lake	5	0.077	1.342	0.759	3.050	0.698	2.170	0.173	1.634	0.689	2.530	1.147	1.610	0.152	2.544
6	N. Keewatin	6	-0.624	1.351	0.168	1.984	-0.480	1.704	0.501	1.651	0.013	1.459	0.220	1.606	-0.169	1.721
7	C. Keewatin	7	-0.531	1.112	-0.085	1.873	-0.163	1.990	-0.134	1.844	0.024	1.707	-0.028	1.829	0.248	1.628
8	S. Keewatin	8	-0.254	1.541	-0.178	1.883	-0.116	1.489	-0.145	1.906	-0.299	2.005	-0.151	1.873	-0.358	1.895
9	C. Saskatchewan	9	0.854	2.061	-0.103	1.885	0.888	2.109	-0.395	1.175	0.785	1.605	0.862	2.470	-0.752	1.690
10	N. Alberta	10	1.419	1.140	-0.012	2.224	0.237	2.191	0.030	1.794	0.270	2.208	-0.121	2.189	0.205	2.068
	F- Ratio		22.050		1.152		2.447		2.154		3.123		2.293		3.128	
	F- Prob.		< 0.000		0.331		0.013		0.029		< 0.002		0.020		< 0.002	
	Eta ^{2}		0.595		0.071		0.140		0.126		0.172		0.133		0.173	

In order to determine whether the mean factor scores ± 2 S.D. could be used to distinguish the wolf populations, these values were plotted for each geographic location by sex (Appendix 7). The resultant plots illustrate the variation among the wolf populations for each component. In both sexes, the cline in size among these populations was apparent in PC I. In females, PC I appeared to completely separate the Queen Elizabeth Island and Baffin Island wolves from N. Alberta wolves (Appendix 7). Interpretation of these data should be done cautiously due to the small sample sizes involved in some instances.

Discriminant Analysis of Cranial Parameters

All 45 variables were included in the discriminant analysis of the cranial data. Standardized canonical discriminant function coefficients for males (Table 10) and females (Table 11) indicate the relative importance of each variable on each of the 9 discriminant functions. A summary of the eigenvalues and % variance for each discriminant function is listed at the bottom of each table. As indicated, the first, second, and third functions contributed 36.8%, 19.0%, and 11.1% of the variance for males, respectively (Table 10). For females, the first, second, and third functions contributed 49.8%, 13.2%, and 11.4% of the variance, respectively (Table 11). The relative importance of each variable to each function can be determined by considering their relative absolute distance from zero. For example, in males (Table 10), Sym-Condy (1.414), I^1-Palat (1.020), and Condy L (-0.619) contributed significantly to the first function, while I^1-SagC (-0.672), InterOr W (-0.663), and W of M_1 (-0.627) contributed most significantly to the second discriminant function. A breakdown of eigenvalues, % variation, canonical correlation coefficients, Wilk's Lambda values, Chi-squared values, degrees of freedom, and significance values, for each of the 9 discriminant functions is presented by sex in Appendix 8.

Plots of the relative positions of the 10 male (A) and female (B) groups representing the entire study area on the first two discriminant functions are shown in Figure 9. Males from the Queen Elizabeth Islands and Banks / Victoria Islands had some overlap with each other, but were separate from the remaining groups. Similarly, males from C. Saskatchewan and N. Alberta overlapped, but were separate from the remaining groups. Males from the N.W.T. mainland and Baffin Island showed varying degrees of overlap. Female groups (B)

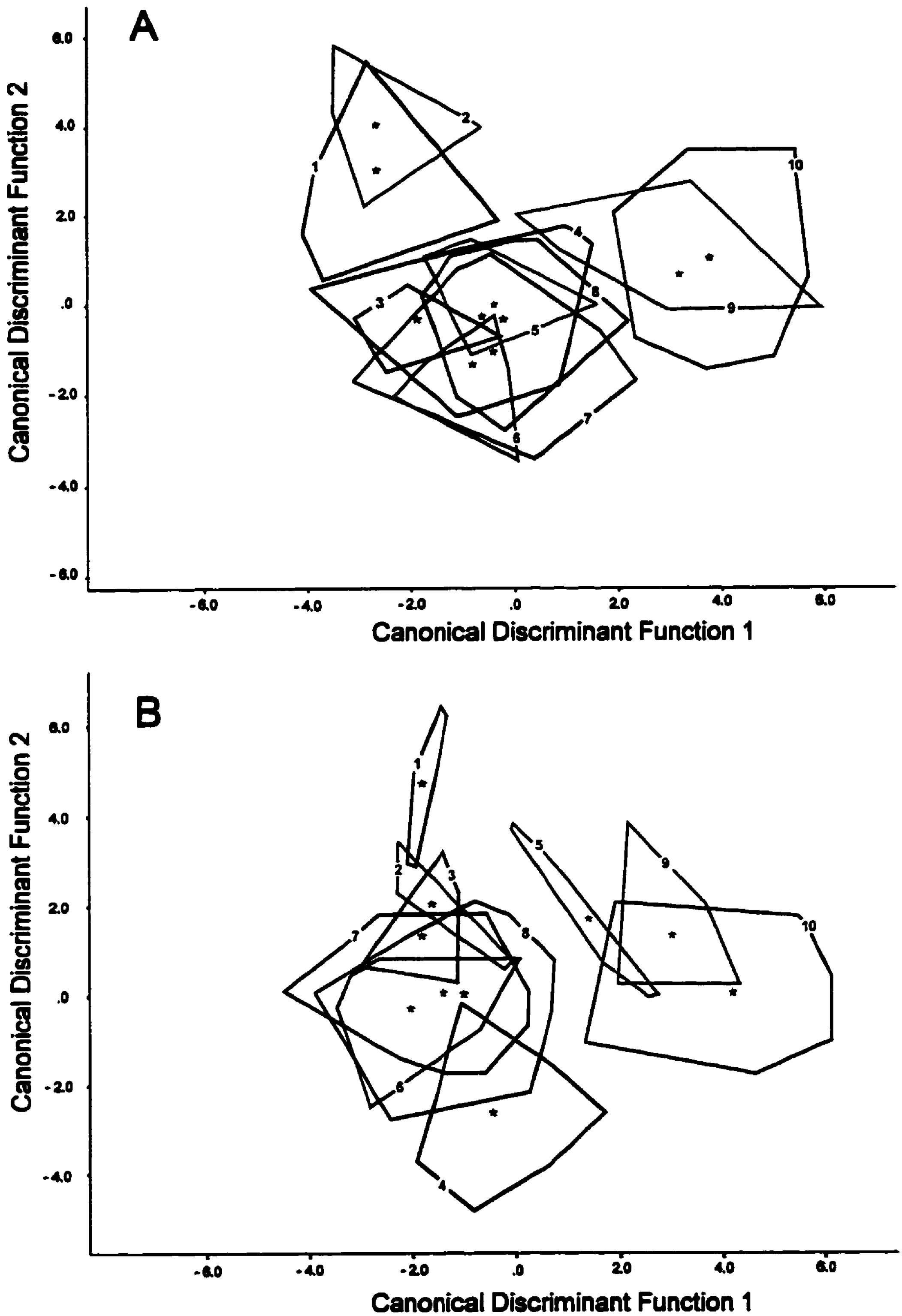
Table 10. Standard canonical discriminant function coefficients for 9 functions used for discriminant analysis of 10 populations of male wolves.

Variable	DF 1	DF 2	DF 3	DF 4	DF 5	DF 6	DF 7	DF 8	DF 9
Condy L	-0.619	-0.216	-0.626	-3.034	-0.216	-0.327	-0.577	0.232	2.208
I^1- Sag C	-0.156	-0.672	-0.137	-0.734	-0.326	0.550	0.204	-0.014	0.101
Nasal L	0.004	0.366	-0.317	0.254	0.461	0.118	0.206	0.625	-0.300
I^1- Palat	1.020	0.001	-1.544	2.683	-0.462	0.265	0.020	-0.107	-0.365
I^2- Palat	-0.747	-0.036	2.541	-0.545	1.018	0.696	0.587	-0.201	-0.202
Pos Pal L	0.087	0.365	0.674	1.617	-0.063	0.771	0.709	-0.441	-0.576
C^1- M^2	0.373	-0.092	0.604	-0.949	-1.147	0.019	-0.542	0.255	-0.059
W of C^1	-0.266	0.298	0.041	0.276	-0.124	0.358	0.017	0.088	-0.302
W of P^4	-0.068	-0.162	-0.255	-0.387	0.167	0.329	0.155	0.460	0.015
L of P^4	0.098	0.359	-0.213	0.128	-0.130	0.340	0.350	0.190	0.612
W of M^1	0.249	0.327	-0.142	0.389	-0.127	-0.224	-0.413	-0.220	0.195
L of M^1	0.112	-0.010	-0.120	0.210	-0.199	0.140	0.285	0.209	0.048
W of M^2	0.028	0.066	0.349	-0.342	0.131	-0.123	0.160	0.032	0.111
I^3 to I^3	-0.018	0.103	-0.262	0.434	-0.419	0.304	0.033	-0.161	0.097
P^1 to P^1	0.069	0.117	-0.008	-0.341	-0.013	-0.007	0.130	-0.503	0.345
P^2 to P^2	-0.239	-0.075	-0.052	0.047	0.143	0.274	-0.279	-0.034	-0.019
C^1 to C^1	0.130	-0.133	0.094	0.234	-0.335	-0.732	0.431	0.461	-0.357
M^1 to M^1	-0.076	-0.345	-0.431	-0.061	0.476	-0.021	0.051	0.278	0.057
Cheek T W	0.088	0.768	0.635	0.153	0.172	-0.119	0.066	-0.052	0.357
Pos For W	-0.213	-0.121	0.301	-0.338	0.047	0.310	-0.017	-0.078	-0.346
Aud Bul W	0.180	0.100	-0.280	-0.084	0.314	0.012	0.455	-0.348	0.039
Occ Cre W	-0.286	0.358	-0.047	0.367	0.342	-0.279	-0.136	0.034	-0.370
Condyle W	0.291	0.063	-0.290	-0.006	-0.081	-0.157	-0.140	0.033	0.046
Condyle L	0.380	-0.490	0.070	0.242	-0.312	0.058	-0.253	-0.331	-0.253
Occ Con W	-0.209	0.154	0.317	-0.108	0.105	-0.201	-0.190	0.143	0.153
InterOr W	-0.185	-0.663	0.186	0.497	0.032	0.341	-0.766	-0.070	-0.195
Postorb W	0.240	0.281	0.133	-0.397	-0.210	0.049	0.623	0.001	0.367
Tem Fos W	-0.074	0.147	-0.324	-0.089	0.087	-0.055	0.501	0.005	0.243
Pari-Temp W	0.167	-0.320	-0.074	-0.185	0.153	-0.106	-0.237	-0.003	0.319
Zygom W	0.176	-0.025	-0.431	-0.035	-0.380	0.734	-0.741	-0.136	-0.181
M^1 to Orb	0.520	-0.016	0.127	-0.010	0.307	-0.356	-0.503	-0.343	-0.229
Jugal H	0.137	0.217	-0.313	-0.430	-0.101	-0.158	-0.351	0.113	-0.332
SagC-AudB	-0.216	0.546	-0.186	0.476	-0.360	-0.548	-0.166	-0.043	0.132
Sym-AngPr	-0.777	-0.236	-0.072	-0.588	1.145	0.911	1.306	-0.166	-0.064
Sym-Condy	1.414	0.388	-0.561	0.795	-0.433	-2.291	-0.885	-0.251	-0.737
C_1 - M_3	0.064	-0.399	-0.181	0.486	0.171	-0.240	-0.155	0.079	-0.008
W of P_4	-0.328	-0.306	0.553	0.341	0.554	-0.412	-0.148	0.174	0.482
L of P_4	-0.481	0.563	-0.115	-0.363	-0.509	0.051	-0.136	-0.183	0.079
W of M_1	-0.432	-0.627	-0.347	-0.296	-0.313	-0.759	0.083	-0.445	-0.681
L of M_1	0.033	0.052	0.706	0.119	0.520	0.132	-0.416	0.245	-0.052
Mandib W	0.230	0.022	-0.394	-0.309	0.236	0.392	0.549	-0.294	-0.428
Art Con W	0.224	-0.055	0.422	0.443	0.020	0.192	-0.059	0.002	-0.063
Art Con L	-0.336	-0.087	0.460	0.120	0.272	0.080	0.442	0.260	0.233
H of Ramus	-0.130	0.218	-0.064	0.187	-0.412	-0.076	0.320	0.726	-0.003
AngP - CorP	0.264	-0.198	-0.020	0.456	-0.124	0.296	-0.326	0.070	0.390
Eigenvalue	**3.55**	**1.89**	**1.08**	**0.89**	**0.67**	**0.57**	**0.50**	**0.32**	**0.25**
% Variance	**36.8**	**19.0**	**11.1**	**9.2**	**6.9**	**5.9**	**5.2**	**3.3**	**2.6**
Cum. %	**36.8**	**55.8**	**66.9**	**76.1**	**83.0**	**88.9**	**94.1**	**97.4**	**100.0**

Table 11. Standard canonical discriminant function coefficients for 9 functions used for discriminant analysis of 10 populations of female wolves.

Variable	DF 1	DF 2	DF 3	DF 4	DF 5	DF 6	DF 7	DF 8	DF 9
Condy L	-1.666	-1.433	-0.124	1.317	0.283	-0.234	-1.791	-0.875	0.252
I^1- Sag C	0.153	-0.329	0.032	-0.137	0.869	0.615	-0.183	0.375	-0.785
Nasal L	0.468	0.453	0.087	0.519	0.395	0.061	0.114	-0.402	-0.051
I^1- Palat	0.615	0.930	-2.137	0.737	-0.381	-1.104	1.053	-0.974	-1.242
I^2- Palat	0.684	0.095	1.847	-2.338	-0.346	1.694	0.405	1.239	1.357
Pos Pal L	0.880	0.927	-0.011	-0.648	-0.452	0.174	1.544	1.084	-0.288
C^1- M^2	-0.080	-0.642	0.097	0.134	0.424	-0.739	-1.072	-0.123	0.369
W of C^1	-0.204	0.157	-0.077	0.076	0.248	0.069	0.370	-0.088	-0.007
W of P^4	0.127	-0.165	0.637	0.607	-0.292	0.530	-0.114	0.352	0.183
L of P^4	0.251	-0.189	0.066	-0.074	-0.699	0.166	-0.142	-0.215	-0.082
W of M^1	-0.277	-0.404	-0.062	-0.167	-0.274	0.450	0.091	0.050	0.261
L of M^1	0.075	0.007	0.430	-0.478	0.036	0.215	-0.183	0.107	0.402
W of M^2	0.227	-0.218	-0.391	0.252	0.254	-0.364	0.386	-0.063	0.017
I^3 to I^3	-0.061	-0.214	0.190	-0.068	-0.153	-0.287	0.264	0.209	-0.146
P^1 to P^1	0.654	0.284	-0.524	-0.135	-0.060	0.582	0.282	0.353	-0.243
P^2 to P^2	-0.532	-0.154	0.496	-0.022	0.266	-0.282	-0.481	-0.246	0.176
C^1 to C^1	-0.097	-0.173	-0.143	-0.060	0.209	-0.612	0.325	0.061	-0.212
M^1 to M^1	-0.334	0.289	0.189	-0.030	-0.584	-0.257	0.364	0.227	0.308
Cheek T W	0.553	0.459	-0.265	-0.122	0.039	-0.038	-0.321	-0.267	0.243
Pos For W	0.189	0.042	-0.180	0.268	0.026	0.563	0.099	0.269	-0.153
Aud Bul W	0.262	-0.270	-0.215	-0.044	-0.123	-0.196	-0.014	0.265	0.496
Occ Cre W	-0.190	0.525	0.320	0.072	0.006	-0.041	-0.513	-0.193	0.080
Condyle W	0.290	-0.040	0.183	0.058	0.031	-0.214	0.083	0.460	-0.252
Condyle L	0.179	-0.048	0.131	-0.444	-0.150	0.240	-0.049	-0.080	0.332
Occ Con W	0.076	0.012	-0.079	-0.358	0.569	-0.125	0.511	0.038	0.117
InterOr W	-0.166	0.161	-0.040	-0.381	0.385	-0.082	-0.047	-0.083	-0.381
Postorb W	-0.001	-0.188	0.450	0.411	-0.295	0.101	0.114	-0.070	0.108
Tem Fos W	0.424	-0.390	0.234	0.090	0.172	0.045	0.127	-0.352	0.104
Pari-Temp W	-0.499	-0.271	0.297	0.126	0.185	0.110	0.018	-0.069	0.120
Zygom W	-0.078	0.379	-0.578	-0.652	-0.240	0.067	-0.366	-0.160	0.397
M^1 to Orb	-0.003	-0.379	-0.485	0.299	-0.310	0.098	-0.227	-0.271	-0.001
Jugal H	0.091	-0.136	0.631	0.205	-0.298	-0.163	0.297	-0.089	0.114
SagC-AudB	-0.188	0.278	-0.031	0.196	-0.387	0.010	0.278	-0.068	0.097
Sym-AngPr	-0.266	-0.456	-0.435	0.065	-0.524	0.613	-0.278	0.687	0.113
Sym-Condy	1.028	0.702	1.299	0.010	-0.061	-1.335	-0.191	-0.906	0.422
C_1 - M_3	-0.713	-0.750	-1.031	0.527	-0.446	0.041	0.806	-0.013	-0.464
W of P_4	-0.228	0.074	-0.314	-0.311	0.203	0.045	0.526	0.185	0.560
L of P_4	-0.513	0.340	-0.315	0.687	0.159	-0.473	0.107	0.112	0.210
W of M_1	-0.087	0.510	0.112	-0.727	0.224	0.396	-0.227	-0.418	-0.436
L of M_1	0.208	0.670	0.010	0.414	0.508	-0.112	-0.192	0.070	-0.278
Mandib W	0.631	-0.167	0.356	-0.047	0.184	0.229	-0.243	-0.405	-0.184
Art Con W	-0.141	0.286	-0.041	0.216	0.224	0.495	-0.116	0.162	-0.226
Art Con L	-0.588	-0.386	-0.291	0.285	0.098	0.244	0.189	-0.079	-0.432
H of Ramus	-0.464	0.889	0.228	-0.170	0.400	-0.465	0.089	0.573	-0.227
AngP - CorP	0.567	-0.731	0.049	0.022	0.299	-0.032	-0.212	0.053	0.080
Eigenvalue	**5.47**	**1.45**	**1.25**	**0.80**	**0.59**	**0.42**	**0.38**	**0.33**	**0.29**
% Variance	**49.8**	**13.2**	**11.4**	**7.3**	**5.4**	**3.8**	**3.5**	**3.0**	**2.6**
Cum. %	**49.8**	**63.0**	**74.4**	**81.7**	**87.1**	**90.9**	**94.4**	**97.4**	**100.0**

Figure 9. Dispersion of 10 geographic samples, from the entire study area, of male (A) and female (B) *C. lupus* on the first two canonical discriminant functions. Asterisks indicate group centroids. Numbers define groups; sample sizes enclosed in brackets (*n* males, *n* females): 1, Queen Elizabeth Islands (13M, 3F); 2, Banks Island and Victoria Island (8M, 5F); 3, Baffin Island (8M, 3F); 4, Mackenzie (27M, 12F); 5, Great Slave Lake (9M, 4F); 6, Northern Keewatin (26M, 13F); 7, Central Keewatin (44M, 49F); 8, Southern Keewatin (30M, 22F); 9, Central Saskatchewan (10M, 6F); and 10, Northern Alberta (27M, 28F).



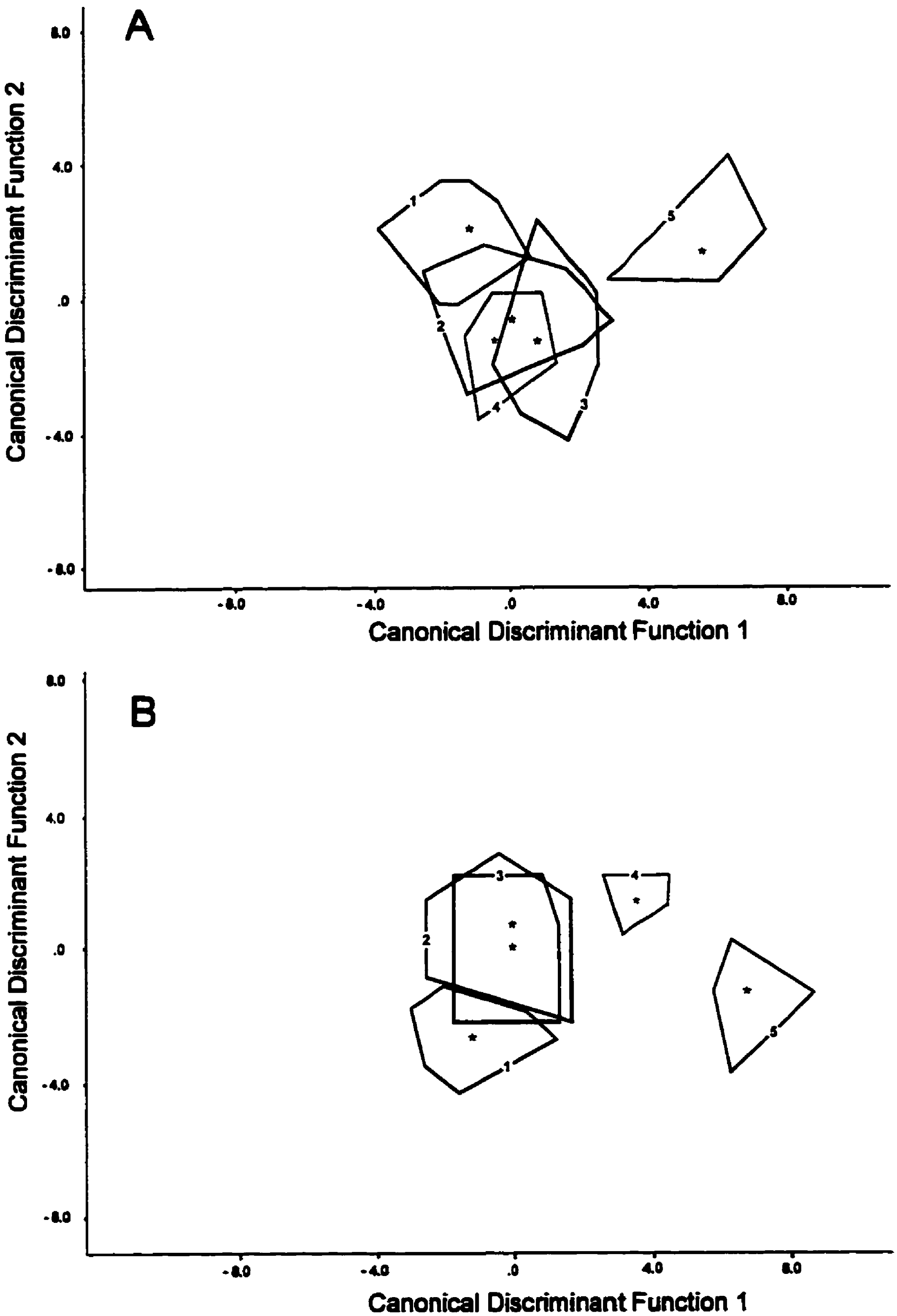
A
B
Canonical Discriminant Function 2
Canonical Discriminant Function 1
6.0
4.0
2.0
.0
-2.0
-4.0
-6.0

had patterns of distribution similar to the males (A). Females from the Queen Elizabeth Islands were separate from the mainland groups. Banks / Victoria Island females overlapped slightly with Baffin Island females and appeared to have a closer relationship to the mainland populations than with the Queen Elizabeth Island females. The N. Alberta, C. Saskatchewan, and Great Slave Lake females overlapped, but were separate from the remaining populations. The affinity of Great Slave Lake females to the N. Alberta and C. Saskatchewan populations was not reflected for the male groups. Males from Great Slave Lake appeared to have a closer relationship to populations from the Keewatin and Mackenzie regions than with the C. Saskatchewan or N. Alberta populations.

In order to examine the relationship of wolves in Keewatin with adjacent groupings, plots of the relative positions of 5 male (A) and female (B) groups (representing N. Keewatin, C. Keewatin, S. Keewatin, Great Slave Lake, and C. Saskatchewan) on the first two discriminant functions are presented in Figure 10. The group relationships confirmed patterns evident in Figure 9, but focused on the 5 groups of interest. Keewatin males overlapped with each other with northern, central, and southern groups appearing to follow a gradient, which was consistent with the univariate data. Males from Great Slave Lake overlapped considerably with both C. Keewatin and S. Keewatin males. Males from C. Saskatchewan were separate from the N.W.T. groups and had their closest affinity to the S. Keewatin and C. Keewatin groups. This analysis suggests that S. Keewatin males have closer ties with other N.W.T. groups than with C. Saskatchewan males. There was considerable overlap of S. Keewatin females with C. Keewatin females. Northern Keewatin females were immediately adjacent to the two southern groups, but had relatively little overlap with them. The small sample of Great Slave Lake females (n=4) was separate from Keewatin females, as initially shown in Figure 9. Central Saskatchewan females were distinct from N.W.T. groups and were positioned more closely to the Great Slave Lake group than to Keewatin wolves. This analysis would suggest that S. Keewatin males have closer ties with other N.W.T. populations than to C. Saskatchewan males.

The classification of male wolves (Table 12) illustrated the success of the discriminant analysis, as 82.7% of the cases were correctly classified. A high proportion of the male cases

Figure 10. Dispersion of 5 geographic samples, from the eastern barrens and Saskatchewan, of male (A) and female (B) *C. lupus* on the first two canonical discriminant functions. Asterisks indicate group centroids. Numbers define groups, sample sizes enclosed in brackets (*n* males, *n* females): 1, Northern Keewatin (26M, 13F); 2, Central Keewatin (44M, 49F); 3, Southern Keewatin (30M, 22F); 4, Great Slave Lake (9M, 4F); and 5, Central Saskatchewan (10M, 6F).



A
B
Canonical Discriminant Function 2
Canonical Discriminant Function 1
8.0
4.0
.0
-4.0
-8.0
1
2
3
4
5

Table 12. Classification results of discriminant analysis for adult male wolves using 45 cranial measurements.

		PREDICTED GROUP MEMBERSHIP									
ACTUAL GROUP	*N*	Queen Elizab. Is.	Baffin Island	Banks / Victoria Is.	Mackenzie Delta	Great Slave Lake	Northern Keewatin	Central Keewatin	Southern Keewatin	Central Saskatchewan	Northern Alberta
Queen Elizabeth Is.	*13*	12 92.3%	1 7.7%								
Baffin Island	*8*		8 100.0%								
Banks / Victoria Is.	*8*			8 100.0%							
Mackenzie Delta	*27*				21 77.8%	1 3.7%	2 7.4%	1 3.7%	1 3.7%		1 3.7%
Great Slave Lake	*9*				1 11.1%	7 77.8%		1 11.1%			
Northern Keewatin	*26*						24 92.3%	2 7.7%			
Central Keewatin	*44*				4 9.1%		5 11.4%	31 70.5%	4 9.1%		
Southern Keewatin	*30*				3 10.0%	1 3.3%	2 6.7%	4 13.2%	20 66.7%		
Central Saskatchewan	*10*	1 10.0%								9 90.0%	
Northern Alberta	*27*										27 100.0%

Percentage of "grouped" cases correctly classified: 82.67% (300 cases processed, 98 cases had at least one missing variable, 202 cases used) from Queen Elizabeth Islands (92.3%), Baffin Island (100%), Banks / Victoria Island (100%), C. Saskatchewan (90%), and N. Alberta (100%) were correctly assigned. The level of successful classifications was lower for male groups from across the N.W.T. mainland, specifically the N. Keewatin (92.3%), Great Slave Lake (77.8%), Mackenzie (77.8%), C. Keewatin (70.5%), and S. Keewatin (66.7%). The classification of female wolves (Table 13) illustrated a similar pattern with 83.5% of the cases correctly classified. All (100%) female cases from Queen Elizabeth Islands, Baffin Island, Banks / Victoria Island, Great Slave Lake, N. Keewatin, and C. Saskatchewan were correctly assigned. The classification rate was lower for females from N. Alberta (92.9%), Mackenzie (83.3%), S. Keewatin (77.3%), and C. Keewatin (69.4%).

In addition to running discriminant analysis for all 45 cranial parameters, two smaller subsets were considered for each sex. Principal component analysis identified 25 variables which contributed a significant level (≥ 0.7) of the variation for males (highlighted in Table 6) and 24 variables for females (highlighted in Table 7). As well, discriminant analysis was also done with the 10 parameters used by Nowak (1995). A slight modification to Nowak's parameters is outlined in Appendix 5. A summary of the classification success for each combination is listed in Table 14. In males, the use of 45, 25, and 10 variables resulted in the successful assignment of 82.7%, 66.7%, and 40.0% of all cases, respectively. For females, the use of 45, 24, and 10 variables resulted in the correct assignment of 83.5%, 67.5%, and 42.1% of all cases, respectively. In general, the more data (number of variables) used in the analysis, the higher the percentage of correctly classified cases. The use of the larger data set (45 variables) appeared to be particularly effective over the smaller data sets in correctly classifying cases on the mainland N.W.T. (areas in close proximity to each other).

The calculation of F-statistics and significance levels between pairs of groups provided a measure of statistical distance for wolf populations of each sex (Table 15). This analysis suggested that most group differences were significant and that the overall pattern of variation was consistent with the classification tables. The F-statistic values for adjacent male populations are presented in Figure 11.

Table 13. Classification results of discriminant analysis for adult female wolves using 45 cranial measurements.

		PREDICTED GROUP MEMBERSHIP									
ACTUAL GROUP	*N*	Queen Elizab. Is.	Baffin Island	Banks / Victoria Is.	Mackenzie Delta	Great Slave Lake	Northern Keewatin	Central Keewatin	Southern Keewatin	Central Saskatchewan	Northern Alberta
Queen Elizabeth Is.	*3*	3 100.0%									
Baffin Island	*5*		5 100.0%								
Banks / Victoria Is.	*3*			3 100.0%							
Mackenzie Delta	*12*				10 83.3%			1 8.3%	1 8.3%		
Great Slave Lake	*4*					4 100.0%					
Northern Keewatin	*13*						13 100.0%				
Central Keewatin	*49*				1 2.0%	1 2.0%	5 10.2%	34 69.4%	8 16.3%		
Southern Keewatin	*22*				2 9.1%			3 13.6%	17 77.3%		
Central Saskatchewan	*6*									6 100.0%	
Northern Alberta	*28*					1 3.6%			1 3.6%		26 92.9%

Percentage of "grouped" cases correctly classified: 83.45% (230 cases processed, 85 cases had at least one missing variable, 145 cases used)

Table 14. Classification results of discriminant analysis comparing 3 sets of cranial measurements (as outlined in the text) for male and female wolves from 10 geographic locations.

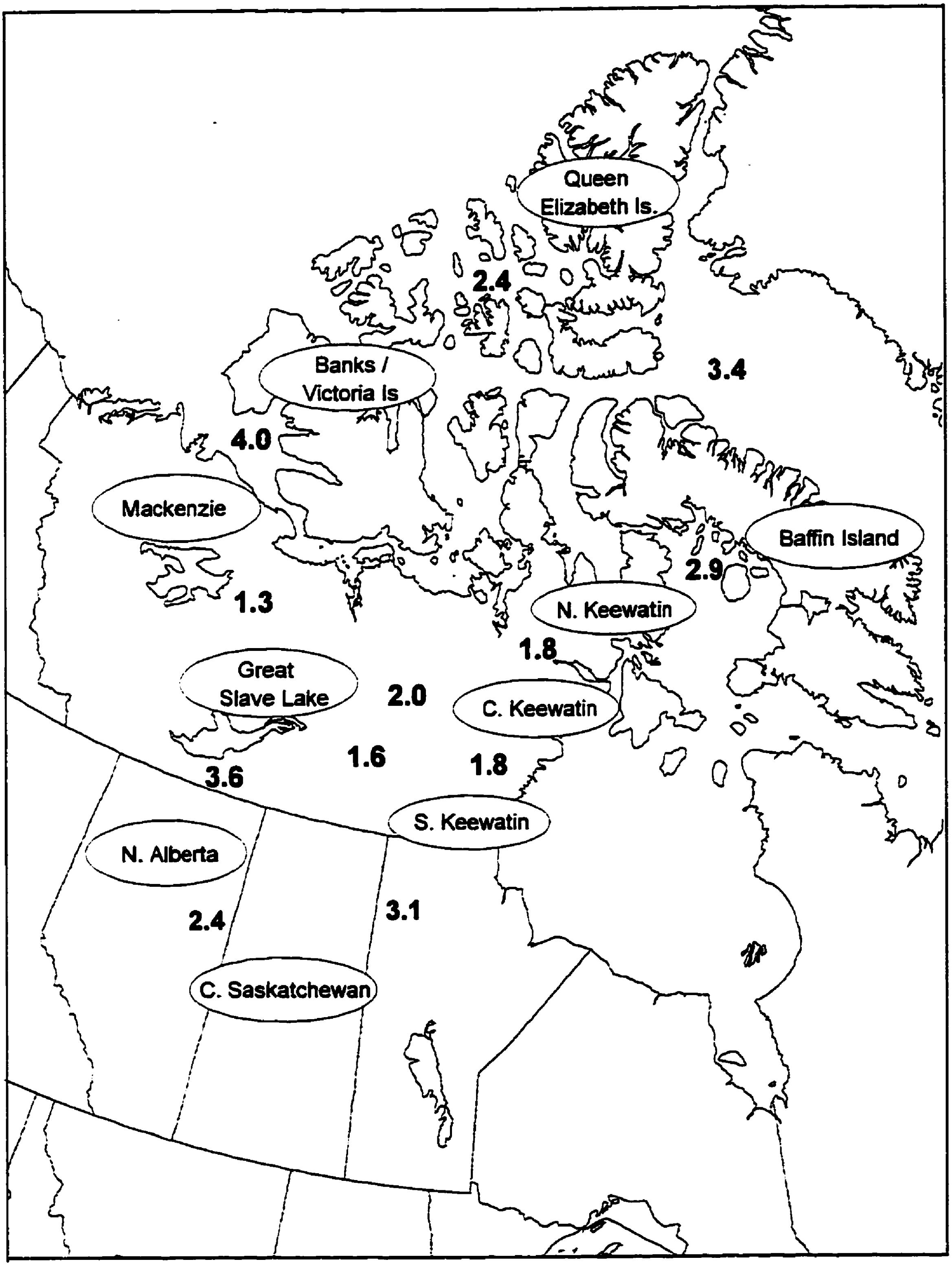
		PREDICTED GROUP MEMBERSHIP									
Number of parameters used in analysis	Percent of All Cases Correctly Classified	Queen Elizabeth Islands	Baffin Island	Banks / Victoria Islands	Mackenzie Delta	Great Slave Lake	Northern Keewatin	Central Keewatin	Southern Keewatin	Central Saskatchewan	Northern Alberta
MALES											
45	**82.7%**	92.3 %	100 %	100 %	77.8 %	77.8 %	92.3 %	70.5 %	66.7 %	90.0 %	100 %
25	**66.7 %**	94.4 %	81.8 %	100 %	61.8 %	46.7 %	60.7 %	47.9 %	57.6 %	91.7 %	86.2 %
10	**40.0 %**	58.8 %	83.8 %	88.9 %	27.5 %	9.5 %	43.8 %	25.0 %	37.5 %	61.5 %	68.8 %
FEMALES											
45	**83.5 %**	100 %	100 %	100 %	83.3 %	100 %	100 %	69.4 %	77.3 %	100 %	92.9 %
24	**67.5 %**	100 %	100 %	75.0 %	68.4 %	60.0 %	58.8 %	51.9 %	58.3 %	100 %	86.2 %
10	**42.1 %**	50.0 %	100 %	50.0 %	37.5 %	26.7 %	46.7 %	32.7 %	32.0 %	33.3 %	72.4 %

Table 15. Statistical distance, expressed as F-Statistic and significance level, between pairs of groups from 10 sampling locations. Males involved 51 iterations; each F-Statistic has 41 and 152 degrees of freedom. Females involved 59 iterations; each F-Statistic has 29 and 107 degrees of freedom. Probability values < 0.05 indicate significance.

Males	Q. Eliz. Is.	Banks / V.	Baffin Is.	Mackenzie	Gr. Slave	N. Keew.	C. Keew.	S. Keew.	C. Sask.
Banks / Victoria Is.	**2.41** 0.000								
Baffin Island	**3.36** 0.000	**3.57** 0.000							
Mackenzie	**4.14** 0.000	**4.03** 0.000	**2.15** 0.001						
Great Slave Lake	**2.95** 0.000	**2.70** 0.000	**2.39** 0.000	**1.31** 0.123					
N. Keewatin	**4.41** 0.000	**4.66** 0.000	**2.91** 0.000	**2.67** 0.000	**1.90** 0.003				
C. Keewatin	**4.97** 0.000	**4.73** 0.000	**3.12** 0.000	**2.12** 0.001	**1.96** 0.002	**1.78** 0.007			
S. Keewatin	**4.34** 0.000	**4.13** 0.000	**3.39** 0.000	**1.82** 0.005	**1.64** 0.018	**2.57** 0.000	**1.84** 0.004		
C. Saskatchewan	**5.52** 0.000	**5.01** 0.000	**4.66** 0.000	**4.13** 0.000	**3.06** 0.000	**4.53** 0.000	**4.04** 0.000	**3.09** 0.000	
N. Alberta	**8.20** 0.000	**6.78** 0.000	**5.67** 0.000	**6.44** 0.000	**3.60** 0.000	**7.42** 0.000	**7.41** 0.000	**6.18** 0.000	**2.42** 0.000

Females	Q. Eliz. Is.	Banks / V.	Baffin Is.	Mackenzie	Gr. Slave	N. Keew.	C. Keew.	S. Keew.	C. Sask.
Banks / Victoria Is.	**1.29** 0.177								
Baffin Island	**3.18** 0.000	**2.01** 0.005							
Mackenzie	**3.45** 0.000	**1.95** 0.007	**4.10** 0.000						
Great Slave Lake	**2.24** 0.002	**1.71** 0.026	**2.64** 0.000	**2.31** 0.001					
N. Keewatin	**2.62** 0.000	**1.30** 0.170	**2.85** 0.000	**2.11** 0.003	**2.28** 0.001				
C. Keewatin	**2.59** 0.000	**1.38** 0.121	**3.08** 0.000	**2.52** 0.000	**2.00** 0.006	**1.53** 0.061			
S. Keewatin	**2.44** 0.001	**1.23** 0.221	**2.83** 0.000	**2.09** 0.004	**1.77** 0.019	**1.66** 0.033	**1.02** 0.450		
C. Saskatchewan	**3.07** 0.000	**2.37** 0.001	**3.78** 0.000	**3.37** 0.000	**1.21** 0.241	**4.36** 0.000	**3.64** 0.000	**3.04** 0.000	
N. Alberta	**4.64** 0.000	**2.91** 0.000	**5.76** 0.000	**5.20** 0.000	**1.96** 0.007	**7.96** 0.000	**12.36** 0.000	**7.79** 0.000	**1.86** 0.012

Figure 11. Statistical distance, expressed as an F-statistic, between 10 sampling locations for male wolves in northern Canada. A complete list of F-statistics and significance levels between all pairs of groups, for males and females, is provided in Table 15.


