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## Prey specialization and morphological conformation of wolves associated with woodland caribou and moose

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*Abstract:* Morphological analysis of wolves associated with woodland caribou in late succession boreal coniferous forests north of the commercial cut line and those associated with moose in early succession boreal deciduous forests south of the commercial cut line were studied in Ontario. So-called “moose-wolves” could readily be distinguished from “caribou-wolves” in both genders using a few morphological measurements. Wolves associated with woodland caribou were significantly smaller in most measurements, and increased in size within seven years post-harvest as moose totally replaced caribou in the ecosystem. Whether this change in wolf morphology is related to micro-evolutionary change, the migration of larger “moose-wolves” into the area, or both, remains unclear.

Key words: caribou; logging; moose; morphology; wolf diet; wolves.

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### Introduction

Historically, woodland caribou (*Rangifer tarandus caribou*) dominated most of the Boreal Forest Biome throughout Canada (Bergerud, 1974) and few moose (*Alces alces*) existed in the northeast of Ontario prior to the mid-1800s (Krefting, 1974). Woodland caribou originally extended as far south as Manitoulin Island and north to approximately 46° latitude (Cumming and Beange, 1993). However, since the 1880s this subspecies has disappeared in the southern part of the range. The present range distribution is north of 50° latitude (Cumming & Beange, 1987; Cumming & Beange, 1993), which approximates the northern limit of commercial timber harvest between Cochrane and Kenora (Racey *et al.*, 1991).

Moose have benefited from early succession forests created by timber harvest (Krefting, 1974) and it has been hypothesized that wolves increase pack sizes (Bergerud, 1974; Messier, 1985; Seip, 1992; Rettie & Messier, 1998) and body mass (Hillis, 1990; Mallory & Hillis, 1995) due to increased prey size. This shift in the predator–prey system is hypothesized to result in the extirpation of local woodland caribou populations due to greater wolf numbers and wolf body mass and the loss of prime habitat (Hillis, 1990; Seip, 1992; Mallory & Hillis, 1995). Bergerud (1990) hypothesized that rareness was an anti-predator strategy of caribou, and Lariviere *et al.* (2000) and Cumming (1975) suggested the clumping strategy of caribou would fail when moose were present in high

densities. Evidence indicates that disturbance has a major negative impact on caribou (Schaefer & Pruitt, 1991; Cumming, 1992; Antoniak, 1993; Chubbs *et al.*, 1993; Cumming & Beange, 1993; Antoniak & Cumming, 1996; Hillis *et al.*, 1998; Hillis & Mallory, 2004). Woodland caribou are now listed as vulnerable by COSEWIC because of the historical recession of their range associated primarily with commercial logging (Brown *et al.*, 2003). No declines in caribou have been recorded in undisturbed Ontario populations. The primary goals of this study were: (1) to assess the status of woodland caribou in northwestern Ontario, (2) to understand habitat utilization by this subspecies, and (3) to understand the impact of human-related land use activities on this species and its predators.

Moose are the largest member of the Cervidae and are found only in boreal forest dominated by spruce, fir, and pine, where disturbance is a major factor shaping the vegetative communities (Odum, 1983; Telfer, 1984; Karns, 1998). In late winter, moose are commonly found on south-facing slopes at higher elevations, in association with protective cover; while in summer they are found near water with abundant aquatic plants (Karns, 1998). Moose numbers were few in the area north of Lake Superior until the early twentieth century; due to the predominance of old growth coniferous forest, and have only recently become common in response to logging and other disturbance (Peterson, 1953, 1955; DeVos, 1958; Karns, 1998). Since the middle of the twentieth century, moose populations have shown positive growth across the continent (Bergerud, 1981; Crete, 1987; Thompson & Euler, 1987; Karns, 1998), which is believed to be due to a reduction in predators, reduced deer populations in the north due to the reversion of farmland to forest, larger clearcuts, and increased legal protection (Aldous & Krefting, 1946; Karns *et al.*, 1974; Peek *et al.*, 1976; Hicks, 1986; Boer, 1992; Alexander, 1993; Bontaites & Guftason, 1993; Morris & Elowe, 1993; Karns, 1998; Peek, 1998).

Resource partitioning facilitates the coexistence of sympatric ungulates and may take the form of spatial or temporal segregation, species-specific preferences for forage or plant parts, and different feeding heights (Stelfox & Taber, 1969; Hudson, 1976; Boer, 1992). Woodland caribou and moose inhabiting the Boreal Forest have limited competition (Davis & Franzmann, 1979; Fuller & Keith, 1981; Boer, 1992), as caribou prefer herbaceous forbs and deciduous foliage in summer and arboreal and ground lichens in the winter, while moose consume woody browse in winter and aquatic succulents, forbs, and deciduous foli-

age in summer (Dodds, 1960; Darby & Pruitt, 1984; Eastman & Ritcey, 1987; Servheen & Lyon, 1989; Boer, 1992; Proceviat, 2003; Proceviat *et al.*, 2003).

Woodland caribou and moose populations may also remain segregated by habitat partitioning and seasonal altitudinal preferences (Boer, 1992). Caribou prefer mature coniferous forest much of the year, open fens during the rut, and frozen lakes and large rivers during the late winter (Bergerud, 1974; Fuller & Keith, 1981; Darby & Pruitt, 1984; Servheen & Lyon, 1989; Boer, 1992; Wilson, 2000; Metsaranta, 2002; Brown *et al.*, 2003; Metsaranta *et al.*, 2003). Moose are associated with aquatic habitats in summer and prefer upland conifer areas with shrub layer in late winter (LeResche *et al.*, 1974; Cairns & Telfer, 1980; Boer, 1992; Hillis & Mallory, 2004).

It is hypothesized that the decline in woodland caribou (*Rangifer tarandus caribou*) in Ontario is due in part to predation. Since moose predation exposes wolves to greater risk of injury or death (Weaver *et al.*, 1992; Mallory *et al.*, 1994), natural selection would favor larger wolves in habitats dominated by moose and smaller wolves in habitats dominated by caribou. As wolves select for the most common ungulate in the system (Lamothe & Parker, 1989), if moose dominate, the increased numbers of wolves and selection for larger wolves would subject the smaller, less common caribou to increased predation risk and population decline into a "predator pit" or local extirpation (Mallory *et al.*, in press). Presumably, if the smaller prey is more abundant, natural selection would result in smaller-sized wolves (less food) and the larger, less common prey would present a more dangerous prey choice and tend to be avoided by the predator, resulting in sustained or increasing populations of the larger prey species.

## Material and methods

Wolf carcasses were obtained from trappers across northwestern Ontario between 1997 and 1998 and wolf scats were collected from moose and caribou ranges. Necropsy procedures for wolf carcasses were followed as outlined by Roffe *et al.* (1996) and measurements were taken as described by Hillis (1990) and Mulders (1997). Wolf skulls were fleshed and dried prior to cleaning by dermestid beetles and the suture between the basiosphenoid and basioccipital bones was checked for ossification to identify adult animals. Only skulls of adults were used in the statistical analysis (Kolenosky & Stanfield, 1975; Skeel & Carbyn, 1977; Mulders, 1997). A total of 45 cranial, mandibular, and dental measurements to the nearest

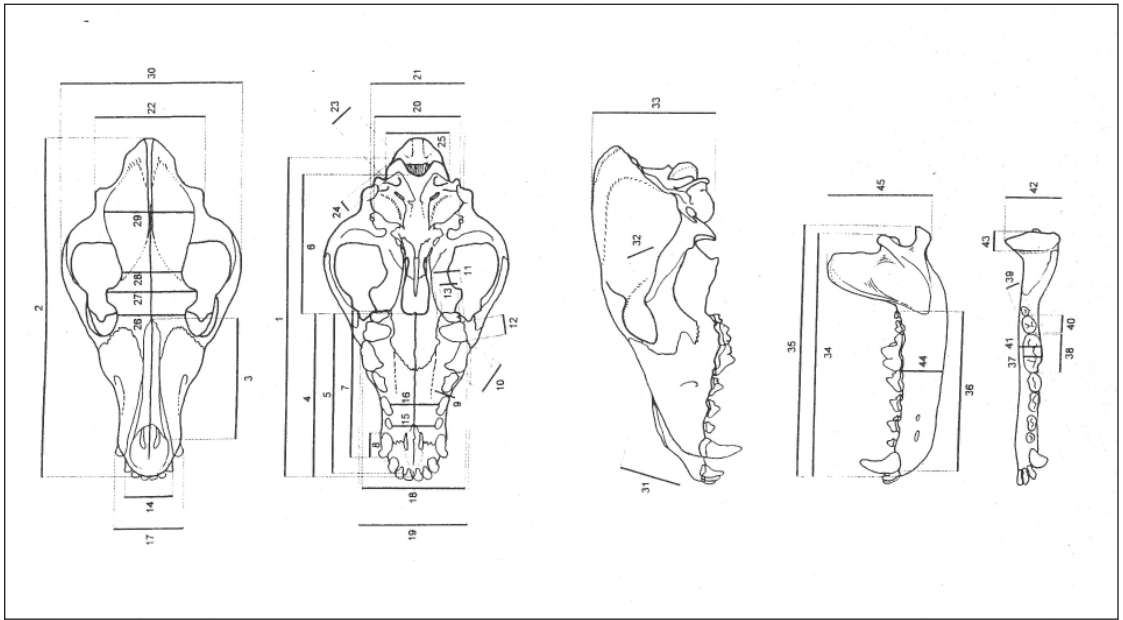


Fig. 1. Cranial, mandibular, and dental parameters ( $n = 45$ ) taken from adult moose- and caribou-wolves (*Canis lupus*). Corresponding descriptions are listed in Table 1.

