MASS, MORPHOLOGY, AND GROWTH RATES OF MOOSE IN NORTH DAKOTA

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ABSTRACT: This paper provides predictive formulas to estimate live weights of moose (Alces alces andersoni) from hunter-harvested animals and evaluate growth rates of moose in North Dakota, and reviews weight-related measurements among moose populations. From 1978–1990, morphometric data were collected on 224 hunter-killed moose harvested after the rut (10 November-12 December) in North Dakota. Body mass increased rapidly for both sexes from 0.5 years to 1.5 years-of-age. Whole weight and total body length reached an asymptote for both sexes by 5.5 years; mean whole weight appeared to decline among older individuals. Although field dressed weight was the best predictor of whole weight ($r^2 = 0.93$; n = 154), total body length provided reasonably good estimates of whole weight ($r^2 = 0.76$; n = 153). Whole weight estimates based upon shoulder height ($r^2 = 0.33$; n = 158) and hind-foot length ($r^2 = 0.46$; n = 163) were less reliable. We also used morphometric variables to predict field dressed weight, carcass weight, and visceral weight. Field dressed weight was the best predictor of antler width ($r^2 = 0.72$; n = 108) and antler width was a good predictor of male age $(r^2 = 0.70; n = 119)$. When compared to other North American populations, average weights of moose harvested in North Dakota tended to be higher in all age classes. Additionally, the calf-to-yearling growth rate of female moose in North Dakota was as high, or higher than in other populations. Morphometric comparisons of free-ranging moose from various North American populations had much size overlap, with southern and eastern moose populations tending to have largest average adult body mass. Sexual dimorphism of mature North Dakota moose (> 4.5 years) was comparable to that in other populations.

ALCES VOL. 49: 1-15 (2013)

Key words: Alces alces, body mass, morphometrics, sex, age, growth rates, North Dakota.

Body weights and measurements of cervids provide insight on condition and health of local populations (Clutton-Brock et al. 1982, Sauer 1984, Verme and Ullrey 1984, Loudon 1987). They allow for the analysis of energetic requirements, energetic capability, and other metabolic parameters (Schwartz et al. 1987), and how subspecies vary in size, shape, and rate of growth (Bubenik 1998, Geist 1998). Comparative morphometric data on North American moose (*Alces alces*) are limited (Blood et al. 1967, Timmerman 1972, Schladweiler and Stevens 1973, Peterson 1974, Franzmann et al. 1978, Crichton 1980, Adams and Pekins 1995, Lynch et al. 1995, Broadfoot et al. 1996). Additionally, measurement and definition of morphometric variables vary among studies making comparisons among populations problematic. Difficulties in accessing hunter-killed moose, and the physical labor involved in handling these animals have undoubtedly limited data collection.

Historically, moose in North Dakota were restricted to the heavily forested areas of the Turtle Mountains, Pembina Hills, and the major tributaries of the Red River. Accounts of early traders in the area indicated that they were not as abundant as elk (Cervus elaphus) or other big game species, and apparently disappeared from the state during the early 20th century (Knue 1991). By the 1960s, moose had returned to North Dakota and small numbers were occupying portions of their historic range. In 1977, the first modern moose hunting season allowed the harvest of 10 moose in Cavalier, Pembina, and Walsh Counties. The expansion of moose into the relatively accessible farmland of North Dakota, coupled with the willingness of local farmers to assist hunters with loading and transporting animals with farm equipment, made it feasible for the North Dakota Game and Fish Department (NDGFD) to collect morphometric data. We provide analyses of 1) age and sex-specific weights and measurements, 2) measurement-weight relationships, 3) age and morphometric relationships, and 4) growth rates of hunter-killed moose from North Dakota. Our goal is to provide predictive formulas for estimating whole, field-dressed, carcass, and viscera weights of hunter-killed moose and to make comparisons with other North American and European populations.

METHODS

Morphometric data were collected on 224 hunter-killed moose examined between 1978 and 1990. Hunters were asked whenever possible to bring their moose in whole to a check station (i.e., prior to removal of viscera, hide, head, or legs). All moose were harvested between 10 November and 12 December after the rutting season; date of kill, sex, and legal descriptions (section, township, range) for all kill sites were recorded. The distribution of the animals examined was between 47.10 and 48.99° N and 97.14 and 100.41° W (Fig. 1). Moose hunting units M1C and M4 are comprised primarily of aspen (*Populus* spp.) forests with intermingled cropland; the remainder of the harvest area was drift prairie with heavy conversion to cropland (Fig. 1). For a more complete description of habitat see Maskey (2008).

Weight was measured with local grain elevator scales with an accuracy of ± 4.5 kg. Recorded weights were whole weight (WW) which comprised a completely intact carcass except for loss of blood and tissue resulting from gunshot wounds; field dressed weight (FDW) which included carcass weight minus all thoracic and abdominal viscera; viscera weight (VW) which included all thoracic and abdominal organs and their contents including blood and the contents of the digestive system; and carcass weight (CW) which comprised the dressed carcass minus the head, hide, and legs below the hock joint.

