

Decline and Extermination of an Arctic Wolf Population in East Greenland, 1899–1939

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(Received 4 August 2009; accepted in revised form 19 October 2011)

ABSTRACT. The decline and extermination of an arctic wolf population in East Greenland between 1899 and 1939 were investigated through analysis of 40 years of archival data, which contained records of 252 sightings of wolves or their tracks. Prior to the start of exploitation by Europeans, this small, isolated wolf population probably consisted of about 38 wolves during an average year. Of 112 wolves sighted in early winter, 31.3% were lone wolves, 23.2% were in pairs, and the rest were in larger groups. Mean pack size was 3.3 wolves, and packs of more than four wolves were rare. The population was concentrated in the central part of its range, making it vulnerable to exploitation by Danish and Norwegian commercial hunters, who exterminated the population. Poison was the primary agent of destruction. There was no evidence that other proposed causes of the decline were influential. This study provided the first evidence of an arctic wolf population that was eradicated and highlights the vulnerability of small, isolated wolf populations to excessive harvest. Wolves in the High Arctic may be particularly vulnerable because of their exceptionally low densities, smaller pack sizes, lower pup production, infrequent reproduction, and insular or disjunct distributions.

Key words: arctic wolf, High Arctic, extermination, poison, Greenland, harvest

RÉSUMÉ. Le déclin et l'extermination d'une population de loups arctiques dans l'est du Groenland entre 1899 et 1939 a fait l'objet d'une enquête prenant la forme de l'analyse de données archivées s'étendant sur 40 années. Ces données comprenaient l'enregistrement de 252 observations de loups ou de pistes de loups. Avant que cette région ne soit exploitée par les Européens, cette petite population de loups isolée comptait probablement environ 38 loups au cours d'une année moyenne. Au début de l'hiver, 112 loups avaient été observés, dont 31,3 % étaient des loups seuls, 23,2 % se trouvaient en paires et le reste étaient en groupes plus volumineux. La taille moyenne d'une meute était de 3,3 loups, tandis que les meutes comptant plus de quatre loups se faisaient rares. Cette population était concentrée dans la partie centrale de son parcours naturel, ce qui la rendait vulnérable à l'exploitation par les chasseurs commerciaux du Danemark et de la Norvège, qui ont fini par l'exterminer. La principale substance utilisée pour les détruire était le poison. Rien ne prouve que leur déclin était attribuable à d'autres causes importantes. Cette étude a non seulement fourni les premières preuves d'une population de loups arctiques qui a été éliminée, mais a également fait ressortir la vulnérabilité de petites populations de loups isolées à une capture excessive. Les loups se trouvant dans l'Extrême-Arctique sont susceptibles d'être plus particulièrement vulnérables en raison de leurs densités exceptionnellement faibles, de la plus petite taille des meutes, de la production plus faible de petits, de la reproduction non fréquente et de leurs distributions insulaires ou isolées.

Mots clés : loup arctique, Extrême-Arctique, extermination, poison, Groenland, capture

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

Long-term data are critical for accurate characterizations of populations, especially in the Arctic, where many species display extreme fluctuations in numbers. Despite this importance, few data sets on terrestrial mammals have been collected on a decadal scale. Little long-term information is available on the arctic wolf (*Canis lupus arctos*) found on the Canadian Arctic Islands and in North and East Greenland. Some information is available on a pack on Ellesmere Island (Mech, 1995, 2005), but population data are lacking (Miller, 1998). In East Greenland, wolves arrived as

recently as 1979 (Hansen, 1979) after an original population vanished during the 1930s (Dawes et al., 1986).

Little is known about that original wolf population. A few wolves were sighted when European explorers arrived in the 1890s (Nathorst, 1900; Kolthoff, 1901). Starting in 1908, Danish and Norwegian commercial hunters began to harvest furbearers (Mikkelsen, 1994). Packs of up to 13 wolves were reported (Devold, 1940). Estimates of the total wolf harvest during 1899–1939 revealed considerable uncertainty, ranging from 35 to 60 wolves, depending upon the authority (Devold, 1941; Pedersen, 1942). By 1932, the residual population was guessed to be 10–12 remaining

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wolves (Pedersen, 1936). The last reported evidence of this population was found in 1939 (Sørensen, 1961). In North Greenland, wolves likely persisted (Marquard-Petersen, 2007).

For the next 65 years, the population collapse was not investigated and was poorly understood, prompting speculation about the cause of the extinction. Multiple factors were proposed: 1) the prior extinction of caribou (*Rangifer tarandus*) in 1900, which caused wolves to lose a traditional prey species (Freuchen and Salomonsen, 1958); 2) excessive hunting pressure (e.g., Giæver, 1939); 3) a combination of these factors (e.g., Dawes et al., 1986); or 4) harvest combined with a crash in the arctic hare (*Lepus arcticus*) population (e.g., Vibe, 1967). A better understanding could be achieved through review and analysis of historical records. Human access to the Arctic is projected to increase in the 21st century as a result of climate change (cf. Barber et al., 2008). Factual knowledge on the root cause of the population collapse is therefore important in evaluating the potential vulnerability of this subspecies to increased human activity, particularly in the Canadian High Arctic, where wolves are not protected in most areas. In Greenland, legal protection is given in 94% of wolf range (Marquard-Petersen, 2008).

This paper reports the results of an analysis of the population characteristics and demise of the historical wolf population in East Greenland based on observational data collected opportunistically and available in 40 years of historical records (1899–1939). The goal was to identify and collect available data and combine this new data set with that of the contemporary wolf population to create a combined 60-year record that can be mined for decades (see Marquard-Petersen, 2007). Objectives were to 1) identify the historical abundance, social organization, and distribution of arctic wolves; 2) evaluate their vulnerability to exploitation by conducting a temporal and spatial analysis of wolf harvest to determine whether overexploitation caused the extinction; and 3) evaluate alternative causes of the population collapse.

METHODS

Data Collection

To gather data on this extinct population, I conducted an exhaustive analysis of published and unpublished sources. The former consisted of narratives of expeditions, descriptions of wildlife, expedition reports, and diaries kept by individuals while exploring, hunting, and trapping in central East Greenland during 1899–1960. Unpublished sources consisted of diaries written by Danish and Norwegian commercial hunters during 1908–52 and letters or reports from files of the three fur trading companies of the period. I reviewed Danish records in Denmark at the Arctic Institute, National Archives, Royal Library, Zoological

Museum, and Danish Polar Center, all in Copenhagen, and at Mogens Graae's private collection in Jutland. I reviewed two other private collections by mail: The Peter Schmidt Mikkelsen and the Arne Philbert collections. I examined Norwegian records in Norway at the Norwegian Polar Institute and the National Archives in Oslo. Records of these institutions located in Tromsø were examined by mail.

I recorded three categories of information: sightings of wolves, harvest records, and wolf tracks. I recorded the date, locality, and number of wolves for each sighting. I excluded data that possibly represented repeat sightings. Counts reported as a range were accepted as a midrange estimate; for example, a report of a pack of 11–13 wolves was recorded as 12 wolves. For each reported kill, I recorded the year, location, sex (if known), method of kill, hunter's name, nationality, and affiliation.

Wolves were absent from the southern half of East Greenland presumably because of the absence of large ungulate prey (cf. Pedersen, 1934). Because of this range boundary, little, if any, wolf range in East Greenland lay outside the areas affected by commercial hunting and listed on Figure 1. Therefore, areas visited by hunters and documented in the historical record were representative of all wolf range in East Greenland. I assumed that 1) the kill and sighting data collectively reflected historical abundance and distribution, 2) the information in diaries was accurate and unbiased to the author's best knowledge, and 3) the diaries surviving to this day represented an unbiased sample of diaries written during the period.

