# Makin' some noise

## A study on anthropogenic threats to thick-billed murre (appa, *Uria lomvia*) in Greenland

Aili Lage Labansen
PhD Thesis 2021

AARHUS UNIVERSITY

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Greenland Institute of Natural Resources, Greenland
Graduate School of Technical Sciences, Department of Bioscience, Aarhus University, Denmark

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| Abstract: | The thick-billed murre (*Uria lomvia*) is the culturally most important seabird species in Greenland. It is declining in most areas of Greenland and have shown local extinctions. Recent research indicates that at least some of the population decline can be linked to drivers in the wintering areas, whereas the role of local breeding conditions largely is unknown. We used a suite of different methods to investigate local drivers during the breeding period, suspected to play a role for the population decline in Greenland. The first part of this thesis provides a brief introduction to historical and current challenges for the murre population in Greenland and describes the research questions. The second part consists of four scientific papers. We investigated the effects of gunshots with an experimental approach and show that there was large variation in the distance of first reaction, and that most responded at distances greater than the current no-disturbance zone allow. We also quantified marine traffic using underwater acoustics, which proved to be a promising tool to study vessel activity. Marine traffic near a declining colony was five times larger, compared to at a stable nearby colony. Local ecological knowledge indicates and confirms the assumption that human disturbances are far less common today than 2-3 decades ago, but that they still occur. A need for a higher information level from authorities was also identified. Lastly, statistical analyses on the impact of various local drivers on murre population trends in Greenland showed that both local human factors and the local climate, derived from global warming, have had an impact on population development in Greenland. Drivers linked to global climate change are difficult to mitigate, which make management measures to diminish negative effects of local anthropogenic drivers even more important. |
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# Preface

This thesis represents a partial fulfillment of the requirements for the degree of Doctor of Philosophy (PhD) at the Graduate School of Technical Sciences, Aarhus University, 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 Flemming Merkel (main supervisor) and Anders Mosbech (co-supervisor), both from AU.

Broadly this work is concerning local factors that might affect breeding thick-billed murres in Greenland with a focus on effects of human disturbances.

When I grew up, we occasionally had appa (i.e., thick-billed murre) for dinner and it was one of my favorite dishes! Particularly my mother and I would be full of anticipation during the preparation of the meal and have the mouth full of water, when dinner was finally served. A dinner that was prepared in no other way than the traditional way, boiled in a hearty soup. For my mother though, this delicious meal had, during the winter months of her childhood in Sisimiut, sometimes been a bit too much of the good. My granddad was a paid worker at the shipyard and during the winter months, when appa were abundant in the waters outside of Sisimiut, he would go out during weekends to catch appa for the week. Times have changed, the appa population has been and still is under pressure for different reasons, as this work describes, and the use of appa as a resource nowadays is much more limited. Yet, appa is not only a nutritional resource, but also a food of high cultural importance. Still today, I am too weak to decline when I am offered appa at a meal... Fortunately – in that sense – it does not happen very often. I just hope that my children will be able to enjoy – and themselves serve for their own children – this extremely tasty, healthy, and valued food.

This thesis consists of a general introduction to the subject, followed by four research papers (I-IV), one of which has been published in *Wildlife Biology*, another submitted to *Conservation Letters*, and two that are planned for submission to other peer reviewed scientific journals. There will unavoidably be some overlap among the papers, as they are centered around the same issues. All figures and tables have been imbedded in the texts of the manuscripts, to make it easier for the reader.

We have mostly used the American name, thick-billed murre, for *Uria lomvia*, rather than the British, Brünnichs guillemot. In the last paper we decided to use the Inuit name, appa.

## Acknowledgements

Working with this thesis has taken me far too long and it would never have been finished without help from people around me, and without the goodwill from the Greenland Institute of Natural Resources that, together with “Den danske stats midler til arktisk forskning”, have funded my work with this thesis.

First of all, to my main supervisor Flemming Merkel: Thank you for your patience and great thoroughness. But even more - for having trust in me! I also owe a great thanks to all my co-authors and all the people who have helped during this long journey of exiting field work, data analysis, statistics, writings, and discussions back and forth. The idea of including an interview survey in my thesis was developed together with the late Lene Kielsen Holm, who we had hoped to involve in the further process also. Her contribution would have added an invaluable dimension that we are truly missing. The last days of writing I had invaluable help from Henrik Lund and from Katrine Raundrup, the whole period of PhD life. Thank you!

Last, but not least I am so thankful for all my family, friends, and colleagues. Special thanks to my mother who have made our family everyday life easier, my brother for housing and nursing me the last intense writing period, and for my husband for taking extra care of our wonderful children. I also had my father in my mind in this work. He would have been so proud.

Carey Islands, July 2015
Photo: A. Kristensen

Aili Lage Labansen
Nuuk, Greenland Institute of Natural Resources
March 2021

## List of included papers

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|---|---|
| Paper I | **Labansen AL**, Merkel FR & Mosbech A (2021) Reactions of a colonial seabird species to controlled gunshot disturbance experiments.<br><br>Published in *Wildlife Biology*<br><br>Contribution: Planning and carrying out field work, data analysis and lead writer of the paper. |
| Paper II | Merkel FR, **Labansen AL**, Autzen T, Simon M & Hermannsen L. Quantifying marine traffic intensity in Northwest Greenland and the potential disturbances of two seabird colonies.<br><br>Manuscript planned for submission to *PLOS ONE*.<br><br>Contribution: Planning and coordinating field work. Contributing with initial analysis and with the writing of the manuscript. |
| Paper III | **Labansen AL** & Merkel FR. Local Ecological Knowledge about a traditional game bird in Greenland.<br><br>Manuscript planned for submission to *Arctic*<br><br>Contribution: Planning and carrying out field work, data analysis and lead writer of the manuscript. |
| Paper IV | Huffeldt NP, **Labansen AL**, Frederiksen M, Linnebjerg JF, Witting L & Merkel FR. Global and local anthropogenic threats to a culturally important food animal.<br><br>Manuscript submitted to *Conservation Letters*<br><br>Contribution: Shared first-authorship. Providing data and co-writing the human component of the manuscript. |

## Summary

The thick-billed murre (*Uria lomvia*) is the culturally most important seabird species in Greenland. It is declining in most areas and have shown local extinctions. Locally harvested resources often define cultural identities, which is especially important for Indigenous Peoples and societies with locally based cultures. Recent research indicates that at least some of the murre decline can be linked to drivers in the wintering areas, whereas the role of local breeding conditions largely has been unknown. Identification of the causes of local biodiversity loss is vital for the sustainability of ecosystems and dependent cultures. We used a suite of different methods to investigate local drivers during the breeding period, which was suspected to play a role for murre population decline in Greenland.

First, we studied effects of gunshot disturbance at breeding colonies to explore the distance where effects started, the difference in the behavioural response between presumed disturbed colonies (e.g. by traffic and hunting) and largely undisturbed colonies, and among plots with varying seabird densities. We carried out two different types of controlled gunshot experiments – one measuring the distance at which murres first reacted to gunshots (Flight Initiation Distance, FID) and one measuring the proportion of murres remaining in the colony during and after repeated gunshots (20 gunshots within 78 minutes). FID varied from 0.5 to 5 km. The proportion of murres remaining in the plot after the repeated gunshots ranged from 0.44 to 0.8. Mainly murres not incubating their egg or brooding their chick took off when disturbed by gunshots, but occasionally also murres attending their offspring took off. We found that density of seabirds at the plot area scale was the best explaining factor for FID, and to some extent also for the effect of repeated gunshots, both for disturbed and undisturbed colonies. Murres in denser colonies reacted earlier (larger FIDs) and somewhat more strongly (higher proportions fleeing) to gunshots than murres in less densely populated colonies. FID clearly showed that the current legislation in Greenland regulating gunshots near breeding colonies is insufficient.

In the second study, we quantified marine traffic intensity around two seabird colonies. Marine traffic represents an increasing source of noise pollution in the marine environment, also in Greenland. Murres are potentially highly vulnerable to this type of anthropogenic disturbance because they breed in coastal areas, where marine traffic also is concentrated. Yet, the magnitude of the problem is largely unknown. We explored if underwater noise recordings can be used as a method to quantify the level of critical marine traffic near seabird colonies. The study area was northern Upernavik in Northwest Greenland, where it was speculated if marine traffic could be a contributing driver for population decline. A total of 307 vessels and seven travelling routes were identified for the period 22 June - 10 August 2016, of which

23 vessels were classified as a potential disturbance for one or the other colony, based on the travelling route, their noise emission and boating behaviour. The colony situated closest to an inshore travelling route (Apparsuit) was disturbed nearly five times as much as the other colony (Kippaku). The true nature of the disturbances was not determined, due to lack of direct observations. However, the higher disturbance level at Apparsuit coincides with a declining murre population trend, in contrast to a positive population growth at the more remote Kippaku. Disturbance from marine traffic activity is an understudied conservation issue for seabirds and this study shows that underwater acoustic monitoring is a useful method to quantify the degree of exposure.

In the third study, we collected Local Ecological Knowledge about murres in Southwest- (2016, 24 informants) and Northwest Greenland (2018, 54 informants), where locals are holders of valuable information about the areas they move in and the resources they use. We focused on their knowledge about local breeding populations, various aspects of human use of the areas and their view on murre management in West Greenland. The interviews had a semi-structured approach with a series of up to 54 predetermined questions. The survey showed that helicopters, marine traffic, and landslides locally are of concern, particularly in the Northwest Greenland, while the level of hunting, egging, and disturbances at colonies today generally is considered small and less concerning. Although most considered regulations necessary, many had suggestions to changes. Southwest informants reported that murres nowadays often are farther from the coast during winter. The dissemination level from authorities appears deficient as many seemed uninformed of murre monitoring results and unaware of the biological reasoning behind the management regulations.

In the last study, the influence of potential local drives was statistically analysed for all murre colonies in Greenland, using data on population trends for the period 1983 – 2017. Both local environmental drivers, linked to global climate change, and indicators of human activity were included in the analyses and the results indicate that both had contributed to recent declines. High rates of air temperature change and insolation co-occurred with the largest declines in the extant population, while the lowest growth rates that have resulted in local extinction occurred when human settlements were nearby.

Drivers linked to global climate change are difficult to mitigate with management actions, and this makes measures to diminish negative effects of local anthropogenic drivers even more important. The wish for a continued use of this culturally valued seabird species and the global and local threats it is faced with, makes management highly challenging. The thesis does not provide quantitative measures on the effects of anthropogenic threats, but it represents an important contribution to future research and management priorities.

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# Resume

Polarlomvien (*Uria lomvia*) er den kulturelt vigtigste havfugleart i Grønland. Ynglebestanden er faldende i de fleste områder og nogle steder er kolonier helt forsvundet. Lokalt udnyttede ressourcer definerer ofte kulturelle identiteter, hvilket især er vigtigt for oprindelige folk og samfund med lokalt funderede kulturer. Nyere forskning tyder på, at tilbagegangen af lomvie delvis kan knyttes til faktorer i overvintringsområderne, mens faktorer knyttet til forhold i yngleområderne generelt er dårlig belyst. Her har vi brugt en række forskellige metoder til at undersøge lokale faktorer i yngleperioden, som mistænktes for at spille en rolle for nedgange i lomviebestanden i Grønland.

Som det første studerede vi effekter af skudforstyrrelser i ynglekolonier, for at undersøge afstanden hvor forstyrrelseseffekten startede, forskellen i adfærd mellem formodede forstyrrede kolonier (f.eks. af trafik og jagt) og stort set uforstyrrede kolonier, samt forskellen mellem plot med varierende tæthed af fugle. Vi gennemførte to typer af kontrollerede eksperimenter med skud – et hvor vi målte afstanden, hvor lomvier først reagerede på skud (Flight Initiation Distance, FID) og et der målte andelen af lomvier der var tilbage i kolonien under og efter en serie af gentagne skud (20 skud inden for 78 minutter). FID varierede fra 0,5 til 5 km. Andelen af lomvier tilbage i plottet efter serien af skud varierede fra 0,44 til 0,8. Hovedsageligt lomvier der ikke rugede på æg eller unge, fløj når de blev forstyrret af skud, men lejlighedsvis fløj også rugende lomvier som dermed forlod deres afkom. Eksperimenterne viste, at tætheden af fugle i kolonien var den bedste forklarende faktor for FID og til en vis grad også for effekten af de gentagne skud, både for forstyrrede og uforstyrrede kolonier. Lomvier i kolonier med høj tæthed reagerede tidligere (større FID'er) og kraftigere (højere andel fløj) på skud end lomvier i kolonier med mindre tæthed. FID resultaterne viste tydeligt, at den nuværende lovgivning som regulerer skud nær havfuglekolonier i Grønland, er utilstrækkelig.

I den næste undersøgelse kvantificerede vi intensiteten af skibs- og bådtrafik nær to havfuglekolonier. Skibs- og bådtrafik udgør en stigende kilde til støjforurening i havmiljøet, også i Grønland. Lomvier er potentielt meget sårbare over for denne type forstyrrelser, fordi de typisk yngler langs kysten, hvor den meste trafik foregår. Alligevel er problemets omfang stort set ukendt. Vi undersøgte, om optagelser af undervandsstøj kan bruges til at kvantificere niveauet for potentiel skadelig trafik nær havfuglekolonier. Undersøgelsen blev udført i et område, hvor skibs- og bådtrafik var mistænkt som medvirkende årsag til bestandsnedgange. I alt 307 fartøjer og syv sejlruter blev identificeret for perioden 22. juni - 10. august 2016, hvoraf 23 fartøjer blev klassificeret som potentiel forstyrrende for den ene eller den anden koloni, vurderet på baggrund af sejlrute, støjniveau og sejladsadfærd. Kolonien Apparsuit, der ligger tættest på den officielle sejlrute, blev forstyrret næsten fem gange så meget som den anden koloni, Kippaku. De

specifikke aktiviteter fortaget i forbindelse med forstyrrelserne kunne ikke bestemmes på grund af manglende direkte observationer. Imidlertid falder det højere forstyrrelsesniveau ved Apparsuit sammen med en faldende lomviebestand, i modsætning til en bestandsvækst ved den mere afsidesliggende Kippaku. Forstyrrelser fra skibs- og bådtrafik er dårligt belyst for havfugle, og denne undersøgelse viser, at akustisk overvågning er en nyttig metode til at kvantificere problemet.

I den tredje undersøgelse indsamlede vi lokal viden om lomvien i Sydvest- (2016, 24 informanter) og Nordvestgrønland (2018, 54 informanter), hvor lokalbefolkningen har værdifuld information om de områder de færdes sig i, og de ressourcer de udnytter. Vi fokuserede på deres viden om lokale lomviekolonier, forskellige aspekter af menneskelig brug af områderne og deres syn på lomvieforvaltning i Vestgrønland. Interviewene havde en semistruktureret tilgang, med op til 54 forudbestemte spørgsmål. Undersøgelsen viste, at der lokalt, især i det nordvestlige Grønland, udvises bekymring for helikoptere, skibs- og bådtrafik og stenskred, mens niveauet for jagt, ægsamling og forstyrrelser i kolonierne generelt betragtes som lille og af mindre betydning i dag. Selvom de fleste mente, at regulering er nødvendig, havde mange forslag til ændringer. Informanterne fra Sydvestgrønland rapporterede, at lomvierne om vinteren nu ofte er længere væk fra kysten. Informationsniveauet fra myndighederne synes generelt at være mangelfuld, da mange virkede uvidende om overvågningsresultater for lomvien og om den biologiske begrundelse bag forvaltningstiltag.

I den sidste undersøgelse blev indflydelsen af potentielle lokale faktorer statistisk analyseret for alle lomvie kolonier i Grønland, på baggrund af data om bestandsudvikling for perioden 1983 - 2017. Både lokale miljøparametre, knyttet til globale klimaforandringer, og indikatorer for menneskelig aktivitet var inkluderet i analyserne, og resultaterne indikerer, at begge forhold bidrog til de observerede bestandsnedgange. Store ændringer i lufttemperaturen og eksponering af sollys faldt sammen med de største bestandsnedgange blandt de eksisterende kolonier, mens de laveste vækstrater, der har resulteret i lokal udryddelse, fandt sted i områder med nærtliggende menneskelige bosættelser.

Påvirkninger der er knyttet til globale klimaforandringer, er vanskelige at afbøde med forvaltningstiltag, hvilket gør at foranstaltninger til at minimere negative påvirkninger af andre menneskelige påvirkninger er endnu vigtigere. Ønsket om en fortsat udnyttelse af denne kulturelt vigtige havfugleresurse og de globale og lokale trusler som arten står overfor, er en stor udfordring rent forvaltningsmæssigt. Denne afhandling indeholder ikke kvantitative estimater af påvirkningerne af de menneskeskabte trusler, men den repræsenterer et vigtigt bidrag til den fremtidige prioritering indenfor forskning- og forvaltning af lomvien.

# Introduction

Humans have a negative impact on wildlife, and biodiversity in general, on a global scale (Dirzo et al. 2014, McCauley et al. 2015). A significant and growing type of stressor that is affecting wildlife is anthropogenic disturbance (Burton 1998, Buckley 2004, Green et al. 2005, Davenport and Davenport 2006, Stankowich 2008). Disturbances can influence energy expenditure, habitat use, fitness, and reproduction of animals due to increased stress, displacements, and loss of offspring (Olsson and Gabrielsen 1990, Creel et al. 2002, Beale and Monaghan 2004, Rodríguez-Prieto and Fernández-Juricic 2005, Lundquist et al. 2013). Seabirds are some of the most threatened birds and a group of birds that exhibit declines worldwide (Croxall et al. 2012). Disturbances have been identified as one of five ongoing factors that globally are affecting most seabird species, seabirds breeding in colonies in particular (Dias et al. 2019). However, for some groups of colony breeding seabirds, like the Alcids, the role of anthropogenic disturbances during the breeding period are less well documented (Lorentsen and Follestad 2014).

Human activities in Greenland are mostly concentrated along the coast and all human communities are near the shoreline. The largest industry is fishery, most cargo are shipped into the region, and most of the personal transportation between communities are carried out by boat, as there are no roads connecting inhabited areas (Christensen et al. 2018). The Greenland economy and related activities primarily depend on the marine infrastructure, which is expected to expand in the future as year-round open water areas and commercially exploitable fish species experience a northward shift due to global warming (Merkel and Tremblay 2018).

The thick-billed murre (aka appa, *Uria lomvia*, hereafter “murre”) is a highly abundant cliff nesting seabird with a circumpolar arctic distribution (Irons et al. 2008). The Greenland breeding population consists of about 342,000 breeding pairs distributed in 20 colonies of varying sizes primarily found along the west coast (Fig. 1) (Merkel et al. 2014b). Outside the breeding season, the Greenland breeding population mixes with murres that breed in Canada, Iceland, Norway, and Russia in the productive open water area off Southwest Greenland and the waters off Labrador and Newfoundland (Fig. 2)(Frederiksen et al. 2016). Like most seabirds, the murre is a long-lived species with delayed maturation and a low reproduction rate (Schreiber and Burger 2001). It reaches sexual maturity at the age of 4-5 years and hatches a maximum of one egg per year (Gaston and Hipfner 2000). These life-history characteristics make the murre dependent on a high adult survival rate and even small changes in adult mortality can drastically reduce the population growth rate (Lebreton and Clobert 1991a). Furthermore, depressed populations recover very slowly because of the low reproductive rate.

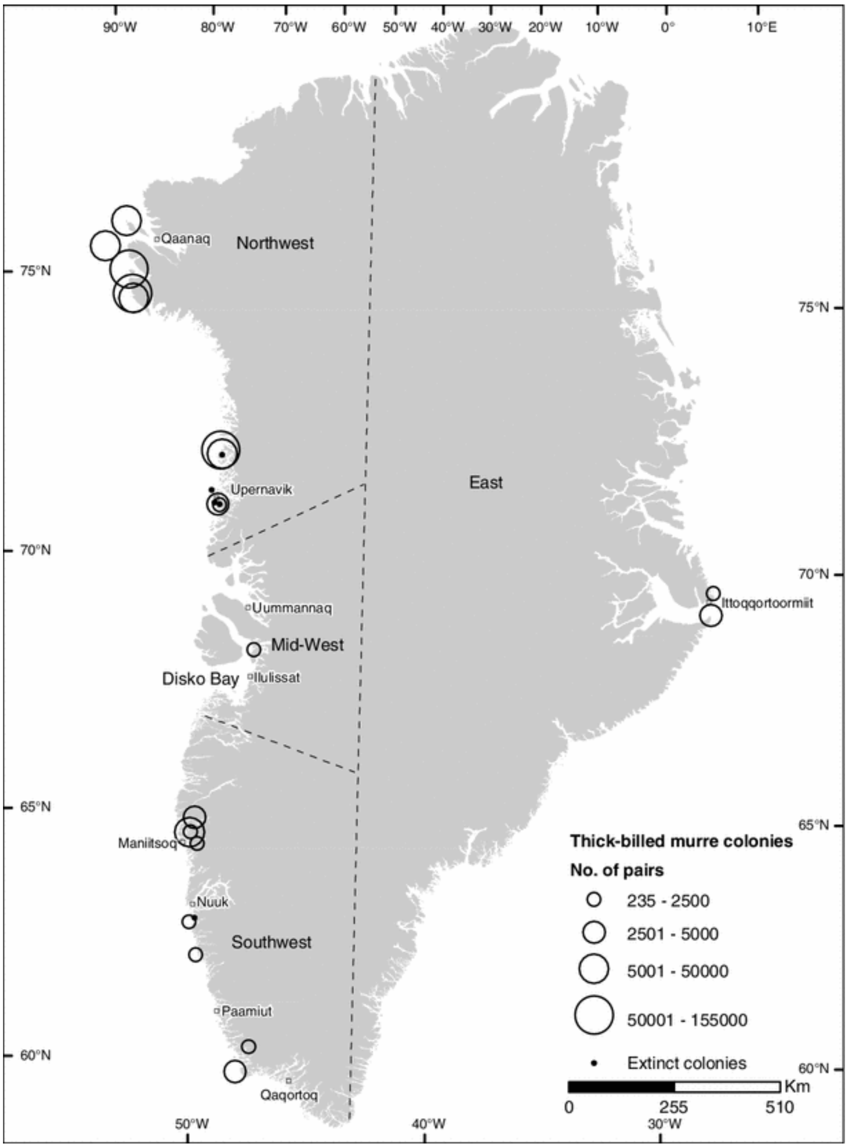


***Fig. 1.*** *Locations and population sizes (pairs) of thick-billed murre colonies in Greenland based on colony surveys in 2006–2011. Main towns (squares) and regions are shown. Colonies shown as 'extinct' correspond to colonies that disappeared in the period 1981–2011. Map from Merkel et al. (2014).*

Being an abundant species, the murre has been, and still is, one of the most important bird food resources for indigenous people in Greenland. Nowadays it is less important for sustenance, yet culturally it is still a highly important food resource, in line with other traditional and valued food sources (Fabricius 1780, Pars et al. 2001, Sowa 2015, Haastrup 2017, Piniarneq 2019). During the 20$^{th}$ century, a range of different human activities caused large reductions and local extinctions of the Greenland breeding population. A growing human population with modern hunting equipment lead to an increased hunting pressure, and human disturbances at breeding colonies reached alarming levels (Chardine and Mendelhall 1998). In addition, hunting was commercialised and in some areas murres were traded and packaged in fish plants to be sold elsewhere in Greenland. Especially the commercial trade in breeding areas during 1960s and 1970s had a large impact on local murre populations (Gilchrist et al. 2005). In the same period, large scale drift nets used in international salmon fisheries caught large numbers of murres in Greenland waters (Tull et al. 1972). During the 1980s and 1990s, hunting and oil spills in Canadian waters also caused a large mortality (Chardine et al. 1999, Wiese and Robertson 2004). All these human factors were gradually mitigated by management and regulations, however often somewhat delayed, resulting in a depressed murre population for posterity.

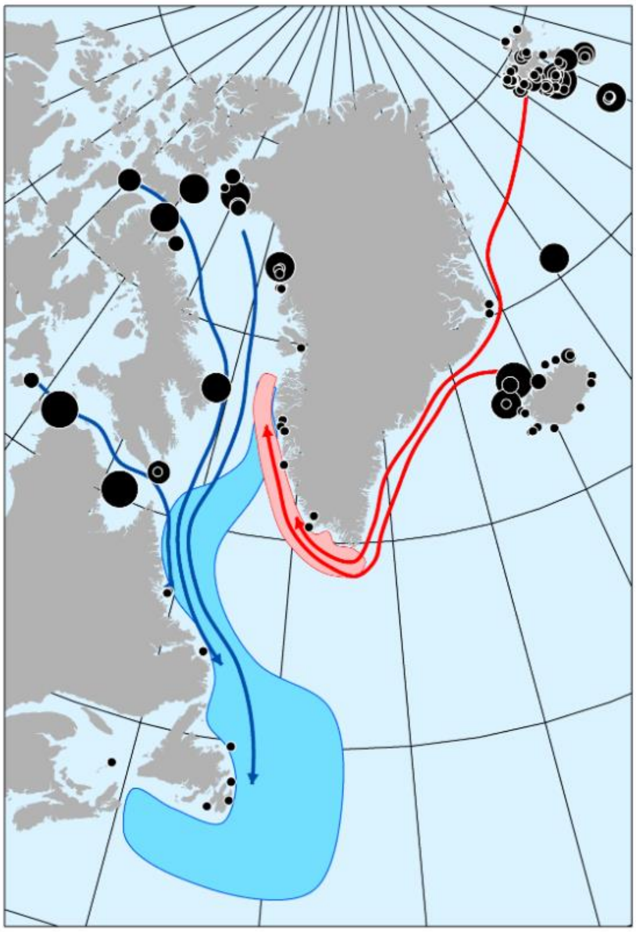

***Fig. 2.*** *Map of the North Atlantic showing migration routes for the eastern and western part of the breeding population (black circles) and the two main wintering areas of thick-billed murre off Southwest Greenland (red area) and Newfoundland (blue area), Canada. Note that migration routes are simplified and not entirely updated.*

The first protective measure involving murres in Greenland was a ban enforced in 1958 on direct hunting at seabird breeding colonies. Murre hunting during the breeding season was prohibited in West Greenland in 1978, but the Uummannaq area and the Northwest region, where most of the colonies are (fig. 1), were exempted. The large scale drift net salmon fisheries, that caught large numbers of murres, were phased out in the early 1970s (Evans and Waterston 1977). The commercial exploitation of murres in the breeding areas in West Greenland was illegalised in 1988 (Falk and Kampp 1997), and the first countrywide hunting regulations of murre were introduced in 1989. Since then, the hunting regulations have slowly moved towards more restricted hunting with the use of restricted seasons and daily hunting quotas.