Queen
Elizabeth Is.
2.4
Banks /
Victoria Is
3.4
4.0
Mackenzie
Baffin Island
2.9
1.3
N. Keewatin
1.8
Great
Slave Lake
2.0
C. Keewatin
1.6
1.8
3.6
S. Keewatin
N. Alberta
2.4
3.1
C. Saskatchewan

Sexual Dimorphism

All cranial parameters were considered for their level of sexual dimorphism using the Student's *t*-test. When all adult specimens (n=525) were considered collectively, the level of sexual dimorphism ranged from 1.8% for Pari-Temp W to 8.9% for W of C^1 (Appendix 9.1). Although the percent sexual dimorphism varied for each parameter, the difference between sexes was significant at the 0.001 level for all 45 parameters.

Considering geographic patterns of sexual dimorphism, however, is of greater interest biologically. For each sampling location, sample size, range, mean, and standard deviation of the mean were determined for each sex, together with a ratio of proportion difference, *t*-value, and probability values (Appendices 9.2 - 9.11). In general, for primary measures of overall size, males were larger than females by approximately 2 to 9%. For a few parameters the level of sexual dimorphism exceeded 10% at several locations. For example, sexual dimorphism in Nasal L was 10.7% in the southern Keewatin; W of C^1 was 11.5 % for central Saskatchewan, 11.6% for Banks / Victoria Is., and 12.5% for the southern Keewatin, and; Art Con L and Art Con W exceeded 12% for central Saskatchewan. Pari-Temp W, a measure of brain case width, had relatively low levels of dimorphism (0.9 to 2.9%) in all localities. InterOr W, Postorb W, and Tem Fos W were larger in females (-0.3 to -3.3% dimorphism) from Baffin Island and Banks / Victoria Island. However, caution should be used in interpreting these differences considering the small female sample sizes (n=8, n=5, respectively) for these two locations. A summary of descriptive statistics for the 3 combined Keewatin samples (northern, central, and southern), which constitute a pooled sample of *C.l. hudsonicus*, is provided in Appendix 9.12. A summary of percent dimorphism for each parameter at each geographic location is provided in Appendix 10, with corresponding descriptive statistics in Appendices 9.2 - 9.11.

The application of discriminant analysis provides another means of comparing group differences and analysing sexual dimorphism. Discriminant analysis of male and female skulls classified 85.3% of the specimens correctly with respect to sex, when 45 cranial parameters were considered (Table 16). The prior probability expected by chance for each

Table 16. Classification of all wolf skulls by sex based on 45 cranial parameters. Discriminant analysis only considers complete cases; 347 cases were processed.

	Classification Matrix		
	Females	Males	% Identified Correctly
All Females	129	16	89.0 %
All Males	35	167	82.7 %
Mean			85.3 %

group is 50%. The classification of specimens within each locality with respect to sex are summarized in Table 17. Since most Great Slave Lake specimens were missing mandibles, discriminant analysis was done without any mandibular parameters (n=12) for this locality, thus allowing additional cases to be included. The percent classification success for discriminating sex, (with Wilk's lambda significance) was 92.2% (0.077) for Queen Elizabeth Islands; 95.0% (0.118) for Banks / Victoria Is.; 76.8% (0.010) for Baffin Island; 100% (0.028) for Mackenzie; 100% (0.172) for Great Slave Lake; 100% (0.006) for N. Keewatin; 97.8% (0.210) for C. Keewatin; 100% (.076) for S. Keewatin; 96.5% (0.110) for C. Saskatchewan; and 100% (0.083) for N. Alberta. Small sample sizes (< 25), particularly for females (< 9), may have contributed to the lower levels of significance for Queen Elizabeth Is., Banks / Victoria Is., and C. Saskatchewan.

Latitudinal Variation in Cranial Parameters

Comparing group means for several cranial parameters (mm ± S.E.) revealed patterns of geographic variation (Table 18). In general, as latitude increased cranial size in each sex decreased, a trend which is in disagreement with Bergmann's Rule. Patterns of changing mean size and percent sexual dimorphism are also presented geographically for the 7 parameters listed in Table 18: I^1-SagC length (Fig. 12), Zygomatic width (Fig. 13), Cheek

Table 17. Classification of all wolf skulls by sex for each location. Forty-five cranial parameters were utilized, except for Great Slave Lake which only involved 33 parameters. Discriminant analysis only considers complete cases. Significance levels were calculated using Wilk's lambda.

		Classification Matrix			
		Females	Males	% Identified Correctly	P *
Queen Elizabeth Is.	Females	6	0	100 %	0.0772
	Males	3	16	84.2 %	
Banks / Victoria Is.	Females	4	0	100 %	0.1183
	Males	1	9	90.0 %	
Baffin Island	Females	6	2	75.0 %	0.0095
	Males	3	11	78.6 %	
Mackenzie	Females	12	0	100 %	0.0281
	Males	0	27	100 %	
Great Slave Lake	Females	30	0	100 %	0.1719
	Males	0	22	100 %	
Northern Keewatin	Females	13	0	100 %	0.0058
	Males	0	26	100 %	
Central Keewatin	Females	49	0	100 %	0.2100
	Males	2	42	95.5 %	
Southern Keewatin	Females	22	0	100 %	0.0763
	Males	0	30	100 %	
Central Saskatchewan	Females	6	0	100 %	0.1098
	Males	1	13	92.9 %	
Northern Alberta	Females	28	0	100 %	0.0828
	Males	0	27	100 %	

* Locations were tested independently, and variation in the data may account for the lower levels of significance observed for several populations.

Table 18. Mean values (mm) ± S.E. for 7 cranial parameters for adult male and female wolves. Data from the 10 sampling locations are organized along western and eastern transects to show latitudinal variation.

MALES

Latitude	Location	Subspecific Designation	*N*	I^1-SagC	Zygom W	Cheek T W	SagC-AudB	L of P^4	Pari-Temp	H of Ramus
> 75 °	Queen Elizabeth Is.	*arctos*	*21*	256.42 2.10	142.38 1.42	82.84 0.65	86.59 0.94	27.12 0.27	64.76 0.40	31.27 0.33
72 °	Banks / Victoria Is.	*bernardii*	*11*	252.14 2.00	140.15 1.49	84.58 1.30	85.60 1.14	27.22 0.23	65.81 0.35	30.44 0.42
68 °	Mackenzie delta	*mackenzii*	*41*	259.17 1.40	141.08 0.71	80.71 0.45	84.70 0.53	26.39 0.15	67.25 0.32	30.45 0.29
62 °	Great Slave Lake	*occidentalis*	*43*	261.92 1.30	140.85 0.69	80.89 0.44	85.41 0.46	26.19 0.19	67.02 0.33	31.62 0.34
< 60 °	Northern Alberta	*occidentalis*	*34*	277.97 1.69	150.51 0.96	86.09 0.60	90.05 0.66	26.82 0.26	68.85 0.45	34.37 0.39
67 °	Baffin Island	*manningi*	*15*	252.67 2.52	136.39 1.17	77.87 0.64	83.17 0.82	25.67 0.33	67.93 0.45	30.95 0.61
67 °	Northern Keewatin	*hudsonicus*	*31*	259.84 1.19	137.97 0.91	80.66 0.51	83.08 0.58	26.09 0.20	67.59 0.42	31.02 0.33
64 °	Central Keewatin	*hudsonicus*	*50*	259.15 1.28	141.12 0.75	81.27 0.40	84.47 0.54	26.02 0.15	67.20 0.28	30.82 0.24
61 °	Southern Keewatin	*hudsonicus*	*36*	265.82 1.29	142.64 0.72	82.39 0.35	86.16 0.47	26.81 0.13	66.51 0.39	32.41 0.29
52 °	C. Saskatchewan	*griseoalbus*	*15*	275.33 2.75	146.18 1.34	84.96 0.94	89.20 1.22	27.06 0.20	67.38 0.67	33.79 0.40

FEMALES

Latitude	Description	Subspecific Designation	*N*	I^1-SagC	Zygom W	Cheek T W	SagC-AudB	L of P^4	Pari-Temp	H of Ramus
> 75 °	Queen Elizabeth Is.	*arctos*	*8*	246.83 0.92	136.56 1.60	79.41 0.96	85.21 1.05	25.80 0.32	63.62 0.88	30.47 0.47
72 °	Banks / Victoria Is.	*bernardii*	*5*	242.98 4.53	138.00 2.11	81.47 2.13	82.81 1.24	25.61 0.64	63.95 1.30	29.31 0.79
68 °	Mackenzie	*mackenzii*	*26*	247.80 1.77	133.96 1.04	76.18 0.64	81.44 0.54	24.98 0.20	66.03 0.43	29.52 0.44
62 °	Great Slave Lake	*occidentalis*	*36*	249.00 1.15	134.19 0.76	77.07 0.55	81.68 0.40	24.99 0.19	65.50 0.36	29.58 0.30
< 60 °	Northern Alberta	*occidentalis*	*30*	263.60 1.11	140.34 0.71	81.32 0.45	85.09 0.55	25.23 0.18	66.89 0.39	32.00 0.33
67 °	Baffin Island	*manningi*	*8*	240.33 2.85	129.97 1.19	76.44 0.77	82.32 0.78	24.78 0.46	67.06 0.79	28.75 0.62
67 °	Northern Keewatin	*hudsonicus*	*19*	243.98 1.87	130.22 0.97	76.57 0.60	79.98 0.68	24.84 0.23	66.74 0.43	28.47 0.41
64 °	Central Keewatin	*hudsonicus*	*60*	245.42 0.98	133.03 0.53	77.48 0.35	80.54 0.46	25.02 0.14	66.05 0.25	28.57 0.21
61 °	Southern Keewatin	*hudsonicus*	*28*	245.66 1.55	133.70 0.79	76.78 0.66	80.98 0.68	24.74 0.19	65.88 0.40	29.03 0.36
52 °	C. Saskatchewan	*griseoalbus*	*6*	258.03 3.20	137.92 0.85	81.28 0.93	82.50 1.20	25.22 0.48	65.50 1.15	32.01 0.91

Teeth width (Fig. 14), SagC - AudB height (Fig. 15), P^4 length (Fig. 16), Pari-Temp width (Fig. 17), and Ramus height (Fig. 18). As well, patterns of variation in Nasal length (Fig. 19) and M^1 to Orbit height (Fig. 20) are provided. These 9 parameters provided a summary of overall size in terms of skull length, width, and height. This pattern of clinal variation held up well on the eastern barrens as males clearly increased in cranial size at lower latitudes. For a number of parameters, however, Queen Elizabeth Island wolves were relatively large and did not fit the north-south gradient more evident for mainland wolves. For example, Queen Elizabeth Island and Banks / Victoria Island wolves had the largest carnassials (L of P^4, Table 18) in the study area. When P^4 length was plotted against Condy L for males, as proposed by Nowak (1983), these 2 parameters helped to distinguish Queen Elizabeth Islands and Banks / Victoria Island populations from other groups of wolves (Fig. 21). Pari-Temp width had relatively little change geographically, when compared with other parameters and exhibited relatively low levels of sexual dimorphism.

When considering subtle morphological changes, interpretation of percent sexual dimorphism (Table 19) should be done carefully, particularly when dealing with smaller sample sizes. The higher levels of sexual dimorphism indicated at lower latitudes within the N.W.T. appeared to have been largely influenced by increased male size. Northern Alberta and C. Saskatchewan females were particularly large, relative to northern females, thereby reducing the level of sexual dimorphism below 60° latitude.

When latitude was incorporated into PCA as a separate variable for male wolves, it resulted in a moderately negative score (- 0.653) on PC I, a component reflecting overall skull size. In female wolves, latitude had a lower negative score (-0.581) on the same component, indicating that cranial size in females had a weaker negative correlation with latitude than did males. When longitude was used in PCA, it identified no clear correlation with any cranial parameter for males and was not positioned on any of the primary components. In contrast, longitude had a moderately positive score (0.629) for females and was positioned on PC I, a component reflecting overall skull size.

Figure 12. Mean I^1-SagC length (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* P < 0.05, ** P < 0.01, *** P < 0.001). Descriptive statistics are listed in Appendices 9.2 - 9.11.

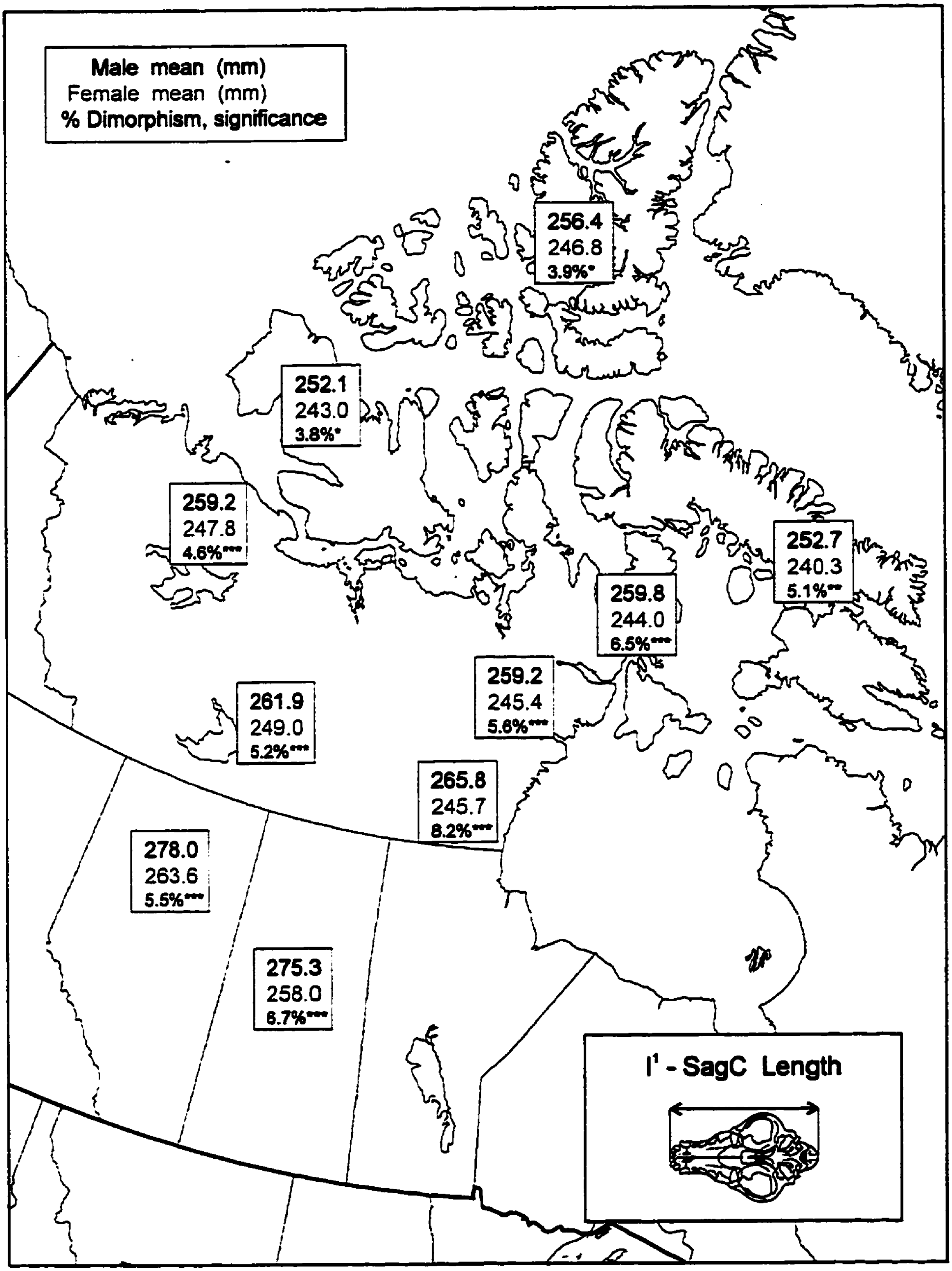
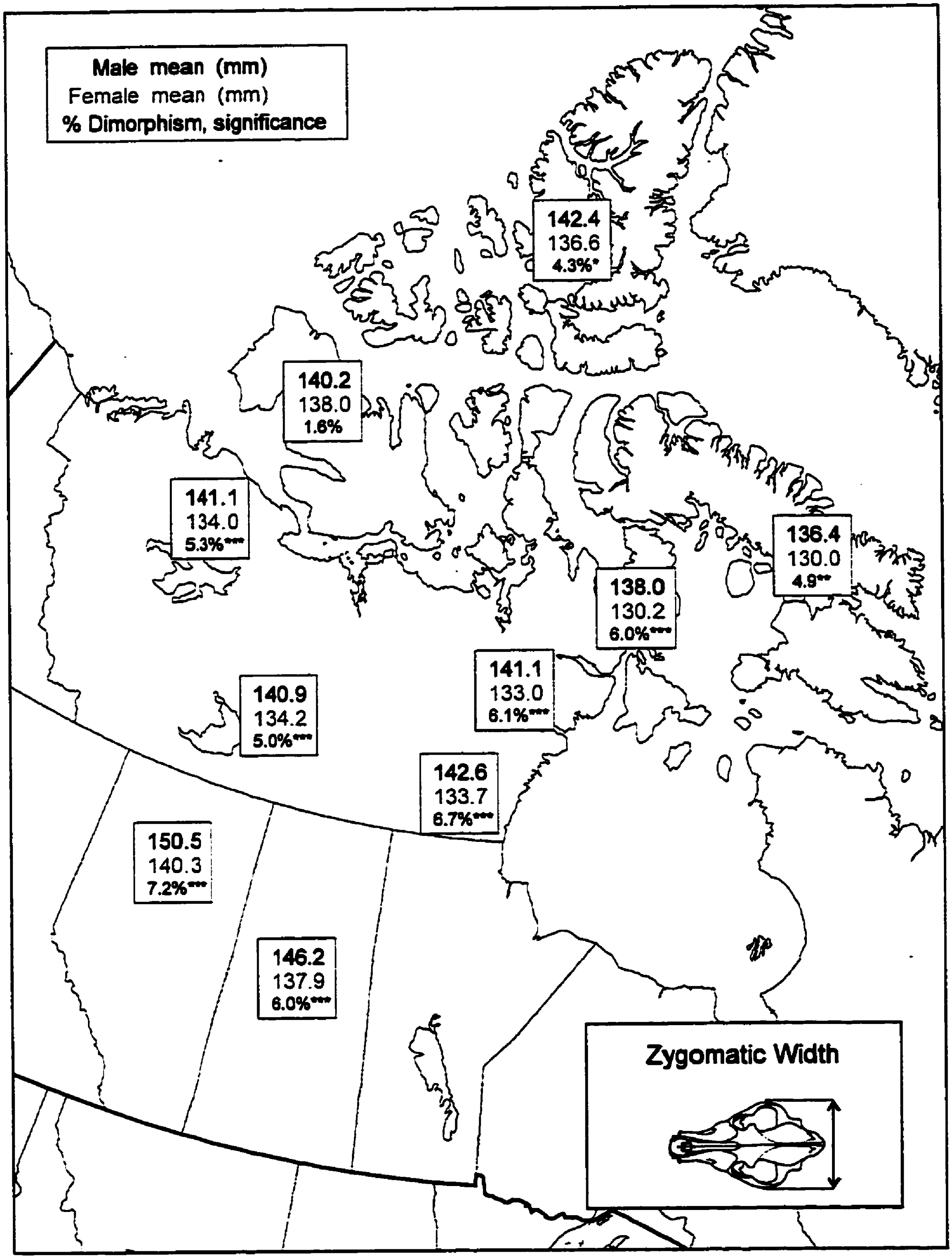

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
256.4
246.8
3.9%*
252.1
243.0
3.8%*
259.2
247.8
4.6%***
252.7
240.3
5.1%**
259.8
244.0
6.5%***
261.9
249.0
5.2%***
259.2
245.4
5.6%***
265.8
245.7
8.2%***
278.0
263.6
5.5%***
275.3
258.0
6.7%***
I1 - SagC Length

Figure 13. Mean Zygomatic width (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Descriptive statistics are listed in Appendices 9.2 - 9.11.



Male mean (mm)
Female mean (mm)
% Dimorphism, significance
142.4
136.6
4.3%*
140.2
138.0
1.6%
141.1
134.0
5.3%***
136.4
130.0
4.9**
138.0
130.2
6.0%***
141.1
133.0
6.1%***
140.9
134.2
5.0%***
142.6
133.7
6.7%***
150.5
140.3
7.2%***
146.2
137.9
6.0%***
Zygomatic Width

Figure 14. Mean Cheek Teeth width (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's t-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Descriptive statistics are listed in Appendices 9.2 - 9.11.

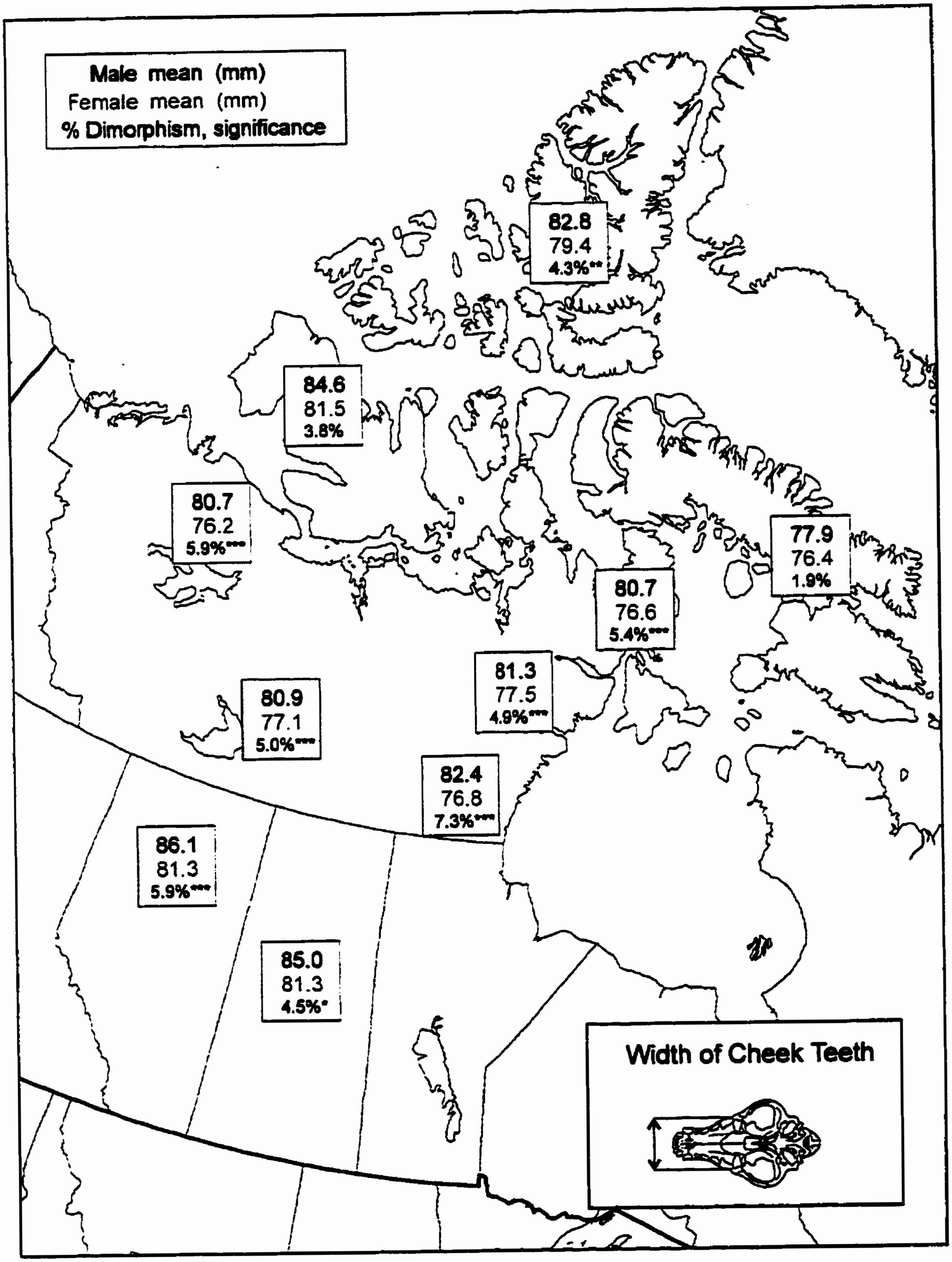

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
82.8
79.4
4.3%**
84.6
81.5
3.8%
80.7
76.2
5.9%***
77.9
76.4
1.9%
80.7
76.6
5.4%***
81.3
77.5
4.9%***
80.9
77.1
5.0%***
82.4
76.8
7.3%***
86.1
81.3
5.9%***
85.0
81.3
4.5%*
Width of Cheek Teeth

Figure 15. Mean SagC-AudB height (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Descriptive statistics are listed in Appendices 9.2 - 9.11.

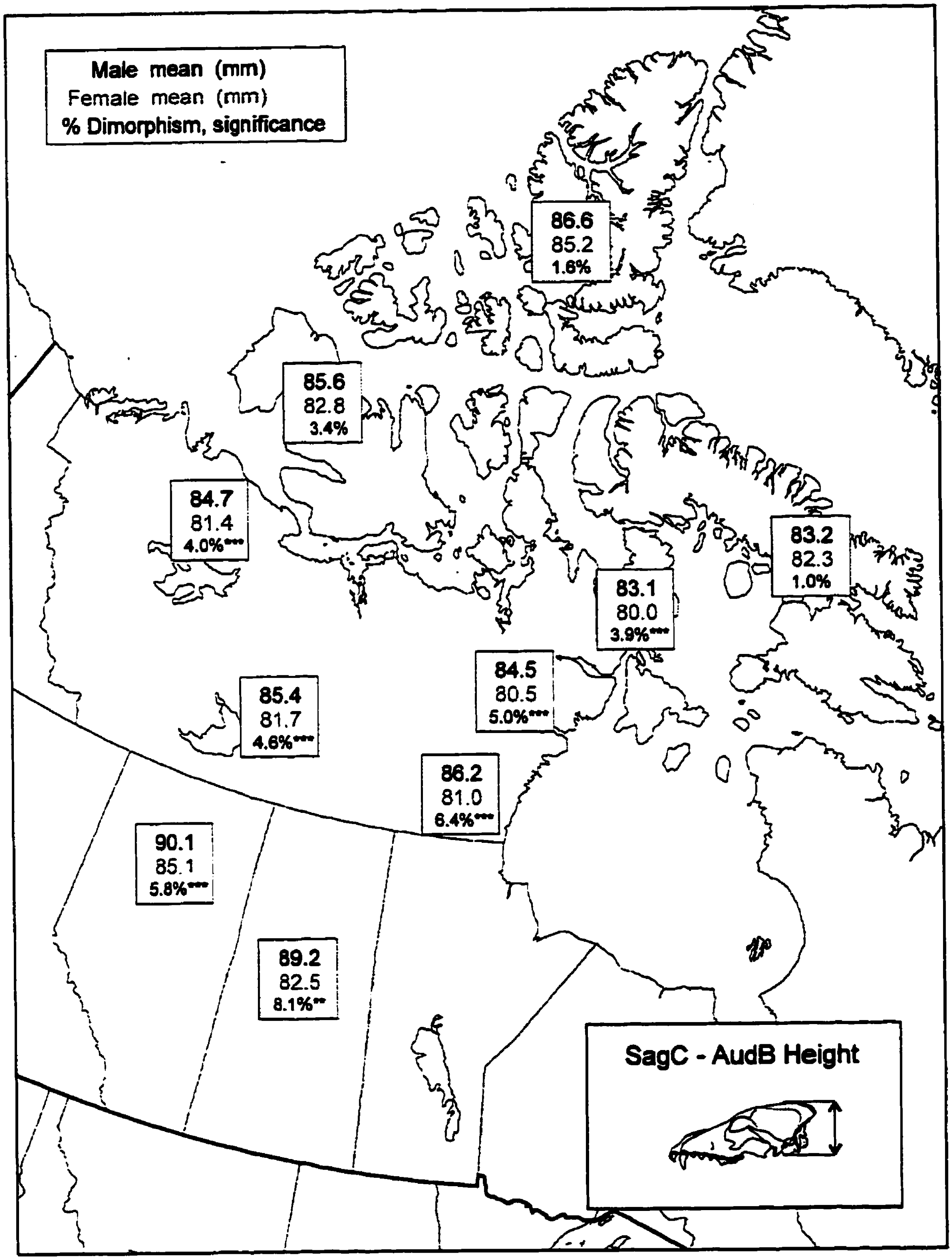
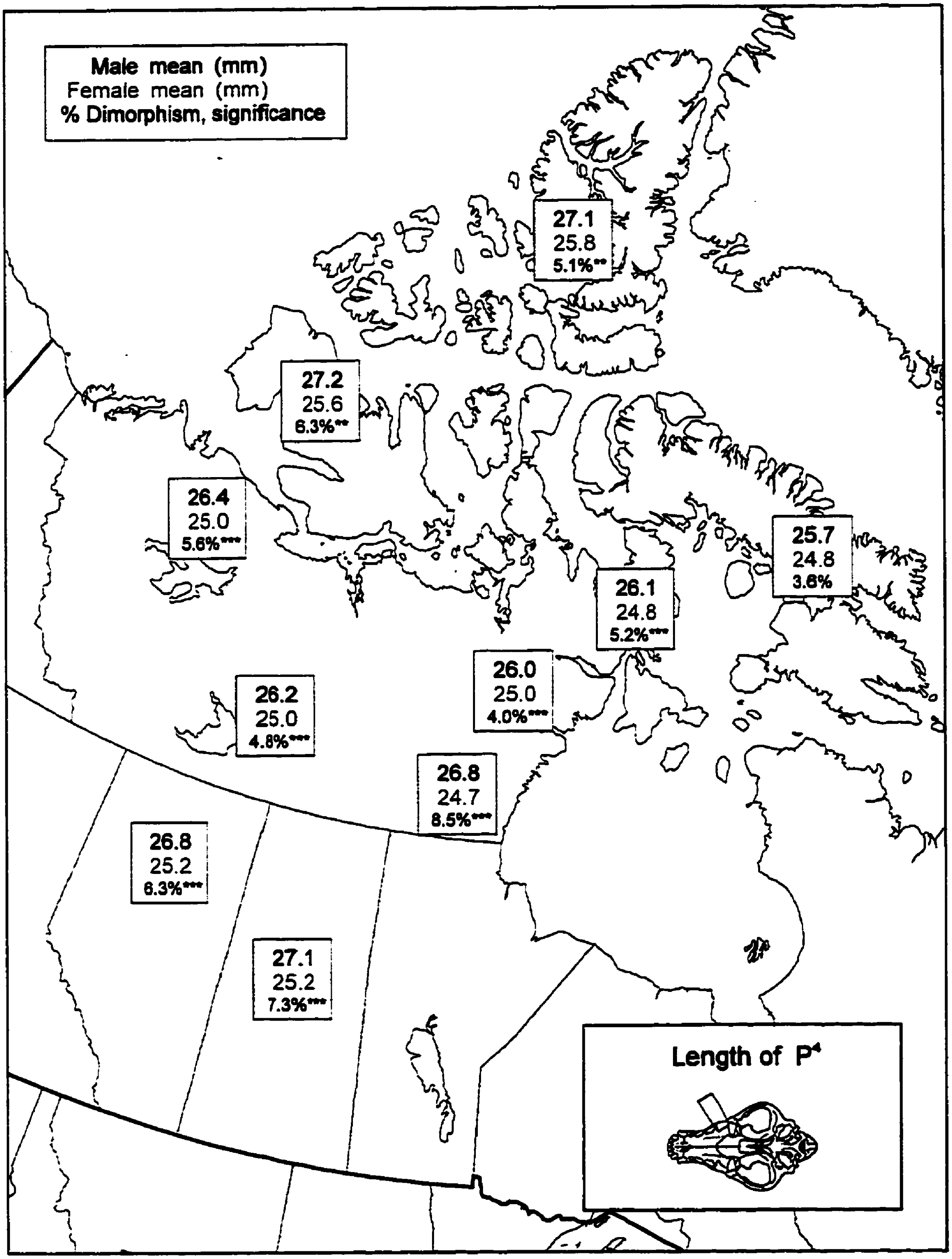

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
86.6
85.2
1.6%
85.6
82.8
3.4%
84.7
81.4
4.0%***
83.2
82.3
1.0%
83.1
80.0
3.9%***
84.5
80.5
5.0%***
85.4
81.7
4.6%***
86.2
81.0
6.4%***
90.1
85.1
5.8%***
89.2
82.5
8.1%**
SagC - AudB Height

Figure 16. Mean P^4 length (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* P < 0.05, ** P < 0.01, *** P < 0.001). Descriptive statistics are listed in Appendices 9.2 - 9.11.



Male mean (mm)
Female mean (mm)
% Dimorphism, significance
27.1
25.8
5.1%**
27.2
25.6
6.3%**
26.4
25.0
5.6%***
25.7
24.8
3.6%
26.1
24.8
5.2%***
26.0
25.0
4.0%***
26.2
25.0
4.8%***
26.8
24.7
8.5%***
26.8
25.2
6.3%***
27.1
25.2
7.3%***
Length of P4

Figure 17. Mean Pari-Temp width (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* P < 0.05, ** P < 0.01, *** P < 0.001). Descriptive statistics are listed in Appendices 9.2 - 9.11.

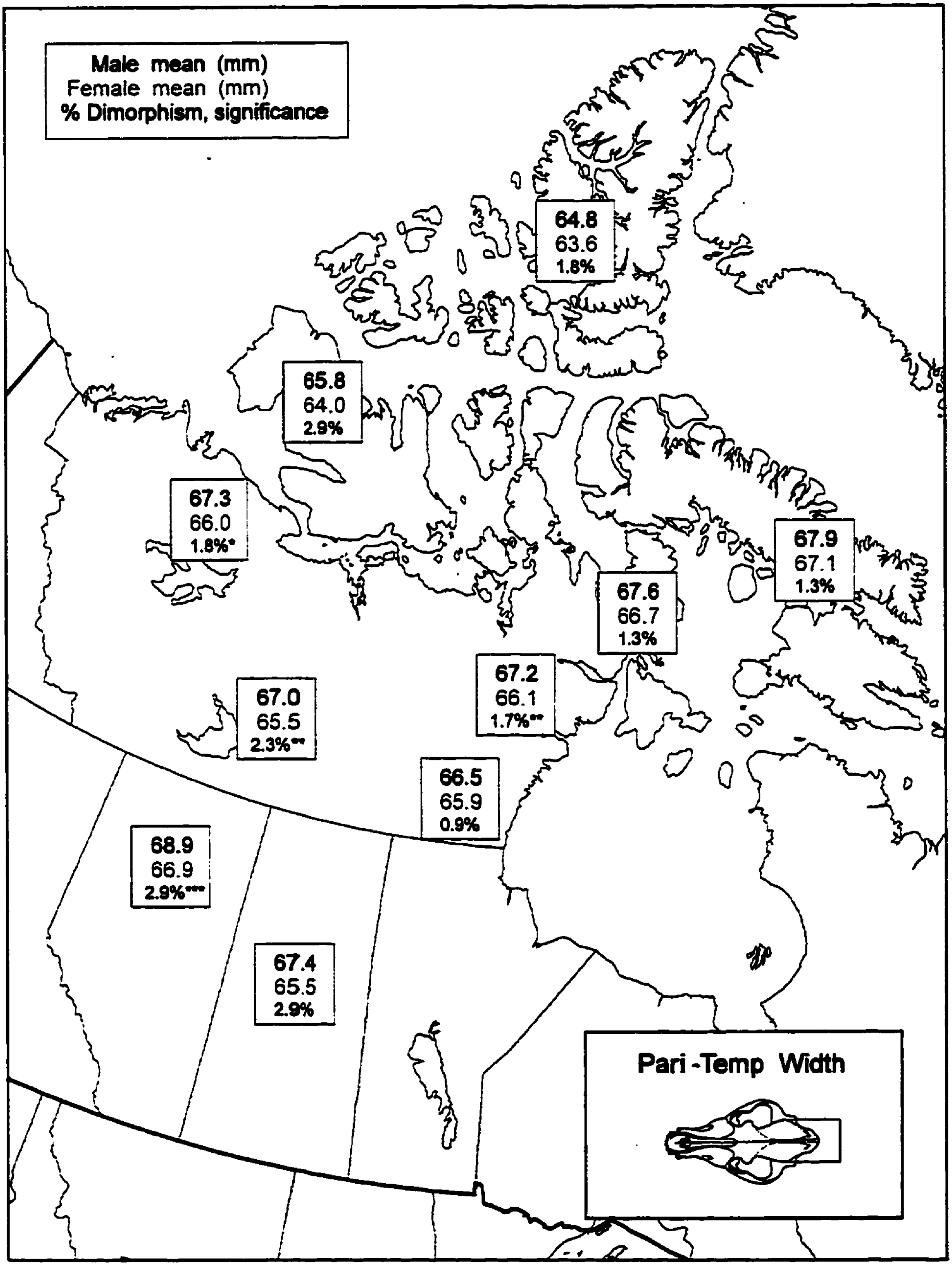

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
64.8
63.6
1.8%
65.8
64.0
2.9%
67.3
66.0
1.8%*
67.9
67.1
1.3%
67.6
66.7
1.3%
67.2
66.1
1.7%**
67.0
65.5
2.3%**
66.5
65.9
0.9%
68.9
66.9
2.9%***
67.4
65.5
2.9%
Pari -Temp Width

Figure 18. Mean Ramus height (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* P < 0.05, ** P < 0.01, *** P < 0.001). Descriptive statistics are listed in Appendices 9.2 - 9.11.

