Movement patterns and habitat selection
– insights from West Greenland caribou
Caribou (*Rangifer tarandus groenlandicus*) in the Akia-Maniitsoq population were found to be partial migrants as ca. 85% were migrants or mixed-migrants while ca. 10% were resident. The average distance between summer and winter home ranges depended on individual movement type; migrants and mixed migrants moved on average 57 km between ranges, whereas resident animals moved only 7 km. Average home range sizes were larger in summer than in winter (96 km² vs. 35 km²), and were dependent on caribou body length. Furthermore, migrants had larger home ranges than residents. The caribou selected annual home ranges, which were characterized by the presence of the vegetation types heath, copse and grassland. This corresponds to findings at patch scale where caribou preferred copse during summer while grassland and snowbed rich in lichens were preferred during winter. Analyses of the late winter diet showed that lichens made up more than 60% of the ingested forage, which stresses the importance of vegetation types rich in lichens as winter habitats. This finding occurred despite the simultaneous expansion of shrubs in the area where the distribution of the vegetation types heath and copse increased by ca. 15% from 1997 to 2008. Although the behavioral plasticity seen in both movement type and home range size variability is likely to favor the long-term survival of the AM caribou, the increasing shrubification of the AM region combined with the declining abundance of this caribou population, suggest that West Greenland caribou in general may become more vulnerable in a warmer climate. If the marked fluctuations in population sizes seen throughout the past 250 years are to be avoided, it is important with a management regime that includes ample areas undisturbed by humans as well as areas comprising the important winter vegetation types. This may not be an easy task as future warming may increase the shrubification even further, and economic interests may pave the way for the establishment of large-scale infrastructures in current day pristine areas.

**Keywords:** Caribou, diet, habitat selection, harvest and trade data, home range, migration, movement, residence time, resource selection, West Greenland
Contents

Preface .................................................................................................................................................. ii
Acknowledgements ............................................................................................................................. iii
List of included manuscripts ............................................................................................................... iv
Summary (English) ................................................................................................................................. v
Summary (Danish) ................................................................................................................................. vi
Introduction ........................................................................................................................................... 1
  Managing large herbivores ..................................................................................................................... 1
  Linking management, habitats and movement ..................................................................................... 2
  Herbivore population dynamics in a changing arctic ......................................................................... 5
  Description of research questions addressed ..................................................................................... 7
Perspectives .......................................................................................................................................... 8
Conclusion .............................................................................................................................................. 10
References ........................................................................................................................................... 12
Manuscript I ....................................................................................................................................... 16
Manuscript II ..................................................................................................................................... 35
Manuscript III ................................................................................................................................... 58
Manuscript IV ................................................................................................................................... 78
Preface

This thesis represents the partial fulfillment of the requirements for the degree of Doctor of Philosophy (Industrial PhD) at the Graduate School of Science and Technology, Aarhus University (AU), Denmark. The research presented is the result of my PhD project conducted at the Greenland Institute of Natural Resources (GINR), Greenland, and at the Department of Bioscience at AU under the supervision of Jacob Nabe-Nielsen (AU), Peter Aastrup (AU) and Josephine Nymand (GINR).

After living in Greenland for 12+ years, I have come to know the importance of caribou both as a fascinating wildlife animal you catch a glimpse of when hiking in the mountains, but also as a valued meat for your freezer. For almost 9 years, I have been employed at the Greenland Institute of Natural Resources in Nuuk. The institute works within three focal areas: research, monitoring and advising the Greenland Government on sustainable exploitation of living resources and safeguarding the environment and biodiversity. To provide the government with science-based advice several caribou surveys have been undertaken during the past 20 years. However, a survey only gives a snapshot in time, and updated knowledge on e.g. seasonal distribution, habitat selection and diet was lacking. In 2008 a GPS-collaring project was initiated and 40 female caribou were tagged, providing information on their spatial and temporal distribution until 2010, when the project was terminated. Data analyses from the collaring project combined with data from a diet study, and historical harvest and trade data comprise the basis of my PhD project and are synthesized in the four manuscripts comprising this thesis.
Acknowledgements

This thesis is the result of years of hard work, which would not have been possible without the help and assistance from people around me. None of it would have been possible without the funding from GrønlandsBankens ErhvervsFond, the Ministry of Education and Research, Government of Greenland, and Greenland Institute of Natural Resources.

My greatest thanks goes to my supervisors Jacob Nabe-Nielsen and Peter Aastrup (Aarhus University) and Josephine Nymand (Greenland Institute of Natural Resources). The support from the three of them made everything fall into place. During the course of this PhD one of my biggest accomplishments was learning a brand new language, R, and without Jacob and his patience, I would never have conquered the statistics needed for the analyses or updated my skills to write scientifically sound papers. Peter always gave valuable advice on caribou in Greenland and I appreciate our many discussions on all possible aspects of herbivore ecology. Jose has saved me countless times, and without her, I would not have finished my thesis. I’m truly grateful for all her help, and for her always lending me an ear when I was frustrated with it al.

Last, but not least, I’m thankful for my family, all of my colleagues and friends in both Nuuk and abroad – none mentioned, none forgotten.

Katrine Raundrup
Nuuk, Greenland Institute of Natural Resources
February 2018
List of included manuscripts

Manuscript I  **Raundrup K**, Nymand J, Aastrup P, Cuyler C, Nabe-Nielsen J. Long-range movements and home range sizes in West Greenland caribou. Manuscript prepared for submission to *Wildlife Biology*. Contribution: Analysed data and leading the writing of the manuscript


Manuscript III  **Raundrup K**, Nymand J, Cuyler C, Aastrup P, Zinglersen KB, Nabe-Nielsen J. Temporal change in caribou winter diet in West Greenland – have 10 years made a difference? Manuscript under review at *Polar Research*. Contribution: Analysed data and leading the writing of the manuscript

Manuscript IV  Moshøj CM, **Raundrup K**, Forchhammer MC. The effect of Inuit hunting pressure on fluctuating harvests of West Greenland caribou populations. Manuscript prepared for submission to *Arctic*. Contribution to writing of the manuscript and data analysis
Summary (English)

Caribou (*Rangifer tarandus groenlandicus*) in the Akia-Maniitsoq population were found to be partial migrators as ca. 85% were migrators or mixed-migrants while ca. 10% were resident. The average distance between summer and winter home ranges depended on individual movement type; migrators and mixed migrators moved on average 57 km between ranges, whereas resident animals moved only 7 km. Average home range sizes were larger in summer than in winter (96 km² vs. 35 km²), and were dependent on caribou body length. Furthermore, migrators had larger home ranges than residents. The caribou selected annual home ranges, which were characterized by the presence of the vegetation types heath, copse and grassland. This corresponds to findings at patch scale where caribou preferred copse during summer while grassland and snowbed rich in lichens were preferred during winter. Analyses of the late winter diet showed that lichens made up more than 60% of the ingested forage, which stresses the importance of vegetation types rich in lichens as winter habitats. This finding occurred despite the simultaneous expansion of shrubs in the area where the distribution of the vegetation types heath and copse increased by ca. 15% from 1997 to 2008. Although the behavioral plasticity seen in both movement type and home range size variability is likely to favor the long-term survival of the AM caribou, the increasing shrubification of the AM region combined with the declining abundance of this caribou population, suggest that West Greenland caribou in general may become more vulnerable in a warmer climate. If the marked fluctuations in population sizes seen throughout the past 250 years are to be avoided, it is important with a management regime that includes ample areas undisturbed by humans as well as areas comprising the important winter vegetation types. This may not be an easy task as future warming may increase the shrubification even further, and economic interests may pave the way for the establishment of large-scale infrastructures in current day pristine areas.
Summary (Danish)

Rensdyr (*Rangifer tarandus groenlandicus*) i Akia-Maniitsoq-bestanden kan betegnes som partiel migrerende, idet ca. 85 % var migrerende, mens ca. 10 % var stationære. Den gennemsnitlige afstand mellem sommer- og vinterområder (herefter home ranges) var afhængig af dyrenes individuelle bevægelsesstil. Idet den afstanden mellem home ranges var 57 km for migrerende dyr, mens den var 7 km for stationære dyr. Sommer home ranges var i gennemsnit større end vinter home ranges (96 km² vs. 35 km²), og størrelsen var afhængig af kropsstørrelse hos rensdyrene. Ydermere viste det sig, at migrerende dyr havde større home ranges end stationære dyr. Rensdyrene valgte årlige home ranges, der var karakteriseret ved tilstedeværelsen af vegetationstyperne hede, krat og græsland. Dette stemmer overens med analyser på mindre skala, hvor rensdyr om sommeren foretrak kratvegetation, mens de om vinteren foretrak græsland og lichen-rig sneleje-vegetation. Undersøgelserne af vinterdien viste, at lichen bestod af ca. 60 % af den spiste føde, og understregede, at de lichenriges vegetationstyper var vigtige vinterhabitater. Dette til trods for den samtidige øgede udbredelse af hede og dværgkrakvegetation i området på 15 % i perioden 1997-2008. Til trods for rensdyrenes adfærdsmæssige plasticitet i valg af bevægelsesstilte samt variationen i størrelsen af home ranges, som begge formodentlig sikrer overlevelsen af rensdyrene på langt sigt, så trækker spredningen af dværgkrakvegetationen muligvis i den anden retning. Rensdyr i Vestgrønland bliver måske mere sårbare i forbindelse med yderligere opvarmning som følge af klimaændringer. Hvis de markante udsving i bestandsstørrelser, der er set i løbet af de seneste 250 år, skal undgås, er det vigtigt, at der forvaltningsmæssigt sikres tilstrækkeligt store uforstyrrede områder samt områder med de vigtige vintervegetationstyper. Dette er ikke nødvendigvis en let opgave, eftersom klimabetinget opvarmning forventes at fortsætte og potentielt drive en yderligere spredning af dværgkrakvegetationen. Ydermere kan fremtidige økonomiske interesser bane vejen for etableringen af stor-skala infrastruktur i områder, der i dag ligger stort set uberørte hen.
Introduction

Managing large herbivores

Herbivore populations provide a considerable resource for both local and regional communities all over the world in the form of e.g. goods and economic income (Gordon et al. 2004). The herbivores may further impact land use and important habitats relevant for conservation (Hobbs 1996). They may be species relevant to conserve due to small population sizes (Bekenov et al. 1998; Wilman and Wilman 2017) or needs to be controlled as a result of increasing numbers (Bråthen et al. 2007).

All of the above examples calls for management regimes to be implemented to safeguard both the herbivores and the habitats they rely on. The concept of adaptive management, which is an approach for concurrent managing and learning about the resources, as developed decades ago (Walters and Hilborn 1978). The term refers to “a structured process of learning by doing, and adapting based on what was learned” (Walters and Holling 1990). The framework consists of two cycles: the set-up phase and the iterative phase (Fig. 1.) The first phase involves gathering stakeholders, defining objectives to be studied, discussing alternative actions, identification of predictive models of the system at hand, and a monitoring program is set in place. During the second phase a management decision based on the objectives and model outputs is taken into action, and the system effects of the decision are monitored and assessed before new decisions are made based on the improved understanding (Williams 2011). Often a resource is responsive to management actions, but the impacts of those actions are uncertain. In those cases adaptive management can be applied as this approach incorporates uncertainties related to e.g. environmental variation, resource status, and understanding of ecological relationships that drive resource dynamics (Williams 2011). By testing hypotheses related to the uncertainties informed decisions can be made and adjustments to the constantly developing management plan can be made (Fig. 1).

Figure 1. Overview of the processes involved in adaptive management. From Williams (2011)
In order to manage herbivore populations in a well-balanced way, information on how population density of the herbivores is related to the vegetation, its productivity and composition is needed (Gordon et al. 2004). That is, hypotheses about resource dynamics needs to be tested and combined with monitoring data to form the basis for adaptive management (Williams 2011). Furthermore, different spatial scales needs to be considered when managing herbivores ranging from small patches of vegetation to seasonal ranges and even to landscape scale. In addition, long-term data on population dynamics (e.g. birth and death rates) are needed to account for changes in the dynamics related to changed land use and climate change (Gordon et al. 2004).

**Linking management, habitats and movement**

For a manager to make valid and effective management of large grazers it is essential to know how and when the animals use and move within the available landscape. That is, information on seasonal habitat selection as well as long- and short-range movement is needed.

Habitat selection can be defined as the disproportionate use of resources relative to the availability, and can be studied at both a temporal and a spatial scale (Fig. 2; Mayor et al. 2009) including selection of specific forage plants (green box in figure 2), selection of patches with forage plants (yellow box), and selection of seasonal ranges with patches (orange box). The mosaic of different patches creates a heterogeneous landscape where animals will have to spend larger proportions of time in patches with profitable forage in order for them to optimize their fitness (Fauchald 1999). This affects the movement patterns of the animals.

*Figure 2. Habitat selection on multiple spatial and temporal scales. Adapted from Mayor (2009).*
Within the heterogeneous landscapes, animals move in response to local resource abundance thereby altering their movement rates and/or turning frequencies. This means that the animals switch between two search modes: extensive and intensive search mode (Fig. 3; Barraquand and Benhamou 2008; Byrne and Chamberlain 2012). When animals are walking between patches of higher quality or quantity of a given resource their search mode is said to be extensive, and their movements are relatively linear and faster compared to the intensive search mode (Barraquand and Benhamou 2008). The intensive search mode (=area concentrated) is seen when animals enter high quality patches, and adapts a slower and more tortuous movement mode (Byrne and Chamberlain 2012).

![Search modes diagram](image)

**Figure 3.** Display of animal movement track when adopting an extensive search mode (relative straight, directed trajectories), and when adopting an intensive search mode (slower, sinuous trajectories; within the circles).

An example of extensive search mode is seen when animals are migrating between seasonal ranges. Migration is generally viewed as an adaptive trait that increases individual’s fitness by improving their access to food, water and mating sites (Dingle and Drake 2007; Avgar et al. 2014; Shaw 2016), and potentially permits animals to escape unfavorable conditions (Hebblewhite and Merrill 2009; Singh et al. 2012; Witter et al. 2012). Migration can additionally be defined by the following concepts: (1) a persistent, undistracted and straightened out locomotory activity; (2) a large-scale animal relocation; (3) a seasonal movement of populations between regions with alternating quantity and quality of resources (Dingle and Drake 2007).

Migration enables animals to seek out seasonal ranges with the forage needed to sustain a diet of energetically suitable forage items. As the environment change during the year (yellow part of Fig. 4), the energy requirements for arctic herbivores change as well (Klein 1990). There are several critical periods throughout the year including calving and calf survival in spring, accumulation of fat reserves for the coming winter during summer and early winter, rut and pregnancy, thermoregulation costs during winter combined with a change to a lichen-dominated diet and increased energy expenditure for crater digging, and growth of foetus during late winter and spring. Especially pregnant females have high energy demands and have to rely on body protein stores build up during summer to early winter to secure a
successful pregnancy; that is, the autumn condition of the female determines the probability of going full term (Cameron et al. 1993). Calving date and calf survival is on the other hand influenced by maternal condition in late winter and spring (Cameron et al. 1993), making the female less dependent on vegetation green-up in spring (Taillon et al. 2013) than previously speculated (Post and Forchhammer 2008). Survival and growth of the calf is on the other hand reliant on ample forage as the availability of green forage improves milk production in the females and secures forage for the growing calf (Aikio and Kojola 2014).

Figure 4. Model of the relationship between seasonal changes in the environment (yellow boxes and arrows) and physiological demands of the caribou (blue boxes and arrows). Adapted from Klein (1990).
Habitat selection and long- and short distance movement may thus affect population dynamics by affecting birth rates and mortality with consequences for population growth and decline.

Herbivore population dynamics in a changing arctic

In the Arctic, management of herbivores poses a huge challenge. Climate change is especially apparent in the Arctic potentially re-shaping landscapes and changing the foundation for both people and animals living there (ACIA 2004; McBean et al. 2005). The most evident changes includes increased temperatures (Xu et al. 2013; Mernild et al. 2014) and increased precipitation (Lucas-Picher et al. 2012; Mernild et al. 2015). The combination of increased temperatures and precipitation is expected to result in increasingly more episodic snowmelt events during winter (Pedersen et al. 2015). The snowmelt will often be followed by re-freezing of the snow and the vegetation below rendering it difficult to reach the forage (Fig. 5).

Furthermore, the availability and quality of forage displays great variation throughout the year – and even between years (Klein 1990).

All of the above have great implications for population dynamics of arctic wildlife and for caribou in particular. The implications include increased winter mortality, increased insect harassment, increased wildfire frequency, changed forage quality and availability all of which may change caribou movement patterns and distributions (Mallory and Boyce 2017). The climate changes are expected to result in increased winter mortality due to icing of the forage as observed for Svalbard reindeer (Hansen et al.)
Even if the icing does not result in fatalities, the added difficulties in reaching the forage negatively impact body condition (Loe et al. 2016) and reproductive success (Helle and Kojola 2008). Increased winter precipitation will further increase snow depth which will impair movement and be energetically costly (Fancy and White 1987). Moreover, the energetically costs of crater digging through the snow to the vegetation below increases (Fancy and White 1985).

During summer caribou in most populations are exposed to varying degrees of insect harassment primarily by the parasitic warble flies and nose botflies (Witter et al. 2012). Increased summer temperatures are likely to prolong the period when the parasitic flies are active. Caribou will actively try to avoid the harassment by moving to windier areas and to snow patches thus reducing the time to forage and increasing their energy expenditure (Toupin et al. 1996). This will ultimately reduce their body condition and thus lower their reproduction (Cuyler et al. 2012).

The increased summer temperatures are expected to increase the frequency of wildfires (Hu et al. 2015). Not only does wildfires have a direct effect on caribou movements as recently burned areas tends to be avoided even when forage starts to regrow (Rickbeil et al. 2017) it also has detrimental effects on the vegetation. This is especially important when referring to lichens which are highly valued forage items during winter for many caribou populations (Manuscript III; Boertje 1984). During summer lichen mats tend to be fairly dry and thus burn easily. Unlike vascular plants, deterioration of lichens may take several decades to regrow (Collins et al. 2011), and burning of large lichen-rich areas may thus have reduce the nutritional status of the caribou during winter ultimately affecting survival.

Wildfires are not the only way vegetation are affected by climate warming. The composition of the vegetation has already been changing and shrubs in particular have become increasingly dominant (Myers-Smith et al. 2011; Elmendorf et al. 2012; Normand et al. 2013; Myers-Smith et al. 2015). The shrubification is expected to negatively affect lichen abundance (Chapin et al. 1995). In some areas the expansion of shrubs have been found to be counteracted by grazing of large herbivores (Manseau et al. 1996; Post and Pedersen 2008) while grazing had no effect in others (Damgaard et al. 2016). The expansion of shrubs corresponds to the expansion of plants with strong anti-browsing defenses thus lowering the quality of the forage (Bryant et al. 2014). The shrubification has thus been correlated with the declines in caribou populations across North America (Fauchald et al. 2017).

In addition to changes directly related to climate change, increased human activity and industry development in previously undisturbed areas have impacts on the caribou. These include changes in migration routes, distribution in the landscape and general avoidance of areas close to the developments (Stankowich 2008; Polfus et al. 2011; Johnson and Russell 2014; Tucker et al. 2018).

Management of caribou is thus not a straightforward task as effects of the above mentioned climate and human induced changes needs to be taken into account.
Caribou and muskoxen (*Ovibos moschatus*) are the only two herbivores in West Greenland. While muskoxen were introduced to the Kangerlussuaq area (66°N) in the late 1960s, caribou are endemic, and have been hunted traditionally for centuries (Manuscript IV; Vibe 1967; Grønnov et al. 1983; Meldgaard 1986). The caribou populations have fluctuated greatly during the past centuries (Manuscript IV; Meldgaard 1986). Data from i.e. hunting and trade statistics have shown that the fluctuations are cyclic, coincide along the entire west coast, and last between 65 and 115 years (Vibe 1967). Four factors are thought to drive the fluctuations: climate change, density dependent overgrazing, hunting, and predation (Meldgaard 1986). Climate plays a large part, and this has been documented in a number of studies, where variation in winter climate e.g. abundance of snow (Solberg et al. 2001; Forchhammer et al. 2002; Tyler 2010), and trophic mismatch (Post and Forchhammer 2008; Post et al. 2008) were found to regulate caribou numbers. Recent data suggest that overgrazing plays a key regulatory role (Post and Klein 1999; Cuyler et al. 2005), while historically, hunting has been mentioned as the most important regulator (Meldgaard 1986). Predation often plays a central regulating role in circumpolar arctic caribou populations (Wittmer et al. 2005; Hegel et al. 2010), but as there are no large predators in West Greenland, predation is not relevant here.

