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Moose Research Center Reports

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Studies 1.45, 1.48, and 1.52
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Moose Research Center Reports

Kris J. Hundertmark
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Study 1.45 Evaluation and Testing of Techniques for Ungulate Management

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Evaluation and Testing of Techniques for Ungulate Management

Thomas R. Stephenson
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Study 1.45
Research Progress Report
Grant W-24-5
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RESEARCH PROGRESS REPORT

STATE: Alaska **STUDY:** 1.45

COOPERATOR: Kenai National Wildlife Refuge, Soldotna, Alaska

GRANT: W-24-5

STUDY TITLE: Evaluation and Testing of Techniques for Ungulate Management

AUTHORS: Thomas R. Stephenson, Kris J. Hundertmark, John A. Crouse, and Charles C. Schwartz

PERIOD: 1 July 1996–30 June 1997

SUMMARY

We continued to collect baseline information on parameters of calving in nutritionally unrestricted caribou (*Rangifer tarandus*) for later comparison with nutritionally stressed animals. We also improved facilities and developed new methods for collecting such information. By allowing a mature bull access to cows only during daylight hours of the rut, we were able to observe 6 planned breedings. An additional yearling and a 2-year-old female were bred during subsequent estruses. Four calves were born and processed (weighed, measured, sexed, eartagged, and blood-sampled) without loss. We evaluated blood parameters to assess immunocompetence in calves. A *Chlostridium* spp. infection caused mortalities of 4 adult cows and 1 2-year-old cow during February and March. An additional yearling female died of unknown causes during the winter. Four of the mortalities were processed to develop predictive equations of total body fat using ultrasonography. Subsequently, we vaccinated the entire herd during April 1997. Using a digital electronic scale, we weighed caribou intermittently, with minimal stress. Seven adult, 1 2-year-old, and 3 yearling females were immobilized during December 1996–April 1997; all but 1 adult and 1 yearling were pregnant based on serum assay. Mean ultrasonic rump fat thickness was 2.81 cm (± 0.29 SE) for pregnant caribou. Mean gestation length was 223 (± 3.7 SD) days. We continued training 6 adult female caribou to use a restrictive feed gate system. The Moose Research Center (MRC) caribou herd remains at 19 animals.

Key words: body condition, caribou, gestation, nutrition, *Rangifer tarandus*, reproduction.

CONTENTS

BACKGROUND

Recent data from the Southern Alaska Peninsula caribou herd (SAP) indicate a reduced population, small adult body size, low birth weights, late calving dates, and low calf survival. Undernutrition is the suspected agent affecting the population dynamics of that herd (Pitcher et al. 1991). It is unclear what the appropriate management strategy for the herd should be because of our uncertainty as to the role of density-dependent food limitation in the decline. Adams (1996) documented an interaction among forage resources, climatic conditions, and previous reproductive success in determining the productivity of female caribou.

Body condition of adult female caribou and reindeer affects reproductive performance and calf survival. Lenvik (1988) found that conception date in reindeer was related to weight (and possibly energy reserves) of females during the breeding season. Pregnancy rate was closely associated with fat reserves and body weights of Peary caribou in Arctic Canada (Thomas 1982). Calves of undernourished female reindeer had reduced birth weights and reduced survival (Espmark 1980, Skogland 1984). Gerhart (1995) determined that body fat content was the body condition parameter that best explained differences in pregnancy rate in Porcupine Herd caribou.

Undernutrition of *Rangifer* females during gestation and possibly before breeding resulted in late calving (Espmark 1980, Reimers et al. 1983, Skogland 1984). Late calving reduces the summer growth season during the first year (Klein et al. 1987) and probably reduces survival of calves into the following winter (Haukioja and Salovaara 1978). For caribou there are strong indications that nutrition, growth, condition, productivity, and survival are linked; however, our knowledge of these relationships is incomplete and additional information is needed to guide management.

OBJECTIVE

Our objectives are to determine the effects of nutrition on breeding chronology, calving chronology, gestation length, birth size, neonatal survival, and maternal body condition. Furthermore, we wish to refine the relationship between nutrition and previous reproductive success in determining future reproductive success.

METHODS

During July 1996–November 1996, captive caribou at the Moose Research Center (MRC) were switched to an ad libitum textured reindeer ration (16% crude protein, 5.5% crude fiber). During November 1996–January 1997, caribou were fed a mixture of the 16% textured ration and the 13% pelleted ration. During January 1997–April 1997, caribou were fed the 13% pelleted ration. Animals were returned to the 16% ration in May to simulate a higher quality natural summer diet. Feed transitions occurred during a 5–6 week period in the fall and spring. Chemical analysis of feed was conducted at Colorado State University's Forage Analysis Laboratory. Feed samples were analyzed using detergent fiber analysis and total nitrogen was determined using a LECO CHN-1000 (Table 1).

Previously, during May/June 1995–July 1996, we provided captive caribou at the MRC an ad libitum pelleted reindeer ration (13% crude protein, 15% crude fiber). Prior to this, animals were fed a 1:1 ratio of pelleted moose ration (10% crude protein, 5% crude fiber; Schwartz et al. 1985) and a different pelleted reindeer ration (16% crude protein), periodically supplemented with alfalfa hay. Caribou were confined to a 4-ha enclosure with access to additional grasses (*Calamagrostis* spp.) and forbs.

We weighed caribou older than neonates intermittently (because of facility remodeling), using a 12-volt electronic platform scale (Tru-Test Limited Model 700, Auckland, New Zealand). During 28 December–4 April 1997, 7 adult, 1 2-year-old, and 3 yearling females were immobilized with a carfentanil citrate/xylazine hydrochloride mixture and reversed with Yohimbine and Naltrexone. Individual-specific "keys" for the self-feeding gates were attached using standard domestic dog collars. Serum was collected by jugular venipunture and frozen (-20 C) for eventual pregnancy-specific protein B assay (Stephenson et al. 1995) to diagnose pregnancy. Portable real-time ultrasound was evaluated for measuring lipid reserves (Stephenson 1995). The rump region was scanned using an Aloka model 210 portable ultrasound device (Corometrics Medical Systems, Inc., Wallingford, Connecticut, USA) with a 5 Mhz, 8 cm linear-array transducer. We measured subcutaneous fat thickness along a line between the spine, at its closest point to the tuber coxae (hip bone) and the tuber ischii (pin bone). Fat thickness was measured with electronic calipers to the nearest 0.1 cm along the line from the midpoint and point of maximum thickness (immediately adjacent to the cranial process of the ischial tuber).

When possible, we determined body composition for fresh mortalities as follows. Whole body mass was determined and then each animal was eviscerated and skinned (subcutaneous fat remained on the carcass). The carcass was bisected longitudinally along the vertebral column; one half was frozen for chemical analysis. The gastrointestinal tract was emptied of ingesta. The concepta and amniotic fluid of pregnant females were removed and their mass determined to permit calculations less the concepta. Kidney fat mass was recorded as the mass, to the nearest 1 g, of trimmed fat attached to the kidney (Riney 1955). The entire viscera and samples of shaved hide were frozen for analysis. The frozen carcass half and visceral mass were sliced at 51 and 25 mm intervals, respectively, on a commercial band saw (Huot and Picard 1988). The homogenate at the base of the blade was collected for each component, mixed, and refrozen. Hide samples were freeze-dried and ground in a Wiley mill to create a homogenate. Chemical analysis of frozen samples was conducted at Washington State University's Wildlife Habitat Laboratory, Pullman,

Washington. Crude fat was determined by ether extraction (AOAC 1975). Samples were analyzed in triplicate.

Percent fat of a body component (e.g., carcass, viscera, hide) refers to its chemical determination. Values for viscera exclude ingesta and uterine contents. Percent ingesta-free body fat (IFBFAT) was calculated by summing the products of each component's percent fat and its respective mass, dividing by ingesta-free body mass, and multiplying by 100.

Newborn calves were weighed using a spring scale (Salter No.235, London, England), ear tagged, sexed, and measured for total length, jaw length, hind foot length 1 (metatarsus), and hind foot length 2 (heel to toe). In addition, blood (5 cc) was collected by cephalic venipuncture using a syringe. We processed calves within 12–24 hours after birth. Serum samples were analyzed at Phoenix Central Laboratories, Seattle, Washington.

During the 1996 breeding season 7 females were confined in a 50 x 50-m enclosure. To insure that breeding dates were known, a 4-year-old male was allowed access to the females 1 hour in the morning and evening and observed.

We tested a controlled-access feeding system (American Calan, Inc., Northwood, New Hampshire, USA) for suitability with caribou. The system utilizes a feed container, accessible only through a neck slot controlled by a 24-volt electronically locking gate, that is unlocked by an individual-specific sensing "key" collar worn by the animal (Mazaika et al. 1988). Animals were trained to use the gate feeders in pairs by initially unlocking the 2 gates specific to their keys and propping the gates open for 1 day. The following day gates were closed but remained unlocked. During subsequent days, gates were locked for both individuals and they were required to use their "keys" to access feed.

In preparation for feeding trials to be conducted this winter, we are currently remodeling our handling facility to better accommodate caribou. In particular, we are constructing a more efficient weighing and immobilization facility. In conjunction with Calan feed gates, an additional enclosure was constructed for confinement of animals during feeding trials.

RESULTS AND DISCUSSION

We observed copulations for 6 confined adult females during the presumptive first estrus. B.Y. (the seventh adult cow) was not confined with the bull due to her history of poor fertility and no apparent indication of estrus. One 2-year-old female (Copper) was not bred during confinement, but upon necropsy on 17 January she carried a second or third estrus calf. Six adult and 2 yearling cows were determined to be pregnant by pregnancy-specific protein B assay during December–April; 1 adult (B.Y.) and 1 yearling (Jade) were not pregnant (Table 2). A bacterial infection (*Chlostridium perfringens and C. sordellii)* caused mortalities of 4 adult cows and 1 2-year-old cow during February and March. An additional yearling female (Berry) died of unknown causes during the winter. Consequently, we vaccinated the entire herd during April 1997. Only 4 females determined to be pregnant calved successfully in May (Table 2). Mean ultrasonic rump fat thickness was 2.81 cm ($\pm$ 0.29 SE) for pregnant caribou during 1997. In contrast, during 1996 rump fat thickness averaged 1.08 cm for pregnant cows. Other than B.Y. (the oldest caribou at

the Moose Research Center), no adult animals exhibited reproductive pauses. In addition, the smallest of 3 yearlings (91.5 kg in January 1997) at the facility did not produce a calf. Gerhart (1995) suggested that lactational infertility may occur regardless of maternal fat reserves, particularly for cows that lactate well into autumn. Cameron (1994) suggested that periodic reproductive pauses were a response by caribou to nutritional stress. The improved nutritional quality of diets provided by feeding the textured ration during the last year appears to have increased fat deposition and possibly reduced the occurrence of reproductive failure at the Moose Research Center.

Upon initial arrival of caribou at the MRC, we began feeding an experimental pelleted 16% crude protein reindeer ration developed by the University of Alaska, Fairbanks. However, because our animals developed scours, we blended this ration 1:1 with a 10% crude protein pelleted moose ration and fed this diet during 1992–1995. During May/June 1995, we began using a 13% crude protein pelleted reindeer ration. However, although MRC captive caribou were intended to be on a high nutritional plane, the poor reproductive performance observed during 1995/1996 indicates our caribou were on a less-than-optimal nutritional plane. Diet analysis of free-ranging caribou in Interior Alaska indicates a summer diet high in crude protein and digestible energy (Boertje 1985, 1990). Currently, animals are fed a 16% textured ration during summer and a 13% pelleted ration during winter.

One male and 3 females were born during 1997 (Table 3). Mean gestation length in 1996–1997 was 225 days (range = 223–227). Mean gestation length for all years (n = 18) was (223 ± 3.7 SD) days (range = 215–231); the median and mode were 224 days (Fig 1).

A baseline serological survey to determine neonatal immunocompetence (Table 4) indicated that mean gamma globulin (1.38 g/dl ± 0.3 SE) and gamma-glutamyl transferase (GGT; 1331.3 U/L ± 387.2 SE) of caribou were high relative to moose and other species (Sams et al. 1996).

All caribou were successful in learning to use the Calan feed gates. We determined that one caribou (B.R.) that had difficulty learning the system last year actually had a malfunctioning gate.

RECOMMENDATIONS

For diets simulating an optimal nutritional plane, we will maintain caribou on a higher quality 16% crude protein textured ration (W. Hauer, UAF LARS), particularly during summer months. Chemical analysis of diets will be used to determine levels of digestible energy and protein provided by diets for comparison to nutritional requirements for maintenance and reproduction. Feeding trials this winter will focus on determining the nutritional quality of optimal nutritional plane diets and ad libitum intake rates. Before placing animals on restricted rations, we need to bring all trial animals to equivalent levels of body condition and reproductive status, particularly if we are to evaluate the existence of cumulative effects.

We also plan to collect first incisor teeth for aging from all wild-caught caribou of unknown ages. This may prove useful in evaluating past reproductive pauses.