0.01 mm were taken using digital calipers (Fig. 1; Appendix 1).

Total body weight with skin removed was measured to the nearest 0.5 kg using a Salter Scale (up to 100 kg) and external body measurements were made to the nearest mm with a fiberglass measuring tape (Fig. 2). A Sartorius Electronic Balance (up to 4 kg) was used to weigh internal organs to the nearest 0.1 g. Differences in morphology between wolves (*Canis lupus*) from caribou range and those from moose ranges were analyzed. Adipose tissue depth measurements were made to the nearest mm with calipers and kidney fat was estimated as described by Harder & Kirkpatrick (1996).

Wolf stomach and scat contents were washed through a 0.21-mm sieve and hairs were selected randomly and rinsed in methyl salicylate. Imprints of each hair were made in clear nail polish for prey species identification (Adorjan & Kolenosky, 1969). Scats were stored in plastic Whirlpak bags and autoclaved to kill endoparasites before handling. Each sample was assigned either a single prey category or—when there were multiple prey items in the stomach or scat—the most abundant item was used (Floyd *et al.*, 1978; Weaver, 1993). Frequencies (%) were calculated within each prey category to allow comparisons among the 3 different habitat types: (1) no disturbance, (2) 0 to 7 years post-harvest, and (3) more than 7 years post-harvest.

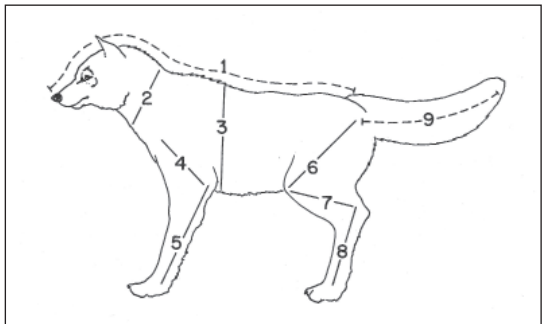


Fig. 2. External morphological measurements taken from wolf (*Canis lupus*) specimens from north-western Ontario (1—contour length; 2—neck girth; 3—chest girth; 4—humerus length; 5—ulna length; 6—femur length; 7—tibia length; 8—tarsal length; 9—tail length).

Statistical analyses were used to identify differences between items in wolf diets, skull morphology, and body and organ morphology for males and females. All multivariate and univariate statistical analyses were done using a SPSSx program, and Discriminant Analysis was used to identify differences in skull and body measurements that best distinguished the wolves from caribou and moose ranges, while Student's *t*-tests, Mann-Whitney U, and Kruskal-Wallis one-way Analysis of Variances were performed on adipose parameters (Zar, 1974).

## Results

### Wolf diet

Stomach and scat contents were analyzed from undisturbed areas (stomachs -  $n = 94$ ; scats -  $n = 16$ ) and from recently logged woodland caribou range 0 to 7 years post-harvest (stomachs -  $n = 89$ ; scats -  $n = 12$ ). Only wolf stomach contents ( $n = 110$ ) were analyzed from logged moose ranges greater than 7 years post-harvest. The percentage of caribou in wolf diets declined significantly, from 21% in areas with no disturbance, to 6% in areas where logging had occurred during the previous 0 to 7 years ( $\chi^2(1) = 7.259$ ;  $P < 0.01$ ) and to 0% in areas logged earlier than 7 years (Fig. 3). The percentage of moose in the diet of wolves was 37% in areas of no disturbance and 33% in areas logged approximately 0 to 7 years earlier and 49% on ranges where logging had occurred earlier than 7 years. The presence of white-tailed deer (*Odocoileus virginianus*) in wolf diets also increased significantly from 0% on ranges with no disturbance to 6% on ranges with logging approximately 0 to 7 years earlier and 9% on ranges where logging had occurred more than 7 years earlier ( $\chi^2(2) = 8.400$ ;  $P < 0.025$ ). In contrast, the percentage of beaver (*Castor canadensis*) in wolf diets declined from 26% on ranges with no disturbance to 22% in ranges with logging approximately 0 to 7 years earlier and to 12% on ranges where logging had occurred more than 7 years earlier. Significant changes in prey classified as "Other" were 0% on ranges with no disturbance, 28% on ranges with logging approximately 0 to 7 years earlier, and 14% on ranges where logging had occurred more than 7 years earlier ( $\chi^2(1) = 4.024$ ;  $P < 0.05$ ); prey diversity was highest in ranges 0 to 7 years post-harvest and lowest in ranges with no disturbance (Fig. 3).

### Skull morphology

#### Male wolves

A comparison of the means of adult male wolf skull measurements using a Student's *t*-test and a non-parametric Mann-Whitney U test is presented in Table 1. Canonical Discriminant Analysis was used to find which of 45 skull measurements best discriminate between moose- and caribou-wolves. Sixty-nine (64%) of the 107 wolf skulls were excluded from the Discriminant Analyses, as they were juveniles or damaged. Twenty-three skulls of adult male wolves

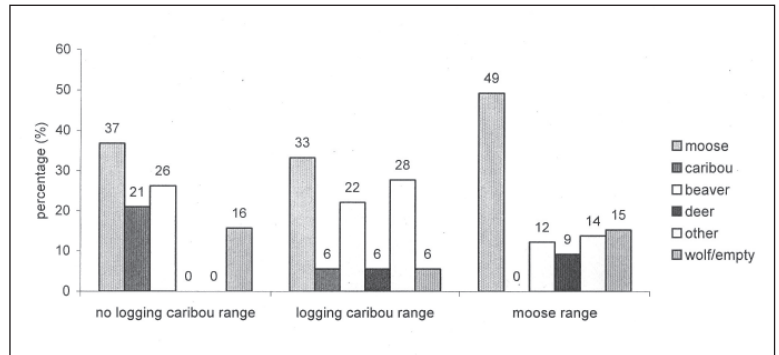


Fig. 3. Percentage of stomach and scat contents of *Canis lupus* in three different habitats (no logging-caribou range; logging-caribou range; logged-moose range) from northwestern Ontario.

were used, 7 from areas within the undisturbed range of woodland caribou and 16 from ranges more than 7 years post-harvest, where moose predominated and caribou were absent. Male moose-wolves had significantly ( $P < 0.05$ ) larger values on numerous skull measures including: Mandible Width, Length of Premolar<sup>4</sup>, Zygomatic Breadth, Cheek T W, and Width Across the 1<sup>st</sup> Molars.

The maximum Zygomatic Breadth, which is associated with bite force (Wiersma, 2001), differed significantly between adult male moose- and caribou-wolves from the two ranges ( $F = 8.3$ ;  $P = 0.009$ ). Zygomatic Breadth entered the discriminant function first and explained 28% of the variance, and the Occipital Condyle Width entered the function next and accounted for an additional 19% of the variance. Only the first five measurements were allowed to enter the Discriminant Analysis to ensure that multiple measurements that vary similarly did not influence the results. Once the 5 measurements had entered the function, only 23% of the variance in all skull measurements remained to be explained, thus 77% of the variance was accounted for by the measurements listed in Table 2. A Wilks' Lambda value of 0.23 indicated that there was a highly significant difference between the two groups of adult male wolves using the 2 value from Table 2 ( $2(5) = 27.15$ ;  $P < 0.001$ ). The discriminant function effectively assigned 100% of the male wolves that were used to generate the function to the range from which they were collected. When the function was tested on adult male wolves not used to generate the function, it correctly classified 95.7% to their respective ranges.

#### Female wolves

One-way Analysis of Variance and Canonical Discriminant Analysis were used to find which of 45 skull measurements best discriminated between

adult female moose- and caribou-wolves. Measurements were made on 19 skulls: 8 wolves were from the undisturbed woodland caribou range and 11 from the moose-dominated and caribou-absent range, where logging had occurred more than 7 years earlier. Adult female moose-wolves had significantly larger values ( $p < 0.05$ ) in Length of Premolar<sup>4</sup> and Width Between the 2<sup>nd</sup> Premolars (Table 3).

A One-way Analysis of Variance indicated that adult female caribou-wolves had greater Palatal Width across the 2<sup>nd</sup> Premolars (mean = 35.1 mm) than adult female moose-wolves (mean = 33.5 mm,  $F = 5.9$ ;  $P = 0.03$ ). Wilks' Lambda indicated that 26% of the variance between the 2 groups was accounted for by the Palatal Width measurement and the five measurements accounted for 85% of the variance. The Wilks' Lambda value (0.15) for the entire function and its 2 value indicated that the two groups separated well using the function. When the Discriminant Analysis was used to calculate discriminant scores (D) for each skull, the function correctly assigned 100% of the adult female wolves used to generate the function to their respective ranges. When the function was tested on wolves not used to generate the function, it correctly assigned 94.7% of them to their respective ranges, with only one of the 19 wolves being erroneously classified as a caribou-wolf (Table 4).

#### *Body morphology*

##### Male wolves

Table 5 compares the morphological parameters of adult male wolves collected from undisturbed caribou ranges and ranges where logging had occurred more than 7 years earlier and where moose dominated and caribou were absent. Levene's test for equality of variances was used to select the appropriate *t*-test. Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney *U* tests and the results of these analyses indicated that adult male moose-wolves were larger than adult male caribou-wolves. Adult male moose-wolves had higher Body Mass (31.6 kg) compared to adult male caribou-wolves (24.7 kg). Male moose-wolves also had greater mean Neck Girth (397.1 mm) than male caribou-wolves (344.3 mm). In addition, adult male moose-wolves had greater Heart, Lung, Liver, and Spleen Weights (Table 5).