Length was measured (nearest cm) before the moose was dressed-out following the methods of Peterson (1974). With the carcass laid flat on its side, with head and spinal column supported on the same plane, total body length (TBL) was measured from tip of nose to tip of tail (point of last coccyx bone, excluding hair) by following the dorsal (spinous) processes of the vertebra. With the carcass laid flat on its side and the front leg positioned so that it was straight and perpendicular to the longitudinal axis of the body, hind-foot length (HFL) was measured from the calcaneum (heel bone of hock) to the tip of hoof, and shoulder height (SH) from the superior angle of the scapula (cartilaginous top of shoulder) to the distal tip of the front hoof. Antler width (AW) was measured at the greatest spread between the tines and at a right angle to the longitudinal axis of the skull. Prior to additional analyses, we



Fig. 1. Locations of 224 moose harvested in North Dakota, USA (1978–1990). Each dot represents the site, to the nearest section, where ≥ 1 moose were harvested.

used t-tests to determine whether any morphometric measurements differed between male and female moose of all ages. Whole weight, FDW, CW, VW, and AW were compared to other morphometric measurements using simple linear regressions. All statistical analyses were conducted using R, version 2.11.1 (R Development Core Team 2010).

Incisor eruption (Peterson 1955) was used to identify young-of-the-year or calves (≤ 6 month-of-age) and front incisors were collected from moose ≥ 6 months of age for cementum annuli analysis (Gasaway et al. 1978, Haagenrud 1978). Ageing was performed by Matson's Laboratory, Milltown, MT, and by co-author R. Johnson (NDGFD) after 1980. The relationship between each morphometric variable and age was examined with linear regression using square-roottransformed age as the dependent variable; to facilitate utility, we present backtransformed equations in Results.

Growth rates for moose have been described as falling into 3 phases: 1) a selfaccelerated phase (Schwartz 1998) of near exponential growth from birth to weaning (4–6 months old) allowing the calf to follow its mother over rough terrain and obstacles (Geist 1998), 2) a second phase of rapid growth from calf to yearling (16-18 months old) allowing young moose to reach a body size (250-280 kg WW) that allows yearlings to confront predators (Geist 1998), and 3) a self-inhibiting growth phase where seasonal peaks and troughs in body mass occur at different times for males and females (Schwartz et al. 1987). Results and discussion focus on these 3 growth phases.

Healthy North American moose calves have a mean birth weight ranging from

12.6-18 kg for single calves (Kellum 1941 in Peterson 1955, Franzmann et al. 1980, Schwartz 1998) and 13.6 kg for twins (Franzmann 1978). The mean weight for 1-3 day-old Alaskan calves was 18.0 kg (n = 109; Franzmann et al. 1980). Average weights of captured calves < 2 weeks old in Ontario averaged 15.7 kg (n = 8) for females and 17.3 kg (n = 10) for males (Addison et al. 1994). The average weight of 43 captured neonate calves in Alberta was 19.6 kg; however, some were captured as late as August (Welch et al. 1985). Lacking information on birth weights for North Dakota moose, we used the range of 13-18 kg as the basis for calculating phase 1 growth rates. We determined percent change of growth rate during phase 1 by dividing calf weight at 0.5 years by the neonate weights of 13 and 18 kg, and we estimated the percent change during phase 2 by dividing the average yearling (1.5 years) weight by the average calf weight.

We measured the level of sexual dimorphism for moose \geq 4.5 years old. Only these moose were included because they would be at or near their maximum size and this age range would best permit comparison to other studies. We calculated dimorphic ratios (male:female) for WW, FDW, CW, VW, TBL, HFL, and SH. We also used t-tests to examine whether these measures differed significantly between males and females \geq 4.5 years old.

RESULTS

Morphometric Measurements

Sample sizes for WW, FDW, VW, and CW were obtained from 160, 166, 146, and 40 moose, respectively (Tables 1 and 2). Sample sizes for TBL, HFL, SH, and AW were obtained from 206, 196, 200, and 121 moose, respectively (Tables 3 and 4). Antler width appeared to plateau at 6.5 years and then decline in older males (Table 4).

Morphometric Relationships

Morphometric measurements were not significantly different for males and females of all ages. Therefore, we combined sexes when conducting regression analyses for these variables. Whole weight was best predicted by FDW ($r^2 = 0.93$, n = 154), followed by TBL ($r^2 = 0.76$, n = 153); FDW was best predicted by TBL ($r^2 = 0.70$, n = 181) and CW ($r^2 = 0.65$, n = 39). Antler width was most highly correlated with FDW $(r^2 = 0.72, n = 108)$. All regression equations for predicting WW, FDW, CW, VW, and AW are provided in Table 5. Age was best predicted by WW ($r^2 = 0.71$, n = 114), followed by FDW ($r^2 = 0.70$, n = 166; Table 6). Antler width was also a reasonable estimator of male age ($r^2 = 0.70$, n = 119; Table 6).

Growth Rates and Patterns

During phase 1, both post-rut male and female calves averaged 196 kg at about 7 months of age, representing a 989–1455% increase in body mass. The average growth rate would be 1% per day assuming a mean age of about 180 days, given a 1 December harvest date. The FDWs of female and male calves were 61 and 72% of WW; FDW of yearling females and males were 73 and 70%, respectively.

During growth phase 2, female and male calves (averaging 196 kg at 6–7 months) increased their WW over the next year by 69 and 65%, respectively. The FDW during phase 2 increased by 102 and 59.3% for females (n = 10) and males (n = 32), respectively (Table 7). The FDWs of female and male calves were 61 and 72% of WW; FDW of yearling females and males were 73 and 70%, respectively. Whole weights, FDW, and TBL plateaued at 5.5 years for both males and females during the self-inhibiting growth phase (Tables 1–4).