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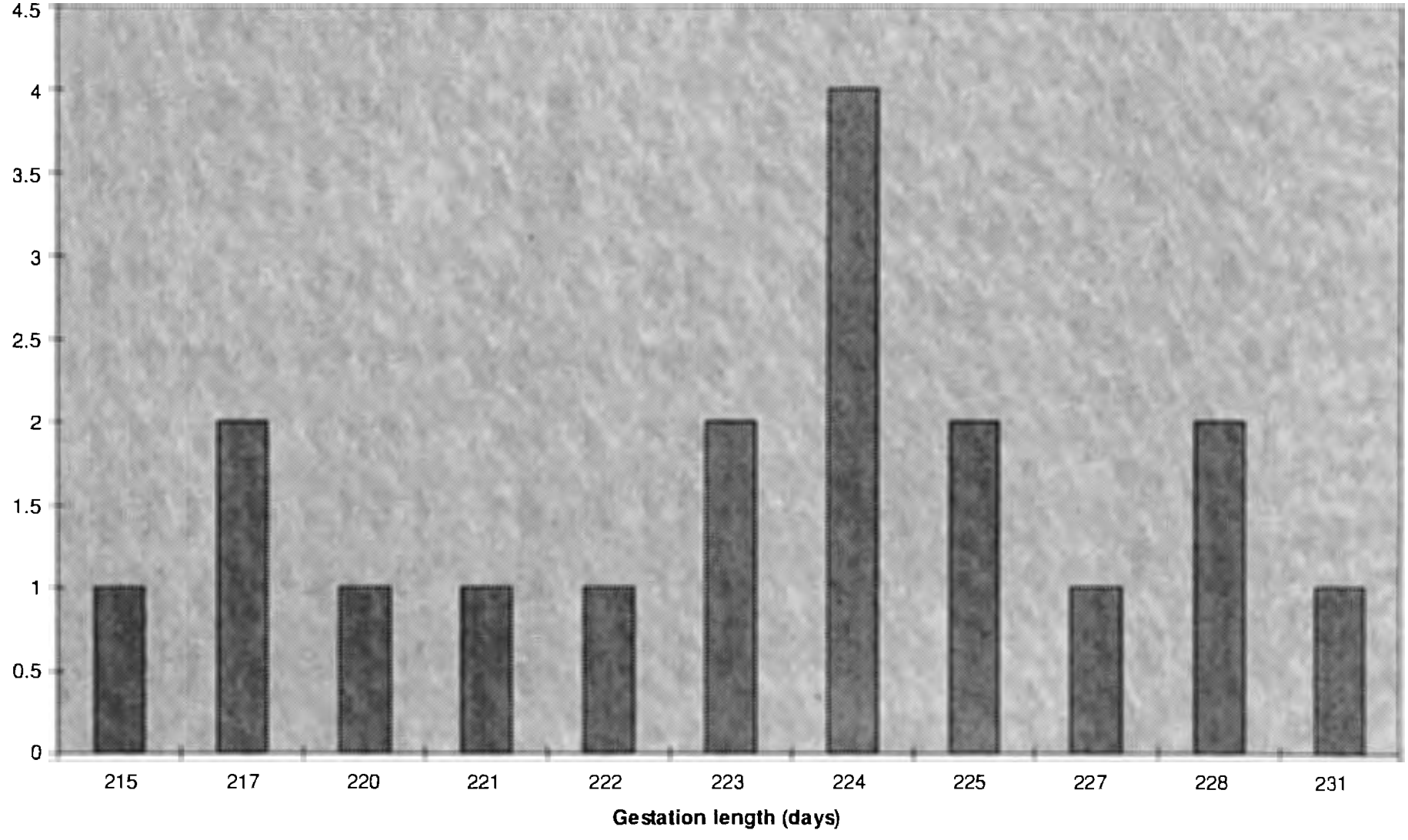

Figure 1 MRC captive caribou share identical mean and mode (224 days) in gestation period, 1996–97

Table 1 Detergent fiber and nitrogen analyses of caribou feeds fed during 1 July 1996–30 June 1997

Type	Sample	NDF	ADF	Cellulose	Lignin	Carbon	Nitrogen	Crude Protein
Pelleted	1	60.66	12.66	10.07	2.32	41.97	2.698	16.86
	2	63.31	12.76	9.78	2.34	42.07	2.725	17.03
	$\bar{x}$	61.985	12.71	9.925	2.33	42.02	2.7115	16.945
Textured	1	78.42	6.04	5.18	0.63	41.66	3.292	20.58
	2	72.21	6.09	4.74	0.77	42.09	3.238	20.24
	$\bar{x}$	75.315	6.065	4.96	0.7	41.875	3.265	20.41

Table 2 Physical and physiological characteristics of caribou immobilized at the Moose Research Center during 28 December 1996–2 April 1997

Animal	Approximate age (yr)	Sex	Recent weight (kg)	Capture date	Rump fat thickness (cm)[a]	Pregnant[b]
Blue	≥11	F	123.5	2/26/97	2.6	Yes
BR	≥11	F	125.0	2/26/97	3.8	Yes
BY	≥12	F	93.5	4/2/97		No
Copper	2	F	122.5	1/16/97	2.0	Yes
Crystal	1	F	103.5	3/5/97	1.3	Yes
Jade	1	F	91.5	2/27/97	1.7	No
Orange	≥7	F	113.0	1/31/97	2.2	Yes
Snow	4	F	125.0	3/5/97	3.6	Yes
Snowflake	1	F		3/5/97	2.7	Yes
Violet	4	F	121.5	12/28/96	3.5	Yes
White	≥11	F		1/22/97	3.6	Yes

[a] Maximum rump fat thickness measured by ultrasonography.

[b] Pregnancy status determined by radio-immuno assay for pregnancy-specific Protein B and confirmed by parturition or necropsy.

Table 3 Descriptive data for caribou calves captured within 24 hours of birth at the Moose Research Center during 22 May–6 June 1997

Animal	Sex	Date		Gestation length (days)	Birth weight (kg)	Total length (cm)	Mandible length (cm)	Metatarsus length[a] (cm)	Hind foot length[b] (cm)	Dam	Sire
		Conception	Birth								
Blossom	F	11 Oct 95	22 May 97	224	17.5		14.5	24.5	34.5	Orange	Hebou
Sharona	F	12 Oct 95	24 May 97	223	17		12.0	25.5	35.0	Violet	Hebou
Casper	M	11 Oct 95	25 May 97	227	22		14.5	28.5	37.0	Blue	Hebou
Gail	F	?	6 June 97	?	13	77.0	13.0	24.0	35.0	Crystal	?

[a] Length of the hind foot minus the hoof.
[b] Length of the hind foot to tip of hoof.

Table 4 Serological data for caribou calves captured within 24 hours of birth at the Moose Research Center during 22 May–6 June 1997 and 21–29 May 1996

Animal	Capture date	Age (hr)	GGT	Albumin	Alpha 1	Alpha 2	Beta	Gamma globulin	Total protein
Sharona	5/24/97	12	684	2.4	1.0	0.2	0.7	1.6	5.9
Casper	5/26/97	15	994	2.1	0.9	0.3	0.7	1.1	5.1
Gail	6/6/97	12	95	2.3	0.9	0.2	0.4	0.2	4.0
Shirley	5/29/96	12	1246	2.3	1.2	0.2	0.7	1.3	5.8
Mindy	5/22/96	12	3130	2.5	1.2	0.3	0.7	2.6	7.5
Radley	5/21/96	12	927	2.2	1.0	0.4	0.6	0.8	5.0
Didley	5/21/96	12	2243	2.4	1.1	0.5	0.9	2.1	7.0

Influence of Selective Harvest Systems on Population Genetics of Alaskan Moose

Kris J. Hundertmark
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Study 1.48
Research Progress Report
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RESEARCH PROGRESS REPORT

STATE: Alaska **STUDY NO.:** 1.48

COOPERATORS: Kenai National Wildlife Refuge, Soldotna, Alaska; Boone and Crockett Club; Gerald Shields and R. Terry Bowyer, University of Alaska Fairbanks; Michael H. Smith, Savannah River Ecology Lab, University of Georgia, Aiken, SC

GRANT NO.: W-24-5

STUDY TITLE: Influence of Selective Harvest Systems on Population Genetics of Alaskan Moose

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PERIOD: 1 July 1996–31 June 1997

SUMMARY

Regional differences in allele frequency and heterozygosity of allozyme loci were documented for Alaskan moose (*Alces alces*). Four variable loci were documented in populations from the Matanuska–Susitna (Mat–Su) valleys and southeastern Alaska (Chilkat valley), and 3 of these loci were variable in the Copper River Delta moose population. Contrary to theoretical predictions concerning inbreeding, the population in the Copper River Delta, which was founded with a small introduction, did not exhibit less genetic variation than other Alaskan populations, and the introduced Colorado population exhibited variation similar to naturally founded Mat–Su population. Conversely, the Colorado population exhibited the lowest number of polymorphic loci, followed by the Copper River Delta, indicating that fixation of alleles due to drift and founder effect can occur in transplanted populations. Analysis of variation in nucleotide sequences of the hypervariable region of the mitochondrial DNA (mtDNA) control region indicates that variation exists within Alaska, but at level probably associated with subspecific differences rather than population subdivision. We recommend that microsatellites be investigated as an appropriate molecular marker to assess population-level genetic variation in moose. When combined with sequences from European and Asian moose, the phylogenetic relationships among North American moose populations indicate that, contrary to prevailing opinion, moose in Alaska represent the founding source for other North American populations. *A. a. andersoni* in southeastern Alaska and western Canada are the populations most closely related to Old World moose, with the bulk of Alaskan populations deriving from individuals now residing in the western Great Lakes region. We simulated moose populations held either at or below nutritional carrying capacity (K) to determine the effect of population density on harvest rate and frequency of alleles favoring antler growth under a selective harvest system. A stochastic model of density-dependent population growth was created to achieve stable populations at K with no hunting. Nonhunting mortality rates were increased to simulate predation losses for a population held below K. The increased nutrition available to this lower density population was assumed to result

in larger age-specific antler size. Each population was subjected to a harvest plan that defined legal bulls as those with either a spike-fork antler as yearlings (small bulls) or with an antler spread of 50 inches (127 cm) or greater (large bulls). Harvest, population composition, and frequency of alleles favorable to antler growth were monitored throughout the simulations. For the population held at K, the frequency of favorable antler alleles declined slightly from that obtained in the population with no hunting. When the population was reduced below K, harvest decreased and the proportion of small bulls in the harvest increased compared to the population at K. In the population below K, the frequency of favorable alleles declined steadily, probably to fixation for unfavorable alleles. Ratios of bulls:100 cows in the two harvested populations were similar, but ratios of small:large bulls were changing, with the lower density population exhibiting a higher proportion of small bulls before harvest. Under the conditions imposed by our model, increases in age-specific antler size associated with increased nutrition resulted in greater selection against alleles favorable for antler growth under a selective harvest scenario. The effect of nutrition on the potential for antler growth must be considered when predicting the outcome of antler-based selective harvests.

Key words: Alaska, *Alces alces*, antlers, control region, genetics, genetic diversity, mitochondrial DNA, moose, selective harvest system.

CONTENTS

BACKGROUND

In 1987 the Alaska Board of Game approved a selective harvest system (SHS) for bull moose (*Alces alces*) on the Kenai Peninsula. This system limited bull harvest to those with either a spike or forked antler, or animals with at least a 50-inch (127 cm) antler spread or at least 3 brow tines on one antler. One of the many reasons cited for instituting this system was that focusing harvest on spike/fork yearlings would serve to eliminate "inferior" bulls from the gene pool. This statement was based on the assumptions that antler characteristics are inherited, that age-specific

variation in antler size is related to genetics, and that antler characteristics are indicative of overall individual fitness.

The SHS implemented on the Kenai Peninsula has proven to be an effective method for managing moose harvest (Schwartz et al. 1992). Consequently, the Alaska Board of Game has adopted this system in many Game Management Units (GMUs) connected by the state road system between Anchorage and Glenallen and most areas of Southeast Alaska. Implementation of this SHS will affect a large proportion of the state's moose populations. In light of this proposal, we need to gain a better understanding of the genetic consequences of harvest systems based upon antler configuration. Specifically, the assumptions driving this system and changes in genetic structure brought about by this system need to be quantified before we can truly understand the effect of SHS on moose genetics.

As public demand for consumptive and nonconsumptive use of moose increases, it is contingent upon the state to manage populations more intensively, which in turn requires a more complete knowledge of population processes. In attempting to understand temporal and spatial differences in the attributes of moose at the population (e.g., natality, mortality) and individual animal (e.g., antler size, body condition) levels, biologists focus primarily on nutrition, predation, and harvest rates. The possibility that genetic factors are responsible for many intra- and interpopulation differences in these parameters is distinct; however, there is a paucity of information concerning population genetics of moose. In order to manage moose populations more effectively, we must understand the degree to which genetics contributes to antler development and the extent to which antler development reflects fitness. Additionally, the potential effects which antler-based management strategies may have on genetics must be described.

The genetic component of phenotypic expression, although universally recognized by biologists, has not been considered in a management context perhaps due to the lack of simple techniques for data collection and analysis or the perception that cause-effect relationships could not be ascertained. However, during the last 2 decades, techniques have been developed to assess population genetics in wild animals (*See* Hedrick and Miller 1992) and subsequent investigations have demonstrated that information gained from such analysis can be useful to managers (*See* Dratch and Pemberton 1992).

The initial efforts to describe genetic variation in wild populations focused on electrophoretic variation of loci coding for enzymes. These studies focused on the relationships between overall genetic variability (most often expressed as heterozygosity) and physiological or morphological characteristics of individuals or populations. Mitton and Grant (1984:489–90) summarized the prevailing theories explaining these relationships as "... (a) the enzymes mark blocks of chromosomes and are fortuitously linked to genes directly affecting growth and development; (b) protein polymorphisms constitute a sample of genes whose heterozygosity reflects a continuum between highly inbred (low heterozygosity) and randomly outbred (high heterozygosity) individuals; and (c) the genotypes of enzyme polymorphisms typically exhibit different kinetic characteristics; these differences affect the flow of energy through metabolic pathways and thereby influence growth, development, and oxygen consumption." In essence, this means that (a) the dynamics of enzyme polymorphisms mirror those of closely linked loci and therefore act as markers, (b) the genotypes observed in a population indicate the breeding history of that

population, and (c) individuals exhibiting heterozygosity are thought to be able to take advantage of multiple metabolic pathways for energy processing, making them better able to adapt to a variable environment.

The most widely studied game species in this context is the white-tailed deer (*Odocoileus virginianus*), which exhibits a great amount of genetic variability (Smith et al. 1984). Studies at the Savannah River Ecology Lab have demonstrated relationships between heterozygosity and body condition of overwintering females (Cothran et al. 1983), conception timing (Chesser and Smith 1987), male body size and antler characteristics (Scribner and Smith 1991), number of fetuses (Johns et al. 1977), and rate of fetal development (Cothran et al. 1983).

Although genetic diversity is thought to be maintained in natural populations by means of stabilizing selection (Pemberton et al. 1991), populations subject to hunting can exhibit unexpected trends in genetic composition due to different mortality rates. Improperly designed hunting seasons can cause dramatic changes in the genetics of populations without causing a decline in population size. Thelen (1991) demonstrated that certain SHS for elk (*Cervus elaphus*) based on antler characteristics actually resulted in a decrease in desirable genetic traits, while others had the opposite effect. Ryman et al. (1981) demonstrated that certain harvest regimes for moose can cause rapid declines in effective population size (N_e), an index of the rate of genetic drift (random loss of genetic material), and that populations in which only males are harvested are more susceptible to these changes because they have an inherently lower N_e because of their skewed sex ratios. Scribner et al. (1985) demonstrated that 2 different hunting methods (still vs. Dog hunting) had different effects on genetic diversity of white-tailed deer populations without changing population composition. Hartl et al. (1991) detected differences in allele frequencies in populations of red deer (*Cervus elaphus*) with dissimilar hunting pressure on spike-antlered yearlings. Therefore, the type of SHS imposed on a population can dramatically affect genetic structure and consequently influence population processes of interest to managers.

Electrophoretic variation has also been used to determine population subdivisions, or breeding units. Species in which population subdivision has been detected include white-tailed deer (Manlove et al. 1976), elk (Dratch and Gyllensten 1985), caribou (*Rangifer tarandus*, Røed and Whitten 1986), mule deer (*Odocoileus hemionus*, Scribner et al. 1991), and moose (Ryman et al. 1980, Chesser et al. 1982). Describing this variation is useful in quantifying such concepts as dispersal and population identity as well as understanding interpopulation differences in population parameters. As populations should be managed at the level of the breeding unit (Smith et al. 1976, Ryman et al. 1981), this information can be of extreme importance to management agencies.