Abundance

Because wolves generally travel as packs in discrete territories, I used the minimum-number-alive method to estimate population size (Krebs, 1999). Because data were separated both in time and in space, I developed a maximum estimate of the pre-exploitation population size as a sum of maximum estimates for each area. I recognized that population size likely was lower in most years because maximum pack sizes reflected wolf abundance during an optimal period. Midrange and minimum estimates were derived using similar methods. I assumed that 1) packs were territorial and occurred in the same core area annually (cf. Ballard et al., 1987, 1997; Mech, 1995); 2) each pack had been sighted and reported at least once, because wolves travel widely, and geographical coverage by hunters was extensive; 3) home ranges were relatively stable, and only one pack occurred in each area; 4) wolves seen in a presumed core area (or on the fjord ice of its immediate surroundings) represented the nearest resident pack; 5) pack size during early winter (October–December) represented maximum pack size in winter; and 6) sightings of wolf packs during seasons other than early winter were conservative estimators of maximum pack size that could substitute for sightings in areas where no packs had been sighted in early winter.

Social Organization

I investigated social organization using sightings from early winter because wolf packs in lower latitudes reach their maximum size, are most cohesive, and travel as a group at this time of year (Peterson et al., 1984; Mech et al., 1998; Adams et al., 2008). I assumed this pattern held true for Greenland, and that the relative proportion of loners sighted in early winter was an accurate estimator of the proportion of lone wolves in the population.

Distribution

Geographical distribution of this wolf population was examined by standardizing sightings of wolves by hunter effort. I assumed that the resulting data set reflected distributional patterns. Hunter effort was expressed as “diary-days,” i.e., one hunter spending one day in the wolf range and recording the day in a diary available for review. Sightings of wolves recorded in diaries were divided by the number of diary-days to achieve a standardized measure for each area. To further compare hunter effort between areas, I established how many individuals overwintered at hunting stations, using Mikkelsen (1994). I expressed this effort as “effort-years” and used it as a relative index of the amount of human activity in each area. For example, attempts at exploiting wolves in Germania Land occurred periodically over a 34-year period (1906 to 1939), but hunters were present during only nine of those years, which is expressed as nine effort-years.

Population Decline

Rate of decrease was investigated by analyzing for trend separately in each wolf core area. Log_e transformations of standardized sightings were necessary to meet the regression assumption of normality. The data were fitted by least squares regression and presented with 95% confidence and prediction intervals. Analysis of covariance (ANCOVA) was used to compare rates of decline in individual core areas. I tested the equality of the regression coefficients ($H_0 = \beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5 = \beta_6$) and related detected disparities to differences in harvest pressures over time and among areas. Unpublished sources, wolf sightings, kills, and areal sizes were listed in Marquard-Petersen (2007).

I assembled descriptive evidence for and against possible causes involved in the population decline: excessive harvest; decline in habitat quality principally through lack of prey; disease; inbreeding depression; decreased reproduction; and factor interaction. I recognized that lack of mention of any potential cause in trappers’ journals did not necessarily mean that those conditions did not exist. I evaluated each factor individually, which led to six predictions:

1. Excessive Harvest: If excessive harvest caused the decline, then the primary mechanism would have been commercial hunters. Harvest would have exceeded maximum sustainable yield (MSY) because the population

declined to extinction. The logistic model was chosen as a means of providing a diagnosis of the decline. An estimate of population rate of increase was needed for calculations. I assumed that a mean exponential rate of increase (r) of 0.24 in the contemporary East Greenland population during 1978–88 (Marquard-Petersen, 2009) was representative of that of the historical population. I recognized that the contemporary population may have experienced an inflated rate of increase due to the recolonization starting in 1979. A possible inflation would cause an exaggerated estimate of MSY. I used maximum population size as an estimate of carrying capacity (K). MSY was estimated through $((1-e^{-r/2})(K/2))$, with “e” constituting the base of natural logs (Caughley, 1977).

I regressed the population decline against each year between 1926 and 1932 for the three population estimates, attempting to reproduce the trajectory derived from the kill data. I limited the regression to these years because model accuracy was potentially influenced by strychnine, introduced by Norwegian hunters in 1926 (cf. Jenov, 1933). The use of poison causes underreporting of harvest, perhaps by up to 100% (Young and Goldman, 1944). In East Greenland, on account of snow or darkness, it could be impossible to locate animals that had eaten poison bait (Devold, 1941). I therefore employed four different regression scenarios with correction factors for undetected kills due to poison use: reported kill plus 0%, 50%, 75%, and 100%. Twelve population trajectories were produced and evaluated, assuming a closed population. I recognized this effort represented a rough approximation of possible population trajectories.

2. Habitat Quality: I defined habitat quality as the ability of East Greenland to support a wolf population by providing sufficient prey for wolves to survive and reproduce. If lack of prey was implicated in the decline, then mechanisms might have been an increase in detrimental weather events that caused over-icing and food shortage among muskoxen (*Ovibos moschatus*), or wolf predation that reduced the muskox population. This factor predicted that one or more severe over-icing events occurred during the 1920s, resulting in catastrophic mortality among muskoxen, or that wolves were reported to be numerous enough to reduce the muskox population.

3. Disease: If disease was an important cause of the decline, then the mechanism would have been a disease or diseases known to affect wolf populations. This factor predicted that harvested wolves or the wolf population had shown signs of disease, or that natural deaths had been found and reported.

4. Inbreeding Depression: If inbreeding depression caused the decline, the primary mechanism would have been closely related wolves breeding with each other. This factor predicted that effects known to be indicators of inbreeding (e.g., congenital bone deformities, blindness, increased juvenile mortality) had occurred, been detected, and reported, or that inbreeding depression had been documented as a factor in wolf population declines elsewhere.

5. Decreased Wolf Reproduction: If decreased reproduction caused the decline, then multiple mechanisms may have been involved (e.g., toxins, inbreeding, disease, and lack of food). Reports of such deleterious agents would have been found in diaries or the published literature.

RESULTS

Published sources consisted of 16 narratives, eight diaries, and 43 descriptions of hunting conditions, containing 55 sightings of wolves or their tracks. Unpublished sources consisted of 12 981 pages in 122 diaries written by Danish and Norwegian hunters who overwintered in East Greenland between 1908 and 1952, as well as 31 letters or unpublished reports recording 197 sightings of wolves or their sign. I reviewed 99.2% of pertinent diaries and documents available in government archives, as well as 23 diaries in private collections (Table 1).

Social Organization

Of 58 sightings made in early winter, totaling 112 wolves, 35 sightings were of lone wolves (60.3%), 13 were of pairs (22.4%), and 10 were of packs with more than two wolves (17.3%). Lone wolves comprised 31.3% of the 112 wolves. Pack sizes ($n = 23$) ranged from 2 to 12 wolves. Packs of more than four wolves were rare (5.0%). Mean early winter pack size was 3.3 wolves.

Harvest

From 1910 to 1920, hunter effort was 14 effort-years. Between 1920 and 1930, effort increased by 800%, and between 1930 and 1940, by another 116% (Table 2). Total hunter effort was 433.5 effort-years.

Forty-six wolves were reported killed from 1899 until the last reported kill in 1932. This low harvest prior to population extinction suggests that the wolf was rare in East Greenland. Most of the harvest (76%) was taken between 1920 and 1932 over 10 effort-years. Shooting was the preferred method of take, followed by strychnine and leg-hold traps (Table 3).

