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Muskoxen in Angujaartorfiup Nunaa, West Greenland: Monitoring, Spatial Distribution, Population Growth, and Sustainable Harvest

C.B. PEDERSEN[1] and P. AASTRUP[2]

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ABSTRACT. In the 1960s, 27 muskoxen (*Ovibos moschatus*) were introduced to Angujaartorfiup Nunaa, which is located next to Kangerlussuaq Airport in West Greenland. Data from 12 aerial surveys of muskoxen from 1986 to 1996 show 1) that the population has stabilized at 3000 muskoxen since hunting was initiated in 1988, 2) that the population has maintained a high level of reproduction during the study period, and 3) that an annual kill of about 700 muskoxen will maintain the population at its current level if natural mortality and reproduction remain unchanged. Using a geographical information system to subdivide data by topography and altitude showed that muskoxen greatly favour valleys and lowland areas. Densities of muskoxen above 500 m above sea level were less than 51% of densities below 500 m above sea level.

Key words: abundance, aerial survey, monitoring, muskoxen, *Ovibos moschatus*, population growth, spatial distribution

RÉSUMÉ. Dans les années 1960, 27 boeufs musqués (*Ovibos moschatus*) ont été relâchés à Angujaartorfiup Nunaa, qui est situé près de l'aéroport de Kangerlussuaq, dans le Groenland occidental. Des données provenant de 12 relevés aériens de boeufs musqués, effectués entre 1986 et 1996, montrent que: 1) la population s'est stabilisée à 3000 individus depuis l'instauration de la chasse en 1988; 2) la population a maintenu un niveau élevé de reproduction durant la période de l'étude; et 3) l'abattage annuel d'environ 700 individus devrait permettre de maintenir la population à son niveau actuel si la mortalité et la reproduction naturelles demeurent inchangées. L'utilisation d'un système d'information géographique pour subdiviser les données selon la topographie et l'altitude a montré que le boeuf musqué manifeste une préférence marquée pour les vallées et les zones de faible altitude. Les densités de boeufs musqués trouvées à plus de 500 m au-dessus du niveau de la mer étaient inférieures à 51 p. cent des densités trouvées à moins de 500 m d'altitude.

Mots clés: abondance, relevé aérien, surveillance, boeuf musqué, *Ovibos moschatus*, croissance démographique, distribution spatiale

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INTRODUCTION

In 1962, nine male and four female juvenile muskoxen were moved from Northeast Greenland to Angujaartorfiup Nunaa in West Greenland (Fig. 1). They were followed by another four male and ten female juvenile muskoxen in 1965. The primary objective of the translocation was to establish a new, stable meat resource for West Greenland Inuit hunters. A secondary objective was to protect the muskoxen from extinction in Greenland by securing a reserve population in case the indigenous muskoxen of Northeast and North Greenland should perish. The muskox population at Angujaartorfiup Nunaa increased rapidly. By 1990, the population was estimated to be 2600 (Olesen, 1993). Olesen estimated a carrying capacity of 5000 animals and concluded that the population should be maintained at 3000 muskoxen. The diet of muskoxen during winter overlaps that of caribou, which are native to the area and occur in small numbers (Olesen, 1993). Forchhammer (1995) found that graminoids were very important year-round for muskoxen in the area, forming 60% to 100% of their diet through the year. As caribou do not have access to lichens in winter, they may feed on graminoids as well. Hunting was initiated in 1988.

Several aerial surveys have been conducted at Angujaartorfiup Nunaa since 1986. Olesen (1993) reviewed population estimates until 1990. These estimates were mainly based on aerial surveys covering valleys and areas with expected high numbers of muskoxen. Estimates based on this survey technique (route method) ignored survey effort (Aastrup et al., 1988; Olesen, 1993). Since 1994, aerial surveys have been conducted using a strip transect method (Buckland et al., 1993).

In this paper, we review the twelve surveys carried out since 1986 to determine the status of the population since hunting began in 1988. We compare the population estimates obtained by route and transect surveys, construct a mathematical population model that incorporates these

[1] Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland; cbp@privat.dk
[2] National Environmental Research Institute, Department of Arctic Environment, P.O. Box 358, 4000 Roskilde, Denmark; pja@dmu.dk