Recently, genetic analyses have identified relationships between alleles at specific loci and selective pressures. Pemberton et al. (1988, 1991) detected a relationship between gene frequencies at a particular locus and juvenile survival and adult fecundity in red deer. Hartl et al. (1991) demonstrated that selective harvesting of spike-antlered red deer caused a decline in frequency over time of a specific allele. This latter study is supported by Templeton et al. (1983), who demonstrated that the number of antler points in white-tailed deer probably is controlled by a single gene. In a subsequent study, Hartl et al. (in press) concluded that red deer that were

homozygous for a particular allele at the Idh-2 locus developed significantly more antler points than did individuals with alternative genotypes. Animals homozygous for a particular allele at the Acp-2 locus exhibited larger antlers, compared to animals with other genotypes.

The degree to which genetics contributes to antler expression (heritability) in moose is unknown. Arguments for either nutrition or genetics as the primary force behind antler growth are common (*see* Goss 1983). The limited data available indicate the form of the antler and its potential size are genetically controlled. Harmel (1983) reported that of the offspring produced by a male white-tailed deer with superior antlers, only 5% exhibited spikes as yearlings, whereas 44% of the offspring of a male with inferior antlers had spikes. As all of the deer in this study were maintained on high-quality feed, it is apparent the size of antlers is heritable. The heritability of brow tines is unknown.

OBJECTIVES

1. Determine genetic structure of moose populations across the state

H_{1O}: Estimates of genetic diversity will not differ among moose populations across the state.

H_{1A}: Estimates of genetic diversity will differ among moose populations across the state.

2. Determine if differences in antler characteristics noted for different regions of Alaska are related to genetic factors

H_{2O}: Populations characterized by superior antlers (larger age-specific antler spreads and palmated brows) will not exhibit more genetic diversity than those characterized by inferior antlers.

H_{2A}: Populations characterized by superior antlers (larger age-specific antler spreads and palmated brows) will exhibit more genetic diversity than those characterized by inferior antlers.

3. Determine the degree to which antler characteristics are heritable

H_{3O}: Antler morphology of offspring has no relation to antler morphology of parents.

H_{3A}: Antler morphology of offspring is related to antler morphology of parents.

4. Determine if antler characteristics are related to other phenetic correlates such as body size and growth rate

H_{4O}: Antler morphology (size) is not related to body size or growth rate.

H_{4A}: Antler morphology (size) is directly related to body size or growth rate.

5. Determine if N_e *of moose populations subjected to SHS changes over time in comparison to control populations*

H_{5O}: Temporal changes in N_e will not differ between populations subject to SHS and general hunts.

H_{5A}: Temporal changes in N_e will differ between populations subject to SHS and general hunts.

6. Determine if SHS causes a decline in the number of animals with inferior antlers

H_{6O}: The percentage of spike-fork yearlings in populations subject to SHS will not decrease over time.

H_{6A}: The percentage of spike-fork yearlings in populations subject to SHS will decrease over time.

7. Determine if genetic diversity of populations is related to historical population trends

H_{70}: Populations characterized by historically low bull:cow ratios and/or low population densities will exhibit no differences in genetic diversity compared to populations that are close to management objectives.

H_{7A}: Populations characterized by historically low bull:cow ratios and/or low population densities will exhibit lower genetic diversity compared with populations that are close to management objectives.

METHODS

JOB 1. DETERMINE GENETIC STRUCTURE OF MOOSE POPULATIONS ACROSS THE STATE

A sample of skeletal muscle, as well as kidney, liver, and heart tissue if possible, were collected from animals shot by hunters. These samples were frozen at -20°C as soon as possible after collection. Additionally, a sample of ear tissue was collected from animals that were collared as part of other research projects and were stored frozen. These tissues were transferred to an ultracold freezer (-80°C) in 1995 to facilitate long-term preservation. A listing of sample sizes and collection locations was presented in Hundertmark et al. (1996).

JOB 3. CONDUCT A CAPTIVE BREEDING PROGRAM TO ASSESS HERITABILITY OF ANTLER AND BODY SIZE

In May 1993, 5 newborn calves (2 male, 3 female) were captured in the Three Day Slough area of the Koyukuk River, an area known for moose with large brow formations. These animals, and a female calf born at the MRC, were hand-reared at the MRC to allow them to become accustomed to human presence and handling. The calves were allowed to forage on natural vegetation during the summer and were provided a formulated ration (Schwartz et al. 1985) ad libitum during the winter to maximize nutritional effects on antler and body growth.

Selective breeding followed the methodology of Harmel (1983). The cows were divided randomly into 2 groups, and a bull was placed with each group based upon random selection and allowed to breed. All offspring were ear-tagged and weighed at birth. Male offspring are placed in a large pen and fed a formulated ration ad libitum. We retained females to be bred to their fathers as yearlings and 2-year-olds. Male offspring will be weighed weekly in September, and their antlers will be removed, weighed, and measured. Weights and antler measurements will be analyzed by partitioning the variance among sires and sibs (Wright 1969). Pedigrees of all MRC moose will be constructed to determine if these data can be used in this analysis.

JOB 5. LABORATORY ANALYSIS OF TISSUE SAMPLES

Electrophoretic analyses of tissue samples were conducted at the Savannah River Ecology Lab at Aiken South Carolina in March 1996. The loci examined are listed in Table 1. Horizontal starch gel electrophoresis was performed according to the procedures of Selander et al. (1971), Manlove et al. (1975), and Harris and Hopkinson (1977). Each gel was loaded with tissue extract from no more than 25 individuals and was exposed to electric current overnight. Gels were sliced and

stained, and allozyme genotypes for each individual were scored. Gels that contained more than 1 genotype were photographed to provide a permanent record.

Tissue samples for 457 individual moose were analyzed for genetic diversity via electrophoresis. These data are being entered into a computer database to assist with analysis. Presently, genotypes at 19 loci for moose from 3 areas (Mat–Su Valley, Southeast Alaska, and Colorado) are entered into the database and are available for analysis. These loci are Mdh-1,-2, Mpi, Pep-2, 6Pgd, aPgd, Ldh-1,-2, Ada, Icd-1,-2, Pgi, Pgm-2, Ck-1,-2, Adk-1,-2, Fh, and Sod-1 and are described in Table 1.

Genetic variability will be analyzed with the computer program BIOSYS-1 (Swofford and Selander 1981) and will be expressed as heterozygosity (h), alleles per locus (A), and percent polymorphic loci (P). Genetic differentiation among populations will be determined by use of F statistics (Wright 1965) and Nei's genetic distance (Nei 1978).

Mitochondrial DNA (mtDNA) was extracted from moose tissue via a standard salt extraction technique. A section of the cytochrome-b gene was amplified using primers MVZ04 and MVZ05 (Table 2). A section of the hypervariable control region was amplified using the primer pairs LGL283-CST39 or ISM015-CST39 (Table 2). We used a cycle sequencing reaction using fluorescent dyes to prepare the sample for sequence determination with an automated sequencer. We edited sequences by examining electropherograms. Individuals with ambiguous sequences were sequenced in both directions. Genetic distances among sequences were computed with the program PHYLIP (Felsenstein 1989), and these distances were used to construct a phylogenetic tree using the UPGMA (unweighted pair group method using arithmetic averaging) algorithm.

JOB 6. CHANGES IN ANTLER TYPE ASSOCIATED WITH SHS

A modeling exercise was conducted to determine if the influence of selective harvest systems on alleles favorable to antler growth would change if antler phenotypes were altered by changing the environmental influence upon them. A previous exercise (Hundertmark et al. 1993) demonstrated that, in populations held near nutritional carrying capacity, a spike/fork-50" selective hunting system had little effect on alleles favorable to antler growth. Complete methodology for the modeling exercise is contained in Appendix A.

RESULTS AND DISCUSSION

JOB 1. DETERMINE GENETIC STRUCTURE OF MOOSE POPULAITONS ACROSS THE STATE

The two naturally founded Alaskan populations (Mat–Su and Southeast) were polymorphic at 4 (Mdh-1, Mpi, Pep-2, and Ck-1) of 19 loci, whereas the introduced Copper River population was polymnorphic at 3 (Mdh-1, Mpi, and Pep-2) loci and the introduced Colorado population was polymorphic for 2 (Mdh-1, Mpi) of these (Table 3). No variation at the Pgm-2 locus was observed, contrary to findings from moose from the Kenai Peninsula (Hundertmark et al. 1992). Other variable loci described by Hundertmark et al. (1992) have not been analyzed at this time. These data support the conclusion of Hundertmark et al. (1992) that moose exhibit levels of genetic variation similar to other mammals and are not monomorphic as previously reported (Ryman et al. 1980).

Estimates of genetic variability for the 4 populations were less than those reported for Kenai Peninsula moose by Hundertmark et al. (1992) (Table 4). This was to be expected for the Colorado population because it originated as a transplant of 23 animals. Moreover, the Southeast population (comprised mainly of animals from the Haines area) was established by migration from Canada, and it would not be unusual if genetic diversity in the founded population was less than that in the parent population. It is surprising, however, to note the lesser amount of diversity in the Mat–Su population compared to animals from the Kenai Peninsula. Mat–Su is a large, open population that would not experience significant amounts of genetic drift, at least in recent times. We should note that measures of genetic variability are influenced by the choice of loci included in the analysis, and the loci included in this analysis were not identical to those of Hundertmark et al (1992). These results may change somewhat in the final analysis.

Allele frequencies differed significantly among the 4 populations for Mdh-1 ($X^2 = 86.5$, $P < 0.0001$), Mpi ($X^2 = 28.2$, $P < 0.0001$), Pep-2 ($X^2 = 11.01$, $P = 0.012$) and Ck-1 ($X^2 = 17.9$, $P = 0.0005$). Genotype frequencies at each locus within populations did not differ from Hardy–Weinberg expectations with the exceptions of Mdh-1 (Mat–Su) and Ck-1 (Southeast). In both of these instances the rare allele was found in the homozygous condition in 1 animal and no instances of heterozygotes were recorded. These data might be attributable to small sample sizes or improperly scored gels and should not be considered as definitive evidence of a heterozygote deficiency.

Allele frequencies for Mdh-1 and Mpi show a geographic trend. The common allele in Mdh-1 in Mat–Su, Copper River Delta, and Kenai samples is the rare allele in Colorado, and these alleles are intermediate in frequency in Southeast Alaska (Table 3). For Mpi, the rare allele in Mat–Su becomes more common in moose from Southeast Alaska and is more common still in Colorado (Table 3). Although the moose from Colorado were introduced, the founding individuals were obtained from Utah and Wyoming, which does not bias this analysis. Nei's (1978) unbiased genetic distances (Table 5) between populations indicate the Copper River Delta population is the most genetically unique of the 4 populations analyzed thus far. Again, this is attributable to founder effect and drift.

Three mtDNA haplotypes were documented in Alaskan moose (Fig. 1, Table 6). Haplotype "Alaska A" was widespread, being excluded only from southern Southeast Alaska. Haplotype B was found in only 1 individual from the Galena area and differed from haplotype A by 1 transition. Haplotype C was found only in animals from the Unuk and Stikine Rivers, Thomas Bay, and from 1 animal from the Haines area. Haplotype C was more closely related to sequences from *A. a. shirasi* from Colorado and *A. a. andersoni* from Ontario than it was to the other Alaska haplotypes (Figs. 2, 3, 4). This lends support to the hypothesis that moose in southern Southeast Alaska are descended from *A. a. andersoni* populations in British Columbia and should be classified as such; this differs from conventional views (Hall 1981, Telfer 1984). Recognizing that moose in this area are a different subspecies than those in the remainder of Alaska is important because *A. a. andersoni* exhibits a tending-bond system of mating, whereas *A. a. gigas* exhibits a harem system. These 2 systems may require different bull:cow ratios to achieve breeding synchrony, which may dictate different management strategies.

Phylogenetic trees constructed from sequence variation indicate that haplotype "Alaska C" and those found in *A. a. andersoni* from the midwest portion of North America are more closely related to Old World moose and New World cervids (represented by *Odocoileus*) than are *A. a. gigas*. According to the current view of moose radiation to North America (Cronin 1992), *A. a. gigas* should be the most ancient subspecies and should be most closely related to Asian moose. The relationships indicated by the UPGMA tree (Fig. 2) indicate a reentry of moose into Alaska from populations to the southeast.

JOB 3. CONDUCT A CAPTIVE BREEDING PROGRAM TO ASSESS HERITABILITY OF ANTLER AND BODY SIZE

The number of dams in the captive breeding program was increased this year to enhance the potential for producing male calves. Five cows were partitioned with each bull, but due to a failure of a fence to keep animals separated, 4 additional cows were bred; the sire in these cases was unknown (Table 7).

JOB 6. CHANGES IN ANTLER TYPE ASSOCIATED WITH SHS

Computer modeling demonstrated that superior nutrition resulting from decreased population density caused antler sizes to increase initially. This trend was short-lived, however, as selection imposed by a selective harvest system caused a general decline in alleles favorable to antler growth. This demonstrates the genetic effects of selective harvest systems can vary, depending on environmental influences on phenotypes. Results of the modeling exercise are contained in Appendix A.

CONCLUSIONS AND RECOMMENDATIONS

Variation in sequences of mtDNA control region, even those within the hypervariable region of the control region, do not vary greatly across Alaska and are therefore not useful for discerning population subdivision within the state. Nuclear systems are inherently more variable due to recombination and are more suited to population level analysis. Allozyme variation in Alaskan moose varies enough that these markers could be used to study population genetics in this species. The difficulty in obtaining organ samples from individuals, however, precludes the collection of large sample sizes. An alternative family of markers, microsatellites, holds a greater potential for studying geographic variation within the state. Microsatellites are neutral markers, display more variation than do allozyme systems, and can be analyzed using a single tissue type due to the advent of PCR (Bruford et al. 1996). We recommend that variation in microsatellite loci of moose be investigated as population-level and perhaps individual-level markers.

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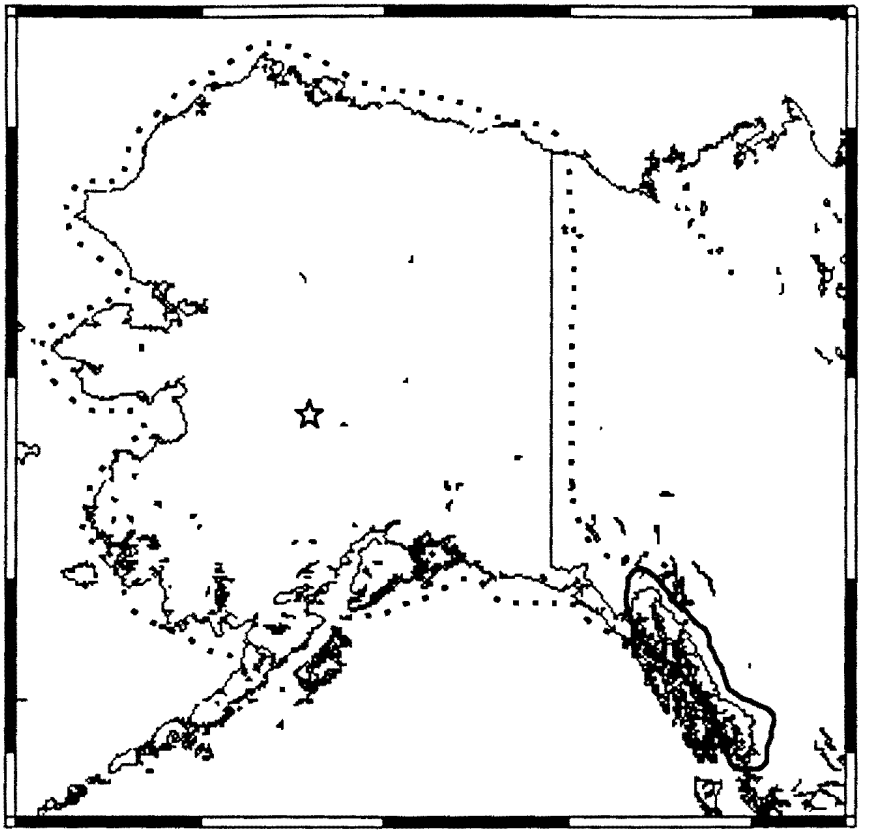

Figure 1 The distribution of haplotypes of the hypervariable region of the control region within Alaskan moose. The most common haplotype (A, broken line) is found statewide with the exception of southern Southeast Alaska, which has its own unique haplotype (B, solid line). A single individual with a variant of haplotype A (C, star) was found near Galena. The distribution of haplotypes A and B overlap in northern Southeast.