Most wolves (90%) killed during the last 10 years of harvest were taken by Norwegians, who killed twice as many wolves during this period as did the Danes; the Norwegian hunters' larger harvest was almost entirely due to the use of strychnine. Poison baits were distributed within the wolf range in large numbers; for example, during the trapping season of 1929–30, a single hunter distributed 56 baits on Ymer Island at a linear density of one bait per 1.5 km of trapline; during the winter of 1932–33, 51 baits were placed on southern Clavering Island; and during the winter of 1933–34, 90 baits were distributed on Hochstetter Forland (see unpublished references in Marquard-Petersen, 2007).

Abundance

Maximum reported pack size in each core area, plus 31.3% lone wolves, suggested that maximum population size in optimal years prior to exploitation consisted of 58 wolves (1 wolf/1817km²; Table 4). During average years, the population likely consisted of about 38 wolves (1 wolf/2774 km²). These estimates indicated a low carrying capacity and a very low population density, supporting the finding of rarity suggested by kill data.

Statements by knowledgeable individuals constituted a third line of evidence, corroborating these findings of rarity. Zoologist A.L.V. Manniche, who overwintered in Germania Land in 1906–08, stated that the wolf was very rare (Manniche, 1910). Zoologist A. Pedersen, who spent five years in wolf range, noted that the wolf was the least abundant terrestrial mammal (Pedersen, 1934). Director J.G. Jennov spent 1929–31 in wolf range, but saw a wolf only twice (Jennov, 1945). Hunter H. Devold overwintered in wolf range in 1926–28 and 1929–32 and reported that wolves were rare (Devold, 1941).

Distribution

Sighting data indicated that this population was distributed in up to six core areas, in part separated by large areas, where wolves were sighted so rarely that these areas effectively constituted gaps in distribution. Overall distribution appeared insular and disjunct except in the central part of the range: Wollaston Forland, Hold with Hope, and areas in between. At 28 kills, this region accounted for 69.6% of the harvest, suggesting that this population was concentrated within 14.3% (15 023 km²) of its range (Fig. 1).

Population Decline due to Excessive Harvest

The linear regression model using the T5 trajectory (Fig. 3) indicated that the population decreased at an average rate of 4.98 wolves per year between 1926 and 1932, including a presumed undetected kill of 50%. Annual harvest rate based on a population size of 38 wolves was 13.1% (Table 4). The logistic model returned an MSY of 3.3 wolves, suggesting that harvest exceeded MSY. ANCOVA indicated that rates of decline differed significantly among areas ($F = 2.86$, $p = 0.03$, $df = 5$). Local population collapses occurred in five of six core areas relatively quickly after arrival of the first commercial hunters, but statistically significant declines were detectable only in Jameson Land, Hold with Hope, and Hochstetter Forland (Fig. 2).

Despite increasing effort in the 1920–30s, harvest success declined from one wolf per hunter in 1926 to 0.06 wolf per hunter in 1932, showing that the decline was real (as opposed to effort-related). Wolves in Hold with Hope were hit the hardest: they were wiped out by Norwegian hunters in only two years, from 1926 to 1928. The killing of eight wolves from a pack of 10 in 1930 left the population severely depleted, which explains both the absence

TABLE 1. Sources in archives in Denmark and Norway with subject matter¹ relevant to the present study and consulted by the author.

Archive	Sources available	Sources consulted	Percent of sources consulted
Arctic Institute, Copenhagen	46	45	99%
National Archives (re. Scoresby Sound), Copenhagen	1 ²	1	100%
Royal Library (Håndskriftsamling), Copenhagen	1	1	100%
Mogens Graae Collection	16	16	100%
Peter Schmidt Mikkelsen Collection	5	5	100%
Arne Philbert Collection	1	1	100%
National Archives, Oslo	5	5	100%
Norwegian Polar Institute, Tromsø	57	57	100%
National Archives, Tromsø	5	5	100%
Total	137	136	99.3%

¹ Hunters, wolves, Nanok, Arktisk Næringsdrift, Østgrønlandsk Kompagni, Scoresby Sound.

² One collection consisting of multiple documents.

TABLE 2. Number of effort-years by decade, known surviving diaries (journals), and effort by the author.

Decade	Effort-years ¹	Known surviving diaries	Diaries consulted	% of diaries consulted
Fall 1900–Summer 1910	22	18	18	100%
Fall 1910–Summer 1920	14	4	4	100%
Fall 1920–Summer 1930	126	27	27	100%
Fall 1930–Summer 1940	271.5	74	73	99%
Total	433.5	123²	122	99%

¹ One hunter spending one winter in East Greenland. Data compiled from Mikkelsen (1994).

² Not equal to number of effort-years because some diaries covered multiple years.

TABLE 3. Method of take during harvest of 46 wolves in East Greenland, 1899–1932.

Nationality	Method of take				Subtotal
	Shooting	Leg-hold trap	Strychnine	Unknown	
Norwegians	10	7	13	1	31
Danes	8	6	0	0	14
Swedes	1	0	0	0	1
Subtotal	19	13	13	1	Total: 46

TABLE 4. Estimates of minimum, midrange, and maximum population sizes of the arctic wolf in East Greenland based upon 60 year-round sightings of wolf packs in six core areas, 1899–1939.

Area	Minimum pack size	Midrange pack size	Maximum pack size	Sightings
Jameson Land	2	3	4	13
Ymer Island	2	8	12	7
Hold with Hope	2	6.5	11 ¹	15
Wollaston Forland	2	6	10	8
Hochstetter Forland	2	3	4	10
Germania Land	2	2.5	3	7
Subtotal:	12	29	44	
No. of lone wolves assumed at 31.3% ²	4	9	14	
Population estimates ³ :	Minimum: 16	Midrange: 38	Maximum: 58	

¹ Conservative. 10–12 wolves were reported seen on one occasion (Devold 1940, 1941).

² Thirty-five lone wolves were reported in sightings totaling 112 wolves or their sign, October–December, 1907–39.

³ Assumed that no core area packs went undetected during the 40 years and that each of the six areas was inhabited by a separate pack.

of reported kills after November 1932 and the subsequent decrease in reported sightings. To the north, Danish hunters tried to eliminate wolves from Hochstetter Forland, but

they were unsuccessful, and tracks of four wolves were reported as late as 1937 (Marquard-Petersen, 2007). To the south, in Jameson Land, few hunters were present, and

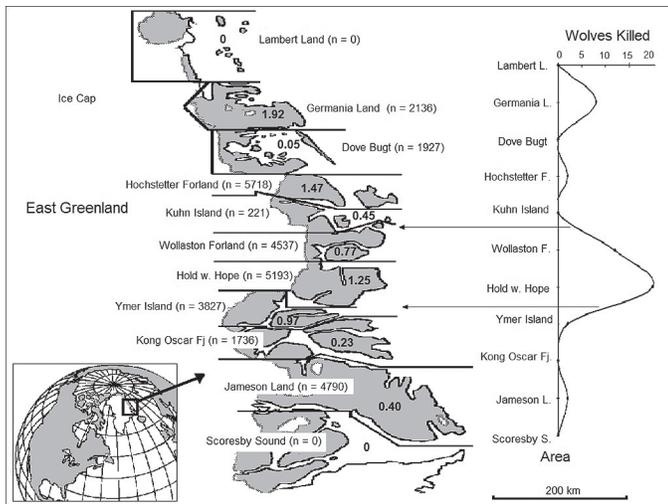


FIG. 1. Map of wolf range in East Greenland, showing areas described in the text. The number of diary-days (n = diary-days), the number of sightings of wolves or their tracks per 100 diary-days (bold figures), and the number of wolves killed during 1899–1932 (line graph to right) are shown for each area. The bold figures also serve as an index of the amount of human activity in each area as documented in the historical record; an index of 0 means the area held little potential for commercial furbearer harvest. Scoresby Sound was the southern range boundary of wolves in East Greenland.

tracks were also reported until 1937. These last remaining wolves appear to have vanished by late 1939.