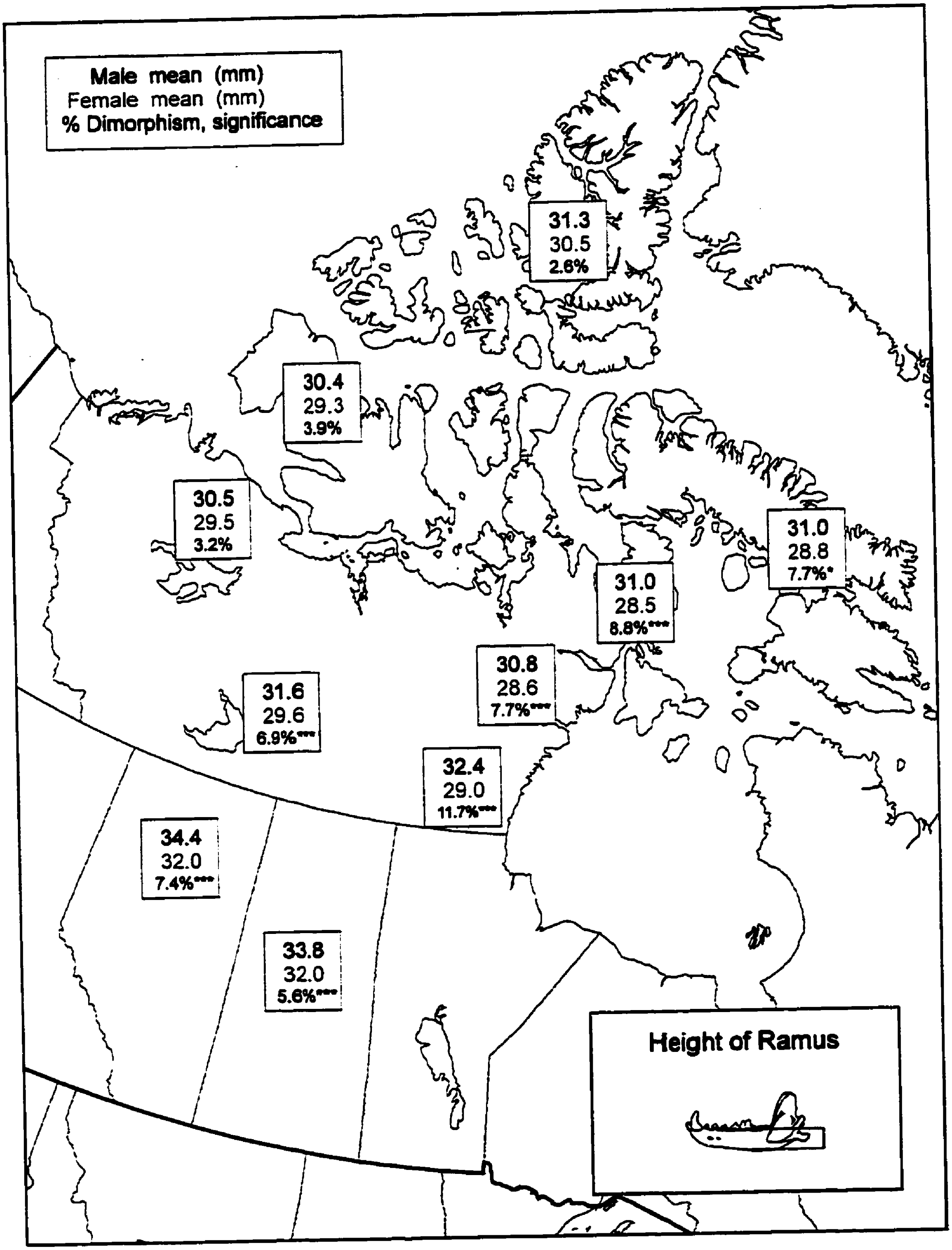
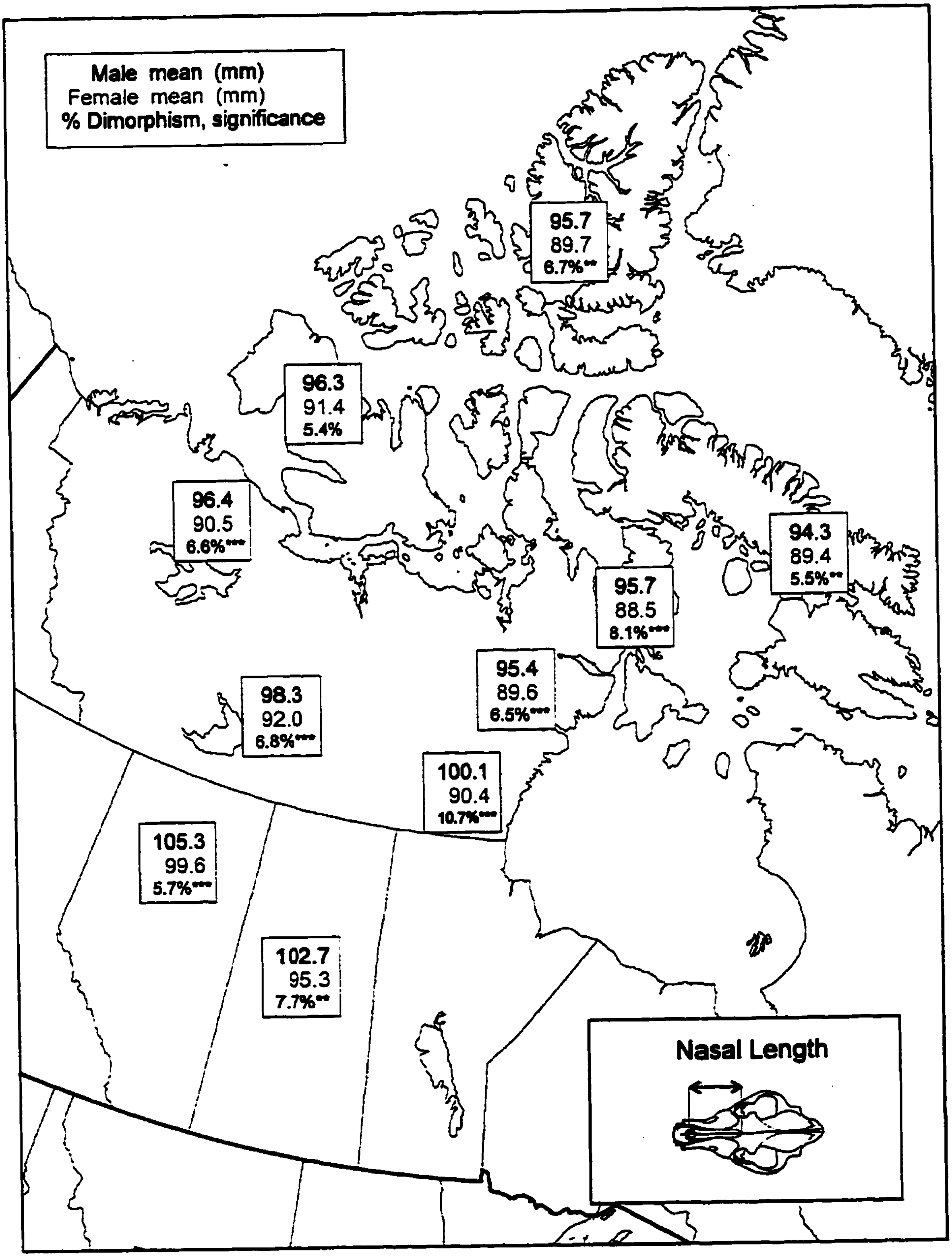

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
31.3
30.5
2.6%
30.4
29.3
3.9%
30.5
29.5
3.2%
31.0
28.8
7.7%*
31.0
28.5
8.8%***
30.8
28.6
7.7%***
31.6
29.6
6.9%***
32.4
29.0
11.7%***
34.4
32.0
7.4%***
33.8
32.0
5.6%***
Height of Ramus

Figure 19. Mean Nasal length (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Descriptive statistics are listed in Appendices 9.2 - 9.11.



Male mean (mm)
Female mean (mm)
% Dimorphism, significance
95.7
89.7
6.7%**
96.3
91.4
5.4%
96.4
90.5
6.6%***
94.3
89.4
5.5%**
95.7
88.5
8.1%***
95.4
89.6
6.5%***
98.3
92.0
6.8%***
100.1
90.4
10.7%***
105.3
99.6
5.7%***
102.7
95.3
7.7%**
Nasal Length

Figure 20. Mean M^1 to Orbit height (mm) and percent sexual dimorphism for male and female wolves from the 10 sampling locations. Means were compared with a Student's *t*-test. Percent sexual dimorphism ((male-female / female) x 100) with a probability < 0.05 indicates significance (* P < 0.05, ** P < 0.01, *** P < 0.001). Descriptive statistics are listed in Appendices 9.2 - 9.11.

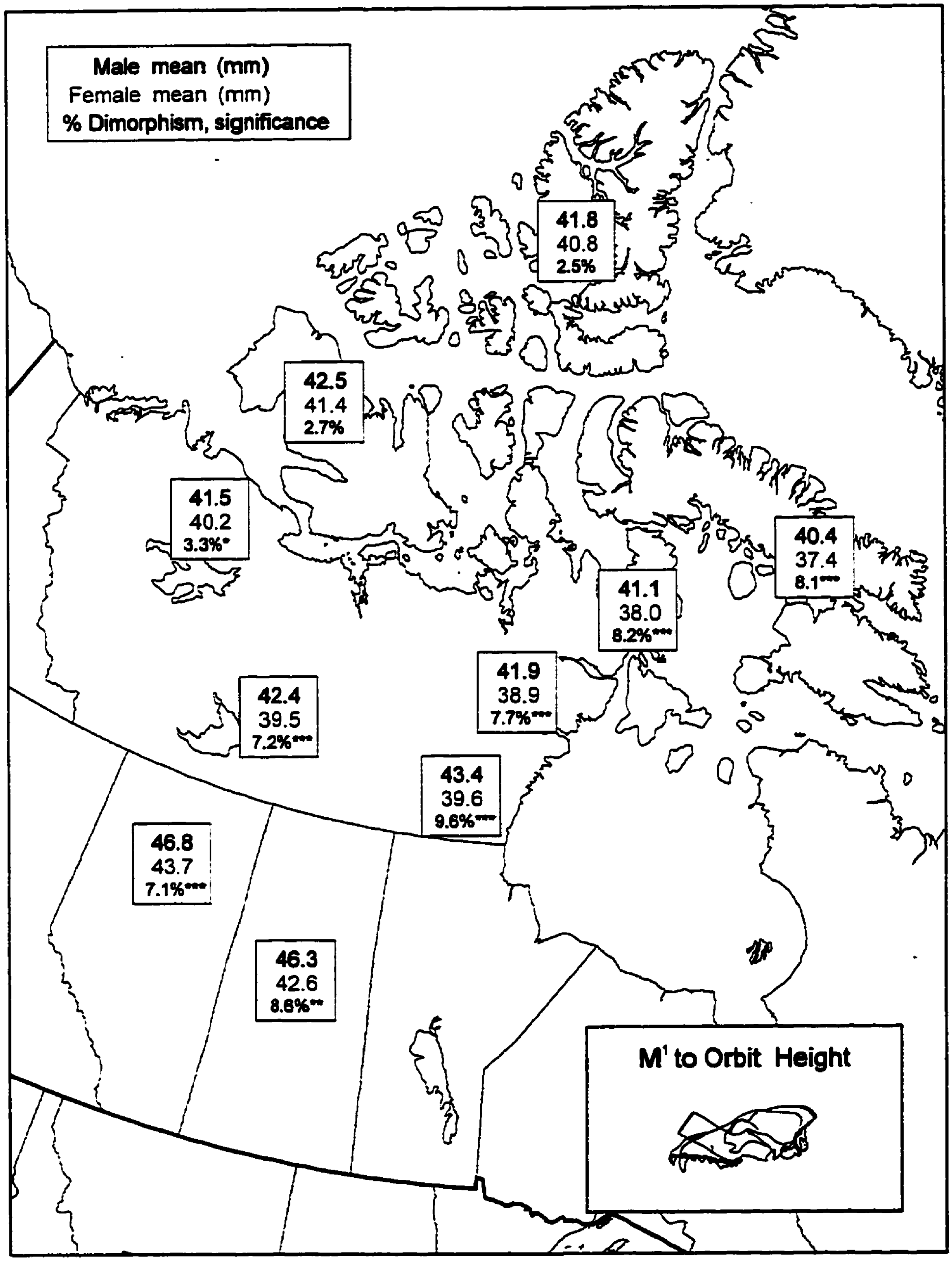

Male mean (mm)
Female mean (mm)
% Dimorphism, significance
41.8
40.8
2.5%
42.5
41.4
2.7%
41.5
40.2
3.3%*
40.4
37.4
8.1***
41.1
38.0
8.2%***
41.9
38.9
7.7%***
42.4
39.5
7.2%***
43.4
39.6
9.6%***
46.8
43.7
7.1%***
46.3
42.6
8.6%**
M1 to Orbit Height

Figure 21. Bivariate plot of mean Condylobasal length (mm) and mean P^4 length (mm) for male wolves from the 10 sampling locations.

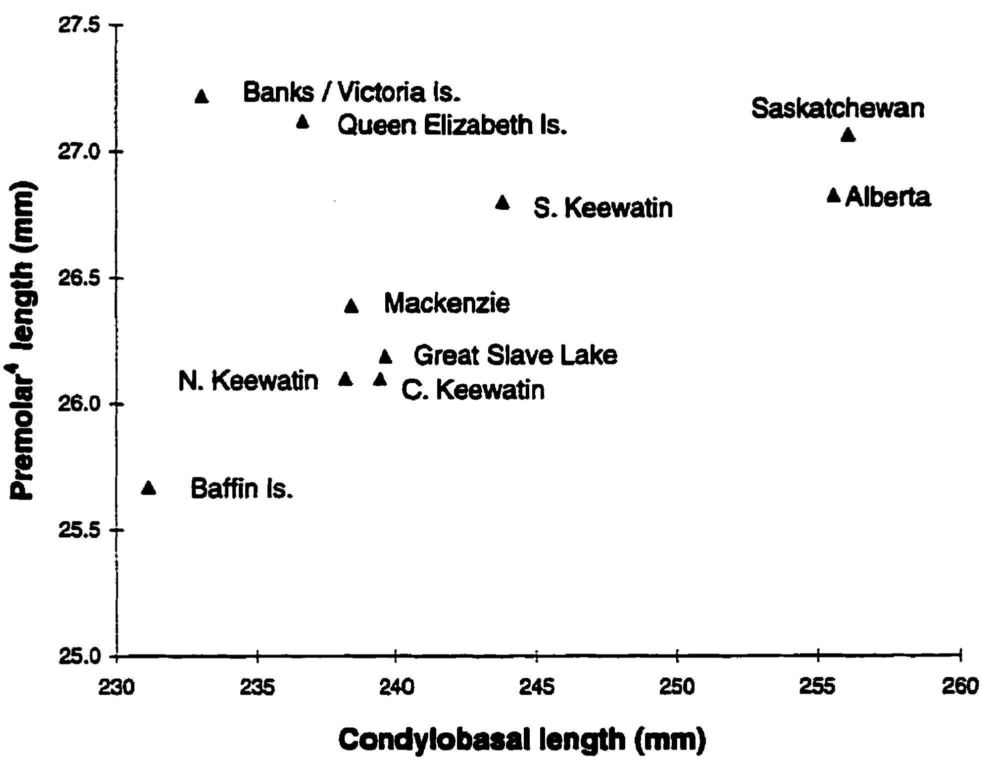

27.5
27.0
26.5
26.0
25.5
25.0
Premolar4 length (mm)
Banks / Victoria Is.
Queen Elizabeth Is.
Saskatchewan
S. Keewatin
Alberta
Mackenzie
Great Slave Lake
N. Keewatin
C. Keewatin
Baffin Is.
230
235
240
245
250
255
260
Condylobasal length (mm)

Table 19. Sexual dimorphic variation of 7 cranial parameters in adult male and female wolves in relation to latitude. Means were compared with a Student's *t-test*. Percent sexual dimorphism ((male - female / female) x 100) with a probability < 0.05 indicates significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Descriptive statistics are listed in Appendices 9.2 - 9.11).

Latitude	Location	Subspecific Designation	*N* M	F	I^1-SagC	Zygom W	Cheek T W	SagC - AudB	L of P^4	Pari-Temp	H of Ramus
> 75°	Queen Elizabeth Is.	*arctos*	*21*	*8*	3.9 *	4.3 *	4.3 **	1.6	4.5 *	1.8	2.6
72°	Banks / Victoria Is.	*bernardii*	*11*	*5*	3.8 *	1.6	3.8	3.4	6.3 **	2.9	3.9
68°	Mackenzie delta	*mackenzii*	*41*	*26*	4.6 ***	5.3 ***	5.9 ***	4.0 ***	5.6 ***	1.8 *	3.2
62°	Great Slave Lake	*occidentalis*	*43*	*36*	5.2 ***	5.0 ***	5.0 ***	4.6 ***	4.8 ***	2.3 **	6.9 **
< 60°	Northern Alberta	*occidentalis*	*34*	*30*	5.5 ***	7.2 ***	5.9 ***	5.8 ***	6.3 ***	2.9 **	7.4 ***
67°	Baffin Island	*manningi*	*15*	*8*	5.1 **	4.9 **	1.9	1.0	3.6	1.3	7.7 *
67°	Northern Keewatin	*hudsonicus*	*31*	*19*	6.5 ***	6.0 ***	5.4 ***	3.9 ***	5.2 ***	1.3	8.8 ***
64°	Central Keewatin	*hudsonicus*	*50*	*60*	5.6 ***	6.1 ***	4.9 ***	5.0 ***	4.0 ***	1.7 **	7.7 ***
61°	Southern Keewatin	*hudsonicus*	*36*	*28*	8.2 ***	6.7 ***	7.3 ***	6.4 ***	8.5 ***	0.9	11.7 ***
52°	C. Saskatchewan	*griseoalbus*	*15*	*6*	6.7 **	6.0 ***	4.5 *	8.1 ***	7.3 ***	2.9	5.6

Ambient Temperature in Relation to Cranial Size

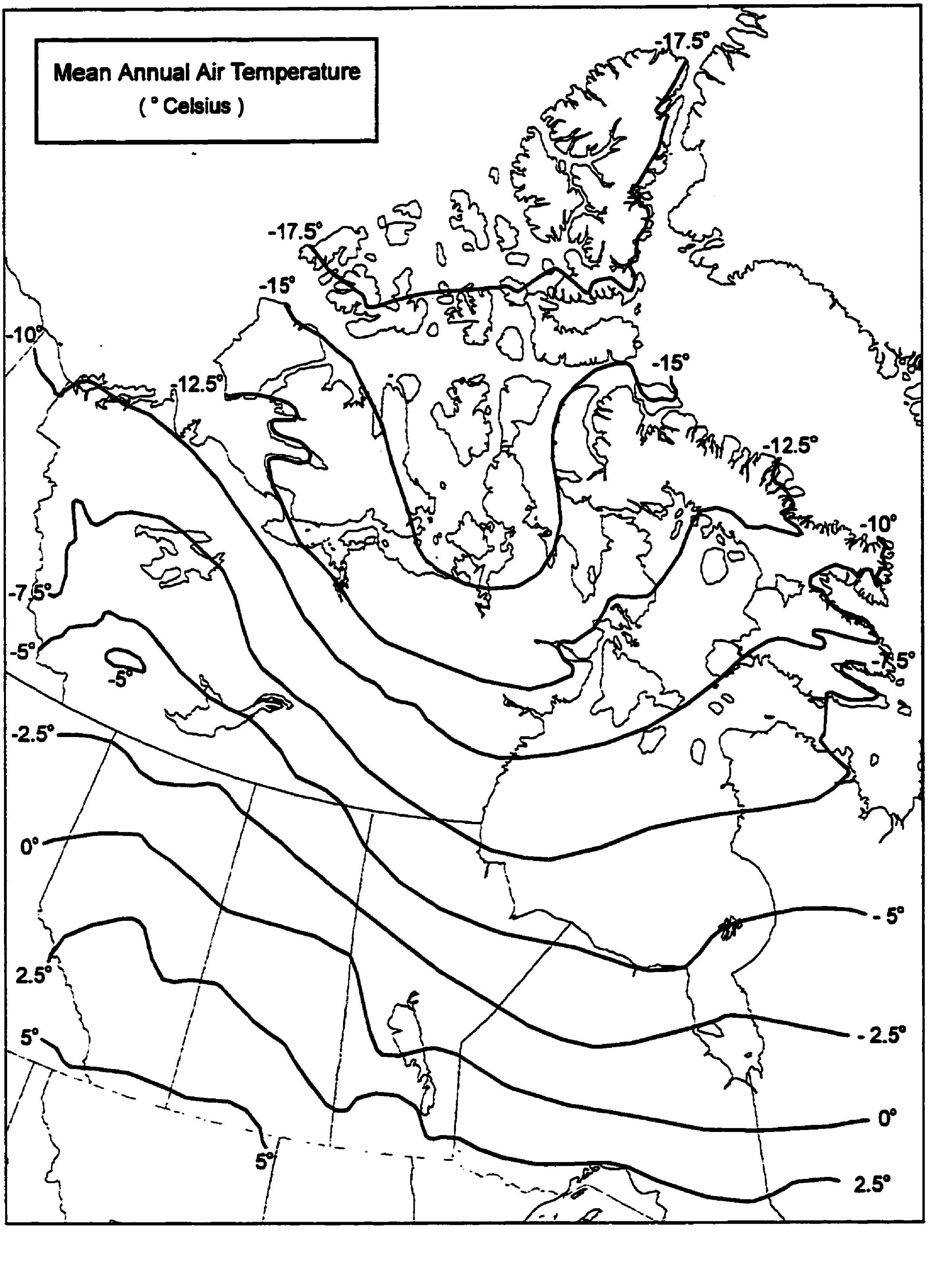
Mean annual, mean summer (July) and mean winter (February) air temperatures were regressed against each of the 3 cranial parameters. A summary of the regession analysis is provided in Appendix 10. In general, isotherms in northern Canada run parallel to the tree-line and move in a north-east to south-west direction (Fig. 22). Mean annual ambient temperature regressed against I^1-SagC for each sex (Fig. 23) resulted in a significant relationship for both males ($R^2 = 0.76$; $P < 0.001$) and females ($R^2 = 0.73$; $P < 0.002$). Mean annual ambient temperature regressed against Palat L. (Fig. 24) also resulted in a significant relationship for males ($R^2 = 0.77$, $P < 0.001$) and females ($R^2 = 0.83$; $P < 0.0003$). Mean annual ambient temperature regressed against Zygom W (Fig. 25) resulted in a significant relationship for males ($R^2 = 0.52$; $P < 0.019$), but an insignificant relationship for females ($R^2 = 0.26$; $P < 0.133$).

Ungulate Prey Weight in Relation to Cranial Size

Adult male and female weights for the two largest ungulate prey species in each geographic location are listed in Table 20. A mean pooled weight was derived by taking the mean value of the largest male and female ungulate species as well as the second largest male and female ungulate species. Mean pooled ungulate prey weight regressed against I^1-SagC (Fig. 26) resulted in a significant relationship for males ($R^2 = 0.81$; $P < 0.0004$) and females ($R^2 = 0.88$; $P < 0.0001$). Mean pooled ungulate prey weight regressed against Palat L (Fig. 27) also resulted in a significant relationship for males ($R^2 = 0.77$; $P < 0.001$) and females ($R^2 = 0.906$; $P < 0.00002$). A regression of mean pooled ungulate prey weight with Zygom W (Fig. 28) resulted in significant relationship for males ($R^2 = 0.87$; $P < 0.0001$) and females ($R^2 = 0.48$; $P < 0.026$). Regression equations with significance levels for the mean body weights of the largest ungulate (M + F) and the second largest ungulate (M + F) prey species considered independently against I^1-SagC and Zygom W are listed in Appendix 12.

A regression of mean pooled ungulate prey with mean annual ambient temperature (Fig. 29) resulted in a significant relationship ($R^2 = 0.77$; $P < 0.0009$).

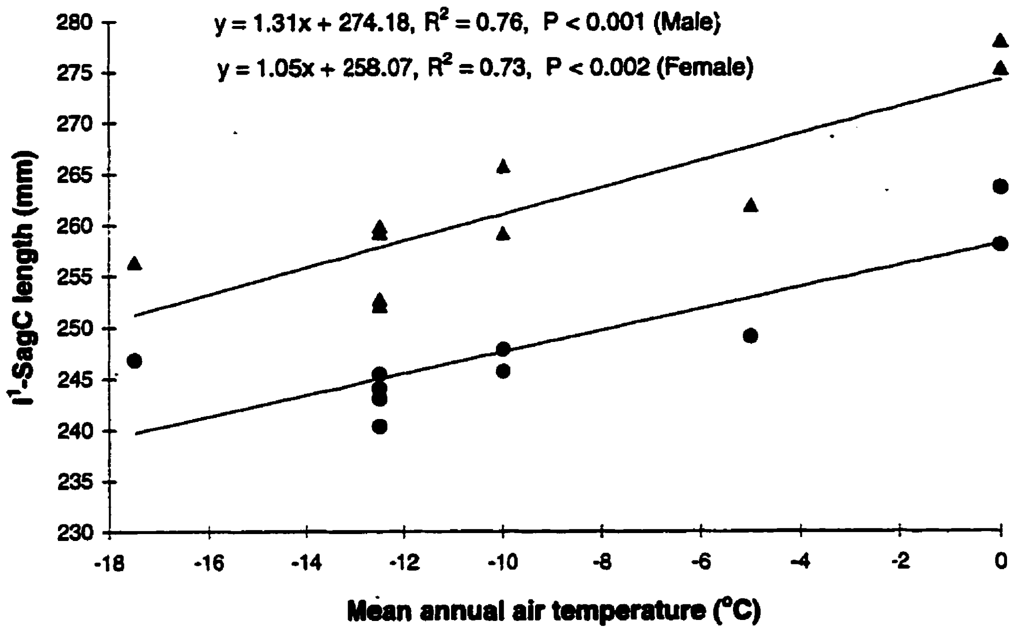
Figure 22. Mean annual air temperatures (°C) for Canada, expressed in isotherms. Data from 1931-1960, adapted from Anonymous (1979).



Mean Annual Air Temperature
(° Celsius)
-17.5°
-17.5°
-15°
-15°
-12.5°
-12.5°
-10°
-10°
-7.5°
-7.5°
-5°
-5°
- 5°
-2.5°
- 2.5°
0°
0°
2.5°
2.5°
5°
5°

Figure 23. Regression of mean annual air temperature (°C) with I^1-SagC length (mm) for male (▲) and female (●) wolves from the 10 sample locations.

Figure 24. Regression of mean annual air temperature (°C) with Palatal length (mm) for male (▲) and female (●) wolves from the 10 sample locations.


y = 1.31x + 274.18, R² = 0.76, P < 0.001 (Male)
y = 1.05x + 258.07, R² = 0.73, P < 0.002 (Female)
I¹-SagC length (mm)
Mean annual air temperature (°C)

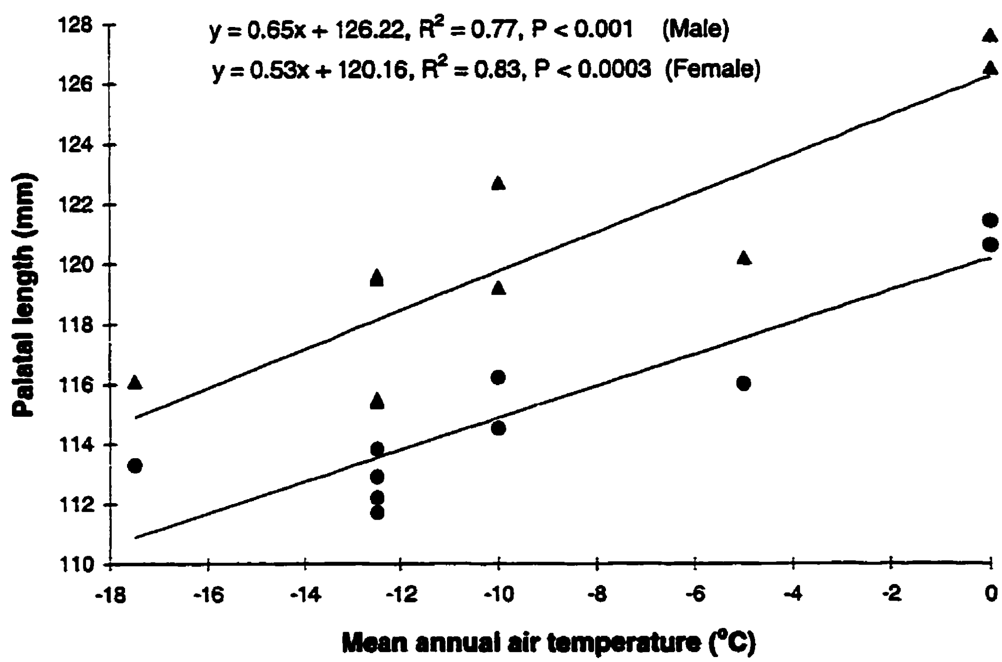
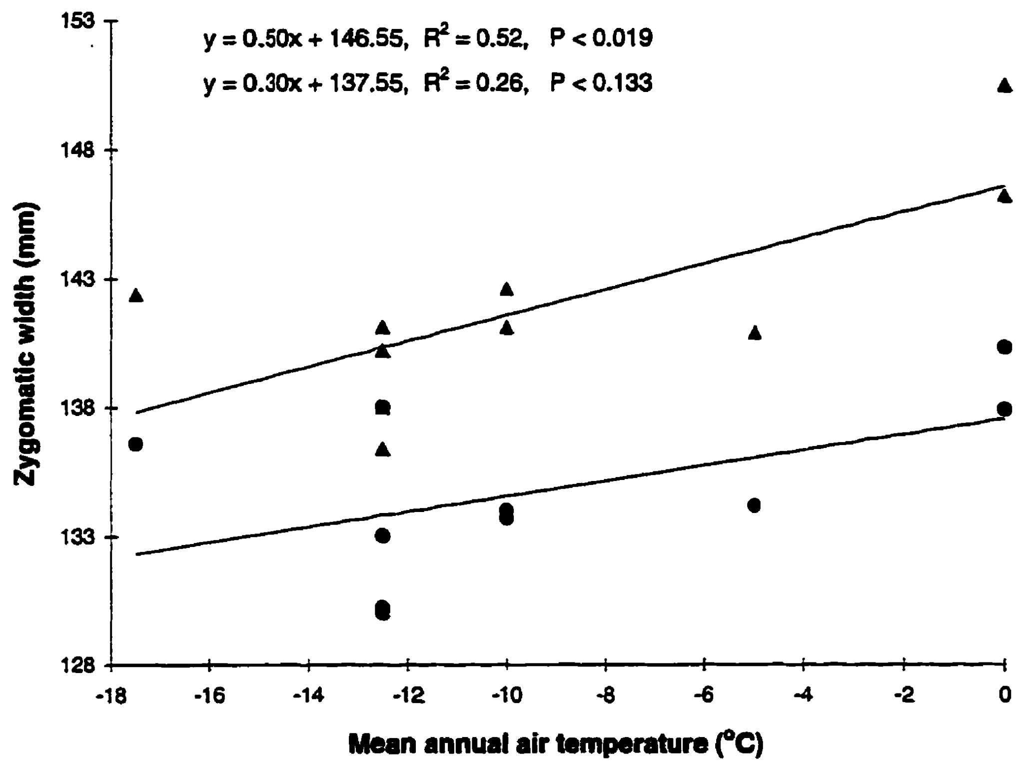

y = 0.65x + 126.22, R² = 0.77, P < 0.001 (Male)
y = 0.53x + 120.16, R² = 0.83, P < 0.0003 (Female)
Palatal length (mm)
Mean annual air temperature (°C)

Figure 25. Regression of mean annual air temperature (°C) with Zygomatic width (mm) for male (▲) and female (•) wolves from the 10 sample locations.



y = 0.50x + 146.55, R² = 0.52, P < 0.019
y = 0.30x + 137.55, R² = 0.26, P < 0.133
Zygomatic width (mm)
Mean annual air temperature (°C)
153
148
143
138
133
128
-18
-16
-14
-12
-10
-8
-6
-4
-2
0

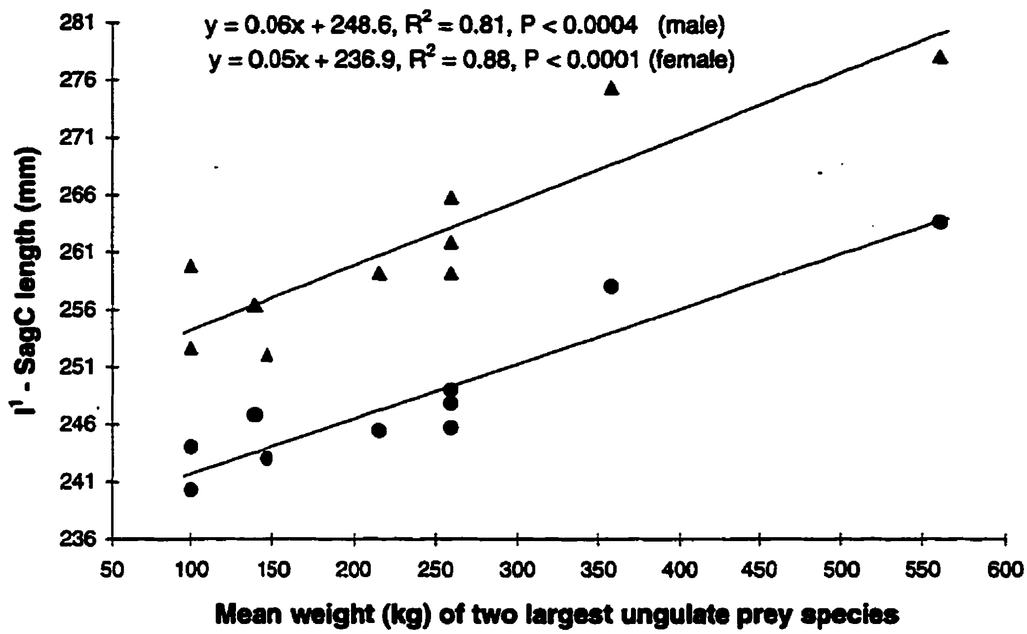
Table 20. Body weights (kg) by sex, for the two largest ungulate prey species utilized by wolves in the study area. Mean pooled weight = (largest M + F prey) + (second largest M + F prey) / 4.

Location	Largest prey item (kg)			Second largest prey item (kg)			Mean Pooled Wt. (kg)
	spp.	M	F	spp.	M	F	
Queen Elizabeth Islands	muskox [a]	262	173	caribou [b]	66	54	138.8
Banks & Victoria Islands	muskox [a]	277	188	caribou [b]	66	54	146.3
Baffin Island	caribou [c]	110	90	none	-	-	100.0
Mackenzie	moose [d]	453	350	caribou [e]	145	90	259.5
Great Slave Lake	moose [d]	453	350	caribou [e]	145	90	259.5
Northern Keewatin	caribou [c]	110	90	none	-	-	100.0
Central Keewatin	muskox [f]	340	288	caribou [e]	145	90	215.8
Southern Keewatin	moose [d]	453	350	caribou [e]	145	90	259.5
Central Saskatchewan	moose [d]	453	350	elk [g]	353	275	357.8
Northern Alberta	bison [h]	850	590	moose [d]	453	350	560.8

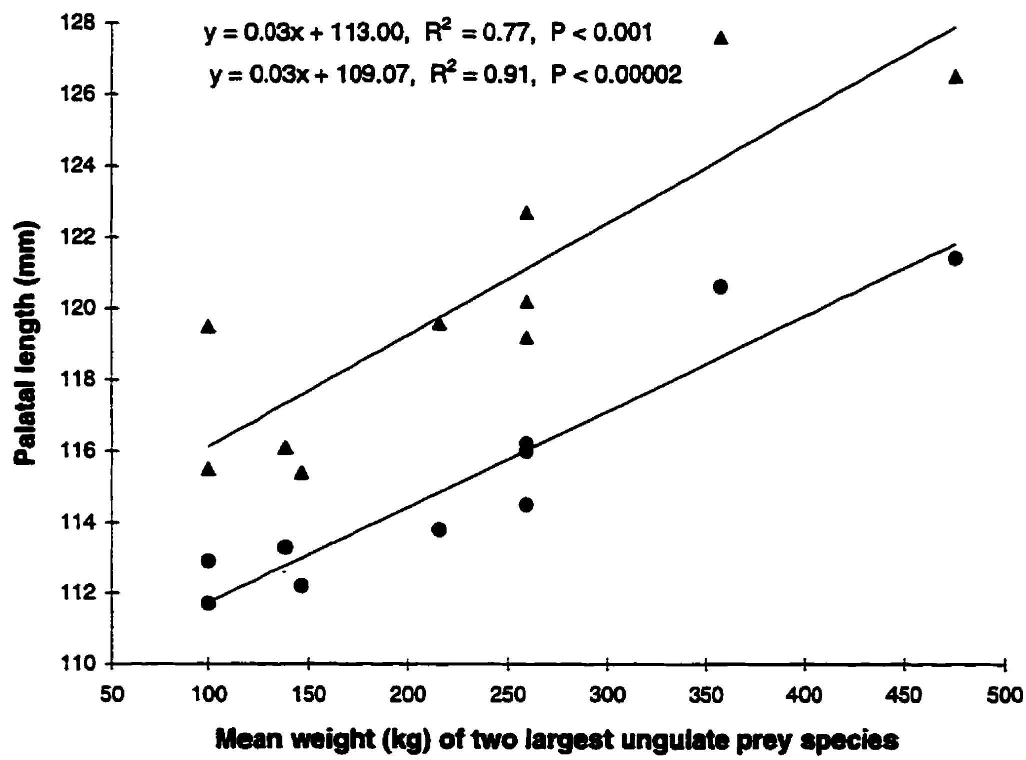
a	*O.m. wardi*	(Latour, 1987)
b	*R.t. pearyi*	(Thomas and Everson, 1981)
c	*R.t. groenlandicus*	(Mike Ferguson, pers. com.)
d	*A.a. andersoni*	(Larter *et at*, 1994)
e	*R.t. groenlandicus*	(Dauphine, 1976)
f	*O.m. moschatus*	(Banfield, 1974)
g	*C.e. manitobensis*	(Blood and Lovaas, 1966)
h	*B.b. athabascae*	(Larter *et al*, 1994)

Figure 26. Regression of the mean body weight (kg) of the two largest ungulate prey species with I^1-SagC length (mm) for male (▲) and female (●) wolves from the 10 sample locations.