Age	Whole Weight (kg)				Field Dressed Weight (kg)			Viscera Weight (kg)			Carcass Weight (kg)		
	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range	
0.5 years	5	196.0 ± 21.6	176.9-226.8	4	119.1 ± 30.2	77.1–145.1	4	73.3 ± 21.1	54.4-99.8	2	127.7 ± 54.5	86.2-163.3	
1.5 years	12	331.1 ± 44.1	272.2-444.5	10	241.1 ± 26.9	204.1-290.3	10	94.6 ± 25.1	68.0–154.2	2	195.0 ± 19.2	181.4-208.7	
2.5 years	5	366.5 ± 20.9	331.1-385.6	6	255.8 ± 12.5	240.4–272.2	5	109.5 ± 17.0	84.8-127.0	4	197.3 ± 14.7	179.2–211.4	
3.5 years	11	410.3 ± 50.9	349.3-526.2	12	285.4 ± 36.5	229.1-358.3	10	158.1 ± 27.6	95.3-172.4	1	281.2	281.2	
4.5 years	2	437.7 ± 22.5	421.8-453.6	3	323.6 ± 42.1	294.8-371.9	2	138.3 ± 16.0	127.0-149.7	1	231.3	231.3	
5.5 years	5	467.2 ± 39.9	417.3-512.6	5	330.7 ± 29.8	292.6-371.9	5	136.5 ± 30.5	90.7-167.8	1	220.0	220	
6.5 years	2	437.7 ± 60.9	394.6-480.8	3	310.0 ± 15.9	294.8-326.6	2	127.0 ± 38.5	99.8-154.2	1	226.8	226.8	
7.5 years	2	435.4 ± 25.7	417.3-453.6	2	310.7 ± 22.5	294.8-326.6	2	124.7 ± 3.2	122.5-127.0	1	239.5	239.5	
8.5 years	3	444.5 ± 64.0	385.6-512.6	3	319.0 ± 41.2	281.2-362.9	3	125.5 ± 22.8	104.3-149.7	0			
10.5 years	1	489.9	489.9	1	335.7	335.7	1	154.2	154.2	0			
≥ 1.5 years	43	397.7 ± 64.9	272.2-526.2	45	285.3 ± 43.2	204.1-371.9	40	127.5 ± 59.2	68.0-172.4	11	216.2 ± 29.1	179.2-281.2	

Table 1. Age-weight relationship for female moose harvested in North Dakota, USA (1978-1990).

Table 2.	Weight categories	(see Methods)	by age	for male moose	harvested in	North Dakota	USA (1978	3-1990).
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	Whole Weight (kg)				Field Dressed We	ight (kg)	Viscera Weight (kg)				Carcass Weigh	nt (kg)
Age	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range
0.5 years	5	196.0 ± 34.3	140.6-226.8	4	141.7 ± 5.7	136.1–149.7	4	68.0 ± 12.3	49.9-77.1	0		
1.5 years	27	323.6 ± 31.4	249.5-403.7	32	225.7 ± 24.5	181.4–290.3	27	96.3 ± 18.5	63.5-163.3	6	177.9 ± 24.4	147.4–207.3
2.5 years	35	402.3 ± 43.3	290.3-485.3	35	292.2 ± 26.7	217.7-349.3	30	119.1 ± 18.9	68.0–158.8	8	219.5 ± 37.9	158.8-281.2
3.5 years	22	446.3 ± 40.4	335.7-503.5	22	322.5 ± 30.1	254.0-367.4	20	121.8 ± 17.9	77.1–154.2	5	236.9 ± 32.2	195.0-270.8
4.5 years	8	444.1 ± 30.1	408.2-499.0	9	320.0 ± 36.6	272.2-381.0	8	123.6 ± 201	90.7-154.2	2	246.5 ± 4.8	243.1-249.9
5.5 years	7	496.6 ± 60.1	408.2–589.7	7	365.5 ± 22.0	340.2-408.2	6	141.7 ± 34.6	95.3-181.4	4	257.3 ± 26.3	235.0-295.3
6.5 years	7	479.5 ± 51.4	403.7-535.2	6	352.3 ± 33.5	303.9–394.6	6	121.0 ± 27.8	99.8-172.4	2	318.2 ± 88.8	255.4-381.0
7.5 years	0			1	349.3	349.3	0			0		
9.5 years	1	453.6	453.6	1	335.7	335.7	1	117.9	117.9	0		
\geq 1.5 years	107	430.6 ± 69.2	249.5-589.7	113	311.7 ± 53.3	181.4-408.2	98	121.0 ± 24.1	63.5–181.4	27	245.5 ± 62.4	158.8-381.0