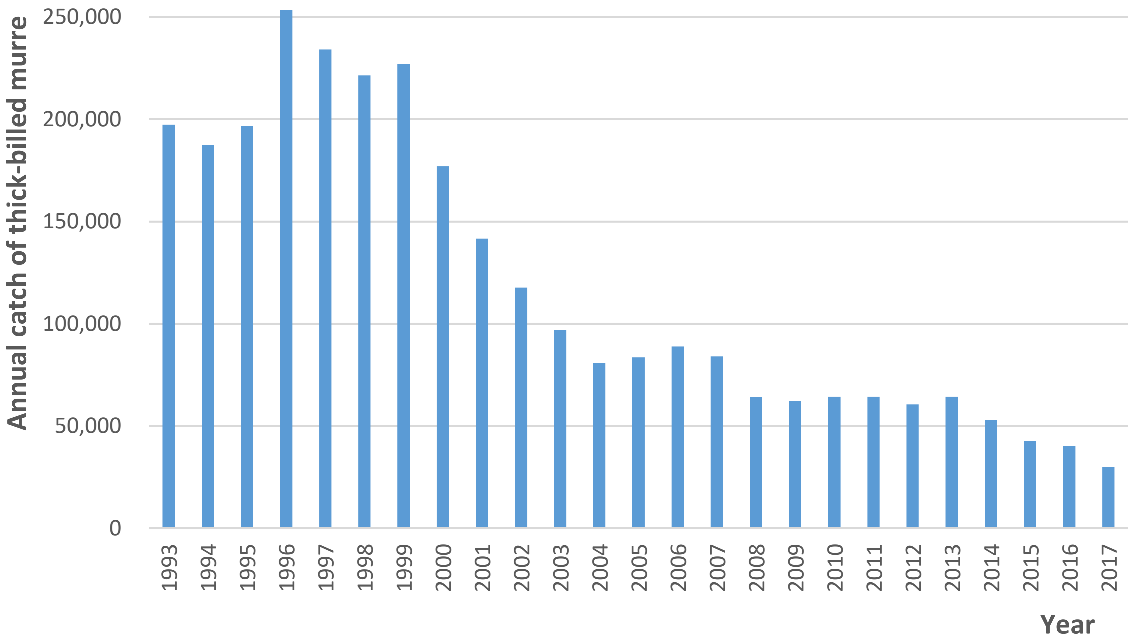


***Fig. 3.*** *Annual catch of thick-billed murre in Greenland from 1993-2017 (Piniarneq 2019).*

Hunting statistics on murre were initiated in 1993 and documented an annual catch surpassing 200,000 murres in the late 1990s (Fig. 3). A significant proportion of the catches consisted of murres shot during spring near breeding areas. This hunting was advised against by scientist because it was significantly taxing adult murres from local breeding populations. Winter catches, on the other hand, consisted of a high proportion of young murres and murres from elsewhere in the North Atlantic region and was considered more sustainable (Lyngs 2003). The spring hunt was banned in 2002 in most of Greenland and the annual hunting levels were generally declining during the early 2000s and have levelled at less than 50,000 murres annually in recent years (Fig. 3) (Piniarneq 2019). However, there has been no sign of recovery, and most of the colonies that were declining before the reduced hunting levels have continued to decline. Similarly, only colonies that were considered stable before the reduced hunting levels appear to be stable or are increasing moderately today (Fig. 4) (Merkel et al. 2014b).

The continued absence of a positive response after more than a decade of a markedly reduced hunting pressure was unexpected and indicated that harvest no longer was the primary driver for the population decline. Not only was the spring harvest markedly reduced in Greenland, but so were winter hunting in Greenland, winter hunting in Canadian waters (Gaston and Robertson 2010) and mortality caused by chronic oiling in Newfoundland waters (Wiese and Robertson 2004, Frederiksen et al. 2019b) was markedly reduced. Studies on breeding colonies in Svalbard, which were also declining, indicated a connection between the declines and climate related factors in the wintering quarters (Descamps et al. 2013b, Fluhr et al. 2017). These climatic factors are likely important also for Greenland colonies, but since murres from decreasing colonies share winter quarters with murres from stable colonies, they were not likely to be the only important factors (Frederiksen et al. 2016).

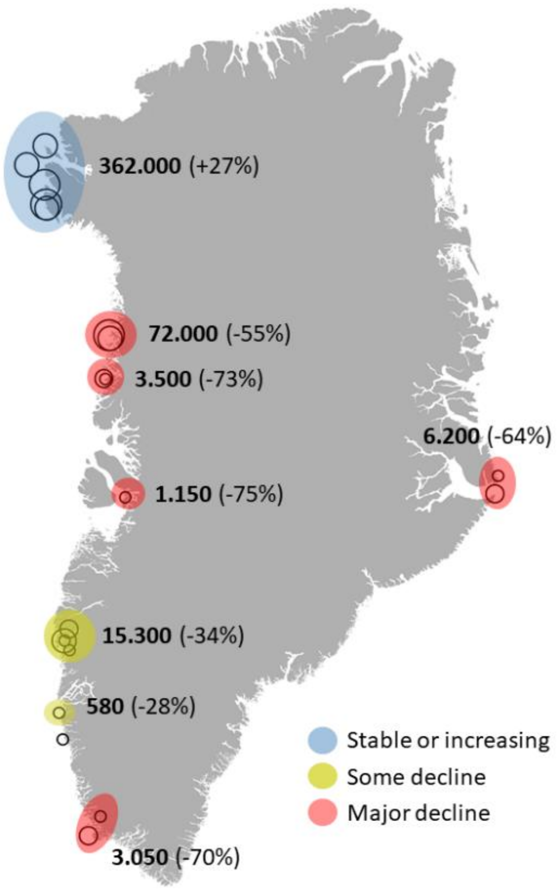


***Fig. 4.*** *The location and population sizes (2017, counted individuals) of the 20 extant thick-billed murre colonies in Greenland in different sub-areas. Population changes (%) for each sub-area in the period from 1990 to 2017 are indicated. One colony that went extinct at Uummannaq in the 1980s and four colonies at Upernavik that became extinct in the period 1989-2003, are not shown on the map.*

## Research questions

The contrasting breeding population trends of some Greenland colonies that share the same wintering quarters indicate that local factors, in effect during the breeding period, somehow contribute to the observed declines. Personal observations during field work, full-season time-lapse photography set up for monitoring purposes, and information from hunting wardens and locals had shown that illegal hunting and egg collection still occurred to an unknown extent in some areas (Merkel et al. 1999, Falk et al. 2000, Mosbech et al. 2009, Linnebjerg 2012, Labansen et al. 2013). Also, disturbances from legal hunting activities (seals etc.), from vessel and aircraft traffic, and influence of local climatic conditions, that could cause lowered breeding success, and increased predation, were all potential contributors to the observed declines in the colonies that were largely unstudied.

In this thesis, a suite of different methods has been used to investigate local factors affecting Greenland murre colonies. Increased knowledge of these factors will provide management with a better foundation on which to act in the effort of halting or reversing the negative population trend of a much-valued resource.

First, we investigated effects of gunshots near murre breeding colonies to document the distance at which murres first reacted to approaching gunshots and the effects of repeated gunshots at a fixed distance. Apart from evaluating the existing legal zones for gunshots at murre colonies, we also wanted to test if murres from colonies with an assumingly high disturbance level reacted differently to disturbances compared to murres from more remote and assumingly less disturbed areas (paper I).

Since human activities in Greenland are highly connected to marine traffic, we recorded vessel activity with passive underwater sound recorders near two neighbouring murre colonies with contrasting population trends. First of all, we wanted to test if the method was useful as a tool to quantify the density of marine traffic near murre colonies. Secondly, we wanted to test the hypothesis that the declining colony, close to a nearby vessel route, was exposed to a higher level of marine activities, and hence human disturbances, than the colony with an increasing murre population (paper II).

Local users of the surrounding environment and its natural resources not only have valuable knowledge of local conditions but are themselves important components of the human-wildlife interactions we were aiming at getting a better understanding of. We collected Local Ecological Knowledge (LEK) by interviewing local users of two important murre areas with very different seasonal availability of murres, in order to uncover important factors affecting colonies and murre populations, and to get a better understanding of different local perspectives, issues, and views on the use and management of the thick-billed murre (paper III).

Finally, we statistically evaluated to what extent a range of potential environmental drivers and indicators of human activities could explain observed trends in all Greenland murre breeding colonies in the period between 1983 and 2017. Global climate change influence sea surface and air temperatures near murre colonies and increasing air temperatures may affect colonies differently depending on the compass orientation of a colony. The purpose was to analyse the relative importance of factors that may influence the population dynamics of murre populations during the breeding period, in order to identify drivers with the most negative impacts (paper IV).


***Fig. 5.*** *Video camera plot (a), recording video camera and a time-lapse photo camera in a sealed metal box (mounted for long-term monitoring purposes) (b), and the time-lapse camera plot named Kippaku C (c) at the thick-billed murre colony Kippaku, Northern Upernavik, during a gunshot disturbance experiment July 21st, 2015.*

# Discussion and perspectives

## Effect of disturbances

Being a cliff nesting seabird species that aggregates in large numbers and is very faithful to its breeding site, the murre is particularly vulnerable to disturbances while breeding (Gaston et al. 1994, Gaston and Hipfner 2000). Birds can show increased tolerance to repeated disturbances (Nisbet 2000), but disturbances can also lead to a sensitisation (Blumstein 2014). Hence the general response to disturbances can differ between birds in different colonies, depending on whether the colony has been exposed to human disturbances through years or largely has been undisturbed (Ellenberg et al. 2009, Ellenberg et al. 2012, Villanueva et al. 2012, Pichegru et al. 2016). When disturbances have significant consequences, as in a hunting situation, they are more likely to cause sensitisation rather than increased tolerance (Bejder et al. 2009). We were not able to relate the difference in response behaviour to assumed difference in disturbance experience, with our gunshot disturbance study (Paper I: Labansen et al. 2021b). The study of approaching gunshots showed that the density of birds in the area of the plots was the best explaining factor for flight initiation: Birds in high density areas reacted at larger distances than birds in areas of less density. However, the results of the study of repeated gunshots were less conclusive. There was some indication of density correlation as well, as the proportion of murres leaving the plot during the repeated gunshots tended to be higher in high density areas. The relation was not statistically significant, though, and the plots that were deviating most from this pattern indicated that former experiences with gunshots could have contributed to the reaction of murres. Murres from a low-density plot in the remote colony of *Kitsissut* reacted relatively strong to gunshots, relative to other low-density areas, whereas murres in a plot in the *Innaq* colony (the Disko Bay), with a low density of murres but a high density of black-legged kittiwakes (*Rissa tridactyla*), reacted more inconclusively. Generally, though, it can be difficult to interpret disturbance behaviour (Gill et al. 2001) and our limited sample size of nine plots in four different colonies did not allow conclusions about effects of former experiments with disturbances. Nonetheless, the repeated gunshot disturbance showed that even if it mainly was murres not attending offspring that took off during extended gunshot disturbances, occasionally also murres that were attending their egg or chick left their offspring exposed. In rare cases offspring were also lost during the experiments. Disturbances may affect populational levels if they have an effect on the survival or reproductive success of individuals (e.g. Nisbet 2000, Gill 2007). The results from paper I were not extensive enough to make any quantitative evaluation of the effects of gunshot disturbances; however, we document that gunshot disturbances have a potential effect on the population through increased energetic costs (flight escape) and occasionally, by loss of offspring.

### Evaluation of the no-shooting zone

With the experiments in paper I, we also documented that the current no shooting zone of 1 km around cliff-nesting seabird colonies in Greenland is ineffectual, as murres from all six colonies of the approaching gunshot experiment exhibited flight initiation distances of more than 1 km (1.5-5 km). It is difficult to know the extent of this problem, i.e., the extent to which hunting for seals, or other types of legal hunting, occurs within 5 km of murre colonies during the breeding period. However, management could consider increasing the no-shooting zone to 5 km or more if a buffer zone is desired for. On the other hand, a wider no-shooting zone could be counterproductive, if people do not understand and accept it and therefore tend to comply less (Falk and Kampp 2002). Furthermore, it is possible that illegal gunshots near colonies due to bird hunting or with the purpose of causing spectacular mass flyouts, is occurring more often than legal hunting within 5 km. In that case, an increased no-shooting zone is unlikely to lead to less shooting disturbance.

### Marine traffic

One way of quantifying anthropogenic disturbance at seabird colonies is by quantifying the level of critical marine traffic. The results from paper II showed that passive underwater sound recorders can be effective tools for identifying levels of marine traffic at murre colonies in Greenland. Hunting is intimately linked with boating in Greenland, especially during the summer months (Boertmann et al. 2013, Boertmann and Mosbech 2017). We knew from our own experiences during field work, and later also from the interview survey of this thesis (paper III), that hunting and gun shooting near murre colonies do occur to some extent. Not all boating disturbs, but most gunshot disturbances are inevitably related to boating. We expected that it would be possible to detect gunshots from the acoustic recordings, so that gunshots could be separated from sounds from cracking icebergs (paper II), but we did not manage to verify this with observations or experimental truthing. We still know little about the extent of gunshot disturbance and hunting at murre breeding colonies, but passive acoustic recorders showed to be a promising tool to quantify marine traffic close to the colonies and in addition, the kind of boating behaviour that typically cause disturbances within seabird colonies. The level of boating activity close to colonies is likely also a good proxy for the level of shooting incidents, although this needs to be verified. The level of shooting is expected to be small, but we know that even very small levels of hunting during the breeding season can have a significant negative effect, particularly at colonies that have shown prolonged declines (Merkel et al. 2015).

### Colonies of contrasting trends

The acoustic recorders were placed at two larger murre colonies, *Apparsuit* and *Kippaku* in Northern Upernavik (Fig. 6), that are situated 8-9 km apart and show the most striking contrast of population trends in Greenland. The two colonies are not only expected to share the same wintering areas, but to a large extent also the same foraging conditions during the breeding period. Yet, *Apparsuit* has declined from about 150,000 murres in the 1990s to about 50,000 murres in 2017, whereas *Kippaku* has grown from about 13,800 to 21,400 murres in the same period (Merkel et al. 2014b). All four studies in this thesis have contributed to a better understanding of conditions that may contribute to the contrasting trends. Paper II documents that the disturbance level at *Apparsuit* was about five times higher than at

*Kippaku*. A higher level of boating is likely followed by a higher level of gunshot disturbances, which we have shown can result in increased energetic costs (flyouts) and breeding failures (paper I). LEK confirmed that disturbances do occur at colonies and that gun shooting and hunting at colonies occur to some extent (Paper III). Additionally, several locals expressed concern about the regional helicopter traffic on the main route between northern settlements and Upernavik town, that pass by the two colonies. The locals explained how the helicopter sounds and vibrations have a larger effect at *Apparsuit* due to the tall and almost vertical cliff sides, than at the small and relatively low-lying island of *Kippaku*. Moreover, locals reported that lands slides are more common at *Apparsuit* than at *Kippaku* (Paper III). Apart from showing that local anthropogenic threats may be important drivers, the statistical analyses in paper IV also showed that south and west facing colonies (like *Apparsuit*), which are more exposed to the sun and the risk of heat stress (Gaston et al. 2002), generally were declining, while north and east facing colonies (like *Kippaku*) generally were stable (paper IV).

***Fig. 6.*** *Picture taken from Kippaku with Apparsuit in the background. Photo: K. Falk.*

Even though murres are considered to have a very high site fidelity (Gaston and Hipfner 2000), there are examples of adult murres that have moved quite far to breed in a different colony, e.g. adult murres banded in Canadian colonies have been observed in the Qaanaaq area (K. Falk, pers. obs.) and *Kippaku* (F. Merkel pers. obs.). We have no knowledge of murres moving from *Apparsuit* to *Kippaku*, because *Apparsuit* is a difficult colony to work in and as a result, very few individuals from this colony have been banded. However, it cannot be ruled out that less optimal conditions at *Apparsuit* may have caused murres to move from *Apparsuit* to *Kippaku* and in that way have contributed to the increase at *Kippaku*. Such a scenario is perhaps not uncommon for new breeders. The site fidelity of established breeders is known to be high (Gaston and Hipfner 2000), but when it comes to the recruitment of new breeders site selection necessarily has to be more flexible since the breeding site where the offspring was born usually remains occupied. In this context it is worth considering, that our definition of a murre colony may not be the same as the murres´ perception of a colony. It could be that young murres "think" of *Apparsuit* and *Kippaku* as one colony and when possible establish breeding at *Kippaku* because local breeding conditions are more favourable here. Thus, in a long-term perspective, a biased site selection during recruitment may have contributed to the observed contrasting populations trends. Supporting such a theory, is the fact that similar pronounced contrasting population trends have been observed in southern Upernavik, where the two colonies in question also are situated very close to each other (< 3 km).

Altogether, our knowledge on mechanisms that may contribute to the contrasting trends observed during the last decades at *Apparsuit* and *Kippaku* has improved. However, it remains unanswered to what extent these factors can explain the observed contrasting population trends, also when it comes to contrasting trends among other colonies that are close to each other, and between larger regions, such as Qaanaaq versus the remaining West Greenland. Paper I indicates that even quite extensive gunshot disturbances only result in a small immediate impact on the breeding success and in some cases, in no detectable impact. The results from Paper IV shows that distance to nearest community have had a negative impact on the growth rate of murre colonies over the last decades, indicating a significant contribution from local anthropogenic drivers. When disregarding the colonies that went extinct over the past decades, Paper IV showed that the rate of air temperature changes had a larger effect, which could explain why the colonies in the Qaanaaq area are doing well, unlike most other colonies in Greenland.

## The human perspectives

Often the perspectives of hunters and biologists are portraited as conflicting in the media and the public debate (Sejersen 2003) and in public debates it is often the loudest voices representing certain interests that are heard most. Apart from learning more about local conditions, from people that are more widely present in the murre breeding areas and for longer periods of time, we were also interested in a more nuanced picture of opinions about murres among normal citizens with a broad interest in murres.

Coming from the Greenland Institute of Natural Resources, however, we represented the part of the authorities who, based on science, have been recommending increasingly more restricted hunting of this valued resource. We have no way of knowing if this have influenced the responses from the informants, but is should be kept in mind. Nonetheless, we generally found that we were well received in the communities.

An opinion that is often expressed in public debates, is that hunting restrictions are unnecessary for a variety of reasons, e.g. that nature protects itself, due to bad weather and general inaccessibility, that hunters never hunt too much, or the like (e.g. Sejersen 2003). This was also mentioned by some in our interview survey, but the majority of our informants believed that hunting restrictions and regulations are necessary in today's society, and somewhat surprising, more in the Northwest than in the Southwest region. The opportunities for hunting murres are relatively good for hunters in the Southwest region, which is an important murre wintering area. Hunters of the Northwest region, on the other hand, have been considerably more affected by murre hunting restrictions since the 2002 stop for spring hunting, that resulted in murres only became available for hunting a short time period in the autumn, before they disappear for the winter.

Some level of spring hunting appeared to have continued in the Northwest region, though, also before a recent reintroduction of a limited spring hunting in 2017 (paper III). Several seemed to be of the opinion, that a limited hunt for own consumption was unproblematic. Another view we also experienced was that hunting for own consumption in general, was unnecessary to report to the hunting statistics. Combined with other indications of a limited information level from the authorities (paper III), these findings suggest a general need for an improved information flow among managers, biologists, and users. This is emphasized by an apparent conflict between the biological recommendations of total hunting ban in the breeding period, the actual conditions in the murre breeding areas, where both disturbances and hunting occasionally occur in the breeding period, and the management, that recently opened up for a month of spring hunting in an area where the local breeding population historically, as well as recently, have shown significant declines.

The murre is not only an important resource for sustenance, but also a food that, as many other traditional food sources for the indigenous people of Greenland, is linked to cultural identity (Sowa 2015). Often people express worry and a feeling of loss when they tell about how young people are ignorant of the taste of murre. This makes it difficult for decision makers to introduce further restrictions. That hunters often argue that biologist survey animals in the wrong areas and at the wrong time of the year, does not make it easier (Sejersen 2002, Andersen et al. 2018).

## Future studies

This thesis has contributed with knowledge that gives a better understanding of local anthropogenic threats to murre colonies in Greenland. However, the net-consequences on population development remains unanswered. The thesis has provided a more solid basis for how to focus future studies in local breeding areas and provided examples on different methods that can be used to improve our knowledge on potential local drivers, both qualitatively and quantitatively. Clearly more studies are needed to quantify the current level of human disturbances, the short- and long-term consequences of disturbances and the intertwined connections to global climate change. Demographic modelling should also be used as a tool to quantify the long-term effect of small changes in local parameters, such as breeding success, or the energetic costs associated with disturbances. Locals also point at the need of investigating the effect of helicopter traffic, landslides, and winter foraging conditions. Finally there is a need to improve our understanding of natural exchange of birds between colonies, especially between closely situated colonies. Auks are known to be highly philopatric to their breeding site, but perhaps our definition of a colony is too simplified, and some of the variation we observe within colonies that are close to each other, could be an expression of neighbouring colonies actually belonging to the same "super" colony.

# Conclusions

This thesis does not provide any quantitative measures on the effects of anthropogenic threats to murres in Greenland, but it documents that disturbances, possibly with some hunting included, likely is contributing to the observed declines. The overall human disturbance level at thick-billed murre breeding colonies in Greenland appears significantly diminished compared to only a few decades ago. Nonetheless, it still seems to be a problem at least in some Greenland murre breeding areas. Part of the problem is also that most of the declining colonies have been declining for an extended period, which this makes them even more vulnerable to small additive negative pressures. The most important driver for the declines in the Northeast Atlantic, and likely also Greenland, may be linked to climate change. This has been documented to impact the murres in the wintering areas (Descamps et al. 2013b, Frederiksen et al. 2019b), but this thesis indicates that climate change also may affect the local breeding conditions. However, effects of climate changes are difficult to mitigate with management actions, which makes it even more important to diminish other human related negative effects. The continued decline of the murre population combined with the increase in human activities in Greenland calls for urgent action.

This thesis also illustrates, that simply increasing the level of restrictions is insuffucient. In order for restrictions to be followed and respected, it is of utmost importance that not only regulative changes are communicated thoroughly to the public, but also the scientific foundation as well as any other management considerations behind the changes. If management decides to prioritise factors like food security or cultural heritage, it should be communicated clearly if this is at the expence of biological sustainability. The scientific basis for the advise that biologist provide to the management clearly needs to be communicated to a much wider audience than it has been so far.

The management could consider re-thinking how users, and the public in general, could be involved better in the decision making process, than today. Better involvement can lead to improved compliance (Noble 2000). This would also require a better knowledge foundation among the public, than we observe today. When it comes to disturbances near breeding colonies, the management could consider encouraging more rekreational use of seabird colonies. This could sound like a contradiction, but promoting a non-disturbing recreational use of seabird colonies, or other types of wildlife, could be a cost effective way of promoting awareness, which could help prevent illegal hunting and disturbing activities. This should also be followed with a thorough outreach campaing about vulnerability and existing rules and provide proper guidelines to how this highly valued species, and other types of wildlife, could be enjoyed without negative consequences.


Kitsissut (Carey Islands), August 2015. Photo: A. Kristensen

## References


Andersen, A. O., M. P. Heide-Jørgensen, and J. Flora. 2018. Is sustainable resource utilisation a relevant concept in Avanersuaq? The walrus case. Ambio **47**:265-280.

Beale, C. M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology **41**:335-343.

Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series **395**:177-185.

Blumstein, D. T. 2014. Attention, habituation, and antipredator behaviour: implications for urban birds. Pages 41-53 *in* D. Gill and H. Brumm, editors. Avian urban ecology: Behavioural and physiological adaptations. Oxford University Press, Oxford, U.K.

Boertmann, D., and A. Mosbech. 2017. Baffin Bay. An updated strategic Environmental Impact Assessment of petroleum activities in the Greenland part of Baffin Bay. 218, DCE - Danish Centre for Environment and Energy, Aarhus University.

Boertmann, D., A. Mosbech, D. Schiedek, and M. Dünweber. 2013. Disko West. A strategic environmental impact assessment of hydrocarbon activities. 71, DCE - Danish Centre for Environment and Energy, Aarhus University.

Buckley, R. 2004. Environmental impacts of ecotourism. CABI Publishing, Wallingford.

