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Invasion of eastern Greenland by the high arctic wolf *Canis lupus* arctos

Ulf Marquard-Petersen

The high arctic wolf *Canis lupus arctos* was exterminated from eastern Greenland during the 1930s by commercial hunters and was considered absent for 40 years. In this study, I examined the recolonisation of east Greenland by wolves from north Greenland through an invasion that began in 1979. The invasion successfully led to the establishment of a new population, because a wolf pair arrived into the core historical wolf range followed by one or two wolves during the next four years. Weight of evidence suggested that the invaders arrived into east Greenland through unintentional, human-mediated jump dispersal. I present two cases of long-distance dispersals by lone wolves following military sled patrols in northern Greenland. Wolves had likely failed to establish a viable population in east Greenland for 40 years for the following reasons: 1) a low propagule pressure, 2) invasions were high risk, occurring through vast areas of the lowest, large ungulate prey biomass reported for wolves in North America, and 3) only singletons made it into eastern Greenland.

Key words: arctic wolf, Canis lupus arctos, dispersal, Greenland, high arctic, invasion, long-distance, recolonisation

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Successful, long-distance dispersal resulting in colonisation of vacant areas is rare and difficult to observe and study, but it is important in shaping the distribution of a species (Lomolino et al. 2006). There are few documented cases involving wolves *Canis lupus* despite their high dispersal potential. In southern Scandinavia, successful recolonisation of former wolf range likely involved a journey of up to 1,100 km (Linnell et al. 2005). Shorter dispersals, i.e. of < 350 km, have resulted in reappearance of wolves in the central Rocky Mountains, USA (Boyd & Pletscher 1999), in Wisconsin, USA (Mladenoff & Sickley 1998) and in the Alps (Breitenmoser 1998).

The arctic wolf *C. l. arctos* inhabits the Canadian Arctic Islands and northeastern Greenland, but little is known about the dispersal characteristics of wolves at this high latitude. In eastern Greenland, a small wolf population was hunted to extinction by 1939 (Marquard-Petersen in press). Wolves were considered absent for 40 years until 1979, when a wolf pair appeared in the area (Hansen 1979). By 1992, a small population was reestablished (Marquard-Petersen

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1995), recently estimated at 23 wolves in three packs separated by vast areas (Marquard-Petersen 2009, 2011). Thus, there is evidence of a successful invasion followed by reproduction and establishment. I use the term 'invasion' *sensu* Alpert (2006) to describe the appearance of an organism in a habitat in which it was previously absent with subsequent adverse effects on organisms already there.

Invasion events in the arctic have received little attention by ecologists, which is likely due to their rarity. The above-mentioned invasion more than doubled the occupied wolf range in Greenland, and at the same time, it represents a 15% increase in the global range of this subspecies (calculated based on Miller 1993, Marquard-Petersen 2007). Yet, the case has not been studied, nor have potential factors contributing to invasion success been evaluated. The 40-year absence of wolves from eastern Greenland contrasted findings at lower latitudes from which rapid repopulation of areas void of wolves has been reported (Fuller 1989, Potvin et al. 1992, Person & Russell 2007). Natural recolonisation of wolves

elsewhere has been hampered by predator control (Peterson & Woolington 1982, Flagstad et al. 2003). But in eastern Greenland, commercial hunting ceased in 1960 (Mikkelsen 1994) without causing wolves to reappear. In 1974, about 88% of the former wolf range became part of a new national park, in which wolves would have received year-round protection if they had been present. An abundant wolf food supply was available in the area: up to 20,000 muskoxen *Ovibos moschatus* (Vibe 1958). Therefore, the cause(s) of the 40-year absence of a wolf population must be sought elsewhere.