Historically, the seasonal migration patterns of the caribou in West Greenland have been found to depend on the population density, as the caribou disperse over larger areas in periods when a population is large. Migrations towards the coastal areas during the winter season have primarily taken place in years with many caribou, while migrations ceased and caribou stayed inland all year round, when population sizes were lower (Meldgaard 1986).

In recent years a general decline in caribou numbers has been observed throughout the Arctic which is also recognizable in some of the populations in Greenland (Vors and Boyce 2009). Although caribou numbers in West Greenland in general were considered as increasing by Vors and Boyce (2009), this is not true for the Akia-Maniitsoq (AM) population studied in this thesis as the numbers have decreased from ca. 46000 in 2001 to ca. 24000 in 2010 (Cuyler et al. 2003; Cuyler et al. 2005; Cuyler et al. 2011). The AM caribou thus follow the trend observed for other *Rangifer* populations in the arctic and northern hemisphere. The reduction was primarily facilitated by a strict management regime, where hunting seasons were extended and harvests were without quotas (Cuyler et al. 2011) although intra-specific competition for food resources can not be ruled out (Cuyler 2007). But has the management resulted in changes in large-scale movement patterns for caribou and has the potential overgrazing facilitated changes in habitat selection and diet? These two questions prompted several overarching research questions to be answered:

1. Are the caribou migratory? Or have they changed behavior due to decreasing density?
2. Are individual long-range movement reflected in seasonal home range sizes?
3. Which habitats are most important during summer and winter?
4. Has the vegetation changed in recent years and is the potential change reflected in the caribou diet?
5. Is the effect of hunting pressure reflected in the historic trade and hunting statistics? And does the effect have potential implications for current day management?

The combined answers from these questions may all have consequences for the current day scientific advice provided for management of the West Greenland caribou.

Perspectives

Caribou in West Greenland is not an easy species to study. They have a large spatial distribution, are often found at remote locations and getting to know their distribution, migration, and diet requires large financial support. Whereas many migratory North American caribou populations aggregate annually on calving grounds enabling aerial surveys with visual counts of animals on relatively confined areas (Rivest et al. 1998; Patterson et al. 2004), caribou in West Greenland do not display gregarious calving (Poole et al. 2013). This adds costs to the surveys which nonetheless are essential for management decisions especially in a time of change at multiple levels.

One of the major challenges facing the caribou is climate change. During the past century the changes include increasing temperatures and precipitation (Mernild et al. 2014; Mernild et al. 2015) that have resulted in changes in vegetation composition (Manuscript III; Sturm et al. 2001; Myers-Smith et al. 2011; Myers-Smith et al. 2015). Furthermore, the almost pristine environment with only little human disturbances may be challenged with the development of tourism, hunting (Fig. 6) and large-scale infrastructures e.g. mining industry including transmission lines, housing facilities and roads (Fig. 6). The cumulative effects of these disturbances are difficult to predict, but it is important to consider the combined effects of human activities when discussing future challenges to caribou populations (Gunn et al. 2011).
Individual Based Modelling (IBM) can be applied to study interactions between individual organisms at different trophic levels using computer simulation models (Huston et al. 1988). In the past decades IBMs have gained increased use within ecology. The output of an IBM model can be regarded as a representation of the “real world” (Grimm and Railsback 2005). It describes a system of individuals and their surroundings (local resources) in which changes at population level are caused by changes in individual behavior, which again is dependent on the local resource availability and interactions between individuals (Grimm and Railsback 2012). The emergent properties derive from adaptive behavior of individuals (Railsback 2001), especially if the ability to adapt to new surroundings affect individual fitness.

Figure 6. Human disturbances in the Akia-Manitsoq area. Caribou hunting intensity during 2001-2016 where higher hunting intensity is plotted as increasingly more red (left). Current map of mineral licenses in the area (right). The licenses include exploration (blue), exploitation (yellow) and new licenses (red) under development. Information on hunting intensity from separate hunting reporting cards and mineral licenses from NunaGIS (http://dk.nunagis.gl, Government of Greenland).

With regard to Greenland caribou populations, an IBM may provide inputs to answer relevant management questions e.g. how will caribou be affected by anthropogenic disturbances including mega-industry in West Greenland? A rational approach to answering the question might be to analyze caribou mortality by two IBMs: One model with uniform risk of dying for all individuals in the population; a second model with variable risk of dying depending on individual behavior. In the first model, the mortality will be constant and can be predicted from the mortality rate of the individuals. In the second model, the population level mortality will emerge based on individual behavior with regard to risk
assessment e.g. behavior towards hunters, roads, or mine sites. The validity of an IBM must be tested by comparing model output with “real world” data (Grimm and Railsback 2005; Railsback and Grimm 2011). That is, either data presented in Manuscript I or II or data collected in a new GPS-collaring campaign.

The use of IBMs for modelling caribou response to future challenges relies on sufficient data on e.g. landscape use (Paper I and II), vegetation composition (Paper II and III), population sizes, and herd structure (Cuyler et al. 2003; Cuyler et al. 2005; Cuyler et al. 2011) as well as behavioral responses to disturbances (e.g. Aastrup 2000; Vistnes and Nellermann 2008; Beauchesne et al. 2014; Johnson and Russell 2014). To aid management decision, collection of more data on particularly behavioral responses are required, but provided that data is available this may be the way forward in identifying the cumulative effects of increased hunting pressure, changes in vegetation composition, large-scale infrastructures, or other human-related disturbances on Greenland caribou populations.

**Conclusion**

Climate is indeed changing in the Arctic and the wildlife living there must either adapt or disappear. Based on the results from Manuscripts I-IV it is not possible to give a single, simple recommendation to managers of the Akia-Maniitsoq caribou. For many years the caribou populations in West Greenland have been managed towards a target density of 1-1.2 km\(^2\) (Cuyler 2007). This target was not based on studies of carrying capacity of the ranges but was expected to favour vegetation quantity, quality and availability beneficial for body condition, health and productivity of the caribou (Witting and Cuyler 2011). The most recent survey of the Akia-Maniitsoq population estimated a total of ac. 24000 caribou with a density of ca. 1.5 km\(^2\) (Cuyler et al. 2011), which is just slightly above the target value and thus should provide for sustainable harvests. In the “simple” West Greenland landscape where predators are absent managers can regulate hunting pressure to increase or decrease the number of caribou. However, hunting pressure is not the only driver of population dynamics as climate, overgrazing and anthropogenic development all participate in creating the multi-faceted world of the caribou.

Management should of course use a target density value as a rule of thumb, but animal density is not to stand alone when managing large grazers. Sufficient information on the quality of both summer and winter ranges for the Akia-Maniitsoq caribou is lacking. Furthermore, the current density may be too low to counteract the observed shrubification of ranges (Manuscript III) which may be detrimental for the caribou. A density of 5 caribou km\(^2\) was needed to counteract shrubification in Northern Norway (Bråthen et al. 2017) but a similar density will be damaging for the vegetation in West Greenland. More
studies are unquestionably needed to visualize the impacts of how density changes and climate driven changes of the vegetation affect movement, habitat selection and diet in the Akia-Maniitsoq caribou.
References


Manuscript I


Manuscript prepared for submission to Wildlife Biology.
Long-range movements and home range sizes in West Greenland caribou
Katrine Raundrup1,2, Josephine Nymand1, Peter Aastrup2,3, Christine Cuyler1, Jacob Nabe-Nielsen2,3

(1) Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland
(2) Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
(3) Arctic Research Centre, Aarhus University, C.F. Møllers Allé 8, 8000 Aarhus C, Denmark

Abstract

Annual migrations between distinct home ranges are common in mammal species although partial migration, where only a fraction of the population migrates, is probably more common than complete migration. Seasonal changes in resource availability are one of the main drivers in large-scale displacements between home ranges. The size of a home range depends on the animal’s requirements for resources, primarily food, during a certain period of time. We therefore studied long-range movement types and home range sizes in the Akia-Maniitsiq caribou population of West Greenland. We used GPS-data from 21 female caribou covering 400 days of data from 8 May 2008 to 12 June 2009 to assess variations in movement. We calculated home range sizes for summer and winter using a utility distribution with 95% kernel and determined possible drivers of home range size using generalized linear models. Caribou showed behavioral plasticity in choice of long-range movement type and was classified as partial migrators with 47.6% mixed-migrators, 38.1% migrators, 9.5% residents and 4.8% dispersers. Home range sizes changed seasonally, with larger home ranges in summer than in winter (mean = 96 km² and 35 km², respectively). Resident caribou had smaller summer and winter home ranges than migrators, and larger animals had relatively large home ranges. The capacity to utilize different long-range movement types makes the Akia-Maniitsiq caribou population well suited to survive in both seasonally variable landscapes and in landscapes with less predictable resource distributions. This behavioral plasticity is likely to enable caribou to cope with landscape variability associated with future climate change.
Introduction

Many mammal species undertake annual migrations between distinct home ranges. Well known examples include wildebeest in Africa (Fryxell et al. 1988; Bolger et al. 2008) and barren-ground caribou in North America (Kelsall 1968; Fancy et al. 1989). Migration is an adaptive trait that increases individuals’ fitness by improving their access to food, water, and mating sites (Dingle and Drake 2007; Avgar et al. 2014; Shaw 2016). It also permits animals to escape unfavorable conditions, such as areas with high levels of insect harassment (e.g. Helle and Tarvainen 1984; Toupin et al. 1996; Witter et al. 2012), severe snow conditions (e.g. Singh et al. 2012) or presence of predators (e.g. Hebblewhite and Merrill 2009; Sivertsen et al. 2016). In the Arctic, annual migrations can provide access to seasonally changing food resources by enabling animals to move to new areas during vegetation greening in spring (Bischof et al. 2012).

Although migration is common in large mammals, other types of long-range movements, including dispersal and nomadism, are seen, and different types of long-range movements are considered beneficial in different environments. Species capable of utilizing more than one type of long-range movement show behavioral plasticity and are expected to be better at responding to changing environmental conditions (Komers 1997). In landscapes where environmental conditions change in a predictable way during the year migration should be favored, while landscapes with little temporal change in resource accessibility are expected to favor resident animals (Mueller et al. 2011). A special case of migration occurs when animals do not return to the original location, but to an area close to the one they started from. Such animals are said to be mixed migrators (Bunnefeld et al. 2011). Partial migration occurs when only a fraction of the animals in a population migrate while others stay in the same area throughout the year (Kaitala et al. 1993; Chapman et al. 2011). Partial migration has been documented in a number of mammal species and is probably more common than complete migration (Dingle and Drake 2007; Chapman et al. 2011) and has among others been observed in roe deer (Cagnacci et al. 2011), red deer (Mysterud et al. 2011), moose (Ball et al. 2001; Singh et al. 2012), Svalbard reindeer (Hansen et al. 2010), and North American caribou (Bergerud 1996). Dispersing animals do not return to previously used ranges once they have settled in a new area, and nomadic animals keep moving to new areas. Nomadism is expected in species that experience temporally unpredictable landscapes (Mueller et al. 2011), such as those in arid areas with unpredictable rainfall (Bekenov et al. 1998). These five movement types, i.e. migration, mixed migration, dispersal, residency and nomadism, cover the span of long-range movement types experienced by animals.

Changes in net squared displacement (NSD) over time, which is a measure of how far an animal has displaced from its starting location, is often used to distinguish different types of long-range movements (Bunnefeld et al. 2011; Börger and Fryxell 2012). For seasonal migrators, NSD increases as animals
move from their summer ranges to the winter ranges and decreases as they return to their summer ranges. For migratory animals, the expected changes in NSD is therefore best described by a double sigmoid curve. For mixed migrators NSD does not return to zero as it does for true migrators. The NSD plot for dispersing animals is best characterized by a sigmoid curve. For resident animals that remain within one foraging range, NSD is small and relatively constant. Finally, for nomadic animals, NSD increases linearly with time (Bunnefeld et al. 2011).

While seasonal changes in resource availability are often associated with large-scale displacement of animals between different confined areas, the amount of resources available to the animals is also related to the size of these areas. Areas where animals stay for an extended amount of time are called home ranges (Burt 1943; Powell 2000). The size of a home range provides information about the area needed to comply with the animals’ requirements regarding food and other resources over a certain period of time (McNab 1963). Home range sizes generally increase with body size, a correlation which is related to the higher basic energetic requirements of larger animals (McNab 1963; Harestad and Bunnell 1979). Home range sizes may also vary among individuals of the same species depending on the individuals’ energy requirements, their knowledge of the landscape, age and health status (Harestad and Bunnell 1979; Powell 2000; Van Moorter et al. 2016). Among ungulates, home range size is often related to age, sex and reproductive status, as has been demonstrated for moose (Cederlund and Sand 1994; van Beest et al. 2011) and roe deer (Saïd et al. 2009). Recently, seasonal home range sizes were found to be larger in migrating than in resident Cape buffaloes (Bennitt et al. 2016). While animals may increase their gross energy intake by migrating (e.g. Rolandsen et al. 2017), they also increase energy expenditure when moving long distances (Fancy and White 1987; Reimers et al. 2014). The net energy intake is thus not necessarily larger for migrators. Animals may therefore choose different strategies to maximize energy intake, e.g. by migrating between relatively small seasonal home ranges with high resource availability, or by being resident within a larger home range. Although crucial for animal energetics, this relationship between long-range movement type and home range size has rarely been analyzed (Bennitt et al. 2016). If both home range sizes and type of long-range movements vary within a population, it shows signs of behavioral plasticity indicative of species that are adapted to habitats that vary in both space and time.

Caribou are known to migrate immense distances, and populations in northern Canada and Alaska may travel more than 5000 km during their annual migration (Fancy et al. 1989; Nicholson et al. 2016). Historically, caribou in West Greenland have also been described as migratory, with summer ranges close to the inland ice and winter ranges closer to the coast (Thing 1984; Meldgaard 1986). A study based on satellite collared female caribou in the late 1990s indicated that some individuals were stationary while others migrated, but the conclusions were based on limited data (Cuyler and Linnell 2004). West
Greenland is characterized by large seasonal climatic variations and the resources are therefore expected to show a high degree of both temporal availability and quality. We therefore expect the caribou to be migratory, as this would enable them to track favorable foraging areas as those distributions change over the year. We also expect home range sizes to vary according to caribou age, size, body condition and seasons. Home ranges are expected to be larger in winter than summer to compensate for limited resources that are spread over large areas as has been observed in another caribou population in West Greenland (Thing 1984). Further, we hypothesize that caribou that only migrate short distances, or remain in the same area year round, have larger seasonal home ranges. In this study we test whether caribou show plasticity in long-scale movement and variation in seasonal home range size. This will provide a better understanding of the West Greenland caribou’s ability to survive in a changing climate and give us valuable insights to the annual movements of this large native ungulate.

**Materials and methods**

**Study area and population**

Caribou (*Rangifer tarandus groenlandicus*) in West Greenland are divided into 5 populations primarily based on geographical barriers that prevent animals from intermixing. The Akia-Maniitsqoq (AM) population is located in an area (ca. 15000 km$^2$) extending approximately 200 km north from Nuuk to the Sukkertoppen Iskappe north of Maniitsoq (Fig. 1). The southwest part is characterized by rugged lowlands under 200m with numerous lakes and streams and several high elevation mountain ridges (up to 600 m above sea level). The remaining areas are mountainous, and divided by steep short fiords, but also including a vast expanse of rugged uplands between 300m and 1100m, which extends east to the inland Ice Cap. The highest elevations are 1300 m above sea level. The size of the AM caribou population was estimated to ca. 24000 animals in the winter of 2010 (Cuyler et al. 2011) and estimations since 2001 (Cuyler et al. 2003; Cuyler et al. 2005) revealed the population to be decreasing. There are no naturally occurring predators in the area, but commercial and sport hunting takes place annually. Most of the hunting is done close to the coast as the interior of the area is relatively inaccessible to hunters (Cuyler et al. 2011). Hunting is therefore not expected to influence the movements of the caribou included in this study.

**Data collection**

Caribou location data were collected using GPS-collars (20 Argos-GPS from Telonics, US, and 20 Iridium-GPS from Vectronics Inc, Germany), which were deployed on 40 female caribou in May 2008. The caribou were caught from a helicopter using a net gun operated by a trained professional. On the ground, the caribou had their legs tied and were blind folded before collaring and assessment of age, body
condition, and body length. The average handling time was 13.5 minutes, with a maximum of 16 minutes. All collars were equipped with automatic release mechanisms set to release after 24–26 months. For the purpose of this study, we used data from 21 animals with collars that logged every 2 or 3 hours and with data from a minimum of 400 days (from the period 8 May 2008–12 June 2009).

At the time of collar deployment (May 2008) caribou were assessed for: (1) age class (sub-adult and adult) based on eruption and wear of incisors (Adamczewski et al. 2008). As all data for this study was from caribou classified as adults (>3 years), age was not used as a variable in any of the analyses; (2) body condition, where fatness was determined by palpation of “shoulder”, “ribs”, and “hips/spine” and assigned a score of 1 (worst) to 4 (best) (Adamczewski et al. 2008). This resulted in a total condition score ranging between 3 (worst) and 12 (best) for each animal; and (3) the length of the animal i.e. body length (cm) along the spine from the tip of the snout to the tip of the last bone in the tail.

Assessment of long-range movement type

Net squared displacement (NSD) was calculated according to Bunnefeld et al. (2011) to determine which movement type best described the movements of individual caribou. Five different models were fitted to the data for each animal:

\[
NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} \quad \text{Migratory}
\]

\[
NSD = \frac{\delta_s}{1 + \exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta_a}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} \quad \text{Mixed migratory}
\]

\[
NSD = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)} \quad \text{Dispersal}
\]

\[
NSD = c \quad \text{Resident}
\]

\[
NSD = \beta \times t \quad \text{Nomadic}
\]

where the asymptotic height (\(\delta\)) corresponds to the annual migration distance, i.e. the distance between summer and winter ranges. For mixed migrators spring and autumn migration distances (\(\delta_s\) and \(\delta_a\)) are not identical. The time at which the migration reaches half of the asymptotic height (\(\theta\)) in spring and autumn is \(\theta_s\) and \(\theta_a\), respectively, while \(\phi\) describes the time between reaching \(\frac{1}{4}\) and \(\frac{3}{4}\) of migration in spring (\(\phi_s\)) and autumn (\(\phi_a\)). The number of days since start (here 8 May 2008) is \(t\), while \(c\) and \(\beta\) are constants. For further information please refer to Bunnefeld et al. (2011). Starting values for the model run were used according to Bunnefeld et al. (2011) with the start date set to 8 May 2008. Analyses were done with the statistical software R (R Core Team 2017) using the package “adehabitat” (Calenge 2006).

Home range analyses
Individual home ranges were calculated using 95% fixed kernel utilization distribution (Worton 1989; Seaman and Powell 1996; Powell 2000) for two seasons: “summer” (GPS-data from August only) and “winter” (GPS-data from January only). The selection of these two periods was made to ensure that migration periods (spring and autumn) were not included in the home range calculations. Generalized linear models (GLMs) were used to determine whether the caribou parameters (body condition and body length; continuous variables) or season and movement type (factor variables) best describe home range size. The full model included main effects and first order interactions with season, except the interaction between movement type and season. Model selection was done by comparing all possible models that contained different subsets of the variables included in the full model. The comparison was based on \( \Delta \text{AIC}_c \) where \( \Delta \text{AIC}_c < 2 \) indicates substantial support for the model(s) (Burnham and Anderson 2002). Since the analysis determines possible differences in home range sizes of migrators/mixed migrators and resident caribou, animals with other movement types were excluded. Only one animal was found to be a disperser (and none were nomadic), hence for this analysis data from 20 animals were included. To aid the movement type assessment the distance (km) between the center of individual winter and summer home ranges was calculated.

Home range size was log\(_{10}\)-transformed prior to all analyses to ensure approximately normally distributed residuals and variance homogeneity. Utilization distribution calculations were done using the R package “adehabitatHR” (Calenge 2006). GLM analyses were done using R (R Core Team 2017).

Results

Long-range movement types

Female caribou in West Greenland used various long-range movement types (Fig. 2), and were not exclusively migratory as we had expected. Using the net squared displacement model output (Supplementary online material), along with re-classifications by visual inspection of the NSD plots (following Singh et al. 2016), and combined with analyses of distances moved between winter and summer home ranges revealed 47.6% (n=10) mixed-migrants, 38.1% (n=8) migrators, 9.5% (n=2) residents and 4.8% (n=1) dispersers. None were nomadic. Three movement trajectories were re-classified before the final movement type was assigned. One of these was originally classified as mixed migratory by model NSD model output, but due to the short distance between summer and winter home ranges (7 km vs. an average distance for migrators and mixed-migrants of 57 km), it was re-classified as resident (caribou id: 615882 in Fig. 2). Further, two were classified as dispersers although one was clearly distinguishable as migratory (albeit with a different temporal scale than the other caribou; caribou id: 613851 in Fig. 2), while the other was mixed-migratory (caribou id: 613856 in Fig. 2). The net distance
moved by the caribou depended on their movement type, as mix-migrators on average moved 84.2 km (range: 46.0–141.2 km), migrators moved 68.8 km (range: 40.6–97.6 km), while residents moved 23.2 km (range: 23.0–23.5 km).

