

ECOLOGICAL AND SOCIAL INFLUENCES ON POPULATION DYNAMICS
AND GENETICS OF MOOSE IN ALASKA

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Presented to the Faculty
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for the Degree of

DOCTOR OF PHILOSOPHY

By

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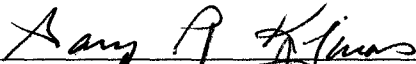
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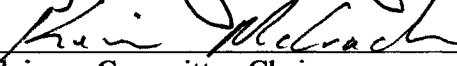
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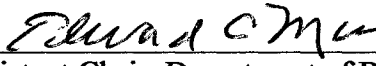






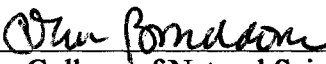


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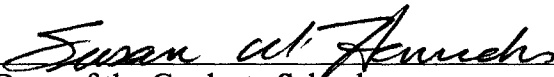


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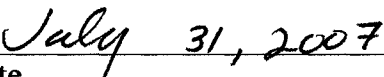
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ABSTRACT

I examined social and ecological influences on moose (*Alces alces gigas*) in Alaska, USA, with respect to hunting success, antler size, and population genetic structure. Catch per unit effort (CPUE) is frequently used to assess hunter success; thus I hypothesized that landscape characteristics and moose density would affect success. Using hunter harvest tickets returned to the Alaska Department of Fish and Game, I modeled CPUE with Weibull regression. I determined success is significantly predicted by hunt location, mode of transportation, hunting regulations, use of commercial services (i.e., guides), year, road density, hunter-to-moose ratio, moose density, and hunter residency status. Antler size is an important factor for hunters and for mating potential in male moose. I hypothesized that moose density, habitat, and use of guides would correlate with antler size of harvested moose. I also predicted that guides would harvest moose with larger antlers and avoid areas where the hunter-to-moose ratio is high compared to nonguided hunters. Results indicated that antler size decreases with increases in moose density and harvest intensity due to density-dependent processes and a younger age structure in heavily harvested areas. Guided hunts tended to harvest larger antlered bulls and avoided areas of high hunter-to-moose ratios.

In addition to age and nutrition, genetics influences antler size. I used eight microsatellites and five sample areas to resolve whether population structure exists among moose in Alaska. I hypothesized that population structure does exist given the intense harvest rates, polygynous mating style of moose, and heterogeneous landscape present in Alaska. Dispersal and gene flow between populations was proposed to occur

via isolation-by-distance (IBD) with a positive linear relationship between geographic and genetic distance. Results indicated weak but significant population structure for moose in Alaska, and IBD was supported. Pairwise comparisons between populations indicated that moose have established separate populations except for between Tanana Flats and Koyukuk and Koyukuk and the Seward Peninsula. Lastly, I hypothesized incorporation of landscape characteristics and subsequent least-cost path would strengthen the significance of IBD. With an additional population, Tetlin, the significance of IBD as a mechanism for dispersal/gene flow for moose in Alaska was improved.

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INTRODUCTION

One recent shift in biological research and wildlife management is the recognition that humans are a part of the ecosystem and their environment. In the context of this shift in thinking, research in wildlife management and conservation needs to incorporate social and ecological issues, regardless of whether species or ecosystem processes are the focus of the research. Clearly, wildlife managers can incorporate both ecology and relevant societal issues into their research designs and management plans.

My dissertation incorporates both ecological and social influences to improve knowledge for effective wildlife management of large ungulates such as moose (*Alces alces*). Population dynamics and life-history characteristics including physical attributes, reproduction, mating strategies, the role of density-dependent processes, predator-prey interactions, and dispersal patterns of moose all necessitate a holistic perspective. Furthermore, moose are a keystone species and can play a dominant role in the boreal-forest ecosystems in Alaska (Molvar et al. 1993; Simberloff 1998). Moose influence many ecological processes such as rates of nutrient cycling and composition of plant and animal communities (Pastor et al. 1993, Kielland et al. 1997, Kielland and Byrant 1998). Moose are also important culturally and provide a vital dietary source of protein for many people (Ballew et al. 2006). Through consumptive (i.e., hunting) and non-consumptive (i.e., viewing) uses, moose are an important economic component of Alaska (Snepenger and Bowyer 1990). In summary, moose are important ecologically, socially, and economically.

The research design and hypotheses of my dissertation included both ecological and social effects on various facets the population ecology of moose (*Alces alces gigas*) in Alaska. My first two chapters focused on social questions relating to moose and their harvest and management; insights from these chapters enabled me to better formulate and understand results from the latter two chapters, which are more ecological and molecular in their orientation.

In Chapter One, I investigated the influence of moose-hunter characteristics and landscapes on harvest success and catch per unit effort (CPUE). Success and CPUE are influenced by the characteristics and motivations of hunters. I predicted that success provided via type of transportation, employment of a guide, moose density, and landscape features would result in spatial variation of harvest and hunter success. In addition, I evaluated whether CPUE could be modeled more effectively with Weibull regression than with previously acknowledged inadequate methods, such as linear regression (Stankey et al. 1973; Solberg et al. 2000), which indicate decreased success with increased effort.

In Chapter Two, I explored the relationship between moose density, harvest intensity, habitat, and antler size. I hypothesized that increased moose density and harvest intensity result in smaller size of moose antlers as a result of lower nutrition available to moose and reduced age of males by intense harvests. Larger-antlered moose would be more likely to occur in areas of good habitat with nutritious foods rather than in areas of low habitat quality and nutrition for moose. I also predicted that guided moose hunts would harvest larger antlered moose than would nonguided hunts in areas with the

same moose density because of the hunting skills of guides. Furthermore, guides would selectively hunt in areas of low hunter-to-moose ratios to meet desires of their clients for harvesting moose with a large antler size.

Chapter Three explored the genetic population structure of moose in Alaska. Even though moose colonized Alaska recently (in evolutionary time), I predicted that population structure of moose in Alaska would occur because of the vast and heterogeneous area, variable selective pressures from hunting, and life-history characteristics such as male-biased dispersal (Hundertmark 1998) and polygamous mating (Schwartz and Hundertmark 1993). In addition, I hypothesized that isolation by distance (IBD) would partially explain observed structure with closer populations more related than more distant populations.

Lastly in Chapter Four, I inferred that incorporation of ecological and social landscape features such as vegetation, fire, past and present glaciers, roads, and railways would improve the positive relationship between geographic and genetic distance. I modeled four different least-cost paths connecting moose populations based on four different friction surfaces that incorporated landscape features with assigned cost values according to four different models. With these four models, I tested whether good or bad moose habitat would be a likely dispersal corridor. I also tested whether the incorporation of habitat and permanent landscape features or only permanent landscape features where effects of habitat were minimized would better improve the relationship between geographic and genetic distance.

In my dissertation I have explored the social, ecological, and genetic components

life-history of a quintessential Alaskan ungulate, the moose. In order to obtain insightful and useful knowledge, one must approach a problem from multiple aspects and disciplines. Scientific research with this approach can address broader and more insightful issues that can be utilized by a wider audience. In the end, my dissertation based on this approach will most certainly improve understanding of the population dynamics, genetics, and wildlife management of not only moose, but other ungulates.

CHAPTER 1

CATCH PER UNIT EFFORT FOR MOOSE: A NEW APPROACH USING WEIBULL REGRESSION¹

1.1 ABSTRACT

The relationship between hunters and their environment is a key component in managing wildlife populations. Hunters' characteristics, motivations, and efforts are crucial to understanding if a hunt will be successful. We predicted that landscape characteristics and moose (*Alces alces*) densities would affect success of hunts. Similar to wildlife management elsewhere, moose hunters in interior Alaska, USA, must return harvest tickets to the Alaska Department of Fish and Game. These tickets provide location of hunts (Uniform Coding Units) and other details. Our modeling of responses (1997–2001) from harvest tickets indicated that location of hunts, mode of transportation, hunting regulations, use of commercial services, year, density of roads, hunter-to-moose ratio, moose density, and residency of hunters were important predictors of success. In addition, we documented that the linear-regression approach to measuring catch per unit effort (CPUE) was inadequate because it produced an inverse, but not significant, relationship between hunting effort and success. This outcome occurred because most hunts, particularly for large mammals, ended with the harvesting of an animal. Likewise, modeling hunter success with logistic regression was similarly biased by measures of hunter effort. We established that a time-to-event Weibull regression provided

¹ Schmidt, J.I., Ver Hoef, J.M., Maier, J.A.K., Bowyer, R.T. 2005. Catch per unit effort for moose: a new approach using Weibull regression. *Journal of Wildlife Management* 69:1112-1124.

substantial improvement over standard models of CPUE. Weibull regression accurately represented the positive relationship between effort and success, and it can be used to model length of hunt and other covariates related to hunters and landscape characteristics for predicting success.

1.2 INTRODUCTION

Rates of hunter success are influenced by characteristics, motivations, and degree of satisfaction of those seeking to harvest animals (Stankey 1973, Albert et al. 2001, Hayslette et al. 2001). Research related to social aspects of hunting ungulates has focused on satisfaction of hunters in relation to management (McCullough and Carmen 1982; Rollins and Romano 1989; Lauber and Knuth 1997, 1999; Fulton and Hundertmark 2004) or on general characteristics of hunters and their hunts (Miller et al. 1994, Ericsson et al. 2000). Preferences, motivations, and effort levels of hunters directly influence harvest success, selection of a particular species, animal harvested, and areas hunted (Stankey et al. 1973, Getz and Haight 1989, Ericsson et al. 2000, Solberg et al. 2000, Albert et al. 2001, Hayslette et al. 2001, Frey et al. 2003).

Previous approaches to modeling hunter effort typically have used regression to analyze catch per unit effort (CPUE; Seber 1992, Lancia et al. 1996, Maunder and Starr 2003, Smith et al. 2003). CPUE is used commonly by the fishing industry to assess status of populations (Dupont 1983, Richards and Schnute 1992, Gould and Pollock 1997, Maunder 2001, Goodyear 2003), and to aid development of fishing and hunting regulations (Lancia et al. 1988, Sigler and Lunsford 2001).

Results from the fishing industry indicate assessment of populations is strengthened when independent estimates of population size are used in combination with CPUE (Worthington et al. 1998, Maunder and Starr 2003). Nonetheless, CPUE for big game often is calculated as the number of animals killed per days hunted without incorporation of independent estimates of population size (Laake 1992, Lancia et al.

1996, Bowyer et al. 1999, Hatter 2001, Van Deelen and Etter 2003). Indeed, this metric has been used to detect changes in moose population sizes (Mercer and Manuel 1974; Crête et al. 1981; Crête and Dussault 1987; Crichton 1993; Hatter 1998, 2001). Bowyer et al. (1999) and Hatter (2001) agree, however, that CPUE is not always reliable and can overestimate increases in population size and underestimate population decreases. Moreover, Bowyer et al. (1999) reported an unexpected inverse relationship between harvest and effort when moose densities were low.

Despite some shortcomings, CPUE is still used widely by wildlife managers (Novak et al. 1991, Laake 1992, Lancia et al. 1996, Cooper et al. 2003). When the bag limit is only a single animal, however, traditional approaches for calculating CPUE may be inadequate. Uncertainty about the expected linear relationships between effort and hunting success has been expressed previously (Bowyer et al. 1999, Lancia et al. 1996, Hatter 2001, Maunder 2001, Van Deelen and Etter 2003), which we believe is related to the all-or-none nature of harvesting of large mammals. Moreover, uncertainty in estimates of CPUE may be associated with changes in regulations, (particularly those affecting size limits), and with a nonlinear relationship between catch and effort (Worthington et al. 1998, Solberg et al. 2000).

Understanding how characteristics of hunters and landscapes influence harvest is equally important in understanding the relationship between effort and success. We predicted that: 1) choice of transportation would influence rates of success because of access, 2) increased motivation and effort of hunters, as measured by employment of guides, would increase hunt success, 3) spatial variation between game management units

(GMU) would affect harvest, and 4) density of moose and the hunter-to-moose ratio would influence success, with areas of high moose density experiencing higher rates of success and reduced effort and areas of high hunter-to-moose ratio experiencing lower rates of success and more effort.

Moreover, we used Weibull regression to assess CPUE, by modeling the length of a successful hunt directly. We compared standard methods used to evaluate CPUE, and illustrated the inability of those procedures to cope with the censored nature of harvesting a moose. These analyses enable prediction of future demand for resources related to moose hunting, and provide insights into the motivation of individuals who hunt.

1.3 MATERIALS AND METHODS

1.3.1 Databases and Study Extent

Licensed moose hunters in Alaska must obtain a harvest tag that is returned to ADF&G whenever a moose is killed. We analyzed data from 1997 to 2001 hunting seasons. Several characteristics of moose hunting, such as transportation, residency, use of commercial services (i.e., transporter or registered guide), and length of trip were recorded on harvest tickets. Registered guides in Alaska must pass certification and become registered with the State, whereas, transporters do not require certification and include anyone who provides travel assistance during a hunt. Returned tickets were coded by Uniform Coding Units (UCU) that established the sampling units for most of our analyses. Although we have no independent method to verify the accuracy of moose-harvest tickets, previous research in Alaska indicates that such tickets provide a reasonable indication of characteristics of most hunters and their harvest (Albert et al.

2001). However, given the remoteness and isolation of many rural villages, a potential bias in our dataset exists in that rural or Native hunters may be underreported in our dataset. Maps for analyses of landscapes, hunter access, and management units were provided by the Alaska Department of Natural Resources and Division of Wildlife Conservation of ADF&G.

1.32 Rivers and Roads

Rivers provide an index of how drainages influence moose habitat and access for hunters via boats during autumn. Rivers also provide trails for snowmobiles and dogsleds and landing strips for aircraft in winter and autumn. Geographic information system (GIS) coverage of rivers was extensive and included all navigable and unnavigable waters within interior Alaska. Roads strongly affect human presence and access. Roads included primary and secondary highways, those under construction, as well as tracks, trails, and footpaths. We calculated density values for rivers and roads by totaling the length (km) of rivers or roads encompassed by an UCU, divided by the area (km²) of the UCU. Alaska contains few roads, so density estimates would have resulted in many zeros. Consequently, we represented the potential effects of roads by estimating the distance from the center point of a UCU to the nearest road. To scale and aid comparisons of model coefficients for roads and river density values, we divided values by 100 and 1,000, respectively.

1.33 Landscape and Habitat Characteristics

Landscape characteristics included slope, aspect, and vegetation, which we obtained from the Spatial Ecology Laboratory at the University of Alaska Fairbanks.

Aspect was sine and cosine transformed for subsequent analyses (Zar 1999). We used variation in aspect and slope to calculate terrain variability (Nicholson et al. 1997). The terrain index, as used by Nicholson et al. (1997) for modeling habitat selection by mule deer (*Odocoileus hemionus*), is a function of the deviation of the mean angular aspect multiplied by the standard deviation of slope. Hence, a higher value for terrain implies an increase in ruggedness, thereby hindering mobility and decreasing the likelihood of ungulate dispersal. Terrain grids were generated at numerous scales based on various pixel sizes. We used the grid with pixel scale of 114 km² for assessing terrain characteristics because that size was more representative of the average UCU and was likely the maximal extent to which a hunter would consider terrain when moose hunting.

1.34 Surveys and Moose Densities

We estimated moose densities via ADF&G aerial surveys during autumn from 1997 through 2001. We based areas selected for aerial surveys on management needs and intensity of hunter use. Survey methods involved counting all moose in randomly selected sample units of 2' latitude and 5' longitude (~12 km²) within survey areas (Ver Hoef 2001, 2002). Use of this survey method helped us establish the spatial extent of our study area. We surveyed 39,332 km², with some sample units within the region were sampled for multiple years. We sampled 2,665 units; when density was estimated in >1 year in a unit, we used the average.

We only used female moose in population density estimates because they show more site fidelity than males (Ballard et al. 1991). We also chose female moose because surveys were conducted after hunting season when estimates of moose density are less

affected by the autumn hunt that targets mostly males (Schwartz et al. 1992). We acknowledge that moose density estimates were based on female moose when males were most likely to be harvested; however, because surveys were conducted after the autumn hunting season, estimates of males would have been confounded by hunter selection, alterations in the sex ratio, and variation in success rates. Because surveys are conducted in autumn shortly after the rut, males are likely to have been congregated around females. Thereby, sexes of moose were aggregated during autumn, and we hypothesize that the extent of females best represents the spatial distribution of both sexes prior to the hunt (Miquelle et al. 1992). We also admit that sex-ratios within interior Alaska were likely to vary. We assume, however, that our estimation of moose density based on female moose was valid given the previously mentioned drawbacks of including males in estimates and our goal of quantifying overall population density of moose. Raw estimates of density were determined by totaling the number of adult females surveyed in sample units, adding 1, and dividing by the area (m^2) within the sample unit. The addition of 1 was necessary because we used a natural-log transformation to normalize data (McKenney et al. 1998, Rew et al. 2001, Ver Hoef 2001) and stabilized variance.

1.35 Kriging

We used ArcGIS 8.3 Geostatistical Analysis Program (Johnston et al. 2001) to krig estimates of moose densities across interior Alaska. Our sample units for hunter characteristics were UCUs, which was larger than moose survey sample units. To aggregate to the UCU scale, we kriged all unsampled moose survey units and then averaged them for each UCU. Kriging has also been used to estimate other populations

of moose (McKenney et al. 1998). The geographic area kriged was formed by all the UCUs that contained moose-survey sample units along with their adjacent UCUs (i.e., those sharing a border with an UCU that contained at least 1 sample unit). We estimated moose densities using ordinary kriging with an exponential variogram model. Because of the abundance of sample units, we used the 20 nearest neighbors of a unit to make predictions that formed a raster-based map. We overlaid predicted values of the raster map on UCUs and then averaged them within each UCU. Values then represented average moose density over our 5-year study in interior Alaska; annual surveys by ADF&G indicated that moose density was relatively stable during our study.

1.36 Human Indices

We examined hunter density as an index to the presence of hunters and their potential interactions with moose. We calculated the number of hunters in a UCU by totaling the number of attempted hunts, regardless of success, for each year. We divided this value by area (km^2) to calculate yearly density of hunters in a particular UCU. We examined the influence of the ratio of hunter-to-moose density when predicting success (Cooper et al. 2003). We based predictions of moose density on a 5-year mean, so we used an equivalent 5-year average of hunter density for determining that ratio. We also explored the influence of residency of hunters on success. We assigned hunters to three categories related to residency: urban, rural, and nonresident (based on postal zip codes). Urban or rural communities were defined as areas with a population of 2,500 to 7,000 residents and considered dependency on the community, utilization of surrounding ecosystem services, and development in the local area according to the joint agreement

between the Subsistence Management for Federal Public Lands in Alaska, the U.S. Department of the Interior, and the U.S. Forest Service (for additional information see ADF&G 2000 subsistence technical document at <http://www.state.ak.us/adfg/subsist/download/tecdoc00.pdf>.)

1.37 Statistical Analyses

We truncated the number of days hunted at 30 because of extreme outliers in our data, but 99% of our samples were retained. We also examined a Spearman rank correlation matrix to remove potentially correlated variables (Zar 1999). Hunter success is a binary response; consequently, we used stepwise logistic regression with PROC LOGISTIC and GENMOD ($\alpha = 0.15$ to enter, $\alpha = 0.10$ to remove) to select significant variables for predicting success (SAS Institute 1999). During stepwise logistic regression, we based model selection on Akaike Information Criterion (AIC; Zar 1999). We determined goodness-of-fit with the Pearson Chi-Square value divided by the degrees of freedom, for which a value near 1 indicated a good fit (Zar 1999). Of 21 GMUs available to enter the model, we excluded three because of incomplete data (19A, 19B, and 21E).

We used the same variables from logistic regression for modeling success and effort with Weibull regression. We assumed a Weibull distribution for CPUE. Weibull regression incorporated censored data and covariates such as landscape and hunter characteristics to estimate both time to achieve a particular rate of success and the proportion of hunters likely to succeed within an area given a specified length of hunting trip. We modeled time to success with PROC LIFEREG (SAS Institute 1999) as the

probability density function. The probability of success is a function of time and is the cumulative distribution function (CDF). We treated unsuccessful hunts as censored values at the time the hunt ended. Survival models based on a Weibull distribution are 1-CDF. Parametric modeling such as Weibull regression can better handle covariates, potential interactions, and provides an approach superior to nonparametric models (i.e., Kaplan-Meier) when parametric assumptions are met (Dupont 1983, Efron 1988). Keech et al. (2000) used this parametric approach to model survivorship of moose, which also has applicability to modeling CPUE. Catch per unit effort was modeled as:

$$\text{Probability of success} = 1 - S(t) = 1 - \exp(-(te^{-\beta x})^{1/\sigma}),$$

where t is time, the values of the covariates are contained in the vector \mathbf{x} , the regression coefficients are contained in the vector $\boldsymbol{\beta}$, and σ is a shape parameter (Allison 1995). For model diagnostics, we examined the relationship between residuals and a negative log-survivorship distribution (Allison 1995), with a linear relationship indicating a good fit. We fit all models with PROC LIFEREG (SAS Institute 1999). We used the estimated regression coefficients to examine relative effects of independent variables related to hunters and amount of time expended to kill a moose. To examine spatial patterns, we needed to hold nonspatial effects constant; thus, we created the typical hunter. For continuous hunter variables, we used the mean, and for categorical variables, we used the most frequent category. By fixing typical characteristics of a hunter and nonspatial coefficients, we analyzed effects of site-specific landscape characteristics (UCUs) on success. We also used the Weibull regression to evaluate hunter success based on use of guides to illustrate its flexibility. In addition, we used the standard approach to

model CPUE and success with linear regression (PROC REG, SAS Institute 1999), with success averaged for each day hunted.

1.4 RESULTS

1.41 Characteristics of Hunts and Success of Hunters

Characteristics of moose hunters, their hunts, and subsequent success were affected by type of hunt, residency, whether they hunted on state or federal lands, their mode of transportation, whether they hired a guide, and the year during which they hunted (Table 1). Success was most variable among GMUs (range = 2-43%), and among modes of transportation used for hunting moose (Table 1). Use of GMUs differed with residency; 19B, 20B, and 20D were used most often by nonresidents, urban residents, and rural residents, respectively. Harvest levels remained relatively constant with a high in 1998 of 3,889 moose to a low of 3,204 moose in 2001 with 18,177 moose harvested during our 5-year study. Surprisingly, median length of hunt did not differ greatly for successful (5 days) and unsuccessful (6 days) hunters; overall the median length of a hunt was 6 days. Median days hunted was shortest for residents with urban hunters spending 5 days and rural hunters 6 days; nonresidents hunted for a median of 7 days.

1.42 Models for Catch per Unit Effort

We modeled hunter success using logistic regression with successful hunts coded 1 and unsuccessful hunts coded 0. Pearson Chi-Square divided by the degrees of freedom, was near 1 ($n = 23,956$, Concordance = 69.5, $\chi^2/DF = 1.01$), indicating a good fit. Remarkably, length of hunt entered the regression model with a negative coefficient (Table 2), demonstrating lower success associated with more effort. This outcome is an

artifact of the successful harvest of a moose ending the hunt, and it illustrates the danger of calculating CPUE in this way. Indeed, when success was regressed with days hunted, we observed a slightly negative, but not significant, trend (Fig. 2A, $P = 0.45$). Lack of a clear relationship between effort and success further illustrates the inability to accurately depict the relationship between success and effort with this traditional approach. When we modeled hunter success with Weibull regression, a plot of residuals resulted in a linear relationship, indicating a Weibull distribution fit the data well. Weibull regression illustrated increased success with increased time to harvest, with a curvilinear and a positive relation between success and effort (Fig. 2B).

The five most influential variables for predicting hunter success from stepwise logistic regression were GMU, type of transportation, length of trip, type of hunt, and whether a guide was used (Table 2). Coefficient estimates computed by logistic regression also indicated increased success with increased density of moose and distance from roads. Moreover, a negative coefficient for days hunted indicated success decreased with additional days hunted. In 1997, rural residency, transportation via snowmobile, and use of a guide and transporter resulted in the highest predicted success (Table 2).

The five most influential variables for Weibull regression included type of hunt, mode of transportation, GMU, year, and the hunter-to-moose ratio (Table 2). Length of hunt was the response variable. Positive values for coefficients of the logistic model indicated increased success; whereas, negative values for coefficients of the Weibull regression indicated shortened time to kill a moose (Table 2). Weibull regression indicated reduced time to achieve success with increased moose density, distance to road,

and river density (Table 2). Attributes that decreased time to success included hunting in 1997, urban residency, use of a snowmobile, use of guide, and transporter usage (Table 2). Coefficients for GMUs in both models varied widely and reflected a strong spatial component to hunter success in interior Alaska. Major differences between the two regressions (i.e., logistic and Weibull) were for residency and success among years. Urban residents had the shortest time to achieve a successful hunt in the Weibull regression; whereas, for logistic regression, rural hunters were most successful. Variables that did not enter the step-wise model consisted of whether a hunt was managed by Federal or State agencies, amount of spruce or deciduous vegetation, slope, aspect, and ruggedness of terrain.

We used Weibull regression coefficients (Table 2) to create a map of standardized hunter success (Fig. 1A and B) by selecting characteristics of a typical hunter and variation from significant spatial components (i.e., GMU, hunter/moose ratio, moose density, distance to road, presence of low shrub vegetation, river density). Landscape and spatial dynamics strongly influenced predicted success for a 6-day hunt in interior Alaska by a typical moose hunter in 2001 (Fig. 1A and B). A typical moose hunter was an urban resident who used a boat, participated in a general hunt, and contracted no guide or transporter services (Table 1).