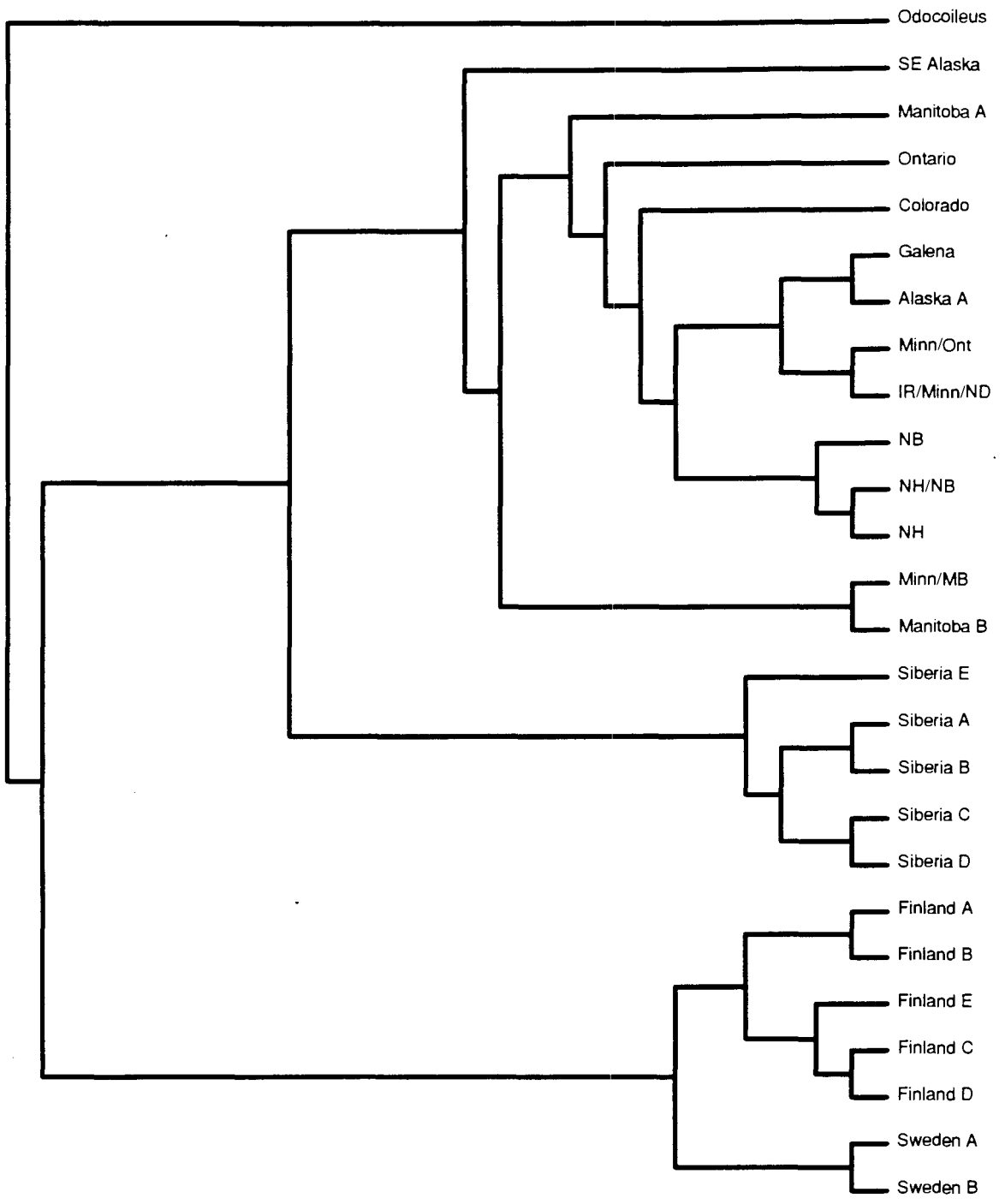

Figure 2 UPGMA tree of phylogenetic relationships of European, Asian, and North American moose. The tree is rooted by the outgroup *Odocoileus virginianus*.

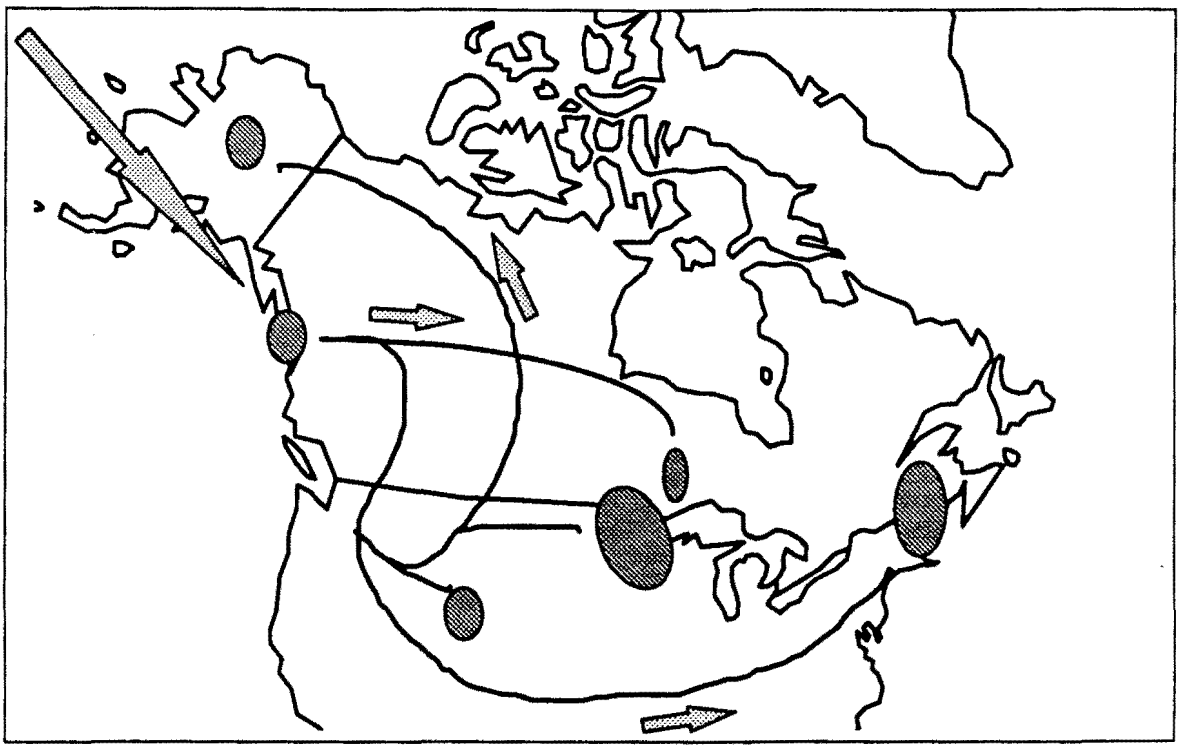

Figure 3 Phylogenetic relationships of populations of North American moose superimposed on a map of their locations. The phylogenetic tree was based on the maximum likelihood tree assuming a molecular clock. Note that lines connecting populations indicate genetic relationship but not necessarily path of migration.

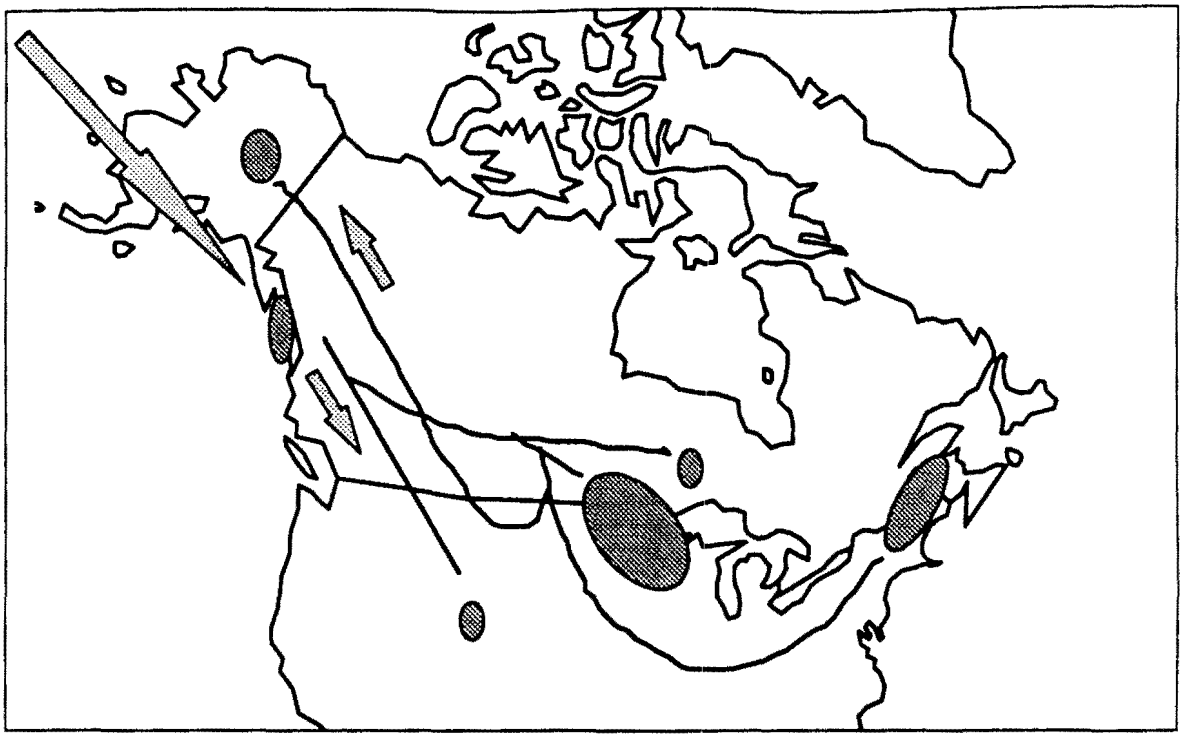

Figure 4 Phylogenetic relationships of populations of North American moose superimposed on a map of their locations. The phylogenetic tree was based on the UPGMA method. Note that lines connecting populations indicate genetic relationship but not necessarily path of migration.

Table 1 Enzymes studied via gel electrophoresis

Enzyme name and locus designations	E. C.[1]	Gel buffer[2]	Stain reference[3]
α-Glycerophosphate dehydrogenase (α-Gpd)	1.1.1.8	LiOH, TC8.0	3
Aconitase (Aco)	4.2.1.3	TM	3
Adenosine deaminase (Ada)	3.5.4.4	LiOH	2
Adenylate kinase (Adk-1,-2)	2.7.4.3	TM, TC8.0	2
Aspartate aminotransferase (Aat-1,-2)	2.6.1.1	LiOH, TC8.0	3
Creatine kinase (Ck-1,-2)	2.7.3.2	TM	2
Esterase (Est, βnp substrate)	3.1.1.1	TM	3
Fumarate hydratase (Fh)	4.2.1.2	TM	3
Glucose-6-phosphate isomerase (Pgi-1,-2)	5.3.1.9	Pk	3
Isocitrate dehydrogenase (Icd-1,-2)	1.1.1.42	LiOH	3
Lactate dehydrogenase (Ldh-1,-2)	1.1.1.27	LiOH, TC8.0	3
Malate dehydrogenase (Mdh-1,-2)	1.1.1.37	AC, TC8.0	3
Malic enzyme (Mod-1,-2)	1.1.1.40	TM	2
Mannose-6-phosphate isomerase (Mpi)	5.3.1.8	LiOH, TC8.0	3
Menadione reductase (mnr)	1.6.99.2	LiOH	3
Peptidase (Pep-1,-2,-3, lgg substrate))	3.4.1.1	LiOH	3
Phosphoglucomutase (Pgm-1,-2)	5.4.2.2	TC8.0	3
6-Phospogluconate dehydrogenase (6Pgd)	1.1.1.44	LiOH	3
Superoxide dismutase (Sod-1,-2)	1.15.1.1	TM	3

[1]Enzyme Commission number

[2]PK (Poulik) = discontinuous tris-citrate (Manlove et al. 1975); LiOH = lithium hydroxide (Manlove et al. 1975); TM = tris-maleate (Manlove et al. 1975); TC8.0 = continuous tris-citrate (Manlove et al. 1975)

[3]1 = Manlove et al (1975); 2 = Selander et al. (1971); 3 = Harris and Hopkinson (1977]

Table 2 Oligonucleotide primers used to amplify mtDNA for this study

Primer	Sequence	Region amplified
LGL283	5'-TACACTGGTCTTGTAAAC-3'	Control region
CST39	5'-GGGTCGGAAGGCGACCAAACC-3'	Control region
ISMO15	5'-ATGGCCCTGTAGAAAGAAC-3'	Control region
MVZ04	5'-GCAGCCCCTCAGAATGATATTTGTCCTC-3'	Cytochrome-b
MVZ05	5'-GCAAGCTTGATATGAAAAACCATCGTTG-3'	Cytochrome-b

Table 3 Allele frequencies and direct-count estimates of heterozygosity (h) for polymorphic loci detected in 3 moose populations

		Locus			
Population	Allele	MDH-1	MPI	PEP-2	CK-1
Mat–Su	A	0.240	0.120	0.045	0.045
(N = 25)	B	0.720	0.880	0.955	0.955
	C	0.040	0.000	0.000	0.000
	H	0.400	0.160	0.091	0.091
Southeast	A	0.560	0.320	0.083	0.200
(N = 26)	B	0.440	0.680	0.917	0.800
	C	0.000	0.000	0.000	0.000
	H	0.400	0.400	0.167	0.000
Colorado	A	0.885	0.442	0.000	0.000
(N = 26)	B	0.115	0.558	1.000	1.000
	C	0.000	0.000	0.000	0.000
	H	0.231	0.577	0.000	0.000
Copper River	A	0.145	0.597	0.158	0.000
(N = 38)	B	0.855	0.403	0.842	1.000
	C	0.000	0.000	0.000	0.000
	H	0.184	0.613	0.211	0.000
Kenai	A	0.000	0.368	0.250	--
(N = 38)	B	0.987	0.632	0.737	--
	C	0.013	0.000	0.013	--
	H	0.026	0.368	0.395	--

Table 4 Estimates of heterozygosity (h), alleles per locus (A), and percent polymorphic loci (P, 0.99 criterion) in 3 moose populations analyzed in this study and compared with a fourth population ("Kenai," Hundertmark et al. 1992)

Population	h	A	P
Mat–Su	0.035	1.2	19.1
Copper River	0.053	1.2	18.2
Southeast	0.046	1.2	19.1
Colorado	0.038	1.1	9.5
Kenai	0.077	1.4	30.0

Table 5 Matrix of Nei's unbiased genetic distance based on allozyme allele frequencies for 4 moose populations

Population	Mat–Su	SE Alaska	Colorado	Copper River
Mat–Su		0.005	0.0233	0.0202
SE Alaska			0.006	0.0202
Colorado				0.0284

Table 6 Condensed dot matrix of sequences examined in this study. Numbers at the top of the table indicate the nucleotide position within the control region where at least one mutation was observed. The consensus sequence was derived from all moose sequences, and each sequence is compared to it. For each sequence, mutations are indicated by the letter of the nucleotide observed (A = adenosine, C = cytosine, G = guanine, T = thymine); dots indicate identity with the consensus sequence. To the right of each sequence is the number of individuals observed with that haplotype.