**Variations in home range sizes**

Home range sizes were highly variable and generally larger in summer (range: 3–1207 km², mean: 96 km²) than winter (range: 0.6–325 km², mean: 35 km²), which was not what we had expected. The size of the home ranges increased with the body length (range: 152–176 cm, mean: 161 cm) of the animals, with season and movement type also being important variables in explaining variations in home range sizes (table 1). There was only weak support for models that included body condition ($\Delta AIC_c > 2$), so this variable did not appear to be important for the size of the home ranges. The predicted home range sizes calculated from two of the top three best GLM models (Fig. 3a and 3b based on model 2, which included body length and season; Fig. 3c and 3d based on model 3, which included body length, movement type and season) fitted observed home range sizes poorly (model 2: $r=0.38$; model 3: $r=0.49$). Animals that migrated far had larger summer and winter home ranges than resident animals (Fig. 3b), though this was less evident when using model 3 for predictions (Fig. 3d). The average distance between seasonal home ranges in the resident caribou was 5.5km (range: 4–7km) while the corresponding distance for migrators/mixed migrators was 56.6km (range: 13–114km).

**Discussion**

Caribou in West Greenland showed great behavioral plasticity in long-range movement types and variation in home range sizes. The Akia-Maniitsoq (AM) population can be classified as partial migrators with ca. 10% of the population being residents and the remainder being mainly migrators or mixed-migrators (ca. 85%). This corresponds to findings in Svalbard (Hansen et al. 2010) and to several caribou populations in North America (Bergerud 1996). Svalbard reindeer have small home ranges and the migration distances are minute (Tyler and Øritsland 1989). Hansen et al. (2010) argue that in Svalbard, large-scale movements are constrained by geographical barriers including glaciers, steep mountains and open sea for part of the population, which prevents animals from performing seasonal migrations. The landscape where the AM population resides is generally lacking dispersal barriers. This suggests that while some of the animals in the AM population are residents, this is not due to barriers. Migration can be viewed as a strategy to limit predation risk, as stationary caribou are likely more susceptible to predation (Schaefer et al. 2000). As there are no predators in West Greenland, animals are not expected to experience reduced fitness by being stationary, and the observed partial migration must be caused by other factors such as differences in resource accessibility of individual animals (Fryxell and Sinclair...
resulting in different survival probabilities (Chapman et al. 2011). Regardless of what causes animals to select a specific type of long-range movement, previous studies suggest that migration may be preferred to residency in many ungulates as migratory animals may have a higher body mass gain (e.g. red deer, Albon and Langvatn 1992) and migrants in general produce more offspring (Rolandsen et al. 2017) than resident animals. The ability to use a more than one type of long-range movements may enable the caribou in the AM population to better survive changing climatic conditions in the future since either dispersal or resident behavior could prove to be more favorable than under current conditions.

Just as the AM caribou used various long-range movement types, the sizes of their home ranges were also highly variable. The majority of the collard females in the AM population were migrators or mixed-migrants, and we expected seasonal home ranges of animals with these movement types to be smaller than those of resident animals. We expected migrating caribou to trade off energetic costs of migration and energetic gains of accessing areas with high quality forage by having smaller seasonal home ranges. Contrary to what we had expected, the resident animals had the smallest home ranges (Fig. 3b). Ample areas with sufficient terrain ruggedness may be an explanation as this type of landscape will provide access to different types of forage throughout the year (Nellemann and Thomsen 1994). Caribou with small home ranges moved across the same elevation gradients as did animals with larger home ranges (data not shown). The rugged terrain found in large parts of the Akia-Maniitsoq area may therefore provide adequate forage at all seasons for the resident caribou to stay within a smaller home range. This illustrates the different ways the West Greenland caribou may be able to maximize annual net energy intake i.e. they can have large home ranges, they can migrate between areas with temporally changing resources, or they can use less energy on movement by being resident, enabling them to survive in spite of restricted access to food. This disparity in home range size corresponds to similar findings in African buffalos, where migrating buffaloes were found to have larger seasonal (wet and dry seasons) home ranges than resident animals (Naidoo et al. 2012). Furthermore, home range sizes depended on season and body length, but not on body condition. Although animal age was not included in the analyses (as the age determination could only discern sub-adults from adult, and all animals thus, were classified as adults), older animals are generally larger (Kelsall 1968). Though body length was found to be positively correlated to home range size, the tendency was relatively weak. It might be biologically more relevant to assume that larger and hence older caribou have greater knowledge of the best resource locations, which permits smaller home ranges and energy conservation, as found in roe deer (Saïd et al. 2009). We only assessed body condition at the time of collaring, and as this index varies during the year (Cameron et al. 1993; Gerhart et al. 1996), and increases as the caribou gains weigh during the summer, it may not be of relevance for assessing home range sizes – at least not during the following winter. Home range sizes were larger in summer than in winter, which was not what we had expected. During winter, snow depth
may hinder caribou in moving over larger areas, thus confining them to smaller areas where they are able to survive by reducing their energy expenditure (Duquette 1988; Singh et al. 2012). Moreover, during summer insect harassment may become so high that the caribou need to move to areas with fewer insects e.g. to mountain slopes with more wind (Colman et al. 2003; Witter et al. 2012). This could result in larger summer home ranges to encompass both the areas with high vegetation cover (valleys) as well as elevations that provide temporary relief from flies, mosquitos and midges.

Caribou are generally expected to select the long-range movement type and home ranges that enables them to select seasonally available resources that maximize their net energy intake (Fryxell and Sinclair 1988; Nicholson et al. 2016). Migrating animals that move between seasonal home ranges may do so to follow the phenological green-up of the vegetation during spring and summer (Bischof et al. 2012), though climate warming may advance vegetation green-up resulting in asynchronous movement (Post and Forchhammer 2008). For resident animals inhabiting landscapes without elevation gradients, the lower net energy intake associated with staying in an environment that is not optimal at all times of the year may be compensated for by avoiding the energetic costs associated with long-range movements (Fancy and White 1985). If this were not the case, it would be more beneficial for them to become migrators. Switches in long-range movement type between years have been observed in e.g. mule deer, where highly variable annual precipitation and snow cover resulted in females changing from being migrators to residents or vice versa (Nicholson et al. 1997). The possibility of varying movement strategies between years (Fieberg et al. 2008) is not uncommon in ungulates and several authors refer to this as a migratory continuum (Dingle and Drake 2007; Cagnacci et al. 2011). Unfortunately, our dataset does not have the temporal resolution to study this interesting aspect of individuals changing long-range movement patterns. In the late 1960s, Vibe (1967) described density dependent migration in a more northerly West Greenland caribou population, where seasonal migrations were only prevalent in periods with higher densities of caribou (Vibe 1967; Meldgaard 1986). This suggests that West Greenland caribou have the ability to change between migration types, but this remains to be validated.

Studies linking long-range movement types and home range sizes in caribou are not common in literature, but here we have gained invaluable insights by combining the two for the West Greenland caribou. This study shows that AM caribou exhibit behavioral plasticity in relation to movement types and variability in seasonal home range sizes. Future climate change in the Arctic and in West Greenland will include both increasing temperatures and elevated precipitation (ACIA 2004), possibly with greater snowfall during winter. The capacity for utilizing multiple movement types as found within the AM caribou population is likely to favor its long-term survival in West Greenland.
Acknowledgements – KR was financially supported by Grønlands Bankens Erhvervsfond and The Government of Greenland.

References


Duquette, L. S. 1988. Snow characteristics along caribou trails and within feeding areas during spring migration. - Arctic 41: 143-144.


Rolandsen, C. M. et al. 2017. On fitness and partial migration in a large herbivore – migratory moose have higher reproductive performance than residents. - Oikos 126: 547-555.


Figure text

Figure 1. Study area where the Akia-Maniitsoq caribou population is located in West Greenland. The blue and red dots are GPS-positions from two individual caribou (no. 5708; migrating and no. 615882; resident) both covering a period of 400 days from May 8 2008–June 12 2009. The first position in the 400-day period is marked by an orange triangle. The digital elevation model used for this map was developed by the BPRC Glacier Dynamics Research Group, Ohio State University.

Figure 2. Net squared displacement (km²) for individual caribou (in grey) during May 8 2008–June 12 2009. Predicted values for the movement models are displayed as migration (blue), mixed-migration (red), dispersal (yellow), and resident (green). No caribou were moving according to the movement model “nomadic”. The number above each of plot is the identification number of each individual caribou.

Figure 3. Observed vs. predicted home range size (km²) with identity line and the correlation coefficient based on model 2 (a) and model 3 (c). Net squared displacement plotted against predicted home range size (km²) calculated using model 2 (b) or model 3 (d). Model 2 included body length and season, while model 3 included body length, movement type and season. Season (summer, winter) and movement type (migration, mixed migration, resident) are plotted for visualization.
Figure 2
Figure 3

(a) Predicted home range size (km$^2$) vs. Observed home range size (km$^2$) with $r=0.38$

(b) Predicted home range size (km$^2$) vs. Season and MovType

(c) Predicted home range size (km$^2$) vs. Observed home range size (km$^2$) with $r=0.49$

(d) Predicted home range size (km$^2$) vs. NSD$_{max}$
Table 1. Top 10 models explaining variations in home range size among individual caribou. The full model included the explanatory variables age, body condition (body con), body length, movement type (MovTyp) and season with first order interactions with season. Models 2 and 3 were used for predicting home range size.

<table>
<thead>
<tr>
<th>#</th>
<th>(Intercept)</th>
<th>con</th>
<th>length</th>
<th>MovTyp</th>
<th>Season</th>
<th>Season</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.495</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>80.418</td>
<td>0.000</td>
</tr>
<tr>
<td>2</td>
<td>-2.085</td>
<td>-</td>
<td>0.022</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>4</td>
<td>81.401</td>
<td>0.984</td>
</tr>
<tr>
<td>3</td>
<td>-5.018</td>
<td>-</td>
<td>0.042</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>6</td>
<td>82.194</td>
<td>1.776</td>
</tr>
<tr>
<td>4</td>
<td>1.434</td>
<td>0.010</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>4</td>
<td>82.846</td>
<td>2.428</td>
</tr>
<tr>
<td>5</td>
<td>1.276</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>82.954</td>
<td>2.537</td>
</tr>
<tr>
<td>6</td>
<td>0.452</td>
<td>-</td>
<td>0.006</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>5</td>
<td>83.252</td>
<td>2.835</td>
</tr>
<tr>
<td>7</td>
<td>1.644</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>5</td>
<td>83.694</td>
<td>3.276</td>
</tr>
<tr>
<td>8</td>
<td>-2.547</td>
<td>0.024</td>
<td>0.024</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>5</td>
<td>83.771</td>
<td>3.354</td>
</tr>
<tr>
<td>9</td>
<td>-2.304</td>
<td>-</td>
<td>0.022</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>83.978</td>
<td>3.561</td>
</tr>
<tr>
<td>10</td>
<td>-2.480</td>
<td>-</td>
<td>0.026</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>7</td>
<td>84.282</td>
<td>3.864</td>
</tr>
</tbody>
</table>
### Model 1: Migration
- **AICc**: Akaike Information Criterion with a correction for small sample size

### Model 2: Mixed-migration
- **d_AICc**: ΔAICc; difference between AICc value for best model and the other models

### Model 3: Dispersal
- **wi_AICc**: AICc weight

### Model 4: Resident
- Movement type based on AICc alone

### Model 5: Nomadic
- Movement type based on additional visual inspection of plots, and distance between seasonal home ranges
Manuscript II


Manuscript submitted to Polar Biology.
Resource selection and drivers of habitat choice in West Greenland caribou
Katrine Raundrup1,2, Peter Aastrup2,3, Josephine Nymand1, Christian Tøttrup4 and Jacob Nabe-Nielsen2,3

1) Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland
2) Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
3) Arctic Research Centre, Aarhus University, C.F. Møllers Allé 8, 8000 Aarhus C, Denmark
4) DHI GRAS A/S, Agern Allé 5, 2970 Hørsholm, Denmark

Abstract
Animals living in heterogeneous landscapes with resources distributed in patches should spend most of their time in profitable areas to optimize individual fitness. Their ability to seek out profitable areas can be studied by looking at their tendency to remain in profitable areas or by studying whether they prefer certain habitat types. We studied this by analyzing movement tortuosity (measured as residence time, RT) and habitat selection (quantified using resource selection functions, RSF) for caribou in central West Greenland. By combing RT and RSF we not only gained insight in habitat selection but also in the movement patterns behind the selection. The relationship between RT and different sets of environmental parameters (NDVI, elevation, snow depth and vegetation type) were modelled using generalized additive models. RT was related to various landscape characteristic. Elevation and vegetation type were included in all models that were supported by data. RT differed among vegetation types, but was not positively correlated with NDVI. Furthermore, RT was higher at low elevations in both winter and summer. We analyzed selection of home ranges within the landscape (2nd order habitat selection) and selection of patches within home ranges (3rd order habitat selection). The preferred home ranges included heath, copse and grassland. Within winter home ranges caribou preferred grassland and snowbed patches, and in summer they preferred copse and heath. As winter is the critical season for caribou survival the grassland and snowbed types are important in securing caribou future, and caribou- and land management must take this into account.
Introduction

When animals live in heterogeneous landscapes the resources needed for survival are likely to be distributed in patches (Johnson et al. 1992). Therefore, in order to optimize individual fitness, animals should spend a relatively large proportion of their time in profitable areas (Faucal 1999; Barraquand and Benhamou 2008). This may be particularly challenging for Arctic caribou that need to move around in the landscape as resource distributions and quality change over the year. Their ability to seek out profitable areas can be studied by either looking at their tendency to remain in profitable areas once they have found them (based on movement track tortuosity) or by studying whether they prefer certain habitat types (using resource selection functions, RSFs, Johnson 1980).

Animals can adaptively change their search mode according to the landscape. Extensive search is seen in animals during inter-patch movements while intensive (area concentrated) search is seen within high-quality patches (Barraquand and Benhamou 2008). Inter-patch movements are characterized by relatively linear movements through unprofitable areas, while area-restricted search with slower speed and increased turning angles are specifics of intra-patch movements (Byrne and Chamberlain 2012). Several different measures of track tortuosity have been suggested, including residence time (RT; Barraquand and Benhamou 2008). RT is an extension of the first-passage time statistic developed by Fauchald and Tveraa (2003) and is a measure of time spent in the vicinity (measured either as moved distance or time away from origin) of any location (Barraquand and Benhamou 2008). RT usually increases when an animal enters a profitable patch and decreases when it moves between such patches (Van Moorter et al. 2016).

One of the factors determining patch profitability for many herbivores is vegetation type, although various abiotic factors and the presence of predators also play a role. Different vegetation types have different forage species compositions and hence dissimilar profitability (e.g. Bliss and Matveyeva 1992; Walker et al. 2005). Herbivores can maximize their energy intake, and thereby increase individual fitness, by seeking out profitable patches with high productivity. In recent years, the normalized difference vegetation index, NDVI, has been found to correlate strongly with aboveground net primary productivity (e.g. Reed et al. 1994; Pettorelli et al. 2005; Westergaard-Nielsen et al. 2013), and the index is therefore often used as a proxy for patch quality for herbivores (Yu et al. 2003; Tveraa et al. 2007). In landscapes where the vegetation undergoes large seasonal changes, grazers may increase their food intake by tracking vegetation green-up during spring and summer (Nellemann and Thomsen 1994; Bischof et al. 2012). Aside from specific vegetation types, patch profitability may also be related to landscape features such as elevation and snow depth (Avgar et al. 2013). The vegetation at higher altitudes is often less dense and more scattered (Sieg and Daniëls 2005) and can therefore be regarded as less profitable. On the other hand higher altitude areas may also be areas with fewer flying insects and can thus alleviate
harassment during summer (Toupin et al. 1996). During winter, lower elevation areas are often connected with deeper snow, hindering access to forage and causing excess energy use to cross (Fancy and White 1987). A thorough understanding of what constitutes a profitable patch can be important for the management of species.

Habitat selection can be quantified using resource selection functions (RSFs) by estimating the relative probability of use of different habitat types (Boyce and McDonald 1999; Manly et al. 2002). If a habitat is used more than expected based on its availability, the habitat is termed preferred (Aebischer et al. 1993). Habitat selection can be assessed at different scales both spatially and temporally and is generally split into orders: selection of landscape (first order), selection of home range within the landscape (second order) and selection of patches within home range (third order; Johnson 1980; Johnson et al. 2002).

Although residency time can be used to describe habitat selection (Freitas et al. (2008) used first-passage time), recent studies suggest that this is best done when combined with RSFs (e.g. Anderson et al. 2008; Bastille-Rousseau et al. 2010). Unintended conclusions may be drawn when selection is based on either of the two alone since e.g. RT may be low in transit areas or at waterholes although those areas may be essential habitats for movement or for acquiring specific resources (Anderson et al. 2008; Benhamou and Riottes-Lambert 2012).

In the Arctic, caribou live in landscapes characterized by large seasonal variations in available habitat. These variations are mainly driven by snow cover during winter and vegetation green-up during spring and summer (Cooper et al. 2011). Caribou may choose to avoid areas with deep snow, as both traversing through a dense snow pack and digging through to the vegetation below is energetically costly (Fancy and White 1985; Ball et al. 2001). Furthermore, the timing of the vegetation greening is to a large extent determined by the distribution of snow patches (Walker et al. 1993), but the amount of snow in different areas can also influence patch productivity through its impact on the length of the growing season. In West Greenland, this heterogeneity is enhanced due to the physical appearance of the landscape with both rugged lowlands and high elevation mountains. Within this landscape, caribou are expected to optimize their individual fitness by adaptively changing their search mode when they encounter patches or habitats with high-quality resources. We therefore expect (1) RT to differ among vegetation types and to be positively correlated with NDVI, as animals should tend to remain in productive habitats with high NDVI. (2) We expect RT to be positively related to elevation during winter, as higher elevations are likely to be snow free or have shallow snow cover, which makes access to the vegetation easier than at lower elevations. The opposite is expected in summer, when it is easy to access the high quality vegetation at lower elevations. (3) We expect RT to be positively correlated with snow depth in winter, as deeper snow would prevent fast and easy movement. (4) We expect caribou to select home ranges in parts
of the landscape which likely indicates that these areas are particularly profitable (second order habitat selection) and similarly to select patches within their seasonal home ranges (third order habitat selection) that are especially profitable. As the distribution of resources changes during the year we expect (5) that the patch scale selection varies seasonally between winter and summer. By combining patch scale movement patterns (here as RT) with traditional habitat selection we intend to identify both the selection as well as the processes behind the selection. To the best of our knowledge, this has not been studied in caribou before.

Materials and methods

Caribou and study area

Caribou (Rangifer tarandus groenlandicus) in West Greenland are divided into 5 populations primarily based on geographical barriers that prevent mixing of animals from neighbouring herds. The Akia-Maniitsoq (AM) population is located in an area stretching from Nuuk in West Greenland and approximately 200 km north to the Sukkertoppen Iskappe (north of Maniitsoq) encompassing approximately 15000 km² (Fig. 1). The area is characterized by lowlands with innumerable lakes and streams towards the coast and steeper elevations in the inland rising to ca. 1300 m above sea level. Approximately 9000 km² are vegetated, while lakes, rivers, fjords, glaciers and un-vegetated boulders and rocks comprise the remainder of the area. The population size of the AM caribou herd is estimated at irregular intervals, most recently in the winter of 2010 with ca. 24000 animals (Cuyler et al. 2011). There are no large predators in West Greenland, but annual quota-based hunting takes place. Most of the hunting occurs close to the coasts (Cuyler et al. 2011), and is therefore not expected to impact RT or habitat selection in the caribou.

Data collection

GPS-collars were fitted on 40 female caribou (20 using Argos-GPS from Telonics, US, and 20 using Iridium-GPS from Vectronics Inc, Germany) in May 2008. All collars were equipped with automatic release mechanisms and logged with varying intervals. For the purpose of this study, data from 24 animals with 6-hour logging intervals (data collected at 00:00, 06:00, 12:00 and 18:00) covering a full calendar year (8 May 2008 to 8 May 2009) were used. Due to GPS-connection failure at some of the logging times, the resulting number of GPS-positions totalled 28555.