Hunter success varied markedly within interior Alaska. Success was high near the rural communities of Huslia and Galena, approximately 50 km south of McGrath, and a 100 km east and northeast of Circle (Fig. 1A and B). Moderate levels of hunter success occurred south of Fairbanks, southwest from Wiseman toward Huslia, and southwest

from Tanana to McGrath. The poorest hunting success was in the area between Circle and 100 km east of Wiseman (Fig. 1A and B).

Although densities of moose south of Fairbanks in GMU 20A were among the highest in the state ($\bar{X} = 0.43$ moose/km², SE = 0.08), hunting success was only moderate when compared to other areas of the State such as Huslia which experienced higher rates of success (Fig. 1A and B). This area also possessed the second highest hunter-to-moose ratios in the State ($\bar{X} = 0.16$, SE = 0.03); only the bordering GMU 20B had higher ratios ($\bar{X} = 0.37$, SE = 0.07). The increase in success near the southern boundary of 20A and below McGrath in 19B corresponded with increased guiding activity. For example, the percent of hunts guided was 748 of 8,074 vs. 1,391 of 31,479 hunts guided for the rest of interior Alaska ($n = 32,227$). in these two GMUs. The area around Huslia also was also more frequently used by guides compared to other places in interior Alaska. Clearly, a guided hunt was more successful than unguided hunt (Fig. 3).

1.5 DISCUSSION

We hypothesize that increased effort (i.e., days spent hunting) for moose in interior Alaska was associated with lack of success, rather than the standard interpretation of effort associated with increasing success. The negative trend between days hunted and CPUE (Fig. 2A) is counter-intuitive. More important is the lack of a significant relationship between effort and success that we assume resulted from a single kill ending the hunt, which occurs frequently for harvests of large mammals. Length of a hunt was a key component of success, and it was used to quantify effort and as an index of hunt quality and status of wildlife populations (Eberhardt 1976, Novak et al. 1991, Laake

1992, Lancia et al. 1996, Bowyer et al. 1999, Van Deelen and Etter 2003). Clearly, a new approach is needed to model CPUE for moose hunting.

Logistic regression models also may not accurately represent the relationship between effort and success (Table 2). Days hunted was estimated with a negative coefficient, again indicating an unrealistic reduction in success associated with longer hunts. Because days hunted is a covariate in the logistic regression model, the negative coefficient for days hunted also influences all other covariates in the model. This outcome can confound the interpretation of other parameters in the model, including those indicated as important in predicting hunting success. Nonetheless, amount of effort expended is an important component of hunting (Table 2). Models should reflect this key variable.

We therefore chose Weibull regression to evaluate the relationship between effort and success for moose hunters within interior Alaska, and we observed a strong relationship between hunter effort and time to success (Fig. 2B). We modeled CPUE using a Weibull distribution that has been commonly used to predict rates of failure over time (Keech et al. 2000) or, in a few instances, catch-effort models (Dupont 1983, Novak et al. 1991). Nonetheless, to our knowledge a Weibull regression approach has never been taken to evaluate hunter success for large mammals.

Weibull modeling of CPUE better reflected effort by placing length of a hunt as an outcome rather than a predictor in the model. Consequently, Weibull regression addressed and effectively removed the inherent bias resulting from confounding effects when we included length of hunt as a predictor (Fig. 2A and B). This approach depicted

a more realistic relationship between CPUE and success, with increases in effort that lead to improved rates of success (Fig. 2B). Weibull regression further allowed for two examinations of success. First, success can be predicted based on characteristics of hunters and a specified length of time in the field. For example, choosing length of hunt on the x-axis yields a prediction of success on the y-axis (Fig. 2B). Conversely, because CDFs are monotonic functions, length of time required to achieve a desired rate of success or harvest level can be predicted. For example, choosing a success rate on the y-axis yields a predicted length on the x-axis (Fig. 2B). Success based on residency provides an example of different performance by logistic and Weibull models towards predicting success, with rural hunters being most successful in the logistic model and urban hunters more successful in the Weibull model (Table 2). We conjecture this outcome occurred for urban hunters because of the necessary preparation and expense to travel outside of the town or employment constraints. Also rural hunters could have multiple attempts to hunt, thereby reducing the time and effort to structure a hunt.

Consistent with our first prediction, rates of success were associated with modes of transportation and were extremely variable (Table 1). Transportation modes that allow access to more remote areas (i.e., boats, airplanes, and snowmachines) offer greater rates of success compared with travel via roads (Table 1 and 2). The model already has corrected for hunter-to-moose ratio, so this effect could be explained by more inexperienced moose in less-accessible areas.

Our prediction that motivations and characteristics of hunters would influence hunting success was supported by the variability of success rates associated with different

attributes of hunters (Table 1). Results indicate that increased effort improved success (Fig. 3). When modeling success and CPUE, Weibull regression exemplified the importance of hunter motivation and effort, with use of a guide or transporter strongly influencing hunting success (Table 2, Fig. 3). Covariate influences in Weibull regression indicated decreased time to success for hunters using guides and provided a quantifiable measure of the increase in effort necessary to influence success.

Game Management Unit was the most important component in predicting success (based on χ^2 values). Why GMU is so important is unclear and may reflect unmeasured local spatial effects. We speculate that variability of sex-ratios among GMUs could explain some of the spatial variation. Year was also important in predicting success (Table 2). Even with use of 5-year means for some parameters, year still clearly had a significant effect on success. Such year effects may be related to fluctuations in weather, access, or regulations. In addition, this outcome implies that success is not solely driven by hunter attributes (Stankey et al. 1973). In our data, numbers of reporting hunters steadily increased (Table 1); if the number of harvested animals was constant, then rates of success decreased.

Consistent with our last prediction, density of moose significantly affected success, with increased densities improving rates of success (Table 2). Our results support Van Deelen and Etter (2003), who illustrated a linear response between deer density and effort, with hunter effort increasing as density of deer decreased. Nonetheless, they questioned whether increased effort resulted in increased success because of small sample sizes and the perception gap by hunters between actual and

perceived density of deer, with hunters increasingly overestimating effort (i.e., underestimated densities of deer) as deer density decreased (Van Deelen and Etter 2003). Our results are similar, although an increase in density of moose was not the best predictor of success. Hunter-to-moose ratio was much more predictive than moose density alone (Table 2). For example, moose were at high density south of Fairbanks but did not yield increased rates of success. This area has high densities of moose, but it also has easy access and close proximity to a substantial human population; consequently, this area attracted many moose hunters. Interference among hunters may decrease rates of success regardless of high moose densities. Other studies also report increases in density of roads and hunter interference associated with decreased rates of success (Cooper et al. 2002, Heberlein and Kuentzel 2002). Several authors have undertaken research incorporating hunter characteristics, motivation, and effort into management schemes (Miller et al. 1994, Albert et al. 2001, Hayslette et al. 2001, Miller and Graefe 2001, Heberlein and Kuentzel 2002); however, more research in this area is needed (Ericsson et al. 2000, Bulte and Horan 2002, Fulton and Hundertmark 2004). Moreover, Ericsson et al. (2000) stated that a better understanding of hunter characteristics could produce hunting regulations that are both economically and biologically sustainable.

1.6 MANAGEMENT IMPLICATIONS

Our regression approach to modeling hunter success with a Weibull distribution allows for more realistic and informative predictions that wildlife managers can use to better estimate harvest levels and structure of hunts. Catch per unit effort is used widely in wildlife management, including detecting changes in population size of moose (Mercer

and Manuel 1974; Crête et al. 1981; Crête and Dussault 1987; Hatter 1998, 2001).

Because days hunted is more a result of success, rather than a reliable predictor of success, wildlife managers should use caution when estimating effort levels or population size based on days hunted.

Weibull estimates for CPUE provide a flexible approach to model success and harvest levels either by predicting the number of days hunted necessary to achieve a desired rate of harvest or by allowing predictions about rates of success for a particular length of trip. Predicting time needed to harvest at a particular rate provides a promising approach for managers when setting hunting seasons. Use of coefficients and covariates from Weibull regression also provides managers with a spatially explicit model that will help establish local regulations and improve site-specific conservation efforts. In addition, we suggest that to understand harvest patterns and effectively manage wildlife, information on combined effects of hunter characteristics, effort, and success are necessary. Weibull regression combines these variables into a unified statistical analysis.

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Section of Alaska Department of Natural Resources. Residency was assessed through the Alaska Community Database maintained by the Department of Community and Development and is available at: <http://www.state.ak.us/adfg/subsist/geninfo/publctns/cpdb.htm>. This research was funded, in part, by the Interdisciplinary Graduate Education and Research Training Program (IGERT) of the National Science Foundation, ADF&G, the Institute of Arctic Biology at UAF, and the Department of Biological Sciences at Idaho State University.

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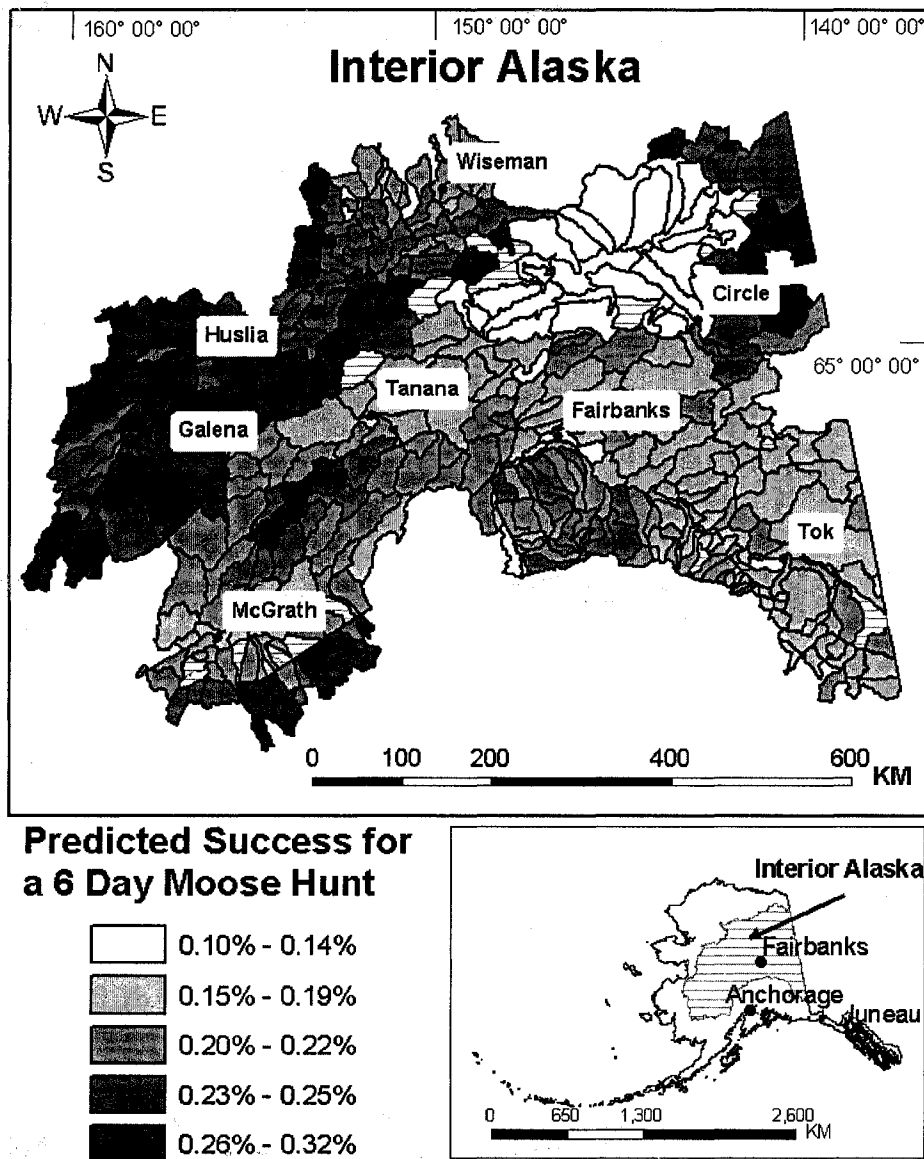


Figure 1.1 Predicted moose hunt success for a 6-day hunt in 2001 by an urban, Alaskan resident with a boat, using no commercial services in interior Alaska, USA, based on hunter-harvest tickets from 1997 to 2001.

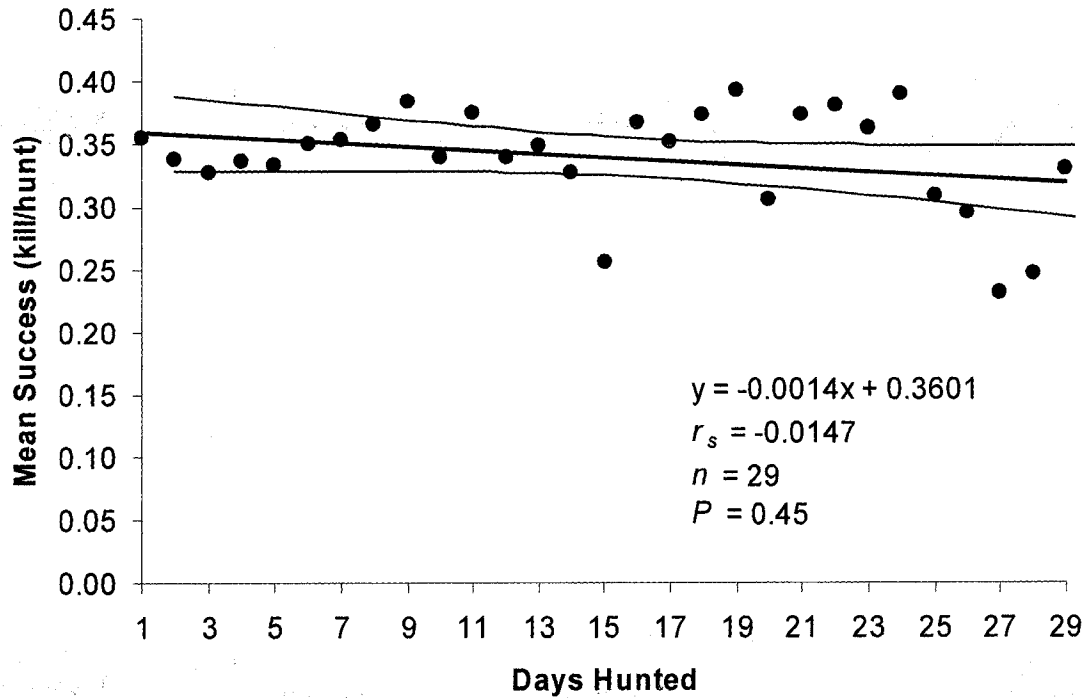


Figure 1.2A Linear regression model of catch per unit effort (CPUE) for moose hunters in interior Alaska, USA, based on hunter-harvest tickets from 1997 to 2001.

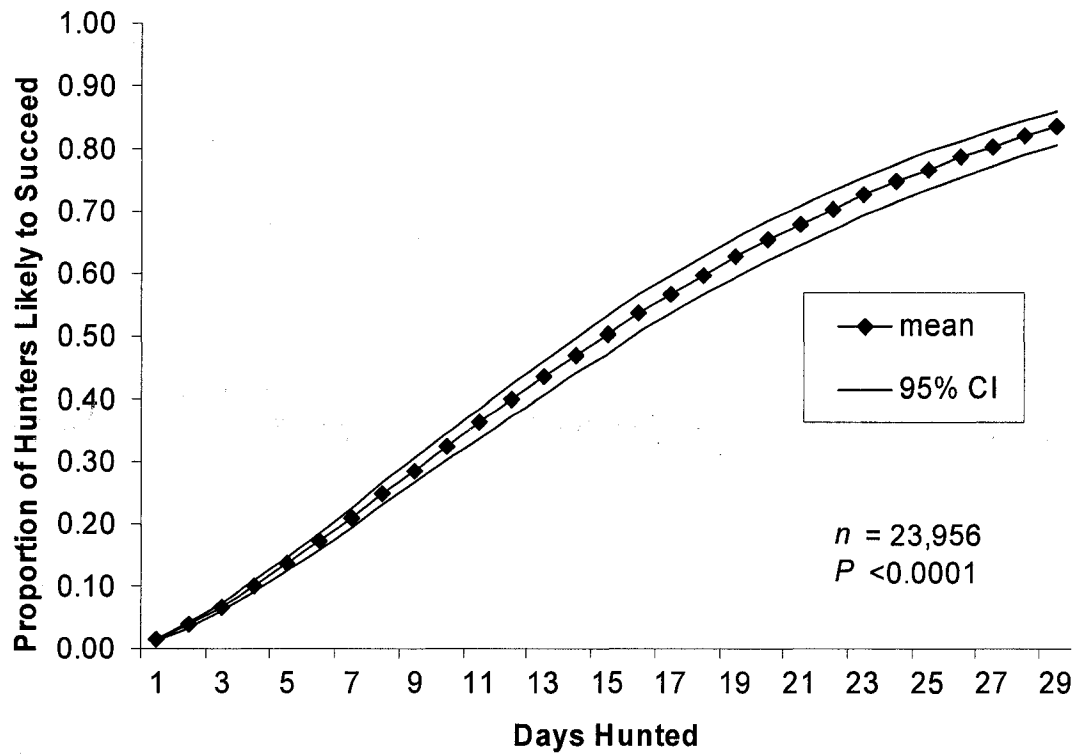


Figure 1.2B Weibull regression model of catch per unit effort (CPUE) for moose hunters in interior Alaska, USA, based on hunter-harvest tickets from 1997 to 2001.

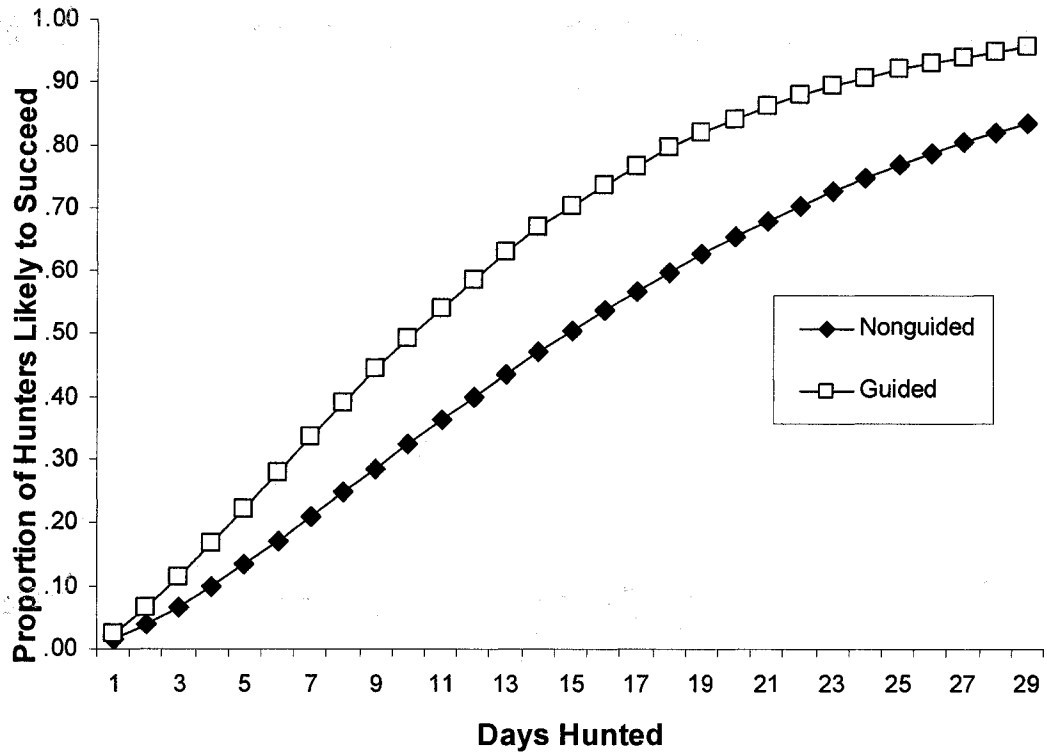


Figure 1.3 Models of catch per unit effort (CPUE) for guided and nonguided hunts for moose hunters in interior Alaska, USA, based on Weibull regression coefficients in Table 1.2.

Table 1.1 Average success for moose hunters from 1997 to 2001 in interior Alaska, USA.

Variables	<i>n</i>	Success	
		(%)	<i>P-value</i>
Hunt type			
Draw	1,335	48.84%	<0.0001
General ¹	48,795	31.92%	
Registration	3,530	46.20%	
Tier II	588	56.97%	
Residency			
Rural	6,920	37.65%	<0.0001
Non-rural ¹	33,596	29.29%	
Non-resident	13,220	45.15%	
Manager			
Federal	103	51.46%	0.0001
State ¹	54,115	33.49%	
Transportation			
Airplane	9,007	44.08%	<0.0001
Horse/dog/foot	616	50.81%	
Boat ¹	17,777	39.52%	
ATV	9,156	30.13%	
Snowmobile	860	61.40%	
ORV	2313	31.60%	

Table 1.1 (continued) Average success for moose hunters from 1997 to 2001 in interior

Alaska, USA

Highway	11,930	18.80%	
Airboat	382	19.37%	
Other	789	40.56%	
Year			
1997	10,380	36.57%	<0.0001
1998	10,618	36.63%	
1999	10,963	33.79%	
2000	11,000	32.58%	
2001 ⁱ	11,259	28.46%	
Use of guide			
Guided	2,129	65.38%	<0.0001
Nonguided ⁱ	37,052	34.71%	
Use of transporter			
Transported	4,138	45.22%	<0.0001
No transporter ⁱ	35,042	35.33%	

ⁱVariables that represent average characteristics of moose hunters..

Table 1.2 Predicted success coefficients from Logistic Regression and Weibull models for moose hunters from 1997 to 2001 in interior Alaska, USA. Note value estimates for categorical variables are offset by base category. Positive logistic indicate increased success; whereas, negative Weibull coefficients represent decreased time needed to successfully harvest a moose.

Variables	DF	Logistic Regression					Weibull Regression				
		Lower ¹	Est ²	Upper ³	X ²	P-value	Lower ¹	Est ²	Upper ³	X ²	P-value
Intercept	1	1.257	1.794	2.332	42.81		1.984	2.256	2.527	265.3	<.0001
Coefficient											
Days Hunted	1	-0.067	-0.06	-0.053	293.89	<.0001					
Distance to											
Road*	1	0.572	0.869	1.167	32.75	<.0001	-0.482	-0.339	-0.197	21.77	<.0001
River Density*	1	-1.002	-0.635	-0.268	11.51	0.001	-0.394	-0.2	-0.007	4.11	0.043
Moose Density	1	0.275	0.467	0.658	22.73	<.0001	-0.299	-0.2	-0.1	15.54	<.0001
Hunter-Moose-											
Ratio	1	-0.472	-0.359	-0.247	39.12	<.0001	0.297	0.363	0.429	115.88	<.0001
Low Shrub	1	-0.436	-0.294	-0.153	16.7	<.0001	0.069	0.142	0.214	14.79	0
Hunt Type	3				154.12					339.16	<.0001
Draw Hunt		-1.017	-0.736	-0.455	26.39	<.0001	-0.043	0.081	0.206	1.64	0.201

Table 1.2 (continued) Predicted success coefficients from Logistic Regression and Weibull models for moose hunters from 1997 to 2001 in interior Alaska, USA. Note value estimates for categorical variables are offset by base category. Positive logistic indicate increased success; whereas, negative Weibull coefficients represent decreased time needed to successfully harvest a moose.

Variables	Logistic Regression						Weibull Regression				
	DF	Lower ¹	Est ²	Upper ³	X ²	P-value	Lower ¹	Est ²	Upper ³	X ²	P-value
Coefficient											
General Hunt		-1.585	-1.33	-1.074	103.74	<.0001	0.486	0.601	0.716	104.87	<.0001
Registered											
Hunt		-1.495	-1.211	-0.927	69.68	<.0001	0.138	0.266	0.394	16.5	<.0001
Tier II		0	0	0			0	0	0		
Year	4				103.55					131.37	<.0001
1997		0.332	0.421	0.511	84.96	<.0001	-0.298	-0.251	-0.204	108.58	<.0001
1998		0.274	0.363	0.451	64.37	<.0001	-0.252	-0.205	-0.157	72.34	<.0001
1999		0.182	0.271	0.359	35.76	<.0001	-0.15	-0.102	-0.055	17.75	<.0001
2000		0.109	0.198	0.287	19.00	<.0001	-0.166	-0.119	-0.071	23.57	<.0001

Table 1.2 (continued) Predicted success coefficients from Logistic Regression and Weibull models for moose hunters from 1997 to 2001 in interior Alaska, USA. Note value estimates for categorical variables are offset by base category. Positive logistic indicate increased success; whereas, negative Weibull coefficients represent decreased time needed to successfully harvest a moose.

Variables	Logistic Regression					Weibull Regression					
	DF	Lower ¹	Est ²	Upper ³	X^2	<i>P</i> -value	Lower ¹	Est ²	Upper ³	X^2	<i>P</i> -value
Coefficient											
2001		0	0	0	.	.	0	0	0	.	.
Residency	2				10.81					22.02	<.0001
Nonresident		-0.166	-0.05	0.067	0.7	0.403	-0.72	-0.505	-0.29	0	<.0001
Nonrural		-0.205	-0.126	-0.048	10.03	0.002	-0.955	-0.745	-0.534	0	<.0001
Rural		0	0	0	.	.	0	0	0	0	<.0001
GMU	17				404.81					144.4	<.0001
Transportation	8				184.91					172.47	<.0001
Airplane		-0.382	-0.159	0.064	1.96	0.162	-0.087	0.028	0.143	0.23	0.629
Horse/Dog/Foot		-0.393	-0.074	0.246	0.2	0.652	-0.152	0.001	0.153	0	0.995

Table 1.2 (continued) Predicted success coefficients from Logistic Regression and Weibull models for moose hunters from 1997 to 2001 in interior Alaska, USA. Note value estimates for categorical variables are offset by base category. Positive logistic indicate increased success; whereas, negative Weibull coefficients represent decreased time needed to successfully harvest a moose.