	1111111122222222223333333333333333344444444	
	2012467890112447788001222333444667880144567 7	
	0549304604131374635019028678035063344978062 4	N
0 Consensus	ATGCTGAGATTATCTGCATATAGATCCATTCCTATCAAGCCTAC	1
1 IR/Minn/ND	G.....T....T.....	9
2 NH/NB	G.....C.....T.....	11
3 NH	G.....C.C.....T.....	1
4 Minn/Ont	G.....T....T..A.....	5
5 Minn/Man	GC.....T...T.C.....T....	5
6 Alaska A	G.....	15
7 Finland B	.....A.A.C...T.....G...T.GC.T....T..ATT...	1
8 Finland C	.....A....C..T.....G...T.GC.T.CG.T..ATT...	4
9 Finland A	.....AGA.....T.....G...T.GC.T..G.T.GATT...	1
10 Finland D	.....A....C..T.....G...T.GC.T.CG.T..ATTat.	2
11 Finland E	.....A....C..T.....G...T.GC.T.CG.T..ATTa..	1
12 Siberia A	G...CA.....CT..TG..C.....C.T....TGG.TT...	1
13 Siberia B	G...CA.....CT..TG..C.....C.T....TG..TT...	1
14 Siberia C	G.....CT...GC.C.....C.T....T...TT...	1
15 Siberia D	G...CA..G...CT..TG..C.....CCT....TGG.TT...	3
16 Siberia E	G.A.CA..G...CT..TG..C.....CCT....TGG.TT...	3
17 Sweden A	.....A.A..C..T.A...G....CT.GC.TTCGCT..ATT...	4
18 Sweden B	.....A.A..C..T.A...G....CT.GC.TTCGCT..ATTa..	2
19 SE Alaska	G.....T..T..GC.....T.....G.....	10
20 Ontario	G.....CG.G.....T.....	1
21 NB	G.....C.....t.....T.....	1
22 Colorado	G.....T.....C.T.....T	3
23 Manitoba A	GC.T.....G.....T....T.....	1
24 Manitoba B	GC.....G.....T...T.C.....T....	1

Table 7 Breeding groups at the Moose Research Center in 1996. Cows with asterisks after their names were bred by unknown sires, as a broken fence allowed mixing of cows and bulls not intended for breeding.

Sire	Dam
Plum	Mustard
	Sue
	Dodger
	Scarlett
	Luna
Green	Deshka
	Laurel
	Caitlin
	Blue
	Sabrina
Unknown	Lara
	Satorene
	Hillary
	Erma

APPENDIX A

EFFECTS OF POPULATION DENSITY AND SELECTIVE HARVEST ON ANTLER PHENOTYPE IN SIMULATED MOOSE POPULATIONS

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ABSTRACT: We simulated moose (*Alces alces*) populations held either at or below nutritional carrying capacity (K) to determine the effect of population density on harvest rate and frequency of alleles favoring antler growth under a selective harvest system. A stochastic model of density-dependent population growth was created to achieve stable populations at K with no hunting. Non-hunting mortality rates were increased to simulate predation losses for a population held below K. The increased nutrition available to this lower density population was assumed to result in larger age-specific antler size. Each population was subjected to a harvest plan that defined legal bulls as those with either a spike-fork antler as yearlings (small bulls) or with an antler spread of 50 inches (127 cm) or greater (large bulls). Harvest, population composition, and frequency of alleles favorable to antler growth were monitored throughout the simulations. For the population held at K the frequency of favorable antler alleles declined slightly from that obtained in the population with no hunting. When the population was reduced below K, harvest decreased and the proportion of small bulls in the harvest increased compared with the population at K. In the population below K, the frequency of favorable alleles declined steadily, likely to fixation for unfavorable alleles. Ratios of bulls:100 cows in the two harvested populations were similar but ratios of small:large bulls were changing, with the lower density population exhibiting a higher proportion of small bulls prior to the harvest. Under the conditions imposed by our model, increases in age-specific antler size associated with increased nutrition resulted in greater selection against alleles favorable for antler growth under a selective harvest scenario. The effect of nutrition on the potential for antler growth must be considered when predicting the outcome of antler-based selective harvests.

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Selective harvest of moose based upon antler size is a common management practice in Alaska and has proven to be an effective management tool (Schwartz et al. 1992). This strategy permits harvest of bulls with either a spike or forked antler (hereafter referred to as small bulls) or having an antler spread of at least 127 cm (50 in, large bulls). Any bull having at least 3 tines on 1 brow palm also is legal to harvest. Such a harvest plan allows a moderate level of harvest while ensuring stability in the proportion of males in the population and a greater mean age among males than does a plan in which any bull is legal. A modeling exercise demonstrated that this harvest plan also maintained allelic diversity among hypothetical loci coding for antler growth with the exception of alleles coding for numerous brow tines (Hundertmark et al. 1993).

The effect of environment on antler growth can be considerable, with estimates of up to 50% of variability in antler size being attributable to environment (Harmel 1983). At population densities below nutritional carrying capacity (K), cervids should be expected to exhibit larger age-specific body and antler size because of greater nutritional quality of forage (McCullough 1984). As the rate of antler growth changes in populations experiencing increasing nutrition, the response of these populations to selective harvest also may change. Many managed populations of moose in Alaska are held near carrying capacity due to hunting policies restricting harvest to males, and the population and genetic effects of selective harvest were evaluated only for populations at or near K (Hundertmark et al. 1993). Some populations in interior Alaska, however, are subject to low-density dynamic equilibria whereby moose exist at densities far below K due to the effects of predation (Gasaway et al. 1983, 1992). We conducted a modeling exercise to determine changes in genetic composition and harvest levels in a moose population held below K and compared our results with those from the model of populations at or near K.

METHODS

A stochastic population model (Fig. 1) reported originally by Thelen (1991) and modified by Hundertmark et al. (1993) was used to simulate populations of moose subjected to different harvest plans. The model took populations through annual cycles of birth of calves, summer mortality of calves, harvest, breeding, and winter mortality of adults and calves. All adult mortality was assumed to occur in winter. Each animal in the population was characterized by age, sex, and antler genotype and phenotype.

The initial population was created using estimates of age structure from a population from the northern Kenai Peninsula, Alaska (Schwartz et al. 1992). Survival rates of females were based upon those reported for the northern Kenai Peninsula by Bangs et al. (1989) but were adjusted slightly to produce a stable population. Summer and winter survival rates of calves were 0.55 and 0.40, respectively. Annual survival rates of females older than calves were 0.88, 0.95, 0.90, 0.85, 0.80, 0.70, 0.60, 0.45, 0.25, and 0.0 for ages yearling, 2-5, 6-10, 11-12, 13-14, 15-16, 17, 18, 19, and 20, respectively. Male survival rates were based upon those of females but were reduced by an exponential decay function in which a bull's antler-size-dependent survival (ASDS) decreased as it aged and its antler size increased. In the function $ASDS = 1 - [(SCORE - SOD)/60]^2$, SCORE is a numerical value (explained later) determined by a bull's genotype and the environment unique to that bull, and SOD is an age dependent value which reflects a score at which survival begins to drop. SOD values for calves and yearlings were 40, and for bulls aged 2-7 were 20, 16, 12, 8, 6 and 4, respectively. For bulls 8 years old or older the value of SOD was 2. We assumed that mortality would increase as a function of antler size because the energy required to produce and carry large antlers, as well as that required to achieve and maintain dominance during rut would place large-antlered animals in a greater energy deficit during winter compared with smaller-antlered animals. With these assumptions, the initial ratios of all bulls and large (>127 cm antler spread) bulls:100 cows were 80 and 34, respectively.

Based upon data from the Kenai Peninsula moose population (Alaska Dept. of Fish and Game, unpubl. data) we assigned a harvest rate equal to 50% of all legal bulls. We did not assume a relationship between the age of the bull and a learned ability to avoid hunters, unlike the model developed for elk (*Cervus elaphus*) by Thelen (1991).

Reproductive rates (calves/cow/yr) at K were 0.0 for calves, 0.22 for yearlings, 1.27 for ages 2-15, 0.14 for ages 16-19, and 0.0 for age 20 (Schwartz and Hundertmark 1993). To produce these rates in the model for the population at K we assumed that 12% of yearlings would produce single calves, 5% would produce twins, and 83% would produce no offspring. Respective values for other age classes were 63%, 32%, and 5% for ages 2-15, and 8%, 3%, and 89% for ages 16-19. To simulate changes in productivity associated with changes in population density relative to K we increased the twinning rate as density decreased (Franzmann and Schwartz 1985). The sex ratio of offspring at birth was 1:1 (Schwartz and Hundertmark 1993).

To simulate a population held below K by predation, we increased mortality rate as moose population size increased. Additional mortality was nil at a population size of 4000 and increased exponentially until it accounted for an additional 5.6% at or above K (10000 animals).

Antler growth was assumed to be an age-dependent polygenic trait. In the model, 5 pairs of genes and environmental influences were assumed to contribute to an antler growth score (SCORE). For each locus, there were two possible alleles: favorable and unfavorable, which contributed 4 and 0 points to the genotype score, respectively. Thus, the genotype score for antler growth varied from 0-40 (allele score x two alleles/locus x five loci). The model tracked the frequency of favorable antler alleles (Q_A). Environmental scores were generated randomly from a distribution with the same mean and variance as the genotype scores and one was permanently assigned at birth to each male. A combination of an individual's genotype and environmental scores created its antler phenotype score which determined age-specific antler size. We assumed a heritability of 0.5. Unlike the prior exercise (Hundertmark et al. 1993) this model did not include an option to take a bull legally if it had at least 3 brow tines on one antler. The hypothetical locus controlling expression of brow tines was considered independent of loci encoding for antler spread and we assumed that any effects attributable to genotype at this locus would be identical for either model.

Slower rates of antler growth in yearlings were manifested in spike/fork antlers. Antlers of this size were assumed to be present only in yearlings, and accounted for 60% of antlers in this age class in a population at K (Schwartz et al. 1992). Other yearlings and bulls older than yearlings have palmated antlers that were characterized by a spread measurement. Age-dependent antler spreads (Table 1) were assigned to the initial population based upon data from hunter check stations on the Kenai Peninsula. Maximum spreads occurred in animals 8-12 years old (Gasaway et al. 1987).

To simulate the effect of increased nutrition on antler phenotype resulting from the better nutrition available to a population below K, we multiplied the antler score by a variable that changed as population size changed. With a population at or below 4000 animals, antler scores were multiplied by 1.36. This value declined exponentially until it equaled 1.00 at a population of 10000 (K). In this way, heritability remained at 0.5 throughout the simulation.

As our model was stochastic, we ran ten simulations of each scenario, from which we generated means and standard deviations of estimates of population and genetic composition. The original modeling exercise (Hundertmark et al. 1993) tracked populations for 50 years, but we extended the model to 100 years in this effort. Estimates of population composition and allele frequencies were generated from the initial population (year 0) and at 5-year intervals to year 100. The

simulation of no harvest (Model A) conducted by Hundertmark et al. (1993) was compared with simulations of harvest in a population at carrying capacity (Model B), and harvest in a population held below carrying capacity by predation (Model C). Comparisons between new simulations and Model A were necessarily limited to the first 50 years due to the length of simulations run by Hundertmark et al. (1993) and are reported here to facilitate comparison with that earlier effort, but comparisons between the current two models included data from the entire 100 year simulations.

Differences in final estimates of parameters between any two simulations were tested with a *t*-test; all comparisons were tested simultaneously and Bonferonni adjusted probabilities were reported. Differences in parameters among all simulations were tested with ANOVA. Post hoc tests among means within ANOVA were conducted with Bonferonni comparisons.

RESULTS

Population size after 50 years differed among the populations ($F_{2,27} = 1350$, $P < 0.0001$). Both harvested populations had significantly fewer animals than the unhunted population and Model C had significantly fewer animals than Model B. Both populations subjected to hunting declined initially as hunting was instituted (Fig. 2a). The population under Model B recovered from this decline as density dependent processes brought the total size back toward K where it stabilized. The population under Model C stabilized at approximately 7000 animals, representing an equilibrium between the greater rates of mortality and increased productivity associated with better nutrition.

Percent declines in Q_A over the first 50 years for Models A, B, and C were 1.1, 5.4, and 15.5 respectively (Table 2). Estimates of Q_A in Year 50 differed significantly ($F_{2,27} = 503.4$, $P << 0.0001$) among the three models, with selective harvest in Model C causing the greatest decline. In the two models involving selective harvest, allele frequencies continued to decline at steady but different rates through the 100 years of the simulation (Fig. 2b).

Total harvest under both models decreased for the first 10 years, primarily because the population was unhunted prior to Year 1. After Year 10, harvest increased initially prior to becoming stable for Model B whereas it decreased slowly for Model C (Fig. 2c). By Year 50, the mean harvest of small bulls under Model C was significantly less than under Model B ($t = 8.35$, d.f. = 18, $P < 0.0001$, Table 2). Mean harvest of large bulls also was less under Model C ($t = 10.68$, d.f. = 18, $P < 0.0001$, Table 2). Moreover, the proportion of spike-fork yearlings in the harvest differed between the two scenarios. Under both models, the proportion of spike-fork yearlings increased concomitant with the decrease in harvest in the first decade; this reflected the harvest of abundant large bulls in the previously unhunted populations. Subsequently, the small bull:large bull ratio in the population prior to harvest increased slightly under Model B but increased at a faster rate under Model C (Fig. 2d). By Year 100, spike-fork yearlings represented 43.8% of the harvest under Model B whereas they represented 51.7% of the harvest under Model C, compared with an approximate 30% share of the harvest initially.