The 12 regression scenarios produced strong downward trajectories (Fig. 3). Three were especially interesting. Starting from a maximum population size of 58 wolves, and using an estimate of actual kill plus an additional unreported harvest of 50% due to underreported poison kills, trajectory T4 produced a residual population of 29 wolves by 1932, which is clearly at odds with the few sightings of wolves or their tracks from 1933 to 1939. Using a minimum population size of 16 wolves produced population extinction by 1931 in all trajectories, which is also at odds with known facts. A mid-range population size of 38 wolves, using known kill plus an additional harvest of 50% unreported poison kill, produced a population trend (T5) most in line with available evidence, bringing the population to eight wolves by 1931, near the probable 10–12 remaining wolves by 1932.

Alternative Causes of Population Decline

There was no evidence that the muskox population was declining as a result of detrimental weather events. To the contrary, several authors stated that the population was increasing during the 1920s and 1930s (Bang, 1944; Jennov, 1945; Vibe, 1967). From 1928 to 1933, conditions were favorable for muskox productivity (Pedersen, 1934). In 1929–31, one-third of the population reportedly consisted of yearlings and two-year-olds (Jennov, 1933; Pedersen, 1936). The population reached a maximum during 1928–30 (Pedersen, 1940). By 1933, it was guessed to be greater than 10 000 (Jennov, 1933; Pedersen, 1934). Other prey species, such as arctic hare, were probably not important, year-round prey to this wolf population (Marquard-Petersen, 2007).

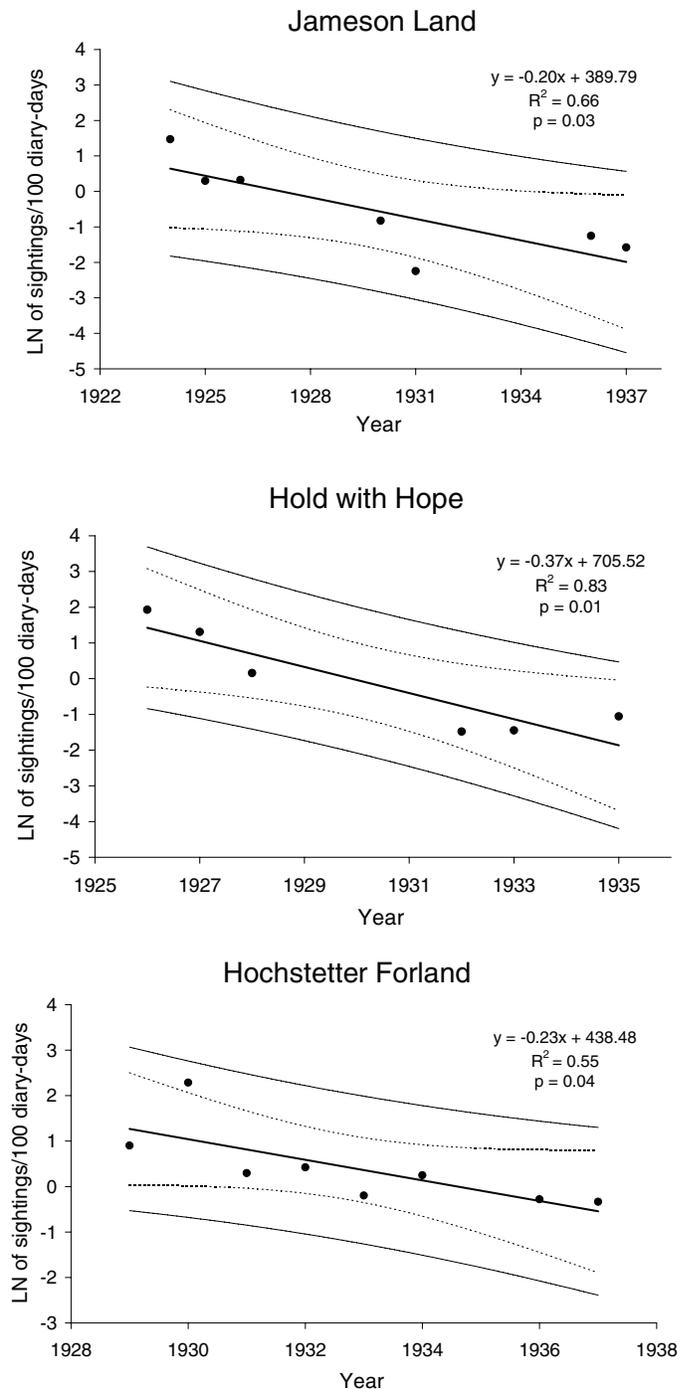


FIG. 2. Regression models of the population decline in three core areas of the arctic wolf in East Greenland. Models are based upon \log_e of sightings of wolves during 1922–38.

There were no reports that 1) wolves had been so numerous that they could have reduced this prey population, 2) killed wolves showed signs of disease, 3) deformities or other symptoms associated with inbreeding were present, 4) high levels of toxins were present or suspected in the environment, 5) a decline in habitat quality had occurred on a scale that could have exterminated a small wolf population, or 6) wolf reproduction had occurred.