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Range	HOT
43.0–164.0	ÔG
57.5-185.2	ΥC
77.3–184.9	FZ
79.8–197.3	NOR
82.9-194.7	HLD
85.0-206.8	D∕
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Table 3.	Morphological	measurements	of female m	oose harvested	in North	Dakota,	USA	(1978–1990).	
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		Total Body Length	(cm)		Hind Foot Length ((cm)		Shoulder Height (cm)				
Age	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range			
0.5 years	5	203.8 ± 12.2	190.0-219.7	5	71.0 ± 2.9	68.0-76.2	4	151.8 ± 9.7	143.0–164.0			
1.5 years	13	248.5 ± 10.3	236.5-265.0	13	77.0 ± 2.6	71.1-81.9	13	175.5 ± 6.8	157.5-185.2			
2.5 years	8	248.2 ± 10.4	232.0-264.7	6	77.9 ± 2.2	74.8-81.0	8	181.2 ± 4.7	177.3–184.9			
3.5 years	15	257.5 ± 17.5	214.0-279.2	14	79.2 ± 3.4	74.1-86.1	15	188.2 ± 5.2	179.8–197.3			
4.5 years	3	271.2 ± 7.7	266.1-280.0	3	79.0 ± 0.6	78.3-79.4	3	190.6 ± 6.7	182.9-194.7			
5.5 years	5	273.2 ± 10.6	259.7-286.1	5	79.4 ± 2.4	77.4-82.9	5	193.4 ± 9.9	185.0-206.8			
6.5 years	3	267.3 ± 5.0	263.6-272.9	3	80.7 ± 1.5	79.2-82.1	3	192.8 ± 0.4	192.4–193.1			
7.5 years	2	263.1 ± 4.0	260.2-265.9	2	81.7 ± 1.2	80.8-82.5	2	190.9 ± 9.7	184.0-197.7			
8.5 years	3	267.4 ± 12.1	255.2 279.4	3	77.9 ± 2.1	75.9-80.0	3	192.3 ± 7.2	188.4–200.6			
10.5 years	1	261.1	261.1	1	80.3	80.3	1	189.1	189.1			
≥ 1.5 years	53	257.5 ± 14.8	214.0-286.1	50	78.6 ± 2.8	71.1-86.1	53	157.5 ± 206.8	157.5-206.8			

Table 4. Morphological measurements of male moose harvested in North Dakota, USA (1978-1990).

	Total Body Length (cm)			Hind Foot Length (cm)			Shoulder Height (cm)			Antler Width (cm)		
Age	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range	n	Mean (± SD)	Range
0.5 years	6	201.4 ± 14.0	176.0-215.0	6	70.6 ± 2.5	66.0-73.5	6	153.0 ± 8.0	141.0-161.5	1	23.5	23.5
1.5 years	40	244.5 ± 11.9	218.0-272.3	38	77.7 ± 2.6	72.2-82.1	38	179.7 ± 7.1	167.5–194.5	28	69.9 ± 10.7	53.3-92.3
2.5 years	48	258.0 ± 12.9	227.0-288.3	46	80.0 ± 3.2	68.9-85.5	46	187.9 ± 9.4	162.0-203.5	40	89.1 ± 11.5	66.4–125.1
3.5 years	26	267.7 ± 13.9	240.0-295.3	26	81.0 ± 2.9	75.0-86.6	26	191.5 ± 8.4	176.0-206.3	26	100.1 ± 9.5	84.4-129.9
4.5 years	9	269.9 ± 9.4	257.5-282.8	7	80.1 ± 2.8	76.2-84.5	9	188.8 ± 6.3	181.0-200.5	9	107.1 ± 14.9	81.3-128.9
5.5 years	9	277.7 ± 12.9	258.0-295.9	9	82.7 ± 1.5	79.1-84.5	9	198.8 ± 6.4	189.0-205.8	9	122.8 ± 8.5	104.8-134.6
6.5 years	7	272.6 ± 12.8	255.9-289.4	7	79.2 ± 2.9	76.4-84.9	7	193.6 ± 13.1	178.5-219.7	7	128.6 ± 23.7	99.8–168.3
7.5 years	1	273.0	273.0	0			0			1	125.7	125.7
8.5 years	1	270.9	270.9	1	82.3	82.3	1	206.4	206.4	1	109.8	109.8
9.5 years	1	274.0	274.0	1	80.0	80.0	1	207.8	207.8	0		
≥ 1.5 years	142	259.0 ± 16.3	218.0-295.9	135	79.7 ± 3.1	68.9-86.6	137	187.7 ± 10.2	162.0-219.7	121	93.6 ± 21.0	53.3-168.3