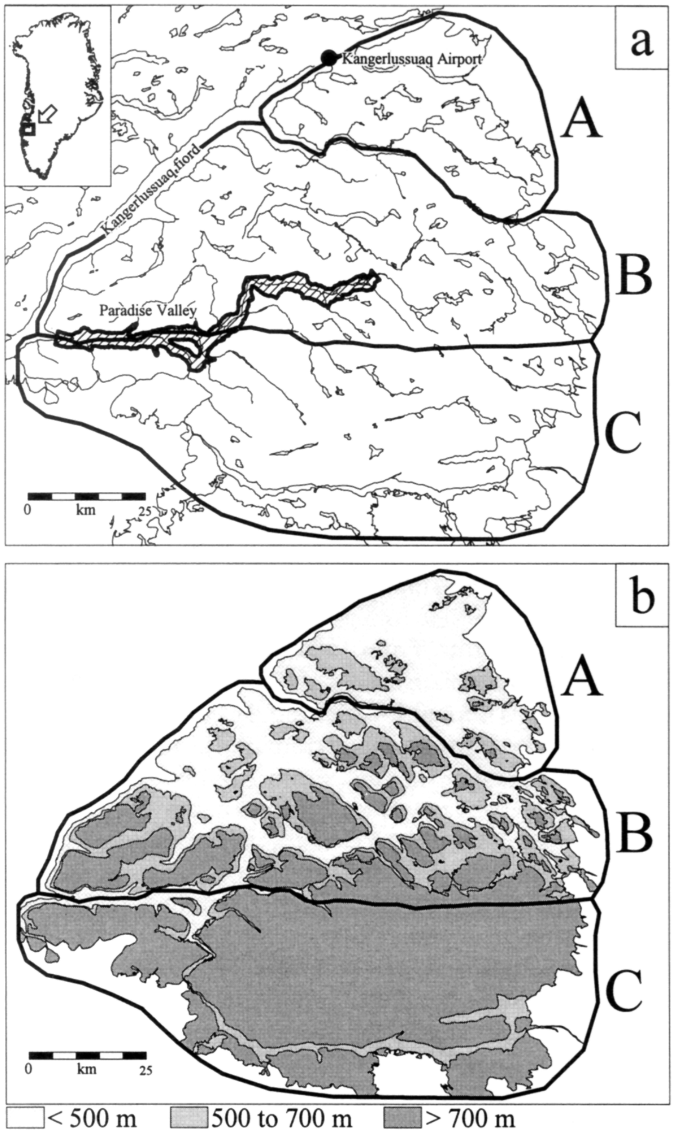

FIG. 1. Map of the study area at Angujaartorfiup Nunaa, West Greenland. Part a) shows the four regions: A, B, C, and Paradise Valley; b) shows the study area subdivided according to height above sea level.

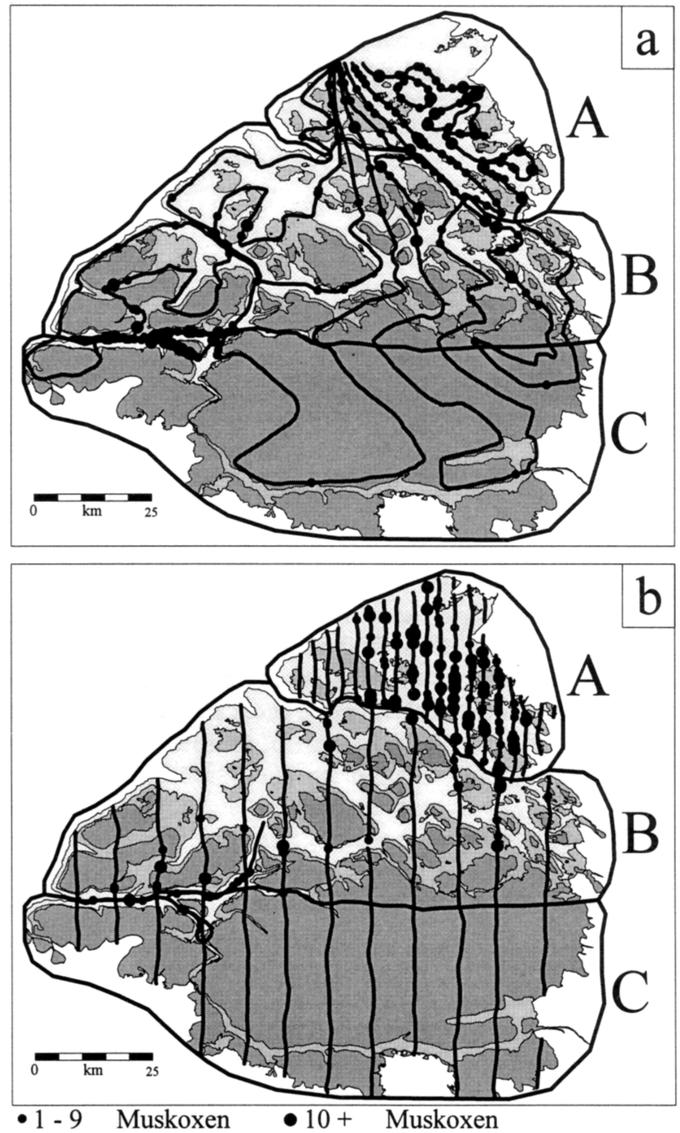

FIG. 2. Map of the study area at Angujaartorfiup Nunaa, West Greenland, showing survey patterns: a) the route survey in August 1987; b) the transect survey in April 1996. Lines indicate survey routes and transects, and dots indicate observed groups of animals.

estimates and the number of animals killed by hunters, and identify the terrain where muskoxen are most likely to be found.