Variables	Logistic Regression						Weibull Regression				
	DF	Lower ¹	Est ²	Upper ³	X ²	P-value	Lower ¹	Est ²	Upper ³	X ²	P-value
Boat		-0.601	-0.389	-0.177	12.91	0	0.097	0.208	0.318	13.59	0
ATV		-0.367	-0.152	0.064	1.9	0.168	0.098	0.21	0.322	13.42	0
Snowmachine		-0.294	0.012	0.318	0.01	0.94	-0.312	-0.165	-0.018	4.81	0.028
ORV		-0.376	-0.137	0.101	1.27	0.26	0.087	0.214	0.34	11	0.001
Highway		-0.925	-0.706	-0.487	39.96	<.0001	0.25	0.366	0.482	38.2	<.0001
Other		-0.648	-0.19	0.268	0.66	0.417	-0.126	0.112	0.349	0.85	0.357
Airboat		0	0	0			0	0	0		
Guide Usage	1				104.39					92.43	<.0001
Nonguided		-1.246	-1.045	-0.845	104.39	<.0001	0.306	0.385	0.463	92.43	<.0001
Guided		0	0	0			0	0	0		

Table 1.2 (continued) Predicted success coefficients from Logistic Regression and Weibull models for moose hunters from 1997 to 2001 in interior Alaska, USA. Note value estimates for categorical variables are offset by base category. Positive logistic indicate increased success; whereas, negative Weibull coefficients represent decreased time needed to successfully harvest a moose.

Variables	Logistic Regression					Weibull Regression					
	DF	Lower ¹	Est ²	Upper ³	<i>X</i> ²	<i>P</i> -value	Lower ¹	Est ²	Upper ³	<i>X</i> ²	<i>P</i> -value
Transporter Usage	1				27.53					0.76	0.383
No transporter		-0.44	-0.32	-0.201	27.53	<.0001	-0.031	0.025	0.08	0.76	0.383
Transported		0	0	0			0	0	0		
Scale of											
Distribution		1	1	1			0.686	0.697	0.709	0	0
Weibull Shape							1.411	1.434	1.458	0	0

¹ Lower limit of 95% confidence interval.

ⁱⁱ Estimate of regression coefficient.

ⁱⁱⁱ Upper limit of 95% confidence interval.

^{iv} We divided distance to roads by 100 and divided river density by 1,000 to scale coefficients.

CHAPTER 2

ANTLER SIZE OF ALASKAN MOOSE: EFFECTS OF POPULATION DENSITY, HUNTER HARVEST, AND USE OF GUIDES²

2.1 ABSTRACT

Moose (*Alces alces gigas*) in Alaska, USA, exhibit extreme sexual dimorphism, with adult males possessing large, elaborate antlers. Antler size and conformation are influenced by age, nutrition, and genetics. These bony structures serve to establish social rank and affect mating success. Population density, combined with anthropogenic effects such as harvest, is thought to influence antler size. Antler size increased as densities of moose decreased, ostensibly a density-dependent response related to enhanced nutrition at low densities. The vegetation type where moose were harvested also affected antler size, with the largest-antlered males occupying more open habitats. Hunts with guides occurred in areas of low moose density, minimized hunter interference, increased rates of success, and harvested moose with larger antler spreads than in nonguided hunts. Knowledge and abilities allowed guides to satisfy demands of trophy hunters, who are an integral part of the economy in Alaska. Heavy harvest by humans also was associated with decreases in antler size of moose, probably via a downward shift in the age structure of the population resulting in younger males with smaller antlers. Nevertheless, density

² Schmidt, J. I., Ver Hoef, J. M., Bowyer, R. T. 2006. Antler size of Alaskan moose: effects of population density, hunter harvest, and use of guides. *Wildlife Biology* 13: 53-65.

dependence was more influential than effects of harvest on age structure in determining antler size of male moose. Indeed, antlers are likely under strong sexual selection, but we demonstrate that resource availability influenced the distribution of these sexually selected characters across the landscape. We argue that understanding population density in relation to carrying capacity (K) and the age structure of males are necessary to interpret potential consequences of harvest on the genetics of moose and other large herbivores. Our results provide researchers and managers with a better understanding concerning variables that effect physical condition, antler size, and perhaps the genetic composition of populations, which may be useful in managing and modelling moose populations.

2.2 INTRODUCTION

Growth, size, and conformation of antlers among cervids are dependent upon a combination of age, nutrition, and genetics (Gross 1983, Hartl et al. 1995, Asleson et al. 1996, 1997). Antler growth and size are directly influenced by forage availability and the ability of cervids to garner foods of high nutritional value (French et al. 1965, Brown 1990, Strickland and Demarais 2000). Population density relative to carrying capacity (K) is important in determining amount and quality of food obtained by individuals (McCullough 1979, Schmidt et al. 2001, Kie et al. 2003, Festa-Bianchet et al. 2004, Stewart et al. 2005). We define K as the number of animals at or near a long-term equilibrium with their food supply (Kie et al. 2003). Nutrients sequestered by male cervids must be allocated first for basic metabolic needs, including growth (Barboza and Bowyer 2000). Indeed, only when these metabolic requirements for growth are met can resources be fully invested in antler growth by males (French et al. 1965, Bowyer 1986, Stewart et al. 2000). Moreover, increased intraspecific competition for resources occurs in ungulate populations at high densities relative to K , which diverts energy away from development of secondary sexual characteristics such as antlers (McCullough 1979, Ferguson et al. 2000, Schmidt et al. 2001, Stewart et al. 2000). Moose (*Alces alces*) invest substantial energy and resources in antler development (Stewart et al. 2000, Bowyer et al. 2001a), which can be limited by forage and nutrient availability in relation to K (Moen and Pastor 1998, Bowyer et al. 2000).

Another critical component determining antler morphology in cervids is age (Clutton-Brock 1982, McCullough 1982, Miquelle 1990, Stewart et al. 2000, Bowyer et

al. 2001a, Yoccoz et al. 2002, Mysterud et al. 2003). The relationship between age and the size and conformation of antlers is especially well documented for Alaskan moose (*A. a. gigas*; Bowyer et al. 2001a). Animals invest differentially based on age, with prime, larger males that have reached asymptotic body growth allocating more resources towards antler growth, symmetry, and size than smaller males (Stewart et al. 2000, Bowyer et al. 2001a, Yoccoz et al. 2002). In Alaskan moose, males do not attain full body growth until about 8 years old (Spaeth et al. 2001). In polygynous mating systems typical of sexually dimorphic cervids (Geist 1966, Ralls 1977, Weckerly 1998, Loison et al. 1999), dominant males often limit mating opportunities of younger, smaller males (Hirth 1977, Bowyer 1986, Van Ballenberghe and Miquelle 1996). In the absence of old, large males, the age at which males mate decreases (McCullough 1982, Strickland et al. 2001, Jenks et al. 2002, Singer and Zeigenfuss 2002). An earlier age of mating may result in younger males making large investments in antler development and size (Mysterud et al. 2003). Moreover, age structure is influenced by population density relative to K and human harvest; populations held away from K by heavy harvests have young age-class distributions (McCullough 1982, Bowyer et al. 1999, Saether et al. 2001). Trophy harvests of young bighorn sheep (*Ovis canadensis*) also have been implicated in increasing mating success of those young animals (Coltman et al. 2002).

Moose provide an excellent opportunity for understanding effects of harvest on antler characteristics. Much is known about moose antlers, including aspects of their physiology (Saether and Haagenrud 1983, Van Ballenberghe 1983, Bubenik 1998, Moen and Pastor 1998), age-related effects on growth (Stewart et al. 2000), size and

conformation (Solberg and Seather 1993, 1994, Bowyer et al. 2001*a*), geographic variation (Sæther and Haagenrud 1985, Gasaway et al. 1987, Sand et al. 1995, Bowyer et al. 2000), effects of management strategies (Stewart 1985, Hundertmark et al. 1998, Solberg et al. 1999, Laurian et al. 2000, Fulton and Hundertmark 2004), age structure (Solberg et al. 1999, Bowyer et al. 2001*a*, Sæther et al. 2001), and characteristics of those hunting them (Sæther et al. 2003, Schmidt et al. 2005). Moreover, antler size and complexity in males are positively related to sperm production and quality (Malo et al. 2005). Yet, almost nothing is known about how population density, intensity of harvest, and motivations of hunters interact to affect antler size of harvested moose. Indeed, debate continues over whether maximal harvests and trophy management are compatible management strategies (Jenks et al. 2002).

Moose populations in interior Alaska occur at low densities because of predation (Gasaway et al. 1992, Bowyer et al. 1998); hence, nutrition would tend not to limit antler growth, except for areas south of Fairbanks, Alaska, USA, where density-dependent responses have occurred (Keech et al. 2000). Moreover, Bender et al. (2003) and Festa-Bianchet et al. (2004) demonstrated that phenotypic responses can be measured when nutritional conditions do not limit potential growth.

Hunters often base harvest decisions on horn or antler size, and wildlife managers have used size restrictions on horns and antlers to limit harvests, which in turn may affect the size of those horn-like structures and demographics of ungulate populations (McCullough 1979, Thelen 1991, Schwartz et al. 1992, Strickland et al. 2001, Festa-Bianchet et al. 2004). Understanding such complex interactions, including

density-dependent responses, as well as influences of harvest on age structure of populations, is essential for the conservation and sound management of these large herbivores.

Motivations and satisfactions that individuals obtain from hunting are diverse, including those derived from subsistence, recreation, mentoring, economics, and trophy harvests (Hendee 1974, Ericsson et al. 2000, Heberlein and Kuentzel 2002, Frey et al. 2003). Sport hunting contributes significantly to the Alaskan economy providing both employment and revenue (Snepenger and Bowyer 1990, Albert et al. 2001). In particular, employment of a guide can be financially costly and is not required by law for moose hunting in Alaska; therefore, hunters typically expect guides to satisfy their goals. Hunters often select for males with large horn-like structures (Stewart 1985, Hartl et al. 2003, Festa-Bianchet et al. 2004). In addition, analyses of hunter harvest tickets indicate that most clients of guides are nonresidents, who invest substantially to harvest moose in Alaska (Schmidt et al. 2005). Guides would be expected to try to satisfy their clients by providing an opportunity to harvest a moose with large antlers.

The forgoing arguments lead us to offer the following hypotheses concerning the influence of harvest and guiding activity in relation to the size of moose antlers: 1) We predict that antler size will exhibit a negative relationship with moose population density, because areas of low density will be on a higher nutritional plane, and in consequence moose will have larger antlers at low than at high densities with respect to K . 2) In areas with moose and similar harvest intensities, habitats with a higher nutritional value for moose will have larger size of antlers than those harvested from areas with lower quality

habitat for moose. 3) Guides will selectively hunt in areas of low moose density compared with nonguided hunts. 4) Regardless of population densities, guided hunts will continue to selectively harvest moose with larger antlers than nonguided harvests within areas with the same stratum of moose density. 5) Also, guides will choose areas with lower hunter-to-moose ratios, thereby demonstrating skill and selectivity in attempting to satisfy the preference of clients for moose with large antlers. 6) Finally, heavily harvested areas, independent of density, will yield moose with smaller antlers, because that harvest will reduce age structure of males in those areas.

2.3 MATERIALS AND METHODS

2.31 Locality and Data

Our study area encompassed most of interior Alaska (569,694 km²) and is bordered by the Alaska Range (1,000–6,000 m elevation) to the south and the Brooks Range (1,000–2,500 m) to the north (Fig. 1A and B). Snow typically remains loose and dry with an average depth <70 cm (Gasaway et al. 1983, Keech et al. 2000, Yarie and Billings 2002); annual precipitation is 24 cm (O'Neill et al. 2002) and daily average temperatures range between 14°C and -30°C (Fleming et al. 2000). Schmidt et al. (2005) provide a comprehensive description of the study area.

Hunter harvest data was obtained from files kept by the Alaska Department of Fish and Game (ADF&G), and are based on harvest tickets collected from all moose hunters regardless of their success. Other researchers have used harvest tickets to accurately reflect hunting activity in Alaska (Albert et al. 2001). We examined results of guided versus nonguided moose hunts and use of transporters (i.e., outfitters) within

interior Alaska between 1997 and 2001. Guides in our analysis were registered in the State of Alaska, and transporters are any persons paid to provide transportation during a moose hunt. Uniform coding units (UCUs) were the basis for our spatial sampling units, because UCUs are the location reported on hunter harvest tags (UCUs, $n = 217$, $\bar{X} = 1,028 \text{ km}^2$, $SE = 5.6 \text{ km}^2$). The UCUs are typically defined by landscape features such as ridge tops and rivers in which often several units occur within the larger Game Management Units (GMUs). Management usually occurs at the level of the GMU, which defined the spatial extent of our study. To minimize spatial differences such as access or use of private landing strips between guided and nonguided hunts, we restricted our analysis to only UCUs where guiding occurred. Therefore nonguided hunts occurred in the same areas used by guides. Maps for UCUs were provided by the Division of Wildlife Conservation of ADF&G.

Aerial surveys conducted by ADF&G during autumn 1997-2001 were used to estimate densities of moose in interior Alaska. Survey methods involved counting moose in randomly selected sample units of 2' latitude and 5' longitude within survey areas from small fixed-winged aircraft (Ver Hoef 2001, 2002). We surveyed 39,332 km^2 ; some units were sampled in multiple years, resulting in a total of 2,665 units used in analyses. Surveys were conducted when snow cover and daylight were adequate, which often was only possible after the hunting season. We selected only females for analysis of density because they exhibited more site fidelity than males (Ballard et al. 1991) and reflected the spatial distribution of both sexes during autumn when the sexes were aggregated (Miquelle et al. 1992). Sampling later in winter might have provided biased results

because the sexes of moose spatially segregate following the mating season (Miquelle et al. 1992; Bowyer et al. 2001*b*, Bowyer 2004). Also, females were used because the hunting season occurred immediately prior to surveys and “male only” harvests are common in interior Alaska (Schwartz et al. 1992, Hundertmark et al. 1998). Consequently, estimates for females are less biased by changes in density from hunting than would be estimates that included males. Schmidt et al. (2005) provide a more detailed description of sampling protocols.

Moose densities (females/km²) within UCUs ($n = 599$) were divided into 3 categories based on “smart quantiles,” which look for natural breaks in data (Johnson et al. 2001). We used categories for two main reasons. Firstly, they are useful for data in which a large portion of samples falls within a small range but may have valid extreme values (Johnston et al. 2001). These extreme values can have undue leverage for continuous models (Rousseeuw and Van Zomeren 1990). Secondly, categories can reveal nonlinear relationships easily. Our categorization resulted in high ($\bar{X} > 0.41$ females/km², $n = 425$), medium ($0.21 < \bar{X} < 0.41$ females/km², $n = 120$), and low ($\bar{X} < 0.21$ females/km², $n = 54$) groupings of moose density, which likely correspond to populations subjected to various levels of predation by large carnivores (*sensu* Gasaway et al. 1992). Even though low density of moose does not necessarily indicate the position of a population in relation to K (Kie et al. 2003), Gasaway et al. (1992) argued convincingly that moose populations in interior Alaska were typically held below K by predation. Areas south of Fairbanks, however, recently have increased in density and measures of physical condition and reproduction indicate those populations may be

approaching K (Keech et al. 2000). These high-density areas provide a benchmark by which to judge other population densities of moose inhabiting the boreal forest.

Mean antler spread (cm) was calculated across the previously defined categories of moose density (females/km²). Antler spread is a reliable index to the overall size of moose antlers (Gasaway et al. 1987; Stewart et al. 2000; Bowyer et al. 2001a).

Moreover, antler spread correlates well with Boone and Crockett scores used to assess trophy antlers in moose (Gasaway et al. 1987).

2.32 Statistical Analyses

We controlled for effects of access between guided and nonguided hunts by sub-setting data for those analyses to contain only hunts that used airplanes for transportation. We used analysis of variance (ANOVA) to explore the relationship of antler size of harvested moose (dependent variable) at low, medium, and high densities and whether a guide was employed (main effects, Zar 1999). In addition, we simultaneously modelled effects of moose density, guide use, and their interaction with antler size (dependent variable). Because harvest can change age structure with possible effects on antler size independent of moose density (i.e., mostly males are harvested), we also modelled antler size with harvest intensity per moose density class as a covariate (ANCOVA) and categories of moose density as the main effect. A posteriori tests were conducted to further explore pairwise differences in moose density for guided and nonguided hunts. Although we do not know the age of harvested moose, this analysis helps control for age differences resulting from intensity of harvest. We used ANOVA with hunter intensity (dependent variable) and moose density (main effect) to predict size

of antlers; harvest intensity was defined as the number of moose taken divided by their population density. All analysis used the GLM procedure in SAS (SAS Institute Inc. 1999).

To further explore effects of habitat on antler size of moose, we used linear regression (SAS Proc REG) to predict size of antlers based on relative proportion of vegetation type present within the UCU where harvest occurred. Vegetation types were low shrubs (< 200 cm tall), deciduous trees and shrubs, which included willow (*Salix* spp.), birch (*Betula* spp.), aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white and black spruce (*Picea glauca* and *P. marina*), and ice or rock. We also assessed aspect, which was transformed to its sine and cosine (Zar 1999).

We used ANOVA to test for effects of hunter-to-moose ratio (dependent variable), with main effects of moose density (low, medium, high), use of guides, and their interaction (Zar 1999). Similar to antler size, pairwise differences between hunter-to-moose ratios were performed to examine differences in moose densities. An index of hunter interference was calculated based on the ratio of hunter density to moose density (Schmidt et al. 2005). Because estimates of moose density are 5-year means, estimates of hunter density also were averaged across those 5 years. Fortunately, the number of moose hunters in interior Alaska remained relatively constant from 1997 to 2001, ranging from 1,781 to 1,865 reported hunters. Hunter presence in UCUs was calculated by totalling the number of hunters in a UCU, regardless of success, from 1997 to 2001. Five-year estimates of hunter presence for each UCU were then divided by 5-year estimates of moose density. An arcsine transformation was needed to normalize

the hunter-to-moose ratio (Zar 1999), although untransformed means are presented for descriptive purposes. Statistical analyses were performed with SAS/STAT software (SAS Institute 1999).

2.4 RESULTS

2.41 Moose Density, Habitat, and Use of Guides

Moose density (females/km²) influenced antler size of harvested moose, with a continual increase ($P < 0.0001$) in size (spread) from areas of high to low densities (Table 1). Furthermore, ANOVA with harvest as a covariate still resulted in significant differences in antler size between areas of low ($\bar{X}_{\text{adj}} = 127.6$, SD = 0.71 cm), medium ($\bar{X}_{\text{adj}} = 117.9$, SD = 1.52 cm), and high ($\bar{X}_{\text{adj}} = 100.1$, SD = 1.17 cm) density ($P < 0.0001$, $n = 27,308$). Relative proportion of vegetation types in UCUs where moose were harvested affected size of antlers: low shrub ($F = 4.28$), deciduous ($F = 3.65$), ice and rock ($F = 3.60$), and spruce ($F = 3.19$).

Guided hunts also resulted in harvest of males with larger antlers ($\bar{X} = 147.4$, SD = 17.5 cm) compared with nonguided hunts ($\bar{X} = 121.0$, SD = 31.9 cm; $n = 2,755$; $P < 0.0001$). Interaction between moose density and guiding, however, was marginally insignificant ($F = 2.22$, $P = 0.11$). Furthermore, the strength of the relationship explained by guiding ($F = 346.34$) was substantially greater than for moose density ($F = 92.63$; $P < 0.0001$; $n = 2,755$). This outcome indicates that even though guiding is the dominant effect on the size of antlers for harvested moose, density of moose still plays a role in affecting size of antlers. Furthermore, when analyses were not restricted to only UCUs where guiding occurred, the strength of the relationship explained by moose density

($F = 448.83$) became substantially greater than guiding ($F = 37.25$) in the same model ($P < 0.0001$; $n = 3,327$).

A large proportion of guided hunts (89.2%; $n = 1,301$) occurred in areas of low-density compared with nonguided hunts (63.8%; $n = 2,966$). If a hunter employed a guide, they were 26 times more likely to hunt in areas of low than high moose density. Nonguided hunts in areas of low moose density made up the largest proportion of hunts; however, hunts in low-density areas were only three times more common than hunts in areas of high density. Consequently, we expected overall antler size of harvested males to be larger in guided hunts because moose in low-density areas possessed larger antlers, and those areas made up a larger proportion of guided compared with nonguided hunts. Indeed, all pairwise differences regarding antler size were significant (Fig. 2, $P < 0.035$). Nonguided hunts also tended to occur in areas with moose at low-densities (Table 1); however, the proportion of nonguided hunts in locations of medium and high density did not decrease as sharply as with use of guides (Table 1).

2.42 Selectivity and Intensity of Harvest

Hunters that employed transporters did not exhibit the same selectivity for areas of low density with potentially larger-antlered males (Table 1). Far less difference in antler size of harvested moose occurred among density categories for hunts with and without the use of a transporter than for guided and nonguided hunts (Table 1). Only a 4-fold increase occurred in use of low- versus high-density areas by hunters who employed a transporter, compared with the 26-fold increase with use of a guide.

We also tested whether guides sought out areas that were less frequently visited by other hunters relative to moose density. Indeed, the hunter-to-moose ratio was lower in areas used by guides in all three categories of moose densities (Fig. 3, $P < 0.0001$). Unlike antler size, however, the interaction term for hunter-to-moose ratio was significant ($P < 0.0001$). Further analyses revealed that among guided hunts, locations with medium densities of moose had a hunter-to-moose ratio that was near equal to that of hunts in areas of high moose density (Fig. 3); all pairwise comparisons were significant ($P < 0.05$).

Intensity of hunter harvest and moose density significantly influenced antler size of moose (Fig. 4, $P < 0.0001$). Antler size decreased as harvest intensity increased within medium- and high-density populations; however, within areas of low density a heavy harvest resulted in larger antlers than from medium-density areas, but less than from lightly harvested ones (Fig. 4). Antler size decreased from high-density areas to areas of low density (Fig. 4).

2.5 DISCUSSION

2.51 Antler Size and Population Density

Our hypothesis that moose density is negatively related to antler size of Alaskan moose was not rejected. Gasaway et al. (1987) demonstrated that site-specific variation in size of moose antlers occurred across Alaska; however, the cause for such variation was unknown. Bowyer et al. (2002) attributed variation in antler size to the habitats occupied by harvested moose, but could not rule out genetic differences in some instances.

Moose in Alaska typically are held at low densities by predation rather than hunter harvest (Gasaway et al. 1992); hunting selectivity by carnivores versus humans may cause substantial differences in the demographics of large mammals (Berger 2005). Hunts in Alaska mostly select only males (Schwartz et al. 1992, Hundertmark et al. 1998) and influences on population size and productivity are minimal. Many areas are difficult for hunters to access, thereby limiting harvest for much of the interior Alaska (Schmidt et al. 2005). Moreover, Alaskan moose have a highly polygynous mating system with female density primarily regulating population dynamics under such circumstances (McCullough 1979, Bowyer et al. 1999, Kie et al. 2003). Indeed, Alaskan moose mate in harems, which differ markedly from the mating system of other subspecies of moose (Molvar & Bowyer, 1994, Bowyer et al., 2003); management objectives for other subspecies often reflect the need for a higher proportion of males in the population to ensure mating synchrony (Crête et al. 1981, Timmermann et al. 1998, Whittle et al. 2000). Males can play a role in the population demography of moose, especially at low density or where their age structure is very young (Mysterud et al. 2002, Sæther et al. 2003, 2004). Even the heaviest harvests of moose in Alaska (Bowyer et al. 1999), however, seldom reach levels reported for Fennoscandia (Sæther et al. 2003, 2004).

Males and females of polygynous ruminants sexually segregate for much of the year (Bowyer 1984, Miquelle et al. 1992, Bleich et al. 1997, Kie and Bowyer 1999; Bowyer et al. 2001*b*, Bowyer 2004). Nevertheless, density-dependent effects on physical condition of females can limit growth of horns and antlers in males (Clutton-Brock et al. 1997, Jorgenson et al. 1998, McCullough 2001). Young Alaskan moose may have

difficulty compensating for low birth weights (Schwartz et al. 1994, Keech et al. 1999), as do some other cervids (Schultz & Johnson 1995, Pélabon 1997). Indeed, harvested moose from low-density areas had larger antlers than those occurring at higher densities (Table 1, Figs. 2 and 4). Effects of population density on antler size were maintained even when harvest was included as a covariate. Because predation is the dominant regulating mechanism for moose in much of interior Alaska (Gasaway et al. 1992), we hypothesize that antler size of males in low-density populations are positively influenced by their enhanced physical condition. Moreover, antlers are ostensibly under strong sexual selection (Bowyer et al. 2001*a*), yet we demonstrated that resource availability strongly influenced the distribution of this sexually selected characteristic across the landscape.