Comparison	n	Equation	r^2
Whole Wt. (WW) (kg) vs. Field Dressed Wt.(FDW) (kg)	154	$WW = (FDW \times 1.28) + 35.5$	0.93
Whole Wt. (WW) (kg) vs. Carcass Wt. (CW) (kg)	39	$WW = (CW \times 1.47) + 67.3$	0.75
Whole Wt. (WW) (kg) vs. Viscera Wt. (VW) (kg)	156	$WW = (VW \times 2.41) + 119.8$	0.65
Whole Wt. (WW) (kg) vs. Total Body Length (TBL) (cm)	153	$WW = (TBL \times 0.36) - 520.2$	0.76
Whole Wt. (WW) (kg) vs. Shoulder Height (SH) (cm)	158	$WW = (SH \times 0.24) - 49.1$	0.33
Whole Wt. (WW) (kg) vs. Hind-Foot Length (HFL) (cm)	163	$WW = (HFL \times 1.51) - 802.8$	0.46
Field-dressed Wt. (FDW) (kg) vs. Carcass Wt. (CW) (kg)	39	$FDW = (CW \times 0.84) + 104.4$	0.65
Field-dressed Wt. (FDW) (kg) vs. Viscera Wt. (VW) (kg)	146	$FDW = (VW \times 1.41) + 119.7$	0.40
Field-dressed Wt. (FDW) (kg) vs. Total Body Length (TBL) (cm)	181	$FDW = (TBL \times 0.26) - 387.8$	0.70
Field-dressed Wt. (FDW) (kg) vs. Shoulder Height (SH) (cm)	165	$FDW = (SH \times 0.17) - 41.0$	0.31
Field-dressed Wt. (FDW) (kg) vs. Hind-Foot Length (HFL) (cm)	174	$FDW = (HFL \times 0.11) + 196.4$	0.03
Carcass Wt. (CW) (kg) vs. Viscera Wt. (VW) (kg)	32	$CW = (VW \times 1.14) + 93.6$	0.56
Carcass Wt. (CW) (kg) vs. Total Body Length (TBL) (cm)	47	$CW = (TBL \times 0.18) - 236.3$	0.33
Carcass Wt. (CW) (kg) vs. Shoulder Height (SH) (cm)	40	$CW = (SH \times 0.24) + 231.0$	0.37
Carcass Wt. (CW) (kg) vs. Hind-Foot Length (HFL) (cm)	46	$CW = (HFL \times 0.013) + 207.8$	0.001
Viscera Wt. (VW) (kg) vs. Total Body Length (TBL) (cm)	156	$VW = (TBL \times 0.09) + 0.011$	0.40
Viscera Wt. (VW) (kg) vs. Shoulder Height (SH) (cm)	147	$VW = (SH \times 0.05) + 22.7$	0.14
Viscera Wt. (VW) (kg) vs. Hind-Foot Length (HFL) (cm)	156	$VW = (HFL \times 0.36) - 173.3$	0.22
Antler Width (AW) (cm) vs. Whole Wt. (WW) (kg)	97	$AW = (WW \times 2.57) - 137.2$	0.65
Antler Width (AW) (cm) vs. Field-Dressed Wt. (WW) (kg)	108	$AW = (FDW \times 3.46) - 102.0$	0.72
Antler Width (AW) (cm) vs. Total Body Length (TBL) (cm)	129	$AW = (TBL \times 0.81) - 1183.0$	0.37
Antler Width (AW) (cm) vs. Shoulder Height (SH) (cm)	116	$AW = (SH \times 0.39) + 198.8$	0.13
Antler Width (AW) (cm) vs. Hind-Foot Length (HFL) (cm)	125	$AW = (HFL \times .024) + 901.0$	< 0.001

Table 5. Simple regression equations for weight-measurement relationships among moose from North Dakota, USA (1978–1990).

Table 6. Regression equations for age-measurement relationships among moose from North Dakota, USA (1978–1990).

Comparison	n	Equations	r^2
Age vs. Whole Weight (WW) (kg)	114	Age = $((WW \times 0.0043)066)^2$	0.71
Age vs. Field Dressed Wt. (FDW) (kg)	166	Age = $((FDW \times 0.06) + 0.022)^2$	0.70
Age vs. Carcass Wt. (CW) (kg)	39	Age = $((CW \times 0.007) + 0.098)^2$	0.53
Age vs. Viscera Wt. (VW) (kg)	145	Age = $((VW \times 0.01) + 0.51)^2$	0.39
Age vs. Total Body Length (TBL) (cm)	203	Age = $((TBL \times 0.0014) - 0.21)^2$	0.53
Age vs. Shoulder Height (SH) (cm)	197	Age = $((SH \times 0.0011) - 0.47)^2$	0.26
Age vs. Hind-Foot Length (HFL) (cm)	153	Age = $((HFL \times 0.00035) + 1.31)^2$	0.014
Age vs. Antler Width (AW) (cm)	119	Age = $((AW \times 0.0016) + 0.26)^2$	0.70

Sexual Dimorphism

Moose \geq 4.5 years old had a sexual dimorphism ratio of 1.04 for WW ($\bar{x} = 485.8$ kg for males [n = 15] and 452.1 kg for females [n = 15]), and 1.07 for FDW ($\bar{x} = 357.2$ kg for males [n = 15] and 321.7

kg for females [n = 17]; Table 8). These ratios were mid-range in comparison with other studies where weight dimorphism for WW and FDW ranged from 0.90–1.19 and 0.70–1.36, respectively (Table 9). Although measurements for male moose were larger for all but

	•				0			
			Females			Males		
Location	Subspecies	Calf FDW (kg) [N]	Yearling FDW (kg) [N]	Change	Calf FDW (kg) [N]	Yearling FDW (kg) [N]	Change	Source
North Dakota	A. a. andersoni	119.1 [4]	241.1 [10]	102.4%	141.7 [4]	225.7 [32]	59.3%	This study
Vermont, New Hampshire, and Maine	A. a. andersoni	108 [23]	216 [65]	100 %	112 [23]	199 [139]	77.7%	Adams and Pekins (1995)
Quebec	A. a. americana	108.6 [26]	192.6 [11]	77.3%	119.6 [19]	199.3 [24]	66.6%	Heyland (1964) in Peterson (1974)
Quebec		108.6 [26]	203.4 [34]	87.3%	119.6 [19]	204.3 [51]	70.8%	Heyland (1966) in Peterson (1974)
Ontario	A. a. andersoni	156.5 [3]	230.9 [7]	47.5%	140.2 [7]	254.5 [19]	81.2%	Timmerman (1972)
Ontario	A. a. andersoni	75.3 [1]	220.9 [2]	193.4%	115.2 [1]	240.4 [1]	108.7%	Simkin (1962)
Ontario	A. a. andersoni		136.3 [3]			228.9 [5]		Broadfoot et al. (1996)
Manitoba	A. a. andersoni		163.3 [1]			205.8 [4]		Crichton (1980), and Pers. Comm.
Alberta	A. a. andersoni	93.9 [27]	161.9 [28]	72.4%	95.3 [21]	152.9 [34]	60.4%	Blood et al. (1967)
Montana	A. a. shirasi	84.4 [14]	163.3 [15]	93.5%	99.3 [14]	170.6 [28]	71.8%	Schladweiler and Stevens (1972)
Norway, Southern	A. a. alces	69.8 [74]	140.2 [115]	100.9%				Saether et al. (1996)
Norway, Interior	A. a. alces	68.5 [298]	139.8 [210]	104.1%				Saether et al. (1996)
Norway, Alpine	A. a. alces	63.2 [625]	125.1 [370]	97.9%				Saether et al. (1996)
Norway, Northern	A. a. alces	72.9 [7]	146.0 [122]	100.3%				Saether et al. (1996)
Norway, Interior Norway, Alpine Norway, Northern	A. a. alces A. a. alces A. a. alces	68.5 [298] 63.2 [625] 72.9 [7]	139.8 [210] 125.1 [370] 146.0 [122]	104.1% 97.9% 100.3%				Saether et al. (1996) Saether et al. (1996) Saether et al. (1996)