Vegetation mapping

Vegetation mapping is important in studies of animal feeding behavior, but up-to-date vegetation maps are often lacking. In this study we used Landsat Enhanced Thematic Mapper Plus (ETM+) to perform the required vegetation mapping. Multiple Landsat scenes were required to cover the entire study area. Image
selection was based on image quality (i.e. minimum of clouds/haze) and date of acquisition i.e. data from July/August 2008 was preferred and only when such data was not available other data was included i.e. anniversary data from +/- 1 year. All Landsat data were obtained with standard terrain correction obtained using ground control points and a digital elevation model (DEM) for topographic accuracy, and which in the absence of other reference material represents the best estimate of absolute positional accuracy (Tucker et al. 2004). Before merging the multiple Landsat images into a full area mosaic we applied a simple atmospheric correction procedure (Chavez 1989) to normalize the images and reduce any effect causing brightness changes not related to actual ground surface changes.

The area of interest is characterized by a complex vegetation cover that made classification based on spectral characteristics alone extremely confusing. The main problem was the patchiness of the vegetation cover along with its diversity making it hard to label with confidence in spite of a well-planned ground-truth data collection. Therefore, and in order to reach the required level of detail, a piecemeal classification approach was used for vegetation cover mapping. The approach is based on the rationale that particular terrain features favor the presence of certain vegetation types, and as such stratification by terrain features can help to reduce classification errors (Thenkabail 1999). First, we performed a preliminary unsupervised classification on the entire image mosaic. This classification was used to separate spectrally distinct classes at the landscape level i.e. water, snow/ice, non-vegetation and vegetation. Hereafter, the vegetation class was stratified into discrete subsets based on elevation and slope. For each of the subsets we performed unsupervised classification and labelling to map the vegetation classes at landscape level into vegetation types of relevance for the caribou population in Western Greenland. Class labelling was greatly facilitated by the use of vegetation indices, bi-spectral plots and field data. In a final step, all the subsets were merged to generate a single classification mosaic of the area with the seven major recognized vegetation types: heath, open heath, copse, fen, grassland, snowbed, and wind exposed ridge (Fig. 1 and Table 1). The spatial resolution of the vegetation map was 30m x 30m.

As a measure of productivity, NDVI from 8-day composite periods were obtained from MODIS satellite images with a resolution of 250 m (data from NASA/Goddard Space Flight Centre, http://modis.gsfc.nasa.gov/). Applying this resolution when extracting NDVI at the caribou GPS-positions resulted in many pixels with missing values (NAs). NDVI was therefore interpolated using the function python gdal_fillnodata.py in GDAL (GDAL 2017) with a maximum distance to search out for values to interpolate set at 3 pixels (corresponding to a maximum of 600 meters from the NA pixel in all four directions). Hence, the resolution of the interpolated NDVI values is \( \leq 1200 \) m. The interpolated NDVI
data was also used for calculating the average summer NDVI (June, July, August) for individual vegetation types within the study area (Table 1).

Elevation data were obtained from the digital elevation model with a resolution of 30m x 30m developed by Howat et al. (2014), while snow depth (measured as water equivalents in meters) was modelled using the regional climate model HIRHAM5 with a resolution of 7.5 km (Christensen et al. 2007; Langen et al. 2015).

Statistical analyses
Residence time (RT) was calculated according to Barraquand and Benhamou (2008). We chose virtual circles around each GPS-position with radii of 500 m based on 6-hour step lengths (average step length = 561m in 94 % of time steps) and with a 24 h limit within which the animal was allowed to walk outside the virtual circle and re-enter. The relationship between RT and different sets of environmental parameters were modelled using generalized additive models (GAMs). The full model included the landscape parameters vegetation type (factor variable), elevation, NDVI, and snow depth (continuous variables) as well as animal id and month (factor variables). Furthermore, the first order interaction between id and month was included since individual caribou are not expected to be equally stationary at different times of the year (Raundrup et al. submitted). Model selection was used to determine which parameters best described variations in RT. This was done by comparing all possible models containing different combinations of the variables using Akaike’s information criterion, AIC, where ΔAIC < 2 indicates substantial support for the model(s) (Burnham and Anderson 2002). Subsequently, model averaging (Johnson and Omland 2004) was used to predict RT in winter (January) and summer (July) based on all models with ΔAIC< 2.

Habitat selection was accessed using resource selection functions (RSF). The selection was studied at two different spatial scales: (1) based on the animals’ annual home ranges, calculated as 100% minimum convex polygons, within the landscape (i.e. 2nd order habitat selection), and (2) based on patches within seasonal (winter: January and summer: July) home ranges (i.e. 3rd order habitat selection). In both cases, the used habitat corresponded to the vegetation types found at the different GPS-positions. Habitat selection was calculated according to Aebischer et al. (1993) using the function compana in the R-package “adehabitat” (Calenge 2006). Significance was assessed using randomization tests with 500 repetitions and the Wilks lambda (Λ) test statistic was used throughout. Here p < 0.05 indicated that animals did not select habitats at random. Habitat(s) used more than expected from availability was classified as preferred. Habitat preference was ranged from most (+) to least (-) preferred and given a ranking value of 0–6 corresponding to the number of vegetation types. Significantly different habitat preferences were visualized by their ranking profiles. If zero values were found in the matrix of used
habitats they were replaced by a small value (0.001), following Aebischer et al. (1993). All statistical analyses were done in R (R Core Team 2017) while maps were made in QGIS (QGIS Development Team 2017).

Results
Residence time was related to various landscape characteristic. Elevation and vegetation type were included in all the models that were strongly supported by data (i.e. the top four models in Table 2). Only two of these included NDVI, and these suggested a negative correlation between RT and NDVI. The exclusion of elevation caused AIC to increase > 5 and excluding vegetation type caused it to increase > 45, showing that models without these variables were poorly supported by data. This only partly supported our expectation (1), as RT differed among vegetation types, but it was not positively correlated with NDVI (Table 2 and Fig. 2) in spite of clear variations in NDVI between the different vegetation types (Fig. 3). Contrary to our expectation (2) caribou had more tortuous movements at low elevations in both winter and summer. The predicted RT was generally higher in winter than in summer corresponding to longer periods in active search mode (Fig. 2). There was some support for our expectation (3), that RT was highest in areas with deep snow, as snow depth was included in two of the four best models. The correlation between snow depth and predicted seasonal RT was, however, weak (Fig. 3).

Animals did not choose habitat at random (expectation 4 and 5), but had specific preferences both when selecting their annual home ranges within the landscape (2nd order habitat selection; $\Lambda_{\text{annual}}$=0.167, p=0.002) and when selecting patches within seasonal home ranges (3rd order habitat selection; $\Lambda_{\text{winter}}$=0.477, p=0.020; $\Lambda_{\text{summer}}$=0.232, p=0.002), supporting expectation (4). Within individual annual home ranges caribou preferred heath, copse and grassland (no significant difference between the three vegetation types), while the remaining four vegetation types were less preferred (Table 3). During winter, caribou preferred grassland and snowbed while fen and ridge were less preferred. The remaining vegetation types were selected to the same degree (no significant difference between the vegetation types). During summer caribou preferred copse and heath while the remaining vegetation types were less selected (Table 3). This supported expectation (5), that caribou selected different habitats at different times of the year.

Comparison of RT and habitat selection revealed the processes behind the selection. Residence time differed among habitat types, and animals appeared to spend less time within the same areas when foraging in copse vegetation than elsewhere (Fig. 4). The animals spent a very large proportion of their time in heath and open heath habitats, reflecting the high availability of these vegetation types in the landscape. The animals spent more time in heath, copse and grassland than would be expected on basis of
the availability of these habitats alone. The animals spent less time in snowbeds and on ridges than expected had they selected habitats at random, but this did not cause them to move faster or have less straight movements than in other habitats (Fig. 4, top).

Discussion
We studied West Greenland caribou and their ability to seek out profitable areas by both looking at their tendency to remain in those areas measured as residence time (RT), and by using resource selection functions (RSFs). The main drivers of variation in RT were found to be vegetation type and elevation but to our surprise both NDVI, which is a proxy for productivity, and snow depth were poor predictors of RT (Table 2). As RT measures path tortuosity, which is influenced by whether the animal is foraging, a direct relationship between NDVI and RT would be expected if NDVI is a good measure of forage quality and/or quantity. At larger spatial scales that might be the case (Pettorelli et al. 2006) but at smaller scales this might not hold true (Mueller et al. 2011) if e.g. lush canopies cover vegetation not actually utilised by the caribou. At our study area the vegetation type with highest summer NDVI was copse (Fig. 3) which primarily is dense growth of willow or alder up to 3 meters tall. Willow or alder in themselves may not be the primary food source, but instead plants below the canopy layer that may or may not be eaten, although the intake of deciduous shrubs increases in the summer compared to winter diet (Thompson and McCourt 1981; Thing 1984; Larter and Nagy 2004).

Caribou selected annual home ranges (2nd order habitat selection) which were characterized by the presence of heath, copse and grassland (Table 3, top). This corresponds well with the selections done at patch scale (3rd order habitat selection), as grassland was the most preferred vegetation type during winter and copse the most preferred during summer (Table 3, middle and bottom). As heath covers ca. 25% of the vegetated area (Table 1) it holds resources utilised during summer, but also during migrations in spring and autumn (periods not included in the patch scale selection). During winter the most preferred habitats were grassland and snowbed. Particularly snowbed is important in this relation as it holds large quantities of lichens (Table 1) which are important parts of the winter diet (e.g. Joly et al. 2010). Furthermore, the wilted grasses and sedges found within the grassland type also constitute a substantial part of the winter diet in West Greenland (Lund et al. 2000; Raundrup et al. in prep.). Even though most of the vegetation at lower elevations is covered by snow during winter, animals appear to prefer digging to the lichens rather than moving to higher altitudes to forage on scattered and less energetically rich, but more easily accessible, vegetation. Although NDVI was found to be a poor predictor of variations in RT, animals appeared to prefer habitats with high NDVI during summer. The vegetation types copse and heath had the highest summer NDVI (Fig. 3) and RSFs indicated that those two habitats where most preferred by the caribou. The productivity in those areas reflect the fresh leaves of the dwarf shrubs as
well as grasses within the copse type. This switch in diet corresponds to findings both in Greenland and elsewhere in the Arctic, where deciduous shrubs and/or graminods make up a large proportion of the summer diet (Thing 1984; Denryter et al. 2017) and is triggered by the development of new, highly nutritious foliage (Klein 1990). The habitat selection during summer to some degree corresponds to previous findings for caribou in the Akia-Manitsoq population since heath but not copse were found to be selected in during a study in 1997-1999 (Tamstorf et al. 2005). Based on vegetation composition in buffer zones around individual caribou, Tamstorf et al. (2005) found the main drives of habitat selection. This method has since been found to tend to underestimate the importance of vegetation types with small areal extent (Boyce 2006).

The apparent difference between RT and habitat selection of the different vegetation types (Fig. 4 top and bottom) may be explained by the selective feeding displayed by caribou (Klein 1992; Larter and Nagy 1997). Seen on an annual scale copse is found to be used relatively much, but RT is relatively low. This may be due to their extensively grazing behaviour while walking (Gunn 1992) as they would seek out scattered but preferred plants under the copse canopy layer while on the move. When they get to an area with high density of their preferred forage e.g. lichens in snowbed the relative habitat use is low (as snowbed is primarily used during winter) but they adapt to feeding mode while there (RT is high).

The profitability of a habitat is not exclusively determined by vegetation type and landscape features such as elevation, but may also be related to their use as mating sites, as a means to avoid predators (DeCesare 2012) or anthropogenic disturbances (Colman et al. 2015). Another key factor affecting habitat profitability is the insect harassment, which during summer may become so severe that it causes animals to change foraging behaviour (Colman et al. 2003), which affects weight gain and survival in calves (Helle and Tarvainen 1984; Weladji et al. 2003). Caribou avoidance of insects can be accomplished by moving to more wind swept, higher elevations or seeking out larger snowbeds where temperatures are lower, which causes insects to be less active (Toupin et al. 1996). As mosquitoes, black flies, and oestrid flies are present in huge numbers on the Akia-Manitsoq range (Cuyler et al. 2012), we expected caribou to select wind exposed ridges or snowbeds to some degree during summer, but this was not the case as they preferred copse and heath types (Table 3). The time spent either on ridges or in snowbed may be of a duration not captured by the temporal resolution (6h) of the gps-locations applied in this study. Nonetheless the variations in RT (Fig. 4) capture this, as the highest RT\text{mean} is found in snowbeds where the caribou apparently adopt a more tortuous movement behaviour. This illustrates the importance of investigating both animal movements and habitat selection to get a full understanding of the factors that influence animal behaviour.
Winter is the most critical time of the year regarding caribou survival, and in this season most of the Akia-Maniitsoq area is snow covered. Climate change is expected to result in increased precipitation and warming especially during winter (ACIA 2004). The increased precipitation may give rise to increased snow cover and depth and may result in increased winter mortality (Tyler 2010). The warming may potentially increase the number of episodic snowmelt events (Pedersen et al. 2015) and warming combined with precipitation is expected to increase the number of rain-on-snow events (Putkonen and Roe 2003). Both are often followed by icing of the vegetation can therefore have severe effects on the caribou as they are unable to reach their forage (Wilson et al. 2013). The preferred winter vegetation types, grassland and snowbed are prone to winter icing as they occur mainly in lowlands or at lower elevations.

To the best of our knowledge this study is the first combining RT with habitat selection in caribou, and it highlights the need for analysing both to get a fuller picture of habitat selection and the related movement patterns. The Akia-Maniitsoq population is one of several caribou populations in West Greenland with the largest being the Kangerlussuaq-Sisimiut population (ca. 98000 caribou; Cuyler et al. 2011) north of AM. Habitat selection and movement patterns in the two populations are likely comparable. This assumption is based on the fact that the vegetation composition at the two locations are relatively similar with more than 55% of the areas covered by heath types (Tamstorf 2001; this study). Furthermore, there are no large predators or currently no large scale infrastructures close the either of the caribou areas (aside from Nuuk, Maniitsoq, Kangerlussuaq and Sisimiut) and in that respect they are comparable. The most important vegetation types for the AM caribou were found to be snowbed and grassland during winter, and heath and copse during summer. These vegetation types aside from heath have limited distributions in both areas, but are highly preferred. Compared to most other Arctic wild caribou populations the caribou in West Greenland are particularly interesting as their habitat selection is expected to display “undisturbed selection”. That is, caribou in other parts of the Arctic have to trade off selection of the most profitable habitats with the presence of predators (e.g. Joly et al. 2010; Dussault et al. 2012; Bastille-Rousseau et al. 2015), anthropogenic disturbances (e.g. Polfus et al. 2011; Johnson and Russell 2014) or repeated wild fires (e.g. Joly et al. 2010). Therefore, future management of both the West Greenland caribou but more importantly, land management should take this into account by securing amble areas where especially snowbed and grassland vegetation is present during winter. This may not be an easy task as both types occur very scattered, but they are essential for the winter survival of the West Greenland caribou.

Acknowledgements
KR was financially supported by Grønlands Bankens Erhvervsfond and The Government of Greenland. The Moderate Resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index
(NDVI) used in this study was processed and produced by the NASA/Goddard Space Flight Center’s Global Inventory Modeling and Mapping Studies (GIMMS) Group through funding support of the Global Agricultural Monitoring project by USDA’s Foreign Agricultural Service (FAS).

References


Benhamou S, Riotte-Lambert L (2012) Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. Ecological Modelling 227:112-116


Klein DR (1990) Variation in quality of caribou and reindeer forage plants associated with season, plant part and phenology. Rangifer Special Issue No. 3:123-130


Thompson DC, McCourt KH (1981) Seasonal diets of the Porcupine Caribou Herd. The American Midland Naturalist 105:70-76


48


Figure legends

**Fig. 1** The Akia-Maniitsoq area with GPS-locations from three caribou plotted in orange, red and blue. The map is based on the distribution seven vegetation types (heath, open heath, copse, fen, grassland, snowbed and wind exposed ridge) with a spatial resolution of 30x30 meter. The black line marks the area of interest.

**Fig. 2** Predicted residence times (RT) as a function of elevation, NDVI and snow depth during January (black) and July (grey), calculated using model averaging of the four best GAM models (ΔAIC <2). Values (mean, minimum, maximum) for RT predictions in January were: elevation (117.306, 29.532, 368.472), NDVI (0.114, 0.000, 0.384) and snow depth (0.211, 0.000, 0.237). In July the corresponding values were: elevation (193.003, 20.736, 717.906), NDVI (0.568, 0.316, 0.664) and snow depth (0.000, 0.000, 0.000). In both months the vegetation type used for model averaging was open heath (the most common vegetation type in the area). Predicted RT represent data from one animal, but the trend was the same for all individuals while the predicted RT was dependent on individual caribou.

**Fig. 3** Variation in summer normalized difference vegetation index (NDVI) in the seven vegetation types (heath, open heath, copse, fen, grassland, snowbed, and wind exposed ridge) in the Akia-Maniitsoq area.

**Fig. 4** Average annual residence time (RT) (top), proportion of time spent (observations in vegetation type/total number of observations; middle), and relative habitat use (observations in vegetation type/area of vegetation type; bottom) in the different vegetation types.
Fig. 1
Fig. 2
Fig. 3
Fig. 4

![Graph showing Relative Time (RT) and Proportion of Time for different habitats.](image)
<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Area (km²)</th>
<th>Area (%)</th>
<th>Dominant species</th>
<th>Moss (%)</th>
<th>Lichen (%)</th>
<th>NDVI</th>
</tr>
</thead>
</table>
| Heath (>20% shrub cover) | 2232.1 | 24.8 | *Empetrum nigrum*  
*Betula nana*  
*Vaccinium uliginosum*  
*Salix glauca*  
*Phyllodoce coerula*  
*Diapensia lapponica*  
*Loiseleuria procumbens*  
*Ledum sp.* | 25 | - | 0.536 |
| Open heath (<20% shrub cover) | 3031.9 | 33.7 | *Vaccinium uliginosum*  
*Betula nana*  
*Cassiope tetragona*  
*Phyllodoce coerula*  
*Ledum palustre*  
*Salix glauca* | 20 | 20 | 0.451 |
| Copse | 574.8 | 6.4 | *Salix glauca*  
*Calamagrostis langsdorfii*  
*Ledum sp.*  
*Coptis trifolia*  
*Empetrum nigrum*  
*Deschampsia flexuosa* | 10-20 | - | 0.599 |
| Fen | 382.1 | 4.2 | *Eriophorum angustifolium*  
*Carex rariflora*  
*Carex saxatilis*  
*Salix arctophila* | >50 | - | 0.455 |
| Grassland | 413.8 | 4.6 | *Calamagrostis lapponica*  
*Carex brunescens*  
*Carex bigelowii*  
*Deschampsia flexuosa*  
*Luca spicata* | 30-40 | - | 0.485 |
| Snowbed | 93.2 | 1.0 | *Salix herbacea*  
*Carex bigelowii*  
*Sibbaldia procumbens*  
*Polygonum viviparum*  
*Silene acaulis*  
*Harrimanella hypnoides*  
*Hierochloë alpina*  
*Luca spicata* | 50 | 20 | 0.443 |
| Ridge | 2274.0 | 25.3 | *Diapensia lapponica*  
*Ledum palustre*  
*Silene acaulis*  
*Hierochloë alpina*  
*Carex bigelowii*  
*Rhododendron lapponicum* | 50-60 | <5 | 0.354 |
Table 2 Top 10 models explaining variations in residence time among individual caribou. The full model included the explanatory variables elevation, id, month, NDVI, snow depth, vegetation type, and first order interaction with id and month

<table>
<thead>
<tr>
<th>(Intercept)</th>
<th>Elevation</th>
<th>ID</th>
<th>Month</th>
<th>NDVI</th>
<th>Snow depth</th>
<th>Veg type</th>
<th>ID: Month</th>
<th>df</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>825.877</td>
<td>-0.020</td>
<td>+</td>
<td>+</td>
<td>-8.472</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>303</td>
<td>0.000</td>
<td>0.282</td>
</tr>
<tr>
<td>824.344</td>
<td>-0.020</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>303</td>
<td>0.063</td>
<td>0.274</td>
</tr>
<tr>
<td>824.147</td>
<td>-0.019</td>
<td>+</td>
<td>+</td>
<td>-4.410</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>303</td>
<td>0.666</td>
<td>0.202</td>
</tr>
<tr>
<td>825.646</td>
<td>-0.020</td>
<td>+</td>
<td>+</td>
<td>-8.233</td>
<td>4.224</td>
<td>+</td>
<td>+</td>
<td>305</td>
<td>0.720</td>
<td>0.197</td>
</tr>
<tr>
<td>824.958</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>301</td>
<td>5.904</td>
<td>0.015</td>
</tr>
<tr>
<td>824.756</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-4.489</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>303</td>
<td>6.457</td>
<td>0.011</td>
</tr>
<tr>
<td>826.231</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-6.907</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>302</td>
<td>6.522</td>
<td>0.011</td>
</tr>
<tr>
<td>825.992</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-6.668</td>
<td>4.341</td>
<td>+</td>
<td>+</td>
<td>304</td>
<td>7.170</td>
<td>0.008</td>
</tr>
<tr>
<td>822.466</td>
<td>-0.025</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>289</td>
<td>45.265</td>
<td>0</td>
</tr>
<tr>
<td>822.261</td>
<td>-0.025</td>
<td>+</td>
<td>+</td>
<td>-4.222</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>291</td>
<td>45.985</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3. Habitat selection with simple ranking matrices for West Greenland caribou. 2nd order habitat selection i.e. selection of home ranges within the landscape (top), and 3rd order habitat selection i.e. locations within home ranges in winter (middle) and summer (bottom). Habitat preference is ranged from most (+++) to least (---) preferred. A triple sign represents significant deviation from random at p<0.05. The most preferred habitats are marked in bold. The rank value provides a rank of the habitat types, and corresponds to the number of “+” for each habitat type.