2.52 Effects of Habitat

We accept our hypothesis that there would be effects of habitat on the antler size of harvested moose. Indeed, that outcome offers further evidence for a nutritional basis for differences in antler size in interior Alaska. Furthermore, the strongest effects occurred in low shrub, which were areas preferred by moose because they often contained willows (*Salix* spp.) and other palatable shrubs (Molvar et al. 1993, Weixelman et al. 1998, Bowyer et al. 2003). Indeed, moose inhabiting tundra areas tend to have larger antlers than those from areas dominated by boreal forest (Bowyer et al. 2000), which likely explains the positive influence of more open habitat types on the size of moose antlers. Indeed, moose density is, in part, a function of the habitats they inhabit in interior Alaska (Maier et al. 2005). Further support for larger antlers in more open

environments was illustrated by males occurring in and adjacent to open areas with ice and rocks having larger antlers than those harvested in dense stands of black spruce common in interior Alaska. We hypothesize that this outcome integrates nutritional quality of habitats and density-dependent effects, which allow the phenotypic expression of large antlers.

2.53 Selectivity of Harvest

We accepted our hypothesis that guides would hunt in areas of lower moose density, resulting in the harvest of large-antlered males (Table 1). Further, we accepted our hypothesis that guides would harvest large-antlered males across a range of population densities in interior Alaska (Fig. 2). We also accepted our hypothesis that guides would hunt in areas with a low hunter-to-moose ratio. These outcomes indicate a high level of hunting skill by guides.

Antler size is often a motivation for sport hunters, and use of guides is common (Stewart 1985, Coltman et al. 2003, Hartl et al. 2003). Accordingly, for guides to be successful, they need to hunt in areas producing large-antlered moose. Indeed, most hunters employing a guide hunted in landscapes with low densities of moose; guides concentrated their hunts in areas of low moose density, which was 26-fold greater than guided hunts in high-density areas (Table 1). There was a lower use of low-density sites by transporters (four times more than for high-density areas). Regardless of mode of transportation or whether a hunter could afford to hire a transporter to attain access to a desired area, guides exhibited selectivity for low-density areas (Table 1). Guides clearly

possessed some skills other than greater means of access or geographic familiarity with areas where they hunted.

Most moose hunters employing guides were nonresidents who invested substantially in their hunts (i.e., travel to Alaska, employment of a guide, time off work, etc., Schmidt et al. 2005). Therefore, the goals of those individuals maybe similar to trophy hunters, who commonly select animals to harvest based on antler size (Stewart 1985, Snepenger and Bowyer 1990, Hartl et al. 2003). Because larger-antlered moose occur in areas of low density (Table 1), guides would be expected to satisfy the aspirations of their clients by hunting in such areas.

As a corollary to our prediction that guided hunts would occur more often in areas with low density of moose, we also proposed that guides would harvest moose with larger antlers across all population densities compared with nonguided hunts (Fig 2), even when both guided and nonguided hunts used aircraft for transportation. Guided hunts occurred more often in areas of low moose density and hunters harvested larger males within all densities categories of moose (Fig 2), indicating additional skill by guides. In addition, previous models of harvest have predicted decreased hunter success with smaller moose-to-hunter ratios (Cooper et al. 2002, Schmidt et al. 2005), resulting in skilled hunters or guides seeking areas with higher ratios. Our results support that finding as well as our prediction that guides would avoid other hunters while maximizing the likelihood of an encounter with a moose (Fig 3).

2.54 Harvest Intensity and Antler Size

We observed a general pattern of decreasing antler size from areas with the heaviest harvests of moose. Contrary to our hypothesis, however, antler size did not uniformly decrease as harvest intensity increased. Instead, at low densities, medium harvest intensity resulted in smaller antler size and ostensibly younger age structure than for moose in heavily harvested areas (Fig. 4).

An inverse relationship is expected between intensity of harvest and age structure; populations with heavy harvests exhibit a downward shift in age structure (McCullough 1979, Bowyer et al. 1999, Jenks et al. 2002). Size of antlers has been used as an index to age moose with larger antlers implying the oldest moose, although some senescence occurs in old age classes (Gasaway et al. 1987 Stewart et al. 2000, Bowyer et al. 2001a). As harvest intensity increases size of antlers should decrease because of a concomitantly younger age structure. Moose experienced reductions in age structure resulting from frequent removal of larger and older males via hunting (Solberg et al. 1999, 2000), leaving mostly younger and smaller-bodied males available for harvest. We demonstrated that successful hunters in areas experiencing heavy harvests and high densities of moose killed males with the smallest antlers. In areas with light harvests of moose, antlers were largest in low-density areas and smallest in high density areas (Fig 4). We hypothesize that this outcome occurred because of both density-dependent effects of physical condition and a reduced age structure among males.

2.55 Genetics and Harvest

Modelling efforts have predicted probable influences of hunting on antlers of Alaskan moose (Hundertmark et al. 1998). Controversy exists, however, over whether sport hunting influences the genetics of ungulate populations via possible consequences of selective harvests (Hartl et al. 1991, Hundertmark et al. 1998, Harris et al. 2002, Coltman et al. 2002, Hartl et al. 2003). Long-term patterns in selective hunting hold the potential to alter population density, sex ratio, and age distribution of ungulates (Ginsberg and Millner-Gulland 1994, Solberg et al. 2000).

Changes in the genetic underpinnings of physical characteristics can be quantified and evaluated (Kurt and Kumarasinghe 1998, Clutton-Brock et al. 1997) where resources are not limiting antler growth; such data would provide information needed for the sound management of moose. Our results also indicated that antler size can be markedly influenced by factors in addition to genetics. Indeed, genes coding for characteristics (large size) of antlers selected by hunters are less likely to be expressed under conditions of high population density in relation to K and, accordingly, the influence of harvest on genetics would be reduced under those circumstances (McCullough 1979). Clearly, more genetic data are needed to test these hypotheses.

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Figure 2.1 Study area where moose were harvested in interior Alaska, USA.

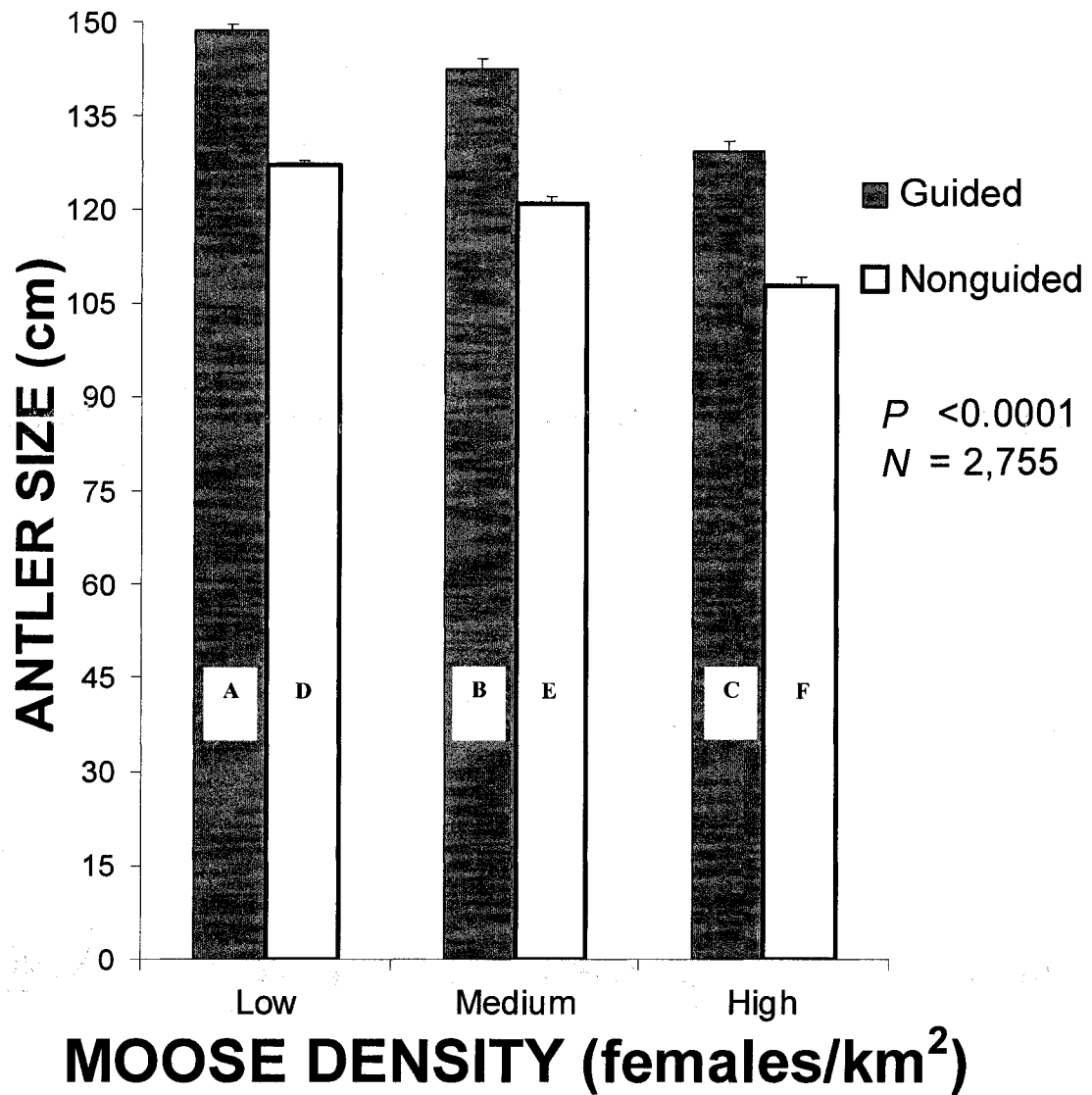


Figure 2.2 Mean (cm \pm SD) antler size of moose harvested by guided and nonguided hunts from 1997 to 2001 in interior Alaska, USA. Whenever a bar has a different letter from any other bar it is significantly different ($P < 0.05$, $df = 5$). P -value on the figure represents the overall significance of comparisons of mean antler sizes.

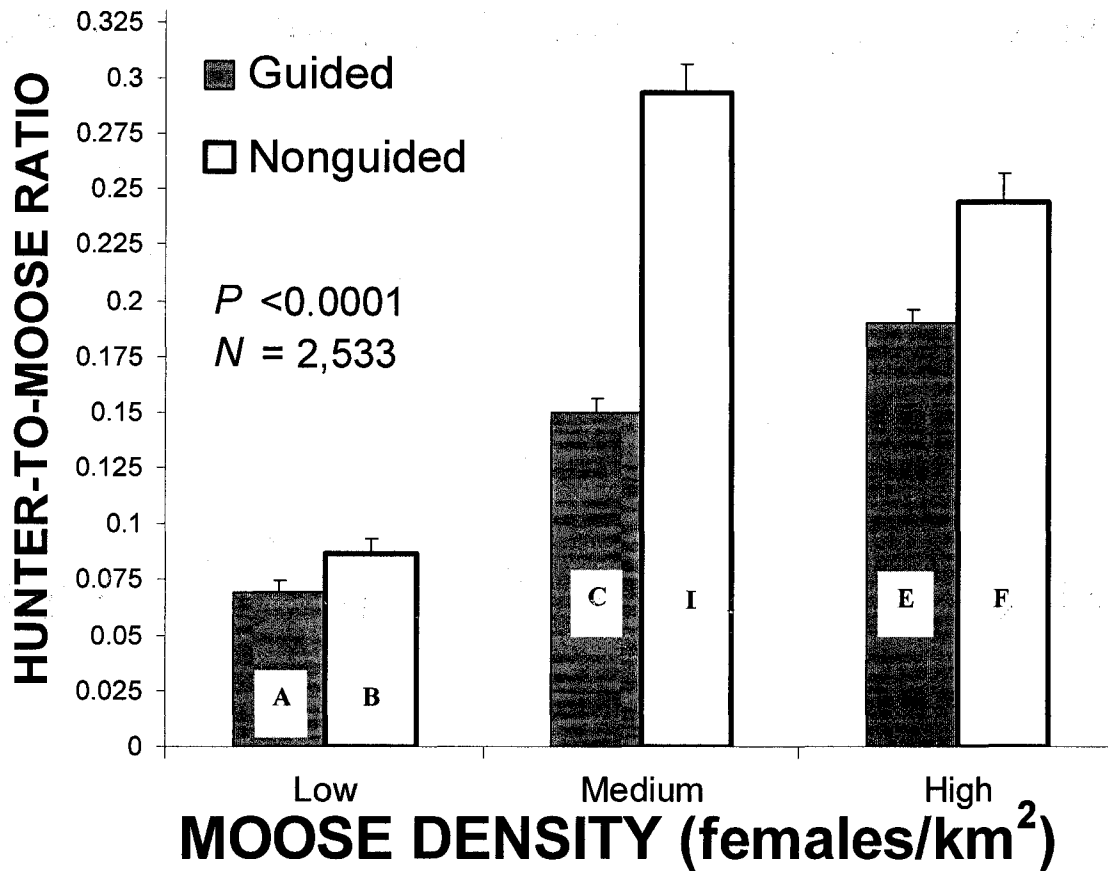


Figure 2.3 Hunter-to-moose ratio in areas used by guided and nonguided hunters from 1997 to 2001 in interior Alaska, USA. Whenever a bar has a different letter from any other bar it is significantly different ($P < 0.05$, $df = 5$). P -value on the figure represents the overall significance of comparisons of hunter-to-moose ratios.

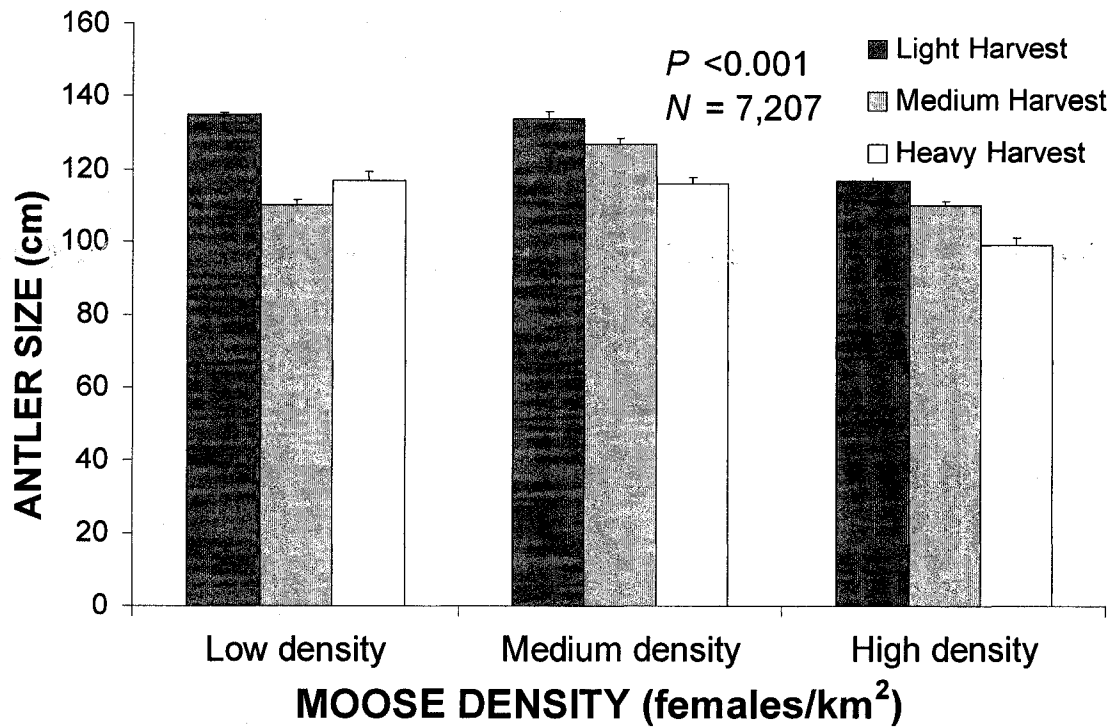


Figure 2.4 Mean (cm \pm SD) antler size of moose by harvest intensity across moose density from 1997 to 2001 in interior Alaska, USA.

Table 2.1 Proportion of guided, unguided, transporter, and nontransported hunts and antler size (cm), as measured by spread, occurring in areas of low, medium, and high densities of moose from 1997 to 2001 in interior Alaska, USA. Different sample sizes occur between hunting characteristics and antler spread because of differential reporting on harvest tickets. *P*-values indicate significant differences in mean antler size (cm) between moose densities.

Moose Density	Guided (<i>n</i> = 1,459)	Nonguided (<i>n</i> = 6,105)	Transported (<i>n</i> = 1,367)	Nontransported (<i>n</i> = 1,960)	\bar{X}	SD	<i>n</i>	<i>P</i> value
Low $X < 0.21$	0.89	0.64	0.70	0.69	113.55	0.38	7,933	<0.0001
Medium								
$0.21 \leq X \leq 0.406$	0.07	0.16	0.15	0.00	106.21	0.37	4,095	<0.0001
High $X > 0.406$	0.03	0.20	0.15	0.18	100.57	0.38	4,009	<0.0001

Note: *P* values indicate significant differences in mean antler size (cm) between moose densities.

CHAPTER 3

POPULATION STRUCTURE AND GENETIC DIVERSITY OF MOOSE IN ALASKA³

3.1 ABSTRACT

Moose (*Alces alces*) are highly mobile, range across much of Alaska, USA, and exert a prominent influence on ecosystem structure and function. Increased knowledge gained from population genetics provides insights into population dynamics and history, dispersal, and can aid in conservation efforts. We examined the genetic diversity and population structure of moose ($n = 121$) with seven polymorphic microsatellites from five regions spanning much of Alaska. Heterozygosity and allelic diversity were generally 80% higher in interior Alaska than in peripheral regions, ranging from 0.603 to 0.529 in the interior, and from 4.57 to 3.14 in surrounding areas. Both F_{ST} and R_{ST} indicated significant population structure ($P < 0.001$). Nonetheless, F_{ST} and R_{ST} values were low, with $F_{ST} < 0.109$ and $R_{ST} < 0.126$. Results of analyses from STRUCTURE indicated five populations. Mantel tests also indicate that isolation by distance partially explained observed structure among moose populations ($r = 0.66$, $P = 0.0041$). Finally, moose from the Alaska Peninsula have likely experienced a genetic bottleneck, but moose in Alaska overall have not. We conclude that weak population structure occurs among moose in Alaska with population expansion from interior Alaska westward towards the coast.

³ Jennifer I. Schmidt, Kris J. Hundertmark, R. Terry Bowyer, and Kevin G. McCracken. (2007) Submitted to the Journal of Heredity.

3.2 INTRODUCTION

Ungulates are important ecologically, culturally, and economically (Regelin and Franzmann 1998; Baskin 2002; Cooper et al. 2002; Gordon et al. 2004); and their evolutionary history and genetics have been well-studied (Coltman et al. 2001; Coltman et al. 2001*a* and *b*; Hundertmark et al. 2002*a* and *b*; Bowyer et al. 2003; Hundertmark et al. 2003; Wilson et al. 2003; Worley et al. 2004). Nevertheless, genetic research on moose (*Alces alces gigas*) in Alaska has been limited to allozymes and mtDNA analyses (Hundertmark et al. 1992, 2002*a* and *b*, 2003, 2006). Understanding the genetic structure of moose populations in Alaska is important because moose are a keystone species that can alter ecosystems (Molvar et al. 1993; Simberloff 1998). In addition to being ecologically important, moose provide a valuable economic and subsistence resource (Nelson 1973; Snepenger and Bowyer 1990; Ballew et al. 2006). Moreover, a more comprehensive understanding of dispersal and gene flow is critical for managing viable populations (Frankham et al. 2002) and moose currently inhabit most of Alaska (Karns 1998).

During the Pleistocene, unglaciated areas in central Alaska likely provided an ice-free corridor for moose as they dispersed towards southern portions of North America (Hundertmark et al. 2003). Even though, fossil and genetic research indicate that moose dispersed into North America from Sweden either 350,000-165,000 (Mikko and Andersson 1995) or 50,000 (Ellegren et al. 1996; Hundertmark et al. 2002*b*) years ago; this does not indicate that sustainable populations were formed in Alaska at this time (Hundertmark et al. 2002*b*). Rather moose at that time left Alaska uninhabited, and

continued to disperse past Alaska in a southern manner (Hundertmark et al. 2002b). Sustainable moose populations in Alaska arrived <15,000 years ago and thereby are more recent in comparison to their southern relatives in North America (Hundertmark et al. 2002b, 2003). From an evolutionary perspective, moose are recent colonists of Alaska (i.e., <15,000); consequently, structure among moose populations might be difficult to detect. Nonetheless, moose have undertaken traditional seasonal movements and exhibit strong fidelity to home ranges (Geist 1963; Houston 1968; Le Resche et al. 1974; Anderson 1991; Ballard et al. 1991; Hundertmark 1998). In addition to the influence of behavior, physical features such as river drainages, presence of glaciers, and mountain ranges have effectively restricted dispersal among moose populations in Alaska (Peterson 1955; Le Resche et al. 1974). Other factors that have been demonstrated to limit range expansion, population density, and dispersal include snow depth (>70 cm), habitat, predation, hunting, and hot temperatures (Coady 1974; Telfer 1978; Telfer and Kelsall 1984; Renecker and Hudson 1990; Gasaway et al. 1992; Bowyer et al. 1997; Maier et al. 2005). Demographic factors, such as isolation by bodies of water and isthmuses, have been shown to significantly influence heterozygosity in moose populations (Broders et al. 1999).

Incorporation of life-history characteristics, mating regimes, population histories, and knowledge of sex-biased dispersal (Bancroft et al. 1995; Scribner et al. 2001; Michaux et al. 2005; Okada et al. 2005) allows for a much more sound reasoning and insightful genetic conclusions. The genetic structure of populations for many species has been better understood by Effects of habitat fragmentation (Wang and Schreiber 2001),

hunting (Coltman et al. 2003), population translocations (Vernesi et al. 2002), and bottlenecks (Broders et al. 1999; Spencer et al. 2000), however, have often made it difficult to infer population status for many species, including ungulates (Wang and Schreiber 2001; Coltman et al. 2003; Coulon et al. 2004). In addition to genetic population structure, assessing genetic diversity is equally important because reductions in genetic diversity have been used to explain abnormalities in antler morphology (Hartl et al. 1991; Bowyer et al. 2002), levels of parasite resistance (Coltman et al. 2001*a* and *b*), and variations in body composition (Hartl et al. 1991; Coltman et al. 2001*b*).

In the past, mtDNA and microsatellites have been used to study phylogenetics and population genetics of moose (Broders et al. 1999; Hundertmark et al. 2002*a* and *b*, 2003, 2006; Wilson et al. 2003). Nonetheless, in Alaska the only published genetic studies of moose used allozymes and mtDNA (Hundertmark et al. 1992, 2002*a* and *b*, 2003, 2006). Previous studies recommended the use of microsatellite markers to better understand population status and dynamics, dispersal, and phenotypic differences among moose in Alaska (Bowyer et al. 2001, 2002; Hundertmark et al. 2002*a* and *b*, 2003, 2006).

The objectives of this study were to assess heterozygosity and investigate the genetic structure of moose in Alaska. In addition, we sought to determine the effective number of migrants among populations, examine evidence for potential past bottlenecks, isolation by distance, and determine to what extent these factors have shaped moose population structure in Alaska. We predicted that (1) Alaskan moose exhibit population structure with evidence of isolation by distance reported for moose in Canada (Broders et al. 1999), (2) populations closer together experience increased number of migrants

between populations (Anderson et al. 2004), and (3) older populations have higher genetic diversity than more recently isolated populations (LeResche 1974; Hundertmark 1998).

3.3 METHODS AND MATERIALS

3.3.1 Tissue Collection and DNA Extractions

Muscle and blood samples of 121 moose were obtained from hunters and biologists throughout Alaska during 2003 and 2004. We sampled moose in five Game Management Subunits (GMU), including Yakutat in Southeast Alaska ($n = 25$), Tanana Flats in interior Alaska ($n = 25$), Koyukuk in West interior Alaska ($n = 26$), Seward Peninsula in Western Alaska ($n = 25$), and the Alaska Peninsula in Southwest Alaska ($n = 20$; Fig. 1A and B). The sample from the Alaska Peninsula was composed entirely of females, whereas the Koyukuk sample was all males. The Seward Peninsula was composed of males and females ($n = 23$, $n = 2$, respectively), and a mixture of males, females, and unknown sex comprised the Yakutat, ($n = 21$, $n = 3$, $n = 1$, respectively) and the Tanana Flats ($n = 4$, $n = 16$, $n = 5$, respectively) samples. To address questions pertinent to population structure and dispersal, a total of 74 males and 41 females were used. We extracted genomic DNA with a Qiagen DNAeasy Tissue Kit, and DNA extracts were stored at -80°C . Moose tissues are archived at the University of Alaska Museum of the North (UAM) in Fairbanks, Alaska. (<http://arctos.database.museum/SpecimenSearch.cfm>).

3.32 Genotyping

We used eight microsatellite loci previously developed for genotyping in moose (Wilson et al. 1997; Roed and Midthjell 1998; Broders et al. 1999; Wilson et al. 2003). These included BM203, BM2830, NVHRT01, NVHRT21, Rt1, Rt5, Rt24, and Rt30. Polymerase chain reaction (PCR) was performed with a total reaction volume of 12.5 μ l and contained ~50 μ g of genomic DNA, 0.5 μ M of fluorescently labeled forward primer and 0.6 μ M of reverse primer, 2.5 mM MgCl₂, 1.25 μ l of 10x buffer B (100mM Tris-HCl, pH 9.0, 500mM KCl), 200 μ M of dNTPs, and 1.0 U of *Taq* DNA polymerase. Bovine serum albumin (1% BSA) was added to optimize PCR for individual loci. PCR cycles were as follows: 94° C for 2 min, followed by 30 cycles of 94° C for 30 s, 58° C for 30 s, and 72° C for 45 s, and a 30 min final extension at 72° C. PCR products were then visualized on a 3% agarose gels stained with 10 μ g/ μ l of ethidium bromide. The forward primers for BM203, Rt1, Rt24, and Rt30 were labeled with HEX dye, whereas BM2830, NVHRT01, NVHRT21, and Rt5 were labeled with 6-FAM. HEX and 6-FAM labeled PCR products were combined and electrophoresed for 2.5 hours at 3V on an Applied Biosystems 377 automated DNA sequencer using 36-cm polyacrylamide gels (5% Long Ranger). We determined allele sizes with the software GENESCAN 3.1.