STUDY AREA

Angujaartorfiup Nunaa is situated on the west coast of Greenland, at 65˚57′N, 52˚14′W to 67˚10′N, 49˚32′W. It covers a total of 7990 km^2 and is bordered to the south by the glacier Sukkertoppen Iskappe and by the inland ice to the east. To the north lies the Ørkendalen valley and Kangerlussuaq inlet. Angujaartorfiup Nunaa is characterized by a continental climate with relatively warm, dry summers and dry, cold winters. The vegetation consists mainly of dwarf shrub heaths, with *Betula nana*, *Salix glauca*, and *Vaccinium uliginosum* as dominant species. Fens and meadows are found along streams, rivers, and lakeshores, both in the lowland and on higher plateaus. The vegetation is luxurious and highly productive compared with that in the ranges of muskoxen in northeastern and northern Greenland (Olesen et al., 1994).

METHODS

The study area was divided into three census zones (regions A, B, and C) on the basis of prior knowledge of the distribution of muskoxen in the area (Fig. 1). Region A, with a mean altitude of 300 m, is mainly lowland with highly productive vegetation. Region B is mainly highland, with an average altitude of 600 m. Region C is almost exclusively highland, with an average altitude of 900 m.

TABLE 1. Aerial surveys (route or transect) of muskoxen at Angujaartorfiup Nunaa, West Greenland, from 1986 to1996. Details shown include distance between transect lines, total survey effort (km), aircraft type, initial location by map or GPS, recording of observations on form or tape, and whether calves were counted in each cluster.

Date	Method	Distance between Transects	Effort in km	Aircraft	Registration		
					Location Method	Recording Method	Calves Counted
Nov. 1986	Route	-	1338	Helicopter	Map	Form	No
June 1987	Route	-	1013	Helicopter	Map	Form	Yes
Aug. 1987	Route	-	1357	Helicopter	Map	Form	Yes
July 1988	Route	-	1011	Piper	Map	Form	No
Aug. 1990	Route	-	1089	Partenavia	Map	Form	No
April 1993	Route	-	779	Partenavia	GPS	Form	No
April 1994	Route	-	992	Partenavia	GPS	Tape	Yes
April 1994	Transect	10 km	717	Partenavia	GPS	Tape	No
April 1995	Transect	10 km	841	Partenavia	GPS	Tape	Yes
May 1995	Transect	A & B: 10 km, C: no cov.	564	Partenavia	GPS	Tape	No
Sept. 1995	Transect	10 km	864	Partenavia	GPS	Tape	No
April 1996	Transect	A: 3.3 km, B & C: 10 km	1215	Partenavia	GPS	Tape	Yes

Using a geographical information system (MapInfo version 4.1), each region was further divided by height above sea level (< 500 m, 500–700 m, > 700 m). One purpose of the detailed subdivision of the study area was to identify the terrain where muskoxen are most likely to be found. Paradise Valley, which is a part of regions B and C, is a narrow valley below 500 m and bounded by steep cliffs that has a known high density of muskoxen. Paradise Valley was defined as a fourth region, as it was evident that strips perpendicular to the valley were insufficient to allow a reliable population estimate.

Survey Design

Table 1 shows the characteristics of each of the twelve aerial surveys discussed in this article.

Two different survey designs were used: the route method and the strip transect method (Fig. 2). In the route method, flights were performed along predetermined routes following land contours, giving high coverage to areas known to be favoured by muskoxen. In the strip transect method, systematic north-south oriented transect lines were flown. Paradise Valley was also covered by the route method. In April 1994, the study area was surveyed by both methods. In April 1996, region A was given greater coverage because the results from previous surveys indicated a high density of muskoxen there (Table 1).

A Bell 206 Jet Ranger helicopter was used for some of the route method surveys. One observer was seated in the right front seat and one in the left back seat. Fixed-wing aircraft (Piper and Partenavia) were used to fly both route and transect method surveys. The Partenavia was flown at a target altitude of 166 m above ground and a target speed of 167 kph. Two observers were seated in the rear seats of the aircraft, which was equipped with plexiglass bubble windows. For each sighting, the observers recorded group size. For some of the surveys, the number of calves in each group was recorded, if possible (Table 1).

Until 1993, the survey route was recorded on a map together with the time for passage between geographically recognizable points. From 1994 on, an onboard computer logged information on time and position every 10 seconds according to a Global Positioning System (Table 1).

Before 1994, observations were transcribed onto standard forms by the observers. From 1994 on, observations were recorded on tape recorders activated by the observer, who pressed a hand-held switch and spoke into a microphone on the headset. Activation of the tape recorder prompted a synchronized time signal, which was fed to the tape from the computer (Table 1).

Observations and survey effort for all surveys were digitized into a geographical information system (MapInfo version 4.1) and subdivided by region and by height above sea level (Fig. 2).

Statistical Analysis

To identify the terrain where muskoxen were most likely to be found, the estimation of abundance was subdivided as follows: region A below 500 m, region A above 500 m, region B below 500 m, region B between 500 and 700 m, region B above 700 m, region C below 700 m, region C above 700 m, and Paradise Valley. The detailed subdivision of the area also served to account for 1) the higher coverage in region A compared with regions B and C in April 1996 and 2) the fact that route surveys give greater coverage of areas known to be favoured by muskoxen.