<table>
<thead>
<tr>
<th>ANNUAL</th>
<th>Heath</th>
<th>Open heath</th>
<th>Copse</th>
<th>Fen</th>
<th>Grassland</th>
<th>Snowbed</th>
<th>Ridge</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heath</td>
<td>0</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>6</td>
</tr>
<tr>
<td>Open heath</td>
<td>---</td>
<td>0</td>
<td>---</td>
<td>+++</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>3</td>
</tr>
<tr>
<td>Copse</td>
<td>-</td>
<td>+++</td>
<td>0</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>5</td>
</tr>
<tr>
<td>Fen</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0</td>
<td>---</td>
<td>+++</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td>Grassland</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+++</td>
<td>0</td>
<td>+++</td>
<td>+++</td>
<td>4</td>
</tr>
<tr>
<td>Snowbed</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ridge</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>+</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>WINTER</th>
<th>Heath</th>
<th>Open heath</th>
<th>Copse</th>
<th>Fen</th>
<th>Grassland</th>
<th>Snowbed</th>
<th>Ridge</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heath</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>---</td>
<td>-</td>
<td>+++</td>
<td>4</td>
</tr>
<tr>
<td>Open heath</td>
<td>-</td>
<td>0</td>
<td>+</td>
<td>+++</td>
<td>---</td>
<td>-</td>
<td>+++</td>
<td>3</td>
</tr>
<tr>
<td>Copse</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>+</td>
<td>---</td>
<td>-</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td>Fen</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Grassland</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>0</td>
<td>+</td>
<td>+++</td>
<td>6</td>
</tr>
<tr>
<td>Snowbed</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>-</td>
<td>0</td>
<td>+++</td>
<td>5</td>
</tr>
<tr>
<td>Ridge</td>
<td>---</td>
<td>---</td>
<td>-</td>
<td>+</td>
<td>---</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>SUMMER</th>
<th>Heath</th>
<th>Open heath</th>
<th>Copse</th>
<th>Fen</th>
<th>Grassland</th>
<th>Snowbed</th>
<th>Ridge</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heath</td>
<td>0</td>
<td>+++</td>
<td>-</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>5</td>
</tr>
<tr>
<td>Open heath</td>
<td>---</td>
<td>0</td>
<td>---</td>
<td>+</td>
<td>---</td>
<td>---</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Copse</td>
<td>+</td>
<td>+++</td>
<td>0</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>6</td>
</tr>
<tr>
<td>Fen</td>
<td>---</td>
<td>-</td>
<td>---</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Grassland</td>
<td>-</td>
<td>+++</td>
<td>---</td>
<td>+++</td>
<td>0</td>
<td>-</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>Snowbed</td>
<td>-</td>
<td>+++</td>
<td>---</td>
<td>+++</td>
<td>+</td>
<td>0</td>
<td>+++</td>
<td>4</td>
</tr>
<tr>
<td>Ridge</td>
<td>-</td>
<td>+</td>
<td>---</td>
<td>+</td>
<td>---</td>
<td>0</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>
Manuscript III

Raundrup K, Nymand J, Cuyler C, Aastrup P, Zinglersen KB, Nabe-Nielsen, J. Temporal change in caribou winter diet in West Greenland – have 10 years made a difference?

Submitted to Polar Research.
Temporal change in caribou winter diet in West Greenland – have 10 years made a difference?

Katrine Raundrup\textsuperscript{a,b,*}, Josephine Nymand\textsuperscript{a}, Christine Cuyler\textsuperscript{a}, Peter Aastrup\textsuperscript{b,c}, Karl Brix Zinglersen\textsuperscript{a}, Jacob Nabe-Nielsen\textsuperscript{b,c}

\textsuperscript{a}Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland
\textsuperscript{b}Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
\textsuperscript{c}Arctic Research Centre, Aarhus University, C.F. Moellers Allé 8, 8000 Aarhus C, Denmark

Abstract

We studied temporal changes of vegetation composition and caribou diet during 10 years in the Akia-Maniitsoq winter range in West Greenland. Vegetation composition was studied using vegetation maps derived from satellite images from 1997 and 2008, and caribou diet changes were assessed using rumen samples collected in late winter from the same two years. The shrubification observed in other parts of the Arctic was also evident in Akia-Maniitsoq. Between 1997 and 2008 heath cover increased by ca. 10% and copse by ca. 5%. The caribou diet composition also changed over this period, with increases in lichen and moss intake by 24% and 11%, respectively. The vegetation composition is likely to have changed in response to a combination of climate changes and decreased grazing intensity associated with a decreasing number of caribou, but the impacts of these changes on habitat use and long-term dynamics of the caribou population remain elusive.

Keywords: caribou, \textit{Rangifer tarandus groenlandicus}, shrub expansion, West Greenland, winter diet
Introduction

Winter is a crucial time for one of the key arctic herbivores, the caribou (*Rangifer sp.*), as temperatures are low, food is scarce, and food quality reduced (Marchand 1996). The vegetation is covered by snow and the forage is characterized by low amounts of nitrogen (N), which is essential for physical processes including body maintenance and reproduction (Barboza and Parker 2006; Barboza and Parker 2008). Poor conditions on the winter ranges can negatively impact individual survival, resulting in population declines (Roby and Thing 1985). For pregnant females a reduced body condition may also adversely influence foetal growth, birth weights of calves, calf growth rates, and milk production (White 1983; Cameron et al. 1993). Therefore, it is important to know the types of vegetation available on the winter ranges, and which are utilized as forage by the caribou.

The composition of the Arctic vegetation is expected to change in response to climate warming and changes in the amount of herbivory. Shrubs, in particular, have already been found to become increasingly dominant (Sturm et al. 2001; Myers-Smith et al. 2011; Myers-Smith et al. 2015) and the predicted negative effect on lichen abundance (Chapin et al. 1995) has already been observed in some areas (Cornelissen et al. 2001; Vanneste et al. 2017). The expansion of shrubs has been found to be countered by grazing of large herbivores in some areas (Manseau et al. 1996; Post and Pedersen 2008; Olofsson et al. 2009) although grazing had no effect on shrub distribution in others (Damgaard et al. 2016). Contrary to shrubs and graminoids, lichens are highly susceptible to grazing and trampling (Helle and Aspi 1983; Manseau et al. 1996) and may need decades or even centuries to regrow following deterioration (Kumpula et al. 2000).

In winter many caribou populations rely on a diet dominated by lichens (Boertje 1984) which are low in N, but energy rich and easily digestible (Helle and Aspi 1983). Caribou can survive on this diet because their lowered winter metabolic rate requires less protein and because they partly rely on energy from fat stores built up during summer (Klein 1990). However, the switch to a lichen dominated diet poses a challenge, especially for pregnant females, as the lowered N intake may result in loss of muscle protein and hamper foetal development, ultimately influencing calf survival (Cameron et al. 1993; Parker et al. 2005). Therefore, though many caribou populations rely mainly on a lichen dominated winter diet, they do need to forage on vascular plants as well to meet their N requirements (Klein 1990). In the Arctic, temperature fluctuations in winter (ACIA 2004) may have a large impact on herbivores relying on the sparse vegetation (Putkonen and Roe 2003; Hansen et al. 2011). When winter temperatures increase above freezing point it may cause the top layer of the snow to thaw (Pedersen et al. 2015). If increased temperatures are combined with precipitation it may result in rain-on-snow events and these are expected to become more frequent in the future (Putkonen and Roe 2003). Both types of incidences are likely to be
followed by refreezing and thereby result in the formation of dense layers of ice on the vegetation (Wilson et al. 2013), making the forage less accessible for the caribou. In winter when the vegetation is covered by snow, caribou need to invest energy in crater digging in up to 1 meter of snow (Fancy and White 1985; Gaio-Oliveira et al. 2006). The amount of energy (and time) invested will have to be traded off with the amount of energy the caribou can get from the forage below the snow (Fancy and White 1985). In years where the snow is covered by ice the caribou may therefore have to use individual feeding craters more extensively and thus deviate from a lichen dominated diet (Ihl 2010).

Micro-histologically analysing epidermal plant fragments in either faecal or rumen samples can be used to assess the diet in herbivores. There are weaknesses to each of these types of samples as different plants have different digestibility and retention time in the gastrointestinal system, but both provide estimates of the diet composition (Anthony and Smith 1974; Leslie et al. 1983; MacCracken and Van Ballenberghe 1993). Faecal samples are often easily available and provide a non-invasive method to assess diet, but the method tends to be less accurate than using rumen samples (Smith and Shandruk 1979) as it often underestimates easily digested forage items, such as lichens and forbs (Thomas et al. 1984; McInnis et al. 1986). Rumen samples are considered to better reflect the animals’ diet as the plants species are less digested, although the readily digestible lichens are prone to be underestimated here as well (Gaare et al. 1977). In spite of this, rumen samples are used when samples from culled animals are possible.

Caribou in West Greenland face the same issues as caribou elsewhere in the Arctic, namely changes in the climate with gradually increasing temperatures and precipitation throughout the past century (Mernild et al. 2014; Mernild et al. 2015) potentially affecting the vegetation composition and therefore ultimately the diet composition. The aim of this study was to describe the decadal changes in vegetation composition in the Akia-Manitsoq area in West Greenland and associated changes in caribou winter diet in the period 1997–2008. As both temperature and precipitation have increased, we expect a change towards increasing shrubification, which would be evident from increased heath and copse cover in 2008 compared to 1997. If shrubification is indeed occurring, we expect the change in vegetation composition to affect winter diet since increased shrub cover may result in fewer lichens (Cornelissen et al. 2001; Vanneste et al. 2017). Caribou are known to be able to change from a lichen based winter diet to a diet with sedges and graminoids when lichens on their winter ranges become scarce (Roby and Thing 1985). We therefore expect a decrease of lichens in the diet in 2008 compared to 1997 along with a corresponding increase in graminoids. In a time where the climate is changing rapidly this study will provide valuable knowledge on how vegetation changes may affect the winter diet of caribou.
Materials and methods

Study area

The study area (ca. 4000 km$^2$) is located in the southwest part of the Akia-Maniitsoq caribou management area (ca. 15000 km$^2$) close to Nuuk in West Greenland (Fig. 1). The study area is characterized by rugged lowlands with an average elevation of 198m. Long-term temperatures (1785–2010) average 6.0°C ± 1.7°C (mean ± SD) in summer (June–August) and -8.8°C ± 4.4°C in winter (December–April), while long term (1890-2010) winter precipitation averages 202.1mm ± 125.4mm. For 1997–2008, summer and winter temperatures were 7.2°C ± 1.3°C and -6.6°C ± 3.7°C, respectively, while the winter precipitation was 326.8mm ± 89.2mm, all of which were above the long term average (Cappelen 2017).

Satellite based vegetation mapping was done in 1997 (Tamstorf 2001) and 2008 (Tøttrup 2009, Raundrup et al. unpubl. ms) and resulted in comparable maps with 5 vegetation types: heath, copse, fen, grassland, and wind exposed ridge (Fig. 1). An additional type (“other”) comprised non-vegetated areas including rocks, sediment, water, snow/ice, clouds and pixels with no data. The 1997 map was based on Landsat 5 (Thematic Mapper, TM sensor) images from 1 July 1993 and 20 July 1995, while the map from 2008 was based on Landsat 7 (Enhanced Thematic Mapper Plus, ETM+ sensor) images from 28 July 2008 (80% of the images). The ETM+ is a further development of the TM, but in general, the two optical sensors are of similar specifications concerning image pixel sizes and divisions of observed wavelengths. The methods for post processing corrections of the images were comparable for the years 1997 (overall classification accuracy: 56%) and 2008 (overall classification accuracy: 81%), and the vegetation maps were, thus, directly comparable. However, two noticeable differences should be taken into consideration. Firstly, the vegetation type categories varied slightly between the two years, but after consultation with C. Bay (senior scientist and expert botanist who participated in the vegetation analyses in both 1997 and 2008), decision was made on the 5 types mentioned previously. This entailed combining two heath types (“heath” with >20% cover of shrubs and “open heath” with <20% cover of shrubs) recognized in 2008 but not in 1997. Secondly, a difference between the two maps originate from the ground-truthing process. In both years ground-truthings were done by analysing the vegetation using either the pinpoint method (in 1997, Molau and Mølgaard 1996) or investigating ca. 25 km transects within a different vegetation types (in 2008, unpubl. data). A total of 116 and 152 vegetation analyses done in 1997 and 2008, respectively (Tamstorf 2001; Tøttrup 2009). A disparity between the two years relates to the GPS-positions taken at each vegetation analysis, as the uncertainties in 1997 (prior to GPS Selective Availability discontinued in 2000) were larger compared to 2008. While uncertainties of GPS-positions in 2008 were well below 10m (Rodgers 2001), the uncertainties in 1997 were ca. 30m when using a stationary GPS and averaging positions over 30 minutes (Tamstorf 2001), which is similar to the pixel size of the final map (25x25m). We assume the uncertainties of the 1997 GPS-positions are the same for all ground-truthing, which makes
the vegetation composition (%) comparable with the 2008 map (spatial resolution 30x30m). Despite the differences on how the maps were produced we feel confident in comparing the vegetation cover (%) in 1997 with 2008.

Study species
The caribou (R. tarandus groenlandicus) in the Akia-Maniitsoq population are partial migrators with ca. 80% classified as migrators while the remainder are resident (Raundrup et al. in prep). The population numbers have been decreasing since the early 2000s with ca. 46000, 36000 and 24000 animals in 2001, 2005 and 2010 respectively (Cuyler et al. 2003; Cuyler et al. 2005; Cuyler et al. 2011).

Rumen samples
During late winters (March–April) of 1997 and 2008 a total of 24 and 41 female caribou were culled within the same area (Fig. 1). Rumen samples were collected for diet analysis. In both 1997 and 2008, for each animal, the rumen and reticulum contents were first mixed and then 1 litre of subsample was stored frozen until analyses could be done. Analysis methodologies of the 1997 and 2008 rumen samples differed but were comparable and resulted in data at plant functional group level (shrub, forb, graminoids, lichen, moss and unknown) or at genus level. In 1997 rumen samples were thawed and mixed and a subsample (ca. 2 teaspoons) was washed onto a gauze net with a mesh size of 2 mm. From each sample, 2x ca. 200 randomly selected plant epidermal fragments within a specific set of cells in the ocular grid were analysed to highest possible taxonomic level using a stereo microscope with 30-100x magnification (Lund et al. 2000). This was done by researchers from the Norwegian Institute for Nature Research and resulted in diet composition at functional plant group level i.e. shrub, forb, graminoid, lichen and moss with an additional group encompassing epidermal fragments where functional group could not be identified with certainty (“unknown”). In 2008, samples were thawed, subsampled at 125–135g wet weight, and dried at 60 °C until stable dry weight was reached (3-4 days). The dried samples were shipped to and analysed at Wildlife Habitat/Nutrition Lab, Washington State University, US. For each sample 2x ca. 100 plant fragments were analysed to highest possible taxonomic level using a stereo microscope. This resulted in functional plant groups (same as for 1997 samples) and when possible, epidermal fragments were identified to plant genera.

Statistical analyses
Changes in the vegetation type cover are only studied as percentage change. We tested if the diet composition differed between 1997 and 2008 using a χ²-test of independence, where H₀ corresponded to no change in diet between the two years. The comparison was done at functional plant group level. The test was done on count data of epidermal fragments in the rumen samples (total number based on the
number of fragment from all individuals). Maps were made using QGIS (QGIS Development Team 2017) while analyses and plots were done in R (R Core Team 2017).

Results
The distribution of vegetation types changed during the study period (Fig. 1, Table 1). The major change occurred with heath and copse as they combined increased their distribution by ca. 15% (from ca. 41% to 56%). This was at the expense of areas with little vegetation e.g. wind exposed ridge and fen areas which decreased ca. 17% and 5% respectively (Table 1).

Akia-Maniitsoq caribou cows showed distinct differences in late winter diet between 1997 and 2008 ($\chi^2=3020.2$, df=5, p<<0.05, Fig. 2). This was evident in all of the functional plant groups within the diet (Table 2). The amount of shrubs and graminoids in the diet decreased from ca. 26% to ca. 7% and ca. 18% to 9% respectively, while the portion of lichens and moss increased from ca. 40% to ca. 64% and 9% to 20% respectively. Although all plant epidermal fragments (aside from 7.4% in the 1997-samples) were identifiable at functional plant group level, diet comparisons at the genus level were impossible, as hardly any of the fragments were identifiable to that level in 1997 (data not presented). In the 2008 diet (Table 3), however, it was clear that important lichens included the genera Cladina/Cladonia, Bryoria and Cetraria/Dactylina, which accounted for >80% of the lichens eaten. The second most abundant diet component was mosses with the genera Polytrichum or Sphagnum making up more than 35% of mosses identified. However, more than 60% of mosses remained unidentified. Of the graminoids, Carex sp. were by far the most abundant, constituting more than 50% of the identified fragments. Empetrum, Betula and Vaccinium were the most abundant shrubs (Table 3).

Discussion
In the period 1997–2008, West Greenland has experienced both increased winter temperature and precipitation (Mernild et al. 2014; Mernild et al. 2015). These appear to have changed the vegetation composition in the Akia-Maniitsoq region, and may be related to the changed late winter diet of Akia-Maniitsoq caribou cows. Furthermore, it has coincided with a decline in Akia-Maniitsoq population abundance.

Precipitation and warming can limit forage availability in winter. Increasing temperatures may potentially raise the number of days where temperature rises above freezing point resulting in episodic snow melt events. These events have become increasingly more frequent in the Nuuk area, and Pedersen et al. (2015) identified up to 16 episodic snow melt events per year during 1979–2013, though not all of those would have consequences for the caribou. Increased precipitation during winter (Mernild et al. 2015) will
likely fall as snow and therefore result in increased snow depth. This alone may be problematic for the caribou as they will need additional energy to dig through increasing amounts of snow to get to the forage beneath (Fancy and White 1985). Increased precipitation combined with winter temperatures above freezing may result in rain-on-snow (Putkonen and Roe 2003). Both episodic snowmelt events and rain-on-snow can be followed by below-zero temperatures. The resultant icing of the snow layer or of the exposed vegetation limits forage availability for caribou, which may have detrimental consequences at population level (Hansen et al. 2011).

Warmer summers (Mernild et al. 2014) appear to have increased plant productivity (Sturm et al. 2001) and may have been the main driver of the shrubification we observed between 1997 and 2008. The most pronounced changes in the vegetation composition were the increase in the vegetation types heath and copse, which increased 10.2% and 4.9% respectively. This expansion appeared to take place into areas that previously had little vegetation cover i.e. the wind exposed ridges. Though not analysed here, we suggest this may be due to heath vegetation (primarily deciduous dwarf shrubs) moving up elevation gradients in the landscape as wind exposed ridges are mainly found at higher elevations. This greening corresponds to findings in other parts of the Arctic (Sturm et al. 2005; Myers-Smith et al. 2011) although the process in Greenland is equivocal as it has been recorded at some locations (Jørgensen et al. 2013) while it is not evident at others (Daniëls et al. 2011; Damgaard et al. 2016). The shrubification is likely not beneficial for the caribou. Lichens are essential in the winter diet for many caribou populations, including this study’s Akia-Maniitsoq cows (Table 4), and shrubs are likely to compete with lichens (Cornelissen et al. 2001). Shrubification could potentially reduce winter forage quantity and quality for caribou that rely on a lichen based winter diet (Sturm et al. 2005). Still, parts of the Akia-Maniitsoq area with open heath have been observed to contain ca. 20% lichens (Raundrup et al unpubl. data). Herbivore grazing can reduce, but not prevent, the expansion of shrubs (Post and Pedersen 2008; Christie et al. 2015), however grazing pressure in the Akia-Maniitsoq area (ca. 3 caribou km\(^2\) in 2001 reduced to ca. 1.6 caribou km\(^2\) in 2010; Cuyler et al. 2003; Cuyler et al. 2011) appears insufficient to counteract the present shrubification. This is also in correspondence with findings in northern Norway where caribou abundance had to be higher than 5 animals per km\(^2\) to impede the expansion of shrubs (Bråthen et al. 2017).