Burton, R. 1998. Maintaining the Quality of Ecotourism: Ecotour Operators' Responses to Tourism Growth. Journal of Sustainable Tourism **6**:117-142.

Chardine, J., B. T. Collins, R. D. Elliot, and H. Lévesque. 1999. Trends in the annual harvest of murres in Newfoundland and Labrador. Bird Trends **7**:11–14.

Chardine, J. W., and V. Mendelhall. 1998. Human disturbances in arctic seabird colonies. 2, C. S. W. Group, Akureyri.

Christensen, T., F. Lasserre, J. Dawson, E. Guy, and J.-F. Pelletier. 2018. Shipping. Pages 243-260 *in* A. Mosbech, M. Lemay, M. Simon, F. Merkel, T. Christensen, R. B. Jacobsen, P. Egede, and K. Falk, editors. Adaptation Actions for a Changing Arctic: Perspectives from the Baffin Bay/Davis Strait Region. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile Activity and Glucocorticoid Stress Responses in Wolves and Elk. Conservation Biology **16**:809-814.

Croxall, J. P., S. H. M. Butchart, B. E. N. Lascelles, A. J. Stattersfield, B. E. N. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International **22**:1-34.

Davenport, J., and J. L. Davenport. 2006. The impact of tourism and personal leisure transport on coastal environments: A review. Estuarine, Coastal and Shelf Science **67**:280-292.

Descamps, S., H. Strøm, and H. Steen. 2013. Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre. Oecologia **173**:1271-1282.

Dias, M. P., R. Martin, E. J. Pearmain, I. J. Burfield, C. Small, R. A. Phillips, O. Yates, B. Lascelles, P. G. Borboroglu, and J. P. Croxall. 2019. Threats to seabirds: A global assessment. Biological Conservation **237**:525-537.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science **345**:401.

Ellenberg, U., T. Mattern, D. M. Houston, L. S. Davis, and P. J. Seddon. 2012. Previous experiences with humans affect responses of Snares Penguins to experimental disturbance. Journal of Ornithology **153**:621-631.

Ellenberg, U., T. Mattern, and P. J. Seddon. 2009. Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. Animal Behaviour **77**:289-296.

Evans, P., and G. Waterston. 1977. Recent salmon netting restrictions in South-west Greenland. Polar Record **18**:507-508.
Fabricius, O. 1780. Fauna Groenlandica - pattedyr og fugle. Det Grønlandske selskabs skrifter VI (translated to Danish by O. Helms), Copenhagen 1929.
Falk, K., and K. Kampp. 1997. A manual for monitoring thick-billed murre populations in Greenland. Technical Report 7, Greenland Institute of Natural Resources, Nuuk.
Falk, K., and K. Kampp. 2002. Lomvien i Grønland: Mulige effekter af forskellige bestands-påvirkende faktorer, og praktiske grænser for ressourceudnyttelse. 38, Greenland Institute of Natural Resources, Nuuk.
Falk, K., K. Kampp, and F. R. Merkel. 2000. Monitering af lomviekolonierne i Sydgrønland, 1999. Greenland Institute of Natural Resources, Nuuk.
Fluhr, J., H. Strøm, R. Pradel, O. Duriez, G. Beaugrand, and S. Descamps. 2017. Weakening of the subpolar gyre as a key driver of North Atlantic seabird demography: a case study with Brünnich's guillemots in Svalbard. Marine Ecology Progress Series **563**:1-11.
Frederiksen, M., S. Descamps, K. E. Erikstad, A. J. Gaston, H. G. Gilchrist, D. Grémillet, K. L. Johansen, Y. Kolbeinsson, J. F. Linnebjerg, M. L. Mallory, L. A. McFarlane Tranquilla, F. R. Merkel, W. A. Montevecchi, A. Mosbech, T. K. Reiertsen, G. J. Robertson, H. Steen, H. Strøm, and T. L. Thórarinsson. 2016. Migration and wintering of a declining seabird, the thick-billed murre Uria lomvia, on an ocean basin scale: Conservation implications. Biological Conservation **200**:26-35.
Frederiksen, M., J. F. Linnebjerg, F. R. Merkel, S. I. Wilhelm, and G. J. Robertson. 2019. Quantifying the relative impact of hunting and oiling on Brünnich's guillemots in the North-west Atlantic. Polar Research **38**:1-11.
Gaston, A. J., L. N. Forest, G. Donaldson, and D. G. Noble. 1994. Population parameters of thick-billed murres at Coats Island, Northwest Territories, Canada613. Condor **96**:935-948.
Gaston, A. J., and J. M. Hipfner. 2000. Thick-billed Murre (*Uria lomvia*). Pages 1-31 *in* A. Poole and F. Gill, editors. The Birds of North America, No 497. The Birds of North America, Inc., Philadelphia, Pennsylvania.
Gaston, A. J., J. M. Hipfner, and D. Campbell. 2002. Heat and mosquitoes cause breeding failures and adult mortality in an Arctic-nesting seabird. Ibis **144**:185-191.
Gaston, A. J., and G. J. Robertson. 2010. Trends in the harvest of Brunnich's guillemots Uria lomvia in Newfoundland: effects of regulatory changes and winter sea ice conditions. Wildlife Biology **16**:47-55.
Gilchrist, H. G., M. Mallory, and F. R. Merkel. 2005. Can traditional ecological knowledge contribute to wildlife management? Case studies of migratory birds. Ecology and Society **10**:20.
Gill, J. A. 2007. Approaches to measuring the effects of human disturbance on birds. Ibis **149**:9-14.
Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation **97**:265-268.
Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the Fate of Wild Nature. Science **307**:550-555.
Haastrup, A. G. 2017. Appaqanngila? - Ingen lomvie? En analyse af forskellige vidensformer om lomvien og bæredygtighedstanker i Grønland. Masters thesis. University of Copenhagen, Copenhagen.
Irons, D. B., T. Anker-Nilssen, A. J. Gaston, G. V. Byrd, K. Falk, H. G. Gilchrist, M. Hario, M. Hjernquist, Y. V. Krasnov, A. Mosbech, B. Olsen, A. Petersen, J. B. Reid, G. J. Robertson, H. Strom, and K. D. Wohl. 2008. Fluctuations in circumpolar seabird populations linked to climate oscillations. Global Change Biology **14**:1455-1463.
Labansen, A., F. R. Merkel, M. Frederiksen, K. Falk, and A. Mosbech. 2013. Monitering af lomvier og rider i det nordlige Upernavik, 2008. 90, Greenland Institute of Natural Resourches, Nuuk.
Labansen, A. L., F. Merkel, and A. Mosbech. 2021. Reactions of a colonial seabird species to controlled gunshot disturbance experiments. Wildlife Biology **2021**.

Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling.*in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: relevance to conservation and management. Oxford University Press, Oxford.

Linnebjerg, J. F. 2012. Foraging ecology of breeding seabirds in Greenland. Aarhus University.

Lorentsen, S. H., and A. Follestad. 2014. Effekter av forstyrrelse på kolonihekkende fugl og effekter av avbøtende tiltak - en litteraturstudie [Effects of disturbances on colony breeding birds and effects of mitigation measures -  a litterature study]. Trondheim, Norway.

Lundquist, D., M. Sironi, B. Würsig, V. Rowntree, J. Martino, and L. Lundquist. 2013. Response of southern right whales to simulated swim-with-whale tourism at Península Valdés, Argentina. Marine Mammal Science **29**:E24-E45.

Lyngs, P. 2003. Migration and winter ranges of birds in Greenland - an analysis of ringing recoveries. Dansk Ornitologisk Forenings Tidsskrift **97**:1-167.

McCauley, D. J., M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, and R. R. Warner. 2015. Marine defaunation: Animal loss in the global ocean. Science **347**:1255641.

Merkel, F., D. Boertmann, K. Falk, M. Frederiksen, K. Johansen, A. L. Labansen, J. F. Linnebjerg, A. Mosbech, and C. Sonne. 2015. Why is the last Thick-billed Murre Uria lomvia colony in central West Greenland heading for extinction? Bird Conservation International **26**:177-191.

Merkel, F., A. L. Labansen, D. Boertmann, A. Mosbech, C. Egevang, K. Falk, J. F. Linnebjerg, M. Frederiksen, and K. Kampp. 2014. Declining trends in the majority of Greenland’s thick-billed murre (Uria lomvia) colonies 1981–2011. Polar Biology **37**:1061-1071.

Merkel, F. R., A. S. Frich, and P. Hangaard. 1999. Polarlomvien i Disko Bugt og det sydlige Upernavik, 1998. Bestandsopgørelse og grundlag for fremtidig monitering af lomviebestandene. Technical Report 25, Greenland Institute of Natural Resources, Nuuk.

Merkel, F. R., and J. E. Tremblay. 2018. Living resources. Pages 133-199 *in* A. Mosbech, M. Lemay, M. Simon, F. Merkel, T. Christensen, R. B. Jacobsen, P. Egede, and K. Falk, editors. Adaptation Actions for a Changing Arctic: Perspectives from the Baffin Bay/Davis Strait Region. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Mosbech, A., F. R. Merkel, D. Boertmann, K. Falk, M. Frederiksen, K. Johansen, and C. Sonne. 2009. Thick-billed murre studies in Disko Bay (Ritenbenk), West Greenland. NERI Technical Report No. 749, National Environmental Research Institute, Aarhus University, Roskilde.

Nisbet, I. C. T. 2000. Disturbance, Habituation, and Management of Waterbird Colonies. Waterbirds **23**:312-332.

Noble, B. F. 2000. Institutional criteria for co-management. Marine Policy **24**:69-77.

Olsson, O., and G. W. Gabrielsen. 1990. Effect of helikopters on a large and remote colony of Brünnich's Guillemot (*Uria lomvia*) in Svalbard. Norsk Polarinstitutt Rapportserie **64**:1-36.

Pars, T., M. Osler, and P. Bjerregaard. 2001. Contemporary use of traditional and imported food among Greenlandic Inuit. Arctic **54**:22-31.

Pichegru, L., T. B. Edwards, B. J. Dilley, T. P. Flower, and P. G. Ryan. 2016. African Penguin tolerance to humans depends on historical exposure at colony level. Bird Conservation International **26**:307-322.

Piniarneq. 2019. Hunting statistics for Greenland, 1993-2017. Department of Hunting, Fishing and Agriculture. Greenland Self Rule, unpublished data.

Rodríguez-Prieto, I., and E. Fernández-Juricic. 2005. Effects of direct human disturbance on the endemic Iberian frog Rana iberica at individual and population levels. Biological Conservation **123**:1-9.

Schreiber, E. A., and J. Burger. 2001. Biology of Marine Birds. CRC Press.

Sejersen, F. 2002. Local knowledge, Sustainability and Visionscapes in Greenland Afdeling for eskimologi og arktiske studier, Københavns Universitet, Copenhagen.

Sejersen, F. 2003. Grønlands naturforvaltning : ressourcer og fangstrettigheder  [Greenland's nature conservation: resources and hunting rights]. Akademisk Forlag, København.

Sowa, F. 2015. Kalaalimernit: The greenlandic taste for local foods in a globalised world. The Polar Record **51**:290-300.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.

Tull, C. E., P. Germain, and A. W. May. 1972. Mortality of Thick-billed Murres in the West Greenland Salmon Fishery. Nature **237**:42-44.

Villanueva, C., B. G. Walker, and M. Bertellotti. 2012. A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic Penguins (Spheniscus magellanicus) at two colonies in Argentina. Journal of Ornithology **153**:219-228.

Wiese, F. K., and G. J. Robertson. 2004. Assessing seabird mortality from chronic oil discharges at sea. Journal of Wildlife Management **68**:627-638.

# Paper I

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# Reactions of a colonial seabird species to controlled gunshot disturbance experiments

**Aili Lage Labansen, Flemming Merkel and Anders Mosbech**

*A. L. Labansen (https://orcid.org/0000-0002-1910-6580) ✉ (aila@natur.gl) and F. Merkel, Greenland Inst. of Natural Resources, Nuuk, Greenland. – ALL, FM and A. Mosbech, Dept of Bioscience, Aarhus Univ., Roskilde, Denmark.*

Gunshots are a worldwide source of anthropogenic disturbance, and knowledge about the potential effect on wildlife is central for conservation and sustainable management of affected species. This study contributes novel insight of the response behaviour and effect of gunshot disturbance on one of the most culturally important seabird species of the Arctic, the thick-billed murre (Brünnich's guillemot, *Uria lomvia*). We studied effects of gunshot disturbance at breeding colonies to explore the distance where effects started, the difference in the behavioural response between presumed disturbed colonies (e.g. by traffic and hunting) and largely undisturbed colonies, and among plots with varying seabird densities. We carried out two different types of controlled gunshot experiments – one measuring the distance at which murres first reacted to gunshots (flight initiation distance, 'FID') and one measuring the proportion of murres remaining in the colony during and after repeated gunshots (20 gunshots within 78 min). FID varied from 0.5 to 5 km. The proportion of murres remaining in the plot after the repeated gunshots ranged from 0.44 to 0.8. Mainly murres not attending offspring took off when disturbed by gunshots, but occasionally also birds incubating their egg or brooding their chick took off. We found that density of seabirds (murres and black-legged kittiwakes *Rissa tridactyla*) at the plot area scale was the best explaining factor for FID, and to some extent also for the effect of repeated gunshots, both for disturbed and undisturbed colonies. Murres in denser colonies reacted earlier (had larger FIDs) and somewhat more strongly (higher proportions fleeing) to gunshots than murres in less densely populated colonies. FID clearly showed that the current legislation in Greenland regulating gunshots near breeding colonies is insufficient. We provide some recommendations for improved management of a popular game species under pressure.

Keywords: flight initiation distance, gunshot disturbance, seabird colonies, thick-billed murre, *Uria lomvia*, wildlife

Anthropogenic disturbances on wildlife, caused by activities such as farming, construction, transport, wildlife tourism and outdoor recreation, is a worldwide and increasing issue (Burton 1998, Buckley 2004, Green et al. 2005, Davenport and Davenport 2006, Stankowich 2008). In some areas, hunting (recreational and/or subsistence) is a noteworthy activity in otherwise remote areas (Dahl 1989, Milner-Gulland and Bennett 2003, Sharp and Wollscheid 2009). However, the disturbance effects of gunshots on wildlife are rarely investigated (Stankowich 2008, Livezey et al. 2016). With this paper we aim to contribute to the limited knowledge about the effect of gunshot disturbances with an experimental approach.

Disturbance of wild animals is, depending on the disturbance level, known to cause increased vigilance, habitat loss, reduced fitness and/or lower breeding success due to increased stress, energetic costs, predation of offspring or loss of offspring when fleeing (Olsson and Gabrielsen 1990, Creel et al. 2002, Beale and Monaghan 2004, Rodríguez-Prieto and Fernández-Juricic 2005, Lundquist et al. 2013). Animals can habituate or show increased tolerance to repeated disturbances (Nisbet 2000, Diego-Rasilla 2003, Stankowich and Blumstein 2005, Walker et al. 2006), but in contrast disturbance can also lead to sensitization (Stankowich 2008, Rankin et al. 2009, Blumstein 2014). This means that the response to disturbances can differ among individuals of the same species due to previous experiences (Stankowich and Blumstein 2005, Ellenberg et al. 2009, Ellenberg et al. 2012, Villanueva et al. 2012, Pichegru et al. 2016).

Cliff-breeding colonial-seabirds, such as the thick-billed murres *Uria lomvia* (hereafter 'murres'), are particularly vulnerable to repeated disturbances, because they aggregate in large numbers and are very faithful to their breeding sites (Gaston et al. 1994, Gaston and Hipfner 2000, Coulson 2002, Bejder et al. 2009). This species is highly abundant with a circumpolar distribution (Gaston and Hipfner

2000, Irons et al. 2008), but is declining in several regions of the North Atlantic (Descamps et al. 2013, Merkel et al. 2014, Fauchald et al. 2015, Frederiksen et al. 2016). Climate-related oceanographic changes at the wintering areas have been associated with population declines in Svalbard (Descamps et al. 2013), and Frederiksen et al. (2016) reported a strong connection between wintering areas and population status of several Atlantic breeding populations. Hunting in the wintering areas off Greenland and Canada is also a contributing factor to the population decline (Frederiksen et al. 2019). However, local factors during the breeding season, such as disturbances, may contribute to some of the contrasting trends observed for different breeding colonies of murres in Greenland – 13 of 19 colonies are declining; the remaining six colonies are stable or increasing (Merkel et al. 2014).

Although never quantitatively measured, it is well known that some murre colonies in Greenland were extensively disturbed in the past by anthropogenic factors, such as hunting, boat traffic, aerial traffic, and by purposefully using guns and other loud noises to initiate fleeing from the colony. Passenger ships and locals regularly used this latter activity, so that they could view the spectacular phenomenon of many birds fleeing the colony simultaneously (Chardine and Mendelhall 1998, Gilchrist 1999, Merkel et al. 1999).

Despite a declining number of families that depend on hunting for subsistence, hunting remains an important source of sustenance for many, as well as a popular recreation activity, now involving larger and faster motor boats (Dahl 1989, Rasmussen 2005, Boertmann et al. 2013, Boertmann and Mosbech 2017). Seal hunting from open boats at sea is one of the most common forms of hunting throughout the year (Boertmann et al. 2013, Boertmann and Mosbech 2017), and, for the summer months of June, July and August, about 25 000–50 000 seals are reported shot every year (2006–2015, PILU/Piniarneq database, June 2017). Furthermore, researchers have witnessed several incidents of illegal bird hunting at or near seabird colonies in Greenland during the field season (Labansen et al unpubl.). In one extreme case in 1998, researchers observed seven hunting episodes over a period of 12 days, involving a minimum of 284 gunshots (Merkel et al. 1999). By Greenland law, murre colonies are protected by a no-shooting zone that was 5 km from the colony from 1958 (Anonymous 1958) until 2009 and was reduced to 1 km in 2009 (Anonymous 2009). However, it is unknown how well the no-shooting zones are respected. In some areas, colonies closest to settlements and boating routes have the largest population declines (Boertmann 2001).

According to the optimal escape theory, potential prey will counterbalance the risks and costs of fleeing from predators during an encounter with a predator (Ydenberg and Dill 1986), and we can control several factors that affect the risk and cost of fleeing (e.g. species, season, life stage and distance to cover) when studying disturbance response behaviours in murre colonies at a specific breeding stage. However, density, or group size in a specific area, is an important factor that can vary among and within colonies. Group size can decrease the fleeing distance (distance from which individuals decide to flee from an approaching predator) due to the diluted predation risk of each individual (Cresswell and Quinn 2011), and the decreased likelihood of predator success with multiple targets (the confusion effect) (Milinski 1984, Parrish 1993, Jeschke and Tollrian 2007). Conversely, group size can cause an increased fleeing distance due to an increased probability of detecting predators and from the increased probability of more vigilant individuals being present in the group (Ydenberg and Dill 1986, Lima 1995, Stankowich and Coss 2006, Stankowich 2008, Braimoh et al. 2018).

We carried out controlled experiments in murre colonies; 1) to investigate the distance at which birds first reacted to approaching gunshots – the so-called flight initiation distance (FID), and 2) to study the response to repeated gunshots, imitating an at-sea hunting situation in Greenland (Merkel et al. 1999, Boertmann et al. 2013, Boertmann and Mosbech 2017). The experiments were carried out in multiple colonies to allow comparison of behavioural responses between disturbed/declining and undisturbed/stable colonies, and in multiple plots within colonies to investigate the importance of group size and colony structure. Based on the FID results of the approaching gunshot experiment, we evaluated whether colonies are sufficiently protected by a no-shooting zone of 1 km. The repeated gunshot experiment illustrates effects of hunting near murre colonies and we discuss possible long-term effects.

## Methods

### Study species and colonies

Murres breed in dense colonies on narrow ledges along steep coastal cliff sides. In Greenland, murres often breed in mixed colonies with black-legged kittiwakes *Rissa tridactyla* and some are homogenous colonies of only murres. Murre colonies can also include one or more of the following species northern fulmar *Fulmarus glacialis*, glaucous gull *Larus hyperboreus*, razorbill *Alca torda* and other alcids. However, these latter species are typically less numerous and generally found in the periphery of the main murre nesting areas. The female lays one egg directly on the cliff ledge and both parents take turns attending (incubating and rearing) the egg/chick (Gaston and Hipfner 2000). The Greenland colonies, including the study colonies vary significantly in size and structure – some consist of relatively uniform cliff sides with continuously occupied breeding ledges, others have a patchy distribution, while others consist of sub-colonies separated by barren cliffs or distributed within an archipelago (Table 1, Fig. 1).

Data were collected in 2015 (four colonies) and 2017 (three colonies) from a total of six colonies, of which four colonies had declining breeding populations (Apparsuit in Northern Upernavik, Kingittoq in Southern Upernavik, Innaq in Disko Bay and Sermilinnguaq in the Maniitsoq area) and two had populations that were stable or slightly increasing (Kitsissut in the Qaanaaq area and Kippaku in Northern Upernavik – Table 1, Fig. 2) (Falk and Kampp 1997, Merkel et al. 2014). The disturbance level of colonies was roughly categorized as high or low based on accessibility. The sub-colonies of Kitsissut, placed on an archipelago about 50 km from the nearest coast of the sparsely inhabited Qaanaaq area, have a very low disturbance level (Burnham and

Table 1. Colony characteristic and latitude of thick-billed murre colonies in Greenland where gunshot experiments were carried out in 2015 and/or 2017. Colony size represents the number of individuals counted on photos in 2015 or 2017 (Greenland Institute of Natural Resources, unpubl.), population trend since the late-nineties is shown as stable (→) or declining (↓) (Merkel et al. 2014), and disturbance level was categorized as low or high. The type of experiment is indicated by AGS (approaching gunshot study) or RGS (repeated gunshot study) with date (and year) of the experiment(s) indicated. Colonies are sorted according to latitude from north to south.

| Colony | Colony description | Size (year) | Trend | Disturbance level | Study type | Date(s) (year) |
|---|---|---|---|---|---|---|
| Kitsissut | 12 sub colonies of varying size and density on three islands in an archipelago 50 km from the mainland. Murre-only colonies. Latitude 76°44′. | 9100 (2015) | → | Low | AGS<br>RGS | Aug 2, 8<br>Aug 7, 8 (2015) |
| Apparsuit | 18 sub colonies of varying size and density, some murre-only some with kittiwakes, along tall coastline of 7 km along S–SW side of large island. Latitude 73°48′. | 50 500 (2017) | ↓ | High | AGS<br>RGS<br>AGS | Jul 23 (2015)<br><br>Jul 23 (2017) |
| Kippaku | More or less continuous along 0.5 km coastline on N–NE side of small island mixed with kittiwakes. Latitude 73°43′. | 21 400 (2017) | → | Low | AGS<br>RGS | Jul 21, 25<br>Jul 21 (2015) |
| Kingittoq | Patchy distribution along tall coastline of 0.6 km on peninsula mixed with kittiwakes. Latitude 72°40′. | 2450 (2017) | ↓ | High | AGS | Jul 11 (2017) |
| Innaq | Patchily distributed in two main areas of respectively 0.8 and 0.2 km within a bay and mixed with kittiwakes. Latitude 69°48′. | 1000 (2015) | ↓ | High | AGS<br>RGS | Jul 12<br>Jul 12 (2015) |
| Sermilinnguaq | Patchily distributed along coast of 0.6 km along north coast of small fjord, mixed with kittiwakes. Latitude 65°40′. | 4600 (2017) | ↓ | High | AGS | Jul 17 (2017) |

Burnham 2010). The remaining colonies are within boating distance of nearby settlements and are all, to some extent, exposed to anthropogenic disturbances. However, the disturbance level at Kippaku is assumed to be relatively low. Kippaku is only about 7 km from the much larger Apparsuit; however, it is somewhat shielded by Apparsuit because the latter is much closer to the boating route.

Data collection was, to a large degree, coordinated with monitoring work or other research projects, due to the high costs of doing fieldwork in the Arctic (Mallory et al. 2018). In some colonies, it was possible to stay and work for a longer period (Innaq, Kippaku and Kitsissut), whereas others were more sporadically visited due to safety and to logistical concerns (Apparsuit, Kingittoq and Sermilinnguaq). The experiments were carried out during the chick rearing period, when most eggs had hatched, which varied from mid-July to early August (Table 1) depending on latitude (Falk and Kampp 2001).

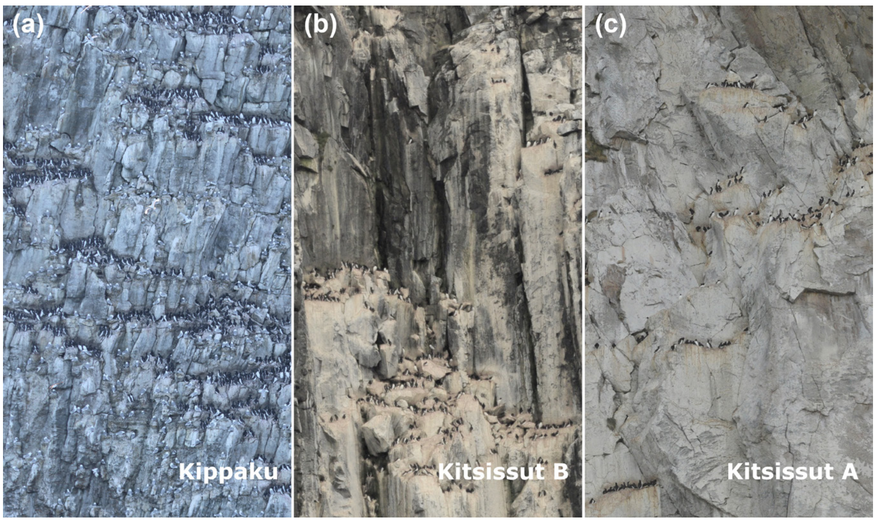


Figure 1. Examples of thick-billed murre breeding colonies of varying density and structure in Greenland: (a) high density area continuously occupied with breeding ledges of thick-billed murre mixed with black-legged kittiwake, (b) partly continuous and partly patchy structure of breeding murres of medium density, (c) patchy distribution of breeding ledges in low density area.