#### *Discriminant analysis*

##### Male wolves

Twenty male adult wolves were used for a Discriminant Analysis with 8 body measurements and 5 organ weights (Table 6). One-way Analysis of

Variance indicated that adult male caribou-wolves had smaller Neck Girths (mean = 335.00 mm) than moose-wolves (mean = 395.70 mm,  $n = 20$ ,  $F = 25.700$ ;  $P < 0.001$ ). Neck Girth entered the discriminant function on the first step and accounted for 59% of the variability between wolves from the two areas. Neck Girth and Kidney Weight were the only two variables to enter the function and accounted for 65% of the total variance. Wilks' Lambda value for the function was 0.35 and its 2 value in Table 6 indicated that there was a significant difference ( $P < 0.001$ ) between the two groups of wolves using the body measurements listed. When scores were calculated for each male wolf used to generate the discriminant function, it correctly assigned 83% of the male wolves to their respective areas. When applied to wolves not used to generate the function, 88% of them were correctly classified (Table 6).

##### Female wolves

Comparisons of the mean organ masses and external body measurements of adult female wolves from undisturbed woodland caribou ranges and ranges where logging had occurred more than 7 years earlier were compared (Table 7). Levene's test for equality of variances was used to select the appropriate *t*-test. Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney *U* tests. The results indicated that no significant differences existed between the female moose-wolves and female caribou-wolves ( $P > 0.05$ ).

#### Discriminant analysis—Female wolves

Seventeen adult female wolves were used for a Discriminant Analysis using 8 body measurements and 5 organ weights (Table 8). One-way Analysis of Variance indicated no differences in the means of body measurements between adult female moose-wolves and adult female caribou-wolves. The Heart Weight ( $F = 1.900$ ;  $P = 0.185$ ) entered the discriminant function on the first step and accounted for 11% of the variability between adult female wolves from the two ranges. Kidney Weight and Neck Girth were the only other variables that entered the function and accounted for 50% of the total variance. Wilks' Lambda value for the function was 0.50 and its 2 value in Table 8 indicated that there was a significant difference ( $P = 0.025$ ) between the two groups of adult female wolves using the body measurements listed. The function correctly classified 86% of the wolves used to generate the function. When applied to a sample of 22 wolves not used to create the function, it correctly classified 73% (Table 8).

Table 1. Skull morphology of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges, where logging had occurred more than 7 years earlier. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range, M = moose range, Wt = weight w[g] (unless otherwise indicated), Lth = length [mm],  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ ).

Variable	Rangev	N	Mean	S.E.M.	<i>t</i> -value	Signif.	Mann-W U
Condyl L	C	7	215.12	14.96	-0.786	0.461	0.789
	M	16	226.99	2.04			
I <sup>1</sup> -Sag C	C	7	256.19	4.25	-0.642	0.528	0.789
	M	16	259.06	2.32			
Nasal L	C	7	95.02	3.49	-0.702	0.49	0.593
	M	16	97.10	1.27			
I <sup>1</sup> -Palat	C	7	125.53	2.29	-0.669	0.511	0.738
	M	16	126.94	0.99			
I <sup>2</sup> -Palat	C	7	123.64	2.33	-0.778	0.459	0.548
	M	16	125.59	0.92			
Pos Pal L	C	7	99.59	1.09	1.190	0.247	0.095
	M	16	97.66	0.96			
C <sup>1</sup> -M <sup>2</sup>	C	7	106.23	1.33	-0.496	0.625	0.738
	M	16	107.00	0.85			
W of C <sup>1</sup>	C	7	14.16	0.38	-2.033	0.055	0.066
	M	16	15.06	0.24			
W of P <sup>4</sup>	C	7	13.93	0.22	-0.274	0.786	0.815
	M	16	14.02	0.20			
L of P <sup>4</sup>	C	7	25.78	0.45	-1.426	0.169	0.109
	M	16	26.51	0.28			
W of M <sup>1</sup>	C	7	20.43	0.24	-0.982	0.338	0.688
	M	16	20.80	0.29			
L of M <sup>1</sup>	C	7	16.71	0.31	-0.490	0.629	0.442
	M	16	16.88	0.18			
W of M <sup>2</sup>	C	7	14.01	0.26	1.077	0.294	0.483
	M	16	13.62	0.21			
I <sup>3</sup> to I <sup>1</sup>	C	7	35.42	0.86	0.016	0.987	0.738
	M	16	35.41	0.50			
P <sup>1</sup> to P <sup>1</sup>	C	7	32.04	0.64	-1.313	0.203	0.350
	M	16	33.11	0.46			
P <sup>2</sup> to P <sup>2</sup>	C	7	34.95	0.72	-1.709	0.102	0.095
	M	16	36.51	0.51			
C <sup>1</sup> to C <sup>1</sup>	C	7	48.83	1.10	-2.015	0.057	0.061
	M	16	50.94	0.50			
M <sup>1</sup> to M <sup>1</sup>	C	7	77.73	0.90	-2.118	0.046*	0.027*
	M	16	80.29	0.69			
CheekTW	C	7	79.67	1.09	-2.491	0.021*	0.033*
	M	16	82.82	0.69			
Pos ForW	C	7	72.92	3.17	-1.955	0.064	0.181
	M	16	77.41	0.70			
Aud BulW	C	7	17.75	0.82	-0.764	0.453	0.738
	M	16	18.45	0.49			
Occ CreW	C	7	80.38	1.53	-1.555	0.135	0.256
	M	16	82.52	0.63			
CondyleW	C	7	12.41	0.35	0.577	0.570	0.229
	M	16	12.15	0.25			
CondyleL	C	7	26.83	0.59	1.709	0.102	0.102
	M	16	25.83	0.29			

Variable	Rangev	N	Mean	S.E.M.	t-value	Signif.	Mann-W U																																																																																																																																																																																																																																												
Occ ConW	C	7	50.87	0.78	1.542	0.138	0.061																																																																																																																																																																																																																																												
	M	16	49.37	0.54				InterOrW	C	7	44.34	1.16	-1.255	0.223	0.256	M	16	46.21	0.84	PostorbW	C	7	60.54	2.13	-1.618	0.120	0.161	M	16	64.78	1.46	TemFosW	C	7	41.38	0.77	-0.303	0.765	0.688	M	16	41.74	0.70	PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462	M	16	67.55	0.50	ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*	M	16	143.56	1.32	M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688
InterOrW	C	7	44.34	1.16	-1.255	0.223	0.256																																																																																																																																																																																																																																												
	M	16	46.21	0.84				PostorbW	C	7	60.54	2.13	-1.618	0.120	0.161	M	16	64.78	1.46	TemFosW	C	7	41.38	0.77	-0.303	0.765	0.688	M	16	41.74	0.70	PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462	M	16	67.55	0.50	ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*	M	16	143.56	1.32	M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09								
PostorbW	C	7	60.54	2.13	-1.618	0.120	0.161																																																																																																																																																																																																																																												
	M	16	64.78	1.46				TemFosW	C	7	41.38	0.77	-0.303	0.765	0.688	M	16	41.74	0.70	PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462	M	16	67.55	0.50	ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*	M	16	143.56	1.32	M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																				
TemFosW	C	7	41.38	0.77	-0.303	0.765	0.688																																																																																																																																																																																																																																												
	M	16	41.74	0.70				PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462	M	16	67.55	0.50	ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*	M	16	143.56	1.32	M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																
PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462																																																																																																																																																																																																																																												
	M	16	67.55	0.50				ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*	M	16	143.56	1.32	M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																												
ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*																																																																																																																																																																																																																																												
	M	16	143.56	1.32				M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640	M	16	41.70	0.62	Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																								
M <sup>1</sup> to Orb	C	7	41.18	1.39	-0.393	0.698	0.640																																																																																																																																																																																																																																												
	M	16	41.70	0.62				Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333	M	16	19.95	0.40	SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																				
Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333																																																																																																																																																																																																																																												
	M	16	19.95	0.40				SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841	M	16	87.51	0.88	Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																
SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841																																																																																																																																																																																																																																												
	M	16	87.51	0.88				Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947	M	16	190.67	1.43	Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																												
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	M	16	190.67	1.43				Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841	M	16	187.31	1.46	C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																								
Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841																																																																																																																																																																																																																																												
	M	16	187.31	1.46				C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548	M	16	120.09	0.80	W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																				
C <sup>1</sup> - M <sup>3</sup>	C	7	119.19	1.24	-0.613	0.547	0.548																																																																																																																																																																																																																																												
	M	16	120.09	0.80				W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256	M	16	11.65	0.15	L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																
W of P <sup>4</sup>	C	7	11.36	0.16	-1.107	0.281	0.256																																																																																																																																																																																																																																												
	M	16	11.65	0.15				L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*	M	16	30.24	0.36	W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																												
L of P <sup>4</sup>	C	7	28.95	0.38	-2.159	0.043*	0.038*																																																																																																																																																																																																																																												
	M	16	30.24	0.36				W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789	M	16	9.21	0.15	L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																								
W of M <sup>1</sup>	C	7	9.22	0.18	0.012	0.990	0.789																																																																																																																																																																																																																																												
	M	16	9.21	0.15				L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789	M	16	12.22	0.13	Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																																				
L of M <sup>1</sup>	C	7	12.17	0.29	-0.165	0.871	0.789																																																																																																																																																																																																																																												
	M	16	12.22	0.13				Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*	M	16	14.99	0.22	Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																																																
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	M	16	14.99	0.22				Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570	M	16	12.73	0.23	Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789	M	16	33.53	0.39	H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																																																												
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	M	16	33.53	0.39				H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867	M	16	31.21	0.53	AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																																																																																				
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	M	16	31.21	0.53				AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688	M	16	77.63	1.09																																																																																																																																																																																																																																
AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688																																																																																																																																																																																																																																												
	M	16	77.63	1.09																																																																																																																																																																																																																																															

Table 2. Canonical Discriminant Analysis of skull measurements of adult male moose- and caribou-wolves ( $n = 23$ ).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
Zygom B	0.72	8.3	1.66
Occ Con W	0.53	10.2	-0.51
SagC-AudB	0.40	12.3	1.48
M1 to Orb	0.29	21.0	-1.10
I <sup>3</sup> to I <sup>3</sup>	0.23	18.2	-0.77

Canonical Correlation Coefficient = 0.88 2 value (5) = 27.15;  $P < 0.001$

Function D = ((-0.37\*v 14)-(0.24\*v 25)+(0.27\*v 30)-(0.38\*v 31)+(1.12\*v 38))-31.46

Table 3. Morphological measurements of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges, where logging had occurred more than 7 years earlier. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests. (C = caribou range, M = moose range, Wt = weight [g], Lth = length [mm]),  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ ).