For the transect method, density was calculated for each subdivision using a strip census estimation technique for a clustered population (Buckland et al., 1993; Laake et al., 1993). For the route method, density was estimated by the total number of observed animals divided by two times the effective strip width and the total length of the route. Although there is no guarantee that density estimates based on the route method are unbiased (or related to the whole area), bias was reduced by the detailed subdivision

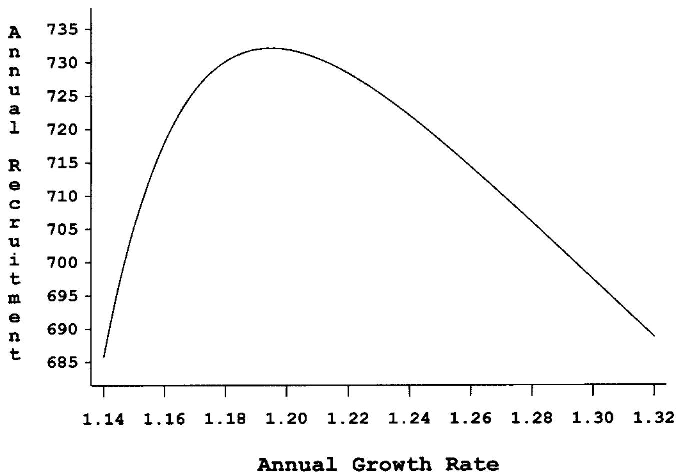

FIG. 3. Annual growth rate of the muskox population of Angujaartorfiup Nunaa, West Greenland, in relation to annual recruitment into the population in 1997.

TABLE 2. Estimates of abundance of muskoxen at Angujaartorfiup Nunaa, West Greenland, from 12 aerial surveys during 1986–96. Abundance figures are shown with confidence limits, overall density (muskoxen/km^2), and, for transect surveys, coefficient of variation (%).

Date	Method	Abundance (95% CI)	Overall Density Muskoxen/km^2	Coefficient of Variation
Nov. 1986	Route	1715	0.22	-
June 1987	Route	1556	0.20	-
Aug. 1987	Route	2379	0.30	-
July 1988	Route	2383	0.30	-
Aug. 1990	Route	4039	0.51	-
April 1993	Route	2524	0.32	-
April 1994	Route	2773	0.35	-
April 1994	Transect	3053 (1981; 4703)	0.39	21.7%
April 1995	Transect	3258 (2093; 5072)	0.41	22.0%
May 1995	Transect	2942 (2215; 3908)	0.37	14.2%
Sept. 1995	Transect	2564 (1778; 3697)	0.33	17.8%
April 1996	Transect	3159 (2383; 4189)	0.40	14.2%

of the study area. For all surveys, an effective strip width of 1 km on either side of the transect line or route was selected on the basis of the findings of Aastrup and Mosbech (1991); if all animals were observed within a distance of 1 km on either side of the transect, then the expected number of animals observed would be the same as the number counted for the actual survey. The reliability of the density estimate was expressed as a log-based confidence interval (Satterthwaite, 1946). The route method does not allow calculation of confidence intervals for the density.

For each survey, total abundance was calculated as the sum of the estimated abundances in all subdivisions. Note that estimates of densities and abundances may be biased because the effective strip width is unknown.

Overdispersed Poisson regression (McCullagh and Nelder, 1986) was used to investigate the possible effect of region and height above sea level on animal densities. These analyses were adjusted for survey year and month to allow for seasonal and yearly variation in the animal density.

The calf fraction was estimated using standard ratio sampling results, i.e., the number of calves observed divided by the total number of animals observed. The variance of the calf fraction was determined using the large sample approximation for ratio estimates with clusters as the sampling unit (Cochran, 1977). Confidence limits were calculated using the normal approximation.

Population Model

A population model was developed to study the relationship between estimates of abundance, kills of muskoxen, and annual growth rate. We define the annual growth rate as the fraction of animals added to the population during one year through reproduction, natural mortality, immigration, and migration out of the area. Births occur in April and May (Olesen, 1993), and since natural mortality, immigration, and migration are negligible, we

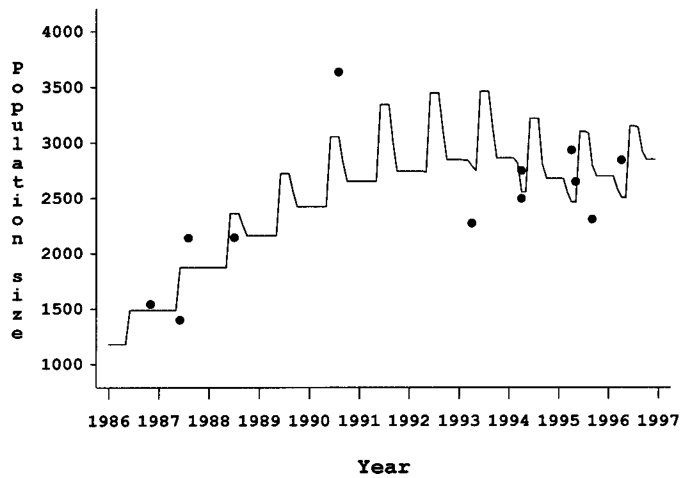

FIG. 4. Estimated population sizes from surveys (dots) and monthly population sizes (curve) predicted for an annual growth rate of 1.26 for the muskox population of Angujaartorfiup Nunaa, West Greenland. Note that the ordinate is a continuous time scale.

assume for simplicity that reproduction, natural mortality, immigration and migration occur in May. Thus reproduction, natural mortality, immigration, and migration can be described by one parameter: the annual growth rate.