Figure 27. Regression of the mean body weight (kg) of the two largest ungulate prey species with Palatal length (mm) for male (▲) and female (●) wolves from the 10 sample locations.



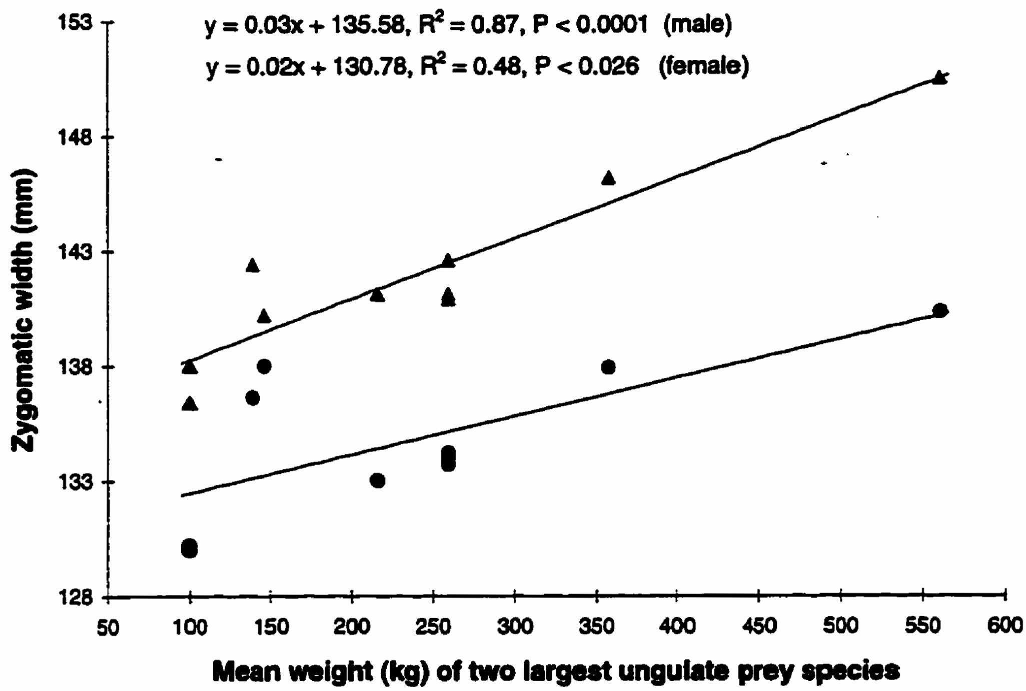
y = 0.06x + 248.6, R² = 0.81, P < 0.0004 (male)
y = 0.05x + 236.9, R² = 0.88, P < 0.0001 (female)
I¹ - SagC length (mm)
281
276
271
266
261
256
251
246
241
236
50
100
150
200
250
300
350
400
450
500
550
600
Mean weight (kg) of two largest ungulate prey species

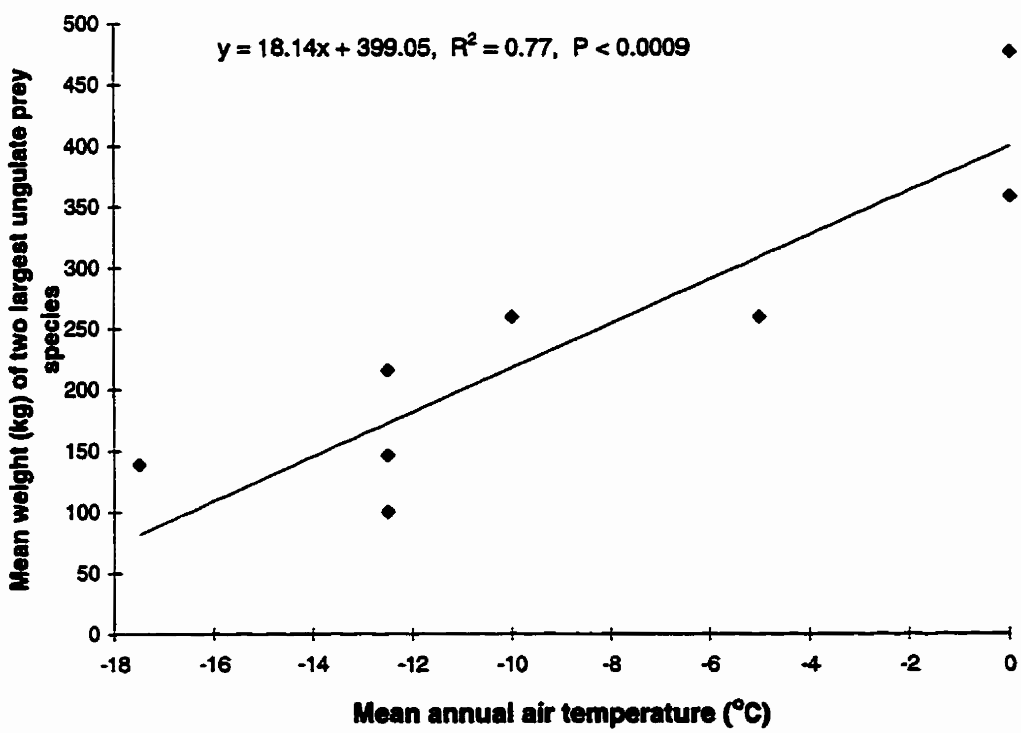


y = 0.03x + 113.00, R² = 0.77, P < 0.001
y = 0.03x + 109.07, R² = 0.91, P < 0.00002
Palatal length (mm)
128
126
124
122
120
118
116
114
112
110
50
100
150
200
250
300
350
400
450
500
Mean weight (kg) of two largest ungulate prey species

Figure 28. Regression of the mean body weight (kg) of the two largest ungulate prey species with Zygomatic width (mm) for male (▲) and female (●) wolves from the 10 sample locations.

Figure 29. Regression of the mean body weight (kg) of the two largest ungulate prey species with mean annual air temperature at the 10 sample locations.


y = 0.03x + 135.58, R² = 0.87, P < 0.0001 (male)
y = 0.02x + 130.78, R² = 0.48, P < 0.026 (female)
Zygomatic width (mm)
Mean weight (kg) of two largest ungulate prey species


y = 18.14x + 399.05, R² = 0.77, P < 0.0009
Mean weight (kg) of two largest ungulate prey species
Mean annual air temperature (°C)

DISCUSSION

Principal Component Analysis of Cranial Parameters

Several authors (Lawrence and Bossert, 1967; Jolicoeur, 1975; Nowak, 1995) reduced the number of cranial parameters under consideration in order to avoid redundancy and to alleviate difficulties in defining and measuring some parameters consistently (measurement error). In this study, it was determined that although some redundancy existed, because overlapping portions of the cranium were measured, there was no possibility of identifying which parameters provided better measures of difference in cranial shape. In addition, Thorpe (1985) suggested that when considering a set of significant characters, the addition of insignificant characters to multivariate analysis had little effect on the geographic patterns obtained. Measurement error in this study was significant in the dental parameters (Appendix 4), but was accepted as an element of the overall variance in the data. It was decided that since the dental parameters contributed useful information to between-group variance on shape, these parameters should be retained in the analysis.

As in similar studies involving cranial morphology, the first 3 principal components accounted for the largest portion of the original sample variance (64.5% for males, 60.2% for females). The first component for males had an eigenvalue of 21.7 representing 48.2% of the variation (Table 5), while females had an eigenvalue of 21.1 representing 46.9% of the female variation (Table 6). The prominence of the first component suggested that nearly half of the variation in both sexes was related to size differences. For both sexes, the second component reflected differences in tooth shape and the third component reflected differences in rostrum width. (As indicated earlier, it is recognized that a portion of the variation in the dental variables reflects variation resulting from measurement error (Appendix 4)).

A one-way Analysis of Variance (ANOVA) was used to identify significant differences between the mean factor scores for each principal component by sex and location (Table 9). Except for PC II in females, a component reflecting dental parameters, this analysis suggested that mean factor scores for all components were significant in terms of representing geographic differences between populations. For both sexes, the high levels of significance for PC I indicated that the mean factor scores on this "size" component contributed the largest portion of the cranial variance among the wolf populations.

Discriminant Analysis of Cranial Parameters

Two assumptions should be met when undertaking discriminant analysis: (1) that data be multivariate normal and (2) that covariance matrices for all groups be equal. Examination of the univariate distribution of each variable by sex provided some assurance that these assumptions were met and a test of data skewness for each of the 45 variables only identified 1 male parameter (P^4 W; -2.30) and 1 female parameter (M^1 - M^1 ; -2.52) which exceeded the threshold (±1.96) for this test (Sokal and Rolf, 1969). Although all individual variables were normally distributed, this still does not necessarily ensure multivariate normality (Manly, 1986). Testing for equality of group covariance is normally undertaken using Box's *M* test (Norusis, 1988b), however, small sample size prevented the determination of group covariances. Skeel and Carbyn (1977) encountered a similar problem. A key assumption of canonical analysis is that dispersions are homogeneous. A violation of this assumption may result in certain desirable properties of the canonical variates being lost and some degree of distortion may occur in the canonical representation of the data (Williams, 1983). This may cause classification results to be overly optimistic (Norusis, 1988b). Despite violation of one or more of these assumptions, it is still recognized that discriminant function analysis is a very useful statistical tool for this type of research (Manly, 1986). If a level of significance can not be determined for these multivariate tests, the results and observed patterns are considered to be more exploratory in nature.

When all 45 cranial variables were used from all 10 populations, 9 canonical discriminant functions were derived for both males and females (Tables 10 and 11, respectively). In males, the first, second, and third components contributed 36.8%, 19.0%, and 11.1% of the variance, respectively. In females, the first, second, and third functions contributed 49.8%, 13.2%, and 11.4% of the variance, respectively. Wilk's lambda indicated that these first 3 functions were significant at the 0.05% level in both sexes (Norusis, 1988b; Appendix 7). A bivariate plot of the first two canonical discriminant functions provided a visual representation of the affinities for the 10 populations of wolves considered in this study (Fig. 9). Both males and females from the Queen Elizabeth Island population were completely separate from the mainland groups. Males from the Banks / Victoria Island population overlapped with the Queen Elizabeth Island population and were totally separate from all the mainland populations. Females from Banks / Victoria Island had a greater affinity with the Baffin Island and mainland females than with Queen Elizabeth Island females, although this conclusion requires caution considering the small sample size (n=3). Both males and females from the C. Saskatchewan and N. Alberta populations overlapped, but were separate from the N.W.T. populations. The small sample of Great Slave Lake females (n=4) overlapped slightly with the N. Alberta and C. Saskatchewan females and were separate from the remaining N.W.T. wolves. In contrast, males from Great Slave Lake were entirely within the N.W.T. mainland populations, overlapping with Mackenzie, S. Keewatin, and C. Keewatin males. Baffin Island males overlapped with all the Keewatin and Mackenzie populations, while females (n=3) overlapped only with the females from Keewatin and Banks / Victoria Islands.

In order to examine the relationships between the 3 Keewatin populations and the Great Slave Lake and C. Saskatchewan populations, a second discriminant analysis was performed among these 5 groups (Fig. 10). Males and females from C. Saskatchewan were completely separate from the N.W.T. populations. Males from the Great Slave Lake population had affinities with the S. Keewatin and C. Keewatin males, while females from Great Slave Lake (n=4) did not overlap with any of the Keewatin females. Males from N. Keewatin had affinities with males from C. Keewatin, but not with males from the S.

Keewatin population. However, the 3 populations formed a cline, a trend also evident in the univariate data. Males from S. Keewatin had affinities with males from C. Keewatin and Great Slave Lake, but not with the N. Keewatin or C. Saskatchewan males. Females from S. Keewatin overlapped with C. Keewatin females and both groups were adjacent to the N. Keewatin females. The higher levels of similarity for females of the 3 Keewatin regions compared with males, may be a reflection of the lower levels of cranial variability in the female sex.

Two points of caution should be raised in interpreting the population affinities in Figures 9 and 10. The small sample sizes, particularly for females from the Queen Elizabeth Islands (n=3), Baffin Island (n=3), Banks / Victoria Island (n=5), and C. Saskatchewan (n=6) may not fully represent the distribution of these populations. Additional samples from these locations would increase the distribution area and possibly result in greater levels of overlap among adjacent groups. Secondly, these plots do not reflect the actual geographic distance separating the wolf populations. In Figure 10, for example, one might conclude that the greater distance separating S. Keewatin males from C. Saskatchewan males would result in an abrupt morphological difference between these populations. However, one must also consider that C. Saskatchewan wolf specimens were collected over 800 km from the S. Keewatin specimens, compared with the relatively shorter 400 km distance separating S. Keewatin from C. Keewatin specimens. Sampling of wolves between S. Keewatin and C. Saskatchewan may reveal that specimens are intermediate in size and represent a broader pattern of clinal variation. The detection of slight shifts in mean values of morphological traits is difficult, if precise geographic locations are unknown. Despite these cautions, Figures 9 and 10 provide the best representation of the affinities of wolf populations in northern Canada to date. The discriminant analysis of each sex separately represents a form of validation, although a true test of the effectiveness of this analysis would involve splitting the sample for each sex. Unfortunately, small sample sizes made this impractical, however, the relative positions of the male and female groups in Figures 9 and 10 revealed similar patterns of distribution, providing a measure of confidence in the results.

Discriminant analysis can also be used to calculate a Mahalanobis Distance (D^2), which is a generalized measure of the distance between two groups (Norusis, 1988b). This approach has been used in a number of taxonomic studies of *C. lupus* (Lawrence and Bossert, 1975; Pedersen, 1978; Schmitz and Kolenosky, 1985; Nowak, 1995). SPSS was unable to generate actual D^2 values with this data, although a similar measure of statistical distance was provided with F-statistic values (Norusis, 1988b). A summary of the between-group values, involving 51 iterations for males and 59 iterations for females (Table 15), offered general support to the relationships established in the earlier discriminant analyses. F-statistic values for male wolves from adjacent populations are presented in Figure 11. The higher F-statistic values separating (1) Queen Elizabeth Island and Banks / Victoria Island populations from other adjacent populations, and (2) N. Alberta and C. Saskatchewan populations from the N.W.T. populations, support the conclusion that there are three primary affinities or subspecies of wolves in north central Canada.

Another means of representing the between-group variability with discriminant functions involves the use of classification tables. When all 45 cranial parameters were employed, a relatively high proportion (82.7%) of the male specimens were correctly classified to geographic location (Table 12). The prior probability of correct classification expected by chance for each group was 10%. Lower classification successes (66.7% - 77.8 %) occurred in the Mackenzie, Great Slave Lake, C. Keewatin, and S. Keewatin populations. Considering the close geographic proximity of these mainland groups to each other and the opportunity for movement and interchange, this lower classification success was expected. The classification success for female specimens (83.5%) was similar to the level of success found for males. In females, lower classification successes (69.4% - 83.3%) were found in the C. Keewatin, S. Keewatin, and Mackenzie populations. This pattern was similar to that derived for the males, and can similarly be explained by the close proximity and opportunity for group interaction. Although interpretation of these results should be viewed with some reservation due to the smaller sample sizes, this analysis involved the largest number of wolf specimens (347 for discriminant analysis; 525 for univariate analysis) considered to date for northern Canada. Similar classification tables have been employed in the study of *C. lupus* crania by Pedersen (1978) and Friis (1985), however, their investigations involved different populations with sample sizes of 150 and 258, respectively.

In order to evaluate the importance of the number of cranial parameters on the ability of the discriminant analysis to correctly classify specimens to specific geographic populations, three combinations of parameters were considered for each sex. In addition to the 45 parameters measured in this study, subsets of significant variables (25 for males and 24 for females) determined by PCA, were also tested. Additionally, the 10 parameters employed by Nowak (1995, Appendix 5) were also used to allow comparison between these two studies. In general, the overall pattern of classification success declined with the reduction in the number of cranial parameters (Table 14). In males, the classification success was 82.7% with 45 parameters, 66.7% with 25 parameters, and 40% with 10 parameters. However, the Baffin Island specimens were an exception, as males were correctly assigned in 100% of the cases with 45 parameters, in 81.8% of cases with 25 parameters, and in 83.8% of cases with 10 parameters, while 100% of the female cases were correctly assigned for each of the three sampling combinations. In contrast, in wolf populations on the N.W.T. mainland, which presumably had greater levels of interchange, 10 cranial parameters provided an insufficient degree of resolution for correctly assigning individuals, while 45 parameters offered greater resolution and correctly assigned a much higher proportion of the cases. The use of a small set of well defined cranial parameters (Nowak, 1995) may be effective in distinguishing isolated populations or populations separated by large distances, however, the number of cranial parameters must be doubled or quadrupled to identify individuals from populations in close proximity or where movement between populations is frequent.

The pattern of classification success in Table 14 suggests that caution is required in drawing conclusions about taxonomic affinities when using discriminant analysis. For example, the application of the "75 percent rule" (Mayr *et al.*, 1953) would be strongly influenced by the number of cranial parameters employed. In previous studies of *C. lupus*, authors have used various numbers of cranial parameters: Goldman (1944) - 15; Jolicoeur (1959) - 12; Kolenosky and Standfield (1975) - 27; Skeel and Carbyn (1977) - 15; Pedersen (1978) - 22; Friis (1985) - 19; Pichette and Voigt (1985) - 9; Schmitz and Kolenosky (1985) - 21; Goldman (1995) - 10. Sokal and Sneath (1963) indicated that there is no clear answer to the optimum number of characters necessary for numerical taxonomy, although it is probably between 50-100. Future studies utilizing cranial morphology of *C. lupus* and other species to identify taxonomic relationships would benefit by a standard approach to the number and selection of cranial measurements. This standardized protocol would provide consistency and additional confidence in the interpretation of taxonomic and genetic relationships.

Geographic Variation

It is well documented that phenotypic variation is influenced by environmental factors (Pianka, 1988), and as Mayr (1970) stated that "the phenotype of every local population is very precisely adjusted to the exacting requirements of the local environment". In addition, evidence suggests that genetic variation in *Canis lupus* may have been influenced by the geographic isolation in refugia during the Wisconsin glaciation (Flint, 1952; Banfield, 1962; Macpherson, 1965). During this period, wolves may have been isolated in primarily three glacial refugia; Pearyland, Beringia, and south of the ice sheet in present day United States (Johnsen, 1953; Guthrie, 1968; Bennike, 1981; Nelson and Madsen, 1986; Youngman, 1993). Subsequent convergence of these isolated populations in the post-glacial period has further complicated the issue. Morphological variation may also be influenced by prey size, ambient temperature, and a wide range of other environmental factors (Jolicoeur, 1975; Geist, 1987; Pianka, 1988; Hillis and Mallory, 1996), however, a review of all environmental parameters influencing cranial morphology was well beyond the scope of this study. The focus of this study was to describe geographical differences in cranial size and shape of *Canis lupus* with a view toward identifying subspecies and their affinities in central and northern Canada.

Subspecific Designations

Nowak (1983) made the comment that "species are created by God, but other taxonomic categories including subspecies are devised in the human mind", and emphasized that attempting to describe and categorize biological variation at the subspecific level can be a subjective exercise. Goldman (1944) made the first major attempt at the subspecific classification of *C. lupus* in North America. His subspecific designations and descriptions of wolf subspecies in Canada and Alaska were based on pelage colour, minor skeletal variation, and variation in body size and weight (Appendix 1) and provided a basis for subsequent taxonomic studies. Goldman (1944) was restricted by small sample sizes, particularly in northern Canada (Appendix 2) and only compared mean values for 15 cranial measurements (Appendix 3). Anderson (1943) described wolves in Saskatchewan as *C.l. knightii*, which was eventually renamed *C.l. griseoalbus* (Hall and Kelson, 1959) and provided an additional subspecies to wolf classification in Canada. The subsequent distributions and subspecific designations portrayed by Hall (1981) represent the standard to which most recent researchers have compared their work (Fig. 1). The more recent application of multivariate statistical procedures to analyse taxonomic variation in mammals has provided a more sophisticated means of studying species and subspecies. The original designations by Goldman (1944) have since come under scrutiny and taxonomic studies in Alaska (Rausch, 1953; Pedersen, 1978) and Canada (Jolicoeur, 1959; Kelsall, 1968; Lawrence and Bossert, 1975; Skeel and Carbyn, 1977; Nowak, 1983; Friis, 1985; Pichette and Voigt, 1985; Brewster and Fritts, 1995; Nowak, 1995) have concluded that consolidation of subspecific classifications is required. Nowak (1983, 1995) has proposed that a review of the North American taxonomy of *Canis lupus* is required and that the number of subspecies should be reduced to five designations (Fig. 2).

No attempt was made in this study to analyse the data of Goldman (1944) for wolves from the Northwest Territories, Canada (Appendix 2), due to his limited sample sizes and restricted distributions for *C.l. hudsonicus* (n=6) and *C.l. arctos* (n=1). The larger sample size of *C.l. occidentalis* (n=26) was broadly based over a wide geographic area (Appendix 2) and the relatedness of individuals within the sample was questionable. A summary of published mean values for I^1-SagC, Zygom W, Cheek T W, and P^4 L for designated subspecies in northern Canada is tabulated in Appendix 6, although no analysis of these data was attempted.

The results of this study tend to support the view of Nowak (1983, 1995) that a consolidation of the subspecific designations of Goldman (1944) is warranted. A simple bivariate plot of mean Condy L and P^4 L as used by Nowak (1983) provides a typical representation of the relative relationships of wolves in northern Canada (Fig. 21). Banks /Victoria Island and Queen Elizabeth Island populations were distinct from the C. Saskatchewan and N. Alberta populations, while the remaining N.W.T. populations were dispersed along a separate sequence (Fig. 21). This pattern was also evident in the multivariate analysis of the first two canonical discriminant functions (Fig. 9), which distributed the specimens from the 10 geographic locations into three primary aggregates. The conclusion of this study is that three subspecies of *C. lupus* are currently found in the central Canadian region and subpopulations within each of these three designations represent ecotypes influenced by localized environmental variation.

1) High Arctic Wolves (*C.l. arctos* and *C.l. bernardi*)

The cranial parameters for males from the Queen Elizabeth Island and Banks / Victoria Island populations were related but were distinct from the mainland populations. Similarly, females from the Queen Elizabeth Island population were different from those of mainland populations, however, the Banks / Victoria Island females had similarities and overlapped with the mainland females. The small number of female specimens (n=3) however, requires cautious interpretation of the results and further sampling in this region should be done. However, the overall results support the conclusion that wolves from the Queen Elizabeth Islands and Banks / Victoria Islands are distinct from all mainland populations. The available data does not distinguish Banks / Victoria Island wolves (*C.l. bernardi*) from Queen Elizabeth Islands wolves (*C.l. arctos*), and clearly until additional data becomes available, the suggestion of Nowak (1995) that *C.l. bernardi* is a subpopulation of *C.l. arctos* appears reasonable.

2) Mainland Tundra Wolves (*C. l. manningi, C.l. hudsonicus, C.l. mackenzii,* and the northern population of *C.l. occidentalis*)

Cranial parameters of both males and females from Baffin Island, N. Keewatin, C. Keewatin, S. Keewatin, Mackenzie, and Great Slave Lake overlapped significantly and indicated that these populations were part of a single, large subspecific complex (Fig. 9). Examination of univariate parameters (Figs. 12 - 20; Table 18) confirmed that a cline in cranial size occurs in the Northwest Territories. Wolves were smallest on Baffin Island and increased in size towards the south central and south western regions. Populations of wolves along the tree-line (northwest - southeast) had a strong similarity with each other. This cline was similar to the pattern reported by Jolicoeur (1959, 1975) for wolves in the western N.W.T. region. Although the cline in cranial size is particularly pronounced for males, this study found no marked discontinuity in the gradient. It is generally acknowledged that subspecific designations are only considered when an abrupt step or a pronounced change in characteristics occurs (Mayr *et al.*, 1953; Pimental, 1958; Mayr, 1963). Since neither of these factors were evident, it was concluded that these populations represent one subspecific designation.

As no specimens were available west of the Mackenzie and Great Slave Lake populations, this study could not define a western boundary for the mainland tundra wolves. It may be that wolves in the N.W.T. share an affinity with Yukon and Alaska populations, or that subspecific populations in northeast Alaska (*C.l. tundrarum*), Yukon (*C.l. pambasileus*), and British Columbia (*C.l. columbianus*) are geographically separated from the N.W.T. populations by the physical barrier posed by the Richardson and Selwyn Mountains. Once published, cranial data collected by V. Walker (pers. comm.) in the Mackenzie delta may help clarify the subspecific status of *C. lupus* in this region.

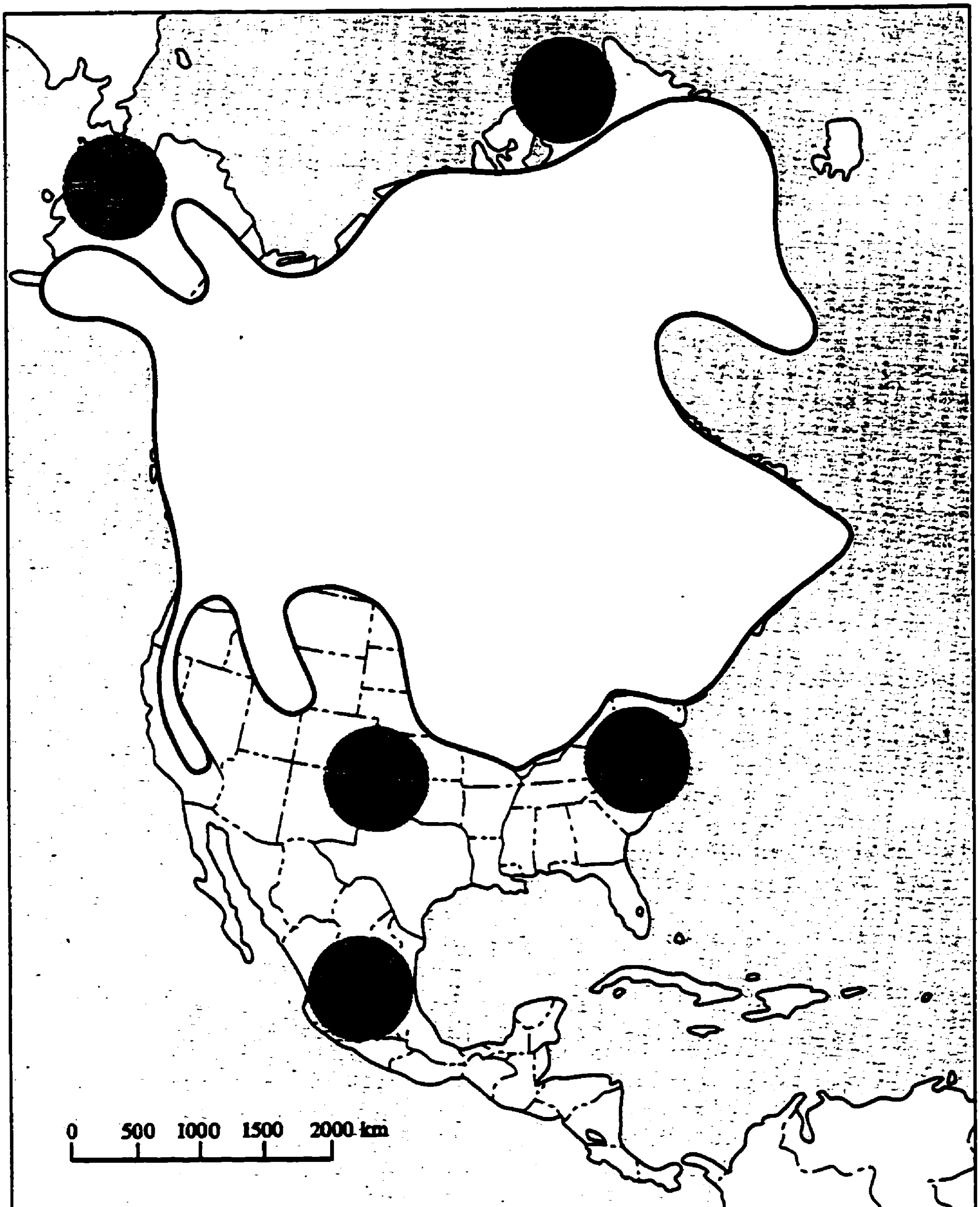
Although the Great Slave Lake population was distinct from the N. Alberta and C. Saskatchewan populations in the west, the relationship in the east between the S. Keewatin population and wolves of northern Manitoba and northern Ontario remains unclear. Additional effort to collect specimens from these regions is required and would allow researchers to clarify the relationships between these populations. In addition, none of the current literature has recognized the considerable variation in cranial size in male wolves of the Keewatin Region. For example, mean total skull length (I^1-SagC) in S. Keewatin males (Appendix 9.9) was 2.3% longer than found in N. Keewatin males (Appendix 9.7). Pooled values for Keewatin specimens (Appendix 9.12) were slightly greater than those previously cited in the description of *C.l. hudsonicus* (Appendix 6). The existing distribution of *C.l. hudsonicus* as described by Goldman (1944) was clearly arbitrary considering his limited and localized sampling (Figs. 1, 3). The suggestion by Nowak (1995) that a single subspecific designation (*C.l. nubilus*) collectively represents the wolves in the eastern arctic as well as wolves in the southwestern United States would also appear to be questionable; however, lack of data for wolves from Manitoba, Ontario, and the central United States prevents an assessment of these relationships and possible clines.

3) Central Boreal Wolves (*C.l. griseoalbus* and southern population of *C.l. occidentalis*)

The third primary group distinguished by multivariate analysis included the C. Saskatchewan and N. Alberta populations (Fig. 9). Both sexes of these two groups overlapped with each other and were distinct from the N.W.T. populations. The females from Great Slave Lake (n=4) were an exception, and were the only group from the N.W.T. with a partial affinity to the N. Alberta and C. Saskatchewan populations. Movement of females between populations is possible as the distance is relatively short and no physical barriers exist. The N. Alberta animals were the largest wolves in this study, similar to the results documented by Gunson and Nowak (1979). Although the C. Saskatchewan and N. Alberta populations were distinct from mainland tundra wolves in the N.W.T., further site specific sampling would be valuable to establish whether a cline exists in size and shape between these two subspecific designations.

In summary, this study identified three primary designations or subspecies of the wolf in northern Canada: (1) High Arctic Wolves - *C.l. arctos* (Pocock, 1935), (2) Mainland Tundra Wolves - *C.l. occidentalis* (Richardson, 1829), and (3) Central Boreal Wolves - *C.l. nubilus* (Say, 1823). The morphological differences among these 3 populations support the hypothesis that subspeciation occurred during the Wisconsin glaciation, when isolated refugia (Fig. 30) existed in the northern part of the continent (Rand, 1954; Macpherson, 1965; Nowak, 1983). Morphological affinities suggest that (1) the High Arctic subspecies evolved in Pearyland (Queen Elizabeth Islands and northern Greenland), (2) the Mainland Tundra subspecies evolved in Beringia (Alaska and Yukon), and (3) the Central Boreal subspecies evolved south of the ice sheet in the central United States. Mayr (1970) also concluded that geographic isolation caused by glaciation was the only effective isolating mechanism influencing wolves in North America. Bryant and Maser (1982) concluded the Wisconsin glaciation influenced the subspecific designations of North American elk (*Cervus elaphus*). The 3 subspecies of caribou (Peary caribou - *Rangifer tarandus pearyi*, barren-ground caribou - *R..t. groenlandicus*, and woodland caribou - *R.t. caribou*) display similar patterns of geographic distribution, lending further support to this theory (Rand, 1954; Banfield, 1961; Røed *et al.*, 1986; Røed *et al.*, 1991). Subsequent postglacial dispersal and convergence of these three wolf populations would have contributed to the genetic diversity

Figure 30. Maximum extent of Pleistocene glaciation in North America and 5 refugia for wolf populations, as proposed by Nowak (1983).



1 Northern group
2 Southern group
3 *Canis lupis arctos*
4 Eastern *C. l. lycaon*
5 *C. l. baileyi*

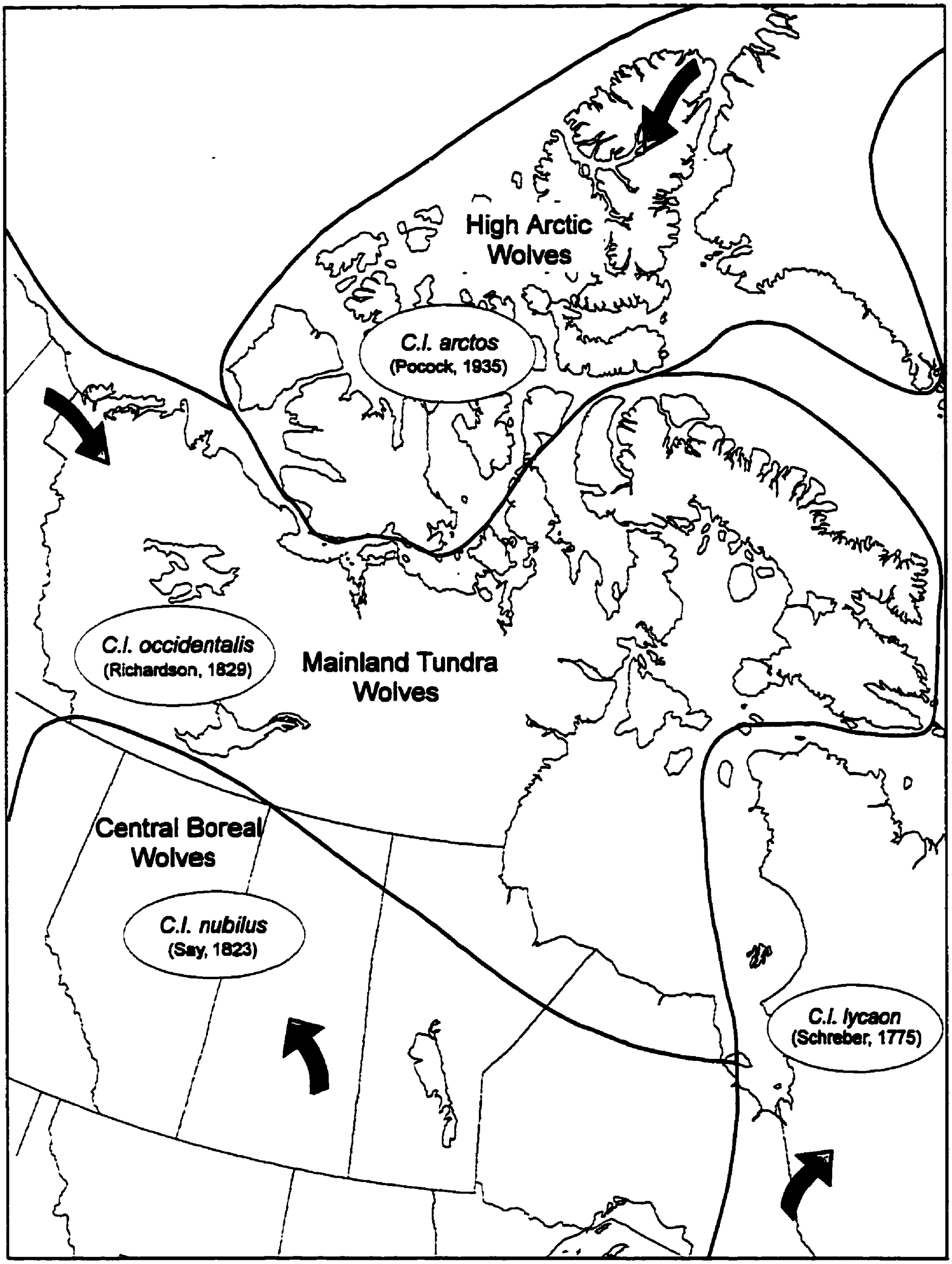
and morphological variation presently evident for *Canis lupus* in North America.

Although this study did not examine cranial samples to the west (Yukon/Alaska) and east (Ontario/Quebec) of central Canada, previous studies have shown that subspecific boundaries are most often associated with physical barriers or habitat change (Banfield, 1961; Røed *et al.*, 1991). In addition, logic would dictate that predators would disperse with prey that they were historically associated with postglacially. Therefore, *C.l. lycaon* which evolved south of the Wisconsin ice-sheet in eastern North America should be associated with the woodland caribou subspecies that evolved in the same region. Similarly, *C.l. arctos*, which evolved in Pearyland should be associated with the Peary caribou subspecies, as it is at the present time. For these reasons, the author suggests that the subspecific boundaries identified by Nowak (1983) should be modified to those indicated in Figure 31. Nowak (1995) indicates that wolves in Alaska and the Yukon are affiliated with the Mainland Tundra Wolves in the western N.W.T., which are associated with the "barren-ground" caribou subspecies originating in Beringia (Røed *et al.*, 1991) and the data from the current study indicates that this association extends eastward to Baffin Island (Fig. 31).

In the center of the continent, the subspecific boundary separating the "Northern group" from the "Southern group" (Fig. 2) should be moved northward towards the N.W.T. border in order to distinguish Mainland Tundra Wolves from the Central Boreal Wolves (Fig. 31). As well, in recognition of the unique characteristics of *C.l. lycaon* in eastern North America, the eastern boundary of the "Northern group" (Nowak, 1983) should be shifted westward to run south of James Bay (physical barrier). These subspecific designations (Fig. 31) would also be consistent with the subspecific designations based on genetic analysis for *Rangifer tarandus* proposed by Røed *et al.* (1991).

If these subspecific boundaries for *C. lupus* in northern Canada (Fig. 31) are accepted, the rules of nomenclature would dictate that the subspecific names should revert to the original descriptions. Therefore, it is proposed that the 3 subspecific designations identified

Figure 31. Subspecific boundaries of *Canis lupus* in northern Canada, as proposed by this study. Arrows reflect possible refugial origins for each subspecific designation.