Variable	Range	N	Mean	S.E.M.	<i>t</i> -value	Signif.	Mann-W U																																																																																																																																																																																																																																																																																
Condyl L	C	8	213.35	2.70	2.211	0.041	0.137																																																																																																																																																																																																																																																																																
	M	11	222.97	3.51				I <sup>1</sup> -Sag C	C	8	240.70	3.10	0.792	0.439	0.509	M	11	244.14	2.75	Nasal L	C	8	88.11	1.73	0.573	0.574	0.509	M	11	89.49	1.50	I <sup>1</sup> -Palat	C	8	119.48	1.72	0.615	0.546	0.509	M	11	121.17	2.17	I <sup>2</sup> -Palat	C	8	118.29	1.69	0.475	0.641	0.680	M	11	119.56	2.11	Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836	M	11	93.04	1.48	C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364
I <sup>1</sup> -Sag C	C	8	240.70	3.10	0.792	0.439	0.509																																																																																																																																																																																																																																																																																
	M	11	244.14	2.75				Nasal L	C	8	88.11	1.73	0.573	0.574	0.509	M	11	89.49	1.50	I <sup>1</sup> -Palat	C	8	119.48	1.72	0.615	0.546	0.509	M	11	121.17	2.17	I <sup>2</sup> -Palat	C	8	118.29	1.69	0.475	0.641	0.680	M	11	119.56	2.11	Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836	M	11	93.04	1.48	C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41								
Nasal L	C	8	88.11	1.73	0.573	0.574	0.509																																																																																																																																																																																																																																																																																
	M	11	89.49	1.50				I <sup>1</sup> -Palat	C	8	119.48	1.72	0.615	0.546	0.509	M	11	121.17	2.17	I <sup>2</sup> -Palat	C	8	118.29	1.69	0.475	0.641	0.680	M	11	119.56	2.11	Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836	M	11	93.04	1.48	C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																				
I <sup>1</sup> -Palat	C	8	119.48	1.72	0.615	0.546	0.509																																																																																																																																																																																																																																																																																
	M	11	121.17	2.17				I <sup>2</sup> -Palat	C	8	118.29	1.69	0.475	0.641	0.680	M	11	119.56	2.11	Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836	M	11	93.04	1.48	C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																
I <sup>2</sup> -Palat	C	8	118.29	1.69	0.475	0.641	0.680																																																																																																																																																																																																																																																																																
	M	11	119.56	2.11				Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836	M	11	93.04	1.48	C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																												
Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836																																																																																																																																																																																																																																																																																
	M	11	93.04	1.48				C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509	M	11	102.20	1.51	W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																								
C <sup>1</sup> -M <sup>2</sup>	C	8	101.02	1.23	0.607	0.552	0.509																																																																																																																																																																																																																																																																																
	M	11	102.20	1.51				W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869	M	11	13.21	0.31	W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																																				
W of C <sup>1</sup>	C	8	13.37	0.21	-0.451	0.657	0.869																																																																																																																																																																																																																																																																																
	M	11	13.21	0.31				W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186	M	11	13.83	0.27	L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																																																
W of P <sup>4</sup>	C	8	13.20	0.37	-1.411	0.176	0.186																																																																																																																																																																																																																																																																																
	M	11	13.83	0.27				L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*	M	11	25.40	0.20	W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																																																												
L of P <sup>4</sup>	C	8	24.47	0.39	-2.129	0.057	0.048*																																																																																																																																																																																																																																																																																
	M	11	25.40	0.20				W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137	M	11	19.84	0.28	L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																																																																								
W of M <sup>1</sup>	C	8	19.55	0.50	-0.544	0.594	0.137																																																																																																																																																																																																																																																																																
	M	11	19.84	0.28				L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679	M	11	16.11	0.21	W of M <sup>2</sup>	C	8	13.64	0.22	1.071	0.299	0.680	M	11	14.31	0.67	I <sup>3</sup> of I <sup>3</sup>	C	8	33.84	0.60	-0.343	0.736	1.000	M	11	34.05	0.29	P <sup>1</sup> to P <sup>1</sup>	C	8	30.66	0.58	1.178	0.256	0.091	M	11	31.58	0.32	P <sup>2</sup> to P <sup>2</sup>	C	8	33.49	0.45	2.433	0.026*	0.026*	M	11	35.10	0.47	C <sup>1</sup> to C <sup>1</sup>	C	8	46.27	0.56	0.769	0.453	0.109	M	11	46.87	0.42	M <sup>1</sup> to M <sup>2</sup>	C	8	76.03	0.96	0.914	0.373	0.409	M	11	77.20	0.71	Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509	M	11	78.42	0.74	Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248	M	11	73.69	1.21	Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804	M	11	16.93	0.66	Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869	M	11	78.86	1.21	CondyleW	C	8	11.07	0.24	1.298	0.212	0.283	M	11	11.58	0.32	Condyle L	C	8	25.02	0.35	1.236	0.233	0.364	M	11	25.69	0.41																																																																																																																				
L of M <sup>1</sup>	C	8	16.11	0.14	0.009	0.993	0.679																																																																																																																																																																																																																																																																																
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Variable	Range	N	Mean	S.E.M.	t-value	Signif.	Mann-W U
Occ Con W	C	8	47.60	0.72	0.816	0.426	0.322
	M	11	48.46	0.73			
InterOr W	C	8	42.80	0.81	0.098	0.923	0.741
	M	11	42.91	0.71			
Postorb W	C	8	60.05	1.76	0.066	0.948	1.000
	M	11	60.21	1.15			
TemFosW	C	8	39.53	0.78	-0.965	0.348	0.364
	M	11	40.51	0.65			
Pari-TempW	C	8	65.35	0.84	-0.677	0.507	0.409
	M	11	66.14	0.78			
Zygom B	C	8	132.17	2.01	1.259	0.225	0.248
	M	11	135.56	1.50			
M <sup>1</sup> to Orb	C	8	38.16	0.41	0.649	0.525	0.509
	M	11	38.71	0.83			
Jugal H	C	8	18.00	0.46	-0.520	0.610	0.650
	M	11	18.30	0.37			
SagC-AudB	C	8	83.22	1.34	-0.024	0.981	0.869
	M	11	83.27	1.15			
SymAngPr	C	8	177.35	2.22	1.721	0.103	0.083
	M	11	182.79	2.08			
Sym-Condy	C	8	174.89	2.44	1.666	0.114	0.160
	M	11	180.27	1.73			
C <sup>1</sup> -M <sup>3</sup>	C	8	113.74	1.33	0.398	0.696	0.741
	M	11	114.50	1.28			
W of P <sup>1</sup>	C	8	10.79	0.12	-1.369	0.189	0.090
	M	11	11.07	0.15			
L of P <sup>4</sup>	C	8	28.22	0.37	-0.307	0.762	0.509
	M	11	28.39	0.39			
W of M <sup>1</sup>	C	8	8.67	0.17	-1.061	0.304	0.409
	M	11	8.88	0.12			
L of M <sup>1</sup>	C	8	11.82	0.22	-0.071	0.944	0.934
	M	11	11.84	0.16			
MandibW	C	8	13.72	0.28	0.579	0.570	0.321
	M	11	13.95	0.24			
Art ConW	C	8	10.75	0.58	-1.063	0.303	0.741
	M	11	11.40	0.32			
Art Con L	C	8	31.14	0.53	-0.167	0.870	0.934
	M	11	31.28	0.61			
H of Ramus	C	8	28.03	0.59	1.909	0.073	0.021
	M	11	29.44	0.27			
AngPCorP	C	8	72.16	0.80	0.573	0.574	0.741
	M	11	72.90	1.06			

Table 4. Canonical Discriminant Analysis of skull measures of adult female moose- and caribou-wolves ( $n = 19$ ).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
P <sup>2</sup> to P <sup>2</sup>	0.74	5.9	-1.87
L of P <sup>4</sup>	0.49	11.8	1.77
Pos For W	0.34	15.0	0.90
Art Con L	0.27	13.7	1.24
L of P <sup>4</sup>	0.15	47.7	-1.12

Canonical Correlation Coefficient = 0.92 2 value (5) = 27.22;  $P < 0.001$

Function D =  $((2.03 * v_{10}) - (1.31 * v_{16}) + (0.19 * v_{20}) - (0.94 * v_{38}) + (0.68 * v_{43})) - 13.97$

Table 5. Morphological parameters of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and ranges where logging had occurred more than 7 years earlier where moose dominated and caribou were absent. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range; Wt = weight [g] (unless otherwise indicated); Lth = length [mm]),  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ ).