3.33 Statistical Analysis

We screened loci for the presence of null alleles and allelic dropout using the software MICRO-CHECKER (Oosterhout et al. 2004). To test for Hardy-Weinberg equilibrium (HWE), linkage disequilibrium (LD), and effective number of migrants (Barton and Slatkin 1986), we used GENEPOP 3.4 (Raymond and Rousset 1995).

FSTAT (version 2.9.3; Goudet 2001) to calculate observed (H_O) and expected (H_E) heterozygosities (Nei 1987), adjusted allelic richness (Goudet 2001), and pairwise F_{ST} statistics (Weir and Cockerham 1984). Bootstrap replicates of 10,000 were performed to assess 95% confidence intervals (CI), and Bonferroni corrections for multiple comparisons were performed (Rice 1989). We also used ARLEQUIN (version 3.0; Excoffier et al. 2005) to calculate R_{ST} (Slatkin 1995) and perform analysis of molecular variance (AMOVA). Genotypic linkage disequilibrium was tested based on 150,000 permutations of the data. Jackknifing was conducted over all loci with 10,000 replicates to determine significant differences overall.

To determine if isolation by distance (IBD) was evident in moose populations, we used linear regression with SAS (version 9.0; SAS Institute 1999) and Mantel tests in GENEPOP and ARLEQUIN (Smouse et al. 1986). With both linear regression and Mantel tests, we compared various regression models including F_{ST} and R_{ST} versus both geographic distance and the natural log (ln) of geographic distance. We also calculated $F_{ST}/(1-F_{ST})$ versus ln of distance (Rousset 1997). Distance between populations was calculated with straight line paths. Because the extent of our analysis included the entire state of Alaska, all maps were projected into Alaska Albers equal area, which results in less distortion than other projections (Snyder 1987). To test for possible genetic bottlenecks, we used the program BOTTLENECK with a modified 2-phase model (TPM; Garza and Williamson 2001). Parameters were set so that 88% of mutations followed a stepwise mutation model (SMM; Kimura and Ohta 1978) and 12% followed a multi-step mutation model. For the multi-step mutation model, the variance was assumed (σ_g^2) to be

9 for the geometric distribution of number of repeat units per multi-step mutation (Di Rienzo et al. 1994). Our analysis used 3 repeat units as the mean step size for multi-step mutations (Δg), approximately equal to σg (Di Rienzo et al. 1994). Significance ($\alpha = 0.05$) was determined with a one-tailed Wilcoxon test (Cornuet and Luikart 1996). We also used the Bayesian analysis implemented in the program STRUCTURE (version 2.0; Pritchard et al. 2000) to infer population structure. To estimate the likelihood of population structure, we let the number of populations (k) vary between 1 and 10. After examining various burn-in lengths, we determined that a chain length of 10,000 was sufficient, and 100,000 Markov-Chain Monte Carlo repetitions were used. A total of 10 simulations were completed for each estimated k with an admixture model and inferred λ (Pritchard et al. 2000). Originally, we used the estimate of the number of populations that gave the best log-likelihood score along with the model that resulted in the highest value for percentage membership (q). We also analyzed our results according to Evanno et al. (2005), in which the number of populations were plotted against $\Delta k = m |L''(k)|/s|L'(k)|$ (i.e., second-order rate of change in the log probability of data between successive values of k) to determine the correct number of populations.

3.4 RESULTS

A total of 121 moose was analyzed with eight microsatellite markers. The only locus out of overall HWE as NVHRT01 ($P = 0.0024$), in which two populations had a deficiency of heterozygotes (Tanana Flats and Alaska Peninsula). We subsequently removed NVHRT01 from the analysis. Of the remaining loci, results from MICRO-CHECKER did not indicate the presence of null alleles or allelic drop out. All other tests

for HWE and LD within the 2003 and 2004 samples within populations were not significant ($P > 0.05$). Evidence of population differentiation between years was not detected. The largest number of alleles occurred in the Tanana Flats ($n = 31$) and the smallest in the Alaska Peninsula sample ($n = 22$). Overall number of alleles ranged from a low with BM2830 and Rt1 ($n = 3$) to a high with Rt30 ($n = 13$). Private alleles occurred in Yakutat (Rt5, Rt24, and Rt30), Koyukuk (Rt30), Seward Peninsula (NVHRT21), and Tanana Flats (BM2830). The only region that did not possess private alleles was the Alaska Peninsula. Of the seven loci, three (BM203, Rt1, and Rt24) had negative F_{IS} values with the overall value positive (0.011). F_{ST} loci estimates were greater than R_{ST} for all but one locus (Rt 1); overall F_{ST} and R_{ST} values were 0.059 and 0.048, respectively. Observed heterozygosity was greatest in the Tanana Flats and was followed closely by the Yakutat; however, Koyukuk was expected to have the second largest heterozygosity (Table 1). There was similar expected heterozygosity for the Seward Peninsula and Yakutat, followed by the Alaska Peninsula (Table 1). Global F_{ST} values were highest in the Alaska Peninsula and lowest in the Koyukuk and Tanana Flats (Table 1). The only two samples with negative F_{IS} values were those from the Tanana Flats and Yakutat (Table 1). The Alaska Peninsula had the highest F_{IS} , followed by Koyukuk, and Seward. In addition, F_{IS} was larger for males than females for all loci, and males also displayed more overall gene diversity, with four of seven loci exhibiting higher gene diversity in males than females. Both males and females had a locus that exhibited heterozygote deficiency, BM2830 and NVHRT21, respectively.

Population structure evaluated with both F_{ST} and R_{ST} estimates exhibited significant structure for moose populations within Alaska, with R_{ST} larger for only two of the pairwise population estimates (Fig. 2). Furthermore, F_{ST} estimates over all loci were larger than R_{ST} . Of these pairwise comparisons more were significant with F_{ST} estimates versus R_{ST} (Fig. 2). F_{ST} values ranged from 0.05 to 0.15 (Fig. 2), which is indicative of low to moderate levels of structure. The largest genetic differentiation was between Yakutat and the Alaska Peninsula (Fig. 2).

Bayesian analysis from STRUCTURE originally indicated that Alaska moose comprised one population, contradicting results from F_{ST} and R_{ST} . Nevertheless, using the method of Evanno et al. (2005), we determined that our samples represented five populations (Fig. 3). Subsequent results from IBD plots of F_{ST} versus geographic distance indicated a slight but significant relationship ($P = 0.01$). When we regressed $F_{ST}/(1-F_{ST})$ versus \ln of geographic distance, we observed a stronger relationship ($P = 0.0041$; Fig. 4). In addition, Mantel tests with ARLEQUIN indicated that the only significant correlation between two matrixes was obtained when one was $F_{ST}/(1-F_{ST})$ and the other the \ln of geographic distance ($P = 0.024$).

We used GENEPOP to estimate the effective number of migrants between populations. Migration was greatest between Koyukuk and Seward Peninsula, followed by Koyukuk and Tanana Flats, and between Tanana Flats and Seward Peninsula (Fig. 2). We also observed more migration between the Seward Peninsula and the Alaska Peninsula than between Koyukuk and the Alaska Peninsula. Lastly, we tested for potential genetic bottlenecks. Overall, we observed no evidence that moose as a single

population in Alaska have experienced a bottleneck; however, the Alaska Peninsula ($P = 0.012$) appeared to have experienced a recent bottleneck.

3.5 DISCUSSION

Ungulates commonly exhibit population structure (Chesser 1991*a* and *b*; Mathews and Porter 1993; Wang and Schreiber 2001; Worley et al. 2004). Even though past research has indicated low levels of mtDNA and nuclear diversity in moose (Hundertmark et al. 2002*a* and *b*; 2003; Wilson et al. 2003), population structure has been observed for moose with the use of microsatellites (Broders et al. 1999; Wilson et al. 2003). Therefore, results from both F_{ST} and R_{ST} statistics (Fig. 2) and Bayesian inference (Fig. 3) that indicate significant population structure in Alaskan moose were expected. Nevertheless, the degree of population structure was more difficult to predict. Given that levels of population structure differed among the methods used, we conclude that structure does indeed exist, but at low levels, especially in interior Alaska.

F_{ST} and R_{ST} values differed in population structure, with F_{ST} indicating more structure than R_{ST} (Fig. 2). The major difference occurred among the population comparisons that contained the Alaska Peninsula, with F_{ST} revealing much more structure. One reason for the differences between the two results could be that F_{ST} incorporates only variance in allele frequencies, and R_{ST} also includes variance in allele size (Balloux and Lugon-Moulin 2002). All samples had private alleles, with the exception of the Alaska Peninsula population (Table 1). The presence of private alleles can cause allelic frequencies between populations to be dramatically different but, meanwhile may have only a slight effect on the variance in allelic size among

populations. Thus, population comparisons that are influenced by private alleles could result in increased population differentiation estimates of F_{ST} while having little effect on R_{ST} estimates. This occurs because F_{ST} estimates are based on differences in allele frequencies while R_{ST} estimates are based on comparisons of allelic range, therefore with the presence of private alleles within our data, F_{ST} estimates were in general larger than R_{ST} . Furthermore, the most discrepancy between statical differentiation between population comparisons occurred with Yakutat and the Alaska Peninsula (Fig. 2) which had the highest and lowest number of private alleles, respectively. Either way, F_{ST} and R_{ST} agreed that Yakutat seems to be the most different among our populations given that all pairwise comparisons with Yakutat were highly significant (Fig. 2). Estimates with F_{ST} and R_{ST} indicated that Koyukuk and the Seward Peninsula are not separate populations at this time, but rather one population. The agreement in ability to decipher these two regions sampled supports ethnographic data, which maintain that moose recently filtered into the Koyukuk region from central interior Alaska around the 1900s and then dispersed into the Seward Peninsula in the 1940s (Nelson 1973).

Similar to previous research with moose, F_{ST} values generally were greater than R_{ST} (Wilson et al. 2003). Moose in both Alaska and Canada, on average, had higher F_{ST} values than R_{ST} values (Wilson et al. 2003), which may be because of the downward bias observed with R_{ST} values (Balloux and Goudet 2002). Differences between F_{ST} and R_{ST} values, however, can provide valuable insights into the balance between mutation and drift (Hardy et al. 2003). R_{ST} does not make assumptions about mutation rates, so when effects of mutation are thought to be larger than dispersal, F_{ST} values will be smaller than

R_{ST} values. Because our values of F_{ST} values were larger than R_{ST} we conclude that dispersal is the dominant factor affecting genetic structure among our moose populations.

F_{ST} values for moose in Alaska are not as large as those reported for moose in Canada, indicating that moose have been established in Canada longer than in Alaska; thereby resulting in relatively more population differentiation and larger F_{ST} values in Canada (Wilson et al. 2003). Furthermore, the range of many of our genetic estimates was narrow (Table 1). For example, F_{IS} values ranged from -0.014 to 0.035, whereas those observed by Wilson et al. (2003) ranged from -0.132 to 0.176. This outcome is consistent with the hypothesis of Hundertmark KJ, Shields GF, Udina IG, et al. (2002) that moose more recently established a sustainable population in Alaska than in Canada. Nevertheless, heterozygosity for Alaskan moose was higher than has been observed for moose populations in Canada (Broders et al. 1999; Wilson et al. 2003). We believe that the elevated heterozygosity could result from increased gene flow or remnants of past gene flow.

Indeed, gene flow could be one of the reasons why our predictions regarding populations with a longer history having higher gene diversity were not fully supported (Dutech et al. 2004). We predicted that populations with an older source such as the Tanana Flats and Yakutat would exhibit higher heterozygosity. The Tanana Flats in central interior Alaska is thought to have the oldest resident moose population among our samples because of past glacial events and re-colonization patterns (Peterson 1955). Evidence that moose can disperse from Canada into Alaska is documented below 58° 45'N (south of Yakutat) in Southeast Alaska; the Alaskan subspecies of moose (*A. a.*

gigas) do not occur there, but are replaced by the Canadian subspecies (*A. a. andersoni*; Hundertmark et al. 2006). Moose around Yakutat likely originated from routes leading into Canada from historically older populations. Yet, the two hypothesized older populations, Yakutat and the Tanana Flats, did not have the highest diversity; but instead Tanana Flats and Koyukuk in the interior had the largest values. Rather than age of an established population, gene flow seems to have greater influence on estimates of heterozygosity. In addition, estimates for the three largest effective number of migrants all were among the populations in interior Alaska and the Seward Peninsula. Our results indicate that substantial gene flow occurs among moose populations in interior Alaska. The Alaska Peninsula had the lowest estimates of heterozygosities and fixation indices. Because sample size is not much smaller for that population, 20 versus 25 or 26, we believe that this is indeed a characteristic of the Alaska Peninsula population in which moose are geographically more isolated than some of our other sampling locations.

Results from the STRUCTURE analysis (Evanno et al. 2005) support the finding that moose in Alaska exhibit population structure with five populations present. With the ability to incorporate multiple gene exchange models, we conclude that the methods of Evanno et al. (2005) are more robust than methods of Prichard et al. (2000), a conclusion also reached by Gompert et al. (2006). This is not the first time that conflicting results concerning population structure have been observed between F_{ST} and the program STRUCTURE (Prichard et al. 2000). In a study that contained similar small F_{ST} values, Martinex-Cruz et al. (2004) reported structure with F_{ST} , but no population structure with the results from STRUCTURE. In addition, Basset et al. (2006) noted no structure in

shrew (*Sorex araneus*) populations with the method of Prichard et al. (2000), but structure was observed with the method of Evanno et al. (2005). We believe that it is best to incorporate multiple methods in reaching conclusions about genetic structure. Therefore, we concluded that the results from F_{ST} , R_{ST} , and STRUCTURE indicate that there is population structure among our samples, although it is weak to moderate.

To explain observed population structure, we suggested that IBD, which has previously attributed moose population structure to Canadian populations (Wilson et al. 2003), would play a role in Alaska. We detected a slight significant positive relationship between F_{ST} and geographic distance, but we continued to explore other regressions and observed that the linear regression between $F_{ST}/(1-F_{ST})$ versus \ln of distance (Rousset 1997) was much stronger (Fig. 4). In addition, results from GENEPOP and Mantel tests detected a significant correlation between $F_{ST}/(1-F_{ST})$ versus \ln of distance. One of the reasons that there might have not been a strong relationship between F_{ST} and straight line geographic distance is because Alaska is very large and has diverse ecological landscapes. Consequently, the topography between populations we compared is very different. Moose in various regions of Alaska may encounter different types of terrain while dispersing, thereby making some paths easier and straighter to traverse versus others, which may be more arduous with impediments that require a convoluted path. Therefore, the Euclidean distances probably are not the actual paths that moose follow during dispersal. Further evidence that straight-line distance might not be very realistic model is that one-half of our population comparisons resulted in greater predicted genetic distance than geographic distances.

Results from the effective number of migrants also indicate that landscape features influence moose dispersal. Even though Koyukuk is 62 km closer to the Alaska Peninsula than the Seward Peninsula, more migration occurred between the Alaska and Seward Peninsula populations (Fig. 2). This outcome indicates that there also appears to be more gene flow along the coastal route through the Yukon Delta between the Seward Peninsula and Alaska Peninsula populations than between Koyukuk and the Alaska Peninsula. We hypothesize that some landscape features, such as the Alaska Range, might reduce gene flow between the Alaska Peninsula and Koyukuk populations more than for moose populations occupying the Seward Peninsula and Alaska Peninsula.

Finally, moose in Alaska do exhibit population structure, but some gene flow still occurs. Understanding the magnitude and geographic pattern of dispersal is a key to maintaining viable moose populations, especially among harvested populations and those separated by habitat barriers (Labonte et al. 1998; Coulon et al. 2004). Because the Tanana Flats is the older population, its moose likely are dispersing westward, given our inability to differentiate between adjacent western neighboring populations (i.e., between the Tanana Flats and its western neighbor Koyukuk and Koyukuk and its western neighbor the Seward Peninsula). The westward dispersal from interior Alaska probably is recent, and migration continues to occur between the Seward Peninsula and Koyukuk and between Koyukuk and the Tanana Flats. One question that remains is whether the current lack of population differentiation reflects a current exchange of moose between the geographic areas or the relatively recent population expansion with no current exchange of individuals. Conservation efforts and management decisions should explore

this issue more closely and consider the current population dynamics, future goals, and evolutionary consequences of their actions.

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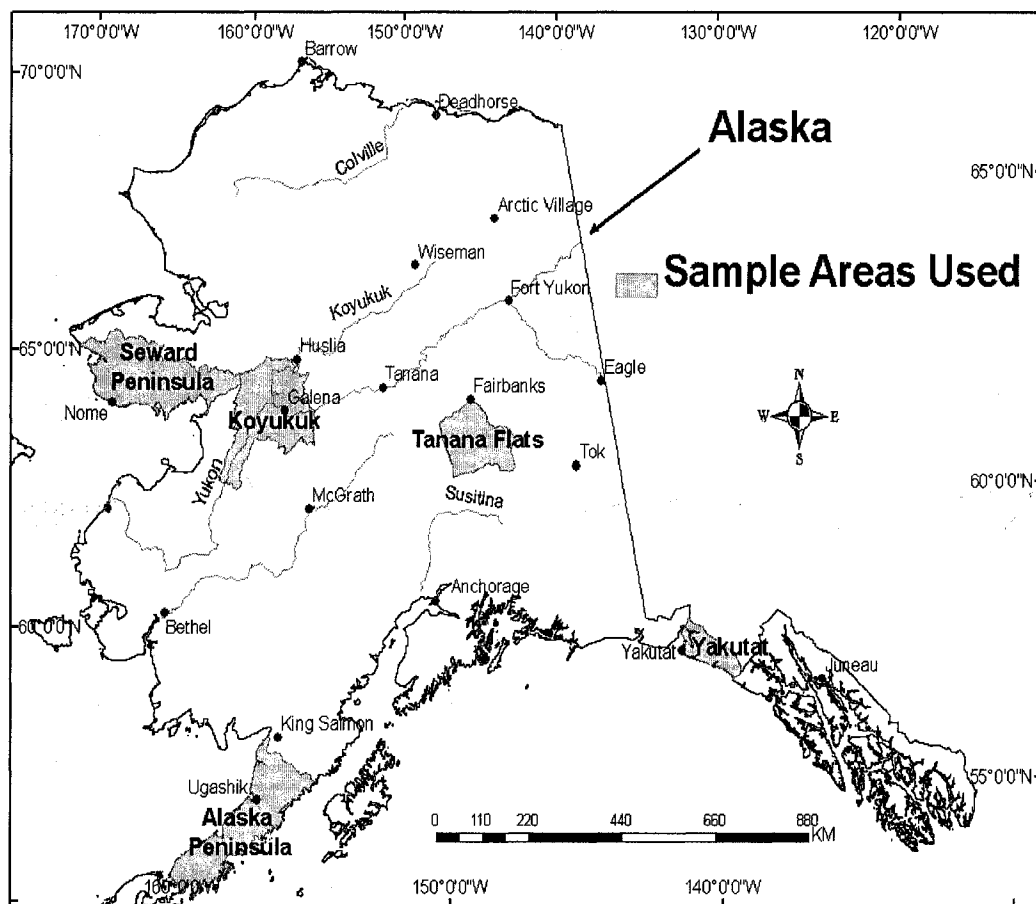


Figure 3.1 Moose populations used for microsatellite analysis in Alaska with boundaries represented by game management subunits for moose in Alaska from 2003 to 2004.

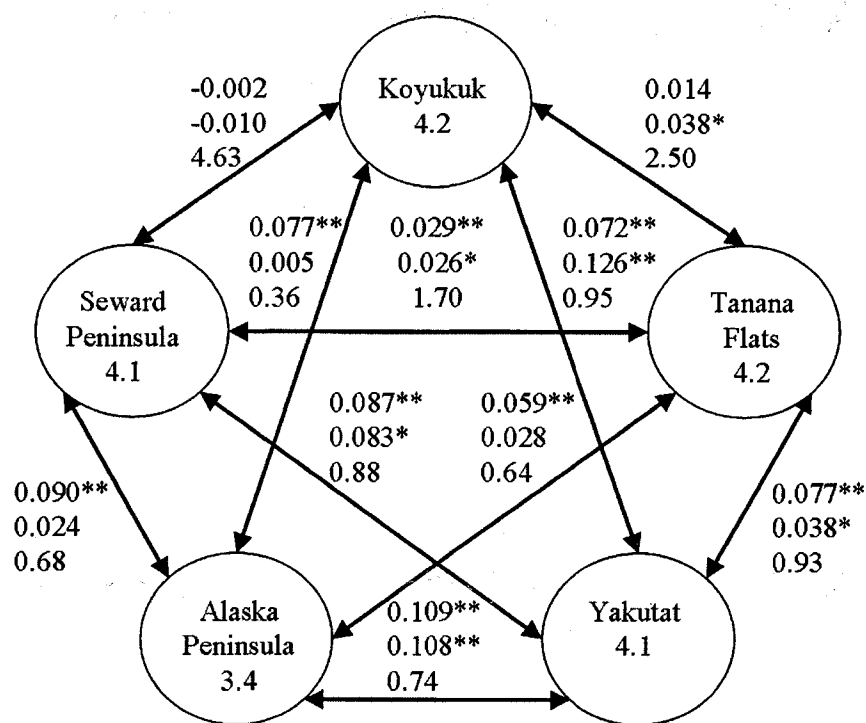


Figure 3.2 Pairwise population comparisons with F_{ST}^{\dagger} values, R_{ST}^{\S} values, and effective number of migrants beside arrows connecting populations and average number of pairwise differences within population in the circles for moose in Alaska from 2003 and 2004. $^{\dagger}F_{ST}$ Weir & Cockerham (1984), $^{\S}R_{ST}$ Slatkins (1995), ** $P < 0.01$, * $P < 0.05$

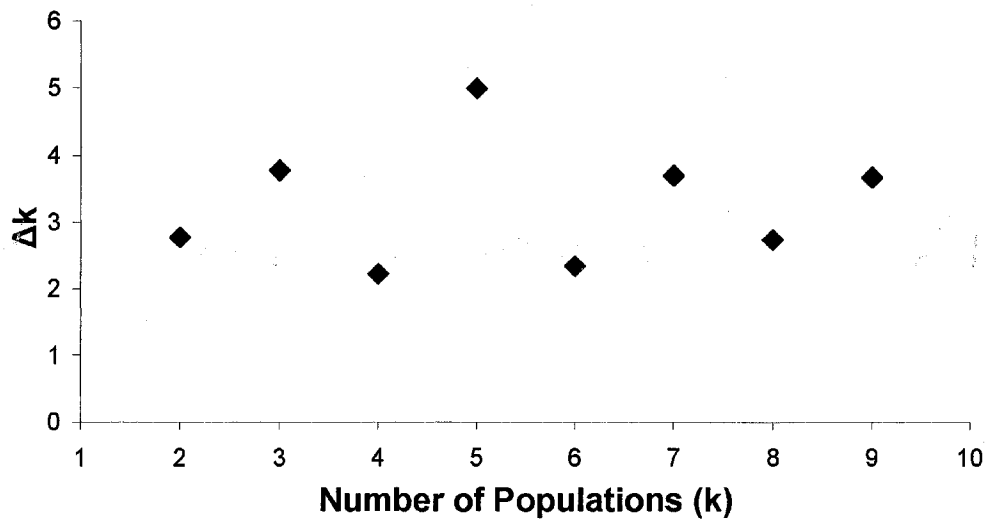


Figure 3.3 Estimated number of populations (k) from STRUCTURE versus the second order rate of change in k (Δk) based on the methods of Evanno et al. (2005) for moose in Alaska from 2003 and 2004. $\Delta k = m(|L''k|)/s[L(k)]$

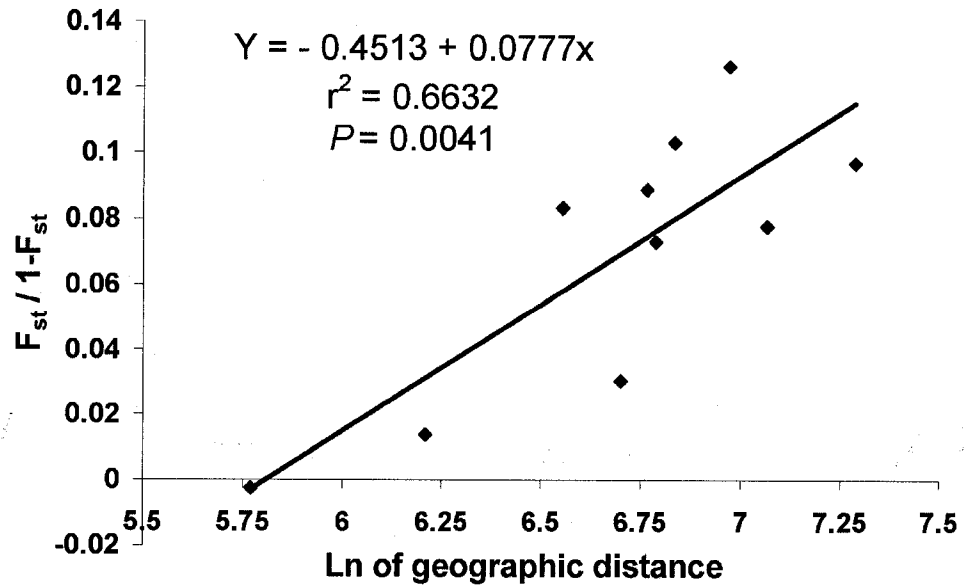


Figure 3.4 Ln of geographic distance versus $F_{ST}/1-F_{ST}$ (Rousset 1997) for moose in Alaska from 2003 and 2004.