Table 7. Comparisons of mean field dressed weight (FDW) of calves and percent change from calf (0.5 years) to yearling (1.5 years) age classes from 7 North American and
northern European moose populations. Note: Broadfoot et al. (1996) used moose of 11 months of age.

Measurement	Sexual Dimorphism	t	Degrees of Freedom	Р
Whole Weight (WW)	1.04	1.3	34	0.21
Field-dressed Weight (FDW)	1.07	2.2	38	0.03
Carcass Weight (CW)	1.27	2.4	8	0.04
Viscera Weight (VW)	0.93	1.1	28	0.27
Total body Length (TBL)	1.02	1.5	40	0.13
Hind-foot Length (HFL)	1.0	0.11	29	0.91
Shoulder Height (SH)	1.16	1.5	28	0.14

Table 8. Sexual dimorphism for 7 morphometric measurements and results of t-tests comparing these measurements between sexes for moose ≥4.5 years old from North Dakota, USA (1978–1990).

VW and HFL, only FDW and CW differed significantly between sexes (Table 8).

DISCUSSION

General Observations

Field dressed weights were the best estimator of WW, although reliable estimates of WW were also obtained using TBL and SH (Table 5). For all sexes the best estimate of age was WW followed by FDW, and AW was also a good estimator of male age (Table 6). Therefore, we suggest that collection of baseline data in local populations focus on FDW, TBL, AW, and incisor collection. Although age can be reasonably predicted by AW for males, and WW and FDW for moose of both sexes, cementum annuli aging remains the most accurate method for determining age. Further, CW and TBL appear to be fairly good predictors of FDW, while other measurements have limited use in estimating FDW (Table 5). Carcass weight and VW were poorly predicted by morphometric measurements (Table 5). Our results also indicate that WW of both sexes can range about $\pm 20\%$ of the mean within an age class. Schwartz et al. (1987) reported overwinter weight loss can range from as little as 7% to as high as 23% of pre-rut body mass; thus, weights of individual moose in fallearly winter that are >20% below the local population average of an age class may indicate nutritional stress or other health concerns such as parasite infection.

Several authors have estimated the relationship between FDW and WW with varying results. In our study the slope of the regression between FDW and WW was 1.28 for both sexes combined (Table 5) which was similar to that in studies with a combined relationship for both sexes. For example, Peterson (1974) and Crichton (1980) calculated slopes of 1.28 and 1.31 for both sexes. Other authors have reported varying results for the relationship between WW and FDW. Blood et al. (1967) estimated an overall carcass yield of 50% (1.50) for all ages, and similarly, Schladweiler and Stevens (1973) estimated WW:FDW ratios of 1.43 for adult females and 1.33 for adult males, and Broadfoot et al. (1996) estimated 1.51 for females and 1.48 for males for 11-month old captive moose.

Other researchers have developed estimators of WW based on a variety of morphometric measurements. Franzmann et al. (1978) developed equations for estimating WW from TBL, chest girth, HFL, and SH, and Wallin et al. (1996) focused on chest circumference to estimate carcass body mass of moose in Sweden after removal of head, skin, lower legs, kidneys, and viscera. Because the methods and outcome of analyses have varied substantially among studies, we suggest that when comparing FDW and WW between populations, eliminate as many biases as possible (e.g., sex, age, and

Table 9. Comparisons of sexual dimorphism based on mean field dressed weight (FDW) and mean whole weight (WW) for adult females and males (≥4.5 years) from various moose populations in North America. * Note: Some references did not permit calculating weight using these age criteria. Therefore, weights for Quinn and Aho (1989) were for mature animals aged as wear class VI (>6.5 years), Schladweiler and Stevens (1973) were for mature animals aged as wear class V (>5.5 years), Blood et al. (1967) and Franzmann et al. (1978) includes animals >3.5 years, Geist (1998) included animals >4.5 years, and Franzmann et al. (1987) were 5 year-old captive animals.