Variable	Range	N	Mean	S.E.M.	<i>t</i> -value	Significance	MannWU
Body Wt (kg)	C	7	24.7	2.5	-3.162	0.005**	0.014*
	M	17	31.6	1.0			
Contour Lth	C	7	123.1	2.8	-1.108	0.280	0.191
	M	17	130.5	4.1			
Tail Lth	C	6	410.0	17.7	-2.045	0.055	0.079
	M	15	448.9	9.8			
Neck Girth	C	7	344.3	14.1	-4.375	0.000***	0.003**
	M	17	397.1	5.3			
Chest Girth	C	7	590.7	29.6	-2.163	0.007**	0.079
	M	17	657.1	8.2			
Humerus Lth	C	7	215.7	6.2	-1.669	0.109	0.114
	M	17	225.3	2.7			
Ulna Lth	C	6	248.3	14.6	-0.757	0.317	0.941
	M	16	259.9	4.4			
Front Paw Lth	C	2	103.0	18.0	-0.281	0.753	1.000
	M	3	108.3	6.0			
Front Paw Wth	C	2	76.5	11.5	0.552	0.529	1.000
	M	3	70.0	2.5			
Femur Lth	C	7	249.3	5.6	-0.278	0.784	0.723
	M	17	251.2	3.7			
Tibia Lth	C	7	239.3	6.9	-0.518	0.610	0.796
	M	17	242.4	2.6			
Tarsal Lth	C	5	169.0	5.6	-1.376	0.188	0.286
	M	13	175.4	2.0			
Hind Paw Lth	C	2	92.5	17.5	-0.234	0.781	1.000
	M	3	96.7	3.3			
Hind Paw Wth	C	2	67.5	4.5	1.496	0.232	0.248
	M	3	61.3	1.9			
Heart Wt	C	7	203.5	70.5	-3.159	0.005**	0.014*
	M	17	424.5	34.6			
Lung Wt	C	7	503.0	42.1	-2.311	0.031*	0.033*
	M	17	667.1	41.8			
Liver Wt	C	7	632.5	67.2	-2.074	0.050*	0.028*
	M	17	862.2	64.9			
Kidney Wt	C	7	189.0	20.4	-1.451	0.161	0.070
	M	17	230.0	16.0			
Spleen Wt	C	7	45.1	7.7	-2.788	0.011*	0.027*
	M	16	68.7	4.5			

Table 6. Canonical Discriminant Analysis of body measures of adult male moose- and caribou-wolves.

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
Neck Girth	0.41	25.7	0.76
Kidney Weight	0.35	8.2	0.50

Canonical Correlation Coefficient = 0.81 2 value (2) = 18.0  $P < 0.001$

Function D = ((0.031\*neck) + (0.015\*kid))-14.95

Table 7. Morphological measurements of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and moose ranges. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range; Wt = weight [g]; Lth = length [mm]),  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ .

Variable	Range	N	Mean	S.E.M.	<i>t</i> -value	Significance	MannWU
Body Wt (kg)	C	8	24.7	2.2	1.007	0.326	0.151
	M	17	22.7	0.9			
Condyl-basal Lth (cm)	C	8	118.9	3.6	0.027	0.979	0.632
	M	14	118.8	2.0			
Tail Lth	C	5	406.0	29.8	-0.094	0.926	0.402
	M	13	408.2	8.9			
Neck Girth	C	8	328.1	11.1	-0.883	0.388	0.471
	M	14	340.1	8.0			
Chest Girth	C	8	599.4	26.4	1.265	0.221	0.132
	M	14	568.8	10.6			
Humerus Lth	C	8	213.1	7.1	1.289	0.212	0.086
	M	14	204.7	2.9			
Ulna Lth	C	6	241.7	13.0	0.407	0.689	0.347
	M	12	236.7	5.9			
Femur Lth	C	8	233.1	6.3	-0.358	0.724	0.629
	M	14	235.1	2.4			
Tibia Lth	C	8	224.5	7.5	0.011	0.991	0.389
	M	14	224.4	2.3			
Tarsal Lth	C	6	164.2	4.9	-0.686	0.503	0.642
	M	11	167.2	1.9			
Heart Wt	C	8	427.6	65.3	1.961	0.027*	0.101
	M	14	292.4	21.9			
Lung Wt	C	8	643.2	63.6	1.454	0.162	0.152
	M	14	530.3	46.2			
Liver Wt	C	8	654.1	70.5	0.262	0.796	0.785
	M	14	633.2	44.9			
Kidney Wt	C	8	168.0	13.7	0.107	0.916	1.000
	M	14	166.2	10.4			
Spleen Wt	C	7	55.3	11.7	0.355	0.659	0.765
	M	14	50.9	3.8			

Table 8. Canonical Discriminant Analysis of body measures of adult female moose- and caribou-wolves ( $n = 17$ ).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
HeartWeight	0.89	1.93	-1.85
KidneyWeight	0.58	9.02	1.47
Neck Girth	0.50	4.05	0.53

Canonical Correlation Coefficient = 0.71 2 value (3) = 9.4;  $P = 0.025$

Function D = ((0.017\*neck)-(0.018\*heart)+(0.039\*kid)-6.51

Table 9. Condition indices of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges (caribou range) and disturbed moose ranges. Levene's test for equality of variances was used to select the appropriate  $t$ -test (equal variances assumed or not). Two-tailed Student's  $t$ -test significance was confirmed by non-parametric Mann-Whitney  $U$  tests (C = caribou range; M = moose range,  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ ).

Variable	Range	N	Mean	S.E.M.	$t$ -value	Significance	MannWU
Sterum Fat (mm)	C	7	7.0	2.8	-0.824	0.419	0.373
	M	17	12.3	3.9			
Rump Fat (mm)	C	7	5.1	2.0	-0.424	0.676	0.617
	M	15	6.2	1.4			
Back Fat (mm)	C	7	3.9	1.9	-1.036	0.312	0.126
	M	17	8.7	2.9			
Inguinal Fat (mm)	C	7	21.9	6.1	-0.777	0.446	0.547
	M	16	28.9	5.3			
Mesentary Fat (index)	C	7	2.1	0.5	-0.806	0.429	0.505
	M	17	2.5	0.2			
Total External Fat (index)	C	7	2.1	0.6	0.045	0.965	0.870
	M	17	2.1	0.3			
Total Internal Fat (index)	C	7	2.1	0.6	-0.702	0.490	0.534
	M	17	2.5	0.3			
Kidney Fat Index	C	7	41.7	13.7	-0.440	0.665	0.462
	M	16	47.9	7.1			

#### Condition indices

The condition of moose- and caribou-wolves determined by adipose measurements is presented in Tables 9 and 10. Levene's test for equality of variances was used to select the appropriate  $t$ -test and two-tailed Student's  $t$ -test significance was confirmed by non-parametric Mann-Whitney  $U$  tests. No significant differences were found in adipose tissue of moose- and caribou-wolves; however, adipose indices were greater in moose-wolves for all variables measured.

#### Male wolves

A comparison of condition indices of adult male wolves collected from undisturbed woodland caribou ranges and disturbed moose-dominated ranges with no caribou was undertaken (Table 9).

#### Female wolves

A comparison of condition indices of adult female wolves collected from undisturbed woodland caribou ranges and disturbed moose ranges with no caribou was undertaken and no significant differences were found (Table 10).

#### Wolf injuries

Old skeletal injuries distinguished by calcification (Phillips, 1984) were evident in 4 of the 106 wolves. Three of the 4 injured wolves were males from moose range. Male injuries included a crushed anterior end of the nasal bones, a shattered humerus and scapula, a cracked and deformed premaxilla, and a cracked back of the skull where the occipital and sagittal crests meet. The single adult female caribou-wolf had a cracked sagittal crest.

Table 10. Condition indices of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range,  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ ).

Variable	Range	N	Mean	S.E.M.	<i>t</i> -value	Significance	MannWU
Sterum Fat (mm)	C	8	7.9	2.0	0.756	0.459	0.585
	M	13	6.1	1.4			
Rump Fat (mm)	C	8	6.4	2.3	0.509	0.616	0.654
	M	14	5.0	1.6			
Back Fat (mm)	C	8	7.3	2.4	0.840	0.411	0.706
	M	14	5.4	1.0			
Inguinal Fat (mm)	C	8	26.6	5.5	1.580	0.077	0.108
	M	14	17.4	2.2			
Mesentary Fat (index)	C	8	2.5	0.4	0.138	0.892	1.000
	M	14	2.4	0.3			
Total External Fat (index)	C	8	1.9	0.5	-0.363	0.720	0.713
	M	14	2.1	0.3			
Total Internal Fat (index)	C	8	2.5	0.4	0.740	0.468	0.570
	M	14	2.1	0.3			
Kidney Fat KFI (index)	C	8	62.3	14.5	0.887	0.385	0.339
	M	14	47.8	9.2			

## Discussion

### *Wolf diet*

Wolf diet changed from essentially a 3 prey system (moose, caribou, beaver) in undisturbed boreal forest to a 9+ prey system in ranges 0 to 7 years post-harvest and finally to a moose-specialized system in ranges more than 7 years post-harvest. However, as moose were available within 10 to 60 km from the core caribou wintering area in this study, their presence in the stomachs and scats of wolves in the "no disturbance" area was expected. Lariviere *et al.* (2000) found the highest wolf densities in areas where wolves had access to white-tailed deer and moose and hypothesized that multiple-prey-based ecosystems sustained higher densities of wolves than systems with single prey bases. Empty stomachs were least frequent (6%) in logged habitats 0–7 years post-harvest compared to the other habitats (15%–16%). Fewer empty stomachs suggest an improvement in the availability of prey for wolves in areas with recent disturbance. McKenney *et al.* (1998) found that moose density increased in the province of Ontario from 0.116 per sq. km in 1975–1980 to 0.145, 0.179, and 0.209 per sq. km for the years 1980–1985, 1985–1990, and 1990–1995, respectively. These increases were not uniform and occurred in spite of moose declines in late successional areas, such as Wabakimi Provincial Park and the area north of Lac Seul that lacked substantial timber harvest.