The relationship between the annual growth rate and the annual recruitment of the population in 1997 (Fig. 3) was established using a population model. The population size in month $m+1$ was predicted by the population size in month m minus the kill in month m. In May, the population size increases by the annual growth rate.

For each aerial survey i = 1,2,...,12, let S_i denote the estimated population size (Table 2), let $N_i(N_0,\eta)$ denote the population size predicted using the population model with an initial population size in January 1986 of N_0 and an annual growth rate of η, and let $\delta_i(N_0,\eta) = N_i(N_0,\eta)/S_i$ denote the correction factor. The value of N_0 that for fixed annual growth rate η minimizes the sample variance of $\delta_1(N_0,\eta)$, $\delta_2(N_0,\eta)$,..., $\delta_{12}(N_0,\eta)$ represents the population

TABLE 3. Annual kill of muskoxen in the Angujaartorfiup Nunaa area, West Greenland, from the start of hunting in 1988 to 1996.

Year	1988	1989	1990	1991	1992	1993	1994	1995	1996
Total annual kill	200	300	400	600	606	700	847	618	500
Non-reproductive animals					6	100	22	618	500
Unrestricted	200	300	400	600	600	600	825	0	0

TABLE 4. Fraction of calves estimated in surveys of muskoxen at Angujaartorfiup Nunaa, West Greenland, during 1987–96. (Calves were counted in five of the total 12 surveys.) Calf fraction (%) is shown with 95% confidence interval.

Date	Calf fraction (95% CI)
June 1987	13.6% (11.6%;15.6%)
Aug. 1987	15.1% (13.5%;16.7%)
April 1994	16.8% (15.6%;17.9%)
April 1995	20.7% (17.3%;24.0%)
April 1996	17.4% (15.6%;19.2%)

size in January 1986 that describes the “most likely” development in the population size. This value is independent of a constant multiplicative bias (e.g., effective search width) in the estimated population sizes S_i. Repeating this procedure numerically, we established a relation between the population size in January 1986 and the annual growth rate, and thus the relation between the annual growth rate and the annual recruitment in 1997, presented in Figure 3. The advantage of this modelling is that it depends on only the relative—and not the absolute—changes in the estimates of population size (Table 2).

Detailed sex and age distributions for the hunt do not exist. Parts of the quotas have been given on the condition that calves and cows followed by calves not be taken, and some quotas allowed only bulls to be hunted. Table 3 summarizes the kill from 1988 to 1996, in relation to reproductive animals. In the first part of this period, quotas were given without restrictions; later, some protection was given to reproductive animals.

RESULTS

Population Size

The population increased from approximately 1700 muskoxen in 1986, to a peak of approximately 4000 muskoxen in 1990. From 1993 to 1996, after a period of three years where population censuses were not performed, the size of the muskox population appeared to stabilize at about 3000 animals (Fig. 4). During this period the mean annual kill was 650 muskoxen per year (Table 3). The overall densities of muskoxen increased from 0.2 muskoxen/km^2 in 1986 to 0.5 muskoxen/km^2 in 1990. Thereafter the density appeared to stabilize between 0.3 and 0.4 muskoxen/km^2 (Table 2). The coefficient of variation, which is a measure of the reliability of the density estimate, is calculated as the standard error divided by the population size and ranged from 14.2% to 22.0%.

In 1994 surveys were conducted both by the route and the transect method. The difference between population estimates based on the two methods are small, indicating that estimates from the two methods are generally comparable. However, the population estimate for 1990 is likely to be an overestimate, as it can only be accommodated by a high annual growth rate from 1988 to 1990 combined with a low annual growth rate from 1991 to 1993.

Calf Fraction

All calf fractions were within the range of 13–21% (Table 4).

Spatial Distribution of Muskoxen

Areas below 500 m in region A and Paradise Valley were clearly the core ranges of muskoxen, although muskoxen could occur anywhere (Fig. 2). Table 5 presents estimates of relative animal density based on data from transect surveys, route surveys, and all surveys. These data indicate that the relative densities based on route surveys were similar to those based on transect surveys, suggesting that estimates of abundance based on route surveys are comparable with those based on transect surveys.