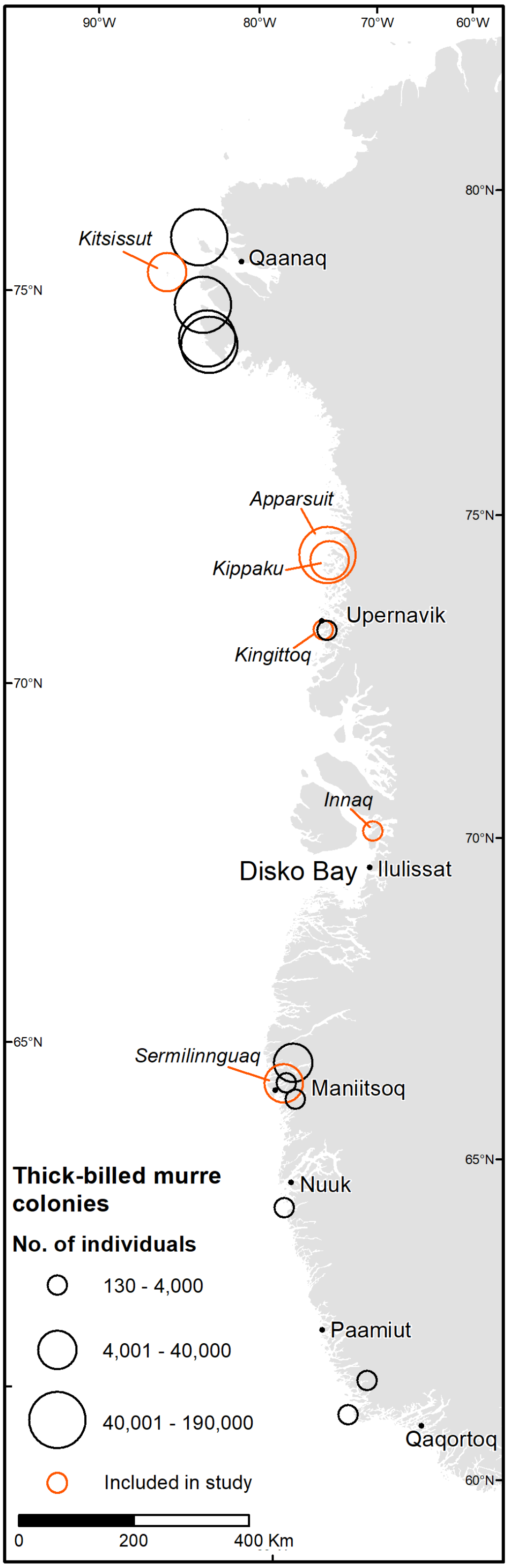


Figure 2. Location and population size of thick-billed murre breeding colonies in West Greenland based on the most recent surveys (2014–2017, Greenland Institute of Natural Resources, unpubl.). Colonies of this study are highlighted with orange. Nearest main town (black dots) for areas with murre colonies are shown.

In the approaching gunshot experiment, a mix of video recordings and direct observation were used to monitor murre reaction (alertness and fleeing) and in the repeated gunshot scenario, video recordings were used to determine the proportion of murres leaving after each gunshot (see later description on the use of cameras). The plots varied in size and were limited to sites where it was possible to mount cameras to record a suitable amount of murres (> 60 murres). For one colony, Apparsuit, this meant that breeding densities at the plots were less dense than typical for this colony. Density of birds at the plots was defined as the number of murres and black-legged kittiwakes (hereafter 'kittiwake') on the cliff within an area of about 75 × 75 m, with the plot as the centre point. The number of birds and the size of the area was determined from high quality photographs taken for colony census purposes, either within the same year of the experiments (4 of the 6 colonies) or within two years of the experiment (Kippaku and Apparsuit B). The size of the area was extrapolated from the pixel height of an upright standing murre assuming the average height of a murre to be about 30 cm from head to tail when standing in a typical upright pose with the ventral side towards the cliff (assessed from taxidermy mounts of murres).

### Camera setup

Video cameras (Panasonic HC-W850 and/or JVC GZ-EX515BE) were placed so that they covered a plot with about 70–400 adult murres within a distance of about 30–200 m; this allowed us to identify chicks on most of the recordings (not at Apparsuit B and Kitsissut B+). Two different plots were filmed during the experiments at Kitsissut, Kippaku and Innaq.

The cameras were started at least 15 min (and preferably an hour or more) before initiation of disturbance experiments and continued 13–536 min after the disturbances were stopped. This varied due to the very different conditions at every plot, both in terms of the physical characteristic of the respective colonies (i.e. accessibility of the plots) and the weather conditions at the time of the experiments.

At Innaq and Kippaku, a video plot from each colony were overlapped significantly with time-lapse photo plots established for monitoring purposes (Huffeldt and Merkel 2013). Data from these plots, originating from the same field season, made it possible for us to identify active breeding sites in the overlapping area at the time of the repeated gunshot experiment (see later description of the repeated gunshot experiment) (Greenland Institute of Natural Resources, unpubl.).

### Gunshot experiments

Murre response was observed while conducting two types of controlled gunshot experiments: 1) the approaching gunshot experiment, and 2) the repeated gunshot experiment at a fixed distance (approx. 500 m). On three occasions, the repeated gunshot experiment was carried out shortly after the approaching gunshot experiment, but first allowing birds to return to the plots (Innaq, Apparsuit and Kitsissut).

A caliber .222 Remington bolt-action rifle (CZ527, 1:14″), with ammunition from Sellier and Bellot (FMJ, 50 g) was used for the experiments. The caliber .222 is a common choice of weapon for the hunting of most seals (NAMMCO 2004). The smaller and less powerful .22 magnum and .17 are also common; more powerful weapons are used for larger seals and other mammals (up to .30-06) (NAMMCO 2004). Shotguns are the primary choice for seabird hunting (e.g. 12 gauge). The noise level of these kinds of recreational weapons has been measured to range from about 140 dB (.22 LR) to 164 dB (.30-06) dB, depending on location of measuring device relative to the weapon, ammunition type, weapon model and location, among other factors (Flamme et al. 2009, Meinke et al. 2014). The .222 is a caliber between the least and the most powerful types mentioned. The experiments were conducted in calm weather with no or little wind, because noise impacts are greatly influenced by conditions like wind speed, wind direction, humidity and landscape (Pater et al. 2009). The shooter was in contact with an observer via VHF radios during the disturbance event. The observer at the colony, was located well away from the birds so that they were not disturbed by the observer. The gunshots were directed towards the colony and plot(s), with an upward shooting angle of about 45 degrees, making sure not to compromise the safety of people or birds.

***Approaching gunshot experiment***

This experiment was carried out from a boat. The first gunshot was fired at a distance of at least 7 km (measured using a Garmin GPS with a waypoint near the relevant plot(s)) – well away from the detection range of birds at the colony. The colony was approached by the boat with the shooter at max. 3 knots when nearing the colony – well below the speed that might elicit responses from the birds due to boating (personal experience and following general guidelines for boating near seabirds colonies in Greenland, Anonymous 2019). The propulsion of the boat was briefly halted while a single gunshot was fired by the shooter towards the colony at the following distances: 6, 5, 4, 3, 2, 1.5, 1 and 0.5 km – or until flight initiation of murres from the plot(s) (i.e. the FID) was detected by the observer, in which case the observer signalled the shooter to stop.

For each gunshot, the following were recorded: wind speed and direction, time of the gunshot and the effect of the shot (reaction of murre (alertness and flight initiation) and kittiwake (flight initiation)) in the colony in general and reactions within the plot.

At Apparsuit and Kitsissut the experiment was repeated within the same colony but in different sub-colonies. At Kippaku it was repeated at the same location due to fog during the first experiment. At Sermilinnguaq and Kingittoq, the approaching gunshot experiment was conducted without video cameras, and the reaction of murre and kittiwake within defined focus areas were observed from a boat.

***Repeated gunshots experiment***

At a consistent distance of approx. 500 m from the plot(s), four series of five gunshots were fired at an interval of 10 min between each series with 3 min between gunshots within a series (20 gunshots over 79 min in total). With no prior experience, it was assumed that all plots would show fly-outs at a distance of about 500 m and show the effect of hunting activities near murre colonies. The shooting was performed from a boat, except at Kitsissut where the topography of the island allowed for doing this on land while facing the colony at a similar distance. Time and general reactions in the colony were noted for each shot. The results from one plot at Kitsissut was excluded due to adverse wind conditions.

The number of murres present at the plots before and after each shot in the repeated gunshot experiment were counted on screenshots from the video recordings using ImageJ (Vers. 1.51j, <https://imagej.nih.gov/ij/> – a public domain image processing software program (Schneider et al. 2012)). When the video footage was of sufficient quality, it was noted when any chicks or eggs were left alone by an attending parent bird. The number of birds in the plot before the first, and after the last, gunshot was counted at least three times (usually more than five times) at 3–10 min intervals, depending on how long the plot was filmed. If filmed for more than an hour before/after the gunshot sequence, then birds were counted every 20–60 min.

For murre it is not possible to distinguish males from females or breeders from non-breeders, and non-breeders in addition to failed breeders are inclined to hang out in the colony, behaving much like breeding birds (Gaston and Hipfner 2000). However, based on attendance patterns, a technique using time-lapse photography and digital image analysis was developed by Merkel et al. (2016) that identifies breeding sites and non-breeding sites and distinguishes between successful and unsuccessful breeding sites. Breeding sites at the Kippaku and Innaq plots that were overlapped with the time-lapse photo plots were individually observed on the video recordings to identify the reaction of the attending bird to every gunshot. The reaction of these birds was categorized as either staying at a site or leaving the site and it was noted whether the site was attended again before the next gunshot. Any egg or chick that was lost, or otherwise relocated, during the disturbance event was noted.

### Data analysis

Regression analyses were carried out in the software R ver. 3.6.1 (<www.r-project.org>) using the 'lm' function and were used in the analysis of both experiment types; in the approaching gunshot experiment to test for the relationship between bird density and FID, and in the repeated gunshot experiment, to test for relationship between bird density and regression coefficients, where the latter was used as a measure of reaction strength. When testing for differences between categorical parameters, low sample size was accounted for by using the Mann–Whitney U test according to Fowler and Cohen (1990). Graphs were made with Microsoft Excel (Office 365) and by using the *ggplot2* package in R (Wickham 2016).

## Results

### Approaching gunshot experiment

Data were obtained from 11 plots of which the two from Kippaku were repeated resulting in 13 data points. Overall, the distance that birds first reacted with alertness ranged from 1 to 5 km and FID ranged from 0.5 to 5 km (Table 2,

Table 2. Alertness distance (A) and flight initiation distance (FID) for thick-billed murre exposed to approaching gunshots from a cal. .222 rifle at 6 breeding colonies in West Greenland. The colonies were classified as with a high (H) or low (L) disturbance level, colony structure as patchy (p) or continuous (c) and densities of murre and black-legged kittiwake (BLK) of the area (75 × 75 m) surrounding and including the plots/center of observations. Wind direction, relative to the shooting direction, is indicated as headwind (h), crosswinds (c) or tailwind (t). The plots are sorted by descending FID.

| | | | Bird density (75 × 75 m) | | | Distance of bird reaction (km) | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Within plot | | Outside plot |
| Colony, plot* | Disturbance | Structure | Murres | BLK | Wind (m s⁻¹) | A | FID | FID¤ |
| Kippaku, C | L | c | 4533 | 3178 | 0 | 4 | 4 | 5 |
| Kippaku, E | L | c | 5672 | 3625 | 0 | 4 | 3 | 5 |
| Kippaku, E (f) | L | c | 5672 | 3625 | 0–1 c | 3 | 3 | 5 |
| Kippaku, C (f) | L | c | 4533 | 3178 | 0–1 c | 3 | – | 5 |
| Kingittoq | H | c/p | 758 | 940 | 0 | 4 | 3 | (5) |
| Kitsissut, B+ (w) | L | c/p | 868 | 0 | 0–3 t/c | 2 | 2 | 2 |
| Sermilinnguaq | H | p | 1154 | 1292 | 1–2 h/c | 2 | 2 | – |
| Apparsuit, B | H | p | 633 | 1 | 0 | 3 | 1.5 | – |
| Innaq, A | H | p | 114 | 277 | 0–1 h/c | 2 | 1.5 | (5) |
| Innaq, H | H | p | 185 | 1547 | 0–1 h/c | 2 | 1.5 | (5) |
| Apparsuit, Q | H | p | 286 | 425 | 0 | 1 | < 1 | 3 |
| Kitsissut, A (f) | L | P | 415 | 0 | 0–1 h | 3 | 0.5 | – |
| Kitsissut, C | L | p | 192 | 0 | 0–3 t/c | 1.5 | 0.5 | 0.5 |

* Experiments carried out in sub-optimal conditions due to wind (w) or fog (f).
¤ FID for BLK in brackets.

Supplementary material Video A1 (<https://youtu.be/C9Y41HZr_zo>)). Kippaku showed lower FIDs during the first experiment when conditions were foggy (Table 2). In the following analyses the results from the second experiment for Kippaku was used.

The difference in median FID between plots from high (median = 1.5 km) and low (median = 2 km) disturbance level colonies was not significant (Mann–Whitney U test: $U = 13$; $p > 0.05$; $n1 = 6$; $n2 = 5$). Rather, a visual inspection of the data implied a relationship between colony structure and density of the observed area and the reaction distance – the FID in particular (Table 2); plots with an FID of 1.5 km or less were characterized by being in areas of relatively small and isolated groups of birds with a density of less than 700 murres per 5625 m² (75 × 75 m), and plots with an FID of more than 2 km were situated within denser and relatively large breeding areas (Table 2).

A regression analysis showed that the FID not only was related to the number of murres, but also the number of kittiwakes within the defined surroundings (75 × 75 m) of the plots. Both murre density and the combined density of murres and kittiwakes showed a linear relationship with murre FID; however, the combined density explained a larger proportion of the variation in FID (murre density, lm: $F(1,9) = 14.78$, $p < 0.004$, $R^2 = 0.6215$; combined density, lm: $F(1,9) = 23.42$, $p < 0.001$, $R^2 = 0.7224$; Fig. 3).

## Repeated gunshots experiment

Data were obtained from 9 plots (Table 3). The proportion of birds leaving the plots at any gunshot ranged from 0 (Kitsissut C) to 0.38 (Kitsissut A) relative to the initial number of birds (before the first gunshot). The number of birds remaining in the plot after each gunshot decreased markedly

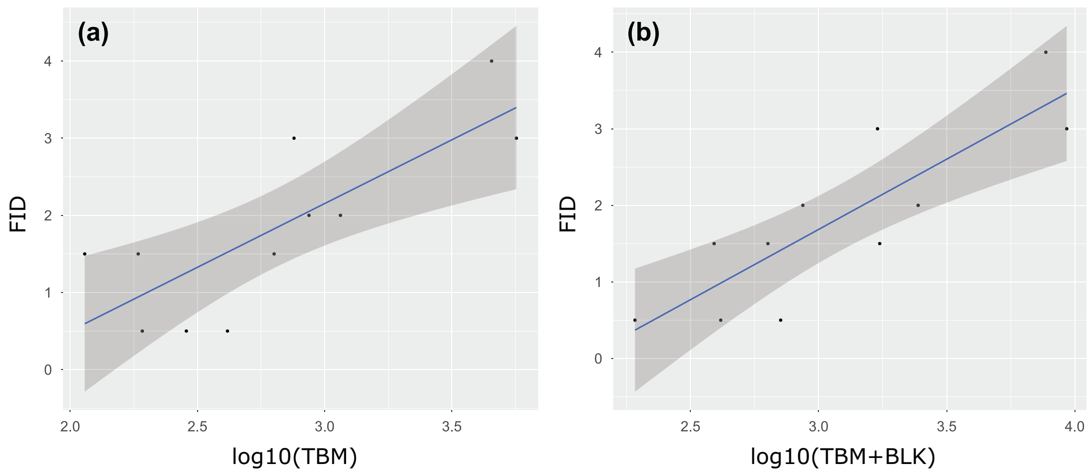


Figure 3. Flight initiation distance (FID) of approaching gunshots in relation to density of birds (a – thick-billed murre (TBM), b – thick-billed murre and black-legged kittiwake (BLK)) in 11 plots from 6 breeding colonies of thick-billed murre in West Greenland. The density was defined as the number of birds within a 75 × 75 m area, containing and surrounding the observed plot/focus area.

Table 3. Escape response to repeated gunshots at four colonies of thick-billed murre (TBM) in Greenland, 2015. Initial number of TBM in video plots of varying size before a repeated gunshot (gs) experiment of 20 gs fired at 500 m, and the proportion of TBM remaining in the plots at the last gs. The regression coefficient represents the blue regression line in Fig. 4 and describes the development and significance ($^{\cdot}$) of the proportion of TBMs remaining in the plot over the course of the gs experiment. Density of birds indicates the number of TBM and black-legged kittiwakes combined, within an area of 75 × 75 m surrounding the plots. The range in number of observed eggs/chicks that were abandoned at each gs and the number of times abandonments occurred during the gs series is indicated. The quality of each video footage was categorized as low (l), medium (m) or high (h). The plots are sorted with ascending proportion of birds at last gunshot relative to the initial number of TBM.

| Colony, plot | Initial no. of TBM | Proportion remaining after last gs | Regression coeffi- cient ($\times 10^3$) | Density of birds | No. of egg/chicks aban- doned; freq. of occurrence | Quality (l, m, h) |
|---|---|---|---|---|---|---|
| Kitsissut, A | 98 | 0.44 | $-2.23^{\cdot\cdot}$ | 415 | 1–5; 15 | m |
| Kippaku, E | 210 | 0.49 | $-2.25^{\cdot\cdot\cdot}$ | 9297 | 1–2; 8 | m |
| **Kippaku, C** | **415** | **0.51** | $-2.35^{\cdot\cdot\cdot}$ | 7711 | **2–19; 20** | **h** |
| Innaq, H | 96 | 0.53 | $-0.98^{\cdot\cdot}$ | 1732 | 1; 1 | m |
| Kitsissut, B | 69 | 0.55 | $-1.83^{\cdot\cdot\cdot}$ | 868 | 1–2; 14 | h |
| Kitsissut, B+ | 175* | 0.67 | – | 868 | – | l |
| Apparsuit, B | 106 | 0.76 | 0.26 | 634 | – | l |
| Kitsissut, C | 147 | 0.78 | −0.56 | 192 | 0 | m |
| **Innaq, A** | **111** | **0.80** | $-0.96^{\cdot\cdot\cdot}$ | 391 | **1; 1** | **h** |

Bold: Plots overlapping with time-lapse photographic monitoring plots (Fig. 5).
* Number of murres before the effect of the flight initiation study (3 shots before the repeated gs experiment started).

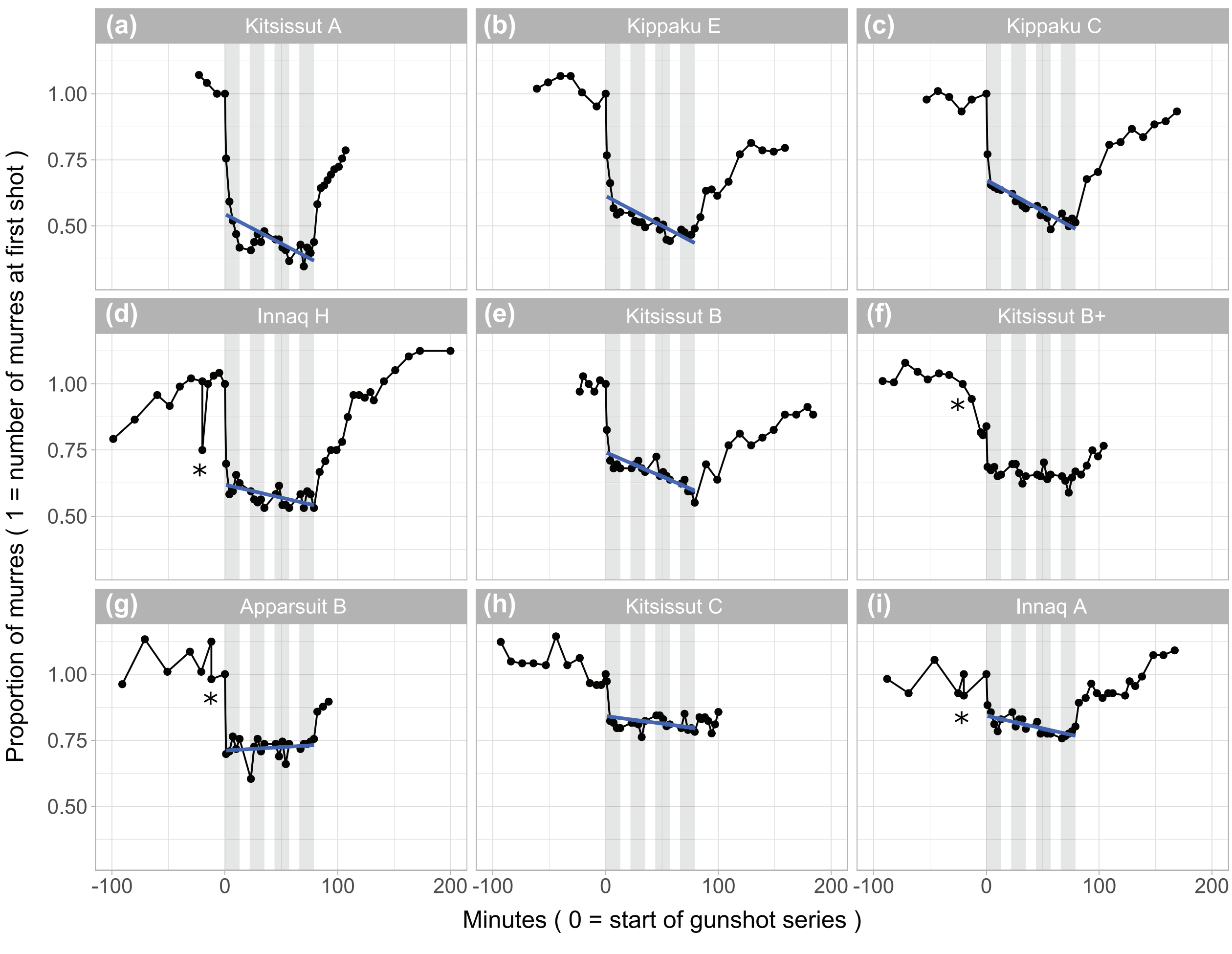


Figure 4. Proportion of thick-billed murres remaining on the ledges at nine different video plots before, during and after a repeated gunshot disturbance experiment of 20 gunshots. The shaded areas indicate the four series of five gunshots with three minutes intervals, showing the proportion of murres just after each gunshot relative to the initial number of murres. Innaq A + H, Apparsuit B and Kitsissut B+ were following an approaching gunshot study and exhibited fly-outs at respectively 1, 1 and 3 gunshots (*) prior to the gunshot series. The number of birds before the three gunshots at Kitsissut B+ are considered as the initial number of birds. The regression lines (blue) are based on the proportion of birds remaining in the plot after each gunshot. The plots are sorted with ascending proportion of murres at last gunshot, see Table 3.

during the first series of five gunshots (Fig. 4). Hereafter, the pattern more or less stabilized at some plots (Apparsuit B, Kitsissut C and Innaq A) at a proportion of about 0.75 or more, whereas the numbers kept decreasing at the remaining plots to somewhere between 0.4 and 0.7 of the initial number of murres (Fig. 4, Table 3).

The repeated gunshot experiment occurred after, and was potentially influenced by, an approaching gunshot experiment in four of the plots (Fig. 4d, f, g and i). At Innaq and Apparsuit a single gunshot caused flight initiations 20 and 12 min prior to the start of the experiment, respectively (both at a distance of 1.5 km), but the number of birds at the three plots went back to previous levels before the gunshot series were initiated. Kitsissut B+ was influenced by three gunshots prior to the repeated gunshot experiment, and, in this case, the count immediately before these three gunshots (21 min before the repeated gunshot experiment) was considered the initial number of murres (Table 3, Fig. 4f). Thus, Kitsissut B+ was not included in the following regression analyses.

Regression analyses of the proportion of birds remaining in a plot after each gunshot showed that high-density plots typically had a regression coefficient that was much lower, i.e. with a steeper negative slope, indicating a stronger reaction, than the low-density plots (Table 3, Fig. 4). However, there was no significant relationship between regression coefficient and bird density (lm: $F(1,6) = 2.942$, $p = 0.13$, $R^2 = 0.329$). Similarly, median regression coefficients overlapped between plots of disturbed and un-disturbed colonies (Mann–Whitney U-test: $U = 2$; $p > 0.05$; $n1 = 3$; $n2 = 5$). Furthermore, median regression coefficients were similar between plots that were observed after an approaching gunshot experiment and plots that were not preceded by such an experiment (Mann–Whitney U-test: $U = 3$; $p > 0.05$; $n1 = 4$; $n2 = 4$).