Moose are the primary prey of wolves throughout the southern half of Quebec, with a direct exponential relationship between wolf and moose densities, particularly when moose exceeded 0.3 animals/km<sup>2</sup> (Lariviere *et al.*, 2000). Below 0.3 moose/km<sup>2</sup>, wolf density remained relatively constant at slightly less than 1 animal/km<sup>2</sup>. Analysis of moose densities in Ontario between 1975 and 1995 (McKenney *et al.*, 1998) indicated that initial scattered patches of higher moose density had expanded to cover a vast area across northern Ontario. The boundary separating areas of moose density above and below the provincial average of 0.209/km<sup>2</sup> closely approximates the southern limit of caribou distribution and the northern limit of timber harvest. Caribou continue to exist along the northern limit of timber harvest where moose densities are below 0.209. Zones of lower than average moose density south of the caribou line are separated from caribou ranges by bands of high moose density. Using the regression line of Lariviere *et al.* (2000), the band of high moose density would represent an ecological barrier of elevated wolf density through which caribou would be unable to re-colonize their former range.

A more varied prey base implies that wolves benefit from a more constant food supply (Cumming, 1975). Prey items such as snowshoe hare, small mammals, fish, birds, and vegetation increased from 0 in undisturbed ranges to 28% in areas 0 to 7 years

post-harvest to 14% in ranges more than 7 years post-harvest. Increases in diversity during the transitional stage (0 to 7 years post-harvest) can be explained by the presence of species associated with both early and late successional habitat.

Forbes and Theberge (1996) found that beaver acted as a buffer prey species when ungulate densities were low. They noted that the inspection of beaver houses was a common activity among Algonquin Provincial Park wolves. In this study, winter observations of wolf tracks in a caribou wintering area indicated that wolves checked a previously opened beaver house. Tracks indicated that wolves had watched the opened house, suggesting that beaver might continue to use a house previously opened by wolves. Beaver were found in 26% of the scat/stomach samples from undisturbed ranges and in 12% of the samples from ranges more than 7 years post-harvest.

While moose were available in remote undisturbed ranges, their densities were low. Dale *et al.* (1995) found that caribou densities below 0.2/km<sup>2</sup> were associated with wolves switching to preying on moose. Messier (1985) found that wolves changed territory boundaries, increased extraterritorial excursions to white-tailed deer areas, and became more susceptible to mortality when moose density was below 0.2/km<sup>2</sup>. In this study—during 8 days of observations including 228 km of transects by snowmobile, snowshoe, and aircraft in the caribou wintering area—the only moose sign observed were tracks and pellet groups found in poplar stands >10 km south of the core caribou wintering area. The absence of moose was also noted while making daily observations of caribou totaling 110 individuals. These observations suggest that, historically, woodland caribou ranges had few to no moose present and that wolf density was low (Bergerud, 1990), as the migratory and clumping behaviour of woodland caribou would leave vast tracts of land seasonally devoid of ungulate prey (Cumming, 1975).

The diet analysis indicated that as sampling moved to areas with increased disturbance, moose increased in importance in the diet, wolves had fewer empty stomachs, and prey diversity increased. It was also concluded that increases in moose density associated with disturbance resulted in the increased use of moose by wolves (Messier, 1995). In addition, it was concluded that increased disturbance subjected woodland caribou to increased predation by wolves, contributing to their extirpation from much of their former range. As timber harvest moved northward, there has been a general increase in moose density (Schwartz & Franzmann, 1991; McKenney *et al.*, 1998) coupled with a decline in woodland caribou

(Bergerud, 1974; Darby *et al.*, 1989; Mallory & Hillis, 1996; McKenney *et al.*, 1998). The decline in caribou and the increase in moose (McKenney *et al.*, 1998) as one moves south was also reflected in the diet of wolves (Fig. 3). Brousseau (1978), using pellet counts, documented a sharp decline in woodland caribou from 0.86/km<sup>2</sup> to 0.00/km<sup>2</sup> within 5 years following the commencement of timber harvest in the Cliff Lake area, northwestern Ontario. Aerial surveys also indicated a 75% decline in the number of caribou using the area during the 11 years of study. Similar to Brousseau (1978) and Kohira & Rexstad (1997), the wolf diet in this study supported the hypothesis that commercial timber harvest changed the predator–prey relationship.

#### *Skull morphology*

Adult male moose-wolves had significantly larger values than adult male caribou-wolves in a number of skull measures including: Mandible Width, Length of Premolar <sup>4</sup>, Zygomatic Breadth, Cheek T W, and Width across the 1<sup>st</sup> Molars. The Canonical Discriminant Analysis correctly classified 95.7% of male wolves to their respective ranges using these 5 skull measures. Adult female moose-wolves had larger values than adult female caribou-wolves in two skull measures: Length of Premolar <sup>4</sup> and Width between the 2<sup>nd</sup> Premolars. The Canonical Discriminant Analysis correctly assigned 94.7% of the adult female wolves to their respective ranges with only one of 19 being erroneously classified. The fact that male wolves were more different than female wolves is significant. Similar results were reported by Hillis (1990) for arctic wolves along the west coast of Hudson Bay, Nunavut. In addition, the fact that adult male moose-wolves had significantly larger skull parameter values that are associated with prey capture, supports the conclusion that these differences are directly related to capture of larger, more dangerous prey. Increased width across the Zygomatic Breadth without a correlated increase in the width of the brain case provides space for larger masseter muscles. Thomason (1991) and Wiersma (2001) demonstrated that bite force increased with greater Zygomatic Breadth and Mandible Width. Larger masseters would increase the bite force and should be selected for in predators preying on larger and more dangerous prey (Mallory *et al.*, 1994). The high classification success of the discriminant functions indicated that there are significant morphological differences in male skull parameters between moose- and caribou-wolves. Mallory *et al.* (1994) and Hillis & Mallory (1996) hypothesized that during hunting, adult male wolves usually make first contact with large ungulate prey and are most

prominent in the capture and killing of risky prey. This behavior would strongly influence the natural selection for male wolf body size and skull morphology in relation to prey specialization, gender, and sexual dimorphism (Mallory & Hillis, 1995; Hillis & Mallory, 1996) and also influence differences between related species, such as the coyote (*C. latrans*) (Mallory & Edwards, 1996).

#### *Body morphology and condition indices*

As diet changed from caribou to moose, the body size of male wolves increased significantly. Male moose-wolves had significantly greater mean neck girth (397.1 mm) than caribou-wolves (344.3 mm) and significantly larger hearts, lungs, livers, and spleen masses. In addition, male moose-wolves had significantly greater body mass (31.6 kg) than male caribou-wolves (24.7 kg), while adult female wolves had few significant differences in body or organ weights. Schmitz & Kolenosky (1985) and Schmitz and Lavigne (1987) found that over a period of 25 years (1959–1984) there was an increase in mean body weight and length of coyotes at the same time as there was a decrease in the mean body length of wolves in southeastern Ontario. Prior to European settlement, wolves in southeastern Ontario were typically predators of large ungulates like moose (Kolenosky & Stanfield, 1975) and Schmitz & Lavigne (1987) concluded that changes in wolves were correlated with an increase in the use of smaller, more abundant white-tailed deer as primary prey. Increases in body size were observed in coyotes that recently arrived in the Maritimes (wolves had been extirpated since the 1800s) and it has been hypothesized that the size increase was due to specialization on the larger prey such as white-tailed deer (Crete & Desrosiers, 1995).

Hillis & Mallory (1996) found that the greatest sexual dimorphism in wolves ( $n = 425$ ) from Nunavut was in body and visceral organ masses, particularly of the heart, lungs, liver, and spleen. They attributed these differences to the division of labor between the sexes, with males being highly specialized for capturing and killing large ungulate prey. In this study, we found that male moose-wolves were larger than male caribou-wolves for the same set of organ measurements and concluded that the differences were due to specialization for capturing larger prey. Thicker necks in moose-wolves would assist in pulling prey down and the increase in bite force due to wider zygomatic arches (Thomason, 1991; Wiersma, 2001) and larger masseter muscles would complement increased neck girth. Larger hearts and lungs would increase the cardiovascular fitness in moose-wolves, and the larger spleen—a blood reservoir—would release more

erythrocytes in response to drops in blood oxygen or blood pressure (Walker and Liem, 1994).

The fact that condition indices did not differ between moose- and caribou-wolves suggests that the body size and pack size of each wolf type adjusted to the nutritional input available from their primary prey. Although no significant differences occurred in condition indices, moose-wolves consistently had higher levels of adipose tissue. Hall (1989), working on arctic fox (*Alopex lagopus*), found larger litter sizes when adipose reserves increased due to an abundance of small mammals. The greater amount of adipose reserves also resulted in higher ovulation rates and we expect a similar relationship in wolves, which would affect wolf pack size.