Data from transect and route surveys were pooled to give overall estimates of the relative animal density (see last column of Table 5). Only the pooled data are referred to in the following results. The animal density varied significantly between regions ($p < 0.0001$) and heights above sea level ($p < 0.0001$). There was no interaction between these variables ($p = 0.32$). For altitude, the animal density below 500 m was used as a baseline. The density above 700 m was 24% (11% to 51%) of the baseline density, and density from 500 to 700 m was 51% (37% to 71%) of the baseline. Region A was used as the baseline density for regions. In Paradise Valley, density was 74% (57% to 96%) of the baseline; in region C, it was 5% (1% to 19%) of the baseline; and in region B, it was 24% (19% to 31%). Overall, the population size increased by 57% (16% to 116%) from 1986 to 1996.

Population Model

Figure 3 shows the estimated relationship between the annual growth rate and the annual recruitment of the population in 1997, and Table 3 shows the annual kill. If the fixed annual growth rate lies between 1.14 and 1.32,

TABLE 5. Estimates of relative density of muskoxen in Angujaartorfiup Nunaa, West Greenland, based on data from transect surveys, route surveys, and all surveys. Density in region A and density at < 500 a.s.l. (indicated as 1) were used as baselines, against which other regions and altitudes are compared.

	Relative Animal Density		
Location	Transect Surveys	Route Surveys	All Surveys
Region:			
A	1	1	1
B	0.21 (0.14, 0.30)	0.26 (0.19, 0.35)	0.24 (0.19, 0.31)
C	0.03 (0.01, 0.17)	0.08 (0.01, 0.43)	0.05 (0.01, 0.19)
Paradise Valley	0.50 (0.35, 0.73)	0.91 (0.66, 1.26)	0.74 (0.57, 0.96)
Height above sea level:			
< 500 m	1	1	1
500–700 m	0.43 (0.28, 0.67)	0.57 (0.38, 0.85)	0.51 (0.37, 0.71)
> 700 m	0.21 (0.08, 0.51)	0.29 (0.11, 0.79)	0.24 (0.11, 0.51)

then the annual recruitment of the population will range from 690 to 730 animals per year. Annual growth rates of 1.14 and 1.32 correspond to correction factors of 1.7 and 0.7, respectively. Olesen (1990) estimated the annual growth rate at 1.26. This annual growth rate corresponds to an annual recruitment of 710 muskoxen and a correction factor of 0.9; that is, estimates of population sizes in Table 2 should be multiplied by 0.9 to estimate the actual population size.

Figure 4 shows the dynamics of the population model for an annual growth rate of 1.26. Each year, the population size increases by 26% during May and then stabilizes until the hunt begins in August, after which it decreases because of hunting. The dips that occur from 1992 onward represent additional hunting in February and March.

DISCUSSION

Population Size

The muskox population in Angujaartorfiup Nunaa has increased rapidly since it was first introduced in 1962 and 1965. Rapid reproduction among two-year-old cows resulted in an annual increase of 32% (Olesen, 1993). Olesen (1993) reviewed the history of the population until 1990. On the basis of the first signs of overgrazing of vegetation and initiation of emigration from the area, he concluded that the carrying capacity had been reached. He recommended quota-based harvesting matching the annual recruitment, and suggested that the muskox population should be maintained at a level of approximately 3000 animals. Hunting was initiated in 1988 and from 1988 to 1992, hunting quotas were 10% of the estimated population size. From 1993 to 1996, hunting quotas were higher: 15% to 30% of the estimated population size (Table 2; Table 3). Until 1991, recruitment into the population was more than 20% (Olesen, 1993). This rate of recruitment appears to have continued for the succeeding years. The data presented here indicate that since hunting began, the population size has stabilized at 3000 muskoxen.

Calf Fraction

The observed calf fraction recorded during aerial surveys is likely to be an underestimate, as calves are often missed (Nagy et al., 1996; Aastrup and Riget, 1999). Fractions between 13% and 21% were observed. These fractions are similar to those in Jameson Land in East Greenland, where the average fraction was 18.2% during 1982–90 (Aastrup and Mosbech, 1999), and to those in Banks Island, Northwest Territories, Canada, where the average fraction was 18.3% during 1982–92 (Nagy et al., 1996). These findings demonstrate a remarkable similarity between the Banks Island herd and the Angujaartorfiup herd in West Greenland.

Annual Kill

The population model suggests that an annual kill of 690–730 muskoxen will balance calf production given the current conditions. However, this reflects an average situation. One or more years with extraordinary mortality among calves would reduce the sustainable kill, and could therefore have drastic consequences on the population size if kills were maintained at the same high level. Inherent in the suggested annual kill is partial protection of calves and of cows followed by calves. This means that a relatively high proportion of the population should be reproductive females. A smaller total production must be expected if the protection of reproductive females is abandoned. It is concluded that, under the present conditions, there is no indication that annual harvest exceeds the productivity of the population.

Density and Range

Olesen (1990) predicted that unless hunting was initiated, muskoxen would emigrate from the Angujaartorfiup Nunaa area because of limited food resources. Data from systematic aerial surveys of caribou in 1993, 1994, 1995, and 1996 in the areas neighbouring Angujaartorfiup Nunaa indicate that the muskox population has not expanded its range (C.B. Pedersen, unpubl. data, 1998). It can therefore be concluded that the muskox population has not expanded its range since hunting was initiated.