The only two plots that were filmed long enough to reach 100% of pre-disturbance levels were the Innaq plots A and H, which had a duration of 69 and 62 minutes, after the last gunshot was fired, respectively. After 14 (plot A) and 35 (plot H) minutes they had reached 95% of pre-disturbance levels. The plots at Kitsissut B and Kippaku C reached 90% of the initial numbers after 100 and 90 min, respectively. Kippaku E appeared to stabilize between 77 and 81% after 40–80 min (Fig. 4). The recording times after the last gunshot for the remaining plots (13–28 min) were not sufficient to determine a return rate (Fig. 4).

### *Reaction among attending breeders*

Without data on breeders/non-breeders for most of the plots, it was not possible to estimate the proportion of breeders leaving after gunshots, but it was, to some degree, possible to observe chicks left alone, indicating a minimum number of attending breeders leaving their offspring. The observed plots showed a noticeable variation in the range of this response – from none to 19 attending breeders leaving their nest sites, and some repeatedly (Table 3). The two time-lapse photo plots at Kippaku and Innaq, in which all breeding sites were identified, represented two extremes. An increasing proportion of attending breeders at the Kippaku C plot left their offspring during the repeated gunshots, and an increasing proportion of these did not return to the plot before the next gunshot (Fig. 5). The number of times the same nest site was abandoned by the attending bird ranged from 1 to 13. In contrast, only a single chick was left alone on one occasion at the Innaq A plot (Fig. 5).

Four of the 114 nest sites identified within the video plot at Kippaku, were classified as failed on the date of the repeated gunshot experiment, based on the time-lapse overlay analyses

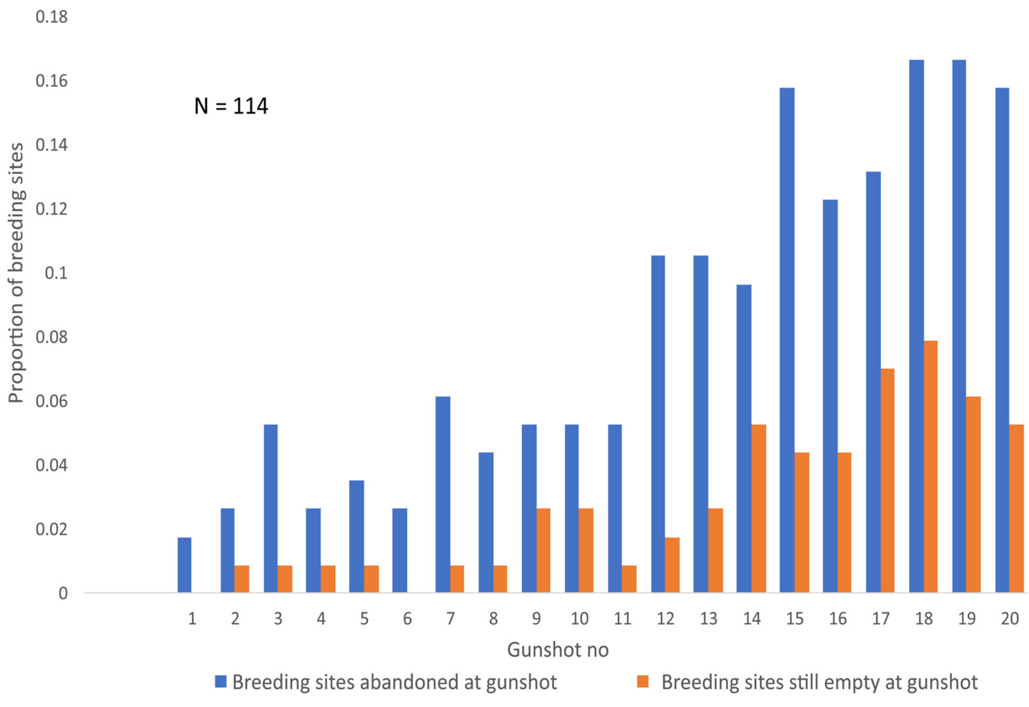


Figure 5. Proportion of 114 breeding sites abandoned by attending thick-billed murres (blue bars) as a reaction to a series of 20 gunshots during a repeated gunshot disturbance study at Kippaku, and the proportion of sites still unattended at each gunshot since the preceding gunshot (orange bars).

8

(Greenland Institute of Natural Resources, unpubl.). However, only one of the failures was verified as a direct result of the experiment, because video footage captured a chick falling off the cliff at the second gunshot. Two other chicks that were dislodged at some point during the experiment, managed to return to their respective nest sites. In addition, one egg outside the plot was observed falling off the cliff.

## Discussion

This study is the first to document effects of gunshot disturbances on colonially breeding birds – both in terms of approaching gunshots and effects of repeated disturbances. The results indicate that murres in larger, more densely populated colonies react to disturbances at greater distances and with a larger proportion of birds fleeing. Thereby, murres in dense colonies are at larger risk of acute reproductive failure from gunshot disturbances, than murres breeding in smaller and more sparsely populated colonies. It was not possible to document a clear link between response behaviour and presumed experience with disturbances in the declining murre colonies. However, the results from the repeated gunshot experiment were less conclusive than the approaching gunshot experiment, and experience with gunshot disturbances could be a contributing factor to the observed variation in response behaviour.

Given the usually remote character of seabird breeding locations, it is difficult to know the extent of the problem from gunshot disturbances caused by illegal seabird hunting, nearby seal hunting, or similar. However, it is our experience that these kinds of incidents occur to a lesser extent today compared to 20 years ago (Merkel et al. 1999). The murres from our six study-colonies probably share similar flyways and winter quarters, which would suggest similar experience with hunting exposure outside the breeding season (Frederiksen et al. 2016). Additionally, this species is adapted to naturally occurring noisy events at the colonies from ice breakup, collapsing icebergs and rock falls, the first two being relatively harmless, while the latter force them to leave their nest sites rapidly or risk death. However, given the varying distances to settlements and boating routes, they most likely have been exposed to different levels of anthropogenic disturbance and sounds of gunfire during the breeding season.

Generally, behavioural responses to disturbances should be interpreted with caution because the same behaviour can be an expression of both robustness and vulnerability (Gill et al. 2001). For example, the lack of a reaction can indicate lack of stress, but it can also indicate a freeze response or limited possibilities to react. Hence, behavioural tolerance does not necessarily equal physiological tolerance. Physiological responses (like heart rate and stress hormone levels) would be more objective measures of the response of individual birds to human disturbance (Tarlow and Blumstein 2007, Ellenberg et al. 2013); although these are not always feasible to perform. From a population perspective, however, leaving a chick or egg behind on the ledge is a more significant measure.

### Approaching gunshots

Generally, group size of a prey species can influence the FID in both directions. Larger groups either allow a closer approach of the predator, due to a larger perception of safety, or the opposite, due to earlier detection of potential danger and the larger probability of more timid individuals in the group (Ydenberg and Dill 1986, Stankowich and Blumstein 2005, Stankowich and Coss 2006). In our case, the gunshot noise was most likely detected at similar distances among the plots, and the FID was more likely dependent on murres assessing whether the risk of staying exceeded the cost of fleeing during an increasingly threatening situation. Timid individuals would make this decision sooner than more tolerant individuals, and flight of timid individuals can initiate fleeing by the rest of the group (Stankowich and Coss 2006, Stankowich 2008). Another possible factor contributing to a larger FID in high density areas could be the swarming effect, where individuals in a swarm gain protection from predation due to the confusion effect (Milinski 1984, Jeschke and Tollrian 2007). Birds in high density areas would gain more protection during a fly-out when leaving the cliff within a swarm than birds in low density areas. Lastly, murres in low density areas have an increased risk of avian predation of offspring and, therefore, a larger incitement to stay at the breeding site (Gilchrist 1999). These density dependent effects are supported by the number of kittiwakes that contribute to the positive correlation between bird density and FID. Also, the sub-colony of Apparsuit Q had a very small FID, whereas murres from the nearby, larger and denser sub-colony were observed to fly off at a noticeably greater distance.

In accordance with existing knowledge (Laursen et al. 2005, Pater et al. 2009, Dehnhard et al. 2019), weather conditions, more specifically wind and fog, also appeared to have an influence on the FID in our study. Kippaku, where the approaching gunshot experiment was repeated due to fog, showed a lower FID during foggy conditions than during calm and clear weather (Table 2). Similarly, the FID for Kitsissut A was relatively low considering the density of birds, which could be explained by the foggy conditions during the experiment. Wind and fog can change the transmission of noise and might weaken the perception of danger (Stankowich and Blumstein 2005).

FID is a relatively easy and widely used measure of fearfulness, but it is also a measurement that is influenced by many factors than can be difficult to control for (Stankowich and Blumstein 2005, Tarlow and Blumstein 2007). This made any conclusion on the significance of former gunshot experience on FID difficult, especially with the limited sample size. Nonetheless, the large variation observed in FID advocates for considering some degree of buffer distances when establishing no-shooting zones based on limited data (Livezey et al. 2016).

### Repeated gunshots

Unlike the approaching gunshot experiment, the repeated gunshot experiment provided information on the fraction of murres fleeing, and to some extent also the type of murres fleeing (attending/non-attending). This presented better opportunities to explore colony-specific differences in effects of and tolerance to gunshot disturbances. The duration of the repeated gunshot setup was likely longer than a typical marine mammal or bird hunting situation near colonies of cliff-nesting seabirds. However, the experiment was within the range (duration and number of gunshots) of what has been observed in the field (Merkel et al. 1999). In addition, the results showed that most of the birds fleeing, fled during the first series of five gunshots, which represent a disturbance level (in number of gunshots) that is likely to occur in most hunting scenarios for marine mammals or seabirds from small open boats in Greenland. A similar mechanism has been observed from an experiment on murre response to drones, where most of the flushing was associated with the initial start up of the rotors by non-breeding birds (Brisson-Curadeau et al. 2017).

At first glance the results from the repeated gunshot experiment appeared to be explained by density, similar to the approaching gunshot experiment (Table 3, Fig. 4). However, this was not supported by the regression analysis. The low-density plot of Kitsissut A displayed a relatively strong negative regression coefficient ($-2.23 \times 10^3$) and a relatively low proportion of birds remaining in the plot at last gunshot. Furthermore, Innaq H was in the low end of the proportion of birds remaining after the last gunshot, indicating a strong reaction. However, the regression coefficient indicated a relatively gradual slope ($-0.98 \times 10^3$), indicating a weak reaction (Table 3). This low-density murre plot had a high density of kittiwakes (Table 2), that did not seem to influence the FID (murre FID = 1.5 km, kittiwake FID = 5 km), but the high density of kittiwakes might have influenced the reaction to repeated gunshots. The deviating characteristics of Kitsissut A and Innaq H may indicate that other factors than density explain some of the observed variation. Kitsissut was representing a stable/undisturbed colony, and the birds could have reacted more strongly to the repeated gunshot disturbances due to less experience with gunshots. Also, the reaction pattern with a more gradual regression slope at Innaq, a declining/disturbed colony, could be influenced by more tolerance to gunshot disturbances.

It is difficult to say whether this difference in behaviour could be a result of birds being more tolerant due to experience with disturbances, or whether the difference is a consequence of more timid individuals already being selected out of this population and thus the remaining birds were more tolerant. Another explanation could be that declining colonies (whether from over-harvesting, climate change, human disturbances or a combination thereof) will have more areas of lower murre density, and, therefore, murres in declining colonies will be less influenced by surrounding birds, which may be reinforced by more motivation to stay at the colony due to risks from avian predation (Gilchrist 1999). This would cause birds at declining colonies to be less reactive due to density alone, irrespective of experience with disturbances. The difference between Innaq A and Kippaku C – the two time-lapse monitoring plots – illustrates how contrasting the reaction pattern can be between a highly reduced and an intact colony. It is difficult to tell whether the difference is due to Innaq being reduced in numbers owing to a general and prolonged negative population trend or due to experience with, and hence increased tolerance to, disturbances – or a combination of both. Our limited sample size makes any inference on this issue difficult and further studies would be needed to make any conclusions on this matter.

The fraction of attending breeders and the fraction of non-breeders in a plot, of which we lacked data, was also likely to influence our results, especially if varying among plots. The number of non-attending breeders and non-breeders varies throughout the day affecting the density of murres, usually in a colony-specific diurnal pattern (Gaston and Hipfner 2000, Merkel et al. 2007, Mosbech et al. 2009, Huffeldt and Merkel 2013). Depending on time of the day, our results could have been affected by this. Attending breeders, unlike non-breeders and non-attending mates, are highly motivated to stay with their offspring during a disturbance event, and to return quickly if they flee, due to the risk of hyperthermia and predation to their egg or chick. This motivation is likely even higher in low density areas because of the higher risk of predation, as mentioned earlier (Gilchrist 1999). The unwillingness to flee may be reinforced by a limited swarming effect by other fleeing birds at these low density colonies. This is supported by the pronounced difference between Kippaku C and Innaq A in the number of attending breeders leaving their site (Table 3). Optimally, the experiments should have been carried out at a time of the day when the conditions were similar at all the plots (e.g. average level of murres present). However, even if we had data for diurnal pattern for all our colonies, we were often restricted to windows of favourable weather regardless of time of day.

Because the two plots at Innaq were recorded for the longest time after the last gunshot, they were, unsurprisingly, the only two plots returning to 100% of the initial numbers. Interestingly, these two plots also reached both 95% and 90% levels relatively quickly compared to plots from other colonies that were recorded for a similar duration. This could, to some degree, support the hypotheses that these plots showed a higher level of tolerance due to more experience with disturbances, were composed of more robust birds, or a combination of the two.

***Reproductive implications***

Ultimately, disturbances at breeding colonies can affect colony size directly through loss of eggs and chicks and indirectly through lowered fitness and breeding propensity of adults. A minimum of one chick and two eggs were lost as a direct consequence of the repeated gunshot experiment events – all the observed cases were from the two stable colonies (Kippaku and Kitsissut). Likewise, the time-lapse data from Kippaku showed a marked increase in breeding failures at the date of the disturbance experiment. However, the failures detected with the time-lapse camera method could have occurred before the experiment, because failures are not recorded by the time-lapse method until the absence of birds coincide with a picture being taken, and only one of the breeding failures was confirmed from the video recordings. Nevertheless, the observed losses of eggs and chick confirm previous knowledge about this type of disturbance causing significant fly-outs, although with relatively small immediate consequences for the breeding success in our study. That said, the loss of offspring might have been larger, if the experiment had been carried out during the incubation period. According to parental investment theory, nest defence should increase as the breeding season progresses (Forbes et al. 1994). Also, as murres do not build nests and lay their egg directly on the cliff (Gaston and Hipfner 2000), eggs are more easily lost than chicks due to eggs' propensity to roll off the ledges.

Apart from the effect of lost offspring on colony size, there is also a potential long-term effect of repeated gunshots on adult fitness. At Kippaku, it was clear that the number of eggs and chicks being left alone increased gradually with the number of repetitions (Fig. 5). In the most extreme case, the same chick was abandoned 13 times over the course of the experiments. The repeated escape behaviour has direct fitness implications for the breeding bird, especially for an auk species like the thick-billed murre, that has the highest wing loading among flying birds (Elliott et al. 2013). This may partly explain why some Greenland colonies are stable while others, including nearby colonies, are declining (Merkel et al. 2014). In a longer-term perspective, repeated disturbances may also influence site fidelity or future breeding propensity (Lima 2009). Although, both are normally considered high for auk species (Gaston and Hipfner 2000), such a mechanism could potentially lead to low recruitment and a bias towards selection by individuals more tolerant to disturbances.

### Management recommendations

Most of the observed FID (11 of 13) and all but one alert distance were longer than the no-shooting zone of 1 km outlined in the current Greenland legislation on the protection of cliff-nesting seabirds (Anon 2019). Disturbance effects from a sound source are very weather dependent (Pater et al. 2009), as our results also have shown; however, shotguns and the larger rifles are more powerful than the caliber .222 used in our experiments, and FIDs are likely to be larger for those calibre firearms compared to those found in our study. Evidently, this study provides a basis for specifying a larger no-shooting zone than the existing no-shooting zone.

Several different methods have been used elsewhere to decide on minimal approach distances for birds, including mean FID, mean FID with a standard deviation added, alert distance and distance of which 95% of birds became alert (Livezey et al. 2016). A minimum shooting distance based on our results could be 5 km if FID is considered a sufficient measure. Some studies have shown physiological effect of disturbances before clear behavioural responses, and this would suggest a zone wider than the FID is necessary to reduce effects by gunshots (Ellenberg et al. 2012). Given the relatively small sample size of this study, it is plausible that some colonies have a larger reaction distance than observed and a safer no-shooting zone would be 1.5 × FID (7.5 km). However, deciding on a meaningful zone can be complicated because a zone too wide could result in a lack of understanding and acceptance of the no-shooting zones by residents (Falk and Kampp 2001). Based on this study, showing that birds in dense areas react at longer distances than birds in less dense areas, the decision makers could consider a differentiated no-shooting zone depending on colony size, as density usually is correlated with colony size. However, it is important to keep in mind that small colonies often are declining colonies that are vulnerable to other pressures.

Larger no-shooting buffer zones should not necessarily lead to changed accessibility for the general public to cliff-nesting seabird colonies. On the contrary, recreational access to wildlife (for tourism or local recreational purposes) can increase awareness and encourage conservation (Gill 2007), provided that no harmful disturbances are caused (Reiertsen et al. 2018). The simple presence of tourists or local recreationists can help limit events of individuals pursuing illegal hunting or other types of severe disturbances at or near seabird colonies. Legal enforcement is difficult and demand many resources in remote areas, and the encouragement of non-disturbing access to cliff-nesting seabird colonies could be considered as a potential conservation tool.

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## References

Anonymous 1958. Landsrådsvedtægt af 12. maj 1958 om fredning af fugle på ynglepladser. – Greenland Land Council Executive Order.

Anonymous 2009. Hjemmestyrets bekendtgørelse nr. 8 af 2. marts 2009 om beskyttelse og fangst af fugle. – Greenland Home Rule Government Executive Order.

Anonymous 2019. Selvstyrets bekendtgørelse nr. 17 af 28. oktober 2019 om beskyttelse og fangst af fugle. – Government of Greenland Executive Order.

Beale, C. M. and Monaghan, P. 2004. Human disturbance: people as predation-free predators? – J. Appl. Ecol. 41: 335–343.

Bejder, L. et al. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. – Mar. Ecol. Prog. Ser. 395: 177–185.

Blumstein, D. T. 2014. Attention, habituation and antipredator behaviour: implications for urban birds. – In: Gill, D. and Brumm, H. (eds), Avian urban ecology: behavioural and physiological adaptations. Oxford Univ. Press, pp. 41–53.

Boertmann, D. 2001. Seabirds. – In: Born, E. and Böcher, J. (eds), The ecology of Greenland. Atuakkiorfik, pp. 170–184.

Boertmann, D. and Mosbech, A. 2017. Baffin Bay. An updated strategic Environmental Impact Assessment of petroleum activities in the Greenland part of Baffin Bay. Scientific Report from DCE – Danish Centre for Environment and Energy, 2018. – Aarhus Univ.

Boertmann, D. et al. 2013. Disko West. A strategic environmental impact assessment of hydrocarbon activities. Scientific Report from DCE – Danish Centre for Environment and Energy, 71. – Aarhus Univ.

Braimoh, B. et al. 2018. Managing human disturbance: factors influencing flight-initiation distance of birds in a West African nature reserve. – Ostrich 89: 59–69.

Brisson-Curadeau, É. et al. 2017. Seabird species vary in behavioural response to drone census. – Sci. Rep. 7: 17884.

Buckley, R. 2004. Environmental impacts of ecotourism. – CABI Publishing.
Burnham, J. and Burnham, K. K. 2010. An ornithological survey of the Carey Islands, Northwest Greenland. – Dansk Orn. Foren. Tidsskr. 104: 26–37.
Burton, R. 1998. Maintaining the quality of ecotourism: ecotour operators' responses to tourism growth. – J. Sustain. Tour. 6: 117–142.
Chardine, J. W. and Mendelhall, V. 1998. Human disturbances in arctic seabird colonies. Circumpolar Working Group Tech. Rep. no. 2. Conservation of Arctic Flora and Fauna,Akureyri, Iceland.
Coulson, J. C. 2002. Colonial breeding in seabirds. – In: Schreiber, E. A. and Burger, J. (eds), Biology of marine birds. CRC Press, pp. 87–109.
Creel, S. et al. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and Elk. – Conserv. Biol. 16: 809–814.
Cresswell, W. and Quinn, J. L. 2011. Predicting the optimal prey group size from predator hunting behaviour. – J. Anim. Ecol. 80: 310–319.
Dahl, J. 1989. The integrative and cultural role of hunting and subsistence in Greenland. – Études/Inuit/Studies 13: 23–42.
Davenport, J. and Davenport, J. L. 2006. The impact of tourism and personal leisure transport on coastal environments: a review. – Estuar. Coast. Shelf Sci. 67: 280–292.
Dehnhard, N. et al. 2019. Boat disturbance effects on moulting common eiders *Somateria mollissima*. – Mar. Biol. 167: 12.
Descamps, S. et al. 2013. Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre. – Oecologia 173: 1271–1282.
Diego-Rasilla, F. J. 2003. Human influence on the tameness of wall lizard, *Podarcis muralis*. – Ital. J. Zool. 70: 225–228.
Ellenberg, U. et al. 2009. Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. – Anim. Behav. 77: 289–296.
Ellenberg, U. et al. 2012. Previous experiences with humans affect responses of snares penguins to experimental disturbance. – J. Ornithol. 153: 621–631.
Ellenberg, U. et al. 2013. Heart rate responses provide an objective evaluation of human disturbance stimuli in breeding birds. – Conserv. Physiol. 1: 1–11.
Elliott, K. H. et al. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. – Proc. Natl Acad. Sci. USA 110: 9380–9384.
Falk, K. and Kampp, K. 1997. A manual for monitoring thick-billed murre populations in Greenland. – Sci. Rep. Greenland Inst. Nat. Res., 7. Nuuk.
Falk, K. and Kampp, K. 2001. Lomvien i Grønland: Mulige effekter af forskellige bestands-påvirkende faktorer, og praktiske grænser for ressourceudnyttelse. – Tech. Rep. Greenland Inst. .Nat. Res., 38. Nuuk.
Fauchald, P. et al. 2015. The status and trends of seabirds breeding in Norway and Svalbard. – NINA Publications, 1151. Tromsø.
Flamme, G. et al. 2009. Estimates of auditory risk from outdoor impulse noise II: civilian firearms. – Noise Health 11: 231–242.
Forbes, M. R. L. et al. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. – Behav. Ecol. Sociobiol. 34: 79–85.
Fowler, J. and Cohen, L. 1990. Practical statistics for field biology. – Wiley.
Frederiksen, M. et al. 2016. Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: conservation implications. – Biol. Conserv. 200: 26–35.
Frederiksen, M. et al. 2019. Quantifying the relative impact of hunting and oiling on Brünnich's guillemots in the north–west Atlantic. – Polar Res. 38: 1–11.
Gaston, A. J. and Hipfner, J. M. 2000. Thick-billed murre *Uria lomvia*. – In: Poole, A. and Gill, F. (eds), The birds of North America.Birds of North America Inc., pp. 1–31.
Gaston, A. J. et al. 1994. Population parameters of thick-billed murres at Coats Island, Northwest Territories, Canada. – Condor 96: 935–948.
Gilchrist, H. G. 1999. Declining thick-billed murre *Uria lomvia* colonies experience higher gull predation rates: an inter-colony comparison. – Biol. Conserv. 87: 21–29.
Gill, J. A. 2007. Approaches to measuring the effects of human disturbance on birds. – Ibis 149: 9–14.
Gill, J. A. et al. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. – Biol. Conserv. 97: 265–268.
Green, R. E. et al. 2005. Farming and the fate of wild nature. – Science 307: 550–555.
Huffeldt, N. P. and Merkel, F. R. 2013. Remote time-lapse photography as a monitoring tool for colonial breeding seabirds: a case study using thick-billed murres *Uria lomvia*. – Waterbirds 36: 330–341.
Irons, D. B. et al. 2008. Fluctuations in circumpolar seabird populations linked to climate oscillations. – Global Change Biol. 14: 1455–1463.
Jeschke, J. M. and Tollrian, R. 2007. Prey swarming: which predators become confused and why? – Anim. Behav. 74: 387–393.
Laursen, K. et al. 2005. Factors affecting escape distances of staging waterbirds. – Wildl. Biol. 11: 13–19.
Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. – Anim. Behav. 49: 11–20.
Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. – Biol. Rev. 84: 485–513.
Livezey, K. B. et al. 2016. Database of bird flight initiation distances to assist in estimating effects from human disturbance and delineating buffer areas. – J. Fish Wildl. Manage. 7: 181–191.
Lundquist, D. et al. 2013. Response of southern right whales to simulated swim-with-whale tourism at Península Valdés, Argentina. – Mar. Mamm. Sci. 29: E24–E45.
Mallory, M. L. et al. 2018. Financial costs of conducting science in the Arctic: examples from seabird research. – Arct. Sci. 4: 624–633.
Meinke, D. K. et al. 2014. Auditory risk estimates for youth target shooting. – Int. J. Audiol. 53: S16–S25.
Merkel, F. et al. 2014. Declining trends in the majority of Greenland's thick-billed murre *Uria lomvia* colonies 1981–2011. – Polar Biol. 37: 1061–1071.
Merkel, F. R. et al. 1999. Polarlomvien i Disko Bugt og det sydlige Upernavik, 1998. Bestandsopgørelse og grundlag for fremtidig monitering af lomviebestandene. – Tech. Rep. Greenland Inst. .Nat. Res. No. 25. Nuuk.
Merkel, F. R. et al. 2007. Monitering af lomvier og rider i Qaanaaq kommune, 2006. – Tech. Rep. Greenland Inst. Nat. Res. No. 69. Nuuk.
Merkel, F. R. et al. 2016. Use of time-lapse photography and digital image analysis to estimate breeding success of a cliff-nesting seabird. – J. Field Ornithol. 87: 84–95.
Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. – Anim. Behav. 32: 1157–1162.
Milner-Gulland, E. J. and Bennett, E. L. 2003. Wild meat: the bigger picture. – Trends Ecol. Evol. 18: 351–357.
Mosbech, A. et al. 2009. Thick-billed murre studies in Disko Bay (Ritenbenk) West Greenland. – Natl Environ. Res. Inst., Aarhus Univ. NERI Tech. Rep. No. 749. Roskilde. <www.dmu.dk/Pub/FR749.pdf>.
NAMMCO 2004. Report of the NAMMCO workshop on hunting methods for seals and walrus. Expert groups/workshops on hunting methods. – Nordic Council of Ministers, Tromsø.