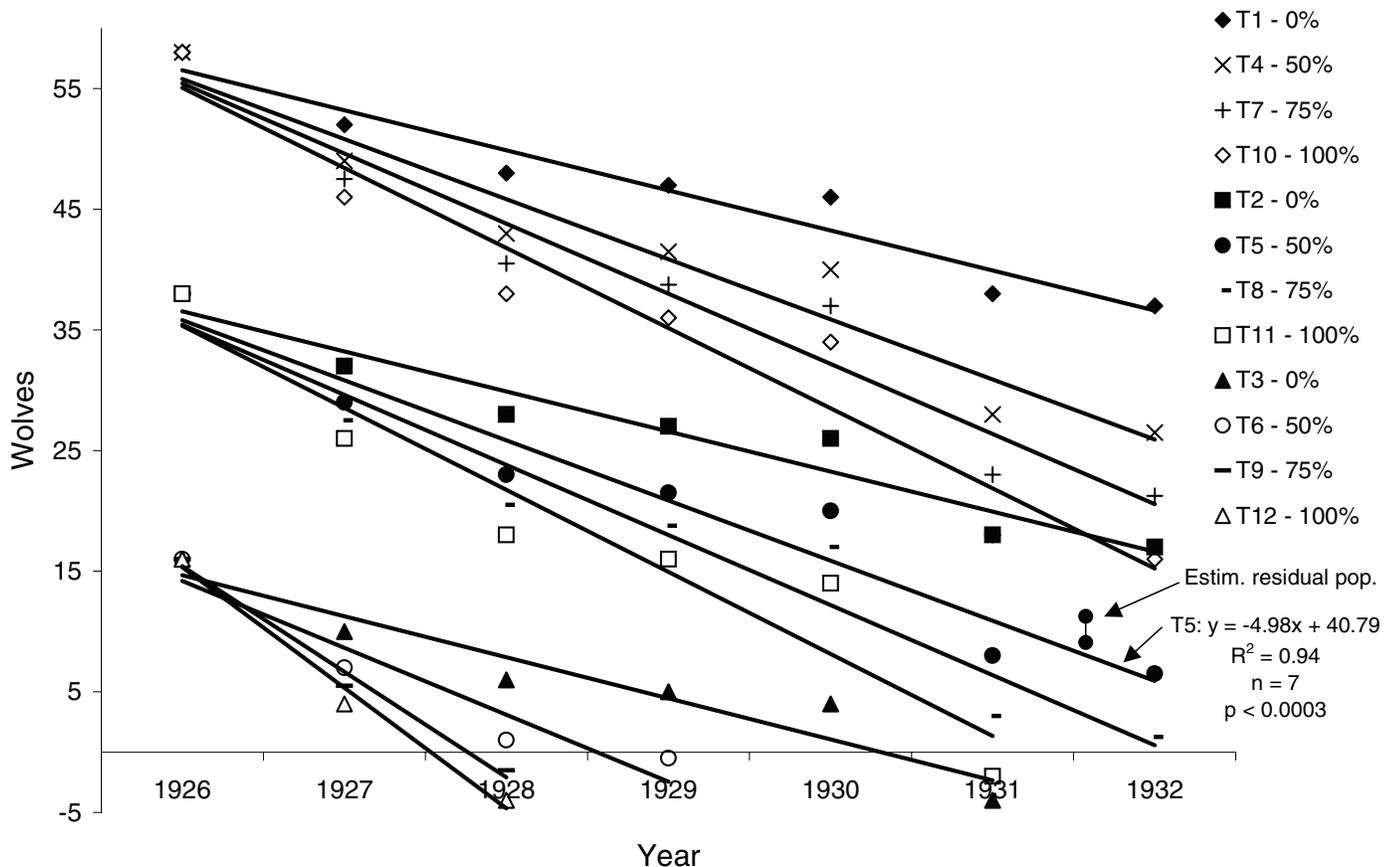


FIG. 3. Estimated East Greenland wolf population trajectories based upon minimum, midrange, and maximum population sizes and reported harvest plus 0%, 50%, 75%, and 100% undetected kill due to poison use, 1926–32.

DISCUSSION

Abundance

The number of wolves observed was an estimate of actual population size, which was unknown. The finding that wolf abundance was exceptionally low was of particular interest because recent work on the contemporary wolf population in East Greenland produced a population estimate of 23 wolves in the same area considered in the historical record (Marquard-Petersen, 2009). Thus, a total of 60 years of data provide a high degree of certainty that the arctic wolf was exceedingly rare on the eastern limit of its distribution during the 20th century. This finding has implications for the assessment of potential impacts on wolves in Greenland from resource development or climate change.

Local declines without subsequent reestablishment of new packs suggest that wolf density in surrounding areas was too low to enable the population to rebound. East Greenland was not recolonized until 1979 (Marquard-Petersen, 2011b). This 40-year delay in reestablishment contrasted with results of studies in lower latitudes, where wolves may quickly reoccupy vacant territories after a decline (Ballard et al., 1987, 1997; Mech et al., 1998).

There were no comparable data on historical abundance of wolves in the Canadian High Arctic. One indicator of the rarity of the wolf in East Greenland relative to Canada may be gleaned from harvest records at the Eureka weather station on Ellesmere Island. There, a crew of six, perhaps supplemented by seasonal personnel, shot 43 wolves in four years (1947–51; Tener, 1952), which is equal to 24 man-years, without exterminating the population. Harvest records from East Greenland indicated that killing 43 wolves took 14 years between 1906 and 1932 by 221 or more overwintering hunters, which is equal to 3094 man-years, and by then the population was depleted. This difference in abundance would also suggest that the concerns of these two populations were different.

Social Organization

Pairs and lone wolves were the most common form of sightings, and packs of more than two wolves were rare. Mean early winter pack size was low relative to wolf populations in lower latitudes, where average pack size ranges between 5.7 and 10.2 wolves, depending upon prey species (Fuller et al., 2003). In the contemporary, largely unexploited Greenland wolf population, mean pack size was

2.6 wolves (Marquard-Petersen, 2009). Packs of more than four wolves in the historical population constituted 5.0% of sightings; in the contemporary population, this index was 3.8% (Marquard-Petersen, 2009). Whereas there was general agreement between these indices, the likely causes for the small pack sizes were different. Pack size depends upon pup production, recruitment, dispersal, and survival (Mech et al., 1998). In heavily exploited wolf populations, pack size is either small or declining (Ballard et al., 1981; Peterson et al., 1984) because hunters rarely kill all wolves in a pack (Rausch, 1967). In contrast, small average pack sizes of contemporary wolves are likely the consequence of low availability and vulnerability of muskoxen (Marquard-Petersen, 2009). Nevertheless, 60 years of data provide compelling evidence that average pack sizes have been low, around three wolves per pack, and that large packs were exceptionally rare.

The percentage of loners was probably biased high because the population was heavily exploited. Pairs were common, and the killing of one wolf in a pair would cause an artificial inflation of the number of solitary wolves. My data appeared to confirm this pattern: between 1899 and 1929, 46% of early winter sightings were of lone wolves, but this proportion increased to 61.7% when data through 1939 were included. This increase likely took place because packs were partly eliminated through hunting and poisoning, fragmenting social organization. Lone wolves comprised 31.3% of the 1899–1939 population and 27.7% of the 1978–1998 population (Marquard-Petersen, 2009). These figures provide long-term evidence of the high frequency of singletons.

Distribution

Most of the population occurred in a few favorable habitats, which were separated by large tracts where wolves appeared to be rare or absent. Both kill and sighting data supported this conclusion. A similar finding of non-uniform distribution was made for the contemporary population in the same area (Marquard-Petersen, 2011a). In the Canadian High Arctic, wolves are rare or absent in large areas, likely because of the limited and clumped distribution of muskoxen (Miller, 1993). This disjunct and insular distribution contrasts with wolf distribution in temperate areas, where territories may abut one another over large areas in an approximately uniform distribution (e.g., Mech et al., 1998; Peterson et al., 1998; Adams et al., 2008).

POSSIBLE CAUSES OF THE POPULATION DECLINE

Excessive Harvest

An annual harvest rate of 13.1% and an MSY of 3.3 wolves (8.7% of the midrange population estimate) were unusually low for any wolf population. Yet the decline of the population to extinction is clear evidence that harvest, in

combination with natural mortality (an unknown), exceeded MSY. The regression results indicated that the population was doomed after the introduction of strychnine in 1926—and perhaps earlier, given the harvest pressure of the early 1920s. I chose the T5 trajectory as the most representative model because it was the regression line closest to the estimated 10–12 wolves remaining by 1932. Undetected kill results in underreporting of harvest, which is more likely to result in unsustainable harvest rates.

Strychnine was the primary agent of destruction because at least 70.6% of kills during the last six years of harvest involved strychnine and large numbers of poison baits were distributed. Not all Norwegian hunters used poison, but it is probable that hundreds of baits were distributed annually, because an average of 13 Norwegian hunters overwintered during 1926–40 (from Mikkelsen, 1994). Greenland wolves were susceptible to strychnine; in one case, eight wolves of a pack of 10 were reportedly poisoned in a single event (Giæver, 1930). Norwegians recognized this vulnerability and began curtailing strychnine use. The fur trading company “Arktisk Næringsdrift” prohibited poison use by 1933 (Giæver, 1939), and the Norwegian government discouraged its use in 1934; however, these restrictions came too late for the wolves. A viable population ceased to exist in East Greenland in 1930 after elimination of wolves in their central core areas. This local extermination bifurcated the population, separating the remaining wolves by hundreds of kilometers, which made it difficult for survivors to find mates (Marquard-Petersen, 2007). The residual population disappeared during the next nine years.