The density of muskoxen in Angujaartorfiup Nunaa varies with topography and altitude. The estimated relative densities of muskoxen indicate that region A and Paradise Valley are the most densely populated regions, and that areas below 500 m are by far the most dense of all regions, supporting 80% of the total population in 20% of the total area.

It may be ambiguous to compare overall densities, as landscape and quality and quantity of forage in muskox ranges vary. Estimates of the overall density of muskoxen in Angujaartorfiup Nunaa ranged from 0.20 to 0.51 muskoxen/km^2. Given that the two survey methods produce comparable results, we may conclude that population size increased by 57% from 1986 to 1996 despite the large hunt. The overall density of muskoxen in Jameson Land in Northeast Greenland, which ranged from 0.27 to 0.57 muskoxen/km^2 during 1982–90 (Aastrup and Mosbech, 1999), was within the same range as that in Angujaartorfiup Nunaa. The similarity of overall densities in Jameson Land and Angujaartorfiup Nunaa could be interpreted as an indication that there is room for more muskoxen in Angujaartorfiup Nunaa because the vegetation and growth conditions are better (Olesen et. al., 1994). The excellent forage conditions seem to result in larger body size (Olesen et al., 1994) and calf recruitment. On the Queen Elizabeth Islands (Canadian Arctic Archipelago), Miller and Russell (1975) reported densities from 0.02 up to 0.07 muskoxen/km^2, and Thomas et al. (1981) reported densities of 0.60–1.0 muskoxen/km^2 in a restricted area in the Bailey Point region in the Canadian Arctic. Aastrup et al. (1986) found extremely low densities (between 0.02 and 2.3 muskoxen per 100 km^2) in high arctic northern Greenland. These comparisons demonstrate that the densities of muskoxen are highly dependent on vegetation characteristics and climate. The Angujaartorfiup Nunaa population lies in the upper range of production and density compared with other muskox populations throughout the circumpolar range.

There has been some concern that the regional distribution of muskoxen in the study area could be affected by hunting, which takes place mainly in region A. The data presented here do not suggest that any such changes have occurred. There is no indication that the relative proportion of the population in each region has changed since hunting began. If a regional redistribution of the population did occur as a result of hunting, it appears to be only temporary, perhaps during and immediately after the hunt. This demonstrates that muskoxen strongly favour specific areas, like region A and Paradise Valley.

Comparing the densities in region A and Paradise Valley indicates that some migration may occur between these two areas. The density appears to be high in Paradise Valley when it is relatively low in region A, and vice versa. It is suggested that muskoxen spread out during summer to the best forage areas. Because of the terrain and good summer forage, a relatively large number of muskoxen stay in Paradise Valley. In winter the muskoxen seem to leave Paradise Valley, probably because of unfavourable snow conditions or lack of forage. There is no indication that a similar relationship exists between region A and regions B and C.

If the density of muskoxen became too high for the available food resources, the densities in regions B and C and at higher altitudes could be expected to increase because of competition for forage in the best areas. Likewise, an expansion of the muskox range to the north could be expected. None of this has occurred, even at the peak population size in 1990, when 84% of the population in region A was found below 500 m.

Forage competition with caribou has been a concern among scientists and the public. Our data do not support the view that competition with caribou adversely affects the muskoxen. On the contrary, caribou occur in relatively small numbers, and we cannot exclude the possibility that the caribou in the area suffer from competition with muskoxen.

Methodological Problems

The potential methodical problems are three: 1) whether abundance estimates based on route surveys are comparable with abundance estimates based on transect surveys; 2) whether abundance estimates based on summer surveys are comparable to those based on winter surveys, and 3) whether abundance estimates (Table 2) are subject to bias due to uncertainty of the effective strip width.

Although the route method has inherent bias, the relative densities based on route surveys were similar to those based on transect surveys, and the population estimates based on the two methods in April 1994 were comparable, suggesting that bias is negligible in this case. We conclude that the two survey methods have produced comparable population estimates. Since the route method does not allow an estimation of the precision of the population estimate, and transect surveys are inadequate in Paradise Valley, it is proposed that future surveys should be based on the transect method, except in Paradise Valley, which should be covered by the route method.

Muskoxen are dark, large-bodied animals that are relatively easy to detect on a snow-covered surface in winter within about 1 km. In summer, muskoxen are also quite easy to detect on the background of the typical green or greyish vegetation, which in most places is less than 0.35 m in height. Therefore we have no argument against comparing population estimates based on summer surveys with those based on winter surveys. There seems to be no reason to expect substantial differences between summer and winter surveys.

Uncertainty may be associated with the effective search width. Although 1 km on either side of the transect line seems reasonable from practical experience, there is no objective evidence on this point for the Angujaartorfiup

Nunaa area. Therefore, the absolute values of the abundance estimates and animal densities presented may be biased. Nevertheless, the results of the population model and the ratios between the population estimates are not subject to bias. Some justification of an effective search width close to 1 km on either side of the transect line comes from the population model, in which an annual growth rate of 1.26 (Olesen, 1990) corresponds to a correction factor of 0.9, or an effective search width of 1110 m on either side of the transect line.