The Akia-Maniitsoq caribou winter diet changed significantly between 1997 and 2008. Since samples were only analysed at the functional plant group level, the difference would not be attributable to samples being processed at two laboratories. However, we acknowledge differing analyses may play a role for assessment to the genus level and thus we did not analyse diet changes at this level. The dietary changes were particularly evident in the caribou intake of lichens, which increased from 40.1% in 1997 to 63.3% in 2008. The shrub intake decreased from 25.9% to 6.9% in the same period. This finding is the opposite
of what we had expected in a landscape where dwarf shrubs and copse become increasingly dominant, but as we are only able to discern between “heath” and “open heath” in the 2008 vegetation map, the shrubification may be towards the “open heath” type where lichens cover can be ca. 20%. If this is the case, the caribou will have better opportunity to graze on lichens. If this is not the case, the finding could result from caribou becoming increasingly selective in their forage choices (Klein 1992); however, we do not have data to determine which explanation is more likely. An alternative explanation that needs to be mentioned relates to the halving of the numbers of caribou in the AM-population that took place between 2001 and 2010. Giving a zero-vegetation change scenario a 50% decrease of grazers would result in effectively doubling the available lichen area per caribou.

Another distinct difference between the winter diet in 1997 and 2008 is the amount of moss. Almost 20% of the rumen contents in 2008 were mosses compared to 8.5% in 1997. As the digestibility of mosses is generally thought to be low (Thomas et al. 1984) this may have negative implications for winter survival in the Akia-Maniitsoq population. Compared to other caribou populations, the moss intake in late winter was above the norm (Table 3). We suggest two possible explanations. First, the high intake of moss in 2008 may have arisen from the snow conditions that year, e.g. deep snow in combination with ice layers from thaw-refreeze episodes. Combined these would increase the energetic cost of cratering through the snow (Fancy and White 1985). Under these conditions, caribou might utilize each feeding crater more intensely, which potentially could increase the intake of a mixture of mosses and lichens (Ihl 2010).

Excess intake of mosses can be connected to overgrazed lichen-depleted winter ranges (Ihl and Barboza 2007), and was the suggested primary cause for the extremely high moss intake observed in the Isortoq population, South Greenland (Nymand 2004). Figure 2 indicates that this explanation is not supported for Akia-Maniitsoq. Caribou are considered selective feeders and it is therefore counterintuitive that they ingest mosses by chance alone (Klein 1992). However, the most plausible explanation for the high dietary component of mosses is the involuntarily intake while feeding on lichens.

Defining good or poor winter ranges may not be a straightforward task. Lichen rich ranges may be considered good, but if the lichens are covered by icing due to episodic snowmelt events or rain-on-snow, or high snow depth, the ranges would be considered less good or even poor. Shrubification may result in reduced lichen cover, which would result in poor quality ranges, but if shrubification results in increased cover of open heath it may favour expansion of lichens and result in better quality ranges. In Arctic North America the shrub expansion has resulted in plants with strong anti-browsing defences, which therefore affected the range quality negatively. This has been associated with dramatically declining caribou populations in recent decades (Fauchald et al. 2017). Given the current increasing shrubification of the Akia-Maniitsoq region combined with the declining abundance of this caribou population, we suggest
that all West Greenland caribou populations may become more vulnerable to decline with climate warming.

Acknowledgement
We would like to thank two anonymous reviewers for providing valuable comments to previous versions of this manuscript.

References


Figure legends

Figure 1.
The Akia-Maniitsoq area with GPS-locations of the caribou culled in 1997 and 2008. The background vegetation maps are from 1997 and 2008 with five vegetation types (heath, copse, fen, grassland, and WER: wind exposed ridge). The black line frames the area of interest regarding vegetation changes. The spatial resolution of the 1997 and 2008 maps are 25x25m and 30x30m, respectively.

Figure 2.
Caribou rumen content of the different dietary components at plant functional group level in late winter 1997 and 2008 (mean ± standard error). The category “Unknown” was only used in 1997, while “Forb” was only used in 2008.
Figure 1.
Figure 2.
Table 1. Comparison of vegetation type cover (%) in the area of interest in the vegetation maps from 1997 and 2008. WER: wind exposed ridge.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>1997</th>
<th>2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heath</td>
<td>39.9</td>
<td>50.1</td>
</tr>
<tr>
<td>Copse</td>
<td>1.2</td>
<td>6.1</td>
</tr>
<tr>
<td>Fen</td>
<td>8.3</td>
<td>3.3</td>
</tr>
<tr>
<td>Grassland</td>
<td>1.9</td>
<td>1.1</td>
</tr>
<tr>
<td>WER</td>
<td>22.8</td>
<td>5.4</td>
</tr>
<tr>
<td>Other</td>
<td>25.9</td>
<td>33.9</td>
</tr>
</tbody>
</table>
Table 2. The 1997 and 2008 winter diet composition (%) analysed from rumen contents of the Akia-Maniitsoq caribou cows and split into functional plant groups. Data represent composition based on the total number of epidermal fragments analysed.

<table>
<thead>
<tr>
<th>Plant group</th>
<th>1997</th>
<th>2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub</td>
<td>25.5</td>
<td>6.9</td>
</tr>
<tr>
<td>Forb</td>
<td>0.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Graminoid</td>
<td>18.3</td>
<td>9.1</td>
</tr>
<tr>
<td>Lichen</td>
<td>40.3</td>
<td>63.8</td>
</tr>
<tr>
<td>Moss</td>
<td>8.5</td>
<td>19.5</td>
</tr>
<tr>
<td>Unknown</td>
<td>7.4</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Table 3. The 2008 winter diet composition (%) analysed from rumen contents of the Akia-Maniitsoq caribou cows. Data represent composition based on the total number of epidermal fragments analysed and is split into functional plant groups and genera.

<table>
<thead>
<tr>
<th>Plant group/Genus</th>
<th>2008</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shrub</strong></td>
<td>6.9</td>
</tr>
<tr>
<td>Betula</td>
<td>18.5</td>
</tr>
<tr>
<td>Empetrum</td>
<td>28.3</td>
</tr>
<tr>
<td>Juniperus</td>
<td>0.4</td>
</tr>
<tr>
<td>Ledum</td>
<td>10.7</td>
</tr>
<tr>
<td>Loiseleuria</td>
<td>11.5</td>
</tr>
<tr>
<td>Rhododendron</td>
<td>0.6</td>
</tr>
<tr>
<td>Salix</td>
<td>6.6</td>
</tr>
<tr>
<td>Vaccinium</td>
<td>15.4</td>
</tr>
<tr>
<td>Unknown shrub</td>
<td>8.0</td>
</tr>
<tr>
<td><strong>Forb</strong></td>
<td>0.7</td>
</tr>
<tr>
<td>Cerastium</td>
<td>26.9</td>
</tr>
<tr>
<td>Equisetum</td>
<td>7.5</td>
</tr>
<tr>
<td>Lycopodium</td>
<td>28.4</td>
</tr>
<tr>
<td>Saxifraga</td>
<td>4.5</td>
</tr>
<tr>
<td>Stellaria</td>
<td>3.0</td>
</tr>
<tr>
<td>Unknown forb</td>
<td>29.9</td>
</tr>
<tr>
<td><strong>Graminoid</strong></td>
<td>9.1</td>
</tr>
<tr>
<td>Agrostis</td>
<td>4.2</td>
</tr>
<tr>
<td>Anthoxantum</td>
<td>7.8</td>
</tr>
<tr>
<td>Calamagrostis</td>
<td>2.6</td>
</tr>
<tr>
<td>Carex</td>
<td>50.6</td>
</tr>
<tr>
<td>Deschampsia</td>
<td>0.5</td>
</tr>
<tr>
<td>Eriophorum</td>
<td>3.8</td>
</tr>
<tr>
<td>Festuca</td>
<td>4.0</td>
</tr>
<tr>
<td>Juncus/Luzula</td>
<td>7.4</td>
</tr>
<tr>
<td>Poa</td>
<td>16.6</td>
</tr>
<tr>
<td>Trisetum</td>
<td>0.8</td>
</tr>
<tr>
<td>Unknown graminoid</td>
<td>1.7</td>
</tr>
<tr>
<td><strong>Lichen</strong></td>
<td>63.8</td>
</tr>
<tr>
<td>Cladina/Cladonia</td>
<td>50.1</td>
</tr>
<tr>
<td>Bryoria</td>
<td>20.1</td>
</tr>
<tr>
<td>Cetraria/Dactylina</td>
<td>17.9</td>
</tr>
<tr>
<td>Nephroma</td>
<td>0.3</td>
</tr>
<tr>
<td>Peltigera</td>
<td>10.5</td>
</tr>
<tr>
<td>Stereocaulon</td>
<td>1.1</td>
</tr>
<tr>
<td>Unknown lichen</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Moss</strong></td>
<td>19.5</td>
</tr>
<tr>
<td>Aulacomnium</td>
<td>5.3</td>
</tr>
<tr>
<td>Polytrichum</td>
<td>14.7</td>
</tr>
<tr>
<td>Sphagnum</td>
<td>19.8</td>
</tr>
<tr>
<td>Unknown moss</td>
<td>60.3</td>
</tr>
<tr>
<td><strong>Unknown</strong></td>
<td>0.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Sub-</th>
<th>Sample</th>
<th>Shrub</th>
<th>Forb</th>
<th>Gramin-</th>
<th>Lichen</th>
<th>Moss</th>
<th>Other/Unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alaska</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Denali</td>
<td>1978-1980</td>
<td>gra</td>
<td>fec</td>
<td>6.0</td>
<td>7.0</td>
<td>11.0</td>
<td>62.0</td>
<td>10.0</td>
<td>4.0</td>
</tr>
<tr>
<td>WAH</td>
<td>1995-1996</td>
<td>gra</td>
<td>fec</td>
<td>7.2</td>
<td>3.2</td>
<td>15.0</td>
<td>58.5</td>
<td>16.1</td>
<td>0.0</td>
</tr>
<tr>
<td>WAH</td>
<td>2005</td>
<td>gra</td>
<td>fec</td>
<td>8.6</td>
<td>4.5</td>
<td>21.6</td>
<td>50.6</td>
<td>14.5</td>
<td>0.0</td>
</tr>
<tr>
<td>WAH</td>
<td>2012-2013</td>
<td>gra</td>
<td>fec</td>
<td>6.9</td>
<td>2.2</td>
<td>5.2</td>
<td>73.9</td>
<td>11.7</td>
<td>0.1</td>
</tr>
<tr>
<td><strong>Canada</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alberta</td>
<td>1979-1983</td>
<td>car</td>
<td>fec</td>
<td>20.3</td>
<td>0.5</td>
<td>4.0</td>
<td>71.3</td>
<td>1.0</td>
<td>3.9</td>
</tr>
<tr>
<td>Banks Island</td>
<td>1972-1973</td>
<td>pea</td>
<td>rum</td>
<td>4.0</td>
<td>27.0</td>
<td>59.0</td>
<td>0.0</td>
<td>0.0</td>
<td>10.0</td>
</tr>
<tr>
<td>Melville Island</td>
<td>1974-1977</td>
<td>pea</td>
<td>rum</td>
<td>1.0</td>
<td>5.0</td>
<td>47.0</td>
<td>11.0</td>
<td>34.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Newfoundland</td>
<td>1957-1966</td>
<td>car</td>
<td>rum</td>
<td>30.0</td>
<td>-</td>
<td>7.0</td>
<td>56.0</td>
<td>6.0</td>
<td>1.0</td>
</tr>
<tr>
<td>NWT</td>
<td>1980-1981</td>
<td>gro</td>
<td>rum</td>
<td>20.6</td>
<td>2.4</td>
<td>-</td>
<td>68.5</td>
<td>4.9</td>
<td>3.6</td>
</tr>
<tr>
<td>Yukon</td>
<td>1973</td>
<td>gra</td>
<td>fec</td>
<td>1.2</td>
<td>-</td>
<td>3.2</td>
<td>66.7</td>
<td>28.8</td>
<td>0.1</td>
</tr>
<tr>
<td><strong>Greenland</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AM</td>
<td>1997</td>
<td>gro</td>
<td>rum</td>
<td>25.4</td>
<td>0.0</td>
<td>18.3</td>
<td>40.3</td>
<td>8.5</td>
<td>7.4</td>
</tr>
<tr>
<td>AM</td>
<td>2008</td>
<td>gro</td>
<td>rum</td>
<td>6.9</td>
<td>0.7</td>
<td>9.1</td>
<td>63.8</td>
<td>19.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Isortoq</td>
<td>2000</td>
<td>tar</td>
<td>fec</td>
<td>1.0</td>
<td>0.0</td>
<td>16.5</td>
<td>18.4</td>
<td>63.4</td>
<td>0.7</td>
</tr>
<tr>
<td>KS</td>
<td>1977-1979</td>
<td>gro</td>
<td>rum</td>
<td>11.0</td>
<td>6.0</td>
<td>58.0</td>
<td>6.0</td>
<td>0.0</td>
<td>9.0</td>
</tr>
<tr>
<td>KS</td>
<td>1997</td>
<td>gro</td>
<td>rum</td>
<td>25.0</td>
<td>0.5</td>
<td>42.0</td>
<td>9.5</td>
<td>5.0</td>
<td>18.0</td>
</tr>
<tr>
<td><strong>Svalbard</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colesdalen</td>
<td>1999-2002</td>
<td>pla</td>
<td>rum</td>
<td>29.0</td>
<td>2.5</td>
<td>33.0</td>
<td>2.5</td>
<td>27.0</td>
<td>6.0</td>
</tr>
</tbody>
</table>

Manuscript IV

Moshøj CM, Raundrup K, Forchhammer MC. The effect of Inuit hunting pressure on fluctuating harvests of West Greenland caribou populations.

Manuscript prepared for submission to Arctic.
The effect of Inuit hunting pressure on fluctuating harvests of West Greenland caribou populations

Charlotte Margaret Moshøj¹,²,³, Katrine Raundrup¹,⁴ and Mads C. Forchhammer⁵,⁶

¹Department of Bioscience, University of Aarhus, Frederiksborgvej 399, 4000 Roskilde, Denmark
²Department of Environmental, Social and Spatial Change, Roskilde University, Universitetsvej 1, 4000 Roskilde, Denmark
³Current address: Dansk Ornitologisk Forening / BirdLife Denmark, Vesterbrogade 140, 1620 København V, Denmark
⁴Greenland Institute of Natural Resources, Kivioq 2, 3900 Nuuk, Greenland
⁵UNIS, P.O. Box 156, 9171 Longyearbyen, Norway
⁶Centre for Macroecology, Evolution and Climate (CMEC) and Greenland Perspective, Natural History Museum of Denmark, Universitetsparken 15, 2100 Copenhagen, Denmark

Abstract

Harvest and trade data are often used as proxies for long-term population dynamics. Although such data may provide valuable long-term information of wildlife species, the use of such proxies for population development needs to be treated carefully. Here, we investigate and contrast long-term harvest (1908-1981) and trade (1816-1865) time series from 7 caribou districts in West Greenland using established time series analytical tools including autoregressive, spectral and wavelet functions to describe how the structural development of these are related to concurrent changes in socio-economic conditions. We furthermore test the effect of a proxy for hunting pressure, on the fluctuating harvest and trade data. Combined, our analyses revealed clear structural differences of the harvest and trade time series, respectively. Specifically, the majority of harvest time series had a 3-dimensional autoregressive structure with strong direct temporal dependence (significant first order autoregressive coefficient) with complex long-term dynamics characterized by both long periodicities (21-34 years) and short (3-7 years). In contrast, the trade time series predominantly displayed a 1-dimensional autoregressive structure with no direct temporal dependence. Accordingly, the long-term fluctuations of the trade data were more simply described by single long-term fluctuations with periodicities 10-36 years across districts. We discuss differences in harvest and trade data with respect to observed temporal changes in socio-economic conditions in West Greenland. These results underline the need for future detailed studies of how temporally changing management strategies may be linked to harvest data thereby integrating the apparent temporal dependence into present day wildlife management of caribou in West Greenland.
Introduction

Populations of barren-ground caribou (*Rangifer tarandrus groenlandicus*) in West Greenland have displayed marked fluctuations in both population sizes and temporal distribution throughout the past 250 years (Vibe, 1967; Meldgaard, 1986). These fluctuations reflect similar historical variations, although not synchronous, in caribou abundance and distribution across their circumpolar range. In recent years, they have followed the declining or stagnating trend seen in a majority of the populations on a global scale (Vors and Boyce, 2009) with a single population, the Kangerlussuaq-Sisimiut in West Greenland, as the exception still displaying positive growth rates. The underlying causes of these fluctuations have been debated for as long as they have occurred, with climate, overgrazing, predation and hunting representing the most tenable regulating factors of caribou populations (Meldgaard, 1986). That climate plays a large part has unequivocally been documented in a range of studies, revealing variation in winter climate, i.e. abundance of snow (Solberg et al., 2001; Forchhammer et al., 2002; Tyler et al., 2008; Tyler, 2010; Callaghan et al. 2011) and trophic mismatch (Post and Forchhammer, 2008; Post et al., 2008), while other studies document density dependent lack of forage due to overgrazing or variations in amount and quality of summer forage leading to starvation or affecting reproduction (Post and Klein, 1999). That predation may affect caribou populations is documented across circumpolar populations (e.g. Wittmer et al., 2005; Hegel et al. 2010) but in West Greenland, predation is non-existent, due to the lack of large predators.

Caribou hunting plays an important role in the history, culture and traditions of the Greenland Inuit. Furthermore, caribou are an important source of meat, preferred to many other harvestable terrestrial foods (Anderson and Nuttall, 2004). Historical documentation on caribou hunting and utilization of derived products from the hunt are plentiful (Müller, 1906; Mason et al., 2007; Pasda and Odgaard, 2011), while resolving what effects and at which levels of harvest effort, the Inuit harvest may regulate caribou populations, is not so well defined. Although a newer study based on 6 years of abundance and harvest data demonstrates the effect of hunting on one out of the two populations in the study (Witting and Cuyler, 2011), no long term studies incorporating the available historical data have documented the effects of caribou harvest on the West Greenland caribou populations. Furthermore, although much speculation has been made thereof (Vibe, 1967; Meldgaard, 1986, 1996) no studies have convincingly related harvest effects on populations to caribou population developments or densities. Overcompensating harvest has repeatedly been blamed for caribou population declines in Greenland (Rink, 1852a; Dalager, 1915; Jensen, 1915; MacMillan and Ekblaw, 1925; Rasmussen, 1927; Jensen, 1928; Oldendow, 1935). It seems though, only to be documented that small isolated populations may have been kept from expanding, or led to temporal extinction by high hunting pressure (Rasmussen, 1921; Degerbøl, 1957; Aastrup 1983), prior to the fixation of high hunting quotas in 2001.
The numbers of caribou hunters have also fluctuated throughout the documented period. In 1834, more than 80% of the population were full time hunters (corresponding to 6041 hunters). A century later, the number of hunters was 8281 (corresponding to 49% of the population). In recent years, the number of full time hunters has decreased immensely; in 2013 only 1998 were registered as full time hunters corresponding to 4% of the population (Sørensen, 2009; Anon. 2014). Strandgaard (1983) reports that during the 1930s and 1940s when caribou populations were at low levels only few hunters maintained the traditional caribou hunt, due to the adversities of reaching the caribou on their inland habitats, difficulties in locating the caribou as well as having to carry the meat back to the coast. When only a few hunted caribou, there were less to share in the burden of transportation, and less gains from communal hunting. When caribou numbers rose again in the 1950-60s, and caribou again were accessible in near coastal habitats, caribou hunting increased, albeit with a temporal delay (Caning, 1997) mirroring the seesaw fluctuations in caribou harvest numbers representative for the past 200 years (Vibe, 1967). Hunting tools and weapons also changed extensively through that same time period, from spears and bows to hunting rifles. Along with the firearms that arrived in Greenland around 1820 came the need for ammunition. In order for the hunters to increase their take on blubber and pelt (Hamilton and Rasmussen, 2010), these goods were acquired by trading in exchange for furs, or supplied by Kongelig Grønlands Handel (abbreviated as KGH [the Royal Greenland Trade Department]). Ammunition for these early rifles came in the form of lead, sold or traded by the KGH, and then formed into lead bullets in molding casts. While shotguns and rifles were costly devices that were not acquired on an annual basis, the sales of lead for bullet molding exhibited annual oscillations on a temporal scale, rendering the figures useful as a proxy for hunting pressure (Jensen, 2002).