Strychnine was used against wolves in the High Arctic as early as 1881 (Lanman, 1885; Greely, 1886) and was used widely elsewhere to control or extirpate wolf populations (Cluff and Murray, 1995). Poison is highly effective because a small number of baits can kill entire packs; in Wood Buffalo National Park, Alberta, about 70% of the wolf population was killed by poison in a single winter (Fuller and Novakowski, 1955). On barren-ground caribou range in Canada, 28 baits produced 67 dead wolves (Kelsall, 1968).

Danish hunters did not use poison and deplored its use (Drastrup, 1932; Oldendow, 1935; Munksgaard, 1938). Instead, they killed as many wolves as possible by using rifles and leg-hold traps. Both methods were less effective than strychnine, but for different reasons. Leg-hold traps were too small, allowing wolves to break free (Poulsen, 1991), or too weak, or ineffective because wolves were cautious and often avoided stepping in traps (Manniche, 1909). In contrast, rifles were effective, but wolves could be shy and difficult to get within rifle range of (Manniche, 1910). Furthermore, during the polar night of winter, limited visibility caused numerous hunters to miss their target (e.g., Devold, 1941). In contrast, strychnine was highly lethal and ready to kill night and day.

Two additional factors enabled Norwegian hunters to excel at killing wolves: numerical superiority and geographical location. Norwegians outnumbered Danish hunters by about 4:1 during the years of most intense harvest

from 1926–30 (45 Norwegians vs. 11–12 Danes; from Mikkelsen, 1994). Geographical location was important, because Norwegians maintained a strong presence in the Hold with Hope area, accounting for 43.5% of the total wolf harvest. Danes had no personnel there from 1924 to 1929, and wolves had been locally extirpated by the time Danes returned in 1930.

Habitat Quality

There was no evidence that lack of prey caused the decline or that extinction of caribou was influential. To the contrary, this wolf population survived for 40 years after the demise of the caribou (originally noted by Dawes et al., 1986). The largest packs documented in Greenland were reported during the 1920s (Marquard-Petersen, 2007), more than 20 years after the caribou disappeared. Furthermore, the contemporary wolf population has thrived since 1979 without the benefit of caribou as alternative prey. Smaller prey may be seasonally important (Mech, 2005), but muskox likely constituted the primary prey, because 1) exhaustive studies of wolf food habits in North America have shown that wolves must have access to ungulate prey to secure long-term viability, 2) no other ungulate was available, and 3) muskox is the primary prey of contemporary wolves (Marquard-Petersen, 1998). Published accounts indicated that the muskox population was expanding in the 1920s to early 1930s, when the wolf population was declining precipitously. This expansion resulted in many calves vulnerable to wolf predation. Thus, wolves disappeared from East Greenland during a period characterized by high prey availability/vulnerability.

Anthropogenic sources of habitat destruction, including road construction and human encroachment, were absent, and there were no indications that other factors adversely affected habitat quality. Furthermore, wolves appear to be more tolerant of human disturbance than previously thought (Thiel et al., 1998; Frame et al., 2007).

Disease

Disease has the potential to cause high wolf mortality (see Brand et al., 1995 for a review). Three diseases receive particular attention. Canine parvovirus may pose a considerable threat to wolf populations (Mech et al., 2008), but since it was not reported until 1977 (Mech and Goyal, 1993), it is an unlikely candidate for impacting the East Greenland wolf population. Canine distemper was reported in 1904 (Budd, 1981), but was not considered an important source of mortality in wolves (Brand et al., 1995). Rabies can be locally devastating to wolf packs, but at low densities packs are unlikely to infect each other (Chapman, 1978). Other diseases could have been implicated, but no kills were reported to show signs of disease, and no natural mortalities were reported. Because of the low wolf density, epizootic events likely were rare. There were no records of debilitating parasitic infestation. The parasitic fauna of

the contemporary population was depauperate (Marquard-Petersen, 1997).

Inbreeding Depression

Effects from inbreeding depression in free-ranging wolves may include a correlation between survival of pups during their first winter and inbreeding coefficients (Liberg et al., 2005), lesions (Räikkönen et al., 2006), low litter and pack sizes (Fredrickson et al., 2007), and congenital bone deformities (Räikkönen et al., 2009). Nevertheless, some species endure for decades with one to five breeding pairs, even in populations founded by a single pair (Caughley and Gunn, 1996). The fossil record suggests that small canid populations have remained viable for thousands of years in spite of low genetic diversity (Wayne, 1996). In Sweden, a severely inbred wolf population was rescued by a single immigrant (Vilà et al., 2003). These findings argue against the possibility that inbreeding was an important factor in the decline.

Decreased Wolf Reproduction

Breeding impairment has rarely been found to be involved in population declines of terrestrial mammals. But in this case, the potential contribution of decreased reproduction was uncertain because information on pup production was lacking. This absence of evidence was noteworthy given that hunters distributed across the wolf range spent 433.5 effort-years in the area between 1906 and 1940, totaling 158 228 man-days. The fact that not a single wolf pup or active den was reported suggests that fecundity rates were low.

Perhaps inbreeding depression was implicated in this apparently low reproduction, since reproductive success in wolves is negatively affected by incest, particularly in small and isolated populations (Asa et al., 2007; Fredrickson et al., 2007; Rabon and Waddell, 2010). The East Greenland wolf population was small, but whether it was demographically isolated from the nearest source population (North Greenland) is unclear. The contemporary wolf population in East Greenland inhabits the same area as the historical population and appears to be geographically and demographically isolated (Marquard-Petersen, 2011b). Nevertheless, a possible link between incest and low reproduction in the historical population remains unsubstantiated speculation. It is noteworthy that the contemporary wolf population has the lowest mean litter size recorded for wolves in North America through observations of pups in summer (Marquard-Petersen, 2008).

Reproduction in wolves may also be negatively impacted by disease, but this link is not well documented (cf. Brand et al., 1995). It would have been difficult for hunters to gather evidence that disease, incest, or both were impacting wolf reproduction, given the apparent absence of pups and active dens.

Factor Interaction

On Isle Royale, a declining wolf population was likely affected by multiple factors simultaneously (Peterson et al., 1998). These researchers had access to data from population surveys conducted annually. Data of similar quality were not available from Greenland for my study, making it difficult to analyze possible factor interaction. More than one of the earlier mentioned factors may have affected this wolf population, adding to the impact of harvest. Low reproduction seems a prime candidate.

CONCLUSION

Some uncertainties exist regarding the potential lack of mention of all possible causes in the historical records. Nevertheless, some facts are undisputed. The wolf population in East Greenland had not been harvested by Europeans prior to 1899. Once harvest began, no effort was made to stimulate population growth, partly because principles of sustainable harvest were poorly understood, but primarily because the goal was to maximize profits by killing as many arctic foxes (*Alopex lagopus*) as possible. Wolves were of less economic importance because of their low abundance, but they interfered with commercial hunting by destroying foxes in traps. Prior to 1920, harvest was important in reducing the wolf population only in Germania Land (Marquard-Petersen, 2007), and most wolf range was likely unaffected by this distant harvest, 325 km to the north of the distributional center. Then between 1920 and 1932, over 10 effort-years, 35 wolves were killed in core wolf range, and the population declined precipitously. Actual harvest was probably higher than reported because of undetected kills associated with poison use. In five of six distributional core areas, local population collapses occurred relatively quickly after the arrival of the first commercial hunters. Thus, excessive harvest was the simplest explanation consistent with the facts. There was no evidence that other potential causes were responsible for, or contributed to, the demise of this population.