The results from this study support the conclusion that the greater adult skull and body size of moose-wolves relative to caribou-wolves was related to specialization on larger prey. The data also support the conclusion that wolves adapted to larger prey would be more efficient at capturing smaller ungulate prey and impact these populations negatively. Gates & Larter (1996) observed that after wood bison (*Bison bison atabascaae*) were introduced to the MacKenzie Wood Bison Reserve, moose and caribou populations in that region declined, which likely reflects the same shift in the predator–prey system as described in this study on moose and woodland caribou in Ontario.

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#### References

- Adorjan, A.S. & Kolenosky, G.B. 1969. *A manual for the identification of hairs of selected Ontario mammals*. Ontario Department of Lands and Forests Research Section, Wildlife Branch. Maple, Ontario. 64pp.

- Aldous, S.E. & Krefting, L.W. 1946. The present status of moose on Isle Royale. – *Trans. N. Am. Wildl. Conf.* 11: 296–308.
- Alexander, C.E. 1993. The status and management of moose in Vermont. – *Alces* 29: 187–195.
- Antoniak, F. 1993. *Forest analysis and modeling of wintering areas of woodland caribou in northwestern Ontario*. M.Sc. thesis, Lakehead University, Thunder Bay, Ontario. 122pp.
- Antoniak, F. & Cumming, H.G. 1996. Analysis of forest stands used by wintering woodland caribou in Ontario. – *Rangifer* Special Issue No. 10: 157–168.
- Bergerud, A.T. 1974. Decline of caribou in North America following settlement. – *J. Wildl. Manage.* 38: 757–770.
- Bergerud, A.T. 1981. The decline of moose in Ontario: a different view. – *Alces* 17: 30–43.
- Bergerud, A.T. 1990. Rareness as an anti-predator strategy to reduce predation risk. – *Trans. 19<sup>th</sup> IUGB Congress*, Trondheim, 1989: 3–9.
- Boer, A.H. 1992. History of moose in New Brunswick. – *Alces* 1: 16–21.
- Bontaites, J.M. & Guftason, K. 1993. The history and status of moose management in New Hampshire. – *Alces* 29: 163–168.
- Brousseau, C. 1978. *Trends of the woodland caribou (Rangifer tarandus caribou) population in the Cliff Lake area of the Dryden District, 1972–1978*. Ont. Min. Nat. Res., Dryden, Ontario. 46pp.
- Brown, G.S., Mallory, F.F., & Rettie, W.J. 2003. Range size and seasonal movement for female woodland caribou in the boreal forest of northeastern Ontario. – *Rangifer* Special Issue No. 14: 227–233.
- Cairns, A.L. & Telfer, E.S. 1980. Habitat use by four sympatric ungulates in boreal mixedwood forest. – *J. Wildl. Manage.* 44: 849–857.
- Chubbs, T.E., Keith, L.B., Mahoney, S.P., & McGrath, M.J. 1993. Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. – *Can. J. Zool.* 71: 487–493.
- Crete, M. 1987. The impact of sport hunting on North American moose. – *Swedish Wildl. Res.* 1: 553–563.
- Crete, M. & Desrosiers, A. 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Quebec. – *Can. Field-Nat.* 109: 227–235.
- Cumming, H.G. 1975. Clumping behavior and predation with special reference to caribou. – In: Luick, J.R. (ed.). *Proceedings of the First International Reindeer and Caribou Symposium*, Biological Papers of the University of Alaska, Special Report, No. 1 (pp. 474–497). University of Alaska, Institute of Arctic Biology, Fairbanks, Alaska.
- Cumming, H.G. 1992. Woodland caribou: facts for forest managers. – *Forest Chron.* 68: 481–491.
- Cumming, H.G. & Beange, D.B. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. – *J. Wildl. Manage.* 51(1): 69–79.
- Cumming, H.G. & Beange, D.B. 1993. Survival of woodland caribou in commercial forests of northern Ontario. – *Forest Chron.* 69(5): 579–588.
- Darby, W.R. & Pruitt Jr., W.O. 1984. Habitat use, movements and grouping behaviour of woodland caribou, *Rangifer tarandus caribou*, in southeastern Manitoba. – *Can. Field-Nat.* 98: 184–190.
- Darby, W.R., Timmermann, H.R., Snider, J.B., Abraham, K.F., Stefanski, R.A., & Johnson, C.A. 1989. *Woodland caribou in Ontario; background to a policy*. Ontario Ministry of Natural Resources, Toronto, Ontario. 38pp.
- Dale, B.W., Adams, L.G., & Bowen, R.T. 1995. Winter wolf predation in a multiple ungulate prey system: gates of the Arctic National Park, Alaska. – In: Carbyn, L.N., Fritts, S.H., & Seip, D.R. (eds.). *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, Occasional Publication No. 35, 642pp.
- Davis, J.L. & Franzmann, A.W. 1979. Fire-moose-caribou interrelationships: a review and assessment. – *N. Am. Moose Conf. Workshop* 15: 80–118.
- DeVos, A. 1958. Summer studies of moose in Ontario. – *Trans. N. Am. Wildl. Conf.* 21: 510–525.
- Dodds, D.G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. – *J. Wildl. Manage.* 24: 52–60.
- Eastman, D.S. & Ritcey, R. 1987. *Moose habitat relationships and management in British Columbia*. Ministry of the Environment, Victoria, B.C. 45pp.
- Floyd, T.J., Mech, L.D., & Jordan, P.A. 1978. Relating wolf scat content to prey consumed. – *J. Wildl. Manage.* 42: 528–532.
- Forbes, G.J. & Theberge, J.B. 1996. Response by wolves to prey variation in central Ontario. – *Can. J. Zool.* 74(8): 1511–1520.
- Fuller, T.K. & Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. – *J. Wildl. Manage.* 45: 197–213.
- Gates, C.C. & Larter, N.C. 1996. Growth and dispersal of an erupting large herbivore population in northern Canada: The MacKenzie Wood Bison (*Bison bison athabasca*). – *Arctic* 43: 231–238.
- Hall, M.N. 1989. *Parameters associated with cyclic populations of arctic fox (Alopex lagopus) near Eskimo Point, Northwest Territories: morphometry, age, condition, seasonal and multi-annual influences*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 164pp.
- Harder, J.D. & Kirkpatrick, R.L. 1996. Physiological methods in wildlife research. – In: Bookhout, T.A. (ed.). *Research and Management Techniques for Wildlife and Habitats*, 5<sup>th</sup> edition. (pp. 275–306). The Wildlife Society, Bethesda, Maryland.