In this study, I gathered and analysed pertinent data surrounding the invasion of eastern Greenland to acquire insight into factors that might influence the ability of wolves in this part of the high arctic to disperse successfully, colonise new areas and to reproduce to overcome the small population size and the extreme isolation. Such knowledge seems important to the conservation of the small, isolated wolf population in eastern Greenland. The invasion is of general scientific significance, because it occurred in a little-studied ecosystem, and because factors that influence transport, establishment and spread of invasions in the Arctic are poorly documented. Paucity of data from this remote, largely uninhabited region, involving non-instrumented wolves, rendered speculative some aspects of a reconstruction of this invasion. However, known facts regarding appearance of the invaders, combined with research on wolf and invasion ecology elsewhere, provide insight into factors underlying the success of this invasion and why wolves failed to recolonise eastern Greenland for 40 years.

Material and methods

Details on the study region are given in Marquard-Petersen (2009). Two agencies maintained a permanent presence in eastern Greenland and became primary sources of information. The first one is a weather station named Danmarkshavn located in Germania Land (Fig. 1).

It took on a central role in the invasion due to the year-round human presence in an otherwise largely uninhabited region. Sled dogs Canis familiaris were tethered outside and were used for recreational travel. Garbage was burned at a nearby, open garbage dump. This disposal method was imperfect. Maagaard (1994) reported watching a wolf leaving the dump with an 80-cm long smoked saddle of pork, indicating that the dump acted as an easy food source. The second agency in the area is a Danish military unit which served as the police authority responsible for conducting patrols to maintain national sovereignty. Sled dog teams were used for winter transportation, averaging 14,876 km/year during 1978-1998, during which all sightings of wildlife were recorded (Marquard-Petersen 2007).

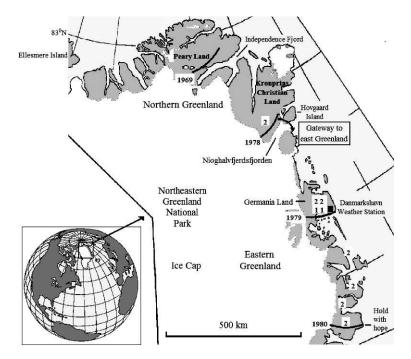


Figure 1. The study region showing place names mentioned in the text, wolves sighted and advance of the invasion front during 1978-1980. Note the geographically isolated gateway to eastern Greenland.

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I reconstructed the invasion by gathering firsthand information on the events. I travelled to eastern Greenland and visited Danmarkshavn to record information on wolf sightings from the weather station log book and from discussions with personnel. I visited Kronprins Christian Land in northern Greenland to evaluate wolf habitat quality by examining important variables, e.g. the availability of prey and suitable den sites. In Denmark, I received unprecedented access to military archives at Air Station Værløse, containing original reports by sled patrols. I recorded all travel routes during the years of 1978-1998 and contacted military personnel to ask follow-up questions. I then stratified northern and eastern Greenland into 21 areas, using a digitised map of Greenland published by the Danish National Survey and Cadastre on CD-ROM (NordicMap Version 1.0) to calculate distances travelled by wolves and military patrols. Finally, I conducted a literature search. The military reports used as sources and measurements of patrol effort are listed in Marquard-Petersen (2007).

Results

The invasion was first detected in northern Greenland in April 1978, when military patrols in southern Kronprins Christian Land encountered a pair of wolves; the first wolf sighting in eastern north Greenland since 1954 (Marquard-Petersen 2007). A year later, in April 1979, a wolf pair was photographed 363 km to the south at Danmarkshavn (Hansen 1979); the first wolf pair confirmed in eastern Greenland since 1939. These wolves came in from the north, following sled patrol tracks and continued southwards following the patrol (Maagaard 1988). Seven weeks later, in June 1979, a wolf pair was again observed at Danmarkshavn (Dawes et al. 1986). Thereafter, no wolves were reported at the weather station until February 1980 when a single

wolf was seen once (Maagaard 1988). During the remainder of 1980, patrols reported a wolf pair in various areas up to 358 km to the south of the weather station; one patrol stated that the pair consisted of a male and a female (Marquard-Petersen 2007). The method used for sex determination was not described in the report. The sled patrols had daily experience with the differences in urination posture of male and female sled dogs, and it is probable that they used this method for sex determination. These sightings suggested that at least three wolves were present in eastern Greenland. Then, for four years, no wolves were reported at Danmarkshavn until May 1984, when a single male came in from the north, again following patrol tracks (Maagaard 1994). After 1984, the possible immigration of wolves into this northern part of east Greenland became less defined, as the frequency of sightings increased with multiple sightings of single wolves during 1984-1985 and a pack of four wolves in 1986 (Maagaard 1988).