The finding that packs were quickly wiped out in the treeless environment added perspective on the contemporary wolf population in the Canadian High Arctic by demonstrating the potential consequences of inadequate protection as human access increases. A report by Miller (1993) that 85% of the wolves seen by hunters on Melville Island had been killed raises questions about whether adequate protection is in place. In lower latitudes, wolf populations appear largely unaffected by annual harvest rates of 29% or higher (Fuller, 1989; Adams et al., 2008). It is questionable whether wolf populations in the High Arctic can withstand similar mortality levels because of a number of depressed variables. First, smaller pack sizes (Marquard-Petersen, 2007) tend to reduce recruitment (Adams et al., 2008). Second, wolf densities are exceptionally low (Riewe, 1975; Miller, 1993; Marquard-Petersen, 2009). Both of

these factors increase the risk of local extinctions from deleterious events. Third, low pup production and infrequent reproduction (Mech, 1995, 2005; Marquard-Petersen, 2008) make it more difficult for packs to replace harvested wolves. And finally, a non-uniform distribution (Miller, 1993; Miller and Reintjes, 1995; Marquard-Petersen, 2011a) may slow recolonization of vacant areas if nearby packs are absent in the impoverished polar desert or semidesert.

ACKNOWLEDGEMENTS

Frank L. Miller with the Canadian Wildlife Service, Claudio Sillero-Zubiri, University of Oxford, U.K., Mads Forchhammer of the National Environmental Research Institute and Torben Dabelsteen of the University of Copenhagen, Denmark, and three anonymous reviewers provided thoughtful comments on earlier versions of the manuscript. In Denmark, Mogens Graae, Peter Schmidt Mikkelsen, and Bent Philbert graciously gave me access to their private collections of hunters' diaries. In Norway, Fred Inge Presteng, Norwegian Polar Institute, and Tor L. Larsen, Norwegian National Archives, were instrumental in my gaining access to original diaries. Elsebeth Thomsen, University of Tromsø, helped me acquire copies of yearbooks published by the Balsfjord Historical Association. I gratefully acknowledge their contributions to this research.

REFERENCES

- Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T., and Demma, D.J. 2008. Population dynamics and harvest characteristics of wolves in the central Brook Range, Alaska. *Wildlife Monographs* 170. 25 p.
- Asa, C., Miller, P., Agnew, M., Rebolledo, J.A.R., Lindsey, S.L., Callahan, M., and Bauman, K. 2007. Relationship of inbreeding with sperm quality and reproductive success in Mexican gray wolves. *Animal Conservation* 10(3):326–331.
- Ballard, W.B., Stephenson, R.O., and Spraker, T.H. 1981. Nelchina basin wolf studies. Final report. Federal Aid in Wildlife Restoration, Projects W-17-8 thru 11, Jobs 14.8R thru .10R. Juneau, Alaska: Alaska Department of Fish and Game.
- Ballard, W.B., Whitman, J.S., and Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs* 98. 54 p.
- Ballard, W.B., Ayres, L.A., Krausman, P.R., Reed, D.J., and Fancy, S.G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs* 135. 47 p.
- Bang, O. 1944. Blant fangstfolk og bikkjer i Eirik Raudes Land [Among trappers and sled dogs in Eirik Raude's Land]. Kamban Forlag.
- Barber, D.G., Lukovich, J.V., Keogak, J., Baryluk, S., Fortier, L., and Henry, G.H.R. 2008. The changing climate of the Arctic. *Arctic* 61(Suppl. 1):7–26.
- Brand, C.J., Pybus, M.J., Ballard, W.B., and Peterson, R.O. 1995. Infectious and parasitic diseases of the gray wolf and their potential effects on wolf populations in North America.

- In: Carbyn, L.N., Fritts, S.H., and Seip, D.R., eds. Ecology and conservation of wolves in a changing world. Occasional Publication Series 35. Edmonton, Alberta: Canadian Circumpolar Institute. 419–429.
- Budd, J. 1981. Distemper. In: Davis, J.W., Karstad, L.H., and Trainer, D.O., eds. Infectious diseases of wild mammals. Ames: Iowa State University Press. 31–44.
- Caughley, G. 1977. Analysis of vertebrate populations. New York: John Wiley & Sons.
- Caughley, G., and Gunn, A. 1996. Conservation biology in theory and practice. Cambridge, Massachusetts: Blackwell Science.
- Chapman, R.C. 1978. Rabies: Decimation of a wolf pack in Arctic Alaska. *Science* 201(4353):365–367.
- Cluff, H.D., and Murray, D.L. 1995. Review of wolf control methods in North America. In: Carbyn, L.N., Fritts, S.H., and Seip, D.R., eds. Ecology and conservation of wolves in a changing world. Occasional Publication Series 35. Edmonton, Alberta: Canadian Circumpolar Institute. 491–504.
- Dawes, P.R., Elander, M., and Ericson, M. 1986. The wolf (*Canis lupus*) in Greenland: A historical review and present status. *Arctic* 39(2):119–132.
- Devold, H. 1940. Polarliv [Life in the Arctic]. Oslo: Gyldendal Norsk Forlag.
- . 1941. Polarulven på Nordøstgrønland [The arctic wolf in Northeast Greenland]. *Norges Jeger- og Fiskerforbunds Tidsskrift* 70:137–144.
- Drastrup, E. 1932. Blandt danske og norske fangstmænd i Nordøstgrønland [Among Danish and Norwegian trappers in Northeast Greenland]. Copenhagen: Nordisk Forlag.
- Frame, P.F., Cluff, H.D., and Hik, D.S. 2007. Response of wolves to experimental disturbance at homesites. *Journal of Wildlife Management* 71(2):316–320.
- Fredrickson, R.J., Siminski, P., Woolf, M., and Hedrick, P.W. 2007. Genetic rescue and inbreeding depression in Mexican wolves. *Proceedings of the Royal Society B* 274:2365–2371.
- Freuchen, P., and Salomonsen, F. 1958. The Arctic year. New York: G.P. Putnam's Sons.
- Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105. 41 p.
- Fuller, T.K., Mech, L.D., and Cochrane, J.F. 2003. Wolf population dynamics. In: Mech, L.D., and Boitani, L., eds. *Wolves: Behavior, ecology, and conservation*. Chicago: University of Chicago Press. 161–191.
- Fuller, W.A., and Novakowski, N.S. 1955. Wolf control operations, Wood Buffalo National Park, 1951–52. *Wildlife Management Bulletin Series* 1, No. 11. Ottawa: Canadian Wildlife Service.
- Giæver, J. 1930. Fangsthytterne. Jegerliv på Østgrønland [In the land of the musk-ox: Tales of wildlife in Northeast Greenland]. Oslo: Gyldendal Norsk Forlag.
- . 1939. Den norske fangstvirksomheten på Østgrønland [Norwegian trapping activities in East Greenland]. In: *Dansk og Norsk fangstvirksomhed paa Østgrønland*. Publikationer om Østgrønland No. 8. Copenhagen: Poul Petri's bogtrykkeri.
- Greely, A.W. 1886. Three years of Arctic service. New York: Charles Scribner's Sons.
- Hansen, K. 1979. Ulve ved Danmarkshavn [Wolves at Danmarkshavn]. *Tidsskriftet Grønland* 8:252.
- Jennov, J.G. 1933. Der Moschusochse in Ost-Grønland [Muskox in East Greenland]. *Zeitschrift für Säugetierkunde* 8(1-2):40–46.
- . 1945. Moskusoksebestanden i Nordøstgrønland og nogle spredte iagttagelser og betragtninger vedrørende dyrelivet i Nordøstgrønland [The muskox population in Northeast Greenland and various observations and opinions regarding the wildlife of Northeast Greenland]. Copenhagen: Østgrønlandsk Fangstkompani Nanok A/S.
- Kelsall, J.P. 1968. The migratory barren-ground caribou of Canada. *Canadian Wildlife Service Monograph* 3. Ottawa: Queens Printer.
- Kolthoff, G. 1901. Till Spetsbergen och Nordöstra Grönland år 1900 [To Spitsbergen and Northeast Greenland in the year 1900]. Stockholm: Fr. Skoglund's Förlag.
- Krebs, C.J. 1999. *Ecological methodology*, 2nd ed. New York: Addison Wesley Longman.
- Lanman, C. 1885. Farthest north: Or, the life and explorations of Lieut. James Booth Lockwood, of the Greely Arctic expedition. New York: D. Appleton and Company.
- Liberg, O., Andrén, H., Pedersen, H.-C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M., and Bensch, S. 2005. Severe inbreeding depression in a wild wolf *Canis lupus* population. *Biology Letters* 1(1):17–20.
- Manniche, A.L.V. 1909. Midnatssol og mørketid: Stemninger og hændelser paa Danmark-ekspeditionen [Midnight sun and polar darkness: Moods and events on the Denmark Expedition]. Copenhagen: Forlaget af 1907.
- . 1910. The terrestrial mammals and birds of North-East Greenland - Biological observations. *Meddelelser om Grønland* 45(1). 199 p.
- Marquard-Petersen, U. 1997. Endoparasites of arctic wolves in Greenland. *Arctic* 50(4):349–354.
- . 1998. Food habits of arctic wolves in Greenland. *Journal of Mammalogy* 79(1):236–244.
- . 2007. Ecology of the High Arctic wolf in northeast Greenland, 1899–1998. PhD thesis, University of Copenhagen, Denmark.
- . 2008. Reproduction and mortality of the High Arctic wolf (*Canis lupus arctos*) in northeast Greenland, 1978–1998. *Canadian Field-Naturalist* 122(2):142–152.
- . 2009. Abundance, social organization, and population trend of the arctic wolf in North and East Greenland during 1978–1998. *Canadian Journal of Zoology* 87(10):895–901.
- . 2011a. Insular and disjunct distribution of the arctic wolf in Greenland, 1978–1998. *Polar Biology* 34(10):1447–1454.
- . 2011b. Invasion of eastern Greenland by the High Arctic wolf. *Wildlife Biology* 17(4):383–388.
- Mech, L.D. 1995. A ten-year history of the demography and productivity of an arctic wolf pack. *Arctic* 48(4):329–332.
- . 2005. Decline and recovery of a High Arctic wolf-prey system. *Arctic* 58(3):305–307.
- Mech, L.D., and Goyal, S.M. 1993. Canine parvovirus effect on wolf population change and pup survival. *Journal of Wildlife Diseases* 29(2):330–333.
- Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., and Dale, B.W. 1998. *The wolves of Denali*. Minneapolis: University of Minnesota Press.