Table 3.1 Sample size, mean number of alleles (N_A), private alleles, expected heterozygosity (H_E), observed heterozygosity (H_O), F_{ST} , and F_{IS} values per population and over all loci for moose in Alaska from 2003 and 2004.

Population	n	N_A	No of private				
			alleles	H_E	H_O	F_{ST}	F_{IS}
Yakutat	25	4.429	5	0.581	0.589	0.059	-0.012
Tanana Flats	25	4.571	1	0.603	0.611	0.058	-0.014
Seward							
Peninsula	25	4.429	1	0.583	0.575	0.059	0.025
Koyukuk	26	4.143	1	0.601	0.582	0.058	0.031
Alaska Peninsula	20	3.143	0	0.529	0.520	0.062	0.035

CHAPTER 4

EFFECTS OF LANDSCAPE CHARACTERISTICS ON POPULATION CONNECTIVITY OF ALASKAN MOOSE: A COMPARATIVE TEST⁴

4.1 ABSTRACT

Landscape genetics is a rapidly developing field that has provided considerable insight into the influence of landscape features on gene flow. Moose (*Alces alces gigas*) in Alaska, USA, are a highly vagile species with well documented dispersal. Eight microsatellite loci were used to genotype a total of 141 individuals from six moose populations in Alaska. We then tested whether models of least-cost paths outperformed Euclidean distance in their ability to relate geographic and genetic distances. Four hypothetical least-cost paths of dispersal were drawn based on four friction maps constructed from multiple habitat and landscape features that were assigned cost values based on current knowledge of moose biology. One-half of the models were assigned costs in which good habitat facilitates dispersal, whereas the other two models assumed that good habitat impedes dispersal. We developed two models for each of these sets of assumptions, one that contained habitat and more permanent landscape fixtures, whereas habitat effects were minimized for other models. Models were evaluated with Mantel tests (AIC_C) and linear regression (R_{ADJ}^2). We also explored rates of current and historic dispersal, population structure, and evidence of bottlenecks. Results indicate that the relationship between geographic and genetic distance is significantly improved when

⁴ Jennifer I. Schmidt, Kris J. Hundertmark, R. Terry Bowyer, and Kevin G. McCracken (2007) for submission to *Molecular Ecology*.

modeled with least-cost paths than with Euclidean models. Models with habitat features minimized outperformed models with more habitat features included due to over-parameterization of the latter. Nonetheless, even at large spatial scales, the inclusion of habitat and landscape features provided a much better understanding of gene flow and population structure of moose in Alaska.

4.2 INTRODUCTION

Animals respond to their surrounding landscape in ways that affect density, growth, dispersal, gene flow, and population structure (Hass 1995, Krebs et al. 1995; Akcakaya et al. 2004; Coulon et al. 2004; Funk et al. 2005; Said & Servanty 2005; Vignieri 2006). The field of landscape genetics, which incorporates many subdisciplines within landscape ecology, is rapidly emerging (Manel et al. 2003; Storfer et al. 2007). Indeed, population structure and distribution has been dictated largely by landscape features (Manel et al. 2003; Geffen et al. 2004; Spear et al. 2005). Aspects of landscape characteristics such as adequate habitat, presence or absence of other species (Manel et al. 2003; Said & Servanty 2005), and barriers or corridors to dispersal and gene flow have a direct effect on population genetics (Manel et al. 2003). Because individuals perceive and respond to their environment in a holistic manner, studies of landscape genetics must evaluate a patchwork of potential corridors and barriers to dispersal and gene flow that reflect ecological, physical, and anthropogenic features. The heterogeneous environment occupied by organisms influences dispersal (Slakin 1994), associated gene flow (Bohonak 1999), and distribution of populations (Wiens 2001).

Geographic information system (GIS) provides a powerful tool to integrate landscape information with genetic data to infer population structure and dynamics (Degen et al. 2001; Michels et al. 2001; Hardy & Vekemans 2002; Kie et al. 2003; Coulon et al. 2004, 2006; Geffen et al. 2004; Pállson et al. 2004; Spear et al. 2004; Guillot et al. 2005). In particular, the combination of landscape genetics and GIS has been useful for better understanding the genetic population structure and dispersal of ungulates (Coulon et al. 2004, 2006; Worley et al. 2004). Moose (*Alces alces*) in particular are greatly influenced by landscape features such as elevation (Van Ballenberghe 1992), glaciers (Peterson 1955; Klein 1965 Telfer & Kelsall 1984; Stephenson et al. 2006), rivers (Maier et al. 2005), lakes (MacCracken et al. 1993), snow (Coady 1974; Stephenson et al. 2006), vegetation (Peek 1974; Schwartz 1998), and fire (Bangs & Bailey 1980; MacCracken & Viereck 1990; Weixelman et al. 1998). In addition, moose can be affected by humans through construction of roads (Yost & Wright 1991; Stephenson et al. 2006), power lines (Ricard et al. 1999), railroads (Modafferi 1991), and hunting (Labonté et al. 1998). Previous research on Alaskan moose (*Alces alces gigas*) indicated that population structure does exist and that isolation-by-distance plays a role (Schmidt et al. Chapter three). Because the ability of an isolation-by-distance model to explain moose population structure was significant, but weak, we hypothesize that the influence of landscape properties complicates the association between genetic and geographic distance (Broquet et al. 2006; Vignieri 2006). Increased understanding about distribution and landscape connectivity among populations is imperative to sustaining and conserving viable populations. In addition, maintaining dispersal

corridors reduces effects of inbreeding and genetic loss (Metzger & Decamps 1997; Frankham 2005). Moreover, modeling dispersal paths provides the opportunity to incorporate effects of climate change and evaluate potential future dispersal and shifts in gene-flow paths (Keyghobadi et al. 1999; Spear et al. 2005).

Many species that inhabit subarctic environments, Alaska in particular, have experienced climate change that is likely to become an increasingly dominant force not only on landscape features, but more importantly on moose population structure and regions deemed suitable habitats. Based on previous research in landscape genetics, we used resistance or friction maps that arise from 'costs' (i.e., barriers to dispersal or gene flow) to draw least-cost paths connecting moose populations to explore dispersal of moose in Alaska (Micheals et al. 2001; Coulon et al. 2004, 2006; Spear et al. 2005; Vignieri 2005). The friction-map concept involves adding up several different coverage maps to create a landscape surface that an animal might perceive. Our research builds on previous research in landscape genetics by incorporating many more landscape layers, of both ecological and anthropogenic origin, to form our friction map (Ray et al. 2002; Currant & Excoffier 2005).

Least-cost paths (Michels et al. 2001; Coulon et al. 2004, 2006; Scribner et al. 2005; Spear et al. 2005; Vignieri 2005) were drawn between six populations of moose sampled in Alaska, and these populations were genotyped with eight microsatellite loci. Both standard measurements of genetic distance and Bayesian methods were used to infer population structure. In addition, we predicted that inclusion of landscape features, such as elevation, glaciers, fire, vegetation, and roads would result in more realistic dispersal

paths that better correlate with genetic distance than linear (Euclidian) geographic distance. We also sought to test whether good moose habitat promotes or impedes dispersal. Because dispersal is male-biased in moose, and female moose are thought to remain close to their natal range, often sharing overlapping home range with their mother (Ballard et al. 1991; Hundertmark 1998), we predicted that the best model based on Mantel tests and linear regression would be the one in which good habitat provided a corridor for male dispersal.

4.3 METHODS

4.31 Samples and genotyping

We collected 141 moose samples from six localities within Alaska (Fig. 1A and B) Yakutat ($n = 25$), Tetlin ($n = 20$), Tanana Flats ($n = 25$), Koyukuk ($n = 26$), Seward Peninsula ($n = 25$), and the Alaska Peninsula ($n = 20$). Samples were composed of both muscle and skin, archived at -80°C , and extracted with a DNAeasy Tissue Kit (Qiagen). Yakutat and Koyukuk sampling dates were 2003 and 2004, Tetlin 2004 and 2005, and Tanana Flats and the Seward Peninsula 2003. Samples were a mixture of males, females, and unknown individuals, respectively, for Yakutat ($n = 21$, $n = 3$, $n = 1$), Tanana Flats ($n = 4$, $n = 16$, $n = 5$), and the Seward Peninsula ($n = 23$, $n = 2$, $n = 0$). The Tetlin and Alaska Peninsula samples were all female.

Microsatellite genotyping was performed with eight primer pairs previously used for moose (Wilson et al. 1997, 2003; Roed & Midthjell 1998; Broders et al. 1999, Schmidt et al. Chapter three). BM203, Rt1, Rt24, and Rt30 were labeled with HEX dye; BM2830, NVHRT01, NVHRT21, and Rt5 were labeled with 6-FAM. Polymerase chain

reaction (PCR) was performed following methods previously outlined in Schmidt et al. (Chapter three). An ABI377 DNA sequencer with 36-cm polyacrylamide gels (Cambrex: 5% Long Ranger) was used for 5 h at 3V. We used GENESCAN 3.1 with a 500 base pair size standard to determine allele sizes.

4.32 Genetic statistical analysis

All loci were examined for the presence of null alleles and allelic dropout with the software MICRO-CHECKER (Oosterhout et al. 2004). We used GENEPOP (v. 3.4; Raymond & Rousset 1995) to examine Hardy-Weinberg equilibrium. FSTAT (v. 2.9.3; Goudet 2001) was used to assess linkage disequilibrium (1,680,000 permutations) and calculate expected and observed heterozygosities (Nei 1987), private alleles (El Mousadik & Petit 1996), allelic richness adjusted for sample size (Goudet 2001), and pairwise F_{ST} statistics (Weir & Cockerham 1984). We performed Bonferroni adjustments for tests that involved multiple comparisons (Rice 1989). We used the methods of Barton and Slatkin (1986) to estimate the effective number of migrants in GENEPOP (Slatkin 1985). We used ARLEQUIN 3.0 (Excoffier et al. 2005) to perform analysis of molecular variance (AMOVA; 10,000 permutations), calculate R_{ST} statistics and log-likelihood assignment values for each moose (Paetkau et al. 1995 & 1997; Waser & Strobeck 1998), and calculate population pairwise differences between the six populations. Given the genetic distance among our population comparisons and the mating behavior of moose, we used a Bayesian approach with BAYESASS 1.2 (Wilson & Rannala 2003) to estimate more recent rates of dispersal and direction, rather than migration. To assure consistent and accurate estimates, we tested various burn-in lengths, initial seed numbers, and

maximization of log-likelihood values were maximized when the proposed changes were between 40 and 60% of the total iterations (Wilson & Rannala 2003). After several trial runs with BAYESASS (Wilson & Rannala 2003), we concluded that after a burn-in length of 10^6 iterations accurate data collection could begin, followed by 3×10^6 iterations to collect data. Convergence and stitization was obtained with a sample frequency of 2,000 Monte Carlo Markov Chain (MCMC; Wilson & Rannala 2003).

To test for possible bottlenecks of past populations, we used the program BOTTLENECK with a modified two-phase model (TPM; Garza & Williamson 2001). Parameters for BOTTLENECK were set so that 88% of mutations followed a stepwise mutation model (SMM; Kimura & Ohta 1978) and 12% a multi-step mutation model (Rienzo et al. 1994); the variance was assumed (σ_g^2) to be nine (Di Rienzo et al. 1994). Our analysis contained three repeat units with the mean step size for multi-step mutation (Δ_g) approximately equal to σ_g (Di Rienzo et al. 1994). Significance was determined with a one-tailed Wilcoxon test (Cornuet & Luikart 1996).

To test for isolation-by-distance, we performed Mantel tests with FSTAT (Mantel 1967; Smouse et al. 1986; Manly 1991). The geographic distance connecting samples was represented by either Euclidian distances, or one of the four least-cost paths and the ln of those distances (Rousset 1997). Genetic distances were calculated with F_{ST} , R_{ST} , and $F_{ST}/(1-F_{ST})$. Because we performed multiple Mantel tests and wanted to discriminate whether there was a significant improvement between tests in a two-step process, we calculated corrected Akaike Information Criterion for small sample sizes (AIC_C) and

ΔAIC_C (Burnham & Anderson 2002). From the residuals in FSTAT we first we calculated log-likelihood values by:

$$\text{Log-likelihood} = \frac{(n \times \text{number of genetic values}) \times (\text{Log}(\text{variance of residuals}))}{2}$$

Next, we used the resultant log-likelihood to calculate AIC_C values and delta according to the standard AIC_C equations (Burnham & Anderson 2002). With the same geographic and genetic comparisons we used the statistical program R to perform linear regression (v. 2.5; R development Core Team). Calculations of AIC_C scores for Mantel tests and linear regression allowed the number of parameters within the model to be defined. Therefore least-cost models one and two with habitat and permanent landscape layers have the largest number of parameters ($n = 23$), least-cost models with only permanent landscape layers next fewest ($n = 15$), and lastly Euclidian models with the least number of parameters ($n = 3$). Unlike AIC_C calculations, estimates of adjusted r-square with linear regression contained the same number of parameters ($n = 3$) since all were regressions between genetic versus geographic distance.

We used Bayesian analysis implemented in the program STRUCTURE 2.1 (Pritchard et al. 2000) to infer population structure and explore population assignments of moose. To estimate the likelihood of population structure, we let the number of populations (K) vary between 1 and 10. After examining various burn-in lengths we observed that a chain length of 100,000 was sufficient with 1,000,000 MCMC repetitions. A total of 10 simulations were completed for each estimated K. Other parameters included the use of an admixture model, correlated alleles, and no population information

provided (Prichard et al. 2000). We used the estimation of the number of population that gave the best log-likelihood score along with the model that resulted in the highest percentage membership value (q ; Prichard et al. 2000). In addition, we analyzed our results according to Evanno et al. (2005), in which the number of populations were plotted against $\Delta K = m |L''(K)|/s|L(K)|$ to determine the correct number of populations from the program STRUCTURE. We used AMOVA in ARLEQUIN to analyze the groups identified by results from the STRUCTURE analysis.

In addition, we explored population structure with a neighbor-joining tree (NJ; Saitou & Nei 1987) based on unbiased Nei's genetic distances (Nei et al. 1983). Genetic distances were calculated and the neighbor-joining tree constructed with the program DISPAN (Ota 1993) and FIGTREE (v. 1.0; Rambaut 2006).

4.33 Study area and landscape features

Most of our study area was in Alaska with smaller areas in Yukon Territory and British Columbia, Canada (2,192,000 km²; Fig. 1A and B). Most of the landscape features we used had been used previously to model moose density and distribution (Maier et al. 2005), catch-per-unit effort (Schmidt et al. 2005), and effects of habitat on antler size (Bowyer et al. 2003; Schmidt et al. 2007) for moose in Alaska. Thus the rank and assigned cost values were made according to previous knowledge of their significance and effect on multiple aspects of moose biology. Landscape layers for coverage in the Yukon Territory and British Columbia were collected from a wide variety of sources. Landscape features that were not in grid form (i.e., polygons and polylines) were converted into 100 x 100-m grids. Appendix 4A lists the map layers used, some of

which were classified as habitat layers with the remainder being physical features of the landscape. The physical features tested were landscape coverages that are relatively permanent potential barriers such as roads, past glaciers, or the ocean (Coulon et al. 2006). All maps provided full coverage of the entire study area and units of measurement in Alaska, the Yukon Territory, and British Columbia maps were equivalent. Since the maps came from different sources the scale differed; thereby subsequent histogram and assignment of categories was done by region. River density (m/m^2) was calculated by totaling the length (km) of rivers encompassed by a uniformed coding unit (UCU), which are defined by ridges and river drainages, then dividing by the area (km^2) of the UCU. Because river density was predicted to increase moose density (Maier et al. 2005), we choose to include this habitat layer to model dispersal paths. The wide range of river density values necessitated us to define five categories which were based on natural breaks in the dataset. Based on the five categories, we classified the outermost levels as poor river density for moose, the next two innermost categories as moderate river density, and lastly the middle category as good river density for moose. Maier et al. (2005) calculated river density in a slightly different manner than our research by using amount of river edge rather than length of river, but our methods reflected their conclusions. Maier et al. (2005) also predicted that moderate elevation would increase moose density; therefore, we sub-divided elevation into two categories (i.e., good and poor). Good moose habitat was defined as extending from sea level to 1,200 m (the general location of treeline) (Van Ballenberghe 1992; Molvar et al. 1993). Poor elevation extended from 1,200 to 1,500 m and areas below sea level. Areas >1,500 meters were defined as

mountains. We implemented a broad classification scheme for elevation because the elevation of treeline and the quality of moose habitat can vary among locations even though they occur at the same elevation. Precipitation (mm/year) was included as a habitat layer because it is an index of snowfall; heavy snowfall can interfere with movements of moose (Coady 1974; Stephenson et al. 2006). Precipitation was averaged (mm/year for Alaska from 1900 to 2000), Yukon (1971 to 2000), and British Columbia (1919 to 2000) and then ordinarily kriged (Johnston et al. 2001), resulting in nine categories. Because only heavy snowfall (> 70 cm; Coady 1974) impedes movements of moose, we choose to assign a cost value to only the two highest categories of nine categories were coded as medium or high resistance.

Consistent with previous studies that predicted moose density as a function of vegetation type (Maier et al. 2005), we recognized four vegetation communities: (1) low shrubs (willow, *Salix* spp.; dwarf birch, *Betula glandulosa* and *B. nana*); (2) deciduous tall shrubs (willow, *Salix* spp.; alder, *Alnus tenuifolia*); (3) deciduous trees (balsam poplar, *Populus balsamifera*; aspen, *P. tremuloides* paper birch, *Betula papyrifera*); and (4) spruce (black, *Picea mariana*; white *Picea glauca*). Moose are known to prefer willows (*Salix* spp.), but they also browse aspen, birch, and poplar (Weixelman et al. 1998).

Preliminary analysis indicated moose density was predicted with logistic regression based on these habitat classes and several other map layers; low shrub was more strongly correlated with high moose density than was deciduous tall shrub. Next in order of moose preference are deciduous trees and lastly conifers and spruce (Van Ballenberghe et al. 1989; Weixelman et al. 1998). This pattern of forage preference leads to a habitat

preference of low shrub > deciduous tall shrub > deciduous tree > spruce. In addition to vegetation, fire history markedly influences moose distribution and density (Peek 1974; Bangs & Bailey 1980; MacCracken & Viereck 1990; Renecker & Schwartz 1998; Schwartz 1998). Therefore, fires from 11 to 20 years old were categorized as best for moose habitat followed in decreasing order by fires 21 to 30 years old, fires 31 to 40 years old, fires less than 11 years old, and finally older fires or unburned forest (Franzmann & Schwartz 1998; Gasaway et al. 1989; LeResche et al. 1974; Weixelman et al. 1998; Maier et al. 2005). Unburned areas were ranked based on the vegetation and its associated preference for moose with spruce the least favored, next deciduous, and most preferred tall shrub. Landcover types covered by ice and rock are avoided by moose and were considered poor habitat for moose (Maier et al. 2005).

4.34 Friction maps and population connectivity

Cell values of the various grid layers were chosen according to current understanding of the influence of habitat on moose. Three main steps were used to determine a least-cost path. First, appropriate values were assigned to the various landscape layers based on biological data. Next, because moose respond to multiple variables in their environment (Bowyer et al. 1999; Maier et al. 2005), the landscape layers were summed to represent an overall cost or friction map composed of 100 x 100-m cells. Lastly, an algorithm was implemented in PATHMATRIX (Ray 2005), which aims to minimize the cost for traversing the cell to calculate a least-cost path connecting the center of our samples (Fig. 1A and B). We chose to model four different least-cost scenarios (Appendix 4A), which resulted in four different friction maps from

which to construct a least-cost path. The first model assumed that preferred habitat would impede moose dispersal because, if either areas of poorer moose habitat contain few moose then due to density-dependence moose would traverse avoid areas of preferred moose habitat. The second model took the opposite approach by assuming that good habitat would provide useful corridors for dispersal into new areas. Stevens et al. (2006) also used this approach to determine whether preferred habitat would impede or facilitate gene flow in the natterjack toad (*Bufo calamita*). In the third and fourth models, permanent landscape features (e.g., elevation, road density, river density) were retained in the model, but transient landscape features (e.g., vegetation types that might change after fire) were excluded (coded as one for the entire map). These two models attempted to hold habitat features constant or at least equal to each other (Appendix 4A). This method does not mean that habitat layers are unaccounted for because with an assigned value, their presence or coverage area is represented. To calculate AIC_C and BIC_C scores we estimated the number of model parameters by counting the number of landscape layers included in the model. Because the first two models contain both habitat and more permanent landscape features, all the layers were counted ($n = 23$; Appendix 4A). Models three and four had far fewer parameters because habitat layers that were held constant with a value of one were not counted as a parameter ($n = 15$; Appendix 4A). With the use of least-cost paths we also tested whether at such a large spatial scale, background noise provided by the vast geographic distances and landscape heterogeneity might result in too much background noise. Landscape noise could potential negate the ability to use landscape genetics to result in improves of the relationship between genetic

and geographic distance over Euclidean models. We also explored the influence of negating habitat features (i.e., least-cost paths three and four) versus the inclusion of habitat (i.e., least-cost paths one and two) would have on the relationship between genetic and geographic distance. Some of the values we defined as more long lasting or permanent landscape layers include such as roads, lakes, mountains, and Pleistocene glaciers; meanwhile habitat layers included vegetation type and age of fire (Appendix 4A). Because elevation and river density were categorized, they were ranked, so the third approach maintained the assumption of the first model: good habitat impedes dispersal. Moreover, the fourth model mimicked the second approach where good habitat favored dispersal. Consequently, the various calculated least-cost paths represent theoretical moose dispersal paths across complex landscapes.

4.35 Landscape interpretation of paths

We choose two different approaches beyond visual inspection to discern the relationship between landscape and the hypothesized dispersal paths. We first identified the segments of the paths that occurred in each individual landscape feature, using the “clip” feature in GIS. The length of the line identified by the ‘clip’ was then summed. Each individual landscape layer was used to ‘clip’ dispersal paths in all four models. This procedure identified the portion of the dispersal path that traversed the landscape feature on which the ‘clip’ was based. Then the total length of the ‘clipped’ portion of the line was calculated. This method gave the length of the dispersal path within each landscape feature. A larger calculated length of line indicates that more of that dispersal path occurs within the given landscape feature. Lengths of each least-cost models were

calculated given the landscape utilized (Appendix 4A). These calculated values for length of paths were used in both the following approaches.

For the first approach, however, we calculated the percent of the path that occurred within each landscape feature for all four models. This procedure was implemented for each individual model, and we then calculated the total length of paths connecting the populations. Next, for each landscape feature, we divided the previously calculated portion of the least-cost within a layer by the total length of least-cost paths connecting the populations. Then, with the length of the least-cost path in a landscape calculated, we determined for each of the models the total length of least-cost paths for all of all possible pairwise connections between populations. We termed this the “percent in cover” scheme:

$$\text{Percent in cover} = \frac{\text{Sum of clipped path in a landscape layer}}{\text{Sum of all the pairwise paths among populations.}}$$

Sum of all the pairwise paths among populations.

The second scheme is termed the “use/availability” scheme in which we attempted to account for the presence or area of each landscape feature used. The “use to availability” ratio is calculated relative to available area (Manly et al. 2002). Consequently, we divided the length of a least-cost path in a landscape calculated by the calculated area representing each landscape feature. We termed this the “use to availability” scheme:

$$\text{Use/availability} = \frac{\text{Length of the least-cost path within a landscape feature}}{\text{Area of the landscape feature examined.}}$$

Area of the landscape feature examined.

4.4 RESULTS

AIC_C results from Mantel tests and linear regression indicated that the inclusion of landscape features significantly improved the relationship of geographic to genetic distance compared to the use of Euclidean distance measurements alone (Table 1). Results from AIC_C and BIC_C scores both ranked the models in the same order, so we report only AIC_C values. Examination of AIC_C scores from Mantel tests and from linear regression supported least-cost models three and four, which only included permanent features and did not include transient (e.g., successional) habitat features (Table 1). In addition, significant support for isolation-by-distance with linear regression was determined to occur between least-cost path two, which assumes that good moose habitat facilitates dispersal and R_{ST} (Table 1; $p < 0.001$). This difference in results probably occurred because even though AIC_C scores and R_{ADJ}^2 estimates account for the number of parameters in the model and penalize for over-parameterization, the number of parameters were constant among the models for R_{ADJ}^2 estimates. When penalties for the different number of parameters due to the landscape features are not included, R_{ADJ}^2 estimates from linear regression indicated that the best model is least-cost path two and second is least-cost path four, both of which assumed that good moose habitat facilitates dispersal (Table 1).