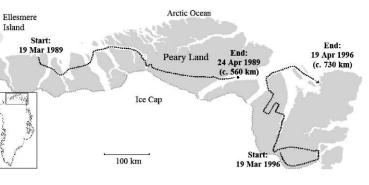
Military reports confirmed that it was not uncommon for single wolves or packs to follow teams of travelling sled dogs for periods of up to one month. During 1978-1998, 21 cases were reported of which 52.4% involved single wolves (Marquard-Petersen 2007). Two of these cases represented record-breaking 560 and 730 km lone-wolf-travelling-with-dog-sled dispersals in northern Greenland (Fig. 2). During all winters except 1991, sled dog teams from northern Greenland entered eastern Greenland via Hovgaard Island. Thus, dispersing wolves had almost yearly opportunities to follow patrols heading south. I considered this route the gateway to eastern Greenland.

Several models have been presented to explain the

mechanisms underlying invasions. The model of

steps and stages separates the invasion process into

Discussion



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Figure 2. Long-distance dispersals by two lone wolves following military sled patrols in northern Greenland in 1989 and 1996. discrete stages that the invader reaches by overcoming a number of sequential steps (Heger & Trepl 2003). This model is helpful in evaluating characteristics of the invading wolves (invasiveness traits) and their environment (invasibility traits).

Why did wolves fail to reestablish a viable population during 1939-1978?

The first step of the model represents immigration into a new area. At this stage, success of invasions is associated with propagule pressure (number of invaders and invasion attempts; Kolar & Lodge 2001, Colautti et al. 2006). In eastern Greenland, during December 1939 - April 1979, only an occasional single wolf, its tracks or a sighting of a large, white, elusive canid were reported (Marquard-Petersen 2007). The military began patrolling the region during World War II, and Danmarkshavn weather station was constructed in 1948-1949. Therefore, observer effort and the related probability of sighting wolves were probably not much different during 1939-1979 compared to the period after 1979. Such rarity of sightings, despite a 40-year period, provides evidence that the source population for this invasion was too small to produce an adequate number of dispersers that could meet, pair up and form new packs. Thus, the propagule pressure was low; a conclusion which was supported by recent findings that pack sizes, wolf densities and reproductive output in Greenland were the lowest reported for wolves in North America (Marquard-Petersen 2008, 2009). In Alaska, effective recolonisation of the Kenai Peninsula was believed to be hampered by low wolf numbers on the mainland (Peterson & Woolington 1982).

Some eastern Greenland invasibility traits likely contributed to this absence of invasion success. First, resource availability is critical to the ability of invaders to overcome low numbers and establish a viable population (Davis et al. 2000, Colautti et al. 2006). But, in the polar desert and semi-desert of northeastern Greenland, large ungulate prey biomass was the lowest facing wolves in North America (Marquard-Petersen 2009). Invaders were therefore at risk of higher mortality from malnutrition (cf. Messier 1985). Second, immigration rates decline with increasing distance from a source area (Lomolino et al. 2006). And, as distance increases, so does the probability that invaders do not arrive, because stochastic events may interfere with invasion success (Crawley 1989). For example, one of two founding wolves may be gored by a muskox (Savile & Oliver

1964), be killed by an avalanche (Mech et al. 1998) or fall through the ice and drown (Peterson et al. 1998). Long distances were a key characteristic of this invasion. Third, geographical factors preempted invasion into northern east Greenland through multiple loci. There was one dispersal corridor into eastern Greenland, hidden behind the 22 km wide Nioghalvfjerdsfjorden glacier at 79°N. Access to eastern Greenland therefore appeared restricted, and the wolf range to the south may constitute an island within Greenland with decreased rates of immigration similar to wolf range on the Kenai Peninsula, where the wolf population was considered nearly isolated (Peterson & Woolington 1982, Bailey et al. 1995). These factors indicated that stage 2 of the model of steps and stages (spontaneous establishment) failed to occur for 40 years, because the invasion process floundered in stage 1 (presence of an occasional dispersing wolf in east Greenland).