- Mech, L.D., Goyal, S.M., Paul, W.J., and Newton, W.E. 2008. Demographic effects of canine parvovirus on a free-ranging wolf population over 30 years. *Journal of Wildlife Diseases* 44(4):824–836.
- Mikkelsen, P.S. 1994. Nordøstgrønland 1908–60; fangsmandsperioden [Northeast Greenland 1908–60; the trapping period]. Copenhagen: Danish Polar Center.
- Miller, F.L. 1993. Status of wolves in the Canadian Arctic Archipelago. Technical Report Series 173. Edmonton, Alberta: Canadian Wildlife Service.
- . 1998. Status of Peary caribou and muskox populations within the Bathurst Island complex, south-central Queen Elizabeth Islands, Northwest Territories, July 1996. Technical Report Series 317. Edmonton, Alberta: Canadian Wildlife Service.
- Miller, F.L., and Reintjes, F.D. 1995. Wolf-sightings on the Canadian Arctic Islands. *Arctic* 48(4):313–323.
- Munksgaard, E. 1938. Fredning af dyrebestanden i Nordøstgrønland [Protection of wildlife in Northeast Greenland]. Copenhagen: Levin & Munksgaard.
- Nathorst, A.G. 1900. Två somrar i Norra Ishavet. Kong Karls Land, Spetsbergens Kringsegling, spanandende efter Andrée i nordöstra Grönland [Two summers in the Arctic Ocean. King Charles Land, circumnavigation of Spitsbergen, searching for Andrée in northeastern Greenland]. Stockholm: Beijers Bokförlagsaktiebolag.
- Oldendow, K. 1935. Naturfredning i Grønland [Nature conservation in Greenland]. Copenhagen: G.E.C. Gads Forlag.
- Pedersen, A. 1934. Polardyr [Arctic animals]. Copenhagen: Nordisk Forlag.
- . 1936. Der grönländische moschusochse [The Greenland muskox]. *Meddelelser om Grønland* 93(7).
- . 1940. Moskusoksen i Grønland og dens fremtid [The muskox in Greenland and its future]. *Det Grønlandske Selskabs Aarskrift* 1940:40–67.
- . 1942. *Canis lupus tundrarum* Miller (in German). *Meddelelser om Grønland* 128(2):20–21.
- Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88. 52 p.
- Peterson, R.O., Thomas, N.J., Thurber, J.M., Vucetich, J.A., and Waite, T.A. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79(3):828–841.
- Poulsen, C. 1991. Yngstemandens dagbøger fra Danmarks-ekspeditionen 1906–08 [Diaries of the youngest member of the Denmark Expedition 1906–08]. Copenhagen: Rhodos.
- Rabon, D.R., Jr., and Waddell, W. 2010. Effects of inbreeding on reproductive success, performance, litter size, and survival in captive red wolves (*Canis rufus*). *Zoo Biology* 29(1):36–49.
- Räikkönen, J., Bignert, A., Mortensen, P., and Fernholm, B. 2006. Congenital defects in a highly inbred wild wolf population (*Canis lupus*). *Mammalian Biology* 71(2):65–73.
- Räikkönen, J., Vucetich, J.A., Peterson, R.O., and Nelson, M.P. 2009. Congenital bone deformities and the inbred wolves (*Canis lupus*) of Isle Royale. *Biological Conservation* 142(5):1025–1031.
- Rausch, R.A. 1967. Some aspects of the population ecology of wolves, Alaska. *American Zoologist* 7(2):253–265.
- Riewe, R.R. 1975. The High Arctic wolf in the Jones Sound region of the Canadian High Arctic. *Arctic* 28(3):209–212.
- Sørensen, L.N. 1961. Henry Rudi, isbjørnkongen [Henry Rudi, the polar bear king]. Oslo: Gyldendal Norsk Forlag.
- Tener, J.S. 1952. A preliminary study of the muskoxen of Slidre Fiord District, Fosheim Peninsula, Ellesmere Island. MA thesis, University of British Columbia, Vancouver.
- Thiel, R.P., Merrill, S., and Mech, L.D. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. *Canadian Field-Naturalist* 112(2):340–342.
- Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. *Meddelelser om Grønland* 170(5).
- Vilå, C., Sundqvist, A.-K., Flagstad, Ø., Seddon, J., Bjørnerfeldt, S., Kojola, I., Casulli, A., Sand, H., Wabakken, P., and Ellegren, H. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Royal Society of London. Proceedings B* 270(1510):91–97.
- Wayne, R.K. 1996. Conservation genetics in the Canidae. In: Avise, J.C., and Hamrick, J.L., eds. *Conservation genetics: Case histories from nature*. New York: Chapman and Hall. 75–118.
- Young, S.P., and Goldman, E.A. 1944. *The wolves of North America*. New York: Dover Publications.