Bull:100 cow ratios of hunted populations after 50 years were reduced significantly ($F_{2,27} = 2800$, $P < 0.0001$, Table 2) from that of the unhunted population and differed significantly from each

other although this latter difference likely had no biological significance. Moreover, these ratios were well above the objective level of approximately 30 bulls:100 cows (Schwartz et al. 1992). Ratios of large bulls:100 cows also differed among the simulations ($F_{2,27}$ = 4592, P < 0.0001), with hunting causing a marked decrease. At 50 years, the low density population had a significantly higher large bull:100 cow ratio than did the hunted population at K (Table 2).

The most notable difference in composition between the two hunted populations was the decrease in the number of large bulls in Model C (Fig. 2e). After the initial decrease in the first decade, numbers of large bulls increased slightly under Model B and stabilized. Under Model C, numbers of large bulls continued to decrease. After 100 years, large bull:100 cow ratios for Model B (4.2 [SD 0.32]) and Model C (4.5 [SD 0.41]) did not differ (t = -1.75, d.f. = 18, P = 0.097) but the ratio of the population in Model C would be expected to continue to decline. The number of spike-fork yearlings in each population increased at relatively constant rates (Fig. 2f). Thus, the proportion of spike-fork yearlings in the harvest under Model C initially was less than that under Model B, but increased at a faster rate and was greater than that in Model B by year 50 (Fig. 2d).

DISCUSSION

We caused an increase in expression of antler size via increased nutrition in a population in which density was decreased relative to K. This increase in phenotype initially caused an increase in the proportion of large bulls in the population (relative to a population at K) and a decrease in the proportion of spike-fork yearlings. These changes were short-lived, however, as changes in harvest of these groups caused changes in allele frequencies. Specifically, the decrease in number of spike-fork yearlings available for harvest caused a decrease in selection against unfavorable antler alleles. Under the original simulations conducted by Hundertmark et al. (1993), the harvest of animals with inferior genotypes as spike-fork yearlings balanced the harvest of animals with superior genotypes as large bulls and acted to stabilize allele frequencies over time. In the current simulation, more inferior animals grew palmated antlers as yearlings due to better available nutrition and thus were protected from harvest. This caused an increase in the frequency of unfavorable antler alleles and a corresponding decrease in the frequency of favorable alleles. Moreover, animals with superior genotypes would, due to increased nutrition, spend less time in the protected class of animals and would thus get less of an opportunity to breed. The outcome of these changes in phenotype was an increase in selection pressure against favorable alleles and a consistent decrease in the proportion of bulls in the population with antler spreads greater then 127 cm.

McCullough (1984) demonstrated that trophy harvest from a white-tailed deer (Odocoileus virginianus) herd was higher when both males and females were harvested. He argued that reducing population density below K caused an increase in nutritious forage and a corresponding increase in age-specific antler size. The absolute decrease in number and harvest of large bulls in Model C seemingly runs counter to this idea, but McCullough was considering harvest as a random process whereas we harvested males based on antler size. Harvest based on antler size always decreased the frequency of favorable antler alleles compared with random harvest in previous simulations (Hundertmark et al. 1993).

Changes in antler size were gradual in this simulation and likely would escape detection for a number of years. Ultimately, however, there likely would be adequate time to detect and rectify the problems observed. Managers should monitor ratios of large:small bulls in their post-hunt surveys and in their harvest reports. Any significant and lasting change in this ratio not accounted for by changes in population density would indicate potential changes in genetic composition in the population.

We assumed that nutritional carrying capacity of the habitat did not change throughout the simulations; this assumption is unlikely to hold in most populations. Nonetheless, our results are informative because they demonstrate that alleles controlling antler growth are subject to a continuum of selective force ranging from balancing selection at or near K to selection against favorable alleles below K. This information is particularly relevant to Alaska moose populations that are being considered for intensive management (Hundertmark and Schwartz 1996).

This exercise demonstrates the contribution of environment to antler growth and the effect this may have on management of moose populations by selective harvest. The relative position of the population with respect to K will determine the success of selective harvest management. The trends observed in this simulation were dramatic only when extended many years into the future, allowing time to detect and rectify problems. The true relationships between nutrition and expression of antler size in moose needs to be documented before real effects of selective harvest can be accurately assessed.

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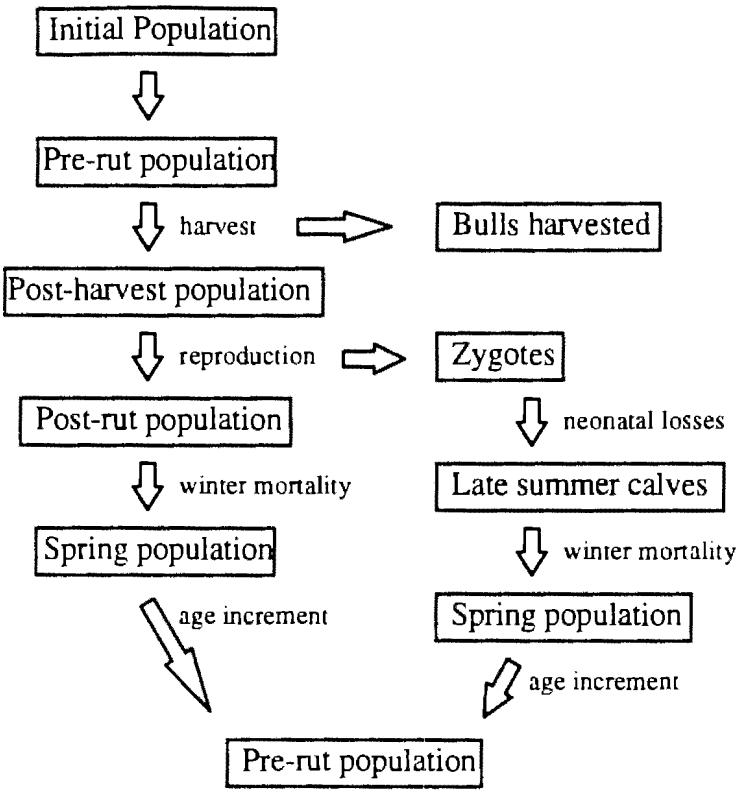

Figure 1 Flow chart of the stochastic model

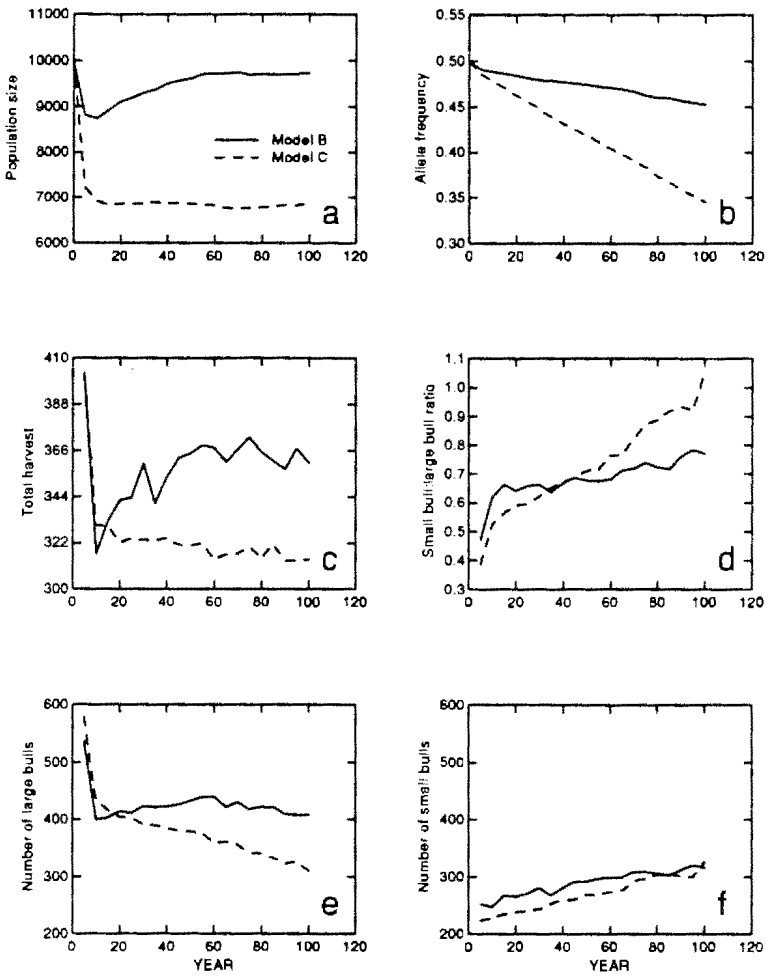

Figure 2 Temporal changes in a) total population size, b) frequency of favorable antler alleles, c) total harvest, d) small bull:large bull (preharvest) ratio, e) number of large bulls in the preharvest population, and f) number of small bulls in the preharvest population for simulated moose populations subjected to either harvest Model B or C (*see* Methods section)

Table 1 Percentage of bulls in four age classes in the initial populations characterized by antler spread

Age (yrs.)	Spike/fork	<91 cm	≥91 and < 127 cm	≥127 cm
1	60	25	15	0
2-3	0	25	60	15
4-5	0	0	60	40
≥6	0	0	5	95

Table 2 Population parameters of simulated moose populations at Year 50. Data for Model A taken from Hundertmark et al. (1993). Values represent means (SD) of 10 simulations. Harvest data are means of years 30–50 of the simulations.

Model	Frequency of favorable alleles	Population size	Harvest of small (spike/fork) bulls	Harvest of large (> 127 cm spread) bulls	Number of bulls per 100 cows	Number of large bulls per 100 cows
A	0.490^{A}	9956^{A}	0	0	79.4^{A}	33.5^{A}
	(0.0033)	(167)			(1.65)	(1.2)
B	0.470^{B}	9457^{B}	140^{a}	210^{a}	43.4^{B}	4.4^{B}
	(0.0024)	(166)	(3)	(3)	(0.88)	(0.3)
C	0.420^{C}	6805^{C}	126^{b}	195^{b}	37.2^{C}	5.1^{C}
	(0.0079)	(90)	(4)	(3)	(1.09)	(0.5)

^{A,B,C} Means within a column differ significantly (ANOVA and Bonferonni post hoc comparisons)

^{a,b} Means within a column differ significantly (*t*-test)

APPENDIX B

GENETIC TECHNIQUES AND THEIR APPLICATION TO MOOSE MANAGEMENT

Kris J. Hundertmark[1]

Analysis of genetic variation can entail the study of phenotype or genotype. The study of phenotype is confounded by gene and environmental interactions but is essential when studying heritability or fitness correlates. Numerous techniques exist for analysis of genotype. Allozymes are allelic enzymes (gene products) that can eb resolved on a gel and represent one of the oldest techniques available. Analyses of allozymes have been used to examine population subdivision, systematics, and the relationship between genetic diversity and fitness correlates. Allozymes are relatively inexpensive to analyze; however, obtaining enough loci for analysis requires tissues that can only be collected from deaad animals. The advent of the polymerase chain reaction and sequencing technology has allowed intensive genetic analyses to be conducted on extremely small samples of tissue, and has permitted analysis at the nucleotide level in both nuclear and mitochondrial genomes. Mitochondrial DNA (mtDNA) is a maternally inherited genome that is useful for determining phylogenies on time scales ranging from recent to millions of years before present. The high degree of female philopatry characteristic of moose (Alces alces) and numerous other wildlife species makes this molecule particularly useful for determining population identity on a spatial scale.

[1]Published as part of an expanded abstract entitled *New Technologies for Moose Management: a Workshop*, written by A. R. Rodgers, S. M. Tomkiewicz, E. J. Lawson, T. R. Stephenson, K. J. Hundertmark, P. J. Wilson, B. N. White, and R. S. Rempel

Physiological Ecology of Moose: Nutritional Requirements for Reproduction with Respect to Body Condition Thresholds

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Study 1.52
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RESEARCH PROGRESS REPORT

STATE: Alaska **STUDY NO.:** 1.52

COOPERATORS: Kenai National Wildlife Refuge, Soldotna, Alaska

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STUDY TITLE: Physiological Ecology of Moose: Nutritional Requirements for Reproduction with Respect to Body Condition Thresholds

AUTHORS: Thomas R. Stephenson, Kris J. Hundertmark, John A. Crouse, and Charles C. Schwartz

PERIOD: 1 July 1996–30 June 1997

SUMMARY

We collected data on fat reserves and reproductive performance of adult female moose (*Alces alces*) during 1996 and 1997. Animals were primarily maintained on a natural browse diet during June–August and an ad libitum pelleted diet during September–May. Mean ultrasonic rump fat thickness and corresponding ingesta-free body fat were 5.0 cm (0.4 SE) and 15.9% (0.7 SE), respectively, for adult cows during November 1995–June 1997. Twelve of 13 adult female moose that mated with a bull during fall 1996 were subsequently diagnosed pregnant. During June–August 1996 and 1997, 6 of 11 (54.5%) and 1 of 6 (16.7%) radiocollared calves survived, respectively. In addition, during June–August 1997 only 2 of a minimum of 9 additional unmarked calves survived. Black bear predation was the primary cause of neonatal calf mortality. Neonatal immunocompetence was assessed by evaluating serum for mean gamma globulin (1.65 g/dl ± 0.2 SE) and gamma glutamyl transferase (GGT; 243.7 U/L ± 40.4 SE). We conducted extensive remodeling of the animal facility to facilitate upcoming feeding trials and permit more efficient animal handling. We also began training moose to use electronic controlled-access feed gates.

Key words: *Alces alces*, body condition, fat reserves, reproduction, immunocompetence, ultrasound.

CONTENTS

BACKGROUND

To facilitate intensive management of moose populations, we must be able to predict survival and reproductive success of individuals within these populations. Although population size is dictated by numerous factors such as weather and predation, ultimately habitat quality defined by the nutritional quality of diets will determine the maximum number of moose that an area can support. Reproductive performance of cow moose is probably related to their body condition. We intend to refine the use of an individual animal's condition as an indicator of the nutritional quality of its habitat and as a predictor of its potential for reproduction and survival.

Recently, methodology for applying the "animal indicator concept" (Franzmann 1985) was validated. Stephenson (1995) developed equations to predict total body fat in moose from ultrasonographic fat measurements. Hundertmark et al. (1994) also developed equations to

predict body composition using bioelectrical impedance analysis. The animal indicator approach assumes that because the animal is a product of its environment, it represents the quality of its environment. Thus, rather than define carrying capacity in numbers of animals, this approach provides a relative indication of the proximity of the population to K. Recently, Grubb (1995) defined nutritional condition as "the state of body components controlled by nutrition and which in turn influence an animal's fitness." Saltz et al. (1995) noted that Grubb's definition clearly identifies the role of nutrition in determining an animal's condition and ultimately its reproductive success.