To further examine the top two least-cost paths, three and four, based on the “percent in cover” and “use/availability” methods we calculated the amount of each path that occurs within the landscape features used (Table 2). Least-cost paths three and four were largely excluded from areas with permanent landscape features such as oceans and

glaciers (0.18% & 7.89%, respectively) and predominately utilized habitat areas without permanent features (99.8% & 92.1%, respectively). This pattern also was observed with the full model least-cost paths, one and two, in that they occurred mostly in permanent areas (87.76% & 91.17%, respectively).

Results from the full models (i.e., one versus two) indicated that when good moose habitat was thought to facilitate dispersal a slightly higher percentage of the least-cost path occurred in permanent landscape features (12.24% & 8.83%, respectively). Moderate elevation ranked first in both “percent cover” schemes because almost 90% of elevation fell within the elevation boundaries that moose are known to inhabit. Nevertheless, the “use/availability” scheme takes into account the amount of poor elevation and mountains, and thus ranked moderate much lower in both models (Table 2). Even though linear landscape features such as railroads, roads, major rivers contain minimal area, such features were ranked higher in both models in the “use/availability” scheme.

Of the eight microsatellite loci used, none showed signs of allelic dropout or null alleles; all were in Hardy-Weinberg equilibrium, and no linkage disequilibrium was present. As previously noted in moose (Wilson et al. 2003), observed heterozygosity was moderate, and our observed values were not vastly different from expected heterozygosity (Table 3). The range of mean number of alleles and allelic richness was minimal, and F_{IS} values were small (Table 3). Locus Rt30 had the most alleles ($n = 16$), and BM2830 and NVHRT01 had the least ($n = 3$); there was a total of 51 alleles sampled across all eight loci. Private alleles were present in Yakutat (Rt24, $n = 2$; Rt30, $n = 3$),

Tanana Flats (BM2830, $n = 1$; Rt30, $n = 1$), Seward (NVHRT21, $n = 2$), Koyukuk (Rt30, $n = 1$), and Tetlin (Rt24, $n = 1$; Rt30, $n = 3$). The only moose sample without private alleles was from the Alaska Peninsula. Results indicated that Tetlin had the greatest gene diversity (0.48) and was near equal to Yakutat and Tanana for the largest average number of alleles per locus (4.25). When all moose samples were examined as one population, there was Hardy-Weinberg disequilibrium with the overall observed heterozygosity ($H_O = 0.53$) significantly less than expected heterozygosity ($H_E = 0.58$). Also, there was no evidence of bottlenecks within populations or when Alaska was tested as a single population.

Population structure differed between F_{ST} and R_{ST} results (Fig. 2). F_{ST} yielded 13 population comparisons that were significant, whereas R_{ST} yielded only five significant comparisons, indicating that migration (as implied strongly by F_{ST}) had greater effect than mutation (as indicated most strongly by R_{ST}) on the structuring of the Alaskan moose populations. Both F_{ST} and R_{ST} estimates were not significant between pairwise comparisons of Tanana Flats versus Koyukuk and Seward Peninsula versus Koyukuk. Overall F_{ST} (0.063) was greater than R_{ST} (0.046); in addition, F_{ST} was larger for five of eight loci (BM203, BM2830, NVHRT21, Rt24, and Rt30). The only population with a negative F_{IS} was Tanana, and the largest occurred in Tetlin (Table 3).

Estimates of dispersal rates and direction of dispersal varied based on the programs used. First, GENEPOP estimated the overall effective number of migrants was 1.13 per generation. The greatest number of migrants occurred between the Seward Peninsula (4.55) and Koyukuk, and the least was between Koyukuk and the Alaska

Peninsula (0.40). Evaluation of dispersal with BAYESASS indicated that the overall dispersal rate was lower than the non-dispersal rate ($0.033 \pm 1.58 \times 10^{-6}$, 0.83 ± 0.16 , respectively), with most individuals assigned to their source population. Furthermore, Tetlin likely was a source for several other populations, including Koyukuk, Seward, and the Alaska Peninsula (Table 3). Furthermore, the Alaska Peninsula received individuals not only from Tetlin but also from the Tanana Flats and Seward Peninsula. Assignment indices from ARLEQUIN, placed all moose sampled from Yakutat, the Alaska Peninsula, and Tetlin in their hypothesized population. The samples with the most individuals assigned to populations other than those from which they were sampled were Koyukuk ($n = 3$ in Seward Peninsula, $n = 3$ in Tanana) and Seward Peninsula ($n = 4$ in Tanana, $n = 2$ in Koyukuk). In addition, Tanana had individuals assigned to the Seward Peninsula ($n = 2$) and Koyukuk ($n = 1$) populations, indicating that these three populations were most genetically similar. In depth exploration of dispersal with STRUCTURE to and from the Alaska Peninsula between the nearest areas sampled (i.e., Koyukuk and the Seward Peninsula), indicated that equally assigned to three populations (33%, 33%, & 34% respectively). Although only one individual in the Alaska Peninsula was misassigned, many were misassigned in Koyukuk ($n = 21$) and the Seward Peninsula ($n = 6$). Of moose misassigned to the Koyukuk sample, the split was similar between the Alaska Peninsula ($n = 10$) and the Seward Peninsula ($n = 11$). All misassigned moose in the Seward Peninsula were assigned to the Alaska Peninsula. Overall, the various results indicate that dispersal currently occurs especially among the more westward populations with less dispersal to and from Yakutat.

Suggested population structure based on genetics with AMOVA results from ARLEQUIN, indicated that the only sampled regions that among our five areas sampled which were not genetically distinct was between Koyukuk and the Seward Peninsula (among groups 6.82%, among populations within groups -0.24%, and within populations 93.42%). Furthermore, the results of a neighbor-joining tree based on unbiased Nei's genetic distances place the Seward Peninsula and Koyukuk closely together. Also, both the neighbor-joining tree (Fig. 3) and F_{ST} and R_{ST} (Fig. 2) estimates illustrate that Yakutat is the most different of the six populations.

Bayesian analysis with both STRUCTURE and BAYESASS indicated only two populations of moose among our samples. One was the Yakutat population with the remaining samples forming one population. By examining the population assignment of individuals when the number of populations was set at six, two moose in the Tetlin population were assigned to the Yakutat population, which is the closest sample to Yakutat. Thus, the program STRUCTURE indicated two populations, and the percentage of inferred ancestry to population one was dominated by the Alaska Peninsula (75.84%), Koyukuk (75.68%), Seward (67.91%), and Tanana Flats (64.70%). Moreover, population two consisted of Tetlin (80.10%) and Yakutat (78.32%). The result of only two populations and evidence of past and current gene flow among the regions sampled indicate support for the weak population structure we observed, which is more likely a recent phenomenon, and moose appear to be dispersing into areas of suitable moose habitat.

4.5 DISCUSSION

Previous research in landscape genetics that utilizes least-cost paths has not attempted to test their usefulness at large spatial scale (Michels et al. 2001; Broquet et al. 2006; Coulon et al. 2004 & 2006; Scribner et al. 2005; Spear et al. 2005; Vignieri 2005), with the exception of research on the highly mobile grey wolf (*Gulo gulo*; Geffen et al. 2004). Given that moose in Alaska have shown population structure (Schmidt et al. Chapter three) and that support for isolation-by-distance was indicated (Schmidt et al. Chapter three), we predicted that least-cost paths based on landscape features would improve the relationship between geographic and genetic structure. Ecological studies also have identified habitat as a key variable in establishment of moose ranges and dispersal, with important implications for the management and conservation of moose (Karns 1998).

Our results clearly indicate that inclusion of landscape features dramatically improves the relationship between geographic and genetic distance, especially because all models with Euclidean distance rank last and provided the poorest fit (Table 1). This outcome provides support for the utility of landscape genetic models that incorporate ecological features at large spatial scales. The lower number of parameters in models three and four, ($n = 15$) versus models one and two, ($n = 23$; Appendix 4A), likely is the reason why AIC_C scores R_{ADJ}^2 scores identified models three and four as providing a significantly better relationship between geographic and genetic distance over models one and two (Table 1). Models with Euclidian distance performed least well. All four least-cost models included permanent landscape features such as mountains, glaciers, and

roads (Appendix 4A). Over-parameterization in models one and two reduced their ability to detect isolation-by-distance compared with models three and four. Even though the top least-cost path models, three and four, attempted to minimize more variable habitat features, they nonetheless contain permanent landscape features. Therefore, just as with other vagile species like wolves, the inclusion of habitat improves understanding and predictions of dispersal, population expansion, and resultant gene flow for moose in Alaska (Geffen et al. 2004; Funk et al. 2005; Coulon et al. 2006).

The residual variation observed among the least-cost path models indicates that microhabitats, which are not readily detected at large scales, are important and that future research at finer scales would be valuable. There was also variation depending on the different genetic measurements used (e.g., F_{ST} vs. R_{ST} etc.), although these had less influence than the habitat model (Table 1). We suggest that large-scale models provide a useful context, but finer-scale landscape genetic studies might actually better mimic the ways that a moose perceives its environment during dispersal. Consideration of scale is especially important, since moose in Alaska are known to be influenced by landscape features at different scales (Maier et al. 2005).

The two methods of “percent in cover” and “use/availability” we used to examine importance of landscape features on the least-cost paths drawn provided useful insight into the specific landscape features that are important to consider for moose dispersal. For example, even though railroads, roads, and large rivers make up a small portion of our study area, the crisscross pattern on the landscape increases the likelihood that during dispersal, a moose will likely encounter such landscape features. Given that road kills are

an important cause of moose mortality, especially in deep-snow winters (Del Frate & Spraker 1991; Dussault et al. 2006), future development of roads should take into consideration their potential effects on species dispersal (Rea 2003). We believe the reason least-cost path four provides a better fit with genetic distance than path three in areas once covered by Pleistocene glaciers is its assumption that good habitat facilitates dispersal. Similarly, model two, which includes this same assumption, provides a better fit than model one, which assumes that good habitat impedes dispersal.

Even though we cannot identify a single best model based on AIC_C models, insights about moose dispersal, gene flow, and population structure can still be made. For example, it was previously uncertain whether moose were able to traverse the vast Yukon-Kuskokwim delta region, which is located between the Seward and Alaska Peninsula. Because all of our best least-cost paths clearly traverse this region (Fig. 1A and B), we hypothesize that this has been an important pathway for moose dispersal. The genetic results also indicated that moose utilize this area given that all six misassigned moose from the Seward Peninsula were placed in the Alaska Peninsula. Identification of previously unrecognized potential dispersal corridors is highly valuable to wildlife managers (Hampton et al. 2004, Dixon et al. 2007).

Even the genetics of vagile animals can be influenced by landscape and social effects (Rueness et al. 2003; Geffen et al. 2004; Riley et al. 2006). Because the best models were either least-costs paths three or four in which the effects of habitat was minimized, a more careful examination of these two paths provides insight into which of the permanent landscape features (e.g., mountains, glaciers, and lakes) most strongly

influence moose dispersal (Appendix 4A). All four least-cost paths tend to avoid mountains and currently glaciated regions. The only models that do not indicate dispersal through ice-free corridors at lower elevations are models that include Euclidean distance, which had the lowest AIC_C scores (Table 1). The effect of mountains and extent of current glaciers largely explains differences in dispersal paths between Yakutat and other Alaskan populations (Fig. 1A and B). This result confirms previous research indicating that moose used lower elevation river drainages to populate Yakutat and surrounding areas from interior British Columbia (Hundertmark et al. 2006).

Comparisons between least-cost paths three and four also show the importance of river density and elevation for moose dispersal because they are the only landscape features to vary between the two paths. Given that the two paths differ, sometimes vastly, river density and elevation are clearly important for moose dispersal. This outcome is not surprising because both variables have widespread effects on habitat; elevation influences climate and hence multiple habitat characteristics. Likewise, river density is a highly influential landscape feature that relates to hydrology, succession, and habitat corridors.

Our ability to determine whether good habitat facilitates or impedes dispersal corridor was limited because we could not distinguish statistically between models three and four based on AIC_C values (Table 1). Results from linear regression R_{ADJ}^2 values indicate the good habitat may be the preferred dispersal corridor because both of the top models (i.e., two and four) were coded with good habitat facilitating dispersal. These conclusions from landscape genetics combined with field observations of moose behavior suggest that, because males are the dispersal sex and migrate large distances, males may

require a high level of adequate habitat to facilitate dispersal (Ballard et al. 1991; Hundertmark 1998). In contrast, females often disperse shorter distances than males (Hundertmark 1998) in a 'rose petal' fashion like that of white-tailed deer, *Odocoileus virginianus* (Porter et al. 1991; Mathews & Porter 1993). Females are more inclined to move outward from a desired habitat so to avoid overlap with their maternal relatives (Ballard et al. 1991; Porter et al. 1991; Mathews & Porter 1993). Therefore, if dispersal were female-biased, moose would be more likely expand into undesirable habitats.

Given the role of moose as keystone species that alter predator-prey dynamics, vegetation composition, succession, and nutrient cycling, the ability to predict future moose ranges has important ecological and societal consequences (Molvar & Bowyer 1994; Kielland et al. 1997; Kielland & Bryant 1998; Suominen et al. 1999; Dairmont et al. 2005; Ballew et al. 2006; Nelson & Mech 2006). Recent climate changes are currently altering moose distribution and use of habitats (Darimont et al. 2005; Stephenson et al. 2006). A changing climate may have dire consequences for moose (Bowyer et al. 1999). Models that simulate projected changes in climate and landscape could therefore be used in conjunction with the relationships that we have observed regarding the influence of landscape on moose dispersal to predict future distributions of moose. Thus incorporation of available GIS data which model climate change scenarios provides a quantitative tool to predict the future consequences of changing abundance and distribution of keystone species, such as moose in Alaska (Simberloff 1998).

As reported previously for moose in Alaska (Schmidt et al. Chapter three), F_{ST} values were larger than R_{ST} values. This outcome may result from the relatively recent

colonization of Alaska by moose (Hundertmark et al. 2003). Therefore, mutations, which primarily influence R_{ST} , likely have not accumulated within populations and would not be the dominant evolutionary process. Rather, we hypothesize that gene flow and dispersal are the dominant forces affecting genetic structure. Results for population differentiation with F_{ST} and R_{ST} (Fig. 2) indicate that two of eight markers do not follow a strict stepwise mutation model, and therefore, estimates with R_{ST} may be somewhat inaccurate and in general lower than F_{ST} (Lugon-Moulin et al. 1999; Balloux et al. 2000). Similarly, Balloux et al. (2002) noted that F_{ST} estimates can be misleading when mutation rates are high. Nevertheless, the recent colonization of moose in Alaska reduces the likelihood that mutations have accumulated; therefore F_{ST} estimates based on dispersal are likely more valid than R_{ST} . Accordingly, we conclude that the only population comparisons that show no differences in genetic structure are between Koyukuk and Tanana Flats and between Koyukuk and the Alaska Peninsula (Schmidt et al. Chapter three).

Results from our various assignment indices and estimates of dispersal rates and directions illustrate that population structure does indeed exist, but it is subtle. Assignment indices from ARLEQUIN indicate that Yakutat, Tetlin, and the Alaska Peninsula are not a likely source for other populations in that all individuals were assigned to their respective population. When only Koyukuk, the Seward Peninsula, and the Alaska Peninsula were examined with STRUCTURE a large amount of gene flow occurred from Koyukuk to the Seward and Alaska Peninsulas; however, little dispersal occurred in the opposite direction from the Seward Peninsula to Koyukuk. Instead, all of

the misassigned individuals from the Seward Peninsula were placed in the Alaska Peninsula. These results are consistent with the analysis we conducted in GENEPOP, which showed that, of all pairwise population comparisons, the highest rate of gene flow was between Koyukuk and the Seward Peninsula. Results from GENEPOP differed from those in STRUCTURE in showing the least amount of dispersal between Koyukuk and the Alaska Peninsula, probably because GENEPOP estimates the historical average rates of dispersal across past generations (Slatkin 1995). Therefore, the more recent dispersal between Koyukuk and the Alaska Peninsula would be more difficult to detect with this method. Nonetheless, given that Koyukuk had 21 of 26 individuals misassigned, this region appears to be a crucial area of genetic mixing with moose from Koyukuk dispersing into surrounding areas.

Both Bayesian methods used to explore assignment indices and dispersal agreed that the Alaska Peninsula is a population sink. Results from BAYESASS indicated that dispersal into the Alaska Peninsula was primarily from the Tanana Flats, Seward Peninsula, and Tetlin populations (Table 4). Most migrants from the Alaska Peninsula went to Yakutat. BAYESASS, however, contradicts previous results in that Tetlin is the dominant source of most other populations studied (Table 4). Given the different methods used to estimate dispersal between STRUCTURE and GENEPOP versus BAYESASS a more current understanding of dispersal is gained with results from BAYESASS ((Faubet et al. 2007); whereas, STRUCTURE and GENEPOP results are diluted by past dispersal and mutation either before or after population establishment (Faubet et al. 2007).

Lastly, AMOVA results indicated a low amount of variation among all the groups compared with considerable variation within groups, suggesting that there is not a large amount of genetic differentiation among sampling areas, relative to within-population diversity.

In summary, evidence for dispersal, presence of misassigned individuals, and differences between F_{ST} and R_{ST} , indicate that moose in Alaska have not reached a mutation-migration equilibrium. STRUCTURE furthermore supported this conclusion with the identification of only two populations in Alaska, an eastern population (i.e., Yakutat and Tetlin) and a second homogenous mixture of the remaining populations. The lack of equilibrium and inability to precisely identify population structure is not surprising, given that the relatively recent arrival and expansion of moose in Alaska (Hundertmark et al. 2003). Another likely reason for the uncertainty of population structure and inability to identify unique populations, especially in interior Alaska, is that given such a large study area, there are probably several small sub-populations we did not sample and which may have interacted with the populations we sampled. Support for the presence of sub-structure within our samples used is consistent with our observation that heterozygosity was less than expected. This pattern suggests a Wahlund effect indicating sub-structure within our sampled populations (Hartel & Clark 1987). Therefore, we conclude that structure is present, but, based on the issues noted previously; precise identification of discrete populations requires further study.

Additional evidence for population structure at the large scale with two very large populations was identified by STRUCTURE. With this in mind, we used STRUCTURE

to examine the assignments of moose with our six hypothesized populations. This outcome suggests that Yakutat is different from the other five sample areas, but shows some evidence of historic gene flow with Tetlin. The Yakutat population also may be distinct if moose in the panhandle of Alaska are composed of an admixture of the subspecies *A. a. gigas* and *A. a. andersoni* (Hundertmark et al. 2006). Although this mixing was presumed to occur 80 kilometers south of Yakutat, dispersal of much greater distances than 50 miles by moose is not uncommon (Ballard et al. 1991; Hundertmark 1998).

Our results provide evidence for the hypothesis that moose populations in interior Alaska are oldest in the interior (i.e., Tanana Flats) and radiated outward towards western Alaska (i.e., Seward and Alaska Peninsulas) (Peterson 1955; Klein 1965). This westward dispersal occurred in stepping-stone fashion from the Tanana Flats as the source, then to the Koyukuk region, and ultimately towards the Seward Peninsula (Schmidt et al. Chapter three). We believe that dispersal occurred in this direction because the historical average number of migrants is greater between Koyukuk and Seward than likely older gene flow between Koyukuk and the Tanana Flats.

Several important questions are unresolved. Undoubtedly, there are processes that influence moose dispersal and genetics but are not included in our models. For example, density significantly influenced dispersal in white-tailed deer (Nixon et al. 2007), so a map of moose density would likely provide additional insights. Other factors that might influence moose dispersal and would be desirable to include as map layers include predator densities (Nelson & Mech 2006), logging (Dairmont et al. 2005),

topography (Farmer et al. 2006), and an index of habitat heterogeneity (Diekötter et al. 2007). Also, methods that yield stronger statistical differences among least-cost paths would have provided more conclusive evidence of sex-biased dispersal in moose. This methodological limitation in the field of landscape ecology also has been noted by Storfer et al. (2007).

Another issue that requires consideration for interpretation from our current and future genetic research and dispersal is the behavioral differences between male and female moose (Hundertmark 1998; Goudet et al. 2002). Thus, the dispersal paths of females and males most likely differ; we have modeled overall gene flow rather than that specific to a particular sex. One possible approach would be to model sexes separately with a female model in which the dispersal path follows a 'rose petal' or similar stepping-stone pattern. This pattern could be compared with a separate model for males that follows an isolation-by-distance dispersal pattern based on landscape features. In addition, least-cost paths will likely differ between the sexes, regardless of the dispersal pattern, because of sex-biased habitat preferences (Bowyer et al. 2001; Spaeth et al. 2004). The two different dispersal paths will likely differ and could improve our understanding of ungulate population dynamics. Another genetic consideration is that males ($n = 74$) slightly outnumbered females ($n = 61$) in our sample, so a more even balance would be preferred. Nevertheless, we do not know whether this male-bias in our sample is greater or less than that which actually occurs in moose dispersal (Ballard et al. 1991; Hundertmark 1998). Through genetic exploration of the sex chromosomes, sex-biased issues could be resolved in that the X-chromosome is from the mother; where

as the Y-chromosome is from the father (Seielstad et al. 1998; Perez-Lézaun et al. 1999; Haig 2000). Further issues that can also influence the proportion of male dispersal from a population are the sex ratio (Symington 1987), population density (Deickmann et al. 1999; Bowler & Benton 2005), and hunting intensity (McCoy et al. 2005; Forget & Jansen 2007).

As GIS and landscape genetics become more widely integrated, other useful map layers such as a density map of moose predators or habitat quality index for moose habitat. Landscape layers that address sex-biased issues include a harvest intensity/regulation or sex ratio maps. The future holds the potential for access to such useful maps and future research that provides novel understanding of moose biology potential could reveal important landscape features current not considered. In addition, there also is a need for a least-cost path algorithm that incorporates more than the adjacent cells, but rather selects from an average value of a given radius. This is crucial because animals vary on the scale at which they perceive their environment so the ability to choose the appropriate scale would vastly improve theoretical dispersal paths (Kie et al. 2003; Bowyer & Kie 2006). Lastly, there is a crucial need for more communication between genetic and landscape ecology professionals so that more knowledge can be extrapolated from landscapes to help explain genetics and ultimately further both the separate disciplines and their integration (Manel et al. 2003; Storfer et al. 2005).

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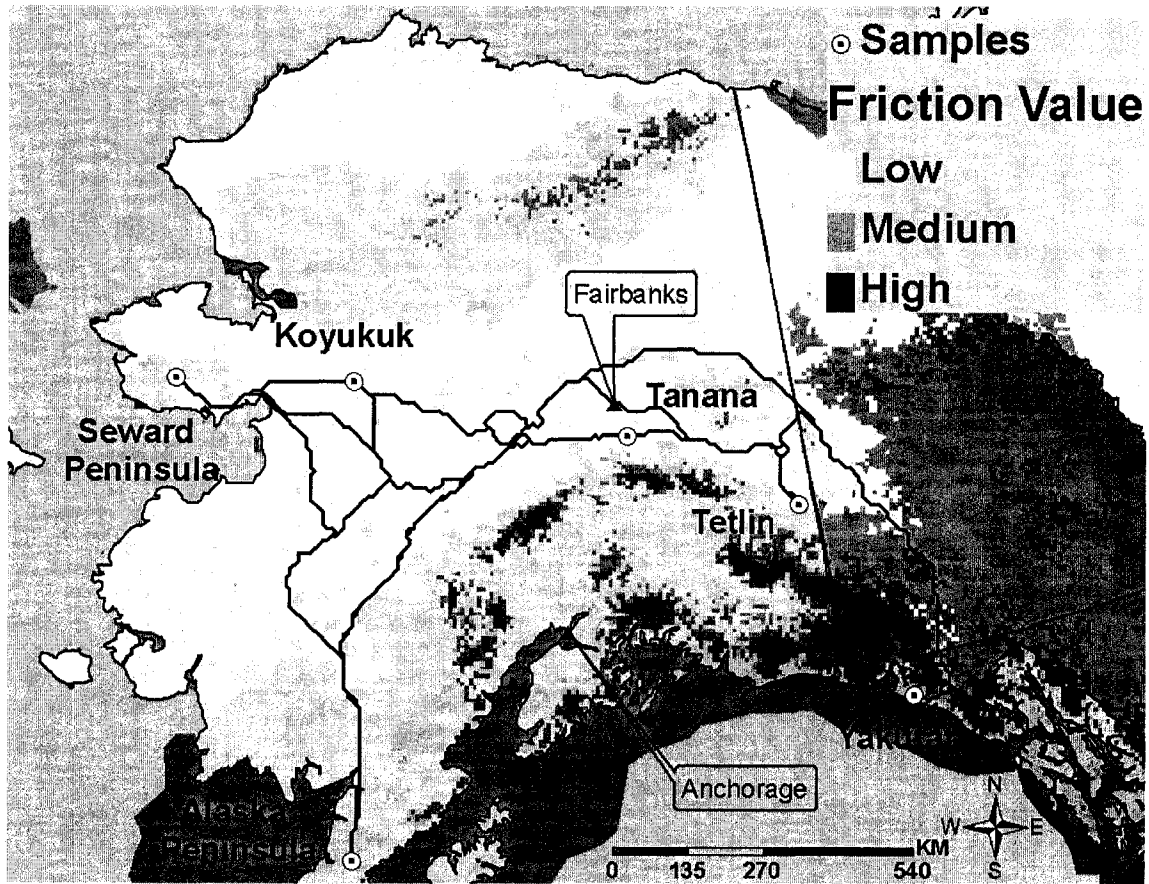


Figure 4.1A Least-cost path three based on friction costs among six moose populations sampled in Alaska, USA, from 2003 through 2006.