High Arctic
Wolves
C.l. arctos
(Pocock, 1935)
C.l. occidentalis
(Richardson, 1829)
Mainland Tundra
Wolves
Central Boreal
Wolves
C.l. nubilus
(Say, 1823)
C.l. lycaon
(Schreber, 1775)

by this study be renamed: (1) High Arctic Wolves - *C.l. arctos* (Pocock, 1935), (2) Mainland Tundra Wolves - *C.l. occidentalis* (Richardson, 1829), and (3) Central Boreal Wolves - *C.l. nubilus* (Say, 1823). Wolves presently occuppying northern Alberta may represent remnant populations of a large subspecies associated with bison and may be distinct from wolves in the southwestern United States, also classified as *C.l. nubilus*.

Sexual Dimorphism

Sexual dimorphism has been documented in the crania of *Canis lupus* (Anderson 1943: Jolicoeur 1959, 1975; Gipson *et al.*, 1974; Kolenosky and Standfield, 1975; Pedersen, 1978, 1982; Walker *et al.*, 1993). In this study, sexual dimorphism ranged from 1.8% (Pari-Temp W) to 8.9% (W of C^1) and was highly significant ($P < 0.001$) for all 45 cranial parameters (Appendix 8.1). In general, males were larger than females by 2 - 9% in all cranial traits, with a few exceptions.

Sexual dimorphism was analysed geographically (Appendices 9.2 - 9.11), although levels of significance may have been influenced by small sample sizes in some regions. Females from Baffin Island (n=8) and Banks / Victoria Island (n=5) had larger measures of InterOr W, Postorb W, and Tem Fos W than males and additional cranial samples from these regions are required to confirm whether these differences reflect a sampling bias. Pari-Temp W, a measure of brain case width, was the least dimorphic trait (0.9 - 2.9%) of the 45 cranial parameters measured. In contrast, sexual dimorphism exceeded 10% in the Nasal L (10.7%), Art Con L (12.2%), and Art Con W (12.0%) at several locations.

Sexual dimorphism was also examined in terms of patterns of geographic variation. Nine parameters representing primary measures of cranial size reflected a general increase in the level of sexual dimorphism from the northeast to the southwest (Figs. 12 - 20). Jolicoeur (1959, 1975) found a similar pattern of clinal variation for wolves in the western N.W.T. The levels of sexual dimorphism for all 45 cranial parameters are summarized in Appendix 10. The pooling of these values, represented at the bottom of Appendix 10, appears to confirm an overall pattern of clinal variation with levels of sexual dimorphism lowest in the northeast (Baffin Island) and highest in the southwest (N. Alberta).

Sexual dimorphic difference can be caused by size changes in either sex. On the N.W.T. mainland, increased male size was the primary contributor to the increasing levels of dimorphism. Although male and female wolves from C. Saskatchewan and N. Alberta were larger than N.W.T. wolves in absolute size, the lower levels of sexual dimorphism for a number of parameters in these animals were attributed to the distinctly larger females. In addition, wolves from Banks /Victoria Island and Queen Elizabeth Islands were larger than wolves from the adjacent Mackenzie region, which influenced the levels of sexual dimorphism. In general, the observed clinal pattern of sexual dimorphism was distinct for the N.W.T mainland and Baffin Island wolves. Slight deviations from this clinal pattern were observed for Banks /Victoria Island and Queen Elizabeth Island populations to the north and for C. Saskatchewan and N. Alberta populations to the south. These anomalies represent regions where wolf populations appear to be genetically different due to isolation during the last glaciation (Rand, 1954; Macpherson, 1965; Røed *et al.*, 1991; Brewster *et al.*, 1995).

Considering the sexually dimorphic variation in the cranial morphology of *C. lupus*, discriminant analysis was able to correctly assign 85.3% (Table 16) of the specimens with respect to sex, when all 347 complete cases were considered. The prior probability expected by chance for each group was 50%. When discriminant analysis was used to classify specimens by sex for each geographic area (Table 17), specimens were correctly assigned in 95.8% of the cases. An exception were the females from Baffin Island, where 75% (6 of 8) of specimens were correctly assigned. All female cases from the remaining 9 geographic locations were correctly assigned (100%). It is possible that the lower levels of sexual dimorphism observed in wolf crania on Baffin Island may have contributed to the lower level of classification success. The overall classification success for males (94.1%) was lower than for females and may be due to the greater variation found in males, as evident by S.D.

of mean values (Appendices 9.1 - 9.12). In addition, the lower levels of classification success for males on the arctic islands could be influenced by lower levels of sexual dimorphism observed in this area. Interpretation of these results must be done with caution considering the small sample sizes involved and the fact that only 3 of the tests were found to be statistically significant at the 0.05 level (Wilk's lambda, Table 17). The use of discriminant analysis holds promise as a classification tool to distinguish male and female specimens of *C. lupus*, however, the use of larger sample sizes and a detailed evaluation of how the quality and quantity of individual cranial measurements actually influences discriminant analysis classification success needs to be more fully explored. These results support the conclusions that (a) with few exceptions, cranial parameters of male wolves are larger than female wolves and (b) clines in the levels of sexual dimorphism occur in wolf populations throughout most of the northern parts of the continent.

Latitudinal Variation in Relation to Cranial Size

Although Bergmann's Rule addresses patterns of variation in terms of body mass, the principle has been applied to variation in the cranial size of *C. lupus* (Jolicoeur, 1975; Skeel and Carbyn, 1977). Comparing population means of several cranial parameters reflecting overall measures of skull length, width, and height revealed patterns of clinal variation (Table 18). In general, as latitude increased, cranial size in both sexes decreased in apparent contradiction of Bergmann's Rule as evidenced from the following figures: I^1-SagC length (Fig. 12), Zygomatic width (Fig. 13), Cheek Teeth width (Fig. 14), SagC - AudB height (Fig. 15), P^4 length (Fig. 16), Pari-Temp width (Fig. 17), Ramus height (Fig. 18), Nasal length (Fig. 19), and M^1 to Orbit height (Fig. 20). The Queen Elizabeth Island and Banks / Victoria Island wolves were slightly larger than the adjacent Baffin Island and Mackenzie populations and represented an exception, possibly caused by genetic divergence during the Wisconsin glaciation. When latitude and longitude values were incorporated into principal component analysis, the results confirmed that male cranial size and to a lesser extent female cranial size were both negatively correlated with latitude. In contrast, female cranial size was positively correlated with longitude (east to west) while male cranial size had no significant relationship with longitude. The results of this analysis further support the conclusions of Geist (1987) that Bergmann's Rule does not apply to wolf populations north of the tree-line (53° to 60° latitude) and that the reduction in cranial size appears to be due to the lower productivity of the ecosystem, largely influenced by ambient temperature.

Ambient Temperature in Relation to Cranial Size

Changes in latitude are generally assumed to reflect differences in ambient temperature, however, in central and northern Canada the mean annual temperature gradient is from the southwest to the northeast, rather than a direct north - south orientation (Fig. 22). For both male and female wolves, a significant relationship was found between total skull length (I^1-SagC) and mean annual temperature (Fig. 23). The rostrum length (Palat L) was also significantly related to mean annual temperature in both sexes (Fig. 24). Skull width (Zygom W) was significantly related to mean annual temperature for males, but not for females (Fig. 25). Although mean July and mean February temperatures were also regressed against these three cranial parameters (Appendix 11), mean annual temperature provided the best measure of this relationship. The observed patterns of clinal variation in this study are consistent with the findings of Jolicoeur (1959, 1975) studying wolves in the western N.W.T. He suggested that the differences in skull length and width were not necessarily due to genetic differences, but rather a result of changes in climate and photoperiod. In addition, he suggested that the overall pattern of variation between populations indicated the presence of a panmictic continuum, rather than a series of distinct subspecific units (Jolicoeur, 1959).

Allen's Rule states that body extremities in homeotherms such as tails, ears, beaks, and limbs are longer in warmer, more tropical regions and shorter in cooler, more polar regions (Remmert, 1980; Pianka, 1988). Although Palat L was significantly correlated with mean annual temperature in both sexes (Fig. 24), this was to be expected as Palat L is essentially a component of I^1-SagC. In fact, the ratio of Palat L /^{1}I -SagC was relatively constant for males (0.453 to .463) and females (.459 to .468) from all 10 geographic locations, suggesting that these two parameters are not independent variables. The significant relationship of Palat L with mean annual temperature appears to be a reflection of the strong association between I^1-SagC and temperature. Since Palat L relative to I^1-SagC was not found to be shorter in the high arctic populations, there was no evidence to support Allen's Rule, of shorter extremities in colder environments.

Skull width (Zygom W) was significantly correlated with ambient temperature for males, but not for females. Since temperature should affect the sexes equally, there is no obvious explanation for this sexual dimorphic difference. These results supported the conclusion that other environmental variables such as primary prey size may be the dominant evolutionary force influencing skull width.

Ungulate Prey Weight in Relation to Cranial Size

Wolves prey primarily upon the largest mammalian prey species present in their environment, which are usually represented by ungulates of the Cervidae and Bovidae families (Pimlott, 1967; Mech, 1970). It has also been suggested, however, that the smaller and more vulnerable of the ungulate species present typically dominates in the wolf diet (Pimlott, 1969; Gauthier and Theberge, 1987; Dawes *et al.*, 1986); although this hypothesis has not been tested adequately (F.F. Mallory, pers. comm.). Except for Baffin Island and the northern Keewatin Region where only *R.t. groenlandicus* is available, most wolf populations in northern Canada have access to two or more large ungulate prey species. Predator size has often been found to be correlated with prey size (Rosenzweig, 1968; McNab, 1971; Schmitz and Lavigne, 1987).

Geographic variation in diet usually reflects regional variation in available prey species. Wolves on the N.W.T. mainland feed primarily on caribou with occasional use of moose in the south and muskox in the north (Kelsall, 1968; Kuyt, 1972; Heard and Williams, 1988; Lamothe and Parker, 1989; Lamothe, 1991). On the high arctic islands, wolves prey on Peary caribou and on muskoxen (Tener, 1965; Miller, 1975; Mech, 1981; Miller, 1995). On Baffin Island, the only available ungulate species is caribou (Clark, 1971) and in Prince Albert National Park in central Saskatchewan, wolves prey primarily on moose and elk (Banfield, 1951; E. Kowal, pers. comm.). Wood Buffalo National Park wolves feed primarily on bison and secondarily on moose (Oosenbrug and Carbyn, 1982; Van Camp, 1987; Carbyn *et al.*, 1993; Larter *et al.*, 1994), while wolves in northern Alberta, south of Wood Buffalo National Park, rely primarily on moose and to a lesser extent on woodland caribou (Fuller and Keith, 1980). In winter, wolves tend to focus on large ungulate species, while summer diets are usually more varied and include a higher proportion of smaller mammals (Kuyt, 1972; Voigt *et al.*, 1976; Fuller and Keith, 1980; Gauthier and Theberge, 1987). Research on winter diet of wolves in the Keewatin Region supports the view that wolves utilize the ungulate prey species according to availability (Lamothe, 1991). For example, the winter diet by volume for wolves from the Keewatin Region was: (1) Arviat (S. Keewatin) comprised of caribou (76%) and moose (24%), (2) Baker Lake (C. Keewatin) comprised of caribou (92%) and muskox (5.3%), and (3) Repulse Bay (N. Keewatin) caribou (92%).

Mean pooled ungulate prey weight regressed against I^1-SagC (Fig. 26) and Palat L (Fig. 27) resulted in significant relationships in both males and females. Since Palat L was found to be a relatively constant component of I^1-SagC as discussed in the previous section, it was felt that these two parameters share a colinear relationship. Considering this close association, attempts to separate out the contribution of Palat L from I^1-SagC would not add anything to our understanding of causal factors as both I^1-SagC and Palat L reflect a size component along the same dimension.

Regression of mean pooled ungulate prey weight with Zygom W (Fig. 28) resulted in a significant relationship for both males ($R^2 = .87$; $P < 0.0001$) and females ($R^2 = 0.48$; $P < 0.026$), however, the greater level of significance in males suggests sexually dimorphic differences may be associated with the taking of primary prey. A larger Zygom W would result in a broader skull and increased attachment for a larger masseter muscle and neck muscle complex. These attributes would be selected for in individuals capturing large, dangerous prey. Although there is limited documentation on the role of each sex while killing prey, there is evidence to suggest that males are more specialized for hunting and killing large ungulate prey (Mallory *et al.*, 1994). The suggestion that adult males tend to initiate contact with primary prey and as a result are at greater risk is supported by the observation that males have greater injury or death rates, than females (Mech and Nelson, 1989; Weaver *et al.*, 1992; Mallory *et al.*, 1994).

Although significant relationships for the mean weight of the largest ungulate prey species and the second largest ungulate prey species each regressed independently against I^1-SagC and Zygom W were identified (Appendix 12), it was felt that the mean pooled ungulate weights (Table 20) provided a broader and more representative measure of the typical primary prey item which wolves encounter in each geographic area.

The differences between males and females in Zygom W and the highly significant regression coefficient between suggest ungulate prey size is the primary causal factor influencing zygomatic width in the male of this species. In an attempt to further understand the relationship between (1) cranial size with ambient temperature, and (2) cranial size with mean primary prey weight, a regression between ambient temperature and mean prey weight was calculated. A significant association ($R^2 = 0.77$; $P < 0.0009$) was similarly identified between these variables (Fig. 29), suggesting that a colinear relationship exists between ambient temperature, mean primary prey weight, and cranial size in *C. lupus*. The apparent interdependence of these three factors requires further study and interpretation, however, the relative strength of the regressions; I^1-SagC with mean annual temperature (male, $R^2 = 0.76$; female, $R^2 = 0.73$) and I^1-SagC with mean prey weight (male, $R^2 = 0.81$; female, $R^2 = 0.88$)

suggests that temperature is the primary environmental influence, which influences prey size and ultimately predator size. As temperature also appears to be influencing prey weight (Fig. 29), it was concluded that prey weight is an additive colinear factor, which results in a stronger relationship between mean primary prey weight and wolf cranial size.

CONCLUSIONS

In summary, the results of this study support the following conclusions;

(1) three subspecies of *C. lupus* currently occur in north-central Canada, described in this study as High Arctic Wolves, Mainland Tundra Wolves, and Central Boreal Wolves,

(2) subpopulations within each of these three subspecific designations represent ecotypes adapted to local environmental conditions,

(3) the subspecific designation used by Goldman (1944) for *C.l. hudsonicus* is invalid and can not be supported by this study,

(4) the consolidation of subspecific designations as proposed by Nowak (1983) is a better reflection of the taxonomic relationship of wolves in northern Canada,

(5) the subspecific boundaries between the "Northern group" and "Southern group" (Nowak, 1983 - Fig. 2) should be moved northward towards the N.W.T. border, and the eastern boundary of the "Northern group" should be shifted westward to James Bay, as represented in Figure 31.,

(6) the four proposed subspecies of *C. lupus* in Canada are distributed as outlined in Fig. 31 and originated after being isolated in separate refugia during the Wisconsin glaciation (refugia include: Pearyland, Beringia, southwest of the ice sheet, and southeast of the ice sheet),

(7) wolves in the S. Keewatin have a greater morphometric affinity to C. Keewatin and N. Keewatin wolves, than to wolves in C. Saskatchewan,

(8) wolves are sexually dimorphic and, with few exceptions, male cranial parameters are 2-9 % greater than females,

(9) wolves in northern Canada follow a cline in the level of sexual dimorphism, with the lowest levels occurring in the northeast and the highest levels in the southwest,

(10) in northern Canada, wolves of both sexes follow a cline in cranial size with the smallest wolves occurring in the northeast and the largest wolves occurring in the southwest,

(11) cranial size in *C. lupus* decreases with increasing latitude, thus constituting an exception to Bergmann's Rule,

(12) there is a significant positive relationship between total skull length (I^1-SagC) and mean annual ambient temperature for wolves of both sexes,

(13) there is a significant positive relationship between Palat L and mean annual ambient temperature for wolves of both sexes, although Palat L as a variable may not be independent of I^1-SagC,

(14) the ratio of Palat L / I^1-SagC was relatively constant geographically for both sexes, providing an exception to Allen's Rule,

(15) there is a significant positive relationship between Zygom W and mean annual temperature for males, but not for females,

(16) there is a significant positive relationship between cranial size (represented by I^1-SagC, Palat L, Zygom W) and mean primary prey weight in wolves of both sexes,

(17) the higher level of significance in the relationship between Zygom W and mean primary prey weight for male wolves relative to females, suggests that males are more specialized for hunting and killing large ungulate prey,

(18) there is a significant positive relationship between mean annual ambient temperature and mean primary prey weight,

(19) a colinear relationship appears to exist between mean ambient temperature, mean primary prey weight, and cranial size in *C. lupus*,

(20) future studies involving cranial morphology of *C. lupus* would benefit by a standard approach to the number and selection of cranial parameters under consideration,

(21) additional specimen collection and analysis is necessary to firmly establish the subspecific and ecotypic relationships of *C. lupus* for: Banks / Victoria Islands, Queen Elizabeth Islands, Baffin Island, west of the Mackenzie and Great Slave Lake region, and south of the Keewatin Region through Saskatchewan, Manitoba, and Ontario,

(22) genetic analysis of *C. lupus* across North America would help to clarify the taxonomic relationship of wolves and evaluate the theory that some of the morphological variation in wolves may have resulted from the genetic isolation and subsequent convergence of populations after the Wisconsin glaciation,

and

(23) mean annual temperature and mean primary prey weight constitute only two environmental variables from a broad range of environmental parameters which may be influencing the variation in cranial morphology of *C. lupus*.

LITERATURE CITED

Anderson, R.M. 1943. Summary of the large wolves of Canada, with description of three new arctic races. J. Mammal. 24(3): 386-393.

Anderson, R.M. 1946. Catalogue of Canadian recent mammals. Nat. Mus. Can. Bull. 102: 238 pp.

Anonymous. 1979. Climatic Atlas of North and Central America. Vol. I. UNESCO - Cartographic, Geneva. 30 pp.

Anonymous. 1988. Red list of threatened species. Int. Union Conserv. Nat. and Nat. Res., Gland, Switzerland.

Bailey, R.C. and Byrnes, J. 1990. A new, old method for assessing measuring error in both univariate and multivariate morphometric studies. Syst. Zool. 39(2): 124-130.

Banfield, A.W.F. 1951. Populations and movements of the Saskatchewan timber wolf (*Canis lupus knightii*) in Prince Albert National Park, Saskatchewan. Can. Wildl. Ser., Wildl. Manag. Bull. Ser. 1 No. 4. 24 pp.

Banfield, A.W.F. 1954. Preliminary investigation of the barren-ground caribou. Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1. 10A and 10B. 74 pp.

Banfield, A.W.F. 1962. A revision of the reindeer and caribou, genus *Rangifer*. Nat. Mus. Can. Bull. 177: 137 pp.

Banfield, A.W.F. 1974. The mammals of Canada. Univ. Toronto Press, Toronto, Ont. 438 pp.

Banville, D. 1983. Status and management of wolves in Quebec. Pp. 41-43, *in* Wolves in Canada and Alaska (ed., L.N. Carbyn), Can. Wildl. Ser. Rep. Ser. No. 45: 135 pp.

Bennike, O. 1981. Subfossil terrestrial mammals from North Greenland. Unpubl. report. Grønlands geologiske Undersøgelse. 6 pp.

Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Gottinger studien. (3)1: 595-708.

Blackith, R.E. and Reyment, R.A. 1971. Multivariate Morphometrics. Academic Press, New York. 412 pp.

Blood, D.A. and Lovaas, A. L. 1966. Measurements and weight relationships in Manitoba elk. J. Wildl. Manage. 30(1): 135-140.

Bogan, M.A. and Mehlhop, P. 1983. Systematic relationships of gray wolves (*Canus lupus*) in southwestern North America. Mus. Southwest. Biol., Occas. Pap. 1:1-20.

Bookstein, F. L. 1989. "Size and shape": a comment on semantics. Syst. Zool. 38(2): 173-180.

Brewster, W.G. and Fritts, S.H. 1995. Taxonomy and genetics of the gray wolf in western North America: a review. Pp. 353-373, *in* Ecology and Conservation of Wolves in a Changing World (eds. L.N. Carbyn, S.H. Fritts, and D.R. Seip). Can. Circumpolar Inst., Univ. Alberta, Edmonton. 620 pp.

Bryant, L.D. and Maser, C. 1982. Classification and distribution. Pp. 1-59 in Elk of North America: ecology and management (eds. J.W. Thomas and D.E. Toweill). Stackpole Books, Harrisburg. 698 pp.

Carbyn, L.N. 1987. Gray Wolf and Red Wolf. Pp. 358-377, *in* Wild furbearer management and conservation in North America. (eds, Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B.). Minis. of Nat. Res., Ontario. 1150 pp.

Carbyn, L.N., Oosenbrug, S.M. and Anions, D.W. 1993. Wolves, bison . . . and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Circumpolar Res. Ser., No. 4, Can. Circumpolar Instit., Univ. Alberta, Edmonton. 270 pp.

Chiarelli, A.B. 1975. The chromosomes of the Canidae. Pp. 40-53, *in* The Wild Canids, (ed. M.W. Fox), Van Nostrand Reinhold Comp., New York. 508 pp.

Child, D. 1970. The essentials of factor analysis. Holt Rhinehart and Wilson, London. 108 pp.

Clark, K.R.F. 1971. Food habits of the tundra wolf of central Baffin Island. Ph.D. Thesis, Univ. Toronto, Toronto, Ontario.

Clarkson, P. and Liepens, I. 1989a. Inuvialuit wildlife studies: western arctic wolf research project progress report 1987-1988. Tech. Rep. No. 2. Available from the Dept Ren. Res., G.N.W.T., Inuvik, N.W.T., Canada, X0E 0T0. 104 pp.

Clarkson, P. and Liepens, I. 1989b. Inuvialuit wildlife studies: western arctic wolf research project progress report 1988-1989. Tech. Rep. No. 7. Available from the Dept. Ren. Res., G.N.W.T., Inuvik, NWT, Canada, X0E 0T0. 71 pp.

Coleman, A.P. 1941. The last million years: a history of the Pleistocene in North America. Univ. Toronto Press, Toronto. 216 pp.

Dauphine, Jr., T. C., 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: growth, reproduction, and energy reserves. Can. Wildl. Serv. Rep. Ser. No. 38. 71 pp.

Dawes, P.R., Elander, M. and Ericson, M. 1986. The wolf (*Canis lupus*) in Greenland: a historical review and present status. Arctic 39(2): 119-132.

DeBlase, A.F. and Martin, R.E. 1974. A manual of mammology. WM. C. Brown Comp., Dubuque. 329 pp.

Flint, R. F. 1952. The ice age in the North American arctic. Arctic. 5: 135-52.

Friis, L.K. 1985. An investigation of subspecific relationships of the grey wolf, *Canis lupus*, in British Columbia. M.Sc. Thesis., Univ. Victoria, Victoria. 162 pp.

Fritts, S.H. 1983. Record dispersal by a wolf from Minnesota. J. Mammal. 64: 166-167.

Fuller, T.K. and Keith L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44: 583-602.

Gauthier, D.A. and Theberge, J.B. 1987. Wolf Predation. Pp. 119-127, *in* Wild Furbearer Management and Conservation in North America. (eds., Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B.,). Min. Nat. Res., Ontario. 1150 pp.

Geist, V. 1987. Bergman's rule is invalid. Can. J. Zool. 65: 1035-1038.

Gipson, P.S., Sealander, J.A. and Dunn, J.E. 1974. The taxonomic status of wild *Canis* in Arkansus. Syst. Zool. 23: 1-11.

Goldman, E.A. 1937. The wolves of North America. J. Mammal. 18 (1): 37-45.

Goldman, E.A. 1941. Three new wolves from North America. Proc. Biol. Soc. Wash. 54: 109-114.

Goldman, E.A. 1944. Classification of wolves. Part II, *in* The wolves of North America, (eds., S.P. Young and E.A. Goldman). Dover Publications Inc., New York. 636 pp.

Goodwin, E.A. and Ballard, W.B. 1985. Use of tooth cementum for age determination of gray wolves. J. Wildl. Manage. 49(2): 313-316.

Gunson, J.R. and Nowak, R.M. 1979. Largest gray wolf skulls found in Alberta. Can. Field-Nat. 93 (3):308-309.

Gunson, J.R. 1983. Status and management of wolves in Alberta. Pp. 25-29, *in* Wolves in Canada and Alaska, (ed. L.N.Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Guthrie, R.D. 1968. Palaeoecology of the large-mammal community in interior Alaska during the late Pleistocene. Amer. Mid. Nat. 79(2): 346-363.

Hagmeier, E.M. 1958. Inapplicability of the subspecies concept to North American marten. Syst. Zool. 7:1-7.

Hall, E.R. and Kelson, K.R. 1959. The mammals of North America. Vol. II. The Ronald Press Comp. New York. 1162 pp.

Hall, E.R. 1981. The mammals of North America. John Wiley and Sons, NewYork. 1181 pp.

Harper, F. 1955. The barren ground caribou of Keewatin. Univ. Kansas Mus. Nat. Hist., Kansas. 163 pp.

Heard, D.C and Williams, T.M. 1988. Physical characteristics of wolves shot near Fort Reliance and Lynx Lake in the winter of 1987-88. (unpubl. rep.) G.N.W.T., Dept. Ren. Res., Yellowknife. 37 pp.

Heard, D.C. 1983. Historical and present status of wolves in the Northwest Territories. Pp. 44-47, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. 45. 135 pp.

Heard, D.C. 1984. Historical and present status of wolves in the the Northwest Territories. Rep. 4, Info. Ser., G.N.W.T., Dept. Ren. Res., Yellowknife. 21 pp.

Hillis, T.L. 1990. The demography and ecology of the tundra wolf, *Canus lupus*, in the Keewatin District, Northwest Territories. M.Sc. Thesis., Laurentian University, Sudbury. Ontario. 148 pp.

Hillis, T.L. and Mallory, F.F. 1996. Sexual dimorphism in wolves (*Canis lupus*) of the Keewatin District, Northwest Territories, Canada. Can. J. Zool. 74: 721-725.

Holleman, D.F. and Stephenson, R.O. 1981. Prey selection and consumption by Alaskan wolves in winter. J. Wildl. Manage. 45(3): 620-628.

Johnsen, P. 1953. Birds and mammals of Peary Land in North Greenland including notes from the Northeast Greenland. Meddelelser om Grønland 128(6). 135 pp.

Jolicoeur, P. 1959. Multivariate geographical variation in the wolf, *Canis lupus* L. Evolution 13(3): 283-299.

Jolicoeur, P. 1975. Sexual dimorphism and geographical distance as factors of skull variation in the wolf, *Canis lupus*. Pp. 54-61, *in* The wild canids, their systematics, behavioral ecology and evolution, (ed. M.W. Fox). Van Nostrand Reinhold Comp., New York. 508 pp.

Keith, L.B. 1983. Population dynamics of wolves. Pp. 66-77, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Kelsall, J.P. 1968. The migratory barren-ground caribou of Canada. Dept. Ind. North. Aff., Can. Wildl. Ser., Ottawa. 340 pp.

Kennedy, P.K., Kennedy, M.L., Clarkson, P.L., and Liepens, I.S. 1991. Genetic variability in natural populations of the gray wolf, *Canis lupus*. Can. J. Zool. 69: 1183-1188.

Kolenosky, G. 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. 36: 357-369.

Kolenosky, G. and Stanfield, R.O. 1975. Morphological and ecological variation among gray wolves *Canus lupus* of Ontario, Canada. Pp. 62-72, *in* The wild canids, their systmatics, behavioural ecology and evolution, (ed. M.W. Fox). Van Nostrand Reinhold Comp., New York. 508 pp.

Kolenosky, G. 1983. Status and management of wolves in Ontario. Pp. 35-40, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Krzanowski, W.J. 1977. The performance of Fisher's linear discriminant function under non-optimal conditions. Technometrics 19(2): 191-199.

Kuyt, E. 1962. Movements of young wolves in the Northwest Territories of Canada. J. Mammal. 43: 270-271.

Kuyt, E. 1972. Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories. Can. Wildl. Serv. Rep. Ser. No. 21. Ottawa. 36 pp.

Lamothe, A.R. and Parker, G.H. 1989. Winter feeding habits of wolves in the Keewatin District, Northwest Territories, Canada. Musk-ox 37: 144-149.

Lamothe, A.R. 1991. Winter food habits and foodchain transfer of metals in wolves (*Canis lupus*) of the Keewatin District, Northwest Territories. M.Sc. Thesis. Laurentian University, Sudbury, Ontario. 158 pp.

Larter, N.C., Sinclair, A.R.E. and Gates, C.C. 1994. The response of predators to an erupting Bison, *Bison bison athabascae*, population. Can. Field-Nat. 108: 318-327.

Latour, P. 1987. Observations on demography, reproduction, and morphology of muskoxen (*Ovibos moschatus*) on Banks Island, Northwest Territories. Can. J. Zool. 65:265-269.

Lawrence, B. and Bossert, W.H. 1967. Multiple character analysis of *Canis lupus, latrans* and *familiaris*, with a discussion of the relationship of *Canis niger*. Am. Zool. 7:223-232.

Lawrence, B. and Bossert, W.H. 1975. Relationships of North American *Canis* shown by a multiple character analysis of selected populations. Pp. 73-86, *in* The wild canids, (ed. M.W. Fox). Van Nostrand Reinhold Comp., New York. 508 pp.

Lehman, N., Eisenhawer, A., Hansen, K., Mech, L.D., Peterson, R.O., Grogan, P.J.P., and Wayne, R.K., 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution 45: 104-119.

Lehman, N., Clarkson, P.L., Mech, L.D. Meier, T.J. and Wayne, R.K. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. Behav. Ecol. Sociobiol. 30: 93-94.

Ludwig, J.A. and Reynolds, J.F. 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons. New York. pp.

Macpherson, A.H. 1965. The origin of diversity in mammals of the Canadian arctic tundra. Syst. Zool. 14: 153-173.

Mallory, F.F. 1987. Impact of prey on furbearer predators. Pp. 141-150, *in* Wild Furbearer Management and Conservation in North America. (eds., M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch). Min. of Nat. Res., Ontario. 1150 pp.

Mallory, F.F., Hillis, T.L., Blomme, C.G., and Hurst, W.G. 1994. Skeletal injuries of an adult timber wolf, *Canis lupus*, in northern Ontario. Can. Field-Nat. 108: 230-232.

Manly, B.F.J. 1986. Multivariate statistical methods: a primer. Chapman and Hall Publ. New York. 159 pp.

Mayr, E. 1963. Animal species and evolution. The Belknap Press, Harvard Univ., Cambridge. 797 pp.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Comp., Toronto. 428 pp.

Mayr, E. 1970. Populations, species and evolution: an abridgement of animal species and evolution. The Belknap Press, Harvard Univ., Cambridge. 453 pp.

Mayr, E., Linsley, E.G., and Usinger, R. L. 1953. Methods and principles of systematic zoology. McGraw-Hill, New York. 328 pp.

McNab, B.K. 1971. On the ecological significance of Bergmann's rule. Ecology 52: 845-854.

McNab, B.K. 1989. Basal rate of metabolism, body size, and food habits in the Order Carnivora. Pp. 335-354, *in* Carnivore behaviour, ecology, and evolution, (ed. J.L. Gittleman), New York. 620 pp.

Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. Univ. Minnesota Press, Minneapolis. 384 pp.

Mech, L.D. 1988b. The arctic wolf: living with the pack. Key Porter Books, Toronto. 128 pp.

Mech, L.D. and Nelson, M.E. 1989. Evidence of prey-caused mortality in three wolves. Am. Midl. Nat. 123: 207-208.

Miller, D.R. 1975. Observations of wolf predation on barren ground caribou in winter. Pp. 209-220, *in* Proceedings of the First Int. Reindeer and Caribou Symp., 9-11 August, 1972, University of Alaska, Fairbanks, (eds., J.R. Luick, P.C. Lent, D.C. Kleen, R.G. White). Pp 209-220. Biol. Pap. Univ. Alaska, Spec. Rep. 1.

Miller, F.L., Russell, R.H., and Gunn, A. 1977. Inter-island movements of Peary caribou (*Rangifer tarandus pearyi*) on western Queen Elizabeth Islands, Arctic Canada. Can. J. Zool. 55: 1029-1037.

Miller, F.L. and Gunn, A. 1978. Inter-island movements of Peary caribou south of Viscount Melville Sound, Northwest Territories. Can. Field-Nat. 92(4): 327-331.

Miller, F.L. 1995a. Inter-island water crossings by Peary caribou, south-central Queen Elizabeth Islands. Arctic 48(1): 8-12.

Miller, F.L. 1995b. Status of wolves on the Canadian arctic islands. Pp. 35-42, *in* Ecology and conservation of wolves in a changing world (eds. L.N. Carbyn, S.H. Fritts, and D.R. Seip). Can. Circumpolar Inst. Univ. Alberta, Edmonton. 620 pp.

Morrison, D.F. 1967. Multivariate Statistical Methods. McGraw-Hill, New York. 338 pp.

Neff, N.A. and Marcus, L.F. 1980. A survey of multivariate methods for systematics. Amer. Mus. Nat. Hist., New York. 243 pp.

Nelson, M.E., and Madsen, J.H. Jr., 1986. Canids from the late Pleistocene of Utah. Great Bas. Nat. 46(3): 415-420.

Norusis, M.J. 1988a. SPSS/PC+ V2.0 Base Manual. SPSS Inc. Chicago. 344 pp.

Norusis, M.J. 1988b. SPSS/PC+ Advanced Statistics V2.0. SPSS Inc. Chicago. 178 pp.

Nowak, R.M. 1979. North American Quaternary *Canis*. Monogr. No. 6, Mus. Nat. Hist., Univ. Kansas. 154 pp.

Nowak, R.M. 1983. A perspective on the taxonomy of wolves in North America. Pp. 10-19, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Nowak, R.M. 1995. Another look at wolf taxonomy. Pp. 375-397, *in* Ecology and conservation of wolves in a changing world, (eds. L.N. Carbyn, S.H. Fritts, and D.R. Seip). Can. Circumpolar Inst., Univ. Alberta, Edmonton. 620 pp.

Oosenbrug, S.M. and Carbyn, L.N. 1982. Winter predation on bison and activity patterns of a wolf pack in Wood Buffalo National Park. Pp. 43-53, *in* Wolves of the world: perspectives of behaviour, ecology and conservation, (eds., F.H. Harrington and P.C. Paquet). Noyes Publ. Park Ridge, New Jersey. 474 pp.

Paetkau, D., Calvert, W., Stirling, I., and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Mol. Ecol. 4: 347-354.

Parker, G.R. 1973. Distribution and densities of wolves within barren-ground caribou range in northern mainland Canada. J. Mammal. 54(2): 341-348.

Pearson, K. 1901. On lines and planes of closest fit to asystem of points in space. Philosophical Magazine 2: 557-72.

Pedersen, S. 1978. Geographical variation in Alaskan wolves (*Canis lupus L.*). M.Sc. Thesis, Univ. Alaska, Fairbanks. 107 pp.

Pedersen S. 1982. Geographic variation in Alaskan wolves. Pp. 345-361, *in* Wolves of the world; perspectives of biology, ecology, and conservation (eds., F.H. Harrington and P.C. Paquet). Noyes Publ., Park Ridge. 474 pp.

Pianka, E.R., 1988. Evolutionary ecology. 4th ed. Harper and Row Publ., New York. 468 pp.

Pichette, C. and Voigt, D.R. 1985. A multivariate analysis of some Ontario and Quebec wolf (*Canis lupus*) skulls. Service de la Faune du Quebec, Bull. 13: 3-21.

Pimental, R.A. 1958. Taxonomic methods, their bearing on subspeciation. Syst. Zool. 7:139-156.

Pimlott, D.H. 1967. Wolf predation and ungulate populations. Am. Zool. 7: 267-278.

Pimlott, D.H. 1975. The ecology of the wolf in North America. Pp. 280-286, *in* The wild canids, their systmatics, behavioural ecology and evolution. (ed, M.W. Fox). Van Nostrand Reinhold Comp., New York. 508 pp.

Pocock, R.I. 1935. The races of *Canis lupus*. Proc. Zool. Soc. (Lond.). 3: 647-686.

Preble, E.A. 1902. Biological investigations of the Hudson Bay region. U.S. Dept. Int., North Amer. Fauna Ser. No. 22. 140 pp.

Preble, E.A. 1908. A biological investigation of the Athabaska-Mackenzie region. N. Amer. Fauna. 27: 574 pp.

Rand, A.L. 1954. The ice age and mammal speciation in North America. Arctic 7 (1): 31-35.

Rausch, R.A. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. 7: 253-265.

Rausch, R.A. 1969. A summary of wolf studies in south-central Alaska, 1957-1968. Trans. N. Am. Wildl. Nat. Res. Conf. 34: 117-131.

Rausch, R.L. 1953. On the status of some arctic mammals. Arctic 6(2): 91-148.

Remmert, H. 1980. Arctic animal ecology. Springer-Verlag, New York. 250 pp.

Richardson, J. 1829 Fauna Boreali Americana. Part 1, *in* The wolves of North America, (eds., S.P.Young and E.A. Goldman). Dover Publ. Inc., N.Y. 636 pp.

Røed, K.H, Staaland, H., Broughton, E. and Thomas, D.C. 1986. Transferrin variation in caribou (*Rangifer tarandus* L.) on the Canadian arctic islands. Can. J. Zool. 64(1): 94-98.

Røed, K.H., Ferguson, M.A.D., Crete, M., and Bergerud., T.A. 1991. Genetic variation in transferrin as a predictor for differentiation and evolution of caribou from eastern Canada. Rangifer 11(2): 65-74.

Romesburg, H.C. 1984. Cluster analysis for researchers. Lifetime Learning Publ., Belmont. 334 pp.

Rosenzweig, M.L. 1968. The strategy of body size in mamalian carnivores. Am. Midl. Nat. 80(2): 299-315.

Say, T. 1823. Long's expedition to Rocky Mountians 1819-1820, Vol. 1 & 2, *in* The wolves of North America, (eds., S.P.Young and E.A. Goldman). Dover Publ. Inc., N.Y. 636 pp.

Seal, H.L., 1964. Multivariate statistical analysis for biologists. John Wiley & Sons Inc. New York. 183 pp.