		Females	Males		Females	Males		
Location	Subspecies	FDW (kg) [n]	FDW (kg) [n]	FDW Sexual Dimorphism	WW (kg) [n]	WW (kg) [n]	WW Sexual Dimorphism	Source
North Dakota	A. a. andersoni	321.7 [17]	343.2 [24]	1.07	452.1 [15]	471.3 [23]	1.04	This study
Quebec	A. a. americana	267.3 [156]	348.0 [224]	1.30				Heyland (1964, 1966) in Peterson (1974)
Vermont, New Hampshire, and Maine	A. a. americana	261.9 [76]	342.8 [251]	1.31				Adams and Pekins (1995)
Ontario	A. a. andersoni	301 [5]	408 [10]	1.36				Timmerman (1972)
Ontario	A. a. andersoni	285.0 [3]	360.0 [2]	1.26				Simkin (1962)
Ontario	A. a. andersoni				461.0 [17]	496.0 [9]	1.07*	Quinn and Aho (1989)
Manitoba	A. a. andersoni	281.2 [7]	308.4 [13]	1.10	400.7 [3]	461.7 [8]	1.15	Crichton (1980)
Alberta	A. a. andersoni	205.0 [55]	220.0 [39]	1.07*	417.0 [6]	413.2 [3]	0.99*	Blood et al. (1967)
Alberta	A. a. andersoni				413.0 [32]	456.0 [30]	1.10*	Geist (1998)
Alberta	A. a. andersoni				412.4 [32]	461.1 [23]	1.12	Lynch et al. (1995)
Montana	A. a. shirasi	214.3 [29]	269.0 [35]	1.25*				Schaldweiler and Stevens (1973)
Alaska	A. a. gigas				400.5 [66]	454.6 [5]	1.14*	Franzmann et al. (1978)
Alaska	A. a. gigas				499.0 [3]	594.0 [3]	1.19*	Franzmann et al. (1978)

10

conversions to WW from FDW and morphometric measurements), and make only direct comparisons such as FDW and WW.

Growth Rates and Weights of North Dakota Moose

Our estimates of phase 1 growth rates were similar to that of Schwartz (1998) who estimated a phase 1 accelerated growth of 1.3-1.6% per day for calves <165 days old (pre-rut). Our rates were higher than those reported by Addison et al. (1994) for captive calves with neonatal weights of 15.7 kg (n = 8) and 17.3 kg (n = 10) for females and males, respectively. At 187 days, or approximately 6 months old, their females averaged 149.2 kg (n = 6) and males 165.8 kg (n = 9), representing a 950 and 958% increase in mass, respectively. In short, during phase 1, North American moose display an impressive rate of growth of $\sim 1000\%$ within a 6 month period.

During growth phase 2, our female calves appeared to grow faster than male calves (Tables 1 and 2), particularly when comparing FDW. This was also true for 5 of the 6 North American populations where similar comparisons could be made (Table 7), suggesting that a larger proportion of body mass is being devoted to skeletal and muscle development at an earlier age in males. This additional skeletal and muscle mass may provide a selective advantage for male calves as they are often driven from their mother by courting males during the rut and must briefly survive alone.

During the third (self-inhibiting) growth phase when body mass goes through seasonal peaks and troughs, the maximum weights for females and males occur midwinter and prerut, respectively (Schwartz et al. 1987). Body weight of North American female moose appears to plateau at 3–4 years (Geist 1998), whereas weight of male moose plateaus at 5 years (Peterson 1974). We found that both male and female weights peaked at 5.5 years (Tables 1 and 2). While sample sizes were small, TBL also appeared to plateau at 5.5 years in North Dakota (Tables 3 and 4), which was similar as reported for Alaskan moose (Franzmann et al. 1978). Comparative data are lacking, but these results suggest that North Dakota moose with access to highly nutritious agricultural crops may maximize body weight earlier and continue to grow structurally longer than other moose populations.

Additional Observations about Moose Growth Rates

In 6 of the 7 populations in which comparisons could be made, female calves weighed $\geq 5\%$ less than male calves (Table 7). The exception (Timmermann 1972) where female calves weighted >10% more than males may be an artifact of small sample size (n = 3 female calves). Overall, FDW of North American female and male calves averaged 101.4 kg (n = 69), and 112.0 kg (n = 61), respectively (Table 7). Estimates of WW from FDW using various correction factors are relatively common in the literature. However, actual WW of North American female and male moose calves in the literature are limited to Blood et al. (1967), Lynch et al. (1995), and this study. The average WW of female and male calves was 174 kg (n = 4) and 197 kg (n = 5) in Alberta (Blood et al. 1967), and 171 kg (n = 12) and 197 kg (n = 13) in Ontario (Lynch et al. 1995). We found that WW for female and male calves were identical, but male FDW appears to be higher. In short, the available data suggests that either maternal moose invest more resources in their male calves, or there is a selective advantage for male calves to develop greater muscle mass at an early age.

During growth phase 2, 5 of 8 populations previously described (Table 7) had heavier mean FDW for yearling males, but North Dakota female yearlings grew at a faster rate than most. During this phase, female yearlings are more likely to remain in loose association with their mother during subsequent calving, while male yearlings disperse and are likely at relative disadvantage. Overall, FDW of North American female and male yearlings averaged 202.2 kg (n = 155), and 199.1 kg (n = 313), respectively. Based upon the FDW versus WW proportions for North Dakota moose (Tables 1 and 2), the mean WW of North American female and male moose yearlings would average 278 and 285 kg, respectively. During this growth phase, Geist (1998) suggested that a solitary moose must be at least 250 kg to confront predators, basing his assumption on the size of adult Ussuri or "dwarf" moose of Manchuria (A. a. cameloides) (Heptner and Nasimovitch 1967, p. 72 in Geist 1998). Whole weights of North Dakota moose and data on FDW we provide from other studies (Table 9) are partially supportive of his assumption.