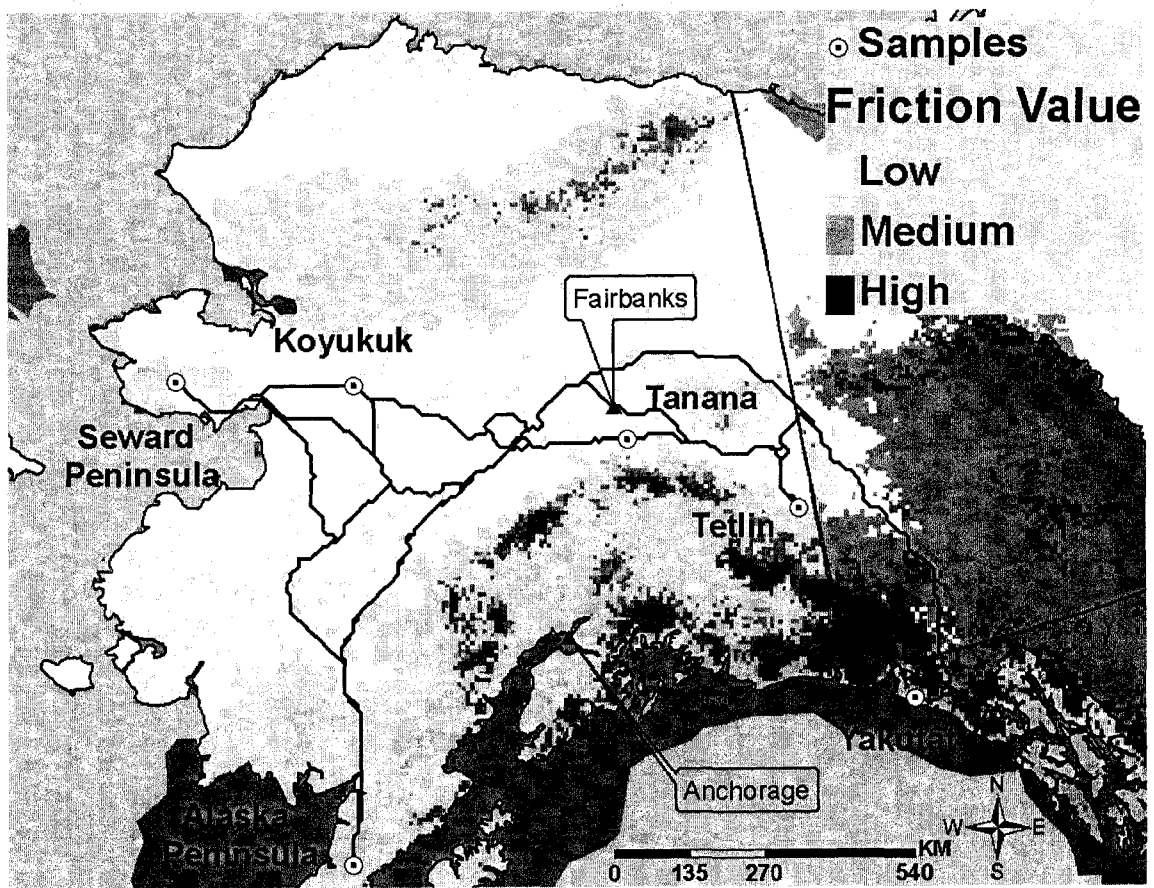


Figure 4.1B Least-cost path four based on friction costs among six moose populations sampled in Alaska, USA, from 2003 through 2006.

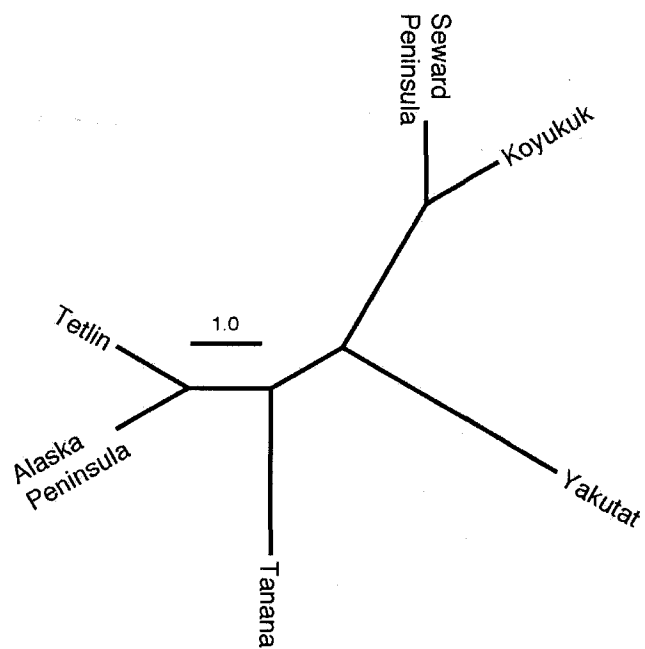


Figure 4.2 Neighbor-joining tree (Saitou & Nei M 1987) based on unbiased Nei's genetic distances (Nei et al. 1983) for six moose populations sampled in Alaska, USA, from 2003 through 2006.

Table 4.1 Results from Mantel tests and linear regression (R_{ADJ}^2) for various path models connecting six moose populations in Alaska, USA, sampled during 2003 through 2006.[§]

Mantel Tests				Linear Regression				
Geographic	Genetic	AIC _C	ΔAIC _C	Geographic	Genetic	AIC _C	ΔAIC _C	R_{ADJ}^2
Ln (Path 4)	$F_{ST}/(1-F_{ST})$	-192.028	0.000	Ln (Path 4)	R_{ST}	-191.714	0.000	0.5215
Ln (Path 4)	R_{ST}	-192.028	0.000	Ln (Path 3)	R_{ST}	-191.709	0.005	0.5218
Ln (Path 3)	$F_{ST}/(1-F_{ST})$	-191.821	0.208	Ln (Path 3)	$F_{ST}/(1-F_{ST})$	-191.139	0.575	0.4014
Ln (Path 3)	R_{ST}	-191.821	0.208	Ln (Path 4)	$F_{ST}/(1-F_{ST})$	-191.139	0.575	0.4482
Path 3	$F_{ST}/(1-F_{ST})$	-190.693	1.335	Path 3	$F_{ST}/(1-F_{ST})$	-191.091	0.623	0.4058
Path 3	R_{ST}	-190.415	1.613	Path 4	$F_{ST}/(1-F_{ST})$	-191.007	0.707	0.4134
Path 4	$F_{ST}/(1-F_{ST})$	-190.254	1.774	Path 3	R_{ST}	-190.594	1.120	0.5971
Path 4	R_{ST}	-190.254	1.774	Path 4	R_{ST}	-190.258	1.456	0.6173
Ln (Path 3)	F_{ST}	-189.388	2.640	Path 3	F_{ST}	-189.810	1.904	0.3955
Path 3	F_{ST}	-189.346	2.682	Ln (Path 3)	F_{ST}	-189.751	1.963	0.401
Path 4	F_{ST}	-189.246	2.783	Path 4	F_{ST}	-189.678	2.036	0.4077
Ln (Path 4)	F_{ST}	-188.856	3.173	Ln (Path 4)	F_{ST}	-189.152	2.562	0.4536

Table 4.1 (continued) Results from Mantel tests and linear regression (R_{ADJ}^2) for various path models connecting six moose populations in Alaska, USA, sampled during 2003 through 2006.[§]

Mantel Tests				Linear Regression				
Geographic	Genetic	AIC _C	ΔAIC _C	Geographic	Genetic	AIC _C	ΔAIC _C	R_{ADJ}^2
Ln (Path 1)	R_{ST}	-29.524	162.504	Ln (Path 1)	R_{ST}	-29.416	162.298	0.4391
Path 1	$F_{ST}/(1-F_{ST})$	-28.710	163.318	Path 1	$F_{ST}/(1-F_{ST})$	-29.044	162.670	0.2762
Path 1	R_{ST}	-28.697	163.331	Path 1	R_{ST}	-28.802	162.912	0.4895
Ln (Path 1)	$F_{ST}/(1-F_{ST})$	-28.601	163.428	Ln (Path 1)	$F_{ST}/(1-F_{ST})$	-28.708	163.006	0.3125
Ln (Path 2)	$F_{ST}/(1-F_{ST})$	-28.147	163.881	Ln (Path 2)	$F_{ST}/(1-F_{ST})$	-28.436	163.278	0.3406
Ln (Path 2)	R_{ST}	-28.075	163.953	Path 2	$F_{ST}/(1-F_{ST})$	-28.399	163.315	0.3443
Path 2	$F_{ST}/(1-F_{ST})$	-28.031	163.998	Ln (Path 2)	R_{ST}	-27.857	163.857	0.5584
Path 1	F_{ST}	-27.218	164.810	Path 1	F_{ST}	-27.611	164.103	0.2805
Ln (Path 1)	FST	-26.916	165.112	Ln (Path 1)	FST	-27.236	164.478	0.3208
Ln (Path 2)	FST	-26.678	165.350	Path 2	FST	-27.066	164.648	0.3383
Path 2	FST	-26.634	165.394	Ln (Path 2)	FST	-27.021	164.693	0.3428
Path 2	RST	-26.310	165.719	Path 2	RST	-26.390	165.324	0.6475

Table 4.1 (continued) Results from Mantel tests and linear regression (R_{ADJ}^2) for various path models connecting six moose populations in Alaska, USA, sampled during 2003 through 2006.[§]

Mantel Tests				Linear Regression				
Geographic	Genetic	AIC _C	ΔAIC _C	Geographic	Genetic	AIC _C	ΔAIC _C	R_{ADJ}^2
Ln (Euclidean)	R_{ST}	55.114	247.142	Ln (Euclidean)	R_{ST}	55.107	246.821	0.4103
Euclidean	$F_{ST}/(1-F_{ST})$	55.554	247.583	Euclidean	$F_{ST}/(1-F_{ST})$	55.227	246.941	0.209
Ln (Euclidean)	$F_{ST}/(1-F_{ST})$	55.658	247.686	Ln (Euclidean)	$F_{ST}/(1-F_{ST})$	55.367	247.081	0.2258
-Euclidean	R_{ST}	55.663	247.691	Euclidean	R_{ST}	55.519	247.233	0.4464
Euclidean	F_{ST}	57.044	249.072	Euclidean	F_{ST}	56.659	248.374	0.2138
Ln (Euclidean)	F_{ST}	57.159	249.187	Ln (Euclidean)	F_{ST}	56.815	248.530	0.2324

[§] Number of parameters for AIC_C and ΔAIC_C path 1 and 2 (K = 23), path 3 and 4 (K = 15), and Euclidean (K = 3). Estimates of R_{ADJ}^2 (K = 3) for all models.

Table 4.2 Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
Moderate		Moderate				Fire < 11	
elevation	25.214	elevation	30.529	Railroads	0.01149	years old	0.00560
		Good river					
Poor elevation	23.633	density	17.177	Poor elevation	0.01037	Railroads	0.00507
		Unburned		Fires 21-30		Fires 31-40	
Good river		spruce	10.567	years old	0.01001	years old	0.00189
density	12.545						

Table 4.2 (continued) Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
Moderate river		Unburned low		Fires 11-20		Good river	
density	10.452	shrub	10.189	years old	0.00796	density	0.00139
Poor river		Moderate river		Fires 31-40			
density	7.147	density	10.042	years old	0.00546	Large rivers	0.00139
Fires 11-20		Pleistocene		Fire < 11		Unburned	
years old	5.511	glaciers	6.066	years old	0.00241	spruce	0.00122
Fires 21-30		Fire < 11		Poor river			
years old	4.043	years old	4.626	density	0.00130	Roads	0.00098

Table 4.2 (continued) Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
Fires 31-40		Unburned				Moderate	
years old	2.533	deciduous	3.174	Large rivers	0.00119	elevation	0.00097
Unburned		Poor river		Good river		Fires 21-30	
spruce	2.476	density	2.995	density	0.00109	years old	0.00088
Unburned		Fires 31-40		Moderate		Fires 11-20	
deciduous	2.438	years old	0.943	elevation	0.00086	years old	0.00085
Unburned low				Moderate river		Unburned	
shrub	1.980	Poor elevation	0.854	density	0.00061	deciduous	0.00074

Table 4.2 (continued) Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
Fire < 11		Medium		Unburned		Moderate	
years old	1.849	precipitation	0.658	deciduous	0.00061	river density	0.00055
Current		Fires 11-20		Unburned		Unburned low	
glaciers	0.045	years old	0.635	spruce	0.00031	shrub	0.00052
						Poor river	
Mountains	0.035	Ice and rock	0.425	Roads	0.00013	density	0.00051
Pleistocene		Fires 21-30		Unburned low			
glaciers	0.030	years old	0.383	shrub	0.00011	Lakes	0.00048

Table 4.2 (continued) Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
				Current		Poor	
Ocean	0.022	Lakes	0.382	glaciers	0.00003	elevation	0.00035
		Current				Medium	
Large rivers	0.016	glaciers	0.141	Mountains	0.00002	precipitation	0.00025
						Pleistocene	
Railroads	0.016	Mountains	0.139	Lakes	0.00001	glaciers	0.00014
				High			
Roads	0.005	Roads	0.044	precipitation	0.00000	Ice and rock	0.00009

Table 4.2 (continued) Percentage of the top two least-cost path models for moose in Alaska, USA, 2003 through 2006, in each landscape feature based on percent in cover and use/availability schemes.

Percent Cover				Use/availability			
Least-cost		Least-cost		Least-cost		Least-cost	
model 3	%	model 4	%	model 3	%	model 4	%
						Current	
Lakes	0.005	Large rivers	0.020	Ice and rock	0.00000	glaciers	0.00008
				Pleistocene			
Ice and rock	0.004	Railroads	0.008	glaciers	0.00000	Mountains	0.00006
High							
precipitation	0.001	Ocean	0.003	Ocean	0.00000	Ocean	0.00000
Medium		High		Medium		High	
precipitation	0.000	precipitation	0.000	precipitation	0.00000	precipitation	0.00000

Table 4.3 Sample size, number of alleles (N_A), allelic richness, number of private alleles, expected heterozygosity (H_E), observed heterozygosity (H_O), and F_{IS} averaged over eight loci for six moose populations sampled in Alaska, USA, from 2003 through 2006.

Population	n	N_A	Allelic	No. private	H_E	H_O	F_{IS}
			richness	alleles			
Yakutat	25	4.250	4.040	6	0.554	0.540	0.026
Tanana Flats	25	4.250	4.022	2	0.533	0.540	-0.014
Seward							
Peninsula	25	4.125	3.880	2	0.550	0.543	0.012
Koyukuk	26	3.875	3.703	1	0.552	0.529	0.042
Alaska							
Peninsula	20	3.000	2.971	0	0.483	0.455	0.060
Tetlin	20	4.250	4.149	4	0.612	0.569	0.078

Table 4.4 Results from Bayesian dispersal proportions (BAYESASS; Wilson & Ranalla 2003) for moose in Alaska, USA, from 2003-2006. Numbers in diagonal are the proportion of non-dispersers within a population. Upper right corner is proportion of dispersal from column population to respective top row population and lower left corner is proportion of dispersal from top row population to respective column population. Italics represent the highest source to the respective row population. Bold values represent the highest source to the respective column population.

		Tanana	Seward	Alaska		
	Yakutat	Flats	Peninsula	Koyukuk	Peninsula	Tetlin
Yakutat	0.8370	<i>0.0336</i>	0.0317	0.0326	0.0316	0.0335
Tanana						
Flats	0.0310	0.8375	0.0329	<i>0.0363</i>	0.0308	0.0315
Seward						
Peninsula	0.0326	0.0346	0.8340	0.0335	0.0297	<i>0.0356</i>
Koyukuk	0.0223	0.0220	0.0194	0.7775	0.0217	<i>0.1371</i>
Alaska						
Peninsula	0.0316	0.0348	0.0348	0.0319	0.8342	<i>0.1596</i>
Tetlin	0.0039	0.0038	0.0033	0.0000	0.0000	0.9231

Appendix 4.A Map layer friction costs used to generate four different least-cost path models for six moose populations sampled in Alaska, USA, from 2003 through 2006.

Habitat features	Friction costs			
	Model 1	Model 2	Model 3	Model 4
Good elevation	10	-10	2	-2
Poor elevation	5	-5	1	-1
Good river density	3	-3	3	-3
Moderate river density	2	-2	2	-2
Poor river density	1	-1	1	-1
Fires 11-20 years	8	-8	1	1
Fires 21-30 years	7	-7	1	1
Fires 31-40 years	2	-2	1	1
Unburned spruce	-8	8	1	1
Unburned deciduous	-6	6	1	1
Unburned low shrub	-4	4	1	1
Fires < 11 yr	-3	3	1	1
Physical features				
Ocean	50	50	50	50
Current glaciers	50	50	50	50

Appendix 4.A Map layer friction costs used to generate four different least-cost path models for six moose populations sampled in Alaska, USA, from 2003 through 2006.

Habitat features	Friction costs			
	Model 1	Model 2	Model 3	Model 4
Mountains	40	40	40	40
Pleistocene glaciers	20	20	20	20
High precipitation	15	15	15	15
Medium precipitation	10	10	10	10
Railroads	10	10	10	10
Roads	10	10	10	10
Lakes	10	10	10	10
Ice/rock	10	10	10	10

CONCLUSIONS

Social and ecological influences must be explored to better understand moose population dynamics and genetics. Since moose in Alaska play a dominant role in the boreal forest ecosystem (Molvar et al. 1993, Simberloff 1998) and are a valuable protein source for many people (Ballew et al. 2006), knowledge gained will provide valuable insight. With this holistic approach, not only will the current understanding of moose biology and genetics increase, but my research will also benefit those who depend on moose. Some of the social issues addressed relate to the influence of harvest rates, hunting regulations, and characteristics of hunters such as the use of guides, modes of transportation, or residency status on success rates, catch per unit effort (CPUE), and antler size of moose in Alaska. Other social dynamics explored included the role of man-made landscape features and potential consequences of hunting on moose genetics and dispersal. In addition to social aspects, some ecological components included were moose density, habitat, and various landscape features to explore their effects on success, CPUE, and antler size. Furthermore, genetic diversity, gene flow, and population structure of moose in Alaska can in turn be influenced by these same ecological factors.

Harvest success and CPUE were determined to be significantly influenced by both social and ecological factors. Important predictors of success and CPUE were location of hunts, mode of transportation, hunting regulations, use of commercial services, year, density of roads, hunter-to-moose ratio, moose density, and hunter residency status. Increases in moose density, distance to roads, and river density all reduced time to achieve harvest success. Meanwhile, hunts in 1997, urban residency, use

of a snowmachine, use of a guide, and transporter usage also lessened time to success. There was a large spatial effect on CPUE among areas, which indicated potential landscape features not present in the model but likely important for predicting success. Furthermore, I determined that previous approaches, such as logistic regression (Hatter 2001), to model CPUE performed poorly. Weibull regression better captured the all or none event that occurs during hunting. This provided a much more accurate and realistic assessment of hunter effort and allowed for improved predictions of success and CPUE for areas within interior Alaska.

As with harvest success and CPUE, I concluded that moose antler size was influenced by some of these same variables. More specifically, moose density, use of guides, and harvest intensity significantly affected size of moose antlers. As moose density and harvest rates increased, I observed a decrease in antler size. Since moose are a density-dependent species, the downward trend in antler size with increased moose density probably is a result of a density-dependent process. Moreover, moose were more likely to have larger antlers in open habitat than in more closed areas. Decreases in size of antlers associated with increased harvest intensity was likely due to a downward shift in age structure and thus an increased percent of younger males within the population with smaller antlers than older bulls. Another probable factor that cannot be discounted is the influence of harvest on genetics and associated effects on antler size. The skill and experience that guides possess allowed them to hunt in areas of lower hunter-to-moose ratios, harvest larger antlered bulls, and achieve higher rates of success. These results are most likely consistent with the motivations of hunters who employ guides (i.e., trophy

hunters) and therefore guides strive to increase the satisfaction of their clients (Stewart 1985, Hartl et al. 2003, Festa-Bianchet et al. 2004) in order to ensure future employment as a guide.

Moose in Alaska are a commonly hunted species (Snepenger and Bowyer 1990; Ballew et al. 2006), and given that hunting has genetic consequences (Coltman et al. 2003), I explored the genetic diversity, gene flow, and population structure of moose in Alaska. With eight microsatellites and either five or six moose populations, respectively, I examined genetic diversity, population structure, and dispersal issues for moose in Alaska.

In Chapter three, I examined five populations (i.e., Yakutat, Tanana Flats, Koyukuk, Seward Peninsula, and Alaska Peninsula) and determined that population structure does indeed exist for moose in Alaska, albeit to a limited extent. Pairwise comparisons among areas of more recent expansion such as between Koyukuk and the Seward Peninsula (Nelson 1973; Hundertmark et al. 1998), indicated that population structure did not exist. In addition, my results from migration estimates indicated there was a measurable amount of gene flow from Koyukuk towards the Seward Peninsula; thus, my results support both scientific and ethnographic documentation of the recent westward expansion of moose in Alaska (Nelson 1973, Hundertmark et al. 1998).

Since moose have arrived recently in Alaska in evolutionary time and continue to expand, it is likely they have not yet reached a mutation-migration equilibrium. Chapter three and four indicated that F_{ST} estimates were overall larger than R_{ST} estimates, and F_{ST} results indicated more population structure than R_{ST} estimates. Given that moose

are a recent resident in Alaska and continue to disperse into various regions, I concluded that F_{ST} estimates better reflect current population structure for moose in Alaska. The Yakutat population was determined to be consistently differentiated from the other populations in Alaska. Lastly, since dispersal is a vital component of the population dynamics and structure of moose (Hundertmark 1998), I explored whether isolation by distance (IBD), in which increases in geographic distance result in increases of genetic distance, was observed. Previous research on moose in Canada indicated that IBD (Broders et al. 1999) does exist in moose. My results also indicated that IBD also occurred for moose in Alaska.

Even though I previously determined evidence for IBD, I attempted to improve incorporate a more realistic representation and estimation of geographic distance to explain genetic distance with the incorporation of landscape genetics. My research incorporated several social and ecological landscape features, some of which were more variable (i.e., habitat or vegetation) and others more permanent (i.e., mountains, lakes, roads, etc.). Based on the current understanding of moose biology, I assigned cost values (i.e., resistance) to various habitat and landscape layers. The assigned cost values of each layer then totalled to produce a friction map in which a least-cost path was drawn. A total of four friction maps that resulted in four least-cost paths were modelled. Half were assigned values with the assumption that bad moose habitat is a corridor, and the remaining two were coded as good habitat is a dispersal corridor. Within each of these two approaches, one least-cost path was drawn based on habitat and permanent landscape features, whereas the other least-cost path only included more permanent landscape

features. Least-cost paths were then compared with Euclidian distances, and model fit was assessed with AIC_C weights and adjusted r-squared estimates from Mantel tests and linear regression.

My results indicated that least-cost path models are superior to Euclidean distance measurements in their explanation of the relationship between geographic and genetic distance. Of the models explored, all Euclidean distance models ranked last and hence provided the poorest fit between geographic and genetic distance. Results from my research are notable in that the spatial scale I explored was much larger than those in previous landscape genetic studies (Funk et al. 2005, Coulon et al. 2006). Yet, I conclude that small scale habitat effects were still evident given that slight differences were observed among the top eight models. Nonetheless, all top eight models were either least-cost path three or four. The minuscule variations between the best fitting eight models was likely due to smaller scale landscape influences since the difference between the genetic distance measurements was negligible.

Even though least-cost paths three and four, which did not contain habitat, were a better fit than least-cost paths one and two, which were based on both habitat and permanent landscape layers, this does not necessarily indicate that habitat is not important for moose dispersal. However, the first two models (i.e., one and two) with all landscape layers contained far more parameters than the latter (i.e., three and four), which only contained the more permanent landscape layers. Therefore, the least-cost paths one and two were penalized for the large number of parameters in comparison with least-cost paths three and four with AIC_C scores. Even though adjusted r-squared estimates

incorporate the number of parameters, all the models contained the same number, so penalization was equal. With an equal number of parameters, results indicated that the best fit model between geographic and genetic distance was least-cost path two, which contained all landscape features and assigned values in which good moose habitat facilitates dispersal.

Other insights based on least-cost models indicate that moose do indeed traverse the Yukon-Kuskokwim Delta region. Least-cost dispersal paths also tend to utilize ice free corridors at lower elevations, especially around the Yakutat region (Klein 1965 and Hundertmark et al. 2006). Support for ethnographic data that indicated a westward expansion of moose from interior Alaska (i.e., Tanana Flats) towards the Seward Peninsula (Nelson 1973) was also found. Habitat features that have a large influence on moose dispersal were river density and elevation, which is not surprising since both habitat features affect many ecosystem processes. Lastly, linear regression indicated that good moose habitat facilitated dispersal, and documentation indicates that male moose can potentially disperse long distances (Hundertmark 1998). Therefore, a dispersal path in which nutrition was available to maintain stamina would be beneficial.

Results and conclusions drawn from my research undoubtedly contribute to social and ecological knowledge of moose. For example, with improved ability to model CPUE and predict success wildlife managers can better estimate harvest rates, and moose hunters can use insight to improve likelihood of success. Furthermore, the increased success through guiding activity stresses the importance of guides for hunters and areas in Alaska with or potentially seeking an economic benefit (Snepenger and Bowyer 1990).

Meanwhile, rates of harvest and moose density influence size of antlers, gene flow, and the genetics of moose, all of which are concerns for conservation efforts (Harris et al. 2002) and moose hunters (Coltman et al. 2003 and Milner et al. 2007).

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