Because body fat is the primary energy store of the body (Price and White 1985), measurement of lipid reserves has been the focus of much research aimed at estimating nutritional condition (Chan-McLeod et al. 1995, Franzmann and Ballard 1993, Harder and Kirkpatrick 1994, Gerhart 1995). Assessment of body condition provides insight into the ability of individuals in a population to survive and reproduce. However, in order to evaluate the role of body condition in determining an animal's reproductive fitness, we also must be able to assess reproductive performance including ovulation, conception, fetal numbers and survival, and natal survival.

Although summer twinning rates have been used to indicate the quality of moose habitats (Franzmann and Schwartz 1985), undetected predation may lead to biased postpartum estimates (Stephenson et al. 1995). Ultrasonography has been used to successfully determine in utero pregnancy and twinning in moose during both early (Stephenson et al. 1995) and late gestation (J. W. Testa, ADF&G, Anchorage, unpubl. data). Because ultrasonography requires specialized equipment and expertise, a serum assay that diagnoses twinning is of interest. Willard et al. (1995) recently developed a quantitative pregnancy-specific protein B assay for domestic sheep that permitted detection of fetal twins with up to 82% accuracy.

Although the existence of threshold "set points" of body condition have been hypothesized for ungulates (Schwartz et al. 1988*a*; Renecker and Samuel 1991; Gerhart 1995), their existence relative to reproduction in moose has only recently begun to be quantified (J. W. Testa, ADF&G, Anchorage, unpubl. data; M. Keech, ADF&G, Fairbanks, unpubl. data). Aside from identifying the mechanisms of reproductive failure, an understanding of thresholds required for ovulation, gestation, and neonatal calf survival will offer new insights regarding the importance of different seasonal habitats and management of these habitats.

Poor maternal nutrition may lead to failure in the passive immunity process between mother and offspring and increase susceptibility to diarrhea, septicemia, and other diseases in neonates. Sams et al. (1996) identified a relationship between serum immune parameters and neonatal mortality of white-tailed deer fawns. Low neonate serum levels of colostral antibodies may occur from inability to efficiently nurse, poor colostral absorption, or depressed colostrum production (Sams et al. 1996). Indices of fawn viability such as immunocompetency or maternal condition may provide insight relative to the additive or compensatory nature of predation.

To validate the animal condition approach, we will conduct experiments with animals foraging on natural browse in addition to animals on trials using pelleted rations. As a

population approaches carrying capacity, increased competition for forage resources should reduce average body condition. Hobbs and Swift (1985) hypothesized that as population density increases, the upper limit on nutritional quality of diets obtainable will decline progressively. Deterioration in the nutritional status of individuals would be expected as population density increases, and the condition of individuals could be monitored to assess diet quality. However, ruminants may be able to increase intake rate in response to declining forage quality. Determining the ability of moose to compensate as density changes will enable us to understand limitations of using the animal–condition approach to assess habitat quality and the mechanisms of density dependence.

OBJECTIVES

1. Determine overwinter nutritional requirements for reproductive success in female moose

2. Determine thresholds in body condition at which reproductive performance declines

3. Evaluate the existence of cumulative effects in female moose relative to body condition, reproductive performance, and nutrition

4. Refine estimation of moose body composition

5. Using ultrasonography and a quantitative serum assay, develop and refine methodology for diagnosing twinning in moose

6. Evaluate effects of density dependence on body condition, reproductive performance, and diet quality of habituated moose on natural browse

STUDY AREA

We conducted this research at the Moose Research Center, located on the Kenai Peninsula, Alaska (60°N, 150°W).

METHODS

JOB 1. CONDUCT FEEDING TRIALS TO EVALUATE THE RELATIONSHIP BETWEEN MOOSE NUTRITION, BODY CONDITION, AND REPRODUCTIVE PERFORMANCE

Extensive remodeling of the animal handling facility was conducted during this period. Alleyways were redesigned to better accommodate moving and weighing animals. We began testing a controlled-access feeding system (American Calan, Inc., Northwood, New Hampshire, USA) for use in individualized feeding trials. The system utilizes a feed container, accessible only through a neck slot controlled by a 24-volt electronically locking gate that is unlocked by an individual-specific sensing "key" collar worn by the animal (Mazaika et al. 1988).

JOB 2. EVALUATE RELATIONSHIP BETWEEN CALF HEALTH AND THE DAM'S NUTRITION AND BODY CONDITION

Moose were immobilized during September and November–January using carfentanil hydrochloride/xylazine hydrochloride. Portable, real-time ultrasound was used to measure fat reserves of adult females. The rump region was scanned using an Aloka model 210 ultrasound device (Corometrics Medical Systems, Inc., Wallingford, Connecticut, USA.) with a 5 MHz 8 cm linear-array transducer. Ultrasonic fat thickness was measured at 2 sites along a line between the spine, at its closest point to the coxal tuber (hip bone), and the ischial tuber (pin bone). We measured subcutaneous fat thickness with electronic calipers to the nearest 0.1 cm at the midpoint and point of maximum thickness (immediately adjacent to the cranial process of the ischial tuber) along the line. We determined 2 fat thickness indices: 1) the maximum fat thickness detected along the line (MAXFAT), and 2) the sum of the maximum thickness and the thickness at the midpoint (SUMFAT). Stephenson et al. (In press) developed an equation to predict percent ingesta-free body fat from rump fat thickness ($R^2 = 0.96$, SEE = 1.09). Ingesta-free body fat was calculated using the equation:

$$\text{ingesta-free body fat (\%)} = 5.61 + 2.05 \text{ (maximum fat thickness)}.$$

In addition, we weighed adult females periodically. Serum was collected during November–January to determine pregnancy-specific protein-B (PSPB). Transrectal ultrasonography also was used to diagnose pregnancy (Stephenson et al. 1995).

We captured newborn calves by hand after locating them by ground surveillance. Calves were handled after >12 hours had elapsed since birth to avoid abandonment by the mother. Captured calves were equipped with expandable break-away radio collars and numbered ear tags. We recorded sex, body mass, total body length, and hind foot length at capture. Serum was collected and evaluated for determination of immunocompetence (Sams et al. 1996), specifically concentrations of gamma-globulins (colostral antibodies) and gamma-glutamyl transferase (GGTP; used to indirectly measure the efficiency of colostral absorption). Lab analyses were conducted by Phoenix Central Labs, Seattle, Washington, USA. To evaluate the effects of calf age on cholostral indices, we regressed age on gamma globulin and GGT concentration.

JOB 3. FURTHER VALIDATE APPROACHES FOR DETERMINING BODY FAT AND BODY PROTEIN IN LIVE MOOSE

No activity on this job occurred during this reporting period.

JOB 4. DEVELOP SERUM ASSAY TO DETECT TWINNING

This is a cooperative project with the University of Idaho, Department of Animal and Veterinary Sciences. Placentas were collected from road-killed pregnant female moose during winter (middle to late gestation), stored frozen, and shipped to Idaho. Pregnancy-specific protein B (PSPB) was isolated from moose cotyledonary tissue by radioimmunoassay at the University of Idaho and is being used to develop a standard curve that will permit quantitative assessment of PSPB in moose sera (Willard et al. 1995).

JOB 5. MONITOR BODY CONDITION AND REPRODUCTIVE PERFORMANCE OF COW MOOSE STOCKED AT DIFFERENT DENSITIES AND FEEDING ON NATURAL BROWSE

No activity on this job occurred during this reporting period.

RESULTS AND DISCUSSION

JOB 1. CONDUCT FEEDING TRIALS TO EVALUATE THE RELATIONSHIP BETWEEN MOOSE NUTRITION, BODY CONDITION, AND REPRODUCTIVE PERFORMANCE

Moose were successful in learning to use the Calan feed gates. Appropriate height of the gates relative to the "key" collar was essential for proper functioning of the gate. The mean height above ground of the electronically active section of the door was 50.5 inches (range = 49–54 inches). Gate slot width and base height were 9.5 and 40.5 inches, respectively. The edge of the feed bowl was 13 inches behind the gate, and the maximum depth of the bowl was 22 inches below the base of the door.

The Calan feeding system eliminates experimental bias associated with individually confining animals during feeding trials. Furthermore, experimental treatments may be assigned to individual animals contained within a common pen.

JOB 2. EVALUATE RELATIONSHIP BETWEEN CALF HEALTH AND THE DAM'S NUTRITION AND BODY CONDITION

Mean ultrasonic rump fat thickness and corresponding ingesta-free body fat (IFBFAT) were 5.0 cm (0.4 SE) and 15.9% (0.7 SE), respectively, for adult cows during November 1995–June 1997 (Table 1). Means were not partitioned by pregnant and nonpregnant animals because a portion of the females were intentionally withheld from breeding and consequently retained fat because they were not expending energy on pregnancy and lactation. However, for comparison with pregnant females fed a submaintenance ration during 1994, mean IFBFAT of 4 nonpregnant adult females was 17.2% (1.9 SE) and 18.0% (1.4 SE) during January and March, respectively (Table 1). During November 1996, Deshka had a predicted 118.9 kg of body fat representing endogenous energy reserves of 1,082,814 kcal. In contrast during September 1996, Dodger, who had reproduced and lactated since she was a yearling, had 18.6 kg of body fat (169,446 kcal). Because animals were provided pelleted feed ad libitum during winter, minimal decline in body condition occurred in many animals during winter and, therefore, these values probably represent a baseline approaching maximum body condition in adult female moose. Twelve of 13 (92.3%) adult female moose confined with mature bulls during fall 1996 were subsequently diagnosed pregnant.

Eighteen neonatal moose calves were handled during 1996 and 1997 (Table 2). During June–August 1996 and 1997, 6 of 11 (54.5%) and 1 of 6 (16.7%) radiocollared calves survived, respectively. In addition, during June–August 1997 only 2 of a minimum of 9 additional unmarked calves survived. Black bear predation was the primary cause of neonatal calf mortality.

Serological data to determine neonatal immunocompetence (Table 3) indicated that mean gamma globulin (1.65 g/dl ± 0.2 SE) and gamma glutamyl transferase (GGT; 243.7 U/L ± 40.4 SE) were higher than values for white-tailed deer (*Odocoileus virginianus*; Sams et al. 1996) and much lower than for caribou (*Rangifer tarandus*; this report). Mean values for gamma globulins in this

study were twice those reported for wild moose on the Kenai Peninsula during 1977–1978 (Franzmann et al. 1980). No relationship was detected when both gamma globulin and GGT (Fig. 1 and 2) were regressed on age ($r^2 < 0.17$, $P > 0.14$).

CONCLUSIONS AND RECOMMENDATIONS

In preparation for upcoming feeding trials, we have formulated and are testing pelleted rations of differing nutritional quality.

Sera collection and ultrasonography from cows immobilized as part of Job 1 and routine immobilizations will be used to evaluate the accuracy of the PSPB test. Repeated collections of sera from individual moose will enable evaluation of the pattern of increased PSPB concentrations with increasing placental mass as gestation proceeds. Calving observations will provide further evaluation of the test's accuracy. The assay will be evaluated for accuracy in diagnosing twin and singleton litters and in predicting breeding date.

To develop neonatal calf age/weight relationships, we plan to collect daily weights of neonatal calves during the week following birth. Bottle-raised cows at the MRC should permit frequent handling of their calves.

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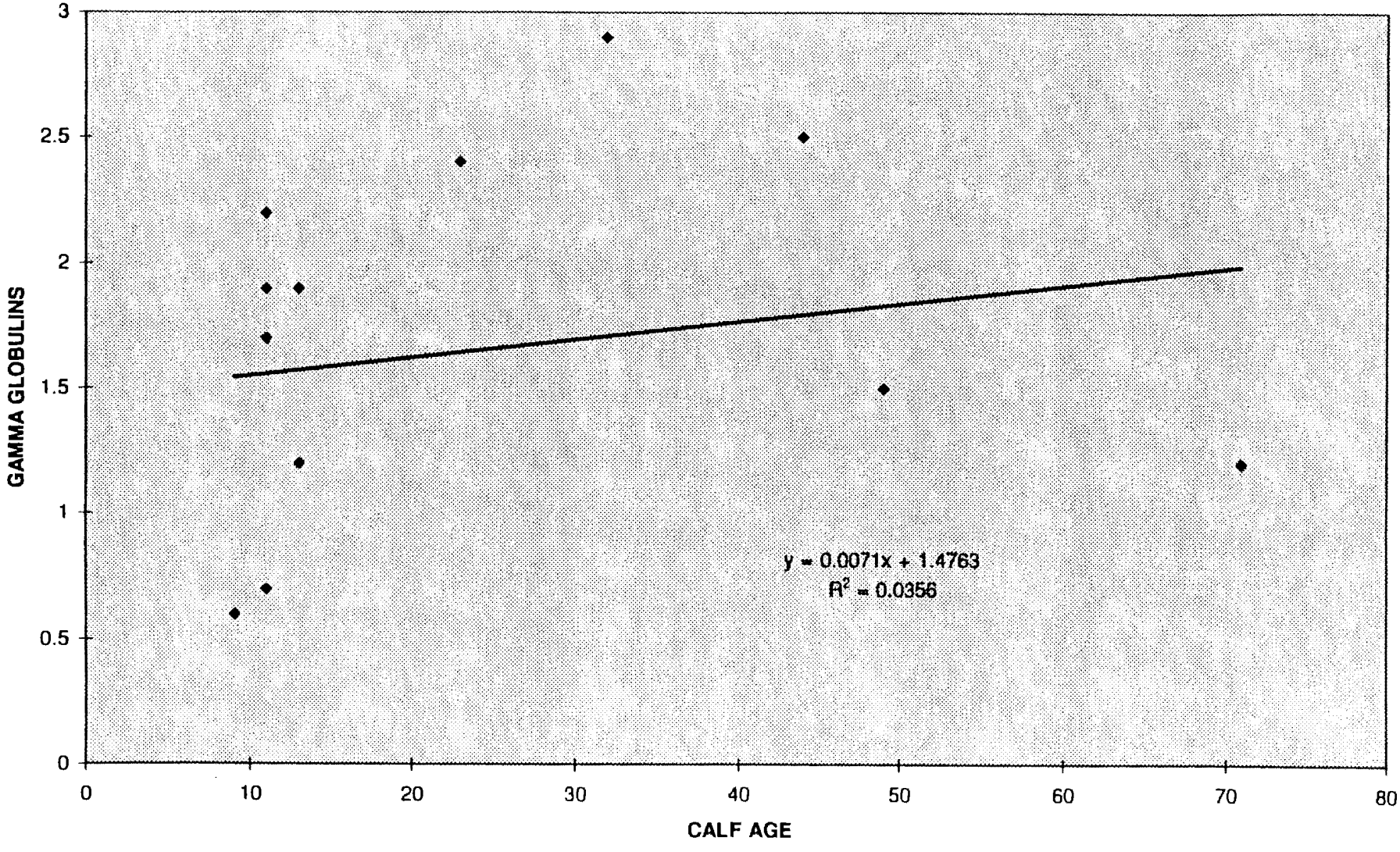


Figure 1 Relationship between serum gamma globulins and age of neonatal moose calves at the Kenai Moose Research Center, 1996–1997