Schmitz, O.J. and Kolenosky, G.B. 1985a. Wolves and coyotes in Ontario: morphological relationships and origins. Can. J. Zool. 63: 1130-1137.

Schmitz, O.J. and Lavigne, D.M. 1987. Factors affecting body size in sympatric Ontario *Canis*. J. Mammal. 68(1): 92-99.

Schreber, J.C.D. 1775. Die säugthiere in abbildungen nach der Natur mit beschreibungen. 8 vols., *in* The wolves of North America, (eds., S.P.Young and E.A. Goldman). Dover Publ. Inc., N.Y. 636 pp.

Skeel, M.A. and Carbyn, L.N. 1977. The morphological relationship of gray wolves (*Canis lupus*) in national parks of central Canada. Can. J. Zool. 55: 737-747.

Smith, B. L. 1983. The status and management of wolves in the Yukon Territory. Pp. 48-50, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Somers, K.M. 1986. Multivariate allometry and removal of size with principal components analysis. Syst. Zool. 35(3): 359-386.

Somers, K.M. 1989. Allometry, isometry, and shape in principal components analysis. Syst. Zool., 38(2): 169-173.

Sokal, R.R. and Sneath, P.H.A. 1963. Principles of Numerical Taxonomy. W.H. Freeman and Comp. San Francisco. 359 pp.

Sokal, R.R. and Rohlf, F.J. 1969. Biometry. (2nd ed). W.H. Freeman and Comp., New York. 859 pp.

Stardom, R.R.P. 1983. Status and management of wolves in Manitoba. Pp. 30-34, *in* Wolves in Canada and Alaska, (ed. L.N. Carbyn). Can. Wildl. Ser. Rep. Ser. No. 45. 135 pp.

Sundberg, P. 1989. Shape and size-constrained principal components analysis. Syst. Zool. 38(2): 166-168.

Taylor, M.K. 1986. Determination of spatial boundaries of polar bear populations by animals of non-metrical skull characters. Michigan State Univ., Dept. Fish Wildlife (unpubl. rep.). 13 pp.

Tener, J.S. 1965. Muskoxen in Canada - a biological and taxonomic review. Queen's Printer. Ottawa. 166 pp.

Thomas, D.C. and Everson, P. 1982. Geographic variation in caribou on the Canadian arctic islands. Can. J. Zool. 60: 2442-2454.

Thorpe, R.S. 1985. The effect of insignificant characters on the multivariate analysis of simple patterns of geographic variation. Biol. J. Linn. Soc. 26: 215-223.

Tompa, F. S. 1983. Status and management of wolves in British Columbia. Pp. 20-24, *in* Wolves in Canada and Alaska. (ed. L.N. Carbyn). Can. Wildl. Serv. Rep. Ser. No. 45. 135 pp.

Van Camp, J. 1987. Predation on bison. Pp 25-33, *in* Bison ecology in relation to agricultural development in the Slave River Lowlands. (eds., H.W. Reynonds and A.W.L. Hawley). N.W.T., CWS. Occ. Pap. 63.

Van Camp, J. and Gluckie, R. 1979. A record long distance move by a wolf (*Canis lupus*). J. Mammal. 56: 44-63.

Voigt, D.R., Kolonosky, G.B., and Pimlott, D.A., 1976. Changes in summer foods of wolves in central Ontario. J. Wildl. Manage. 40(4): 663-668.

Walker, V., Clarkson, P.L., Liepens, I.S., and Lennie, J. 1993. A comparison of skull dimensions and characteristics of wolves in the western Northwest Territories, 1986-1993. (unpubl. rep.) G.N.W.T. Ren. Res., Inuvik. 35 pp.

Wayne, R.K., Benveniste, R.E., Janczewski, D.N. and O'Brien, S.J. 1989. Molecular and biochemical evolution of the Carnivora. Pp. 465-494, *in* Carnivore behavior, ecology, and evolution. (ed. J.L. Gittleman). Cornell Univ. Press, New York. 620 pp.

Wayne, R.K., Lehman, N., Allard, M.W. and Honeycutt, R.L. 1992. Mitochondrial DNA variability of the gray wolf: genetic consequences of population decline and habitat fragmentation. Cons. Biol. 6: 599-569.

Wayne, R.K., Lehman, N., and Fuller, T.K. 1995. Conservation genetics of the gray wolf. Pp. 399-408, *in* Ecology and conservation of wolves in a changing world. (eds. L.N. Carbyn, S.H. Fritts, and D.R. Seip). Can. Circumpolar Inst., Univ. Alberta, Edmonton. 620 pp.

Weaver, J.L., Arvidson, C., and Wood, P. 1992. Two wolves, *Canis lupus*, killed by a moose, *Alces alces*, in Jasper National Park, Alberta. Can. Field-Nat. 106: 126-127.

Williams, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64(5) 1283-1291.

Williams, T.M. and Heard, D.C. 1989. Physical characteristics of wolves shot near Fort Reliance, N.W.T. between 4 February 14 and April 1989. (unpubl. rep.), G.N.W.T. Dept. Ren. Res., Yellowknife. 30 pp.

Williams, T.M. 1991. Physical characteristics of wolves shot near Fort Reliance and Lynx Lake N.W.T. between 1 November 1989 and 1 April 1990. (unpubl. rep.), G.N.W.T. Dept. Ren. Res., Yellowknife. 34 pp.

Williams, T.M. 1991. Physical characteristics of wolves shot near Bathurst Inlet, N.W.T. between 26 February and 5 May 1990. (unpubl. rep). G.N.W.T. Dept. Ren. Res., Yellowknife. 13 pp.

Young, S.P. and Goldman, E.A. 1944. The wolves of North America. Dover Publ., New York. 636 pp.

Youngman, P.M. 1993. The Pleistocene small carnivores of eastern Beringia. Can. Field - Nat. 107(2): 139-161.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs. 620 pp.

Appendix 1. Goldman's (1944) description of *C. lupus* subspecies in Canada and Alaska.

The subspecific designations currently in use for wolves in Canada and Alaska were defined by Young and Goldman (1944). The following excerpts of Goldman's descriptions concentrate on skull characteristics, especially those that can be easily compared among populations:

a) ***Canis lupus occidentalis*** Richardson; Type locality - Fort Simpson, N.W.T. Type specimen - not designated. "Size among the largest of North American wolves . . . skull very large and massive. . ." Skull - " About the size of *pambasileus*, but rostrum and palate slightly shorter; maxillary tooth row shorter. About like that of *tundrarum* in size and general structure, but molariform teeth usually smaller...similar to that of *columbianus*, but usually larger; postorbital processes stouter, less tapering, more bluntly pointed; dentition as a whole heavier...larger than that of *mackenzii* . . . Compared with *arctos*: size larger, more massive; brain case broader; frontal region broader and flatter . . . postorbital processes stouter, more bluntly pointed; auditory bullae smaller . . . Compared with *hudsonicus*. . . size larger, postorbital processes stouter, more bluntly pointed, the posterior borders turned less abruptly inward." Specimens examined: 42 skulls, 2 skins.

b) ***Canis lupus hudsonicus*** Goldman; Type locality - Head of Schultz Lake, Keewatin District, N.W.T. Type specimen - adult male, No. 180281, U.S. National Museum. "Light colored species . . . medium size . . . skull with rather broad postorbital region and narrow, acutely pointed postorbital processes." Skull - "Similar . . . to that of *occidentalis*, but differs in decidedly smaller size; postorbital processes more slender and more acutely pointed, the posterior boarders turned more abruptly inward. Apparently larger than that of *mackenzii*. Similar in size to that of *arctos* but flatter, the frontal region less highly arched and convex in lateral view . . . postorbital processes narrow and acute as in *arctos*; dentition similar, but antero-internal cusps of upper carnassials less prominent." Specimens examined: 6 skulls, 9 skins.

c) ***Canis lupus arctos*** Pocock; Type locality - Melville Island, Franklin District, N.W.T. Type specimen - adult, probably male, skull only, No. 55.11.26.4 British Museum. "Nearly white subspecies of medium size . . ." Skull - "Compared with *occidentalis*: size smaller, less massive; brain case narrower, more highly arched, frontal region decidedly narrower, . . . postorbital processes slenderer, more acutely pointed; . . . dentition similar, but rather light; protocone of upper carnassial prominent. Compared with *orion*: very similar in general form, but frontal region less elevated and less convex in outline." Specimens examined: 1 skull, 1 skin.

d) ***Canis lupus bernardi*** Anderson; Type locality - Cape Kellet, S.W. Banks Is, Franklin District, N.W.T. Type specimen - adult male, skin and skull, No. 2796 National Museum of Canada. Skull - "Distinguished by great comparative length, narrow zygomatic breadth, long, slender rostrum and exceedingly large carnassials. Nasals narrower than in *tundrarum* and extending much farther behind posterior extensions of maxillaries and with shorter distance across postorbital processes. From its nearest neighbor on the north, *Canis lupus arctos . . . bernardi* differs the most widely, with skull of only slightly less length, but much less massive, with narrower rostrum, less zygomatic breadth, lighter lower mandible, of less depth and more nearly straight. The tooth-row is about the same length as in *arctos*, but the molars and premolars are all longer, broader, and heavier; canines and incisors project forward at a noticeably greater angle." Specimens examined: 8 skulls, 6 skins.

e) ***Canis lupus mackenzii*** Anderson; Type locality - Bathurst Inlet, Mackenzie District, N.W.T. Type specimen - adult male, skin and skull, No. 2792 National Museum of Canada. Skull -From original description: "Much larger than in *manningi* of Baffin . . . smaller than in *hudsonicus* . . . and *tundrarum* . . . with teeth about the same size as in the last tow forms but larger than in *manningi*. Compared with *bernardi* . . . the teeth of *mackenzii* are much smaller, particularly the upper and lower carnassials. Ramus of mandible short and heavy, with lower edge of ramus much more convex than in *tundrarum* . . ." Specimens examined: 8 skulls, 2 skins.

f) ***Canis lupus manningi*** Anderson; Type locality - Hantzsch River, Baffin Island, N.W.T. Type specimen - female young adult, skin and skull, No. 17236 National Museum of Canada. "Considerably smaller than any of the other Arctic wolves . . . Color somewhat variable . . . adults generally white . . ." Skull - "From original description: "Much smaller and less massive than in *arctos* in all respects, with rostrum more slender and zygomata proportionately much smaller; bullae much smaller; carnassials much shorter and less massive; tooth-row shorter and all teeth smaller, palate more narrow and with posterior end of nasals projecting less far behind maxillaries . . . Compared with *tundrarum*, from which it is still farther separated geographically, *manningi* shows even greater difference in size . . . " Specimens examined: 13 specimens.

g) ***Canis lupus orion*** Pocock; Type locality - Cape York, N.W. Greenland. Type specimen - apparently male adult, skin and skull, No. 97.3.5.1 British Museum. "Described as a "whitish gray" subspecies, perhaps smaller than arctos . . ." Skull - "Type skull of doubtful sex, described as smaller than that of *arctos*, with less elevated and convex frontal profile. The skull of a female from Greenland is very similar to that of a male believed to represent *arctos* from Ellesmere Island in general form. The frontal region is less elevated, and thus in accord with the description of the type, but the range of individual variation is unknown." Specimens examined: 2 skulls, 1 skin.

h) ***Canis lupus labradorius*** Goldman; Type locality - Fort Chimo, Quebec. Type specimen - probably male, adult skull only, No. 23136 U.S. National Museum. "Size medium, color light; frontals remarkably broad behind postorbital processes" Skull - "Compared with that of *lycaon*, the skull is larger, more massive; rostrum heavier; postorbital region relatively broader...dentition heavier." Specimens examined: 1 skull.

i) ***Canis lupus lycaon*** Schreber; Type locality - Quebec, Quebec. Type specimen - not designated. "A small, dark-colored subspecies; skull with remarkably slender rostrum." Skull - "Similar in general to *nubilus*, but smaller, with much slenderer rostrum; supraoccipital shield less projecting posteriorly over foramen magnum; . . . Differs from that of *hudsonicus* in much smaller size and relatively slenderer rostrum. Compared with that of *labradorius*, the skull is much smaller and slenderer; frontal region narrower; nasals more emarginate anteriorly; dentition in general lighter, but posterior upper molars relatively large. Similarity in size and cranial details to large subspecies of *niger* is rather close; but in *lycaon* the skull is usually broader,with higher brain case and more massive in general form; zygomata more widely spreading; postorbital processes with posterior margins turned less abruptly inward . . ." Specimens examined: 71 skulls, 14 skins.

j) ***Canis lupus tundrarum*** Miller; Type locality - Point Barrow, Alaska. Type specimen - probably female, No. 16748, U.S. National Museum. "Size large; color light; . . . closely allied to *pambasileus* of Mt. McKinley . . . skull with heavy dentition . . . similar also to *occidentalis* and *mackenzii* in size, but color darker" Skull - "in close agreement with that of *pambasileus* in size and general structure, but dentition usually heavier, the difference most noticeable in the molariform teeth; crowns of 2nd and 3rd upper premolars, and of 2nd, 3rd, and 4th lower premolars usually distinctly longer. Not very unlike that of *occidentalis*, but dentition usually heavier." Specimens examined: 9 skulls, 4 skins.

k) ***Canis lupus pambasileus*** Elliot; Type locality - Susitna River, region of Mount McKinley, Alaska. Type specimen - male adult, No. 13481, Field Museum of Natural History. "Size among the largest of North American wolves; black color phase frequent; skull very large with elongated rostrum. Similar in size to *occidentalis*. . . skull with longer palate. Similar in size to *tundrarum* of the Arctic coast of Alaska; . . . skull very similar in general form, but dentition lighter." Skull - "Closely approaches that of *occidentalis* in size and general form, but rostrum and palate slightly longer; maxillary tooth row longer. In close agreement with that of *tundrarum* in size and general structure, but molariform teeth usually smaller . . . Distinguished from *columbianus* by larger usual size; supraoccipital shield narrower; postorbital processes broader, less tapering, more bluntly pointed; carnassials relatively broader, less elongated . . ." Specimens examined: 77 skulls, 17 skins.

l) ***Canis lupus alces*** Goldman; Type locality - Kachemak Bay, Kenai Peninsula, Alaska. Type specimen - male adult, skull only, No. 147471 U.S. National Museum. "Size large, perhaps largest of North American wolves; skull elongated with broad rostrum and narrowly spreading zygomata; canines large, but molariform teeth comparatively small." Skull - "Similar in general form to *pambasileus*, but apparently larger, more elongated; rostrum and palate longer; nasals broader, more divergent anteriorly; supraoccipital shield broader; dentition similar, but molariform teeth relatively narrower." Specimens examined: 5 skulls.

Appendix 2. Goldman's (1944) cranial data for: *C.l. hudsonicus* and *C.l.arctos*
Standard deviation values have been calculated for Goldman's data.

Locality	I.D. No.	Greatest length	Condylobasal length	Zygomatic breadth	Squamosal constriction	Width of rostrum	Interorbital breadth	Postorbital constriction	Length of mandible	Height of coronoid process	Maxillary tooth row, crown length	Upper carnassial, crown length	Upper carnassial crown width	First upper molar, ant-post. diameter	First upper molar, transv. diameter	Lower carnassial crown length
C.l. hudsonicus																
Keewatin																
Cape Fullerton	19493	260.0	240.7	146.1	80.5	46.7	46.0	38.8			111.0	27.3	16.0	18.7	25.9	
Hudson Bay	19348	254.0	233.2	137.0	78.1	46.2	46.1	37.3	183.1	73.7	107.8	26.9	14.6	18.5	24.2	30.0
Schultz Lake	180281	258.3	241.0	146.4	83.9	46.0	47.2	41.8	190.3	84.6	110.1	26.8	14.2	17.4	24.2	32.6
Schultz Lake	180282	262.1	237.7	145.5	80.2	44.2	47.6	38.8	186.3	75.1	107.2	25.5	14.5	17.6	22.1	28.8
Wager River	22940	263.3	240.8	137.2	80.1	43.2	47.0	41.2	187.3	73.7	109.7	25.6	14.0	17.5	23.5	29.1
MALE (n=5)	**Mean**	**259.5**	**238.7**	**142.4**	**80.6**	**45.3**	**46.8**	**39.6**	**186.8**	**76.8**	**109.2**	**26.4**	**14.7**	**17.9**	**24.0**	**30.1**
Standard Dev.		3.64	3.35	4.89	2.09	1.49	0.70	1.87	2.97	5.26	1.60	0.82	0.79	0.61	1.37	1.73
Keewatin																
Schultz Lake	180283	251.0	228.8	134.8	77.4	42.4	44.4	43.2	181.9	75.4	104.1	24.5	13.8	17.4	22.6	27.6
FEMALE																
C.l. arctos																
High Arctic																
Ellesmere Islands	42119	264.7	236.9	138.7	79.4	46.0	45.6	40.4	186.8	76.1	108.6	26.4	15.3	17.6	23.0	30.1
MALE																

No FEMALE Samples

(con't)

Appendix 2. (con't) Goldman's (1944) cranial data for: *C.l. occidentalis*
Standard deviation values have been calculated for Goldman's data.

Locality	I.D. No.	Greatest length	Condylobasal length	Zygomatic breadth	Squamosal constriction	Width of rostrum	Interorbital breadth	Postorbital constriction	Length of mandible	Height of coronoid process	Maxillary tooth row, crown length	Upper carnassial, crown length	Upper carnassial crown width	First upper molar, ant-post. diameter	First upper molar, transv. diameter	Lower carnassial crown length
Alberta																
Edmonton	242907	276.7	248.1	144.3	81.0	45.8	50.8	44.8	194.6	79.0	111.3	27.6	13.9	18.3	23.9	30.3
Smith Landing	177370	274.0	250.0	148.8	82.5	50.2	51.5	41.9	196.5	85.1	110.7	25.5	15.3	16.4	21.8	28.5
Wood Buffalo Park	98230	278.2	262.5	145.5	90.5	47.2	46.2	44.6	197.6	80.8	114.1	27.2	14.4	17.6	24.2	30.8
Wood Buffalo Park	98226	274.2	258.8	144.0	84.5	50.7	46.1	43.2	199.0	82.8	115.4	28.5	15.6	18.0	25.2	33.6
British Columbia																
Cache Creek	4698	283.0	255.2	152.7	86.6	51.3	51.4	46.8	204.7	83.6	114.5	26.9	15.9	16.9	24.4	31.2
Mackenzie																
Artillery Lake	262688	281.0	258.0	149.8	82.3	44.4	50.0	43.8			120.4	28.6	15.9	18.9	25.5	
Aylmer Lake	29040	272.0	245.3	143.4	81.7	43.3	50.7	45.6	191.7	83.0	100.8	27.2	14.1	17.9	24.2	30.0
Coronation Gulf	236104	278.5	256.0	142.5	83.3	45.6	49.0	46.1	198.3	81.0	118.7	27.7	14.7	19.2	24.7	31.0
Dease River	34446	265.3	240.8	146.2	85.2	43.0	51.4	44.1	186.5	84.3	108.7	25.3	13.4	16.3	24.0	29.9
Fort Simpson	9001	292.8	266.0	156.5	85.4	50.1	53.2	44.9	204.8	85.3	116.4	30.6	17.1	18.8	24.8	33.8
Fort Simpson	9003	270.3	245.0	147.8	84.4	49.6	49.9	41.0	190.9	82.5	111.1	27.9	15.2	16.8	22.4	30.0
Fort Simpson	134131	272.0	253.5	132.7	84.1	48.0	41.8	41.8	193.2	78.2	112.6	27.0	15.0	17.7	24.6	29.7
Yukon																
Macmillan River	134496	283.3	255.7	148.0	87.2	47.5	49.0	42.8	204.0	87.2	111.0	26.5	14.5	17.2	24.6	31.0
Pelly Lakes	214478	276.5	253.6	152.3	83.5	51.3	53.4	46.1	200.5	86.1	110.0	27.0	14.5	17.8	24.2	31.0
Pelly Lakes	214479	275.0	256.9	150.2	85.4	47.5	52.0	47.1	202.7	92.9	112.1	28.2	15.8	17.7	24.0	31.7
Pelly Lakes	214477	270.9	247.7	143.7	83.1	46.2	47.8	44.3	195.4	84.2	111.6	26.4	14.6	16.7	23.0	29.1
Pelly Lakes	214481	277.3	256.3	145.2	82.2	49.1	46.4	40.7	202.7	87.2	116.7	26.8	14.8	18.1	24.4	30.2
MALE (n=17)	**Mean**	**276.5**	**253.5**	**146.7**	**84.3**	**47.7**	**49.4**	**44.1**	**197.7**	**84.0**	**112.7**	**27.3**	**15.0**	**17.7**	**24.1**	**30.7**
Standard Dev.		6.28	6.59	5.26	2.34	2.69	3.01	1.97	5.44	3.56	4.44	1.24	0.90	0.86	0.94	1.41
Alberta																
Wood Buffalo Park	130266	257.3	237.5	143.0	83.1	44.6	42.3	45.0	185.5	76.4	104.8	25.8	14.2	17.0	23.4	29.7
Wood Buffalo Park	92227	265.8	244.7	140.5	84.3	44.9	42.5	38.8	188.7	75.2	110.1	25.0	13.9	16.3	23.4	29.2
Wood Buffalo Park	98232	256.0	245.5	134.0	81.8	44.4	41.7	42.6	184.4	76.3	107.6	26.3	13.1	16.9	23.4	28.7
Wood Buffalo Park	130170	256.5	243.5	131.4	80.5	44.9	41.9	41.5	185.5	76.6	106.7	25.2	13.4	16.3	21.9	29.7
Mackenzie																
Fort Anderson	6508	257.8	241.9	139.5	81.3	45.9	44.6	39.5			110.0	26.1	15.1	17.8	23.5	
Fort Smith	134781	249.5	233.2	133.0	79.9	40.5	40.0	37.2	183.2	74.0	102.7	24.4	13.4	16.1	21.8	26.9
Great Bear Lake	34447	249.5	233.0	130.0	75.5	42.7	42.3	36.0	176.7	70.1	106.6	26.5	14.2	18.0	24.1	29.0
Great Slave Lake	121469	255.5	239.0	135.4	79.8	41.0	44.5	40.0	182.4	77.0	105.9	24.6	13.3	15.7	22.8	27.8
Yukon																
Macmillan River	134497	254.0	233.7	137.4	77.7	42.7	42.8	42.8	180.8	78.9	102.0	23.9	13.8	15.4	22.2	27.4
FEMALE (n=9)	**Mean**	**255.8**	**239.1**	**136.0**	**80.4**	**43.5**	**42.5**	**40.4**	**183.4**	**75.6**	**106.3**	**25.3**	**13.8**	**16.6**	**22.9**	**28.6**
Standard Dev.		4.87	5.04	4.39	2.67	1.88	1.41	2.87	3.60	2.62	2.83	0.91	0.62	0.89	0.81	1.06

Appendix 3. Description of 15 cranial measurements used by Goldman (1944).

1. **Greatest length** - Length from anterior tip of premaxillae to posterior point of inion in median line over foramen magnum.

2. **Condylobasal length** - Length from anterior tip of premaxillae to posterior plane of occipital condyles.

3. **Zygomatic breadth** - Greatest distance across zygomata

4. **Squamosal constriction** - Distance across squamosals at constriction behind zygomata.

5. **Width of rostrum** - Width of rostrum at constriction behind canines.

6. **Interorbital breadth** - Least distance between orbits.

7. **Postorbital constriction** - Least width of frontals at constriction behind postorbital processes.

8. **Length of mandible** - Distance from anterior end of mandible to plane of posterior ends of angles, the right and left sides measured together.

9. **Height of coronoid process** - Vertical height from lower border of angle.

10. **Maxillary tooth row, crown length** - Greatest distance from curved front of canine to back of cingulum of posterior upper molar.

11. **Upper carnassial, crown length** - Antero-posterior diameter of crown on outer side.

12. **Upper carnassial, crown width** - Transverse diameter at widest point anteriorly.

13. **First upper molar, antero-posterior diameter** - Greatest antero-posterior diameter of crown on outer side.

14. **First upper molar, transverse diameter** - Greatest transverse diameter of crown.

15. **Lower carnassial, crown length** - Antero-posterior diameter at cingulum.

Appendix 4. Measurement error calculated by remeasurement of 19 cranial specimens. Percent difference was calculated by taking the absolute value of: (M1 - M2 / M1) x 100. The mean and standard deviation was calculated for the 19 "% difference" values.

Variable	Mean % Difference	S.D.
Condy L	0.189	0.139
I^1- Sag C	0.180	0.130
Nasal L	0.784	0.736
I^1- Palat	0.261	0.250
I^2- Palat	0.230	0.198
Pos Pal L	0.337	0.640
C^1- M^2	0.288	0.245
W of C^1	3.106	3.010
W of P^4	4.702	2.530
L of P^4	0.358	0.278
W of M^1	1.595	1.366
L of M^1	0.940	0.841
W of M^2	1.309	1.228
I^3 to I^3	1.111	0.872
P^1 to P^1	1.062	1.013
P^2 to P^2	1.059	0.897
C^1 to C^1	0.404	0.447
M^1 to M^1	1.633	1.220
Cheek T W	2.219	1.286
Pos For W	0.347	0.387
Aud Bul W	2.073	1.527
Occ Cre W	0.230	0.122
Condyle W	1.184	1.706
Condyle L	1.219	0.825
Occ Con W	0.331	0.247
InterOr W	0.572	0.635
Postorb W	0.456	0.448
Tem Fos W	0.408	0.320
Pari-Temp W	1.027	0.589
Zygom W	0.207	0.185
M^1 to Orb	0.510	0.390
Jugal H	0.742	0.490
SagC-AudB	1.472	1.129
Sym-AngPr	0.319	0.453
Sym-Condy	0.263	0.239
C_1 - M_3	0.462	0.291
W of P_4	1.038	1.059
L of P_4	0.328	0.376
W of M_1	0.808	0.725
L of M_1	0.682	0.545
Mandib W	1.923	1.475
Art Con W	1.106	0.830
Art Con L	0.303	0.261
H of Ramus	1.176	2.657
AngP - CorP	0.115	0.092

Appendix 5. List of 10 cranial measurements used by Nowak (1995).

Nowak	Equivalent in this study
1. Greatest length of skull	I^1 - Sag C
2. Zygomatic width	Zygom W
3. Alveolar length of maxillary toothrow (P^1- M^2)	C^1-M^2 *
4. Maximum width across upper cheek teeth (at P^4)	Cheek T W
5. Palatal width at first premolars (inner P^1)	P^1 - P^1
6. Width of postorbital processes	Postorb W
7. Height from toothrow to orbit at M^1	M^1 to Orb
8. Height of jugal	Jugal H
9. Crown length of P^4	L of P^4
10. Width of M^2	W of M^2

* Nowak's measure of maxillary toothrow excludes the canine. This study has no equivalent measurement, but offers C^1- M^2 as a similar substitute for purposes of a discriminant analysis comparison. C^1- M^2 is longer than Nowak's measure by the ant.- posterior length of the canine as well as the diastema between C^1 and P^1.

Appendix 6. Summary of published mean values for I^1 - SagC, Zygom W, Cheek T W and P^4 L, for subspecific designations of *C. lupus* in northen Canada.

C.l. hudsonicus

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Goldman (1944)	Central	64°	5	259.5	142.4	-	26.40
Skeel & Carbyn (1977)	Southern	61°	25	261.5	140.6	81.9	26.15
Nowak (1995)	(not specified)	-	14	258.7	139.8	82.1	26.07
This study	Northern	67°	31	259.8	138.0	80.7	26.10
This study	Central	64°	50	259.2	141.1	81.3	26.00
This study	Southern	61°	36	265.8	142.6	82.4	26.80
This study	Pooled	61-67°	117	261.4	140.7	81.5	26.28
Females							
Goldman (1944)	Central	64°	1	251.0	134.8	-	24.50
Skeel & Carbyn (1977)	Southern	61°	25	248.3	133.4	78.8	28.15[a]
This study	Northern	67°	20	244.0	130.2	76.6	24.80
This study	Central	64°	60	245.4	133.0	77.5	25.00
This study	Southern	61°	28	245.7	133.7	76.8	24.70
This study	Pooled	61-67°	108	245.2	132.7	77.1	24.92

a this value appears to be unusually large and may be an error.

C.l. occidentalis

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Anderson (1943)	Artillery L	63°	2	269.3	142.8	-	26.50
Jolicoeur (1975)	N. Great Slave L.	64°	106	-	143.3	80.5	-
This study	Great Slave	61-63°	43	261.9	140.9	80.9	26.19
Anderson (1943)	WBNP	60°	5	269.0	148.5	-	26.70
Goldman (1944)	(wide ranging)	54-68°	17	276.5	146.7	-	27.30
Skeel & Carbyn (1977)	WBNP	60°	24	265.1	143.4	83.3	26.45
Nowak (1995)	(not specified)	-	50	276.2	148.2	85.1	26.81
This study	N. Alberta	54-61°	34	278.0	150.5	86.1	26.82
Females							
Anderson (1943)	Artillery Lake	63°	4	259.7	137.0	-	26.50
Jolicoeur (1975)	N. Great Slave L.	64°	103	-	135.2	76.4	-
This study	Great Slave Lake	61-63°	34	249.0	134.2	77.1	24.99
Anderson (1943)	WBNP	60°	5	260.6	131.5	-	25.90
Goldman (1944)	WBNP-Great Bear	60-67°	4	255.8	136.0	-	25.30
Skeel & Carbyn (1977)	WBNP	60°	5	264.3	138.9	79.9	25.78
This study	N. Alberta	54-61°	30	263.6	140.3	81.3	25.23

C.l. mackenzii

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Anderson (1943)	Coronation Gulf	68°	*3*	251.0	132.8	-	26.70
This study	Mackenzie Reg.	63-70°	*41*	259.2	141.1	80.7	26.39
Females							
Anderson (1943)	Coronation Gulf	68°	*2*	241.0	129.8	-	25.40
This study	Mackenzie Reg.	63-70°	*26*	247.8	134.0	76.2	24.98

C.l. griseoalbus

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Anderson (1943)	PANP	54°	*3*	282.2	147.0	-	27.3
Skeel & Carbyn (1977)	PANP	54°	*22*	274.4	147.7	86.4	27.33
Nowak (1995)	(not specified)	-	*10*	271.5	144.8	89.3	27.18
This study	PANP	54°	*15*	275.3	146.2	85.0	27.06
Females							
Anderson (1943)	PANP	54°	*3*	267.5	135.8	-	27.30
Skeel & Carbyn (1977)	PANP	54°	*27*	253.6	136.3	80.4	25.53
This study	PANP	54°	*6*	258.0	137.9	81.3	25.22

C.l. arctos

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Goldman (1944)	Ellesmere Is.	> 76°	*1*	264.7	138.7	-	26.4
Anderson (1943)	Ellesmere Is.	> 76°	*3*	261.9	142.2	-	26.80
Jolicoeur (1975)	A. Archipelago	> 75°	*10*	-	142.4	81.7	-
Nowak (1995)	Queen Eliz. Is.	> 75°	*22*	256.5	142.4	86.8	27.45
This study	Queen Eliz. Is.	> 75°	*21*	256.4	142.4	82.8	27.12
Females							
Jolicoeur (1975)	A. Archipelago	> 75°	*6*	-	137	79.23	-
This study	Queen Eliz. Is.	> 75°	*8*	246.8	136.6	79.4	25.80

C.l. bernardii

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Anderson (1943)	Banks Island	72°	*3*	245.3	129.3	-	27.40
This study	Banks / Victoria	69-72°	*11*	252.1	140.2	84.6	27.22
Females							
Anderson (1943)	Banks Island	72°	*2*	238.8	120.0	-	26.00
This study	Banks / Victoria	69-72°	*5*	243.0	138.0	81.5	25.61

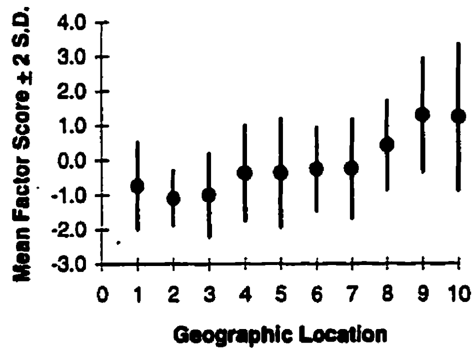
C.l. manningi

Reference	Location	Lat.	*n*	I^1- SagC L.	Zygo. W.	Cheek T W.	P^4 L.
Males							
Anderson (1943)	Baffin Island		*2*	253.5	137.5	-	24.30
This study	Baffin Island	62-70°	*15*	252.7	136.4	77.9	25.67
Females							
Anderson (1943)	Baffin Island		*3*	247.8	129.5	-	24.30
This study	Baffin Island	62-70°	*8*	240.3	130.0	76.4	24.78

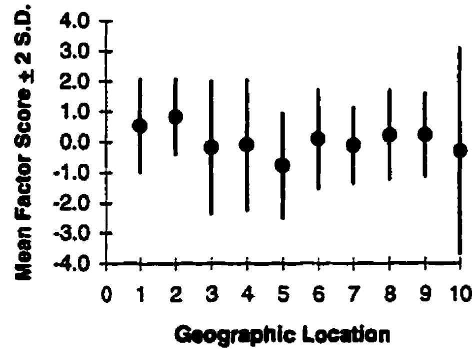
Appendix 7. Plot of mean factor scores ± 2 S.D. for male (PC1-PC6) and female (PC1-PC7 wolves from the 10 geographic locations, (1) Queen Elizabeth Is., (2) Banks / Victoria Island, (3) Baffin Island, (4) Mackenzie, (5) Great Slave Lake, (6) N. Keewatin (7) C. Keewatin, (8) S. Keewatin, (9) C. Saskatchewan, and (10) N. Alberta.

MALES

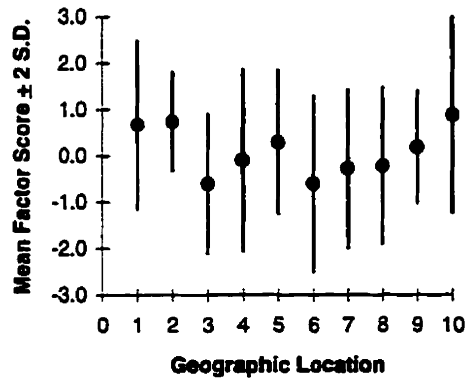
PC I



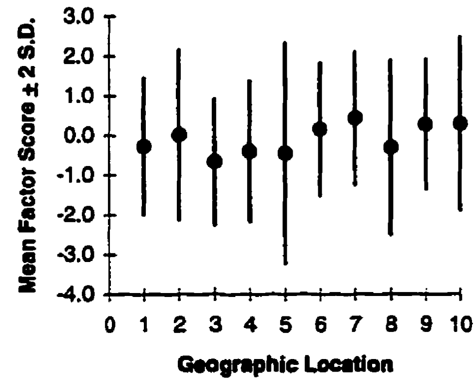
PC II



PC III



PC IV



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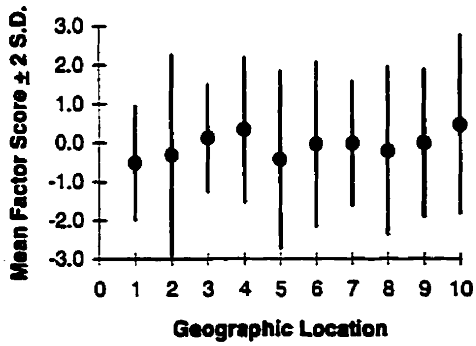
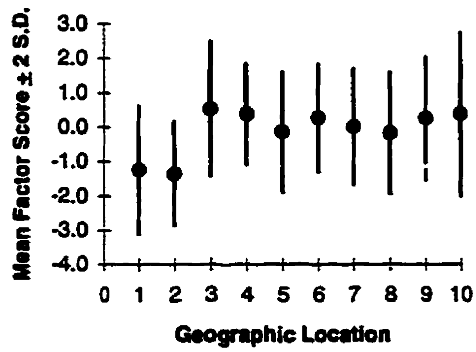


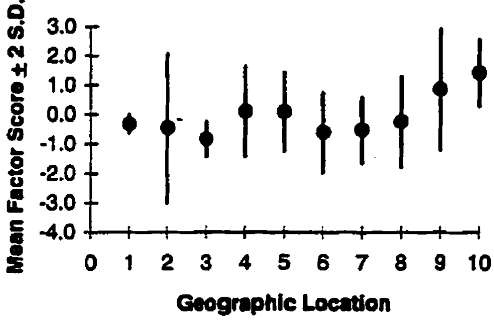
PC VI



Appendix 7. (Con't)

FEMALES

PC I



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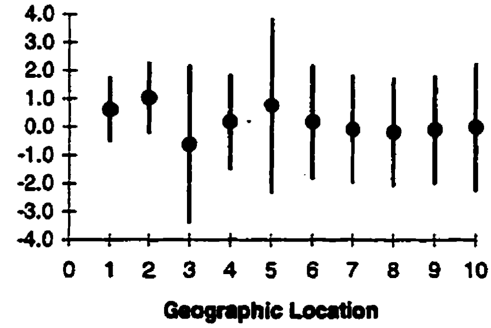

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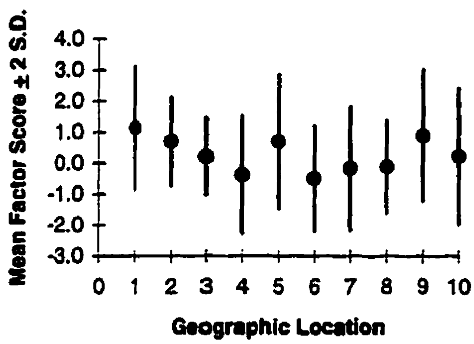

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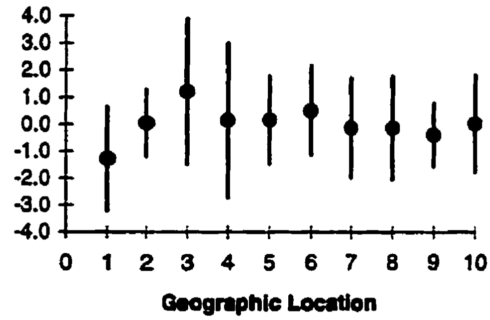

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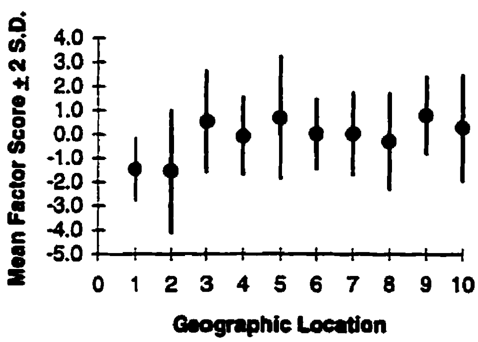

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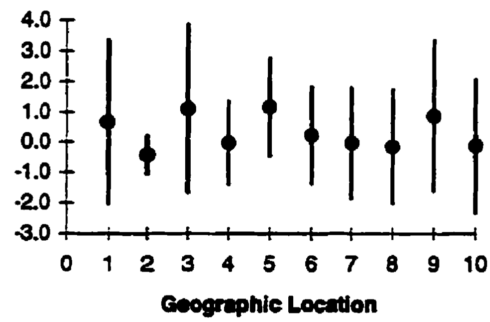
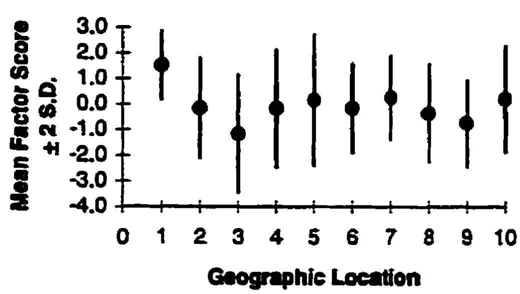


PC VII



Appendix 8. Eigenvalues, % variation, canonical correlation coefficients, Wilk's lambda values, Chi-square values, degrees of freedom, and levels of significance for canonical discriminant functions (DF) used for discriminant analysis of cranial parameters in male and female wolves.