Nisbet, I. C. T. 2000. Disturbance, habituation and management of waterbird colonies. – Waterbirds 23: 312–332.
Olsson, O. and Gabrielsen, G. W. 1990. Effect of helikopters on a large and remote colony of Brünnich's guillemot *Uria lomvia* in Svalbard. – Norsk Polarinstitutt Rapportserie 64: 1–36.
Parrish, J. K. 1993. Comparison of the hunting behavior of four piscine predators attacking schooling prey. – Ethology 95: 233–246.
Pater, L. L. et al. 2009. Recommendations for improved assessment of noise impacts on wildlife. – J. Wildl. Manage. 73: 788–795.
Pichegru, L. et al. 2016. African penguin tolerance to humans depends on historical exposure at colony level. – Bird Conserv. Int. 26: 307–322.
Rankin, C. H. et al. 2009. Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. – Neurobiol. Learn. Mem. 92: 135–138.
Rasmussen, R. O. 2005. Analyse af fangererhvervet i Grønland [Socio-economic analysis of the Greenland hunters]. – Unpubl. Rep. Dep. of Fisheries and Hunting, Greenland Home Rule, Nuuk.
Reiertsen, T. K. et al. 2018. Effektstudie av turisme på sjøfugl. Hvordan påvirker ferdsel hekkende sjøfugl på Hornøya? – NINA Rapport, 1528. Tromsø.
Rodríguez-Prieto, I. and Fernández-Juricic, E. 2005. Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. – Biol. Conserv. 123: 1–9.
Schneider, C. A. et al. 2012. NIH Image to ImageJ: 25 years of image analysis. – Nat. Methods 9: 671–675.
Sharp, R. and Wollscheid, K. U. 2009. An overview of recreational hunting in North America, Europe and Australia. – In: Dickson, B. (ed.), Recreational hunting, conservation and rural livelihoods: science and practice. Blackwell Publishing, pp. 25–38.
Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. – Biol. Conserv. 141: 2159–2173.
Stankowich, T. and Blumstein, D. T. 2005. Fear in animals: a meta-analysis and review of risk assessment. – Proc. R. Soc. B 272: 2627–2634.
Stankowich, T. and Coss, R. G. 2006. Effects of risk assessment, predator behavior and habitat on escape behavior in Columbian black-tailed deer. – Behav. Ecol. 18: 358–367.
Tarlow, E. M. and Blumstein, D. T. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. – Appl. Anim. Behav. Sci. 102: 429–451.
Villanueva, C. et al. 2012. A matter of history: effects of tourism on physiology, behaviour and breeding parameters in magellanic penguins *Spheniscus magellanicus* at two colonies in Argentina. – J. Ornithol. 153: 219–228.
Walker, B. G. et al. 2006. Habituation of adult magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. – Conserv. Biol. 20: 146–154.
Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.
Ydenberg, R. C. and Dill, L. M. 1986. The economics of fleeing from predators. – In: Rosenblatt, J. S. et al. (eds), Advances in the Study of Behaviour. Academic Press, pp. 229–249.

Supplemental material available at Youtube <https://youtu.be/C9Y41HZr_zo>.

# Paper II

Merkel FR, **Labansen A**, Autzen T, Simon M & Hermannsen L. Quantifying marine traffic intensity in Northwest Greenland and the potential disturbance of two seabird colonies.

Manuscript planned for submission to *PLOS ONE*.

Apparsuit. Photo: C. Isaksen

## QUANTIFYING MARINE TRAFFIC INTENSITY IN NORTHWEST GREENLAND AND THE POTENTIAL DISTURBANCE OF TWO SEABIRD COLONIES

*Flemming Ravn Merkel[1,2], Aili Lage Labansen[1], Thyge Feldskou Autzen[1], Malene Simon[3] and Line Hermannsen[2]*

[1]Greenland Institute of Natural Resources, Kivioq 2, PO Box 570, 3900 Nuuk, Greenland

[2]Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

[3]Greenland Climate Research Centre, Greenland Institute of Natural Resources, Kivioq 2, PO Box 570, 3900 Nuuk, Greenland

**ABSTRACT**

Marine traffic represents an increasing source of noise pollution in the marine environment with possible negative consequences for a wide range of marine animals. Seabirds are potentially highly vulnerable to this type of anthropogenic disturbance, because they often aggregate in large and dense colonies in coastal areas, where marine traffic also is concentrated. However, the magnitude of the problem is largely unknown. In this study we aimed to explore if underwater noise recordings can be used as a method to quantify the intensity of marine traffic around seabird colonies, and thereby approximate the potential level of disturbance. We studied two colonies of thick-billed murre (*Uria lomvia*) in Northwest Greenland, for which it was speculated that marine traffic could be a contributing driver for population decline. Known vessel tracks from automatic monitoring systems (AIS and VMS) and GPS recordings were used to study the acoustic noise characteristics of these vessels and to assess the influence of landmasses and seabed topography on the noise landscape. Subsequently, this knowledge was used as a reference to acoustically detect other vessels and their approximate travelling routes. A total of 307 vessels and seven travelling routes were identified for the period 22 June - 10 August 2016, of which 23 vessels were classified as a potential disturbance for one or the other colony, based on the travelling route, their noise emission and boating behaviour. As much as 96% of all the vessels were unaccounted for by means of AIS and VMS data, including all the potentially disturbing vessels. The colony situated closest to an inshore travelling route (Apparsuit) was disturbed nearly five times as much as the other colony (Kippaku). The true nature of the disturbances could not be determined, as they were not visually observed. However, the higher disturbance level at Apparsuit coincides with a declining population trend for this murre colony, in contrast to a positive population growth at the more remote Kippaku. Disturbance from marine traffic activity is an understudied conservation issue for seabirds, however, this study shows that underwater acoustic monitoring is a useful method to quantify the degree of exposure.

## INTRODUCTION

The potential for anthropogenic disturbances on wildlife caused by marine traffic is increasing on a global scale, due to the rapid increase in numbers of both commercial (UNCTAD 2020) and recreational vessels (Davenport and Davenport 2006, ICOMIA 2015). In Arctic regions, climate change is resulting in many regions formerly impassable due to ice covered waters now are accessible by boat and open to expansion of shipping routes (PAME 2009, Moore et al. 2012, PAME 2020).

In Greenland, this development is facilitating economic growth in the northern areas. Fishery is the largest industry and is expanding northwards, partly because warmer waters result in a northward shift of the catch species and because open water allow fisheries and shipping to southern destinations (Merkel and Tremblay 2018). Because most towns and settlements in Greenland are not connected by roads, the marine infrastructure is an important driver for all economic activity, and is also important for regional travels between communities (Christensen et al. 2018). Furthermore, the smaller boats typically used for personal transportation are getting larger and faster, making it possible to travel farther and more frequently. Airplanes and helicopters are part of the infrastructure, but has a limited capacity and is often a very expensive solution for regional travels (Mallory et al. 2018).

Marine traffic generates broadband underwater noise, which can lead to negative impacts on a wide range of marine animals (Richardson et al. 1995, Nowacek et al. 2007, Simpson et al. 2016, Hansen et al. 2020). Seabirds that breed in coastal areas and forage exclusively in the marine environment, are among the wildlife potentially affected by vessel noise, both below and above the water surface. Still the knowledge of anthropogenic noise effects on seabirds is very limited and only few data exist on hearing of seabird species. The great cormorant (*Phalacrocorax carbo sinensis*) was recently shown to have its best hearing sensitivity in water at 1 kHz (Larsen et al. 2020). Consistent with this, the common murre (*Uria aalge*), which has a similar amphibious lifestyle as the cormorant, has been found to react to underwater noise with peaks at 1-4 kHz. Reactions included stopping to feed, moving away from the noise source and exhibiting a startle response (Hansen et al. 2020), which would have energetic consequences for the animal. Above the surface, murres have been found to have best hearing at similar frequencies (1-4 kHz, Mooney et al. 2019). Apart from the noise, the physical presence of a vessel may also elicit a behavioural response, in particular if vessels previously have been associated with high-risk events, such as hunting. A bird’s reaction to a stressor is generally linked to the perceived risk, with stronger reactions if they perceive a serious danger (Beale and Monaghan 2004, Stankowich and Blumstein 2005, Ellenberg et al. 2009, Villanueva et al. 2012). Cliff-breeding colonial seabirds are particularly vulnerable to disturbances above the water surface because they aggregate in large numbers and are very faithful to their breeding sites

(Coulson 2002, Gaston and Hipfner 2020). The immediate consequences of disturbance can include increased energetic costs, higher predation of offspring, loss of offspring when fleeing the nest site, or adult mortality if disturbances also involve hunting (Schauer and Murphy 1996, Merkel et al. 1999, Rojek et al. 2007, Labansen et al. 2021).

Among the Arctic seabirds, the thick-billed murre (*Uria lomvia*) is potentially highly exposed to marine traffic, as it breeds in large colonies on steep cliffs directly facing the sea. Within the Arctic Council working group CAFF (Conservation of Arctic Flora and Fauna), this species is considered a species of conservation concern due to direct or indirect effects of human activities, such as hunting, tourism, oil pollution and bycatch (Chardine and Mendenhall 1998, Wiese et al. 2004, Merkel and Barry 2008). Although these threats have been addressed and significantly reduced over the past decades, breeding populations are still declining in several regions of the Arctic, including Greenland, where 12 of 19 colonies are in decline (Merkel et al. 2014).

The main drivers currently identified to impact murre population development in the North Atlantic, all occur during winter when murres are far away from their breeding areas and include factors such as oceanographic changes, winter hunting and oil pollution (Descamps et al. 2013, Frederiksen et al. 2019). However, contrasting population trends in Greenland have been observed among closely situated colonies (with shared wintering areas), indicating that local factors in the breeding area, such as disturbances and local hunting, also may play a role for the observed decline.

Here, we used underwater acoustic recorders to measure vessel noise at two murre colonies in Northwest Greenland. We subsequently used the noise measurements to estimate vessel density, the approximate travelling routes and the potential disturbance at the colonies. One of the study colonies experienced a long-term population decline (Merkel et al. 2014) and a possible link to marine traffic has been speculated due to a nearby inshore vessel route. However, the distance to designated vessel routes can be a poor measure of vessel intensity in an area, particularly in coastal areas where smaller vessels often travel outside common routes. Furthermore, smaller vessels are not monitored by automatic monitoring systems and their movement patterns are therefore not easily mapped (Hermannsen et al. 2019). By conducting this study, we aimed to explore the possibility of using underwater acoustic monitoring as a method to quantify marine traffic around seabird colonies, as a first step to understand the possible impact on seabird populations. The method is not new (e.g. Simard et al. 2016, Hermannsen et al. 2019), but to our knowledge, passive acoustics have not previously been used to quantify the potential problem of marine traffic around seabird colonies.

## MATERIALS AND METHODS

**Study area.** The study was carried out at two seabird colonies (8-9 km apart) in northern Upernavik, Northwest Greenland, in the period June – August, 2015 and 2016. The northernmost colony Apparsuit is approximately 5 km long and is facing south-southwest and had approximately 50,000 attending murres in 2017. In comparison, the Kippaku colony, situated southeast of Apparsuit, is approximately 0.5 km long and is facing mainly northeast and had approximately 21,000 attending murres in 2017 (GINR, unpublished data). The Apparsuit colony is situated just east (1 km) of the inshore in-between settlements boating route and the colony has been declining over the past three decades, while the Kippaku colony is situated 6 km east of the same inshore route and has increased slightly in the same period (Merkel et al. 2014). The offshore cargo shipping route is situated at least 50 km to the west of the colonies, while offshore travels between settlements usually pass the colonies at a distance of 10 – 20 km. Water depths within the study area are typically between 300 and 1000 m, except very close to the colonies. Icebergs are common in the study area, originating from the Giesecke glacier 50 km southeast of the colonies.

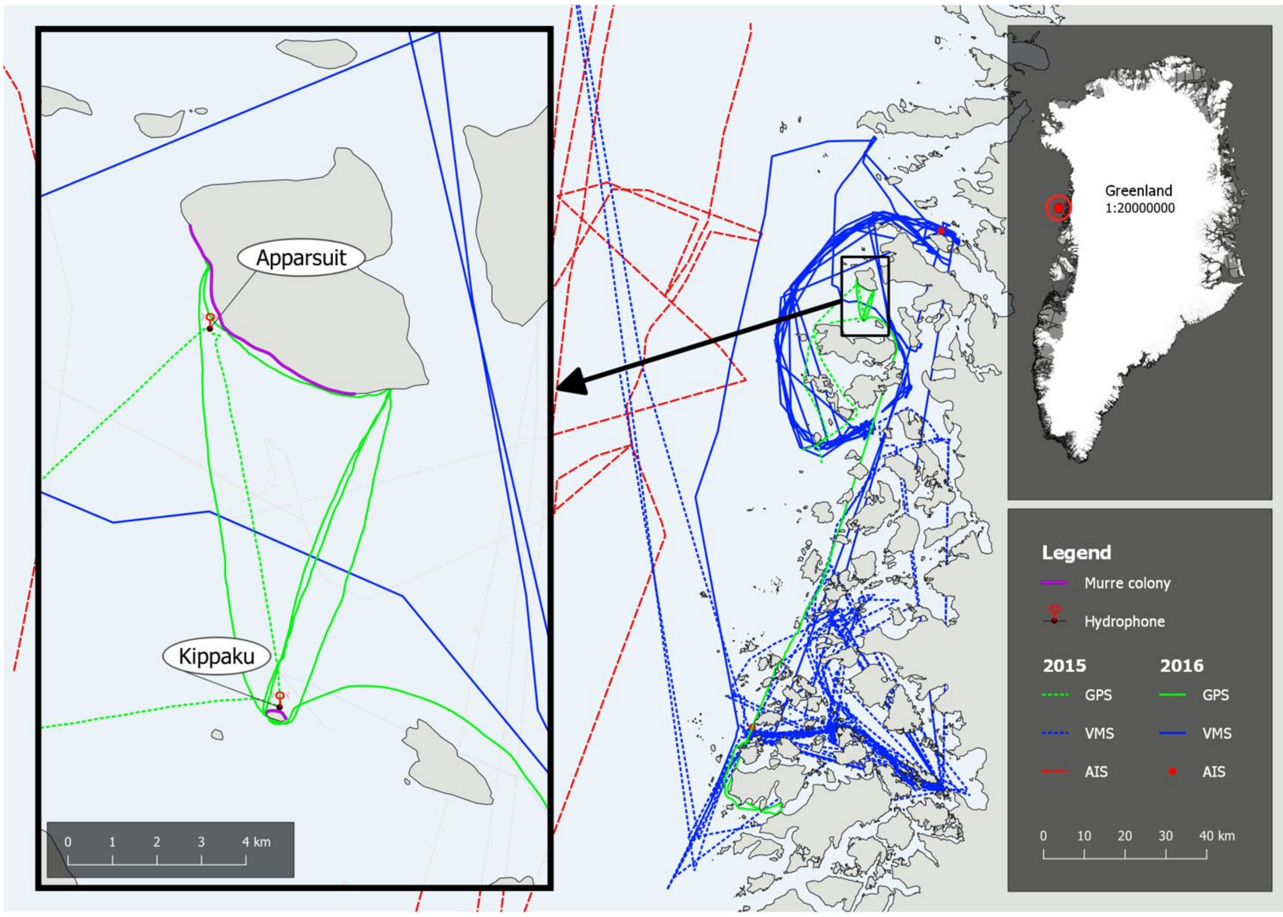


**Fig. 1**. Known vessel tracks within and around the study area in the northern Upernavik area, June – August, 2015 and 2016, obtained from automatic vessel monitoring systems (AIS and VMS) and from own GPS tracking. AIS and VMS source: The Gatehouse Group and the Greenland Fisheries License Control Authority.

**Underwater sound recordings.** Recordings of underwater sound were made in the period June 28 – August 18, 2015 and June 22 – August 16, 2016 with two stationary acoustic loggers (DSG, Loggerhead Instruments) recording at a sampling rate of 20 kHz (clip level 169 dB re 1 µPa). In 2016 the loggers recorded continuously, while only in intervals of 10 minutes every 30 minutes in 2015. The recorders were deployed at a horizontal distance of 100 m from the seabird cliff, resulting in a moored depth of 100 m at Kippaku and 290 m at Apparsuit. The recording rig consisted of a 100 kg anchor, an acoustic release, the DSG logger placed approximately 12 m above the seafloor, and sub-surface buoys to keep the mooring vertical in the water column and to allow for surfacing, when the acoustic release was signaled to detach from the anchor.

**Vessel positions and tracks.** Automatic Identification System (AIS) and Vessel Monitoring System (VMS) data were obtained from the Gatehouse Group and from the Greenland Fisheries License Control Authority, respectively, for the period June – August in 2015 and 2016 and within a radius of approximately 150 km from each of the colonies. In addition, we tracked our own movements in the area using handheld GPS devices. All vessel tracks were analyzed using GIS (QGIS version 3.4.12-Madeira). Fig. 1 shows all the known tracks from 2015 and 2016.

**Acoustic analyses.** Acoustic analyses of the sound recordings were used to estimate the presence and movements of all vessels around the colonies in 2016, including small vessels that were undetected by monitoring systems. The same analysis could not be made for 2015 due to the non-continuous sound recordings. However, for the initial training exercise, data from both years were used, i.e. step 1 in the following description:

1. For vessels with known tracks (from AIS/VMS/GPS data, 2015 and 2016) we used the corresponding sound recordings as a training dataset. The recordings were visually and aurally inspected as spectrograms in Raven Pro (version 1.5) to learn how to identify vessel noise events and how to distinguish between the different type of vessels (Suppl. Fig. 1-4). Vessel tracks and the corresponding underwater sound were also used to identify sub-areas within the study area, where vessel noise could not be visually detected on the spectrograms due to shielding from landmasses or seabed typography (see Supp. Fig. 4-5 and Fig. 2).

2. From start to end, all sound recordings from 2016 were visually inspected as spectrograms (including the small proportion containing AIS/VMS/GPS tracked vessels). All noise patterns identified as vessels were marked from start to end in Raven Pro and categorised according to presumed vessel type (cargo vessels, fishing vessels or smaller vessels) and activity (see examples in Suppl. Fig 1-6). Vessels

with a uniform noise emission were categorised as passing by at a constant speed, whereas fluctuating noise levels were categorised as vessels making short stops or changing speeds. The visual inspections were supplemented by listening to a subset of the recordings.

3. All identified vessels were organised according to their acoustic detection time and the duration of their noise emission to identify temporal overlap in vessel activity between the two recorder stations. In case of an overlap in time, the vessel noise characteristics and changes in noise levels were inspected to determine if the overlap in activity could be caused by the same vessel. This method was verified by GPS tracks and sound recordings of our own boating activity (see example in Suppl. Fig. 6).
4. In the final step individual vessels were grouped according to their estimated travelling route. This was achieved by studying the duration of the vessel noise, the pattern of appearance and disappearance of the noise, overlap in appearance between the two recorder stations, signal strength and frequency distribution of the noise pattern. When comparing these characteristics with the knowledge gained in step 1, a vessel could be assigned to a specific travelling route (see Tab. 1).

**Potential impact on seabird colonies.** Based on observations in Greenlandic seabird colonies (Merkel et al. 1999, Egevang 2008, F. Merkel & A. Labansen, unpubl. obs.), and studies elsewhere (Nowacek and Wells 2001, Williams et al. 2002, Rojek et al. 2007) showing that proximity and vessel behaviour affects the degree of disturbance of animals, we expected a large potential for disturbance by vessels when being close to the colony (roughly < 1km) and especially when making sudden changes in speed or direction at the same time. Thus, when the acoustic recordings indicated that a vessel was deviating from the normal fixed speed, i.e. acceleration and deceleration combined with periods of slow speed or idle running, and when a high power amplitude ( >3 kU, but depending on vessel type) of the noise indicated that the vessel was close to a colony, it was considered a potential disturbance (see example in Suppl. Fig. 5).

When deviating vessel activity happened at the southern end of the Apparsuit colony, a powerful noise signal was not a useful criterion for being close the colony. Activity in this area was not detected on the Apparsuit recorder because this was placed farther north in the colony and shielded from the southern end by the curved shape of the island and the seabed topography (Fig. 4, Suppl. Fig. 6). However, the activity was detected on the Kippaku recorder (≈ 7 km away), but with a weak power signal. In these cases, the detection of acceleration/deceleration was the main criteria for classifying the vessel as a potential disturbance for the colony and supported by previous knowledge about boating behaviour in this area (see Discussion).

**Tab. 1.** Characteristics and criterions for allocating vessels to different travel routes (see also Fig. 2)

| | |
|---|---|
| Route 1: | Visible only on spectrograms from the Kippaku recorder, but only for a short period (depending on speed). When moving north, the noise pattern typically was highly visible in the first half and subsequently disappeared gradually, while opposite when moving south. |
| Route 2 | Noise pattern similar to route 1, but the normal steady movement with a fixed speed was temporarily interrupted by a shorter or longer period with idle running, combined with acceleration and deceleration. The travel route shown in Fig. 2 indicate that vessels came close to the southern part of the Apparsuit colony. This interpretation was not based only on the noise recordings, as the Kippaku recorder was quite far away (7 km). Knowledge from direct observations in the study area was also used (see Discussion). |
| Route 3 | Visible on the spectrograms on both recorders for a long distance, but when close to the inshore route (1) only visible on the Kippaku recorder. Compared to route 6, the noise signal varied more in strength when travelling on this route, as the distance to the recorders varied more. |
| Route 4 | A gradual increase or decrease in signal strength when approaching or travelling away from the Kippaku recorder. Travels were typically interrupted by a shorter or longer period with idle running, combined with acceleration and deceleration. Not visible on the Apparsuit recorder at any time and when south or southwest of the Kippaku island invisible on both recorders. |
| Route 5 | Characterised as being visible only at the Apparsuit recorder spectrograms when on the northern part of this route, followed by a short period of visibility on both recorders when moving southwards, and subsequently only visible on the Kippaku recorder. Signal strength was shortly very high when passing the Apparsuit recorder at a close distance. The travels on this route were typically interrupted by a shorter or longer period with idle running, combined with acceleration and deceleration. |
| Route 6 | When moving south, the noise pattern became quickly and simultaneously visible on the spectrograms from both recorders and gradually disappeared when moving further south, first on the Kippaku recorder and subsequently on the Apparsuit recorder. The pattern was opposite when moving north. Note that cargo ships were also categorised to this route, although they were assumed to travel much further west (≈ 50-80 km according to AIS data from 2015) than indicated by the line in Fig. 2. Note also that these ships were visible for a longer distance/period than indicated by Fig. 2. |
| Route 7 | Characterised as being moderately visible on the spectrograms from both recorders when located to the west and temporarily visible only on the Apparsuit recorder when farther to the east. |

## RESULTS

A total of 307 vessels were identified based on noise recorded by two sound recorders located at two thick-billed murre colonies in 2016. This number does not include our own boating activity, i.e. when deploying the recorders or visiting the colonies. Based on noise characteristics and speed, 11 vessels were identified as cargo vessels, 50 were classified as fishing vessels and 246 vessels were classified as smaller fast-moving vessels. Only a single cargo vessel and 12 fishing vessels, corresponding to 4% of the vessels identified in 2016, were detected by means of AIS or VMS data.

Based on both vessel monitoring data (AIS and VMS) and acoustical detection of vessels without AIS or VMS, seven approximate boating routes were identified (Tab. 1, Fig. 2). Most vessels passed the colonies along the inshore boating route (route 1), making up 66% (203) of the detected vessels (Fig. 2). The offshore route (6) had the second highest traffic intensity, accounting for 21% (64) of the vessels, while 4% of the vessels used the remaining routes (Fig. 2). Travel directions were identified as 41% of the vessels travelling north, 41% going south, 3% going both north and south, 4% going west or east, while the direction could not be determined for 11% of the vessels.

The 307 vessels were visible as noise on the sound recordings for a total period of approximately 91 hours. The large Apparsuit island was shielding the Apparsuit recorder from most inshore vessel activity and only about 30% (27.2 h) of the identified noise was visible on the Apparsuit recorder, while 70% (63.8 h) of the vessel detected noise originated from the Kippaku recorder. As a result, most of the inshore vessels were identified on the Kippaku recorder, while offshore vessels or vessels travelling between the colonies were identified on the Apparsuit recorder or on both recorders. When summarized for the whole period, vessel activity was relatively high from around mid-day until early night, peaking at mid-afternoon. At this latitude and season continuous light allows even small vessels to travel throughout the night, but relatively few vessels were active from late night to early morning (Fig. 3).