- Hicks, A.C. 1986. The history and current status of moose in New York. – *Alces* 22: 245–252.
- Hillis, T.L. 1990. *The demography and ecology of the tundra wolf, Canis lupus, in the Keewatin District, Northwest Territories*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 144pp.
- Hillis, T.L. & Mallory, F.F. 1996. Sexual dimorphism in wolves (*Canis lupus*) of the Keewatin District, Northwest Territories, Canada. – *Can. J. Zool.* 74: 721–725.
- Hillis, T.L. & Mallory, F.F. 2004. *Ecology of woodland caribou (Rangifer tarandus caribou) in northwestern Ontario: responses to habitat fragmentation*. Interim Report, Ontario Ministry of Natural Resources, Thunder Bay, Ontario 62pp.
- Hillis, T.L., Mallory, F.F., Dalton, W.J., & Smiegielski, A.J. 1998. Preliminary analysis of habitat utilization by woodland caribou in northwestern Ontario using satellite telemetry. – *Rangifer*, Special Issue No. 10: 195–202.
- Hudson, R.J. 1976. Resource division within a community of large herbivores. – *Nature Canada* 103: 153–167.
- Karns, P.D. 1998. Population distribution, density and trends. – In: Franzmann, A.W. & Schwartz, C.C. (eds.). *Ecology and Management of the North American Moose* (pp. 125–140). Washington, D.C.: Smithsonian Institution Press.
- Karns, P.D., Haswell, H., Gilbert, F.F., & Patton, A.E. 1974. Moose management in the coniferous-deciduous ecotone of North America. – *Nature Canada* 101: 643–656.
- Kohira, M. & Rexstad, E.A. 1997. Diet of wolves, *Canis lupus*, in logged and unlogged forests. – *Can. Field-Nat.* 111(3): 429–435.
- Kolenosky, G.B. & Stanfield, R.O. 1975. Morphological and ecological variation among gray wolves (*Canis lupus*) of Ontario, Canada. In: Fox, M.W. (ed.). *The Wild Canids, their Systematics, Behavioural Ecology and Evolution* (pp. 62–72). New York: Van Nostrand Reinhold Company.
- Krefting, L.W. 1974. Moose distribution and habitat selection in North American. – *Nature Canada* 10: 81–100.
- Lamothe, A.R. & Parker, G.H. 1989. Winter feeding habits of wolves in the Keewatin District, Northwest Territories, Canada. – *Musk-Ox* 37: 144–149.
- Lariviere, S., Jolicoeur, H., & Crete, M. 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Quebec. – *Biol. Conserv.* 94: 143–151.
- LeResche, R.E., Bishop, R.H., & Coady, J.W. 1974. Distribution and habitats of moose in Alaska. – *Nature Canada* 101: 143–178.
- Mallory, S.E. & Edwards, C. 1996. *A comparison of standard measurements and fractal techniques for distinguishing gray wolves (Canis lupus) and coyotes (Canis latrans)*. B.Sc. (Hons.) thesis, Laurentian University, Sudbury, Ontario. 76pp.
- Mallory, F.F. & Hillis, T.L. 1995. Correlations of sexual dimorphism and foraging strategies in wolves, *Canis lupus*, from the central Canadian Arctic. *International Symposium on Wolves & Humans 2000*. Univ. Minnesota, Duluth. p. 32.
- Mallory, F.F. & Hillis, T.L. 1996. Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints/releases, and population dynamics. – *Rangifer*, Special Issue No. 10: 49–60.
- Mallory, F.F., Hillis, T.L., Blomme, C.G., & Hurst, W.G. 1994. Skeletal injuries of an adult timber wolf, *Canis lupus*, in northern Ontario. – *Can. Field-Nat.* 108: 230–232.
- Mallory, F.F., Wiwchar, D.M.A., & Hillis, T.L. *in press*. Wolves, caribou and other ungulates. – *Rangifer* Special Issue No. 20.
- McKenney, D.W., Rempel, R.S., Venier, L.A., Wang, Y., & Bisset, A.R. 1998. Development and application of a spatially explicit moose population model. – *Can. J. Zool.* 76: 1922–1931.
- Messier, F. 1985. Social organization, spatial distribution and population density of wolves in relation to moose density. – *Can. J. Zool.* 63: 239–245.
- Metsaranta, J. 2002. *Habitat utilization by woodland caribou (Rangifer tarandus caribou): an assessment of use in disturbed and undisturbed habitats in west central Manitoba*. M.Sc. thesis, Laurentian University, Sudbury, Ontario 145pp.
- Metsaranta, J.M., Mallory, F.F., & Cross, D.W. 2003. Vegetation characteristics of forest stands used by woodland caribou and those disturbed by fire and logging in Manitoba. – *Rangifer*, Special Issue 14: 255–266.
- Morris, K. & Elowe, K. 1993. The status of moose and their management in Maine. – *Alces* 29: 91–98.
- Mulders, R. 1997. *Geographic variation in the cranial morphology of the wolf (Canis lupus) in northern Canada*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 167pp.
- Odum, E.P. 1983. *Fundamentals of Ecology*, 3<sup>rd</sup> edition. New York: CBS College Publishing.
- Peek, J.M. 1998. Habitat relationships. In: Franzmann, A.W. & Schwartz, C.C. (eds.). *Ecology and Management of the North American Moose* (pp. 351–376). Washington, D.C.: Smithsonian Institution Press.
- Peek, J.M., Ulrich, D.L., & Mackie, R.J. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. – *Wildl. Monogr.* 48: 1–65.
- Peterson, R.L. 1953. *Studies on the food habits and the habitat of moose in Ontario*. Royal Ontario Museum, Zoology and Paleontology Section, Toronto. pp.1–40.
- Peterson, R.L. 1955. *North American Moose*. Toronto: University of Toronto Press. 164pp.
- Phillips, M.K. 1984. The cost to wolves of preying on ungulates. – *Austral. Mammal.* 8: 99.
- Proceviat, S.K. 2003. *Impact of careful logging on availability of woodland caribou (Rangifer tarandus caribou) and moose (Alces alces) forage and habitat in northeastern Ontario*

- lowland black spruce stands*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 132pp.
- Proceviat, S.K., Mallory, F.F., & Rettie, W.J. 2003. Estimation of arboreal lichen biomass available to woodland caribou in Hudson Bay lowland black spruce sites. – *Rangifer* Special Issue No. 14: 95–99.
- Racey, G.D., Abraham, K., Darby, W.R., Timmermann, H.R., & Day, Q. 1991. Can woodland caribou and the forest industry coexist: the Ontario scene. – *Rangifer* Special Issue No. 7: 108–115.
- Rettie, W.J. & Messier, F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. – *Can. J. Zool.* 76(2): 251–259.
- Roffe, T.J., Friend, M., & Locke, L.N. 1996. Evaluation of causes of wildlife mortality. In: Bookhout, T.A. (ed.). *Research and Management Techniques for Wildlife and Habitats*, 5<sup>th</sup> edition (pp. 324–348). The Wildlife Society, Bethesda, MD.
- Schaefer, J.A. & Pruitt Jr., W.O. 1991. Fire and woodland caribou in southeastern Manitoba. – *Wildl. Monogr.* 116: 1–39.
- Schmitz, O.J. & Kolenosky, G.B. 1985. Wolves and coyotes in Ontario: morphological relationships and origins. – *Can. J. Zool.* 63: 1130–1137.
- Schmitz, O.J. & Lavigne, D.M. 1987. Factors affecting body size in sympatric Ontario canids. – *J. Mammal.* 68: 92–99.
- Schwartz C.C. & Franzmann, A.W. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. – *Wildl. Monogr.* 113: 1–58.
- Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. – *Can. J. Zool.* 70(8): 1494–1503.
- Servheen, G. & Lyon, L.J. 1989. Habitat use by woodland caribou in the Selkirk Mountains. – *J. Wildl. Manage.* 53: 230–237.
- Skeel, M.A. & Carbyn, L.N. 1977. The morphological relationship of gray wolves (*Canis lupus*) in national parks of central Canada. – *Can. J. Zool.* 55: 737–747.
- Stelfox, J.G. & Taber, R.D. 1969. Big game in the northern Rocky Mountains coniferous forest. – In: Taber, R.D. (ed.). *Coniferous Forests of the Northern Rocky Mountains* (pp. 197–220). University of Montana Foundation, Montana.
- Telfer, E.S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). – In: Olson, R., Hastings, R., & Geddes, F. (eds.). *Northern Ecology and Resource Management* (pp. 145–182). University of Alberta Press, Edmonton.
- Thomason, J.J. 1991. Cranial strength in relation to estimated bite forces in some mammals. – *Can. J. Zool.* 69: 2326–2333.
- Thompson, I.D. & Euler, D.L. 1987. Moose habitat in Ontario: a decade of change in perception. – *Swedish Wildl. Res.* 1: 181–193.
- Walker, Jr., W.F. & Liem, K.F. 1994. *Functional anatomy of the vertebrates*, 2<sup>nd</sup> edition. New York: Saunders College Publishing.
- Weaver, J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. – *J. Wildl. Manage.* 57(3): 534–538.
- Weaver, J.L., Arvidson, C., & Wood, P. 1992. Two wolves, *Canis lupus*, killed by a moose, *Alces alces*, in Jasper National Park, Alberta. – *Can. Field-Nat.* 106(1): 126–127.
- Wiersma, J.H. 2001. *Maximum estimated bite force, skull morphology, and primary prey size in North American carnivores*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 155pp.
- Wilson, J.E. 2000. *Habitat characteristics of late wintering areas used by woodland caribou (Rangifer tarandus caribou) in northeastern Ontario*. M.Sc. thesis, Laurentian University, Sudbury, Ontario. 134pp.
- Zar, J.H. 1974. *Biostatistical Analysis*. Englewood Cliffs: Prentice-Hall Incorporated. 620pp.

Appendix 1. Cranial, mandibular and dental measurements ( $n = 45$ ) taken from *C. lupus* skulls.

No.	Abbrev.	Description
1	Condy L	Condylobasal length (from premaxilla to occipital condyle)
2	I <sup>1</sup> -SagC	Maximum length from premaxilla to sagittal crest posterior
3	Nasal L	Maximum length of nasals
4	I <sup>1</sup> -Palat	Palatal length from alveolar of I <sup>1</sup>
5	I <sup>2</sup> -Palat	Palatal length from alveolar of I <sup>2</sup>
6	PosPal	Post palatal length
7	C <sup>1</sup> to M <sup>2</sup>	Crown length of upper cheek teeth from C to M <sup>2</sup>
8	W to C <sup>1</sup>	Maximum anterior-posterior width of upper canine at base
9	W to P <sup>4</sup>	Maximum buccolingual width of P <sup>4</sup> at enamel line
10	L of P <sup>4</sup>	Maximum anterior-posterior length of P <sup>4</sup> at enamel line
11	W of M <sup>1</sup>	Buccolingual width of M <sup>1</sup> at enamel line (at major cusp)
12	L of M <sup>1</sup>	Maximum anterior-posterior length of M <sup>1</sup> at enamel line
13	W of M <sup>2</sup>	Crown width of M <sup>2</sup>
14	I <sup>3</sup> to I <sup>3</sup>	Crown width across upper incisors
15	P <sup>1</sup> to P <sup>1</sup>	Minimum width between alveoli of P <sup>1</sup>
16	P <sup>2</sup> to P <sup>2</sup>	Palatal width inside the second upper premolars (at hollow)
17	C <sup>1</sup> to C <sup>1</sup>	Width of skull across outside of upper canines
18	M <sup>1</sup> to M <sup>1</sup>	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	CondyL W	Maximum width of long axis of left condyle
24	CondyL 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 <sup>1</sup> to Orb	Minimum distance from alveolar margin of M <sup>1</sup> 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 <sup>1</sup> to M <sup>3</sup>	Maximum crown length from C <sup>1</sup> anterior to M <sup>3</sup>
37	W of P <sup>4</sup>	Buccolingual width of P <sup>4</sup>
38	L of P <sup>4</sup>	Anterior-posterior length of P <sup>4</sup>
39	W of M <sup>1</sup>	Buccolingual width of M <sup>1</sup>
40	L of M <sup>1</sup>	Anterior-posterior length of M <sup>1</sup>
41	Mandib W	Width of mandible at P <sup>4</sup>
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 <sup>4</sup> and M <sup>1</sup>
45	AngP - CorP	Distance from angular process to top of coronoid process