Sexual Dimorphism

It should be noted that WW and FDW in North Dakota are subject to biases that may or may not be obvious. For example, weights of adult males from other studies sampled during pre-rut would likely result in a higher sexual dimorphic ratio because these animals should be in optimal physical condition. The low dimorphic ratio for WW and FDW in North Dakota may relate directly to our data collection period during post-rut when males weigh less. Higher sexual dimorphism of FDW of 1.3 was reported in Vermont, New Hampshire, and Maine (Adams and Pekins 1995), Quebec (Peterson 1974), and Ontario (Timmermann 1972; Table 9). The earliest starting dates for moose hunting seasons in New Hampshire, Maine, Ontario, Quebec, and Vermont range from August-October (Timmermann and Buss 1995), whereas, moose in this study and in Alberta (26 November-6 January; Blood et al. 1967) were harvested post-rut. Further, the sample size of WW in Alberta was small (n = 6 females and 3 males) and included animals 3.5 years of age (Blood et al. 1967). We assume that the value of 1.3 probably represents the pre-rut maximum sexual dimorphism, and ratios <1.1 probably reflect post-rut leaner male weights. Other dimorphic ratios we report (TBL, HFL, and SH; Table 8) were low and should not vary seasonally.

Subspecies Comparisons

Sample sizes reported by Simkin (1962) are too small (i.e., 1-2 individuals per category) for comparative purposes, but are reported here for completeness. North Dakota calf and yearling moose were larger than in all other populations except in Ontario (Timmermann 1972; Table 7). Ontario moose were sampled during the first 2 weeks of an October hunting season from forestland long managed for pulpwood with an abundance of preferred and productive habitat and forage (Timmermann 1972). Comparisons were also made between mean FDW and WW of mature adult moose from North Dakota with 9 other North American populations (Table 9); however, age criteria used for determining adult or mature moose was not uniform for all populations. For example, moose from Alberta (Blood et al. 1967) and Alaska (Franzmann et al. 1978) included animals as young as 3.5 years, and females from North Dakota were comparatively shorter in TBL than those from Alaska (Franzmann et al. 1978). However, our comparisons suggest that female moose from North Dakota are markedly heavier than all other populations, with the exception of 5 year-old captive animals in Alaska (Franzmann et al. 1978) and animals sampled prior to the rutting season in Ontario (Ouinn and Aho 1989).

These data also indicate that moose in North Dakota grow as fast or faster during their initial years when compared to other North American and European moose populations (Table 7). Based upon TBL, moose from North Dakota reached their maximum mass by 5.5 years. Range expansion of moose from northern forested areas into the agriculturally dominated landscape of North Dakota provides a unique opportunity to obtain and evaluate subspecies and regional morphometric variations. During the fall, moose in North Dakota are frequently observed foraging on sunflowers and other agricultural crops. Although food habits information in North Dakota is limited to a single study (Maskey 2008), seasonal use of agricultural foods was high, with row crops (primarily corn [Zea mays]) composing 11 and 22% of the fall and winter diets (Sheridan Co., Moose Hunting Unit M9; Fig. 1). In the Turtle Mountains (Bottineau Co., Moose Hunting Unit M4; Fig. 1) where row crops are limited, alfalfa (Medicago sativa) composed 13% of the summer and fall diet representing $\sim 90\%$ of consumed forbs. This agricultural forage may help maximize growth rate and body mass of moose in North Dakota faster than would occur in traditional forest habitat.

Management Implications

Environmental conditions affect body mass (Sand 1996, Hjeljord and Histol 1999, Ericsson et al. 2002), and in turn, body mass influences reproductive potential (Saether and Haagenrud 1983, Adams and Pekins 1995). Monitoring moose populations is difficult, particularly in forested environments; however, measuring body weight of yearling and adult moose has potential value in predicting the nutritional and reproductive status of moose populations (Adams and Pekins 1995). Growth rates also have predictive value in estimating reproductive potential and habitat conditions. Because measuring body weight of moose is often a difficult task, having reliable equations to predict WW from other morphological parameters provides important alternatives for measuring and monitoring moose populations. The predictive equations provided here will be useful to wildlife managers for estimating various weight parameters and age related to productivity, and may aid in law enforcement and immobilization protocols when body weight and age of moose are often necessary.

ACKNOWLEDGEMENTS

We want to express our sincere thanks to the hunters and landowners for their cooperation during this study. Additionally, we would like to thank the following department personnel for their assistance on check stations: S. Allen, A. Anderson, A. Aufforth, B. Bitterman, S. Brashears, E. Dawson, G. Enyeart, T. Ferderer, T. Frank, J. Gulke, A. Harmoning, L. Johnson, M. Johnson, M. Johnson, M. Kanzelman, S. Kohn, R. Knapp, J. Kobriger, A. Kreil, G. Link, B. Lynott, M. McKenna, R. Parsons, R. Patterson, C. Penner, H. Pochant, C. Pulver, G. Rankin, B. Renhowe, S. Richards, R. Rollings, J. Samuelson, D. Schmidt, J. Schulz, B. Stotts, R. Sohn, L. Tripp, and L. Vetter. Finally, we thank E. Addison and 2 anonymous reviewers for providing helpful editorial comments. Financial support was provided by the North Dakota Game and Fish Department Federal Aid Project W-67-R.

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