How many wolves invaded eastern Greenland?

Although it cannot be proven, the wolf pair that arrived at Danmarkshavn in 1979 likely was the same pair which was sighted the previous year in Kronprins Christian Land (Dawes et al. 1986). First, the wolf pair came in from the north (Maagaard 1988). Second, after a 40-year absence, it seemed unlikely that two pairs of dispersing wolves would occur in the area during the same 12-month period given the low population parameters mentioned earlier. Third, during the three years following the 1978 sightings in Kronprins Christian Land, no wolves were reported sighted by patrols in northern Greenland east of Independence Fjord despite yearly patrols, totalling 6,087 km, including 2,556 km in southern Kronprins Christian Land (Marquard-Petersen 2007), suggesting that the wolf pair had moved on or had died.

The 1980 and 1984 sightings both involved a single wolf but were separated by four years. These sightings may have represented the same animal, but if that were true, then this wolf must have spent four years in the region without being detected. This seems unlikely because it is well documented that arctic wolves are attracted by field camps, weather stations and their garbage dumps (Grace 1976, Miller 1978, Gray 1995, Miller & Reintjes 1995). Such an attraction frequently results in detection.

These sightings suggested that the invasion lasted at least five years (1979-1984) and consisted of two or three pulses, totalling three or four wolves. This scenario is a conjecture, but it is supported by the sighting record and the tendencies of arctic wolves to seek out people/facilities. A small north Greenland population of 32 wolves with low and infrequent reproduction (Marquard-Petersen 2008, 2009) further supports this conjecture by indicating low propagule pressure into eastern Greenland during most years.

Did military sled patrols inadvertently facilitate the invasion?

Human-mediated transport is the main vector for dispersal of many species (Alpert 2006). There were multiple lines of evidence that this vector was active in Greenland. First, it is well-established that teams of travelling sled dogs in northern Canada and Greenland may elicit a response in arctic wolves; > 300 km has been reported (Freuchen 1919, Vibe 1948, Miller 1993). Second, the 21 cases of wolves following sled patrols in northern and eastern Greenland noted earlier. Third, the invading wolves of 1979 came in from the north, following tracks left by a military sled patrol (Maagaard 1988). The 1984 invader also followed a patrol coming in from the north (Maagaard 1994). Therefore, military patrols may inadvertently have played a key role in the invasion of eastern Greenland. The 560 km dispersal in northern Greenland added a geographical dimension, providing evidence of a wolf being attracted from the impoverished western part of northern Greenland, only 77 km from Ellesmere Island, to the more productive central Peary Land. The 730 km dispersal had demographic consequences, as this wolf was shot after conflicts with sled dogs (Marquard-Petersen 2008).

Conservation implications

My findings indicate demographic and geographic isolation and raise questions about the long-term viability of the eastern Greenland wolf population. Despite 30 years of legal protection, the population is still only about 23 wolves. This invasion apparently did not reach stage 3 of the model of steps and stages, i.e. permanent establishment through population growth to a minimum viable population. For example, the red wolf *Canis lupus rufus* of the southeastern United States is estimated to consist of > 100 wolves, yet is classified as 'critically endangered' by the International Union for Conservation of Nature (IUCN 2011). By extension, the 40-year delayed reestablishment highlights the need for adequate protection for wolves on the Canadian Arctic Islands, because the speedy reestablishment of vacant areas reported from lower latitudes may not be the norm in the far north.

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