Males

Parameter	Eigenvalue	% of Variation	Canonical Correlation	Wilk's Lambda	Chi-squared	Degrees of Freedom	P Value
DF 1	3.553	36.76	0.8834	0.0030	1,005.5	405	0.0000
DF 2	1.839	19.02	0.8048	0.0138	742.5	352	0.0000
DF 3	1.079	11.16	0.7203	0.0393	561.5	301	0.0000
DF 4	0.887	9.17	0.6855	0.0817	434.5	252	0.0000
DF 5	0.666	6.89	0.6323	0.1542	324.4	205	0.0000
DF 6	0.573	5.93	0.6037	0.2569	235.8	160	0.0001
DF 7	0.499	5.16	0.5768	0.4042	157.2	117	0.0078
DF 8	0.320	3.31	0.4921	0.6057	87.0	76	0.1827
DF 9	0.251	2.6	0.4480	0.7993	38.9	37	0.3854

Females

Parameter	Eigenvalue	% of Variation	Canonical Correlation	Wilk's Lambda	Chi-squared	Degrees of Freedom	P Value
DF 1	5.472	49.83	0.9195	0.0029	680.4	405	0.0000
DF 2	1.447	13.17	0.7689	0.0188	462.8	352	0.0001
DF 3	1.247	11.35	0.7449	0.0461	358.6	301	0.0126
DF 4	0.804	7.32	0.6676	0.1035	264.3	252	0.2855
DF 5	0.593	5.4	0.6101	0.1867	195.5	205	0.6711
DF 6	0.422	3.84	0.5449	0.2974	141.3	160	0.8537
DF 7	0.382	3.48	0.5257	0.4229	100.3	117	0.8661
DF 8	0.328	2.98	0.4968	0.5845	62.6	76	0.8657
DF 9	0.289	2.63	0.4733	0.7760	29.5	37	0.8034

Appendix 9.1 Descriptive statistics for 45 cranial variables (mm) for all adult male and female wolves considered in this study. Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, are indicated by underlined *t*-values.

	Males					Females							
Variable	*N*	Range		Mean	S.D.	*N*	Range		Mean	S.D.	R	t-value	P
Condy L	284	216	284	241.71	10.04	206	206	255	230.16	8.76	1.050	13.24	< 0.001
I^1- Sag C	294	231	305	262.68	11.28	219	226	280	248.78	9.84	1.056	14.57	< 0.001
Nasal L	296	79	122	98.04	6.01	222	80	107	91.63	5.34	1.070	12.59	< 0.001
I^1- Palat	296	108	139	120.60	5.10	227	104	128	115.48	4.44	1.044	12.04	< 0.001
I^2- Palat	296	105	137	118.17	5.07	227	102	125	113.04	4.36	1.045	12.42	< 0.001
Pos Pal L	286	89	121	101.78	4.92	212	85	108	96.74	4.27	1.052	11.97	< 0.001
C^1- M^2	294	96	126	109.70	4.29	224	93	114	105.08	3.77	1.044	12.77	< 0.001
W of C^1	290	9	18	15.12	1.05	221	12	16	13.88	0.82	1.089	14.44	< 0.001
W of P^4	296	7	13	10.98	0.70	227	9	12	10.42	0.56	1.053	9.79	< 0.001
L of P^4	296	21	30	26.44	1.19	227	22	28	25.03	1.06	1.057	14.16	< 0.001
W of M^1	295	16	24	20.92	1.12	226	16	23	19.88	1.09	1.052	10.58	< 0.001
L of M^1	296	11	19	16.74	0.84	226	14	22	16.18	0.80	1.035	7.74	< 0.001
W of M^2	296	9	16	13.71	0.86	227	11	15	13.15	0.77	1.042	7.66	< 0.001
I^3 to I^3	285	32	43	37.90	1.76	215	31	40	35.80	1.68	1.059	13.47	< 0.001
P^1 to P^1	289	27	38	32.13	1.91	227	26	37	30.55	1.79	1.052	9.60	< 0.001
P^2 to P^2	294	30	43	35.85	2.04	227	29	41	34.02	1.93	1.054	10.38	< 0.001
C^1 to C^1	278	42	58	48.77	2.62	220	28	52	45.60	2.55	1.069	13.54	< 0.001
M^1 to M^1	295	74	93	81.91	3.27	226	47	87	77.78	3.64	1.053	13.61	< 0.001
Cheek T W	292	73	94	82.00	3.55	224	69	87	77.82	3.38	1.054	13.53	< 0.001
Pos For W	292	57	73	65.18	2.57	220	57	70	62.87	2.45	1.037	10.29	< 0.001
Aud Bul W	287	15	26	19.36	1.94	216	13	24	18.43	1.77	1.050	5.56	< 0.001
Occ Cre W	288	74	95	82.57	3.32	215	71	89	79.01	3.15	1.045	12.15	< 0.001
Condyle W	286	10	16	12.39	0.98	209	10	14	11.55	0.72	1.073	11.12	< 0.001
Condyle L	284	22	31	26.13	1.44	206	21	28	24.72	1.23	1.057	11.69	< 0.001
Occ Con W	285	43	59	50.80	2.38	213	42	56	48.10	2.11	1.056	13.12	< 0.001
InterOr W	297	39	59	47.28	3.00	225	39	52	44.66	2.67	1.059	10.36	< 0.001
Postorb W	297	50	78	64.30	4.74	218	47	72	60.74	4.48	1.059	8.61	< 0.001
Tem Fos W	297	33	49	41.94	2.78	224	32	48	40.75	2.95	1.029	4.69	< 0.001
Pari-Temp W	290	61	76	67.17	2.32	220	59	73	66.00	2.17	1.018	5.77	< 0.001
Zygom W	292	122	163	142.09	6.12	220	123	146	134.41	5.07	1.057	15.53	< 0.001
M^1 to Orb	297	35	54	42.72	2.90	226	34	49	39.93	2.66	1.070	11.31	< 0.001
Jugal H	297	16	27	19.46	1.51	227	15	22	18.25	1.47	1.066	9.21	< 0.001
SagC-AudB	290	74	98	85.72	4.03	214	72	93	81.79	3.41	1.048	11.84	< 0.001
Sym-AngPr	266	173	228	193.33	8.00	202	167	206	183.96	7.61	1.051	12.82	< 0.001
Sym-Condy	266	171	225	191.18	8.52	202	163	203	181.66	7.69	1.052	12.47	< 0.001
C_1 - M_3	265	97	139	123.01	4.84	201	105	128	117.95	4.29	1.043	11.74	< 0.001
W of P_4	284	3	10	8.32	0.60	219	7	9	7.86	0.42	1.059	10.18	< 0.001
L of P_4	284	11	19	16.48	0.87	219	14	18	15.67	0.71	1.052	11.15	< 0.001
W of M_1	283	7	13	11.92	0.69	221	10	13	11.17	0.51	1.067	13.95	< 0.001
L of M_1	284	24	33	29.68	1.33	221	25	32	28.24	1.24	1.051	12.41	< 0.001
Mandib W	284	11	19	14.33	0.99	221	12	17	13.42	1.04	1.068	10.00	< 0.001
Art Con W	292	9	16	12.48	1.14	225	9	15	11.64	0.95	1.072	9.10	< 0.001
Art Con L	292	27	38	33.17	2.04	226	27	37	31.11	1.85	1.066	11.88	< 0.001
H of Ramus	284	26	40	31.68	2.23	220	25	36	29.52	2.14	1.073	10.99	< 0.001
AngP - CorP	292	65	94	78.78	4.60	226	65	89	73.55	4.31	1.071	13.17	< 0.001

Appendix 9.2 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from the **Queen Elizabeth Islands** (*C.l. arctos*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined t-values.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	20	222	251	236.66	7.85	7	224	232	228.10	2.45	1.038	4.32	<0.001
I^1 - Sag C	21	239	272	256.42	9.65	8	241	254	246.83	4.68	1.039	2.67	0.013
Nasal L	21	84	108	95.70	5.22	7	84	96	89.65	3.84	1.067	2.81	0.009
I^1 - Palat	20	108	124	116.14	4.13	8	112	115	113.26	1.35	1.025	2.77	0.010
I^2 - Palat	20	105	122	113.85	4.28	8	109	113	110.97	1.48	1.026	1.84	0.077
Pos Pal L	20	92	107	101.10	3.69	7	94	101	97.73	2.35	1.034	2.25	0.034
C^1 - M^2	20	100	114	108.10	3.47	8	104	106	105.02	0.76	1.029	3.75	0.001
W of C^1	20	14	17	15.89	0.69	8	14	16	14.57	0.73	1.091	4.51	<0.001
W of P^4	20	9	12	10.94	0.69	8	10	12	10.29	0.56	1.063	2.35	0.027
L of P^4	20	25	29	27.12	1.19	8	25	27	25.80	0.90	1.051	2.82	0.009
W of M^1	20	18	23	20.93	1.21	8	18	22	19.88	1.08	1.053	2.13	0.042
L of M^1	20	15	18	16.86	0.84	8	15	18	16.31	0.72	1.034	1.60	0.122
W of M^2	20	12	15	13.74	0.78	8	13	15	13.40	0.63	1.025	1.10	0.282
I^3 to I^3	19	35	41	38.21	1.48	6	35	37	36.38	0.69	1.050	2.91	0.008
P^1 to P^1	19	30	37	32.67	1.96	8	31	33	31.83	0.72	1.026	1.64	0.114
P^2 to P^2	20	33	41	36.90	1.86	8	33	38	35.18	1.64	1.049	2.28	0.031
C^1 to C^1	20	45	53	48.38	1.89	8	45	47	45.98	0.67	1.052	4.95	<0.001
M^1 to M^1	20	75	88	81.69	3.25	8	74	87	78.95	3.76	1.035	1.93	0.065
Cheek T W	19	78	87	82.84	2.82	8	76	85	79.41	2.71	1.043	2.92	0.007
Pos For W	19	60	72	66.22	3.03	8	62	66	64.15	1.45	1.032	1.83	0.079
Aud Bul W	19	16	22	18.57	1.66	6	17	20	19.22	1.10	0.966	-0.89	0.385
Occ Cre W	19	77	85	80.82	2.62	6	77	82	79.27	1.89	1.020	1.34	0.195
Condyle W	20	11	13	11.88	0.73	7	10	12	11.33	0.52	1.049	1.81	0.082
Condyle L	20	22	27	25.33	1.16	7	23	25	23.86	0.60	1.062	3.18	0.004
Occ Con W	20	46	52	50.08	1.74	7	46	49	46.98	1.25	1.066	4.32	<0.001
InterOr W	21	41	51	46.27	2.83	8	43	45	44.25	0.91	1.046	2.90	0.007
Postorb W	21	56	71	63.91	4.69	7	58	66	61.53	2.50	1.039	1.27	0.214
Tem Fos W	21	36	44	40.04	2.06	8	34	43	38.97	2.69	1.027	1.15	0.259
Pari-Temp W	20	61	67	64.78	1.8	8	59	66	63.62	2.49	1.018	1.38	0.180
Zygom W	20	129	152	142.38	6.35	7	132	144	136.56	4.24	1.043	2.24	0.034
M^1 to Orb	21	39	46	41.76	2.01	8	39	43	40.76	1.55	1.025	1.26	0.217
Jugal H	21	17	22	19.03	1.19	8	17	20	18.73	1.18	1.016	0.60	0.552
SagC-AudB	20	79	91	86.59	4.2	7	82	89	85.21	2.78	1.016	0.81	0.427
Sym-AngPr	19	176	203	189.23	6.04	8	181	186	183.77	1.56	1.030	3.66	<0.001
Sym-Condy	19	173	199	185.99	6.26	8	175	185	180.36	2.69	1.031	2.43	0.023
C_1 - M_3	19	97	129	119.73	6.82	8	116	120	118.01	1.37	1.015	0.70	0.491
W of P_4	19	7	9	8.33	0.45	8	8	9	8.08	0.34	1.031	1.37	0.183
L of P_4	19	16	19	17.54	0.71	8	16	18	16.79	0.46	1.045	2.71	0.012
W of M_1	19	11	13	12.06	0.57	8	11	12	11.34	0.43	1.063	3.19	0.004
L of M_1	19	27	33	30.37	1.3	8	28	30	28.88	0.99	1.052	2.90	0.008
Mandib W	19	13	16	14.34	0.8	8	12	16	13.59	1.22	1.055	1.89	0.070
Art Con W	19	10	14	12.26	0.97	8	11	13	12.01	0.83	1.021	0.64	0.529
Art Con L	19	29	35	33.24	1.73	8	30	33	31.23	1.17	1.064	2.99	0.006
H of Ramus	19	29	34	31.27	1.42	8	29	32	30.47	1.32	1.026	1.36	0.185
AngP - CorP	19	68	86	76.92	3.62	8	69	76	72.03	2.37	1.068	3.50	0.002

Appendix 9.3 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from **Baffin Island** (*C.l. manningi*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R=male mean /female mean. Unequal variances, identified by Levene's test, are indicated by underlined t-values.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	14	219	244	231.12	7.35	8	206	233	222.57	8.69	1.038	2.46	0.023
I^1- Sag C	15	236	268	252.67	9.75	8	226	252	240.33	8.05	1.051	3.06	0.006
Nasal L	15	87	100	94.31	4.20	8	85	94	89.43	3.21	1.055	2.86	0.009
I^1- Palat	15	109	123	115.50	4.47	8	104	118	111.71	4.15	1.034	1.98	0.061
I^2- Palat	15	107	121	112.70	4.28	8	102	115	109.45	4.05	1.030	1.76	0.093
Pos Pal L	14	92	102	96.49	3.05	8	85	99	93.26	4.87	1.035	1.93	0.690
C^1- M^2	15	99	110	104.98	3.29	8	93	104	100.55	3.38	1.044	3.05	0.006
W of C^1	15	13	16	14.42	0.89	8	12	15	13.61	1.00	1.060	2.00	0.059
W of P^4	15	9	12	10.98	0.87	8	10	12	10.68	0.83	1.028	0.77	0.447
L of P^4	15	23	27	25.67	1.28	8	23	27	24.78	1.31	1.036	1.58	0.129
W of M^1	15	18	22	20.42	1.19	8	18	21	19.57	1.05	1.043	1.69	0.105
L of M^1	15	14	17	16.14	0.99	8	15	17	15.75	0.83	1.025	0.96	0.347
W of M^2	15	11	14	13.13	0.85	8	12	13	12.59	0.49	1.043	1.63	0.118
I^3 to I^3	14	34	42	37.98	2.50	6	33	40	36.37	2.96	1.044	1.25	0.227
P^1 to P^1	13	28	34	30.72	1.91	8	28	31	29.15	1.42	1.054	2.00	0.060
P^2 to P^2	15	32	36	34.00	1.84	8	31	35	33.10	1.62	1.027	1.16	0.261
C^1 to C^1	14	44	50	46.77	1.93	8	42	47	44.24	1.89	1.057	2.97	0.008
M^1 to M^1	15	75	83	79.30	2.47	7	74	82	78.42	2.75	1.011	0.75	0.464
Cheek T W	15	74	83	77.87	2.50	7	73	78	76.44	2.03	1.019	1.32	0.202
Pos For W	15	57	67	62.45	2.52	8	58	63	59.21	1.92	1.055	3.16	0.005
Aud Bul W	15	15	20	17.47	1.56	8	13	19	16.51	1.93	1.058	1.30	0.208
Occ Cre W	15	75	82	79.60	1.99	8	71	81	76.89	3.69	1.035	2.31	0.031
Condyle W	14	10	14	12.40	1.02	8	11	13	11.69	0.75	1.061	1.69	0.106
Condyle L	14	23	27	24.75	0.96	7	21	26	23.95	1.51	1.033	1.51	0.148
Occ Con W	15	45	54	49.03	2.47	8	44	50	46.64	1.82	1.051	2.40	0.025
InterOr W	15	41	50	44.88	2.29	8	40	47	43.57	3.20	1.030	1.14	0.266
Postorb W	15	56	67	60.85	3.62	7	59	66	61.80	2.90	0.985	-0.60	0.522
Tem Fos W	15	39	46	41.48	1.80	8	37	48	42.91	3.60	0.967	-1.05	0.320
Pari-Temp W	15	64	71	67.93	1.72	8	63	69	67.06	2.24	1.013	1.04	0.310
Zygom W	14	129	141	136.39	4.36	8	125	136	129.97	3.37	1.049	3.58	0.002
M^1 to Orb	15	37	43	40.37	1.57	8	34	42	37.35	2.05	1.081	3.96	0.001
Jugal H	15	18	20	18.86	0.78	8	16	21	18.41	1.20	1.024	1.09	0.290
SagC-AudB	15	78	89	83.17	3.16	8	80	86	82.32	2.21	1.010	0.68	0.505
Sym-AngPr	14	173	194	184.32	6.22	8	167	186	177.81	6.14	1.037	2.37	0.028
Sym-Condy	14	173	191	181.84	6.20	8	163	186	175.41	6.73	1.037	2.27	0.034
C_1 - M_3	15	107	125	117.95	4.73	8	106	117	113.22	4.23	1.042	2.36	0.028
W of P_4	15	7	9	8.12	0.47	8	7	9	7.81	0.56	1.040	1.41	0.173
L of P_4	15	15	18	16.19	0.84	8	14	17	15.47	0.92	1.047	1.89	0.073
W of M_1	15	10	13	11.82	0.77	8	11	12	11.22	0.68	1.053	1.85	0.078
L of M_1	15	27	30	28.46	1.25	8	26	30	27.86	1.37	1.022	1.06	0.303
Mandib W	15	12	16	14.23	1.30	8	12	15	12.98	0.77	1.096	2.49	0.021
Art Con W	14	9	14	11.29	1.42	8	10	12	11.15	0.69	1.013	0.30	0.766
Art Con L	14	27	34	30.96	2.26	8	29	32	29.81	1.16	1.039	1.58	0.130
H of Ramus	15	26	34	30.95	2.35	8	26	31	28.75	1.76	1.077	2.31	0.031
AngP - CorP	14	65	81	72.97	3.74	8	66	73	69.97	2.32	1.043	2.04	0.055

Appendix 9.4 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from **Banks / Victoria Is.** (*C.l. bernardi*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined *t*-values.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	10	222	240	233.02	4.94	4	218	238	225.97	9.63	1.031	1.85	0.089
I^1- Sag C	10	242	258	252.14	6.31	5	235	258	242.98	10.12	1.038	2.18	0.049
Nasal L	11	89	103	96.32	5.39	5	87	100	91.42	5.17	1.054	1.71	0.110
I^1- Palat	11	109	121	115.44	3.24	5	108	119	112.19	4.39	1.029	1.67	0.116
I^2- Palat	11	108	118	113.14	2.81	5	105	116	109.24	4.38	1.036	2.16	0.048
Pos Pal L	10	93	103	98.47	2.89	5	91	101	95.44	3.84	1.032	1.73	0.108
C^1- M^2	11	99	114	105.83	4.07	5	99	108	103.40	3.56	1.024	1.15	0.270
W of C^1	11	15	18	15.92	1.00	5	14	15	14.27	0.73	1.116	3.29	0.005
W of P^4	11	10	12	11.05	0.83	5	10	11	10.37	0.56	1.066	1.68	0.115
L of P^4	11	26	29	27.22	0.77	5	24	27	25.61	1.20	1.063	3.26	0.006
W of M^1	11	21	23	21.82	0.64	4	20	21	20.22	0.66	1.079	4.26	0.001
L of M^1	11	16	18	16.92	0.48	4	16	17	16.31	0.47	1.037	2.19	0.048
W of M^2	11	13	15	14.25	0.43	5	13	14	13.51	0.52	1.055	3.00	0.010
I^3 to I^3	11	35	40	37.41	1.53	4	33	37	34.95	1.88	1.070	2.61	0.022
P^1 to P^1	10	29	34	31.79	1.55	5	29	34	31.04	2.13	1.024	0.78	0.450
P^2 to P^2	11	34	39	36.84	1.70	5	34	38	35.32	1.78	1.043	1.64	0.124
C^1 to C^1	11	45	51	47.67	1.99	5	44	49	45.68	2.03	1.044	1.84	0.087
M^1 to M^1	11	78	90	83.47	3.05	5	78	85	80.67	2.84	1.035	1.73	0.106
Cheek T W	11	80	94	84.58	4.32	4	78	87	81.47	4.25	1.038	1.24	0.238
Pos For W	11	63	71	65.60	2.28	5	61	69	63.38	3.05	1.035	1.63	0.125
Aud Bul W	10	17	21	19.32	1.12	5	16	20	18.14	1.78	1.065	1.60	0.134
Occ Cre W	10	80	91	82.95	3.67	5	75	84	79.17	3.50	1.048	1.91	0.078
Condyle W	10	11	13	11.85	0.69	4	10	12	10.84	0.94	1.093	2.25	0.044
Condyle L	10	24	27	24.79	1.17	4	22	26	24.01	1.63	1.032	1.01	0.332
Occ Con W	10	48	54	50.42	2.23	4	45	48	46.57	1.36	1.083	3.18	0.008
InterOr W	11	40	52	45.16	3.89	5	44	51	45.99	2.90	0.982	-0.42	0.678
Postorb W	11	55	73	63.74	6.73	5	63	69	64.67	2.78	0.986	-0.39	0.701
Tem Fos W	11	35	45	40.81	3.16	5	37	44	40.92	2.32	0.997	-0.07	0.947
Pari-Temp W	10	63	67	65.81	1.11	5	60	68	63.95	2.91	1.029	1.83	0.091
Zygom W	11	134	148	140.15	4.95	5	132	145	138.00	4.72	1.016	0.82	0.428
M^1 to Orb	11	40	44	42.52	1.44	5	39	44	41.39	1.98	1.027	1.29	0.217
Jugal H	11	18	21	19.49	0.83	5	18	20	18.79	0.47	1.037	1.76	0.100
SagC-AudB	10	80	90	85.60	3.59	5	80	87	82.81	2.77	1.034	1.52	0.153
Sym-AngPr	11	185	197	189.58	4.16	5	177	190	182.07	5.76	1.041	2.98	0.010
Sym-Condy	11	177	194	186.14	5.17	5	175	190	179.99	6.67	1.034	2.02	0.062
C_1 - M_3	11	113	127	119.56	3.93	5	112	122	116.68	3.75	1.025	1.38	0.190
W of P_4	11	8	10	8.94	0.57	5	8	9	8.31	0.57	1.076	2.07	0.058
L of P_4	11	16	18	17.67	0.64	5	16	17	16.66	0.27	1.061	3.36	0.005
W of M_1	11	11	13	12.07	0.79	5	11	12	11.36	0.49	1.063	1.81	0.092
L of M_1	11	30	32	31.14	0.74	5	29	30	29.42	0.67	1.058	4.46	0.001
Mandib W	11	13	15	14.28	0.62	5	13	15	13.90	0.41	1.027	1.24	0.234
Art Con W	11	10	13	11.83	0.69	5	10	12	10.91	0.76	1.084	2.40	0.031
Art Con L	11	31	36	32.45	1.74	5	29	33	31.80	1.64	1.020	0.71	0.492
H of Ramus	11	28	33	30.44	1.40	5	27	31	29.31	1.77	1.039	1.38	0.189
AngP - CorP	11	74	81	77.01	2.59	5	67	75	71.63	3.58	1.075	3.43	0.004

Appendix 9.5 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from the **Mackenzie Region** (*C.l. mackenzii*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	38	216	259	238.41	7.95	20	215	249	229.95	8.13	1.037	3.82	<0.001
I^1-Sag C	41	238	280	259.17	8.93	26	233	268	247.8	9.03	1.046	5.06	<0.001
Nasal L	41	87	110	96.44	5.73	25	80	101	90.46	5.15	1.066	4.27	<0.001
I^1-Palat	41	109	126	119.18	4.1	26	106	125	116.19	4.44	1.026	2.82	0.006
I^2-Palat	41	108	123	116.65	3.96	26	105	122	113.55	4.23	1.027	3.04	0.003
PosPal L	38	89	114	100.53	4.18	21	91	103	96.68	3.05	1.040	3.71	<0.001
C^1-M^2	41	96	116	107.98	3.75	25	98	112	105.22	3.03	1.026	3.11	0.003
W of C^1	38	13	16	14.8	0.99	24	12	16	13.93	1.03	1.062	3.33	<0.001
W of P^4	41	9	13	10.93	0.73	26	10	11	10.41	0.52	1.050	3.15	0.002
L of P^4	41	24	28	26.39	0.98	26	23	27	24.98	1.00	1.056	5.69	<0.001
W of M^1	41	18	24	20.89	1.17	26	18	22	19.81	1.05	1.055	3.81	<0.001
L of M^1	41	15	19	16.58	0.85	26	14	18	16.09	0.73	1.030	2.43	0.018
W of M^2	41	11	15	13.55	0.9	26	11	15	13.2	0.80	1.027	1.63	0.108
I^3 to I^3	40	34	42	38.15	1.76	25	34	39	35.78	1.47	1.066	5.63	<0.001
P^1 to P^1	41	28	36	31.91	1.79	26	28	35	30.25	1.79	1.055	3.70	<0.001
P^2 to P^2	41	30	39	35.64	1.99	26	31	39	33.55	2.13	1.062	4.08	<0.001
C^1 to C^1	34	42	54	48.13	2.24	20	42	51	45.74	2.57	1.052	3.58	<0.001
M^1 to M^1	41	75	87	81.99	2.83	26	47	85	76.48	6.84	1.072	4.59	<0.001
Cheek T W	41	73	87	80.71	2.87	25	71	83	76.18	3.18	1.059	5.98	<0.001
Pos For W	41	59	70	64.42	2.34	26	57	69	62.43	2.56	1.032	3.27	0.002
Aud Bul W	40	15	23	18.99	1.73	25	15	22	18.01	1.84	1.054	2.16	0.034
Occ Cre W	41	76	86	82	2.99	24	72	83	77.9	2.97	1.053	5.35	<0.001
Condyle W	38	10	13	12.16	0.67	21	10	12	11.33	0.50	1.073	4.91	<0.001
Condyle L	38	24	28	25.75	1.17	19	23	27	24.46	1.02	1.053	4.10	<0.001
Occ Con W	38	46	55	50.02	2.11	22	43	50	47.68	1.90	1.049	4.30	<0.001
InterOr W	41	42	52	47.11	2.3	26	39	50	44.85	3.02	1.050	3.46	<0.001
Postorb W	40	53	71	63.37	3.98	26	53	70	61.16	4.28	1.036	2.14	0.036
Tem Fos W	41	36	47	42.28	2.46	26	34	47	41.37	2.83	1.022	1.39	0.169
Pari-Temp W	41	62	72	67.25	2.04	26	62	72	66.03	2.18	1.018	2.31	0.024
Zygom W	41	133	151	141.08	4.56	26	125	146	133.96	5.29	1.053	5.85	<0.001
M^1 to Orb	41	37	47	41.47	2.32	26	36	49	40.16	2.81	1.033	2.07	0.042
Jugal H	41	16	21	18.87	1.2	26	15	21	18.31	1.44	1.031	1.73	0.089
SagC-AudB	41	79	93	84.7	3.36	26	77	89	81.44	2.78	1.040	4.13	<0.001
Sym-AngPr	41	176	206	190.7	6.33	26	171	199	184.11	6.57	1.036	4.09	<0.001
Sym-Condy	41	174	204	188.61	6.19	26	167	196	181.32	6.34	1.040	4.65	<0.001
C_1-M_3	41	110	131	122.01	4.29	26	110	127	118.88	4.12	1.026	2.96	0.004
W of P_4	41	7	10	8.18	0.56	26	7	9	7.78	0.43	1.051	3.07	0.003
L of P_4	41	14	17	16.16	0.73	26	15	17	15.49	0.64	1.043	3.83	<0.001
W of M_1	41	10	13	11.7	0.73	26	10	12	10.96	0.52	1.068	4.48	<0.001
L of M_1	41	26	32	29.35	1.24	26	26	30	27.86	1.18	1.053	4.90	<0.001
Mandib W	41	12	17	13.97	1.03	26	12	17	13.66	1.25	1.023	1.13	0.262
Art Con W	41	10	13	11.96	0.8	26	9	14	11.14	0.99	1.074	3.70	<0.001
Art Con L	41	30	37	32.7	1.66	26	28	36	30.99	2.15	1.055	3.66	<0.001
H of Ramus	41	27	34	30.45	1.86	26	26	36	29.52	2.26	1.032	1.83	0.071
AngP-CorP	41	71	85	78.5	3.45	26	68	83	73.75	4.12	1.064	5.09	<0.001

Appendix 9.6 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from **Great Slave Lake** (*C.l. occidentalis*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined *t*-values.

Variable	Males					Females					R	t-value	P
	N	Range		Mean	S.D.	*N*	Range		Mean	S.D.			
Condy L	39	222	251	239.59	6.72	27	221	242	229.06	5.60	1.046	6.69	<0.001
I^1-Sag C	42	244	275	261.92	8.43	32	240	263	249.00	6.53	1.052	7.18	<0.001
Nasal L	43	87	109	98.31	4.93	35	86	101	92.01	4.25	1.068	5.97	<0.001
I^1- Palat	43	111	127	120.23	3.67	36	111	122	116.00	3.19	1.036	5.41	<0.001
I^2- Palat	43	109	125	117.87	3.72	36	109	119	113.55	3.05	1.038	5.57	<0.001
Pos Pal L	41	89	107	100.94	3.68	30	91	102	95.93	3.05	1.052	6.08	<0.001
C^1- M^2	43	101	117	109.24	4.15	35	100	111	104.87	2.90	1.042	5.46	<0.001
W of C^1	43	13	18	14.82	0.99	35	12	16	13.78	0.96	1.075	4.68	<0.001
W of P^4	43	9	12	10.86	0.67	36	9	11	10.35	0.48	1.049	3.83	<0.001
L of P^4	43	24	29	26.19	1.24	36	23	28	24.99	1.14	1.048	4.42	<0.001
W of M^1	43	19	23	20.69	1.01	35	18	22	20.06	1.17	1.031	2.56	0.012
L of M^1	43	15	18	16.57	0.72	35	15	18	16.15	0.68	1.026	2.65	0.010
W of M^2	43	12	16	13.49	0.74	36	11	15	13.21	0.76	1.021	1.71	0.092
I^3 to I^3	39	34	41	37.36	1.72	35	31	40	35.53	1.94	1.052	4.32	< 0.001
P^1 to P^1	43	29	35	32.01	1.51	36	26	35	30.71	1.88	1.042	3.42	0.001
P^2 to P^2	43	32	39	35.38	1.63	36	29	39	34.00	2.15	1.041	3.25	0.002
C^1 to C^1	39	44	52	48.39	2.05	34	41	50	45.49	2.22	1.064	5.82	<0.001
M^1 to M^1	43	75	86	81.25	3.25	36	72	84	77.79	2.92	1.044	4.93	<0.001
Cheek T W	43	76	89	80.89	2.86	36	71	84	77.07	3.30	1.050	5.52	<0.001
Pos For W	42	58	70	64.69	2.39	33	58	68	62.79	2.39	1.030	3.42	0.001
Aud Bul W	41	16	22	19.3	1.49	32	15	21	17.93	1.66	1.076	3.69	<0.001
Occ Cre W	42	77	88	82.1	2.37	32	75	84	79.29	2.47	1.035	4.97	<0.001
Condyle W	40	11	14	12.05	0.68	28	10	12	11.28	0.62	1.068	4.73	<0.001
Condyle L	39	23	28	25.83	1.24	28	23	28	24.50	1.06	1.054	4.61	<0.001
Occ Con W	40	43	56	50.5	2.55	33	42	55	47.93	2.56	1.054	4.28	<0.001
InterOr W	43	43	57	47.13	2.80	35	40	51	44.70	2.74	1.054	3.84	<0.001
Postorb W	43	55	78	64.16	4.08	33	51	69	59.81	4.30	1.073	4.51	<0.001
Tem Fos W	43	35	48	42.18	3.15	35	32	45	39.99	3.34	1.055	2.98	0.004
Pari-Temp W	42	62	72	67.02	2.14	33	62	69	65.50	2.06	1.023	3.10	0.003
Zygom W	43	133	152	140.85	4.53	34	126	146	134.19	4.44	1.050	6.46	<0.001
M^1 to Orb	43	38	47	42.35	2.34	35	35	44	39.49	1.85	1.072	5.88	<0.001
Jugal H	43	17	22	19.29	1.08	35	15	21	18.07	1.20	1.068	4.74	<0.001
SagC-AudB	42	80	94	85.41	2.97	31	78	88	81.68	2.21	1.046	5.89	<0.001
Sym-AngPr	18	175	203	190.63	7.48	12	176	195	184.92	7.01	1.031	2.10	0.045
Sym-Condy	18	177	199	187.49	6.54	12	174	193	183.36	6.74	1.023	1.67	0.105
C_1 - M_3	18	114	134	121.78	5.00	12	110	125	119.37	4.02	1.020	1.39	0.174
W of P_4	34	7	9	8.23	0.47	29	7	9	7.75	0.53	1.062	3.83	<0.001
L of P_4	34	15	18	16.14	0.74	29	14	17	15.55	0.82	1.038	3.01	0.004
W of M_1	34	10	13	11.81	0.59	29	10	13	11.15	0.59	1.059	4.40	<0.001
L of M_1	34	27	33	29.33	1.42	29	26	32	28.29	1.43	1.037	2.86	0.006
Mandib W	34	14	17	14.55	0.66	29	12	15	13.62	0.80	1.068	5.09	<0.001
Art Con W	43	11	15	12.3	0.83	34	9	13	11.72	0.89	1.049	2.96	0.004
Art Con L	43	29	36	32.65	1.82	34	27	34	31.38	1.82	1.040	3.06	0.003
H of Ramus	34	28	35	31.62	2.00	29	27	33	29.58	1.64	1.069	4.38	<0.001
AngP-CorP	43	68	85	78.04	3.57	34	65	81	72.90	3.22	1.071	6.54	<0.001

Appendix 9.7 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from the **Northern Keewatin** (*C.l. hudsonicus*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	30	221	252	238.2	6.62	18	217	236	226.2	5.81	1.053	6.35	< 0.001
I^1- Sag C	31	239	272	259.8	6.65	19	230	256	244.0	8.14	1.065	7.51	< 0.001
Nasal L	31	87	102	95.7	3.84	20	80	96	88.5	4.85	1.081	5.95	< 0.001
I^1- Palat	31	111	128	119.5	3.32	21	105	122	112.9	4.02	1.058	6.45	< 0.001
I^2- Palat	31	109	125	117.2	3.43	21	102	119	110.5	4.00	1.061	6.49	< 0.001
Pos Pal L	30	91	105	99.3	3.32	20	91	99	94.5	2.35	1.051	5.57	< 0.001
C^1- M^2	30	102	118	109.6	3.22	21	99	110	104.0	3.12	1.054	6.17	< 0.001
W of C^1	30	14	18	15.1	0.93	19	13	16	14.0	0.88	1.079	4.20	< 0.001
W of P^4	31	10	12	11.1	0.54	20	10	12	10.5	0.44	1.057	4.28	< 0.001
L of P^4	31	24	28	26.1	1.13	20	23	26	24.8	1.02	1.052	3.99	< 0.001
W of M^1	31	19	22	20.6	1.00	21	18	23	20.0	1.20	1.030	2.12	0.039
L of M^1	31	15	18	16.7	0.61	21	15	18	16.3	0.68	1.025	2.57	0.013
W of M^2	31	12	15	13.9	0.75	21	12	15	13.4	0.74	1.037	2.40	0.020
I^3 to I^3	29	35	40	37.6	1.42	20	32	40	35.7	2.05	1.053	3.70	0.001
P^1 to P^1	31	28	36	31.4	1.92	21	27	33	29.8	1.78	1.054	2.93	0.005
P^2 to P^2	30	32	39	35.1	1.78	21	30	38	33.6	1.60	1.045	3.07	0.004
C^1 to C^1	30	43	51	47.9	1.92	21	42	50	45.2	2.29	1.060	4.48	< 0.001
M^1 to M^1	31	74	86	80.6	3.16	20	73	83	76.6	2.77	1.052	4.62	< 0.001
Cheek T W	31	75	87	80.7	2.85	21	72	84	76.6	2.75	1.054	5.14	< 0.001
Pos For W	31	60	70	64.6	2.48	19	58	67	62.0	2.57	1.042	3.43	0.001
Aud Bul W	30	16	23	19.4	1.82	19	16	21	18.1	1.36	1.072	2.65	0.011
Occ Cre W	30	74	85	80.6	2.58	19	74	83	77.8	2.26	1.036	3.81	< 0.001
Condyle W	30	11	15	12.2	0.90	19	11	12	11.6	0.54	1.052	2.74	0.009
Condyle L	30	23	28	25.7	1.26	19	22	26	24.3	0.97	1.058	4.19	< 0.001
Occ Con W	29	48	55	50.3	1.67	18	46	52	48.0	1.71	1.048	4.50	< 0.001
InterOr W	31	42	50	46.3	2.25	20	40	52	44.1	3.03	1.050	2.96	0.005
Postorb W	31	56	72	63.9	3.91	19	48	68	59.5	4.76	1.074	3.62	0.001
Tem Fos W	31	35	46	41.5	2.93	20	35	47	41.2	2.69	1.007	0.29	0.772
Pari-Temp W	30	63	74	67.6	2.30	19	64	73	66.7	1.87	1.013	1.35	0.182
Zygom W	31	128	146	138.0	5.08	19	123	138	130.2	4.23	1.060	5.56	< 0.001
M^1 to Orb	31	35	45	41.1	2.37	21	34	42	38.0	2.11	1.082	4.88	< 0.001
Jugal H	31	17	21	18.6	1.02	21	15	19	17.3	0.98	1.075	4.81	< 0.001
SagC-AudB	29	77	89	83.1	3.15	18	74	84	80.0	2.89	1.039	3.39	0.001
Sym-AngPr	31	176	203	191.0	5.85	21	171	187	179.2	4.40	1.066	7.87	< 0.001
Sym-Condy	31	174	200	188.7	5.16	21	171	186	177.3	4.27	1.064	8.35	< 0.001
C_1 - M_3	30	114	130	122.7	3.42	21	107	124	116.2	4.09	1.056	6.13	< 0.001
W of P_4	31	7	9	8.5	0.53	21	7	9	8.0	0.37	1.063	3.85	< 0.001
L of P_4	31	15	18	16.5	0.80	21	15	17	16.0	0.54	1.031	2.85	0.006
W of M_1	30	11	13	12.0	0.54	21	11	12	11.2	0.42	1.071	5.58	< 0.001
L of M_1	31	27	32	29.5	1.21	21	26	31	28.3	1.25	1.042	3.63	0.001
Mandib W	31	12	16	14.0	0.78	21	12	15	13.0	0.90	1.077	4.18	< 0.001
Art Con W	31	11	15	12.7	0.91	21	10	13	11.6	0.90	1.095	4.39	< 0.001
Art Con L	31	29	36	32.8	1.66	21	28	32	30.0	1.22	1.093	6.71	< 0.001
H of Ramus	31	28	35	31.0	1.82	21	25	33	28.5	1.88	1.088	4.88	< 0.001
AngP - CorP	31	70	85	76.9	3.62	21	67	77	71.7	2.71	1.073	5.57	< 0.001