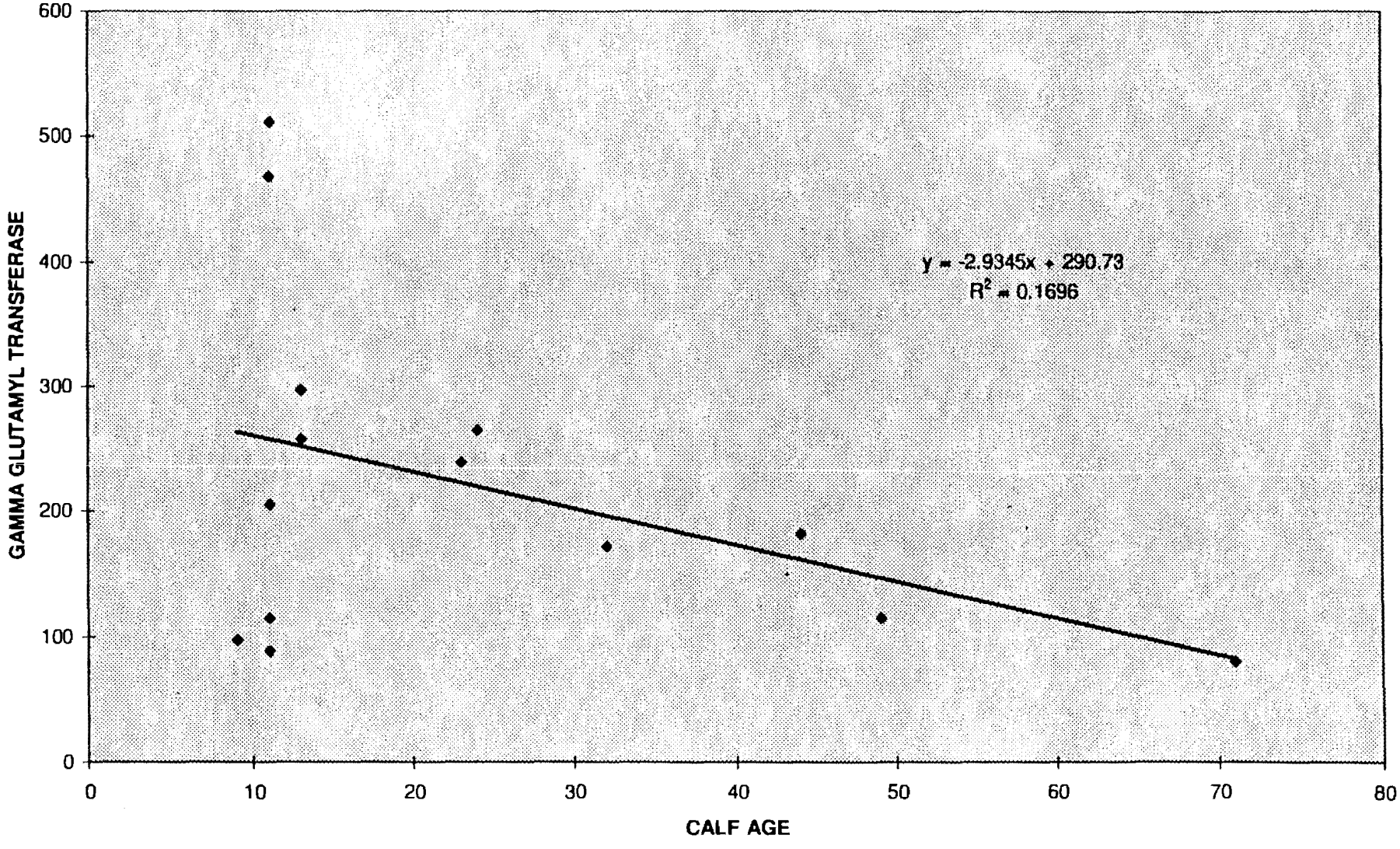


Figure 2 Relationship between serum gamma glutamyl transferase and age of neonatal moose calves at the Kenai Moose Research Center, 1996–1997

Table 1 Ingesta-free body fat (IFBFAT; predicted from ultrasonic maximum rump fat thickness [MAXTH]) and pregnancy status of adult female moose at the Moose Research Center, Alaska, during 1995–1997

Animal	Midth	Maxth	Sumth	IFBFAT (%)	IFBFAT (kg)	Mass	Pregnant
11/20/95 Sabrina	1.4	3.4	4.8	12.58	48.57		Y
01/29/96 Deshka	4.4	7.6	12	21.19	93.3		N[1]
01/29/96 Lara	1.2	3.1	4.3	11.965	45.375		N[1]
01/29/96 Luna	4.4	6.2	10.6	18.32	78.39		N[1]
01/30/96 Satorene	3	5.7	8.7	17.295	73.065		N[1]
02/01/96 Erma	1.6	3.1	4.7	11.965	45.375	407	N[1]
02/01/96 Hillary						366	Y
02/01/96 Sabrina	2.2	5.6	7.8	17.09	72		Y
02/01/96 Sue						516	N[1]
02/05/96 Erma	1.6	3.1	4.7	11.965	45.375	407	N[1]
03/05/96 Blue	2.9	5.7	8.6	17.295	73.065	491	Y
03/05/96 Caitlin	2.3	5.3	7.6	16.475	68.805	513	Y
03/05/96 Dodger	4.5	7	11.5	19.96	86.91	502	Y
03/05/96 Laurel	3.5	6	9.5	17.91	76.26	515	Y
03/05/96 Mustard	2.3	6.3	8.6	18.525	79.455	498	Y
03/05/96 Scarlet	1.2	4.7	5.9	15.245	62.415	502	Y
03/31/96 Deshka	3.7	6	9.7	17.91	76.26	522	N[1]
03/31/96 Lara	2.4	4.1	6.5	14.015	56.025	454	N[1]
03/31/96 Luna	4.5	7.4	11.9	20.78	91.17	521	N[1]
03/31/96 Sato	2.5	6.7	9.2	19.345	83.715	508	N[1]
03/31/96 Sue	2.1	6.2	8.3	18.32	78.39	518	N[1]
09/24/96 Dodger	0.4	0.7	1.1	7.045	19.815		NA[2]
09/24/96 Luna	6.8	9.3	16.1	24.675	111.405		NA
09/24/96 Mustard	0.3	2.5	2.8	10.735	38.985		NA
09/24/96 Sue	2.2	6.5	8.7	18.935	81.585	550	NA
11/18/96 Dodger	0.9	2.6	3.5	10.94	40.05	421	Y
11/19/96 Blue	0.8	1.9	2.7	9.505	32.595	413	N
11/19/96 Deshka	6.4	10	16.4	26.11	118.86	574	Y
11/19/96 Mustard	1.2	3.6	4.8	12.99	50.7	440	Y
11/21/96 Laurel	3.1	6.4	9.5	18.73	80.52	521	Y
11/21/96 Luna	5.4	8.6	14	23.24	103.95	570	Y
11/21/96 Scarlet	0.8	3.3	4.1	12.375	47.505	478	Y
11/21/96 Sue	3.6	7.8	11.4	21.6	95.43	570	Y
11/22/96 Sabrina	0.8	1.5	2.3	8.685	28.335		N
12/19/96 Caitlan	1.5	4	5.5	13.81	54.96	445	Y
12/19/96 Satorene	1	5.8	6.8	17.5	74.13	455	Y
01/30/97 Lara	0.4	3.6	4	12.99	50.7	436	Y
01/31/97 Erma	2	4.4	6.4	14.63	59.22		Y

Table 1 Continued

Animal	Midth	Maxth	Sumth	IFBFAT (%)	IFBFAT (kg)	Mass	Pregnant
01/31/97 Hillary	0.7	1.7	2.4	9.095	30.465		Y
06/26/97 Satorene	1.6	4	5.6	13.81	54.96		NA

[1]These animals were intentionally withheld from mating as part of another study.
[2]Not applicable.

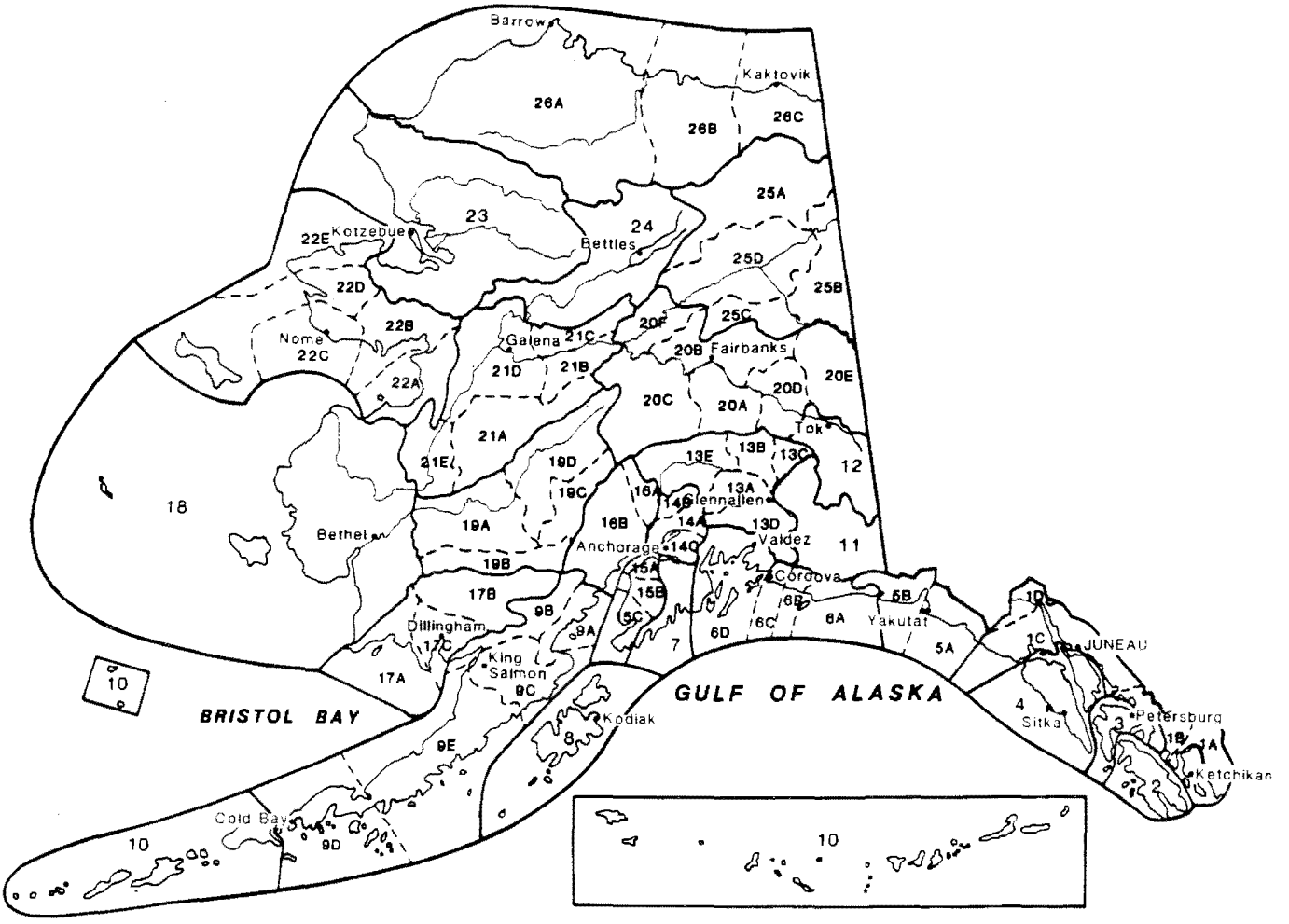
Table 2 Descriptive data for neonatal moose calves at the Moose Research Center during 1997

Name	Dam	Date	Time	Age (hours)	Sex	Mass (lbs)	HF (cm)	TL
Levi	Blue	05/28/96	1035	11	Female	41	47	105
Renny	Sabrina	05/28/96	0950	13	Male	44	49	104
Mattie	Hillary	05/26/96	1605	44	Female	29	44	100
Laur96	Laurel	05/26/96	1550	10	Male	39	49	105
Clay	Scarlett	05/25/96	1000	13	Male	43	48	103
Daisy	Dodger	05/24/96	1250	11	Female	35	45	79
Danny	Dodger	05/24/96	1235	11	Male	36	47	96
Must96	Mustard	05/20/96	2000	11	Female	29	41.5	91
Clover	Mustard	05/20/96	2000	11	Female	31.5	43	93
Cait961	Caitlin	05/19/96	0745	9	Female	36	47	102
Cait962	Caitlin	05/18/96	2250	1	Female	34	46	99
Laur97	Laurel	05/28/97	1500	23	Male	30	45	
Shaq	Laurel	05/31/97	1515	71	Male		47	107
Flo	Dodger	05/31/97	1200	49	Female	37	44	100
Diana	Luna	05/31/97	1600	32	Female	40	50	104
Isabelle	Scarlett	06/12/97	1700	24	Female	24	42	93
Horton	Satorene	06/14/97	1900	50	Male	43	46	96

Table 3 Serological data for neonatal moose calves at the Moose Research Center, 1996–1997

Name	Date	Time	Age (hours)	GGT	Albumin	Alpha 1	Alpha 2	Beta	Gamma	Tot. Prot
Levi	05/28/96	1035	11	206	2.1	1.1	0.2	0.4	1.7	5.5
Renny	05/28/96	0950	13	297	2.3	1	0.3	0.4	1.2	5.5
Mattie	05/26/96	1605	44	182	2.3	1	0.3	0.6	2.5	6.7
Clay	05/25/96	1000	13	258	2.3	1	0.3	0.3	1.9	5.8
Daisy	05/24/96	1250	11	511	2.2	1.1	0.5	0.5	2.2	6.5
Danny	05/24/96	1235	11	468	2	1.1	0.2	0.3	1.9	5.5
Must96	05/20/96	2000	11	114	2	1.3	0.2	0.3	0.7	4.5
Clover	05/20/96	2000	11	89	2.1	1.2	0.2	0.3	0.7	4.5
Cait961	05/19/96	0745	9	97	1.9	1.3	0.4	0.3	0.6	4.5
Laur97	05/28/97	1500	23	239	2.2	1	0.1	0.5	2.4	6.2
Shaq	05/31/97	1515	71	80	2.4	1.1	0.2	0.7	1.2	5.6
Flo	05/31/97	1200	49	115	2.8	0.7	0.3	2.2	1.5	7.5
Diana	05/31/97	1600	32	172	2.1	1	0.1	0.5	2.9	6.6
Isabelle	06/12/97	1700	24	265	2.5					4.4
Isabelle	06/22/97		240	563	2.3					4.2

Alaska's Game Management Units



The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer's excise tax collected from the sales of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program allots funds back to states through a formula based on each state's geographic area and number of paid hunting license holders. Alaska receives a maximum 5% of revenues collected each year. The Alaska Department of Fish and Game uses federal aid funds to help restore, conserve, and manage wild birds and mammals to benefit the public. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes for responsible hunting. Seventy-five percent of the funds for this report are from Federal Aid.

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