In this study, we incorporate the effects of intrinsic temporal dependent dynamics of caribou fluctuations with harvest pressure in evaluating the century long caribou harvest records across seven regions in West Greenland (Fig. 1). Furthermore, despite the fact that previous studies have utilized and merged the available harvest and skin trading data (Forchhammer et al., 2002; Post and Forchhammer 2002), corroboration of whether the two datasets display similar underlying properties are lacking. Hence, we furthermore aimed to investigate and contrast the effect harvest effort had on the harvested numbers of West Greenland caribou in time and space, as well as evaluating the affinity of the two caribou data set in terms of autoregressive structure and compatibility as proxies reflecting harvest and fluctuations in the actual populations. This may have importance for evaluating the present day management on hunting and its sustainability, and on modeling the future population fluctuations as well as evaluating the quality and applicability of available historical caribou data.
Methods

The harvesting and management regime of caribou in West Greenland

Although several periods of rise and decline in the caribou population occurred during the 18th and 19th century, no hunting regulations were inferred prior to 1924, following the onset of a decline in the caribou population, where caribou were protected from hunting in Southwest Greenland from 20 May-20 July. In 1927, this restriction was extended to include all of West Greenland from 1 October to 31 July. Hunting statistics are available from 1908 until 1982, when harvest data registration was discontinued until 1993.

The data

Time series data on hunting statistics of caribou originate from two sources (Fig. 2): (1) annual trading records from KGH (henceforth referred to as” trade data”) held at the Danish National Archives (1816-1981) from six caribou districts, and (2) harvest data (henceforth referred to as” harvest data”) (1908-1981) from seven caribou districts (Anon. 1909a, 1909b, 1938, 1960). The trade data from the 19th and 20th century consisted of number, types and condition of pelts and also recorded by-products as e.g. antlers. The pelts were recorded at the regional trading offices, which geographically coincided with the hunting districts of the individual caribou populations (Fig. 1). Therefore, the caribou pelts were recorded in the regions within which they had their range and where they were harvested. An exception of this is Upernavik, which ceased to be an independent colony from 1814-1826, and pelts from Upernavik from this and perhaps later periods, presumably went to Qeqertarsuaq (Vibe, 1967). Therefore, data from Upernavik is only represented by harvest data. Hunters from one region may also hunt caribou in neighboring regions/districts, and then following report them in their home districts, as was documented for hunters from Nuuk who hunted caribou in Sisimiut, which then turned up in the Nuuk trading and game statistics (Grønnow et al., 1983; Meldgaard 1986). This contributed to noise in the data.

The harvest data from the 20th century was collected from the annual reports of hunters. These reports registered number, type and geographic locality of the hunters catch. Since reporting involved transport to the local trading post, and the fact that reporting was not a formal prerequisite for hunting, it is assumed that the number of animals reported hunted reflects a minimum. No limits on the harvest existed during the timeframe of this studies historical data. Furthermore, all products from Greenland were monopolized commodities up to 1950, and therefore both types of hunting statistics in theory should reflect caribou population size, although the trade data do not reveal the number of caribou hides kept for personal use, i.e. for tool crafting and clothing.

When interpreting the harvest and trade statistics there are further biases to be considered. During the early colonial period, Inuit were advised against caribou hunting as well as physically moved to
centralized townships away from caribou hunting grounds. This was due to hunting trips away from the central colonies and into the land of caribou keeping Inuit away from the missions and made religious conversion harder to accomplish, as well as paying less profit than the hunt on marine mammals (Thorhallesen, 1914; Dalager, 1915; Gad, 1976; Grønnow et al., 1983). The hunting and trade statistics from more recent decades also inherently mask underlying biases, since many caribou that are killed, never turn up in hunting or trading statistics, and for some years, some settlements are altogether lacking due to non-registration of reported harvests (Strandgaard, 1983; Holthe and Lassen, 1984; Meldgaard, 1986). Despite all these biases, the use of harvest/trade statistics in a time series analysis context as proxies for actual harvested numbers is supported by previous studies, where correlation between yearly harvest and census numbers were found to be high (Post and Forchhammer, 2004; Reimers et al., 2009; Simard et al., 2010).

The social-economic data were collected from the Greenland National Archives in Nuuk, and consisted of counts of number of inhabitants per district, subdivided by gender and for some groups, also age class. Growth and decline in human population size in the form of births and deaths were also registered, as were data on number of hunters by trade recorded in individual districts dating back to 1800. These data were only available for some of the west coast districts i.e. Qeqertarsuatsiaat, Aasiaat, Disko Bay, Uummannaq and Upemavik (Fig. 1). Another available alternative proxy for hunting and hunting efficiency was the counts of traded weapons (i.e., shotguns and rifles sold) and ammunition (amounts of lead and lead shots sold). These records were assimilated for all districts from the annual registers of KGH (Anon. 1909b) and records from the Greenland Ministry (Anon. 1938, 1960, 1968) as well as from Christian Vibes original notebooks. The caribou data were log-transformed to correct for heteroscedasticity and to enable linear analyses (Royama 1992, Lindström and Forchhammer 2010).

Statistical and autoregressive analyses
Annual synchrony across hunting districts (Fig. 1) was calculated as the inverse coefficient of variance (1/CV) for caribou harvest data as well as the caribou trade data. We modeled the effect of changing hunting pressure on caribou harvest, by integrating autoregressive (AR) analyses of harvest and trade data, separately. For both set of analyses, we selected a third order autoregressive model (AR3) based on overall parsimony using the Akaike Information Criterion (AIC; Sakamoto et al., 1986). Through correlations, we evaluated the relationship between the four available proxies for harvest pressure: 1) Annual number of hunters in districts, 2) Annual number of men in districts, 3) Number of weapons sold/traded per year per district, and 4) Amounts of lead bullets sold. However, we found that proxies 1) and 2) were not available for all districts and proxy 3) would not reflect annual variations in effort, while proxy 4) was found to have the longest overlapping time series for all districts for both trade and harvest
data. Furthermore, proxy 4) was found to be correlated with proxy 2) for two districts (Aasiaat $r = 0.66$, $n=82$, $p<0.001$ and Upernavik $r = 0.86$, $n=84$, $p<0.001$). We therefore chose to use the annual amount of lead bullets sold ($L$) as our proxy for annual hunting pressure. This variable was integrated as a covariate in the AR3 models.

AR and covariate coefficients were estimated using the PROC AUTOREG function with maximum-likelihood estimation in SAS 9.3 for Windows (SAS Institute, 2012). The year of harvest ($Y_t$) was forced in before the AR procedures to rectify non-stationarity of the data (Royama, 1992). In the analyses, we lagged the covariate $L$ up to 2 years ($L_t \ldots L_{t-2}$) because harvesting may indirectly affect recruitment rates (Solberg et al., 1999). Assuming a log-linear temporal relationship in the harvest and trade data the full model may be described as

$$X_t = Y_t + \beta_0 + \beta_1 X_{t-1} + \beta_2 X_{t-2} + \beta_3 X_{t-3} + \omega_1 L_t + \omega_2 L_{t-1} + \omega_3 L_{t-2} + \epsilon_t$$

(Equation 1)

where $X_t$ is the log$_e$-transformed number of harvest or number of traded pelts in year $t$, $Y_t$ the year of harvest/trade and $\epsilon_t$ the remaining variance not described by the deterministic part of the model. The $\beta_{i,n}$ and $\omega_{i,n}$ are the autoregressive and covariate coefficients, respectively. From the full model in Equation 1, the most parsimonious model was found for each district by the minimum AIC value. A difference in AIC between models less than 1 is considered insignificant (Sakamoto et al., 1986).

**Spectral and wavelet analyses**

We performed spectral analysis to estimate the strength of the frequency components (the power spectral density), to detect overall periodicities in the data. Additionally, wavelet analyses were performed on both the data series to quantify the progressive change of periodicity through the length of the time series. The spectral and wavelet analyses were performed in the statistical program PAST (Hammer et al., 2001).

**Results**

**Overall fluctuations and synchrony**

All caribou populations in the study showed considerable short and long-term fluctuations in harvest and trade numbers (Fig. 2). For the first overall period (1816-1860) represented by trade data only, the overall tendency is of an increase from very low numbers in 1810 to a maximum around 1845-1850 and from then on an overall rapid decrease in populations occurs, returning to the initial low numbers as those seen at the periods onset in the 1820s, around 1860-65 (Fig. 2). During this period, the degree of synchrony of the trade data series (Fig. 3) fluctuates with larger variation at onset, and then evens out prior to a peak in oscillation in the early 1850s, decreasing along with the overall trade data curve (Fig. 2) in the 1860s. During this period, no harvest statistics were kept.
Following 1865, there is a gap in available statistics until 1908 where harvest data became available. Here, low numbers prevail throughout the districts in comparison to the maxima in the previous period, but overall the harvest numbers show growth for the period 1908 to 1920. This defined growth period ends first in southern districts and a few years later in the northern (Fig. 2). The synchrony curves for trade as well as harvest statistics (Fig. 3) show initial differences in the onset of this period with an overall decline in harvest statistics paralleled by fluctuating rise and fall in synchrony of trade statistics. In the final growth period of the 1915 to the mid-1920s, both harvest and trade synchrony curves show two sharp trough and peak incidents in between population synchrony (Fig.3).

During the following period, from mid 1920s-1950s, the number of caribou reported shot in West Greenland were at a minimum in all districts (Fig. 2). Sisimiut, which had a record high of nearly 9000 traded skins in the 1845 maxima, did not surpass over 200 registered harvested caribou during the 1920-1950 low, and the highest recorded harvest in any district in this period was just a mere 1000 harvested caribou in Maniitsoq district in 1923. In the early 1950s, an overall tendency of population increases is observed, and this tendency continues for most districts, until early 1970, where the hunting statistics again are observed to be decreasing although large fluctuations in number are seen over approximately 10 year periods in Sisimiut and Maniitsoq and to a lesser degree in Aasiaat and Nuuk (Fig. 2). Contrary to this general pattern, the number of hunted caribou in Paamiut stays at low levels throughout the period 1950-1980. The highest amplitudes are represented in the data from Sisimiut, Aasiaat and Maniitsoq (Fig. 2). The harvest data synchrony curve (Fig. 3) reflects the above described tendencies displaying a slow increasing rise in synchrony, which then again falls and stabilizes around 1 in the early 1970s. The described varying amplitudes during the last decades of the study period, lead to two sharp peaks of less synchronous fluctuations.

*Spatio-temporal changes*

The harvest data

Whereas the spectral analyses provide long-term estimates of the average time-series periodicity, the wavelet analyses also give information of any temporal changes in periodicity over the length of time series. Our spectral analyses supported the above mentioned differences between the trade and harvest data series. The harvest time series from the districts Paamiut, Nuuk, Maniitsoq and Sisimiut all displayed similar long-term periodicity of 50 years (Fig. 4.1a-4.4a) whereas the northern districts Aasiaat and Upernavik showed reduced periodicity of approximately 40 (Fig. 4.5a) and 33 years (Fig. 4.7a), respectively. The harvest time series from Qeqertarsuaatsiaat did not display any significant long-term fluctuation.
Like the spectral analyses, the wavelet analyses of the harvest time series confirmed the presence of long-term fluctuations in all districts but Qeqertarsuatsiaat (Fig. 4.1b-4.7b). In Paamiut (Fig. 4.1b), Nuuk (Fig. 4.2b), Sisimiut (Fig. 4.3b) and Aasiaat (Fig. 4.5b), long-term periodicities of 27-34 years were present throughout the time series, whereas a 32-year periodicity occurred in Maniitsoq series around 1945-50 and remained for the rest of the time series (Fig. 4.4b). In the Upernavik district, a long-term periodicity of 21 years disappeared in the late 1960’s (Fig. 4.7b). In addition, the wavelet analyses demonstrated the shorter periodicities of 16-19 years and 3-7 years in the harvest data, which for most districts appeared in the 1960’s and 1970’s (Fig. 4.1b-4.7b).

The trade data
Spectral analyses showed that the trade time series also had significant long-term periodicities ranging 20-40 years (Fig. 4.1c-4.6c). There were no trade data available from Upernavik (Fig. 4.7). Similarly, long-term periodicities of 16-36 years were found using wavelet analysis (Fig. 4.1d-4.4d). However, in the districts Aasiaat (Fig. 4.5d) and Qeqertarsuatsiaat (Fig. 4.6d) only periodicities of 10-14 years was observed. In contrast to the harvest data, no additional short-term periodicities were seen the trade data (Fig. 4.1d-4.6d).

Autoregressive analyses
The harvest data from all districts displayed significant direct (AR1) temporal dependence (Table 1), since all autoregressive coefficients, apart from Aasiaat, were positively correlated with harvest data from t-1. Data from Sisimiut and Aasiaat furthermore displayed significant delayed temporal dependence (AR2, AR3, Table 1) indicating the influence of previous year’s harvest, lagged 2 and 3 years, on the present year’s harvest outcome. The trade data from Qeqertarsuatsiaat showed significant positive direct temporal dependence (AR1, Table 2) while significant delayed temporal dependence (AR2, AR3, Table 2) was observed for the trade data series from Nuuk only.

All of the most parsimonious models for both harvest and trade data sets included the co-variable, annual number of lead shots sold (L), either directly, or lagged one or two years (Table 1, 2). The most parsimonious models of harvest data indicated two districts (Maniitsoq and Sisimiut) with a direct relationship (L) while the most parsimonious model for the data from Nuuk and Aasiaat included $L_{t-1}$, and Paamiut and Upernavik included $L_{t-2}$. In the trade data, lagged effects had an overall higher order of the variable included (Nuuk, Maniitsoq and Sisimiut all had a two-year lag, $L_{t-2}$, while Paamiut and Aasiaat only included a one-year lag, $L_{t-1}$) and only the Qeqertarsuatsiaat district displayed a direct effect (Table 2). This effect was negative for Nuuk and Upernavik in the hunting data and likewise negative for Nuuk,
as well as Paamiut and Qeqertarsuatsiaat in the trade data. Overall, the effect of $L$, a proxy for harvest effort, was greatest in the southern districts, for both harvest and trade data series (Table 1, 2).

Simple correlation analysis of the standardized variables of harvest and trade statistics from overlapping periods revealed low but significant correspondence between harvest and trade data ($r^2 = 0.1557$, $P<0.001$).

**Discussion**

*Spatio-temporal fluctuations*

The period 1800-1860

Caribou populations in West Greenland have fluctuated in time and space, and affected the people dependent on them as a resource, for as long as humans have inhabited Greenland (Egede, 1770). In the late 1700s caribou hunting had failed altogether, as had the harvest of several alternative harvestable species of seals and whales, and in the settlements starvation was widespread and many were abandoned (Petersen, 1991). The period 1800-1810 was defined by humid winter climate (Vibe 1967), and thus winter conditions that restricted the access of caribou to their winter forage, due to icing or hardening of the snowpack (Tyler, 2010). The number of traded caribou skins in West Greenland stayed at low levels until about 1815, when a steep rise in number of caribou skins purchased by KGH was seen (Fig. 2). This overall trend of rising trade numbers, is believed to be due to more stable climate conditions and fast replenishment of caribou forage due to availability of ground water reserves following the humid climate period (Vibe, 1967), and the rise is mirrored in all the documented trading districts (Fig. 2). Another reason for the steep incline of increase in numbers of traded skins may be found in the change in hunting patterns. During the long prior period where caribou numbers retained low levels, traditions as well as lack of availability and transfer of knowledge on the movement and whereabouts of the caribou were lacking due to e.g. smallpox epidemics in 1782-1785 and in the early 1880s that killed many elders (Rydberg 1903), as well as changed land use due to religious conviction (Thorhallesen 1914). Furthermore, during years where Greenland caribou numbers are low, seasonal migrations are not common (Vibe 1967, Meldgaard 1986). Therefore, hunting was most likely not profitable for those hunters that were left in the settlements, with caribou mainly confined to inland habitats, where access was difficult as was transport of the meat and hide provisions after the hunt. Consequently, there may have been a lag in time, where caribou were gaining in numbers, but hunting traditions were not re-established, and until the point in time where caribou again became more accessible in coastal areas. By then the caribou would be plentiful enough for the harvest to generate the steep rise in trade numbers. This time-lag in harvest, has been documented in other ungulate studies where hunting pressure tended to increase when ungulate density was high, and decline when ungulate density was low, but show less substantial change at intermediate levels (Fryxell et al. 1991). The actual harvested numbers were most
probably even higher, as some caribou hides were kept for own use, and some caribou were left unskinned in the mountains (Vibe, 1967). The number of traded caribou hides may further have been affected by a warming period in the early 1800s (Rink, 1952a) which gave rise to the economically more interesting cod fishery in the areas south of Sisimiut (Rink, 1852b; Smidt, 1983). This most probably affected the summer hunting activities of the resident hunters. This short cod period lasted from 1810-1823, and cod were not numerous again until 1845-1849, when fishing was resumed in Sisimiut and Disko Bay (Rink, 1852b).

The variation in the number of hides traded in Sisimiut and the more southern districts may be explained in part by the prolonged seasonality and possibility of winter hunting north of Maniitsiq, due to the availability of snow and dog sledding traditions, and in part by the northern migration of caribou from southern summer grounds during winter (Müller, 1906). In the Nuuk district, the trading had increased from less than 100 skins annually to more than 4000 skins in the 1830s. Several historical sources verify the existence of a large caribou herd in the region between 1825 and 1850, that then declined in temporal synchrony with the herd at Qeqertarsuatsiaat (Fig. 2; Rink, 1852a; Winge, 1902; Meldgaard, 1986). One of the reasons for the onset of this decline prior to the more northern areas may in part be due to the fact that the area and caribou population around Nuuk, as well as around Qeqertarsuatsiaat formed the basis of social and cultural meetings during summer. During these summer meetings, Inuit from southern districts travelled and took part in not only the social gatherings but also the hunt, leaving the caribou here under a larger cumulative hunting pressure than from just regional hunters (Petersen, 2003). Although this also took place at hunting grounds in the deep fjords of Kangerlussuaq and Nassuttooq (north of Sisimiut) (Amdrup and Ostermann, 1921) these caribou populations were more abundant in number and could better uphold the larger number of hunters on sites. In Qeqertarsuatsiaat where several sources had mentioned the abounding availability of caribou prior to the decline in the early 1940s (Rink, 1857; Winge, 1902), the trading never recuperated, while in Nuuk it remained close to zero until after the 1950s (Vibe, 1967). The caribou hides that were traded in Aasiaat during the 1830s-1860 originated from a population that was interspersed with, at that time, three other populations, namely Sisimiut, Ilulissat and Qasigiannguit (Meldgaard, 1986). The onset of the increase in trading numbers in the first part of the 19th century came later to Aasiaat than its neighboring regions. The reason may be found in the geographical distribution of the caribou during periods of low densities. At low densities, caribou were found in inland regions, and did not become available for harvest and trade for Inuit in the Aasiaat area until they were more numerous and thus expanded their distribution to coastal areas. Sisimiut and Maniitsiq are both located in areas with access to the inland regions where the caribou retreated during low density periods via nearby fiords (Meldgaard, 1986). Aasiaat, on the other hand, lies in the northernmost and coastal part of the caribou range and therefore was one of the first areas to be barren of caribou (Müller, 1906) during
low-density periods, and one of the last to be re-inhabited again, which is reflected in the trading figures. Furthermore, a large percentage of caribou hides traded in Aasiaat stemmed from the summer hunting trips down the coast to camps inland by Nassuttoq (Amdrup and Ostermann, 1921) and with caribou populations at low levels, the risk of low hunting success in addition to the risk involved in undertaking the journey may have deflected the hunters from Aasiaat from this choice. For all regions, the time period between the late 1840s and 1860s was defined by marked decline of traded caribou skins, accounting for only a low percentage of the previous decades. Along with the decline in the West Greenland caribou were reports of similar declines in the Thule district in the north (Rasmussen, 1915), and across Baffin Bay in the Northwest territories (Vibe, 1967) in the following decades. While some sources relate the declines in northern regions to the introduction of firearms and the northern whalers’ meat requirements (Banfield, 1951) others refer to the changes in climate (Vibe, 1967) as the determining factor for caribou declines during this time period.

The period 1900-1960

Harvest statistics (hunting records) which list the numbers of caribou shot by each hunter in every settlement, were kept since 1900. In comparison to the prior period of increasing trade numbers 100 years previously, the maximum number of caribou harvested in the early 1900s was much less than in the previous caribou abundance period. For example, in Maniitsoq, where up to 5000 caribou skins were traded in the 1840s, harvest numbers in the early 1900s “abundant” period was only just over 1300 (in 1918) and the highest number traded was much less: 148 skins in the same year. This disparity between numbers of harvested caribou and traded skins may be due to the proportionate larger need for caribou skins for household use after a long period of meager harvest years, and it has been accounted how a certain restocking of meat and hides take place following low harvest years for caribou (Petersen, 2003).