In 23 cases (8%), vessel activity was characterized as a potential disturbance at one of the colonies (see definition in Methods). In two cases, the vessel was classified as a fishing vessel, whereas the majority of the disturbance events were associated with vessels classified as smaller fast-moving vessels. Close to five times as many of the potential disturbance events occurred at the Apparsuit colony (19 cases) compared to the Kippaku colony (4 cases). At Apparsuit, most potential disturbance events occurred at the southern part of the colony by vessels travelling on route 2 (Fig.2) and thereby deviating from the normal inshore boating route (route 1, Fig. 2). The remaining events occurred when vessels travelled along the entire extent of the colony (route 5, Fig. 2), travelling close to the colony at irregular speeds or making stops. At the Kippaku colony potential disturbance events were also caused by vessels deviating from the inshore boating route and also travelled at irregular speeds and included occasional stops. The four vessels characterized as disturbing the Kippaku colony were detectable on the Kippaku recorder for an approximate duration of 1.5 h, while the 19 vessels potentially disturbing the Apparsuit colony were detectable on the Apparsuit recorder for a total of 7.7 h. This duration included some travel time when approaching and leaving the colony, so the critical exposure time is unknown, but likely shorter. Among the identified disturbances, 65% occurred from 13PM to 19PM, while the remaining 35% occurred from 22PM to 5AM. The nature of the disturbance above the water surface, when boats temporarily stopped or slowed down in front of the colonies, could not be determined. In a few cases, we suspect to have heard gunshots at the sound recordings; however, this could not be verified due to the inability of separating these events from broadband noise events of cracking icebergs.

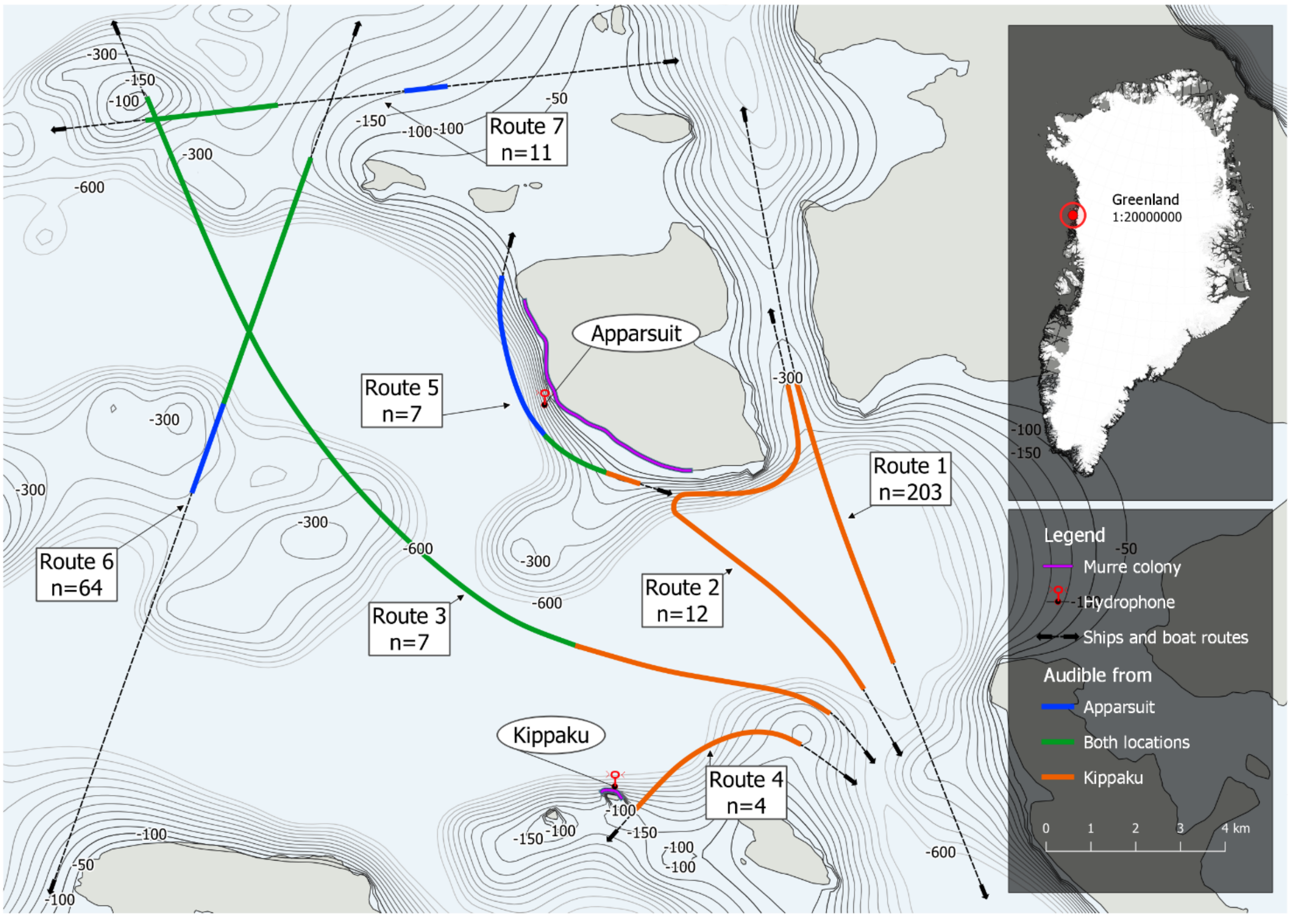


**Fig. 2**. Map showing the identified travelling routes in 2016 and the number of vessels using them (n). The coloring of the routes indicates the audibility of vessel noise at two underwater sound recorders located close to the seabird colonies Kippaku and Apparsuit. A total of 307 vessels were identified.

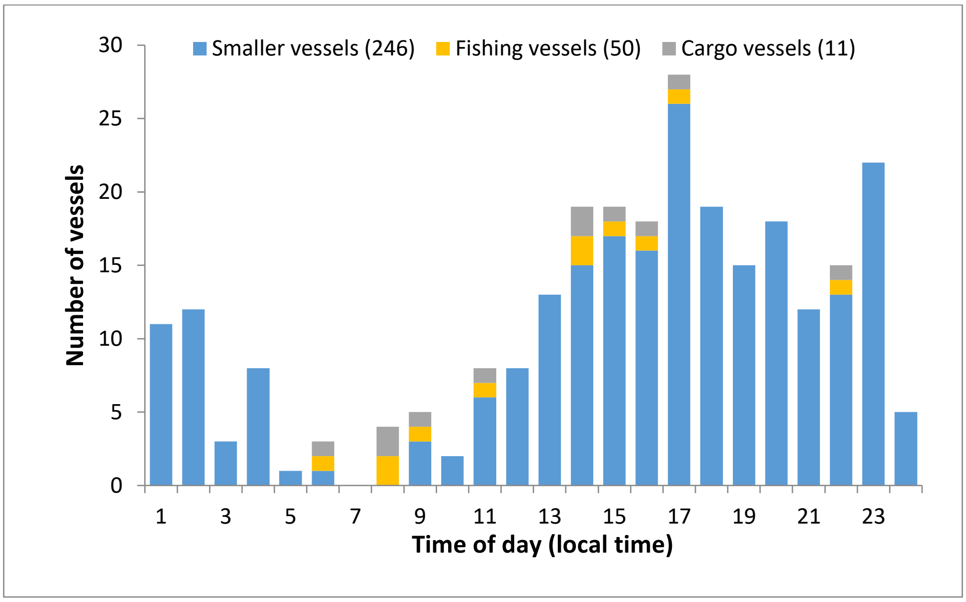


**Fig 3.** Vessel activity around two seabird colonies in Northwest Greenland, Kippaku and Apparsuit, summarised for the period June 22 to August 8, 2016. The total number of times each vessel category appeared, is shown in the figure legend.

## DISCUSSION

### Traffic intensity and potential disturbances of seabird colonies

Based on acoustic detection, 307 vessels were identified in the study area from June 22 to August 10, 2016, of which only 4% could be matched with AIS or VMS data. Most vessels were categorised as fast-moving boats (80%) and the majority (66%) were estimated to follow the inshore travelling route (route 1, Fig. 2). None of these boats had AIS/VMS onboard and would therefore have been unaccounted for if assessing potential anthropogenic effects on the murre colonies only on the basis of AIS and VMS data.

Instead the potential disturbance effect on the colonies was characterised on the basis of underwater recordings, using knowledge from several previous studies showing that the combination of being close to the colony and making sudden changes of speed can cause a significant disturbance at seabird colonies, compared to a boat passing by at a fixed speed (Merkel et al. 1999, Rojek et al. 2007, Egevang 2008, F. Merkel & A. Labansen, unpubl. obs.). In this way, eight percent of the vessels were in total considered a potential disturbance for the colonies, because they travelled close to the colonies and generated erratic engine noise, with the majority of them being a potential disturbance at Apparsuit compared to Kippaku. The results are in line with our expectations that the Apparsuit colony is subject to human disturbances more frequently than the colony at Kippaku, primarily due to the nearby inshore boating route (route 1, Fig. 2) passing on the eastern side of the Apparsuit island (colony on the western side). Both in terms of duration and frequency of disturbances, the Apparsuit colony was exposed approximately five times more than the Kippaku colony in 2016. The frequency of disturbance corresponds to, on average, one disturbance every third day at Apparsuit, and one every 14 days at Kippaku.

Although the true impact of the identified disturbance events here is unknown, as they were not observed directly, this acoustic method can help to pinpoint areas of concern, where vessels may affect fitness of seabird colonies. The relatively high degree of disturbance at the Apparsuit colony, i.e. on average one disturbance every third day, may have contributed to the large population decline reported for this colony (Merkel et al. 2014), especially if hunting occasionally is involved. Attempts were made to identify potential hunting incidents, as this would naturally add to the level of disturbance impact. Recent studies have shown that seabirds in some colonies respond to gunshots at a distance up to 4-5 km (Labansen et al. 2021). Although we acoustically did identify possible gunshots near both colonies, we could not verify if these were in fact gunshots or noise from icebergs cracking. It is known, however, from other fieldwork activity that shooting occasionally does occur at murre colonies in Greenland (Merkel et al. 2014). The most recent observation from this study area was in 2020, where shooting was observed at the southern part of the Apparsuit colony (F. Merkel, unpubl.).

Although we believe that the previous level of illegal hunting close to seabird colonies (see Merkel et al. 2014 and references therein) is much reduced nowadays, it is known that even small increases in adult mortality in species with a slow life-history pattern, like the thick-billed murre, can pose a threat to long-term viability (Lebreton and Clobert 1991). Apart from the direct mortality from hunting, the combination of erratic engine noise and hunting may also have entailed a lower tolerance or a sensitization to engine noise stimuli, causing birds to perceive unpredictable engine noise events as high-risk events (Stankowich and Blumstein 2005, Stankowich 2008, Bejder et al. 2009). This could lead to more extensive escape responses with consequences on energy budgets and breeding success (Carney and Sydeman 1999, Rojek et al. 2007) and potential future reductions in breeding propensity and recruitment. Long-term exposure to disturbances could also lead to a direct population effect if the most noise-sensitive individuals abandon the area on a permanent basis, as shown for other marine animals (Bejder et al. 2006a, Bejder et al. 2006b). An amplifying factor for this study species, is that disturbances are likely to mainly affect one of the sexes. Studies on thick-billed murre have shown that one sex is primarily nocturnal while the other is primarily diurnal when it comes to colony attendance. In Greenland, including this study area, it appears that females are the diurnal sex (Linnebjerg et al. 2015, Huffeldt and Merkel 2016), and consequently more likely to be disturbed when attending the colony, as human activities occur mainly during daytime. Due to the reproductive role of the females, a biased impact on this sex can amplify long-term consequences on population viability (Lebreton and Clobert 1991).

**Study limitations and recommendations**

Optimally, if all vessels were fitted with reliable monitoring systems, it would be easier to allow for inclusion of boat disturbances in population consequence models. However, since AIS and VMS is currently only required on large and commercial vessels (IMO 1998), and coverage of these systems is mostly incomplete (Robards et al. 2016, Hermannsen et al. 2019, this study), it is necessary to develop a simple method for detecting the presence of vessels around areas that are important for marine species. Here, underwater sound recordings proved to be useful in quantifying the intensity of marine traffic around two seabird colonies, and in most cases also the travelling routes and behavior of vessels could be estimated. To a large extend, this was possible because the two recorder units captured the noise landscape differently, due to the geographical positions of the units and the surrounding landscape. Both the presence of landmasses and the topography of the seabed caused noise signals to be shadowed out from some areas, which in our case made it possible to make an interpretation of the whereabouts of the vessels, which was verified with a large test dataset with known vessel movements. Thus, a similar setup in a different landscape may not work equally well. In all cases, the method requires a decent amount of position data (AIS, VMS or GPS) to verify the influence of landmasses and seabed topography on the noise landscape.

The detection and approximated location of vessels can be improved by having more recording stations. In this study, an additional hydrophone at the southern end of the Apparsuit colony would have been helpful for the interpretation of boating activity in this area (route 2, Fig. 2), in particular because the colony stretches over 5 kilometers. With the current setup this activity was only detectable on the Kippaku recorder, which was approximately 7 km away. Our interpretation that the deviating boating activity (deceleration, idle running and acceleration) happened in front of the southern part of the colony, was partly based on prior knowledge about boating behavior in this area. During annual fieldwork activity here (2008 – 2020), several direct observations were made of boats deviating from the inshore boating route (1) to visit the southern and nearest part of the Apparsuit colony.

Optimally, an automatic detector should be developed to detect vessels based on relevant spectral and temporal characteristics, in order to enable more cost-effective analysis of large datasets, as in the case of Simard et al. (2016). Developing a region-specific detection algorithm is a time-consuming task though and since our pilot-study covered a relative short period with relatively few vessels, at least compared to Simard et al. (2016), the manual identification of vessels was likely more efficient in our case. However, a wider use of passive acoustics to quantify human activity in the Arctic marine environment would clearly benefit from an automatic detection algorithm. The estimation of travelling routes will be difficult to automate, but when using passive acoustics mainly to quantify the potential disturbance of a predetermined sensitive area, knowledge about travelling routes is likely not needed or needed only in the early study-phase. In our study area for example, continued monitoring of disturbance levels would need only to focus on the proximity of the vessels and the movement behavior of the vessels.

In Greenland, vessel presence may be a useful proxy for hunting events around seabird colonies. However, we were unable to explore this as we could not verify possible shooting events. The main challenge was the frequent occurrence of cracking icebergs; however, detections may be possible if collecting ground truth data on gunshots fired at increasing distances from a recorder unit. The most obvious alternative solution would be to measure gunshots with aerial noise recorders; however, these would probably face the same challenge as in water, namely the difficulty in distinguishing ice cracks from gunshots. In areas with no icebergs, both methods would probably work well.

In this study, we focus on using detected vessel noise to approximate the above-water component of disturbances. However, future research should also focus on the possible impact of underwater noise on seabirds, which is already a recognized conservation issue for marine mammals (Richardson et al. 1995, Nowacek et al. 2007). Recent studies indicate that underwater noise can affect foraging activity in common murres and cause them to deter from an area (Hansen et al. 2020). Both responses will have energetic consequences for a seabird, and such effects should therefore be included when assessing population consequences of anthropogenic stressors.

**Conclusion**

Marine traffic represents a massive source of noise pollution in the marine environment (e.g. Slabbekoorn et al. 2010). With the expected increase of human activity in the Arctic (Moore et al. 2012), it is important to assess how these activities may affect seabirds, which is one of the most threatened groups of birds worldwide (Croxall et al. 2012, Dias et al. 2019). Since seabirds breed at land but dive to forage, both airborne and waterborne noise may affect their behavior. Here we show that current vessel monitoring systems may cause severe underestimations of actual human exposure, as we found that only 4% of vessels travelling in an area with two murre colonies were tracked by AIS or VMS, with none of these being smaller boats that often move unpredictably and erratically. Erratic vessel movements may elicit negative responses in breeding colonies, in particular if these events are associated with hunting events. We compared two murre colonies and found that the murre colony with a declining population, also was the colony with the highest vessel density and more events with erratic engine noise close to the colony. We conclude that underwater noise recording is a simple and relatively cheap method to quantify human activities around seabird colonies, which is an important input for population consequence models.

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**REFERENCES**

Beale, C. M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology **41**:335-343.

Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series **395**:177-185.

Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour **72**:1149-1158.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Krutzen. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology **20**:1791-1798.

Carney, K. M., and W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds **22**:68-79.

Chardine, J. W., and V. Mendenhall. 1998. Human disturbance at Arctic seabird colonies. CAFF Technical Report No. 1, Circumpolar Seabird Working Group (CSWG), Conservation of Arctic Flora and Fauna (CAFF), CAFF International Secretariat, Akureyri, Iceland.

Christensen, T., F. Lasserre, J. Dawson, E. Guy, and J.-F. Pelletier. 2018. Shipping. Pages 243-260 *in* A. Mosbech, M. Lemay, M. Simon, F. Merkel, T. Christensen, R. B. Jacobsen, P. Egede, and K. Falk, editors. Adaptation Actions for a Changing Arctic: Perspectives from the Baffin Bay/Davis Strait Region. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Coulson, J. C. 2002. Colonial breeding in seabirds. Pages 87-109 *in* E. A. Schreiber and J. Burger, editors. Biology of Marine Birds. CRC Press, New York, USA.

Croxall, J. P., S. H. M. Butchart, B. E. N. Lascelles, A. J. Stattersfield, B. E. N. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International **22**:1-34.

Davenport, J., and J. L. Davenport. 2006. The impact of tourism and personal leisure transport on coastal environments: A review. Estuarine, Coastal and Shelf Science **67**:280-292.

Descamps, S., H. Strøm, and H. Steen. 2013. Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre. Oecologia **173**:1271-1282.

Dias, M. P., R. Martin, E. J. Pearmain, I. J. Burfield, C. Small, R. A. Phillips, O. Yates, B. Lascelles, P. G. Borboroglu, and J. P. Croxall. 2019. Threats to seabirds: A global assessment. Biological Conservation **237**:525-537.

Egevang, C. 2008. Forstyrrelser i grønlandske havfuglekolonier. Technical Report no. 71, Pinngortitaleriffik, Greenland Institute of Natural Resources, Nuuk.

Ellenberg, U., T. Mattern, and P. J. Seddon. 2009. Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. Animal Behaviour **77**:289-296.

Frederiksen, M., J. F. Linnebjerg, F. R. Merkel, S. I. Wilhelm, and G. J. Robertson. 2019. Quantifying the relative impact of hunting and oiling on Brunnich's guillemots in the North-west Atlantic. Polar Research **38**:ARTN 3378.

Gaston, A. J., and J. M. Hipfner. 2020. Thick-billed Murre (*Uria lomvia*).*in* S. M. Billerman, editor. Birds of the World, Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.thbmur.01.

Hansen, K. A., A. Hernandez, T. A. Mooney, M. H. Rasmussen, K. Sorensen, and M. Wahlberg. 2020. The common murre (Uria aalge), an auk seabird, reacts to underwater sound. Journal of the Acoustical Society of America **147**:4069.

Hermannsen, L., L. Mikkelsen, J. Tougaard, K. Beedholm, M. Johnson, and P. T. Madsen. 2019. Recreational vessels without Automatic Identification System (AIS) dominate anthropogenic noise contributions to a shallow water soundscape. Scientific Reports **9**:15477.

Huffeldt, N. P., and F. R. Merkel. 2016. Sex-specific, inverted rhythms of breeding-site attendance in an Arctic seabird. Biology letters **12**:20160289.

ICOMIA. 2015. Recreational Boating Industry Statistics 2015. Report by the International Council of Marine Industry Associations, United Kingdom.

IMO. 1998. Guidelines for the control and management of ship's ballast water to minimize the transfer of harmful aquatic organisms and pathogens. International Maritime Organization.

Labansen, A., F. R. Merkel, and A. Mosbech. 2021. Reactions of a colonial seabird species to controlled gunshot disturbance experiments. Wildlife Biology:wlb.00752.

Larsen, O. N., M. Wahlberg, and J. Christensen-Dalsgaard. 2020. Amphibious hearing in a diving bird, the great cormorant (Phalacrocorax carbo sinensis). Journal Of Experimental Biology **223**:10.1242/jeb.217265.

Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling. Pages 105-125 *in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Oxford University Press, Oxford.

Linnebjerg, J. F., A. Reuleaux, K. N. Mouritsen, and M. Frederiksen. 2015. Foraging Ecology of Three Sympatric Breeding Alcids in a Declining Colony in Southwest Greenland. Waterbirds **38**:143-152.

Mallory, M., H. G. Gilchrist, M. Janssen, H. L. Major, F. R. Merkel, J. F. Provencher, and H. Strøm. 2018. Financial costs of conducting science in the Arctic: examples from seabird research. Arctic Science **4**:624-633.

Merkel, F., A. L. Labansen, D. Boertmann, A. Mosbech, C. Egevang, K. Falk, J. F. Linnebjerg, M. Frederiksen, and K. Kampp. 2014. Declining trends in the majority of Greenland's Thick-billed Murre (*Uria lomvia*) colonies 1981-2011. Polar Biology **37**:1061-1071.

Merkel, F. R., and T. Barry. 2008. Seabird harvest in the Arctic. CAFF Technical Report No. 16, Circumpolar Seabird Working Group (CSWG), Conservation of Arctic Flora and Fauna (CAFF), CAFF International Secretariat, Akureyri, Iceland. http://www.caff.is.

Merkel, F. R., A. S. Frich, and P. Hangaard. 1999. Polarlomvien i Disko Bugt og det sydlige Upernavik, 1998. Bestandsopgørelse og grundlag for fremtidig monitering af lomviebestandene. Technical Report No. 25, Pinngortitaleriffik, Greenland Institute of Natural Resources, Nuuk.

Merkel, F. R., and J. E. Tremblay. 2018. Living resources. Pages 133-199 *in* A. Mosbech, M. Lemay, M. Simon, F. Merkel, T. Christensen, R. B. Jacobsen, P. Egede, and K. Falk, editors. Adaptation Actions for a Changing Arctic: Perspectives from the Baffin Bay/Davis Strait Region. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Mooney, T. A., A. Smith, K. A. Hansen, O. N. Larsen, M. Wahlberg, and M. Rasmussen. 2019. Birds of a feather: Hearing and potential noise impacts in puffins (Fratercula arctica). Proceedings of Meetings on Acoustics **37**:010004.

Moore, S. E., R. R. Reeves, B. L. Southall, T. J. Ragen, R. S. Suydam, and C. W. Clark. 2012. A New Framework for Assessing the Effects of Anthropogenic Sound on Marine Mammals in a Rapidly Changing Arctic. Bioscience **62**:289-295.

Nowacek, D. P., L. H. Thorne, D. W. Johnston, and P. L. Tyack. 2007. Responses of cetaceans to anthropogenic noise. Mammal Review **37**:81-115.

Nowacek, D. P., and R. S. Wells. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science **17**:673-688.

PAME. 2009. Arctic Marine Shipping Assessment 2009 Report. Akureyri, Iceland., Arctic Council (PAME), April 2009, second printing.

PAME. 2020. The increase in Arctic shipping 2013-2019. Arctic Shipping Status Report (ASSR) #1. Arctic Council (PAME), March 2020. Akureyri, Iceland. 25 pp. https://www.pame.is/document-library/shipping-documents/arctic-ship-traffic-data-documents/reports/752-arctic-shipping-report-1-the-increase-in-arctic-shipping-2013-2019-pdf-version-1/file.

Richardson, W. J., C. R. Greene, Jr., C. I. Malme, and D. H. Thomson. 1995. Marine mammals and noise. Academic Press, San Diego, US.

Robards, M. D., G. K. Silber, J. D. Adams, J. Arroyo, D. Lorenzini, K. Schwehr, and J. Amos. 2016. Conservation science and policy applications of the marine vessel Automatic Identification System (AIS)—a review. Bulletin of Marine Science **92**:75-103.

Rojek, N. A., M. W. Parker, H. R. Carter, and G. J. Mcchesney. 2007. Aircraft and vessel disturbances to Common Murres Uria aalge at breeding colonies in central California, 1997–1999. Marine Ornithology **35**:61-69.

Schauer, J. H. S., and E. C. Murphy. 1996. Predation on eggs and nestlings of common murres (*Uria aalge*) at Bluff, Alaska. Colonial Waterbirds **19**:186-198.

Simard, P., K. R. Wall, D. A. Mann, C. C. Wall, and C. D. Stallings. 2016. Quantification of Boat Visitation Rates at Artificial and Natural Reefs in the Eastern Gulf of Mexico Using Acoustic Recorders. Plos One **11**:e0160695.

Simpson, S. D., A. N. Radford, S. L. Nedelec, M. C. Ferrari, D. P. Chivers, M. I. McCormick, and M. G. Meekan. 2016. Anthropogenic noise increases fish mortality by predation. Nature Communications **7**:10544.

Slabbekoorn, H., N. Bouton, I. van Opzeeland, A. Coers, C. ten Cate, and A. N. Popper. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends in Ecology and Evolution **25**:419-427.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.