The total abundance estimate in April 1996 (CV = 14.2%) had a higher precision than total abundance estimates in April 1994 (CV = 21.7%) and April 1995 (CV = 22.0%), because of the increased coverage in region A. The coefficient of variation for estimates of abundance based on line transect surveys typically ranges from 15% to 25%. Thus, the confidence intervals in Table 2 are narrow compared with confidence intervals from other aerial surveys. Designing the coverage of an aerial survey so that subdivisions with high density are given higher coverage than subdivisions with low density effectively increases the precision of estimates of total abundance. It is therefore advisable to subdivide study areas in accordance with the prior knowledge of the distribution of animals. The observed groups of muskoxen (Fig. 2) and the results concerning the difference in animal density between regions and heights above sea level (Table 5) justify the chosen subdivision of the Angujaartorfiup Nunaa area.

CONCLUSION

We conclude that 1) hunting has stabilized the population at a constant level of about 3000 individuals; 2) a hunt of about 700 muskoxen per year is sustainable under the present conditions; 3) muskoxen greatly favour valleys and lowland areas; and 4) it is possible to manage a population of wild muskoxen in a sustainable manner for at least 10 years.

Whether the population should be maintained at the present level is a political question. A reduction in population size would decrease the risk of overgrazing and damage to vegetation. An increase in population size might allow an even higher utilization; however, it would increase the risk of overgrazing.

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REFERENCES

AASTRUP, P., and MOSBECH, A. 1991. Transect width and missed observations in counting muskoxen (*Ovibos moschatus*) from fixed-wing aircraft. Rangifer 13(2):99–104.

———. 1999. Population demography of the muskox population in Jameson Land, East Greenland 1982–90. Unpubl. ms. Available at the Department of Arctic Environment, National Environmental Research Institute, P.O. Box 358, 4000 Roskilde, Denmark.

AASTRUP, P., and RIGET, F. 1999. Muskox population estimates of Hold with Hope, Ymer Ø, Geographical Society Ø and Traill Ø. 1996. Unpubl. ms. Available at the Department of Arctic Environment, National Environmental Research Institute, P.O. Box 358, 4000 Roskilde, Denmark.

AASTRUP, P., BAY, C., and CHRISTENSEN, B. 1986. Biologiske miljøundersøgelser i Nordgrønland 1984–85. Copenhagen: Grønlands Fiskeri- og Miljøundersøgelser.

AASTRUP, P., NIELSEN, A.B., and NYGAARD, K.H. 1988. Miljøundersøgelser ved Sarfartoq 1986–89. Vildt og vegetation. Copenhagen: Grønlands Miljøundersøgelser.

BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P., and LAAKE, J.L. 1993. Distance sampling. New York: Chapman & Hall.

COCHRAN, G.C. 1977. Sampling techniques. 3rd ed. New York: John Wiley & Sons.

FORCHHAMMER, M.C. 1995. Sex, age, and seasonal variation in the foraging dynamics of muskoxen, *Ovibos moschatus*, in Greenland. Canadian Journal of Zoology 73:1344–1361.

LAAKE, J.L., BUCKLAND, S.T., ANDERSON, D.R., and BURNHAM, K.P. 1993. Distance user's guide. Fort Collins: Colorado Co-operative Fish and Wildlife Research Unit, Colorado State University.

McCULLAGH, P., and NELDER, J.A. 1986. Generalised linear models. 2nd ed. London: Chapman and Hall.

MILLER, F., and RUSSELL, R.H. 1975. Aerial surveys of Peary caribou and muskoxen on Bathurst Island, Northwest Territories, 1973 and 1974. Canadian Wildlife Service. Progress Notes No. 44.

NAGY, J.C., LARTER, N.C., and FRASER, V.P. 1996. Population demography of Peary caribou and muskoxen on Banks Island, N.W.T. 1982–1992. Rangifer Special Issue 9:213–222.

OLESEN, C.R. 1990. Bestandsudvikling og økologi for moskusokser i Angujaartorfiup Nunaa, Vestgrønland. Teknisk Rapport nr. 16 (April 1990). Nuuk, Greenland: Grønlands Hjemmestyre. Miljø- og Naturforvaltningen.

———. 1993. Rapid population increase in an introduced muskox population, West Greenland. Rangifer 13(1):27–32.

OLESEN, C.R., THING, H., and AASTRUP, P. 1994. Growth of wild muskoxen under two nutritional regimes in Greenland. Rangifer 14(1):3–10.

SATTERHWAITE, F.E. 1946. An approximate distribution of estimates of variance components. Biometrics Bulletin 2: 110–114.

THOMAS, D.C., MILLER, F., RUSSELL, R.H., and PARKER, G.R. 1981. The Bailey Point Region and other muskox refugia in the Canadian Arctic: A short review. Arctic 34(1):34–36.