Characteristic for the harvest data in the period 1908-1930s from all the south central regions (Nuuk, Maniitsoq, and Sisimiut) is the interchanging pattern of increase and decrease in harvest and trade numbers, exhibiting increased stochasticity in comparison to the previous periods formerly discussed. Periodicities in fluctuations are dependent on not only environmental noise, but also on the timing and size of the harvest fraction (Jonzen et al., 2003). After the 50-year caribou low, it is plausible to believe that an initial rise in number of caribou, visualized by their reappearance in the coastal areas when seasonal migrations again procured (Meldgaard, 1986), may have led the Inuit to take a large fraction of a population still in a vulnerable state numerically. In addition to climate change, this may have reinforced the short-term fluctuations. As caribou numbers still were nowhere near the previous level, the reinstatement of caribou migrations may in fact not have made the animals easier prey per se. This is due to the spatial expansions of a still low density population on vaster hunting grounds compared to when
the caribou were concentrated in the inland. The access for the hunters would have been easier, and the presence of the caribou closer to the settlements may have led more hunters to partake in the hunt, thereby leading to the greater bag, and the increase in stochasticity. In 1924, a hunting legislation was passed that banned caribou hunting from 20 May - 20 July in Southwest Greenland, and in 1927 this ban was extended to the rest of West Greenland, for all of 10 months, only allowing harvest in August and September. Nonetheless, the number of caribou hunted and skins traded kept on declining and in the late 1920s, the number of caribou hunted in the southernmost district, Paamiut, was less than 100, while the number available for trade was under 10. This furthermore reflected the trend in the districts of Sisimiut and Upernavik, and although levels at Nuuk and Maniitsoq were higher, the development was still negative. Hunting bans, it seems, had come too late. According to theory, a time delay in the assignment/instatement of harvest may increase the stochasticity and fluctuations in the population (Solberg et al., 1999).

In the following period, from the mid-1930s to the 1960s the development in caribou harvest and trade followed two differing patterns amongst the districts. While Nuuk and Maniitsoq still kept the harvest numbers above 300 on an annual average, harvest and trade in Paamiut, Sisimiut and Upernavik, declined to extreme low values, reflecting other changes in these societies and the environment. Most determining was probably the ongoing transition in southern districts from hunting to fishing (Hamilton et al., 2000). In the northern settlements, Uummannaq and Upernavik, the negative trend in caribou harvests was furthermore enhanced by harsh winters (Vibe, 1967), which deemed detrimental to the residing caribou populations, possibly due to the occurrence of over-icing rendering forage inaccessible under the snow (Tyler, 2010). Consequently, the major changes in hunting life and technical innovations, such as replacement of the umiaq (skin-covered boat) with motorized boats (Petersen, 2003), had an effect on the number of hunters that kept up the tradition of the inland caribou hunts. The transition into using motorized boats made it possible to expand and exploit a larger hunting territory in vicinity of the winter settlement, making the summer moves even more respondent, and further enhanced the economically superior fishing activities (Smidt, 1983). In addition, the turf houses had been abandoned and replaced by wooden houses, which did not need airing in summer, and simultaneously the use of collective hunter’s huts as an advance base lessened the need for periodic nomadism (Petersen, 2003). In the end 1950s through 1960s, caribou harvest and trade numbers rose again in all locations north of Nuuk. The trade numbers in general did not exceed more than 25% of the harvest, underlining the fact that the main aim of caribou hunting was for own consumption and use, and not so much for economic purposes. During this period, more Greenlanders found their livelihood as fishermen and civil servants, and in the 1960s as construction workers in the growing development industry (Petersen, 2003).
The period 1960-1980
After a period of fairly low caribou numbers in West Greenland, the period 1960-1980 is characterized by tremendous increase followed by a crash in numbers in three of the seven regions (Maniitsoq, Sisimiut and Aasiaat). From an estimated maximum of 100,000 animals in the late 1960s (Thing, 1982; Roby and Thing, 1985) the numbers diminished to less than 10,000 in the late 1970s (Roby and Thing, 1985). The main cause for this rapid decline has been allocated to overgrazing (Thing, 1984; Staaland and Olesen, 1992; Fredskild and Holt, 1993) which resulted in lower caribou recruitment (Cuyler, 2007).

The trading of caribou hides is almost non-existent during this period and reflects the changing hunting traditions. Previously the hunting formed the economic basis for most families but during the 1960-1980 less than 20 percent of the population were registered as full time hunters (Sørensen, 2009). Further, the use of caribou hides for traditional use as e.g. clothing was only very limited, hence resulting in the almost complete disappearance of traded hides during these two decades (Fig. 2).

Structural differences in harvest and trade time series
The log-linear structure of autoregression has been linked directly to more general exponential population growth models (Lindström and Forchhammer, 2010). Although linked, our analytical approach differs in that observed changes in autoregressive, spectral and wavelet analyses suggest changes in the temporal processes behind the hunting of caribou (the harvest data) as well as the trading of caribou pelts (the trade data) rather than population density dependent dynamics per se. Interestingly, our autoregressive analyses (Table 1 and 2) corroborate the distinct differences between the harvest and trade data stated above. Whereas the parsimonious AR models for the harvest time series portrayed dimensional more complex models with highly significant direct temporal dependence (Table 1), all AR models for the trade time series but one was 1-dimensional with no direct temporal dependence (Table 2; but see the Qeqertarsuatsiaat series). These distinct structural differences between the harvest and trade time series were also confirmed by our wavelet analyses (Fig. 4.1-4.7). The harvest time series were all characterised by complex fluctuating patterns with long-term fluctuations of 21-34 years together with short-term 16 year and 3-7 year fluctuations (Fig. 4.1b-4.7b). In contrast, the trade time series mostly displayed single long-term fluctuations without a range of additional short-term fluctuations (Fig. 4.1d-4.6d).

Evidently, the processes behind the recorded harvest and trade time series, respectively, deviate considerably. Current year harvest depends strongly on the amount harvested last year, which together with ongoing concurrent changes in caribou management strategies (see above) generate complex temporal dynamics. This is not apparent in the trade data and the lack of direct temporal dependence
suggests more simple, constant mechanisms over time, probably related to a relatively constant market and personal use of caribou skin present the early period 1816-1865.

Influence of hunting pressure on harvest and trade data

In our study we found an overall effect of hunting pressure in both datasets, indicated by the presence of the hunting pressure proxy (L: the annual number of lead shots sold) in all of the most parsimonious models (Table 1 and 2). Overall, the influence of L was more discernible in the trade data than in the harvest data, since all of the most parsimonious models of trade data additionally included lagged effects of hunting pressure (Table 2). To interpret these results, one must take into consideration both the type of data, as well as the temporal window in which it was collected. Most of the longer time series of trade statistics stem from the period 1815-1865, where caribou populations in general were at high levels, or went from low to high levels, while the overlap of trade statistics with periods of low harvest and documented low population is limited. The reverse holds true for the harvest data, where the longest time series in our study overlaps the periods of low caribou harvest numbers in the general time frame of 1908-1960, but also contains the last twenty years (1960-1980) of higher harvest quantities. These results indicate that inasmuch as it is an effect of the type of data (hunting or trade statistics) that are used in the analyses, the concurring respective low and high harvest levels may also in part be determining for the differences found. Hunting pressure affected trade statistics when caribou populations and concurrent trade of skins was high and had less effect when harvests numbers were low. This may be explained by either decreased accessibility to the caribou during population lows, or that the lower level of hunting happened by choice, or a combination of both. The results indicate that the pressure of hunting was significant in the populations with highest caribou numbers (except for Upernavik, which may be due to its isolated proximity) while pressure was non-discernible in populations with low population numbers. Or, in a temporal perspective, hunting was significant when populations had high numbers (in the most hunted populations) and low when caribou population numbers were low. This indicates that the Inuit hunters themselves may have regulated the hunting, perceiving that when caribou were numerous, they could be hunted and killed with little effort, while the opposite was true at low numbers. Also, the changed migratory patterns of populations at high abundancies with more animals along the coastlines (Meldgaard, 1986) might have made the caribou even more available and accessible to hunters.

Conclusion

Collectively, our analyses portray clear differences between the West Greenland caribou harvest and trade data, suggesting rather contrasting causal mechanisms with temporally dependent management strategies as an important component generating the harvest time series in contrast to the relatively constant market and home use conditions resulting in no or little temporal dependence in the trade time series. Two
interesting aspects emerge from our study. First, a more vigorously investigation of harvest data and its relation to wildlife management is needed. Importantly, our analyses and results demonstrate a high temporal dependence in harvesting wild caribou populations, which is relevant to present day management of caribou in West Greenland. Secondly, the use of harvest or trade data as proxies is widespread (e.g. Forchhammer et al., 2002; Post and Forchhammer 2002). Although often justified through comparisons to real population counts (e.g., Forchhammer and Asfærg 2000), our results demonstrate distinct underlying conditions that need to be taken into account when using harvest or trade data, respectively, as a proxy for population dynamics. Indeed, such conditions may not only vary across species but, as demonstrated by our autoregressive and wavelet analyses, also across populations within species.

References


Amdrup, G.C. and Ostermann H. 1921. Greenland 200 years after the arrival of Hans Egede [Grønland i tohundredaaret for Hans Egedes landing]. In Danish only. C.A. Reitzel, Copenhagen, Denmark.


Anon. 1909a. Reports and proclamations regarding the colonies in Greenland [Beretninger og kundgørelser vedrørende kolonierne i Grønland (Styrelsen af Grønland) no. 1-1927]. In Danish only.

Anon. 1909b. Communications from the Royal Greenland Trade Department 1882-1908 [Meddelelser fra Direktoratet for den kongelige grønlandske Handel 1882-1908]. In Danish only. Copenhagen, Denmark.


Banfield, A.W.F. 1951. The barren-ground caribou. Department of Resources and Development, Northern Administration and Lands Branch, Ottawa, Canada.


Degerbøl, M.A. 1957. The extinct reindeer of East Greenland, Rangifer tarandus eogroenlandicus, subsp. nov., compared with reindeer from other arctic regions. Munksgaard Publishing, Copenhagen, Denmark.


Jensen, A.S. 1928. The fauna of Greenland; an attempt to get an overview [Grønlands fauna; et forsøg paa en oversigt]. In Danish only B. Lunos Publishing, Copenhagen, Denmark.


Müller, R. 1906. The game and the hunt in South Greenland [Vildtet og Jagten i Sydgrønland]. In Danish only. Hagerup Publishing, Copenhagen, Denmark.


Rink, H. 1852b. Regarding the monopoly trade in Greenland: considerations regarding the access to Greenland for private people. [Om monopolhandelen paa Grønland: betænkning i anledning af
spørgsmaalet om privates adgang til Grønland. A.F]. In Danish only. Høst Publishing, Copenhagen, Denmark.

Rink, H. 1857. Contributions to the description of the natural history of Greenland [Naturhistoriske bidrag til en beskrivelse af Grønland]. Saerskilt aftryk af tillæggene til "Grønland, geographisk og statistisk beskrevet"]. In Danish only. Kleins Bogtrykkeri, Copenhagen, Denmark.


Rydberg, C. 1903. Regarding the trade- and population conditions in Greenland along with considerations regarding the current condition of the Greenlanders [Om erhvervs- og befolkningsforholdene i Grønland samt bemærkninger til oplysning om grønlændernes nuværende tilstand]. In Danish only. Geografisk Tidsskrift 17:69-92.


Thorhallesen, E. 1914. Description of the South Greenland missions during visits in the years 1774-1775 [Beskrivelse over missionerne i Grønlands søndre distrikt: hvilke han som vice-provst visiterede i aarene 1774-1775]. In Danish only. København: Hoffensbergske etablissement, Denmark.


Table 1. Summary of the autoregressive analyses of harvested caribou in West Greenland.

<table>
<thead>
<tr>
<th>Area</th>
<th>n</th>
<th>AIC</th>
<th>Model</th>
<th>AR</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paamiut</td>
<td>50</td>
<td>56</td>
<td>ln_PA_harvest = year ln(L)<em>PA</em>{t-2}</td>
<td>AR3</td>
<td>**</td>
</tr>
<tr>
<td>Nuuk</td>
<td>50</td>
<td>37</td>
<td>ln_NU_harvest = year ln(L)<em>NU</em>{t-1}</td>
<td>AR3</td>
<td>*</td>
</tr>
<tr>
<td>Maniitsoq</td>
<td>49</td>
<td>80</td>
<td>ln_MA_harvest = ln(L)_MA</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Sisimiut</td>
<td>41</td>
<td>52</td>
<td>ln_SI_harvest = ln(L)_SI</td>
<td>AR3</td>
<td>*</td>
</tr>
<tr>
<td>Aasiaat</td>
<td>39</td>
<td>2.3</td>
<td>ln_AA_harvest = year ln(L)<em>AA</em>{t-1}</td>
<td>AR3</td>
<td>*</td>
</tr>
<tr>
<td>Upernavik</td>
<td>40</td>
<td>25</td>
<td>ln_UP_harvest = year ln(L)<em>UP</em>{t-2}</td>
<td>AR2</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Coefficient AR1</th>
<th>Coefficient AR2</th>
<th>Coefficient AR3</th>
<th>DW</th>
<th>Rtot2</th>
<th>RegR2</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3183 ± 0.1508 ***</td>
<td>-0.0266 ± 0.1609</td>
<td>0.1655 ± 0.1494</td>
<td>1.8634</td>
<td>0.7728</td>
<td>0.517</td>
</tr>
<tr>
<td>0.453 ± 0.1490 ***</td>
<td>-0.0276 ± 0.1662</td>
<td>0.2166 ± 0.1520</td>
<td>1.9082</td>
<td>0.5273</td>
<td>0.1889</td>
</tr>
<tr>
<td>0.5748 ± 0.1540 ***</td>
<td>-0.0909 ± 0.1788</td>
<td>0.0705 ± 0.1682</td>
<td>1.9792</td>
<td>0.4945</td>
<td>0.0985</td>
</tr>
<tr>
<td>0.2128 ± 0.1681 ***</td>
<td>0.527 ± 0.1396***</td>
<td>0.009275 ± 0.1613</td>
<td>1.9236</td>
<td>0.4905</td>
<td>0.1337</td>
</tr>
<tr>
<td>-0.0726 ± 0.1524 ***</td>
<td>0.4787 ± 0.1441**</td>
<td>0.0302 ± 0.1683</td>
<td>1.8229</td>
<td>0.5795</td>
<td>0.3111</td>
</tr>
<tr>
<td>0.5216 ± 0.1572 ***</td>
<td>0.1845 ± 0.1768</td>
<td>0.1380 ± 0.1628</td>
<td>1.8378</td>
<td>0.7614</td>
<td>0.1795</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Coefficient L</th>
<th>Coefficient L (lag1)</th>
<th>Coefficient L (lag2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.0448 ± 0.006686***</td>
<td>0.1951 ± 0.1057</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-0.0147 ± 0.007865</td>
<td>-0.1739 ± 0.0823*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-0.0234 ± 0.0115*</td>
<td>0.1227 ± 0.2074</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-0.0179 ± 0.0125</td>
<td>0.2686 ± 0.1243*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-0.0174 ± 0.004162***</td>
<td>0.0819 ± 0.0828</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-0.0397 ± 0.0149**</td>
<td>-0.001286 ± 0.0529</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Summary of the autoregressive analyses of caribou fur trade statistics in West Greenland

<table>
<thead>
<tr>
<th>Area</th>
<th>n</th>
<th>AIC</th>
<th>Model</th>
<th>AR</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paamiut</td>
<td>35</td>
<td>80</td>
<td>ln_PA_trade = year_L_PA_t_1</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Qeq.</td>
<td>33</td>
<td>75</td>
<td>ln_QE_trade = year_L_QE</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Nuuk</td>
<td>47</td>
<td>102</td>
<td>ln_NU_trade = year_L_NU_t_1 ln_L_NU_t_2</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Maniitsoq</td>
<td>70</td>
<td>132</td>
<td>ln_MA_trade = year_L_MA_t_1 ln_L_MA_t_2</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Sisimiut</td>
<td>49</td>
<td>76</td>
<td>ln_SI_trade = year_L_SI_t_1 ln_L_SI_t_2</td>
<td>AR3</td>
<td></td>
</tr>
<tr>
<td>Aasiaat</td>
<td>33</td>
<td>67</td>
<td>ln_AS_trade = year_L_AS_t_1 ln_L_AS_t_1</td>
<td>AR1</td>
<td>***</td>
</tr>
<tr>
<td>Upernavik</td>
<td></td>
<td></td>
<td>No valid model</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Coefficient AR1</th>
<th>Coefficient AR2</th>
<th>Coefficient AR3</th>
<th>DW</th>
<th>Rtot2</th>
<th>RegR2</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.8594 ± 0.1679</td>
<td>0.164 ± 0.2361</td>
<td>-0.3188 ± 0.1793</td>
<td>2.1379</td>
<td>0.8334</td>
<td>0.2455</td>
</tr>
<tr>
<td>0.6252 ± 0.1902*</td>
<td>0.2677 ± 0.2218</td>
<td>-0.0218 ± 0.2154</td>
<td>1.8854</td>
<td>0.7054</td>
<td>0.1035</td>
</tr>
<tr>
<td>1.0196 ± 0.1648</td>
<td>0.0179 ± 0.2388**</td>
<td>-0.0940 ± 0.1691</td>
<td>1.7717</td>
<td>0.8831</td>
<td>0.1995</td>
</tr>
<tr>
<td>1.0275 ± 0.1333</td>
<td>-0.2089 ± 0.1926</td>
<td>-0.1362 ± 0.1357</td>
<td>2.3664</td>
<td>0.9063</td>
<td>0.0304</td>
</tr>
<tr>
<td>1.0395 ± 0.1541</td>
<td>0.051 ± 0.2457</td>
<td>-0.1895 ± 0.1868</td>
<td>1.7727</td>
<td>0.9245</td>
<td>0.1852</td>
</tr>
<tr>
<td>1.1305 ± 0.2379</td>
<td>0.0237 ± 0.3678</td>
<td>0.2063 ± 0.2525</td>
<td>1.9127</td>
<td>0.8248</td>
<td>0.0497</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Coefficient L</th>
<th>Coefficient L (lag1)</th>
<th>Coefficient L (lag2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.0960 ± 0.0350***</td>
<td>-0.3698 ± 0.2325</td>
<td></td>
</tr>
<tr>
<td>-0.006979 ± 0.0685</td>
<td>-0.5033 ± 0.2890</td>
<td></td>
</tr>
<tr>
<td>-0.009398 ± 0.0203</td>
<td>-0.7407 ± 0.3003**</td>
<td>0.1946 ± 0.1683</td>
</tr>
<tr>
<td>-0.004064 ± 0.0175</td>
<td>0.1623 ± 0.1785</td>
<td>0.242 ± 0.1744</td>
</tr>
<tr>
<td>-0.0205 ± 0.0115</td>
<td>0.5061 ± 0.2258*</td>
<td>0.4968 ± 0.2304*</td>
</tr>
<tr>
<td>0.0160 ± 0.2079</td>
<td>0.3649 ± 0.3950*</td>
<td>0.3687 ± 0.3691*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No valid model</td>
</tr>
</tbody>
</table>
Figure 1. Map of Greenland with larger towns (black dots) in West Greenland. Data from seven towns/regions are included in the analyses (white dots with black circumference). The Greenlandic names are listed with corresponding old Danish names in parentheses.

Figure 2. Caribou population fluctuations based on trade data (grey) or harvest data (black) in seven regions: Paamiut, Qeqertarsuatsiaat, Nuuk, Maniitsoq, Sisimiut, Aasiaat and Upernavik. A combined plot for West Greenland is included for visualization.

Figure 3. Synchrony curves for trade (grey) and harvest (black) statistics.

Figure 4. Spectral and wavelet analyses of periodicity of the two sets of harvest data. a and c display the wavelet power spectrum (the strength of the frequency components) of the harvest (a) and skin trade (c) data and the dotted line shows the corresponding confidence interval indicating the significance of the periodicities. (b) and (d) display the wavelet diagrams. The color symbolizes the strength of the periodicity. Blue is weak, red is strong and contours indicate statistically significant periodicities with the cone of influence indicated. The diagram illustrates the progressive change of periodicity throughout the time series. 4.1: Paamiut; 4.2: Nuuk; 4.3: Sisimiut; 4.4: Maniitsoq; 4.5: Aasiaat; 4.6: Qeqertarsuatsiaat; 4.7: Upernavik (no trade data).
Figure 1.
Figure 2.
Figure 3.
Figure 4.1.

Figure 4.2.
Figure 4.3.

Figure 4.4.
Figure 4.7.