Appendix 9.8 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from the **Central Keewatin** (*C.l. hudsonicus*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	49	216	252	239.40	6.85	58	212	243	226.80	5.74	1.056	10.36	<0.001
I^1- Sag C	49	231	276	259.20	8.94	57	229	267	245.40	7.42	1.056	8.63	<0.001
Nasal L	50	79	109	95.40	4.98	58	82	99	89.60	3.85	1.065	6.73	<0.001
I^1- Palat	50	109	127	119.60	3.55	60	105	120	113.80	3.07	1.051	9.17	<0.001
I^2- Palat	50	107	124	117.30	3.48	60	103	117	111.50	3.05	1.052	9.24	<0.001
Pos Pal L	49	89	109	100.70	4.04	58	88	102	95.10	2.96	1.059	8.27	<0.001
C^1- M^2	50	98	115	109.10	3.19	59	96	112	104.40	3.30	1.045	7.60	<0.001
W of C^1	50	13	17	14.90	0.80	59	12	16	13.90	0.71	1.072	7.10	<0.001
W of P^4	50	9	12	11.00	0.61	60	9	12	10.40	0.53	1.058	5.27	<0.001
L of P^4	50	23	28	26.00	1.07	60	23	27	25.00	1.07	1.040	4.85	<0.001
W of M^1	50	19	23	20.70	0.91	60	17	22	19.80	0.99	1.045	5.05	<0.001
L of M^1	50	15	19	16.80	0.68	60	14	19	16.30	0.73	1.031	3.71	<0.001
W of M^2	50	13	15	13.60	0.61	60	12	14	13.00	0.66	1.046	5.29	<0.001
I^3 to I^3	50	32	40	37.30	1.48	58	33	39	35.80	1.37	1.042	5.52	<0.001
P^1 to P^1	50	27	38	31.70	1.70	60	27	34	29.90	1.50	1.060	5.87	<0.001
P^2 to P^2	50	31	40	35.50	1.66	59	29	39	33.70	1.77	1.053	5.55	<0.001
C^1 to C^1	48	42	53	47.80	2.10	60	41	52	44.90	1.96	1.065	7.28	<0.001
M^1 to M^1	50	74	88	81.40	2.96	60	71	83	77.40	2.82	1.052	7.11	<0.001
Cheek T W	49	74	87	81.30	2.77	60	71	84	77.50	2.75	1.049	7.15	<0.001
Pos For W	49	59	70	65.30	2.35	57	58	67	62.70	1.78	1.041	6.46	<0.001
Aud Bul W	49	15	22	19.30	1.54	57	15	23	18.60	1.42	1.038	2.57	0.012
Occ Cre W	48	77	89	82.40	2.68	57	74	87	78.40	2.81	1.051	7.31	<0.001
Condyle W	50	10	14	12.40	0.81	58	10	13	11.40	0.64	1.088	6.79	<0.001
Condyle L	50	23	29	26.40	1.22	58	23	27	24.60	1.11	1.073	7.78	<0.001
Occ Con W	50	45	55	50.80	1.99	57	45	53	47.90	1.86	1.061	7.75	<0.001
InterOr W	50	39	52	47.30	2.32	60	39	50	43.90	2.29	1.077	7.79	<0.001
Postorb W	50	50	72	63.20	3.99	58	51	72	59.50	3.92	1.062	4.87	<0.001
Tem Fos W	50	33	47	41.30	2.75	59	32	45	39.90	2.92	1.035	2.58	0.011
Pari-Temp W	49	63	73	67.20	1.99	57	61	70	66.10	1.89	1.017	3.07	0.003
Zygom W	49	122	152	141.10	5.28	58	124	146	133.00	4.04	1.061	8.96	<0.001
M^1 to Orb	50	35	46	41.90	2.24	59	34	43	38.90	1.66	1.077	8.01	<0.001
Jugal H	50	16	22	19.10	1.27	60	15	21	17.70	1.24	1.079	6.01	<0.001
SagC-AudB	49	74	94	84.50	3.79	56	72	88	80.50	3.47	1.050	5.55	<0.001
Sym-AngPr	49	178	203	191.50	5.49	60	168	194	181.00	5.10	1.058	10.32	<0.001
Sym-Condy	49	177	200	189.50	5.49	60	168	191	178.40	4.86	1.062	11.15	<0.001
C_1 - M_3	49	116	130	122.60	2.83	60	105	122	116.40	3.42	1.053	10.14	<0.001
W of P_4	49	8	9	8.40	0.41	59	7	9	7.90	0.32	1.063	7.62	<0.001
L of P_4	49	14	18	16.40	0.70	59	14	17	15.60	0.65	1.051	5.68	<0.001
W of M_1	49	11	13	11.90	0.49	60	10	12	11.10	0.48	1.072	8.50	<0.001
L of M_1	49	28	31	29.60	0.96	60	26	32	28.20	1.23	1.050	6.80	<0.001
Mandib W	49	12	16	13.90	0.78	60	12	15	12.90	0.79	1.078	6.96	<0.001
Art Con W	49	11	14	12.40	0.95	59	10	13	11.40	0.76	1.088	5.79	<0.001
Art Con L	49	28	36	32.60	1.65	60	27	35	30.70	1.62	1.062	6.00	<0.001
H of Ramus	49	27	35	30.80	1.69	60	25	32	28.60	1.60	1.077	7.11	<0.001
AngP - CorP	49	70	86	77.70	4.06	60	65	82	72.30	3.07	1.075	7.64	<0.001

Appendix 9.9 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from the **Southern Keewatin** (*C.l. hudsonicus*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	35	232	260	243.80	6.71	28	215	244	227.50	7.24	1.072	9.25	<0.001
I^1- Sag C	36	253	282	265.80	7.73	28	229	261	245.70	8.18	1.082	10.09	<0.001
Nasal L	36	93	110	100.10	4.73	28	82	98	90.40	4.00	1.107	8.73	<0.001
I^1- Palat	36	117	132	122.70	3.72	27	108	121	114.50	3.26	1.072	9.15	<0.001
I^2- Palat	36	114	129	120.20	3.74	27	105	118	112.10	3.29	1.072	9.01	<0.001
Pos Pal L	35	96	108	102.40	3.25	27	87	102	95.60	4.09	1.071	7.31	<0.001
C^1- M^2	36	105	118	111.00	3.13	27	95	111	103.50	3.81	1.072	8.57	<0.001
W of C^1	35	14	17	15.30	0.86	27	13	15	13.60	0.68	1.125	8.60	<0.001
W of P^4	36	10	13	11.10	0.62	28	9	11	10.30	0.56	1.078	5.33	<0.001
L of P^4	36	25	28	26.80	0.79	28	22	27	24.70	1.00	1.085	9.25	<0.001
W of M^1	35	19	23	21.00	1.09	28	18	21	19.50	1.00	1.077	5.40	<0.001
L of M^1	36	15	19	17.00	0.72	28	14	17	16.00	0.78	1.063	5.77	<0.001
W of M^2	36	12	15	13.50	0.81	27	11	14	12.70	0.79	1.063	3.88	<0.001
I^3 to I^3	35	35	43	38.50	1.68	26	31	38	35.20	1.51	1.094	7.91	<0.001
P^1 to P^1	35	28	36	32.10	1.71	28	28	34	30.40	1.44	1.056	4.26	<0.001
P^2 to P^2	36	33	39	36.00	1.78	28	31	40	33.70	1.77	1.068	5.26	<0.001
C^1 to C^1	35	45	54	49.40	2.18	28	43	51	45.40	1.95	1.088	7.56	<0.001
M^1 to M^1	35	77	89	82.50	2.72	28	71	86	76.90	2.97	1.073	7.86	<0.001
Cheek T W	35	77	88	82.40	2.07	27	69	84	76.80	3.44	1.073	7.48	<0.001
Pos For W	35	60	73	65.30	2.35	28	57	68	62.60	2.40	1.043	4.60	<0.001
Aud Bul W	35	16	23	18.80	1.82	28	14	22	18.10	1.86	1.039	1.50	0.123
Occ Cre W	35	76	89	83.30	2.81	28	71	88	78.10	3.42	1.067	6.62	<0.001
Condyle W	35	10	14	12.30	0.84	28	10	13	11.40	0.80	1.079	4.18	<0.001
Condyle L	35	24	29	26.40	1.15	28	22	27	24.60	1.29	1.073	5.77	<0.001
Occ Con W	34	46	55	50.80	2.09	28	43	52	47.60	1.89	1.067	6.26	<0.001
InterOr W	36	41	54	47.70	2.92	27	40	50	44.70	2.77	1.067	4.04	<0.001
Postorb W	36	57	76	64.00	4.57	27	53	70	60.40	4.56	1.060	3.10	0.003
Tem Fos W	36	36	49	41.80	2.31	27	36	44	40.70	2.43	1.027	1.97	0.054
Pari-Temp W	34	61	71	66.50	2.26	28	61	69	65.90	2.10	1.009	1.13	0.264
Zygom W	34	133	154	142.60	4.21	27	127	143	133.70	4.12	1.067	8.32	<0.001
M^1 to Orb	36	40	50	43.40	1.88	28	35	45	39.60	2.22	1.096	7.56	<0.001
Jugal H	36	17	23	19.40	1.30	28	15	21	18.00	1.57	1.078	3.89	<0.001
SagC-AudB	35	83	94	86.20	2.79	27	73	89	81.00	3.56	1.064	6.44	<0.001
Sym-AngPr	36	188	204	195.50	4.54	26	168	196	181.70	6.61	1.076	9.77	<0.001
Sym-Condy	36	171	203	192.80	5.94	26	167	193	179.30	6.16	1.075	8.70	<0.001
C^1 - M^3	36	117	132	124.70	3.25	25	108	125	116.80	3.76	1.068	8.70	<0.001
W of P^4	36	7	10	8.40	0.52	27	7	9	7.80	0.36	1.077	4.85	<0.001
L of P^4	36	15	18	16.50	0.55	27	14	17	15.40	0.53	1.071	8.04	<0.001
W of M^1	36	11	13	12.10	0.59	28	10	12	11.20	0.46	1.080	6.58	<0.001
L of M^1	36	28	32	29.90	0.99	28	25	31	28.00	1.06	1.068	7.66	<0.001
Mandib W	36	13	16	14.30	0.68	28	12	15	13.40	0.88	1.067	4.52	<0.001
Art Con W	36	11	16	12.50	1.01	28	10	13	11.60	0.76	1.078	4.07	<0.001
Art Con L	36	31	37	33.90	1.58	28	28	37	31.40	2.19	1.080	5.31	<0.001
H of Ramus	36	29	37	32.40	1.73	27	25	33	29.00	1.89	1.117	7.38	<0.001
AngP - CorP	36	73	88	80.20	3.85	28	65	81	72.30	3.84	1.109	8.12	<0.001

Appendix 9.10 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from **Central Saskatchewan** (*C.l. griseoalbus*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined *t*-values.

	Males					Females							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	15	234	268	256.10	8.03	6	231	248	240.32	6.74	1.066	4.24	<0.001
I^1- Sag C	15	247	293	275.33	10.65	6	246	266	258.03	7.84	1.067	3.59	0.002
Nasal L	15	91	108	102.65	4.51	6	89	100	95.32	4.36	1.077	3.39	0.003
I^1- Palat	15	117	132	127.62	3.93	6	114	126	120.56	4.86	1.059	3.49	0.002
I^2- Palat	15	114	129	125.06	3.91	6	112	124	118.16	5.02	1.058	3.38	0.003
Pos Pal L	15	101	115	108.51	3.98	6	99	103	101.55	1.85	1.069	4.06	0.001
C^1- M^2	14	107	118	114.52	3.13	6	102	113	108.22	4.2	1.058	3.73	0.002
W of C^1	14	14	18	15.67	0.93	6	13	15	14.05	0.82	1.115	3.70	0.002
W of P^4	15	10	11	10.76	0.40	6	9	10	9.88	0.68	1.089	3.67	0.002
L of P^4	15	26	28	27.06	0.79	6	23	26	25.22	1.18	1.073	4.19	<0.001
W of M^1	15	19	23	21.45	0.91	6	18	21	19.95	1.09	1.075	3.23	0.004
L of M^1	15	16	18	17.23	0.53	6	14	17	16.06	0.93	1.073	3.71	0.001
W of M^2	15	13	15	14.17	0.71	6	13	14	13.39	0.62	1.058	2.36	0.029
I^3 to I^3	14	36	41	38.96	1.94	6	34	38	36.69	1.67	1.062	2.50	0.022
P^1 to P^1	15	31	36	33.35	1.67	6	30	34	32.18	1.62	1.036	1.46	0.160
P^2 to P^2	14	33	40	36.52	2.11	6	34	37	35.36	1.4	1.033	1.23	0.235
C^1 to C^1	14	46	55	51.70	2.61	6	44	50	47.96	2.42	1.078	3.00	0.008
M^1 to M^1	15	76	86	81.81	3.05	6	77	82	79.05	2.18	1.035	2.00	0.059
Cheek T W	14	79	90	84.96	3.52	6	78	84	81.28	2.27	1.045	2.34	0.031
Pos For W	15	63	69	66.04	1.67	6	61	64	62.55	1.39	1.056	4.52	<0.001
Aud Bul W	15	17	24	21.12	1.99	6	17	20	19.09	1.13	1.106	2.33	0.031
Occ Cre W	15	80	90	85.57	3.06	6	78	82	80.51	2.29	1.063	3.64	0.002
Condyle W	15	11	14	13.05	0.73	6	11	13	12.30	0.47	1.061	2.31	0.032
Condyle L	14	26	30	27.99	1.07	6	25	27	26.12	0.6	1.072	3.96	0.001
Occ Con W	15	49	57	53.65	2.42	6	48	51	49.73	1.32	1.079	3.72	0.001
InterOr W	15	42	52	48.24	2.81	6	43	47	45.63	1.31	1.057	2.16	0.043
Postorb W	15	59	77	66.30	4.99	6	56	67	61.93	4.08	1.071	1.90	0.073
Tem Fos W	15	39	48	43.02	2.72	6	40	43	41.47	1.09	1.037	1.34	0.196
Pari-Temp W	15	63	72	67.38	2.61	6	63	70	65.50	2.81	1.029	1.47	0.158
Zygom W	15	136	155	146.18	5.18	6	136	141	137.92	2.07	1.060	5.22	<0.001
M^1 to Orb	15	42	49	46.26	1.93	6	38	45	42.58	2.7	1.086	3.54	0.002
Jugal H	15	19	22	20.35	1.03	6	18	20	19.07	0.89	1.067	2.64	0.016
SagC-AudB	15	82	97	89.20	4.71	6	79	86	82.50	2.95	1.081	3.21	0.005
Sym-AngPr	14	190	210	203.02	5.76	6	182	196	190.85	5.72	1.064	4.34	<0.001
Sym-Condy	14	186	212	203.83	7.02	6	183	198	190.03	6.02	1.073	4.19	0.001
C_1 - M_3	14	121	133	128.08	3.85	6	116	125	121.12	3.94	1.057	3.68	0.002
W of P_4	15	8	10	8.41	0.51	6	7	8	7.72	0.59	1.089	2.66	0.015
L of P_4	15	16	18	16.61	0.54	6	14	16	15.49	0.64	1.072	4.09	0.001
W of M_1	15	11	13	12.20	0.58	6	10	12	11.39	0.57	1.071	2.94	0.008
L of M_1	15	27	32	29.77	1.13	6	26	29	28.29	1.28	1.052	2.62	0.017
Mandib W	15	14	17	14.88	0.74	6	13	16	13.91	1.28	1.070	2.20	0.040
Art Con W	15	12	15	13.24	0.92	6	11	13	11.80	0.53	1.122	3.58	0.002
Art Con L	15	32	38	35.00	2.04	6	29	34	31.23	1.72	1.121	3.98	0.001
H of Ramus	15	31	36	33.79	1.56	6	28	35	32.01	2.24	1.056	2.08	0.051
AngP - CorP	15	76	86	81.94	3.02	6	72	78	76.06	2.39	1.077	4.24	<0.001

Appendix 9.11 Descriptive statistics for 45 cranial variables (mm) for male and female wolves from **Northern Alberta** (*C.l. occidentalis*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined *t*-values.

	Males					Females							
Variable	*N*	Range		Mean	S.D.	*N*	Range		Mean	S.D.	R	t-value	P
Condy L	34	233	284	255.58	8.82	30	231	255	243.67	5.58	1.049	6.36	<0.001
I^1- Sag C	34	252	305	277.97	9.88	30	254	280	263.60	6.07	1.055	6.90	<0.001
Nasal L	33	90	122	105.26	6.47	30	93	107	99.61	3.70	1.057	4.31	<0.001
I^1- Palat	34	116	139	126.50	4.69	30	114	128	121.42	3.46	1.042	4.88	<0.001
I^2- Palat	34	114	137	124.00	4.76	30	111	125	118.88	3.38	1.043	4.90	<0.001
Pos Pal L	34	93	121	107.93	4.73	30	98	108	103.26	2.86	1.045	4.70	<0.001
C^1- M^2	34	106	126	114.14	4.04	30	101	114	109.61	3.01	1.041	5.03	<0.001
W of C^1	34	9	18	15.28	1.53	30	13	15	13.93	0.64	1.097	4.72	<0.001
W of P^4	34	7	12	11.01	0.98	30	9	12	10.70	0.60	1.029	1.50	0.140
L of P^4	34	21	30	26.82	1.50	30	22	27	25.23	1.00	1.063	4.90	<0.001
W of M^1	34	16	24	21.49	1.38	30	16	22	20.28	1.22	1.060	3.71	<0.001
L of M^1	34	11	18	16.73	1.31	30	15	22	16.36	1.18	1.023	1.17	0.248
W of M^2	34	9	16	14.18	1.19	30	12	15	13.62	0.80	1.041	2.19	0.033
I^3 to I^3	34	33	42	38.28	1.91	29	34	40	36.48	1.57	1.049	4.03	<0.001
P^1 to P^1	32	28	37	33.72	2.08	29	29	37	32.15	1.51	1.049	3.33	0.001
P^2 to P^2	34	31	43	37.28	2.59	30	31	41	35.22	1.79	1.058	3.74	<0.001
C^1 to C^1	33	47	58	51.69	2.92	30	28	51	47.30	3.96	1.093	5.04	<0.001
M^1 to M^1	34	78	93	84.80	3.38	30	75	84	79.97	2.19	1.060	6.69	<0.001
Cheek T W	34	79	94	86.09	3.51	30	77	87	81.32	2.49	1.059	6.33	<0.001
Pos For W	34	62	72	67.01	2.29	30	60	70	65.02	2.22	1.031	3.53	0.001
Aud Bul W	33	15	26	21.13	2.23	30	15	24	19.91	1.80	1.061	2.38	0.020
Occ Cre W	33	76	95	86.17	3.69	30	78	89	82.53	2.42	1.044	4.57	<0.001
Condyle W	34	10	16	13.56	1.26	30	11	14	12.25	0.64	1.107	5.30	<0.001
Condyle L	34	23	31	27.36	1.49	30	24	28	25.87	1.09	1.058	4.54	<0.001
Occ Con W	34	46	59	52.44	2.48	30	47	56	49.93	1.92	1.050	4.47	<0.001
InterOr W	34	42	59	50.11	3.61	30	41	50	46.37	2.28	1.081	4.88	<0.001
Postorb W	34	58	78	68.92	5.04	30	47	72	63.67	5.15	1.082	4.12	<0.001
Tem Fos W	34	39	49	43.93	2.46	30	35	47	42.29	2.60	1.039	2.60	0.012
Pari-Temp W	34	65	76	68.85	2.61	30	63	70	66.89	2.03	1.029	3.33	0.001
Zygom W	34	136	163	150.51	5.60	30	132	146	140.34	3.87	1.072	8.34	<0.001
M^1 to Orb	34	42	54	46.84	2.73	30	40	49	43.73	1.84	1.071	5.26	<0.001
Jugal H	34	19	27	21.79	1.65	30	18	22	20.00	1.22	1.090	4.86	<0.001
SagC-AudB	34	79	98	90.05	3.87	30	80	93	85.09	2.99	1.058	5.68	<0.001
Sym-AngPr	33	185	228	203.98	7.61	30	181	206	195.35	5.19	1.044	5.21	<0.001
Sym-Condy	33	185	225	202.71	7.46	30	180	203	193.53	5.07	1.047	5.66	<0.001
C_1 - M_3	32	119	139	127.28	4.33	30	115	128	122.60	2.97	1.038	4.93	<0.001
W of P_4	33	3	9	8.05	1.00	30	7	9	7.85	0.40	1.025	1.07	0.290
L of P_4	33	11	19	16.34	1.24	30	14	17	15.63	0.64	1.045	2.82	0.006
W of M_1	33	7	13	11.85	1.10	30	10	12	11.30	0.52	1.049	2.49	0.016
L of M_1	33	24	33	30.03	1.80	30	25	31	28.67	1.18	1.047	3.50	0.001
Mandib W	33	11	19	15.36	1.31	30	13	17	14.34	1.00	1.071	3.46	0.001
Art Con W	33	9	16	13.71	1.36	30	10	15	12.64	1.01	1.085	3.50	0.001
Art Con L	33	31	38	35.10	2.14	30	30	36	32.37	1.62	1.084	5.68	<0.001
H of Ramus	33	30	40	34.37	2.24	30	27	36	32.00	1.83	1.074	4.57	<0.001
AngP - CorP	33	74	94	84.64	4.71	30	69	89	80.28	3.65	1.054	4.08	<0.001

Appendix 9.12 Descriptive statistics for 45 cranial variables (mm) for male and female wolves for **Entire Keewatin Region** (*C.l. hudsonicus*). Parameters were analyzed for sexual dimorphism using Student's *t*-test. R = male mean / female mean. Unequal variances, identified by Levene's test, indicated by underlined *t*-values.

	Males					**Females**							
Variable	***N***	**Range**		**Mean**	**S.D.**	***N***	**Range**		**Mean**	**S.D.**	**R**	**t-value**	**P**
Condy L	114	216	260	240.44	7.08	104	212	244	226.89	6.15	1.060	15.03	<0.001
I^1- Sag C	116	231	282	261.40	8.49	104	229	267	245.22	7.71	1.066	14.74	<0.001
Nasal L	117	79	110	96.93	5.07	106	80	99	89.62	4.10	1.082	11.79	<0.001
I^1- Palat	117	109	132	120.53	3.80	108	105	122	113.80	3.33	1.059	14.07	<0.001
I^2- Palat	117	107	129	118.14	3.78	108	102	119	111.44	3.32	1.060	14.10	<0.001
Pos Pal L	114	89	109	100.85	3.79	105	87	102	95.10	3.18	1.060	12.11	<0.001
C^1- M^2	116	98	118	109.84	3.26	107	95	112	104.09	3.39	1.055	12.90	<0.001
W of C^1	115	13	18	15.10	0.87	105	12	16	13.84	0.74	1.091	11.56	<0.001
W of P^4	117	9	13	11.06	0.59	108	9	12	10.40	0.52	1.063	8.80	<0.001
L of P^4	117	23	28	26.28	1.06	108	22	27	24.92	1.04	1.055	9.71	<0.001
W of M^1	116	19	23	20.75	0.99	109	17	23	19.74	1.04	1.051	7.49	<0.001
L of M^1	117	15	19	16.84	0.68	109	14	19	16.18	0.74	1.041	6.96	<0.001
W of M^2	117	12	15	13.65	0.72	108	11	15	12.99	0.73	1.051	6.89	<0.001
I^3 to I^3	114	32	43	37.73	1.61	104	31	40	35.62	1.56	1.059	9.82	<0.001
P^1 to P^1	116	27	38	31.74	1.77	109	27	34	30.03	1.54	1.057	7.73	<0.001
P^2 to P^2	116	31	40	35.56	1.75	108	29	40	33.65	1.72	1.057	8.22	<0.001
C^1 to C^1	113	42	54	48.29	2.19	109	41	52	45.09	2.02	1.071	11.32	<0.001
M^1 to M^1	116	74	89	81.51	3.01	108	71	86	77.14	2.85	1.057	11.15	<0.001
Cheek T W	115	74	88	81.45	2.67	108	69	84	77.13	2.93	1.056	11.52	<0.001
Pos For W	115	59	73	65.12	2.39	104	57	68	62.56	2.11	1.041	8.36	<0.001
Aud Bul W	114	15	23	19.15	1.71	104	14	23	18.33	1.54	1.045	3.72	<0.001
Occ Cre W	113	74	89	82.17	2.87	104	71	88	78.22	2.88	1.050	10.10	<0.001
Condyle W	115	10	15	12.29	0.84	105	10	13	11.44	0.67	1.074	8.30	<0.001
Condyle L	115	23	29	26.20	1.23	105	22	27	24.55	1.14	1.067	10.29	<0.001
Occ Con W	113	45	55	50.69	1.94	103	43	53	47.87	1.83	1.059	10.96	<0.001
InterOr W	117	39	54	47.13	2.54	107	39	52	44.11	2.57	1.068	8.84	<0.001
Postorb W	117	50	76	63.64	4.14	104	48	72	59.71	4.23	1.066	6.97	<0.001
Tem Fos W	117	33	49	41.51	2.66	106	32	47	40.34	2.79	1.029	3.21	0.002
Pari-Temp W	113	61	74	67.10	2.18	104	61	73	66.13	1.95	1.015	3.44	<0.001
Zygom W	114	122	154	140.72	5.21	104	123	146	132.69	4.23	1.061	12.41	<0.001
M^1 to Orb	117	35	50	42.15	2.34	108	34	45	38.87	1.96	1.084	11.31	<0.001
Jugal H	117	16	23	19.08	1.25	109	15	21	17.69	1.30	1.079	8.21	<0.001
SagC-AudB	113	74	94	84.64	3.51	101	72	89	80.56	3.38	1.051	8.63	<0.001
Sym-AngPr	116	176	204	192.60	5.62	107	168	196	180.80	5.40	1.065	15.96	<0.001
Sym-Condy	116	171	203	190.30	5.77	107	167	193	178.40	5.10	1.067	16.26	<0.001
C_1 - M_3	115	114	132	123.29	3.24	106	105	125	116.48	3.61	1.058	14.76	<0.001
W of P_4	116	7	10	8.43	0.48	107	7	9	7.89	0.34	1.068	$\underline{9.81}$	<0.001
L of P_4	116	14	18	16.46	0.68	107	14	17	15.65	0.62	1.052	9.20	<0.001
W of M_1	115	11	13	11.99	0.53	109	10	12	11.16	0.46	1.074	12.39	<0.001
L of M_1	116	27	32	29.69	1.04	109	26	32	28.13	1.19	1.055	10.51	<0.001
Mandib W	116	12	16	14.05	0.76	109	12	15	13.04	0.86	1.077	9.40	<0.001
Art Con W	116	11	16	12.51	0.96	108	10	13	11.48	0.79	1.090	8.70	<0.001
Art Con L	116	28	37	33.07	1.72	109	27	37	30.76	1.78	1.075	9.91	<0.001
H of Ramus	116	27	37	31.37	1.86	108	25	33	28.67	1.73	1.094	11.23	<0.001
AngP - CorP	116	70	88	78.24	4.08	109	65	82	72.19	3.20	1.084	12.34	<0.001

Appendix 10. Percent sexual dimorphism observed geographically for 45 cranial parameters. The mean %, at bottom of page, is based on an average of the 45 variables. Appendices 9.2 - 9.11 provide descriptive statistics for each location.

Variable	Baffin Island	Queen Elizabeth	Banks / Victoria	Mackenzie Delta	Great Slave L.	Northern Keewatin	Central Keewatin	Southern Keewatin	Central Saskatch.	Northern Alberta
Condy L	3.8	3.8	3.1	3.7	4.6	5.3	5.6	7.2	6.6	4.9
I^1- Sag C	5.1	3.9	3.8	4.6	5.2	6.5	5.6	8.2	6.7	5.5
Nasal L	5.5	6.7	5.4	6.6	6.8	8.1	6.5	10.7	7.7	5.7
I^1- Palat	3.4	2.5	2.9	2.6	3.6	5.8	5.1	7.2	5.9	4.2
I^2- Palat	3.0	2.6	3.6	2.7	3.8	6.1	5.2	7.2	5.8	4.3
Pos Pal L	3.5	3.4	3.2	4.0	5.2	5.1	5.9	7.1	6.9	4.5
C^1- M^2	4.4	2.9	2.4	2.6	4.2	5.4	4.5	7.2	5.8	4.1
W of C^1	6.0	9.1	11.6	6.2	7.5	7.9	7.2	12.5	11.5	9.7
W of P^4	2.8	6.3	6.6	5.0	4.9	5.7	5.8	7.8	8.9	2.9
L of P^4	3.6	5.1	6.3	5.6	4.8	5.2	4.0	8.5	7.3	6.3
W of M^1	4.3	5.3	7.9	5.5	3.1	3.0	4.5	7.7	7.5	6.0
L of M^1	2.5	3.4	3.7	3.0	2.6	2.5	3.1	6.3	7.3	2.3
W of M^2	4.3	2.5	5.5	2.7	2.1	3.7	4.6	6.3	5.8	4.1
I^3 to I^3	4.4	5.0	7.0	6.6	5.2	5.3	4.2	9.4	6.2	4.9
P^1 to P^1	5.4	2.6	2.4	5.5	4.2	5.4	6.0	5.6	3.6	4.9
P^2 to P^2	2.7	4.9	4.3	6.2	4.1	4.5	5.3	6.8	3.3	5.8
C^1 to C^1	5.7	5.2	4.4	5.2	6.4	6.0	6.5	8.8	7.8	9.3
M^1 to M^1	1.1	3.5	3.5	7.2	4.4	5.2	5.2	7.3	3.5	6.0
Cheek T W	1.9	4.3	3.8	5.9	5.0	5.4	4.9	7.3	4.5	5.9
Pos For W	5.5	3.2	3.5	3.2	3.0	4.2	4.1	4.3	5.6	3.1
Aud Bul W	5.8	-3.4	6.5	5.4	7.6	7.2	3.8	3.9	10.6	6.1
Occ Cre W	3.5	2.0	4.8	5.3	3.5	3.6	5.1	6.7	6.3	4.4
Condyle W	6.1	4.9	9.3	7.3	6.8	5.2	8.8	7.9	6.1	10.7
Condyle L	3.3	6.2	3.2	5.3	5.4	5.8	7.3	7.3	7.2	5.8
Occ Con W	5.1	6.6	8.3	4.9	5.4	4.8	6.1	6.7	7.9	5.0
InterOr W	3.0	4.6	-1.8	5.0	5.4	5.0	7.7	6.7	5.7	8.1
Postorb W	-1.5	3.9	-1.4	3.6	7.3	7.4	6.2	6.0	7.1	8.2
Tem Fos W	-3.3	2.7	-0.3	2.2	5.5	0.7	3.5	2.7	3.7	3.9
Pari-Temp W	1.3	1.8	2.9	1.8	2.3	1.3	1.7	0.9	2.9	2.9
Zygom W	4.9	4.3	1.6	5.3	5.0	6.0	6.1	6.7	6.0	7.2
M^1 to Orb	8.1	2.5	2.7	3.3	7.2	8.2	7.7	9.6	8.6	7.1
Jugal H	2.4	1.6	3.7	3.1	6.8	7.5	7.9	7.8	6.7	9.0
SagC-AudB	1.0	1.6	3.4	4.0	4.6	3.9	5.0	6.4	8.1	5.8
Sym-AngPr	3.7	3.0	4.1	3.6	3.1	6.6	5.8	7.6	6.4	4.4
Sym-Condy	3.7	3.1	3.4	4.0	2.3	6.4	6.2	7.5	7.3	4.7
C_1 - M_3	4.2	1.5	2.5	2.6	2.0	5.6	5.3	6.8	5.7	3.8
W of P_4	4.0	3.1	7.6	5.1	6.2	6.3	6.3	7.7	8.9	2.5
L of P_4	4.7	4.5	6.1	4.3	3.8	3.1	5.1	7.1	7.2	4.5
W of M_1	5.3	6.3	6.3	6.8	5.9	7.1	7.2	8.0	7.1	4.9
L of M_1	2.2	5.2	5.8	5.3	3.7	4.2	5.0	6.8	5.2	4.7
Mandib W	9.6	5.5	2.7	2.3	6.8	7.7	7.8	6.7	7.0	7.1
Art Con W	1.3	2.1	8.4	7.4	4.9	9.5	8.8	7.8	12.2	8.5
Art Con L	3.9	6.4	2.0	5.5	4.0	9.3	6.2	8.0	12.1	8.4
H of Ramus	7.7	2.6	3.9	3.2	6.9	8.8	7.7	11.7	5.6	7.4
AngP - CorP	4.3	6.8	7.5	6.4	7.1	7.3	7.5	10.9	7.7	5.4
Mean %	**3.8**	**3.9**	**4.4**	**4.6**	**4.9**	**5.7**	**5.8**	**7.3**	**6.8**	**5.7**

Appendix 11. Regression equations and coefficients (R^2) of mean Annual, mean July, and mean February air temperatures against I^1-SagC length, Palatal length, and Zygomatic width for male and female wolves. Probability values < 0.05 indicate significance.

Variable	n	Sex	Equation	R^2	P- value
Mean Annual Temperature					
I^1 - SagC length [a]	10	M	y = 1.31x + 274.18	0.758	< 0.001
	10	F	y = 1.05x + 258.07	0.725	< 0.002
Palatal length [b]	10	M	y = 0.65x + 126.22	0.765	< 0.001
	10	F	y = 0.53x + 120.16	0.829	< 0.0003
Zygomatic width [c]	10	M	y = 0.50x + 146.55	0.518	< 0.019
	10	F	y = 0.30x + 137.55	0.026	< 0.133
Mean July Temperature					
I^1 - SagC length	10	M	y = 1.90x + 241.60	0.863	< 0.0001
	10	F	y = 0.30x + 137.55	0.733	< 0.002
Palatal length	10	M	y = 0.95x + 110.03	0.893	< 0.00004
	10	F	y = 0.73x + 107.46	0.843	< 0.0002
Zygomatic width	10	M	y = 0.74x + 133.97	0.624	< 0.007
	10	F	y = 0.41x + 130.39	0.266	< 0.127
Mean February Temperature					
I^1 - SagC length	10	M	y = 1.17x + 295.22	0.808	< 0.0004
	10	F	y = 0.97x + 275.87	0.832	< 0.0002
Palatal length	10	M	y = 0.55x + 135.9	0.749	< 0.001
	10	F	y = 0.47x + 128.5	0.864	< 0.0001
Zygomatic width	10	M	y = 0.48x + 155.55	0.647	< 0.005
	10	F	y = 0.30x + 143.18	0.343	< 0.075

a Regression plotted in Figure 23.
b Regression plotted in Figure 24.
c Regression plotted in Figure 25.

Appendix 12. Regression equations and coefficients (R^2) of mean ungulate weights [a] against I^1-SagC length (A) and Zygomatic width (B) for male and female wolves. Probability values < 0.05 indicate a significant relationship.

Variable	n	Sex	Equation	R^2	P - value
(A) I^1- SagC length					
Largest ungulate	10	M	$y = 0.04x + 255.04$	0.65	< 0.005
(mean weight)	10	F	$y = 0.03x + 237.37$	0.74	< 0.002
Second largest ungulate	10	M	$y = 0.07x + 251.31$	0.86	< 0.0001
(mean weight)	10	F	$y = 0.06x + 239.45$	0.89	< 0.0001
(B) Zygomatic width					
Largest ungulate	10	M	$y = 0.02x + 135.52$	0.80	< 0.0005
(mean weight)	10	F	$y = 0.01x + 130.56$	0.48	< 0.026
Second largest ungulate	10	M	$y = 0.03x + 137.37$	0.74	< 0.001
(mean weight)	10	F	$y = 0.02x + 132.12$	0.35	< 0.070

weights [a] Mean is based on average male + female ungulate weights outlined on Table 20.

IMAGE EVALUATION
TEST TARGET (QA-3)

150mm

6″

APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989