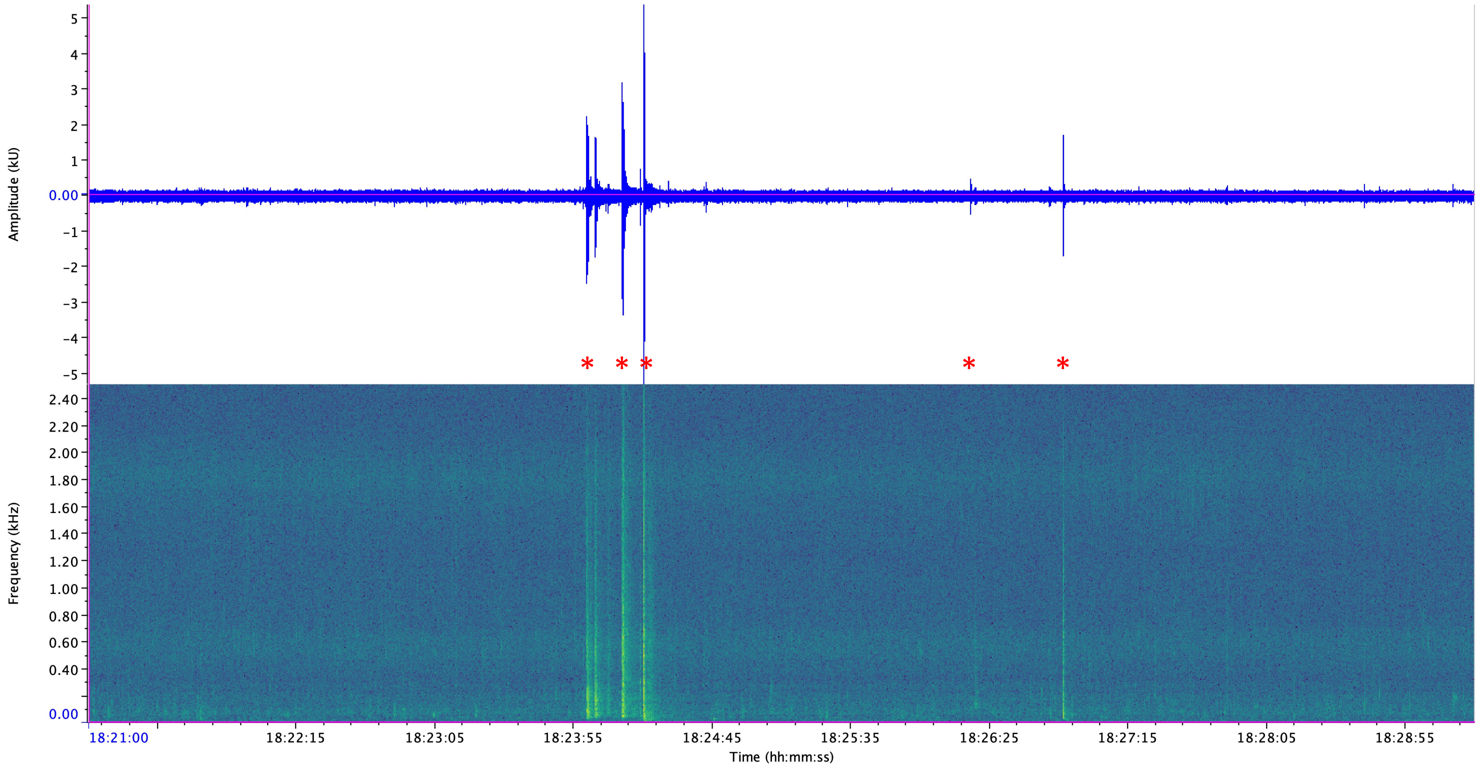
Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc Biol Sci **272**:2627-2634.

UNCTAD. 2020. Handbook of statistics 2020. United Nations Conference on Trade and Development, United Nations, Geneva. https://unctad.org/HandbookOfStatistics.

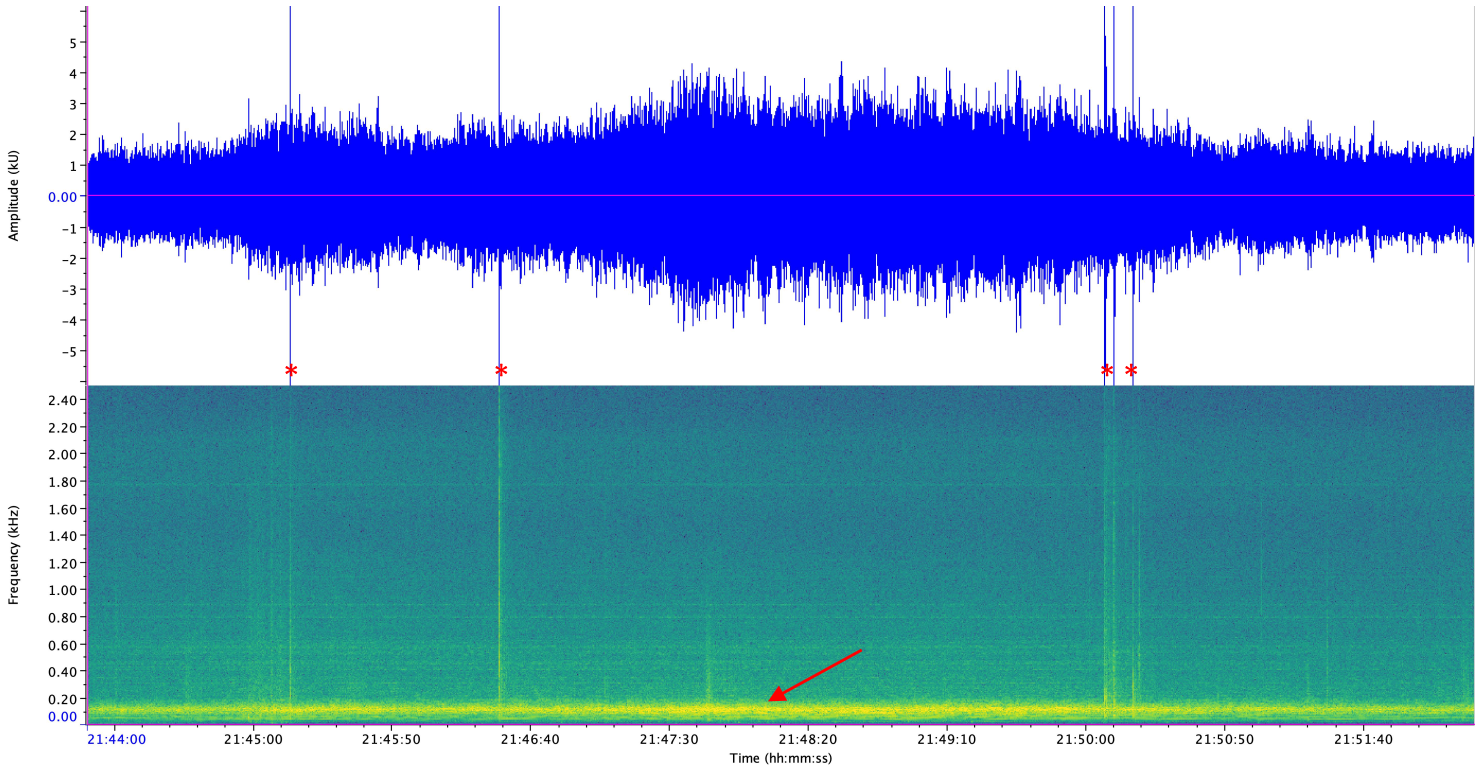
Villanueva, C., B. G. Walker, and M. Bertellotti. 2012. A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic Penguins (Spheniscus magellanicus) at two colonies in Argentina. Journal of Ornithology **153**:219-228.

Wiese, F. K., G. J. Robertson, and A. J. Gaston. 2004. Impacts of chronic marine oil pollution and the murre hunt in Newfoundland on thick-billed murre *Uria lomvia* populations in the eastern Canadian Arctic. Biological Conservation **116**:205-216.

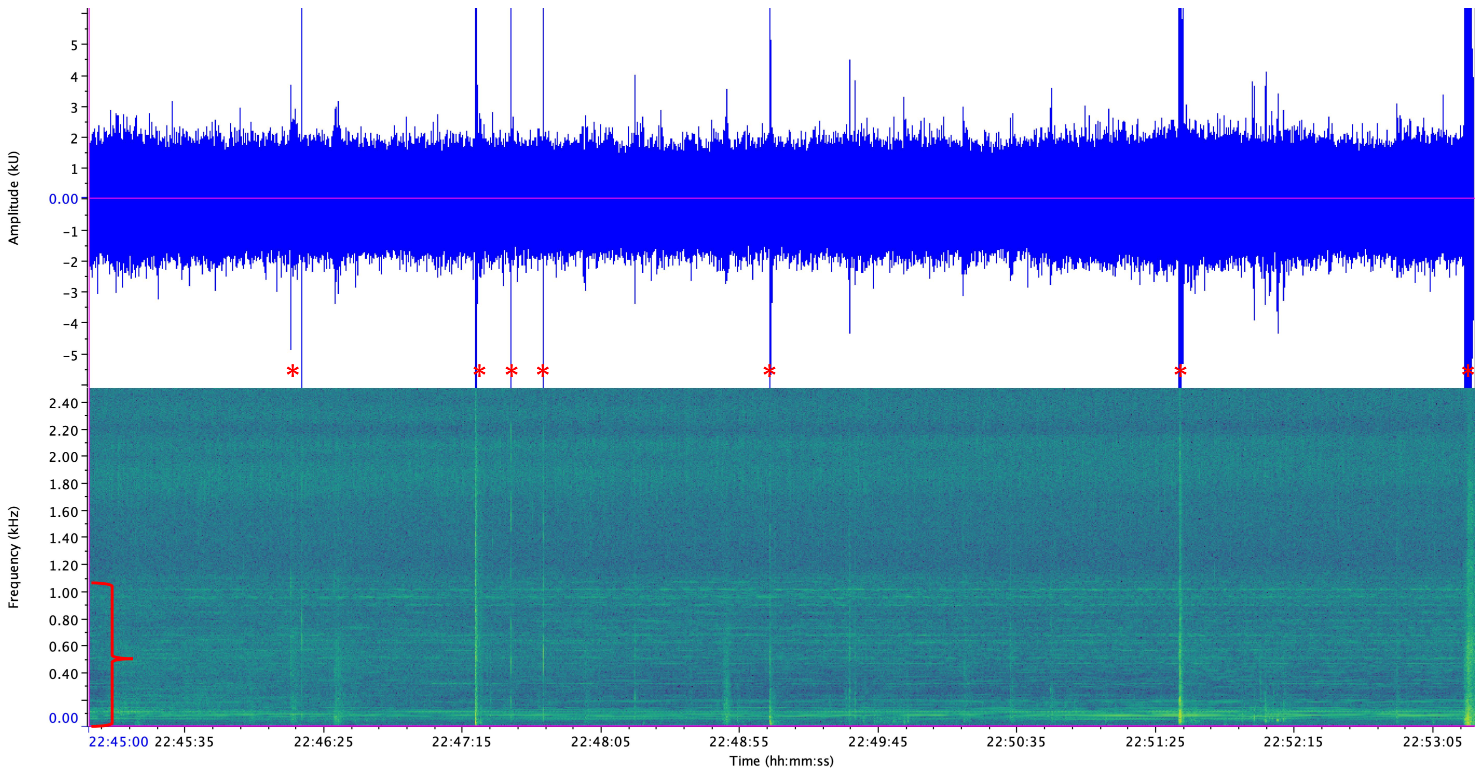
Williams, R., D. E. Bain, J. Ford, and A. W. Trites. 2002. Behavioural responses of male killer whales to a 'leapfrogging' vessel. Journal of Cetacean Research and Management **4**:305-310.



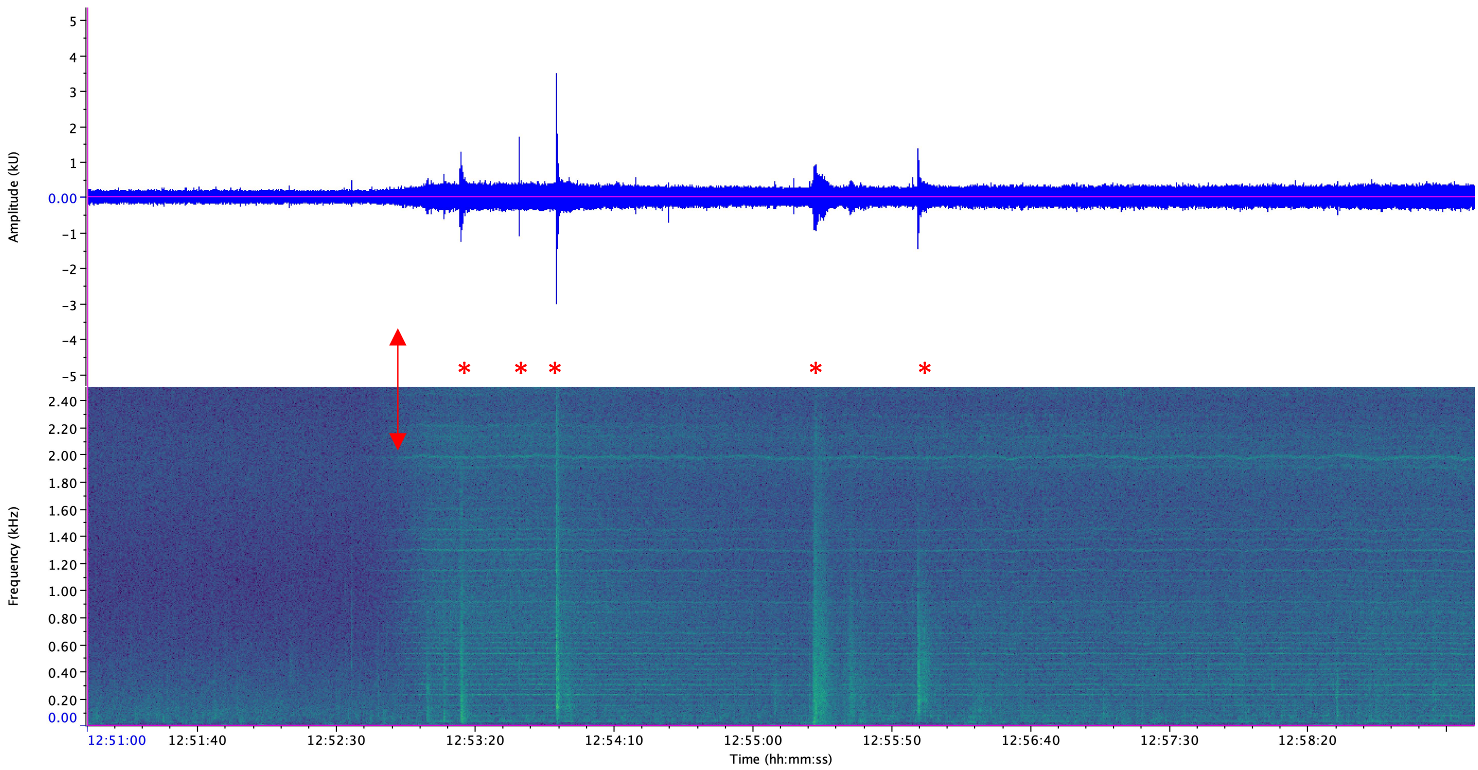

**Supp. fig. 1**. Power amplitude and spectrogram of acoustic underwater recordings of a 8 minute period with **no vessel activity**. Vertical spikes of noise, marked with *, represent cracks from icebergs.



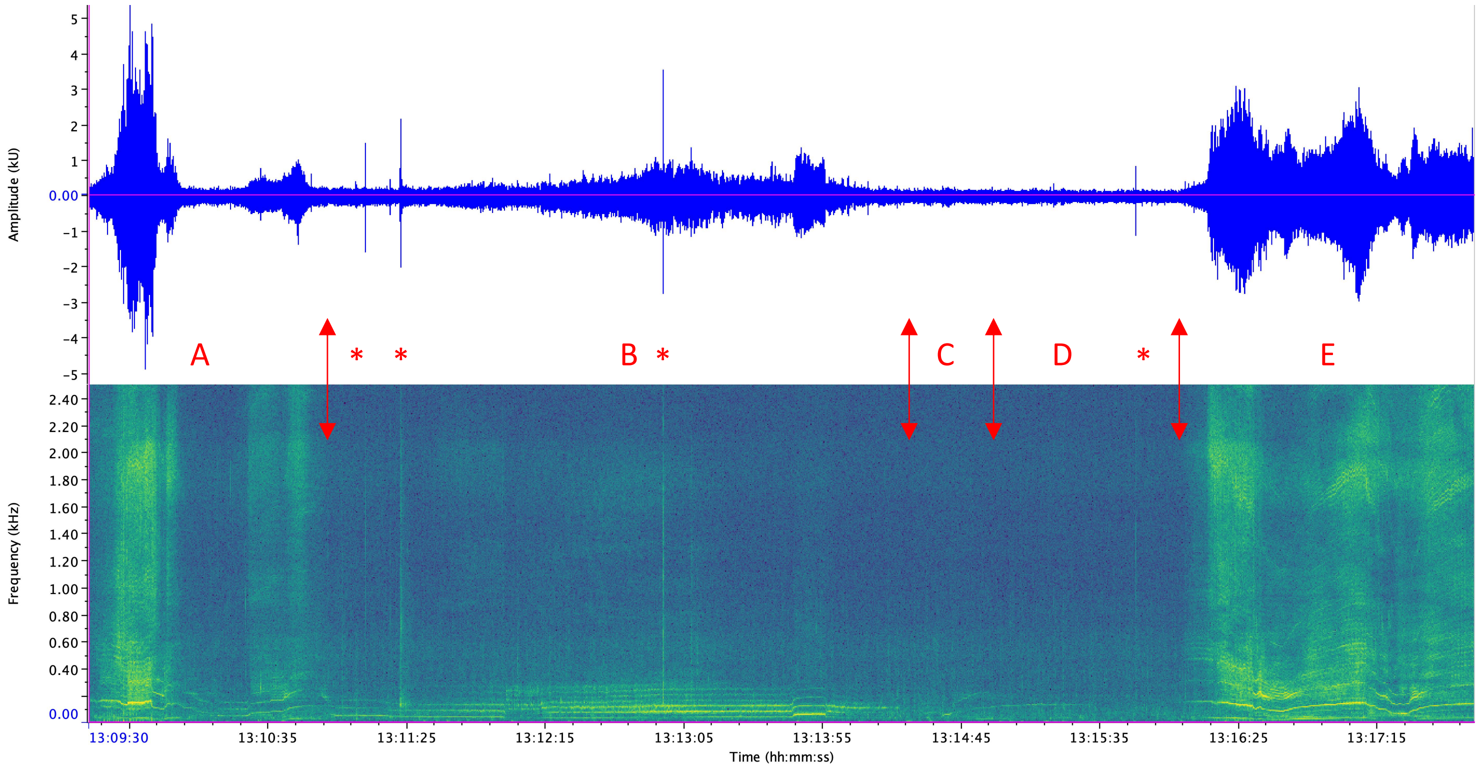

**Supp. fig. 2**. Power amplitude and spectrogram of acoustic underwater recordings for a 8 minute period, showing a **cargo vessel** passing vest of the colonies (distance unknown). Note the distinctive horizontal noise band below 0.2 kHz on the spectrogram (see arrow), which is characteristic for large vessels. Vertical spikes of noise, marked with *, represent cracks from icebergs.



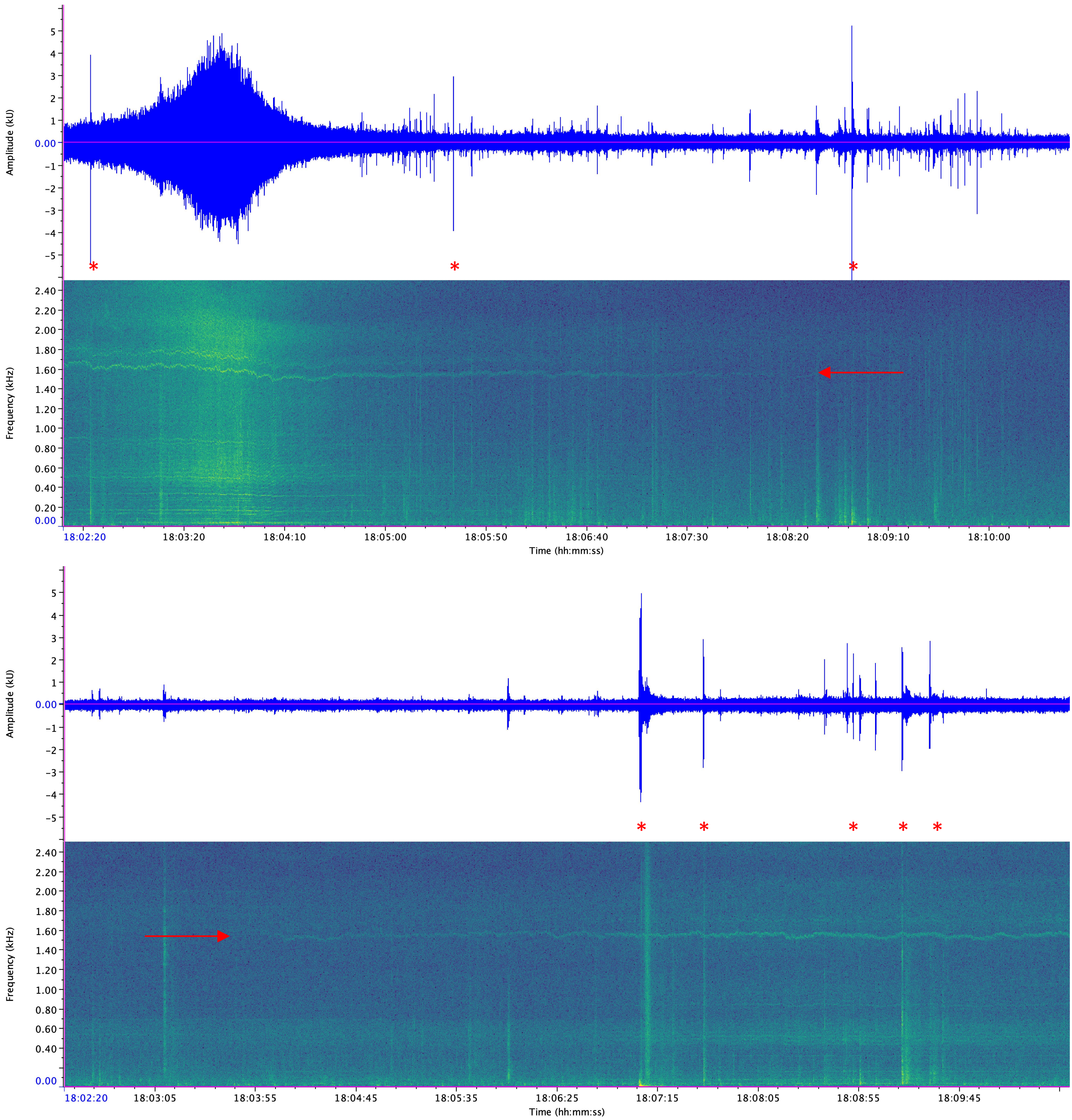

**Supp. fig. 3**. Power amplitude and spectrogram of acoustic underwater recordings for a 8 minute period, showing a **fishing vessel** passing the Kippaku recorder at a distance of 3 km. Note that most of the noise is visible as multiple horizontal bands below 1.0 kHz on the spectrogram (indicated by the brace), which is characteristic for slow moving fishing vessels. Vertical spikes of noise, marked with *, represent cracks from icebergs (tiny cracks not marked).




**Supp. fig. 4**. Power amplitude and spectrogram of acoustic underwater recordings for a 8 minute period, showing a **fast moving vessel** passing the Apparsuit recorder at a distance of approximate 6 km. Vessel noise is shielded by landmasses in the first 2 minutes (up until the red arrow). Hereafter vessel noise is visible as numerous horizontal bands over the entire frequency scale. Vertical spikes of noise, marked with *, represent cracks from icebergs.




**Supp. fig. 5**. Power amplitude and spectrogram of acoustic underwater recordings of a **small vessel** making erratic boating behavior close (< 1 km) close to the Kippaku colony over a period of 8 minutes. Red letters/arrows in figure indicate periods with **A**) high speed, briefly interrupted by slow speed, **B**) a longer period of slow speed, **C**) engine stop and start, and **D**) vessel noise partly of fully shielded behind island, **E**) vessel coming back at high speed and then briefly interrupted twice by low speed. Asterisks * indicate a crack from an iceberg.




**Supp. fig. 6**. Power amplitude and spectrogram of acoustic underwater recordings for a 8 minute period, showing a **research vessel** (Sanna) passing first the Apparsuit recorder at a distance of 100 m (top figure) and shortly afterwards visible on the Kippaku recorder at a distance of 8 km (lower figure). The characteristic noise band around 1.6 kHz (see arrows) makes it easy to see that it is the same vessel on both figures. The gradual but rather quick disappearance on the Apparsuit recorder is due to shielding from seabed topography. Vertical spikes of noise, marked with *, represent sudden resounding cracks from icebergs (tiny cracks not marked).

# Paper III

**Labansen AL** & Merkel FR. Local Ecological Knowledge about a traditional game bird in Greenland.

Manuscript planned for submission to *Arctic*.


Nuussuaq, February 2018

## LOCAL ECOLOGICAL KNOWLEDGE ABOUT A TRADITIONAL GAME BIRD IN GREENLAND

*Aili Lage Labansen[1,2] and Flemming Merkel[1,2],*

[1] Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland

[2] Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark.

Keywords: local knowledge, sustainable hunting, thick-billed murre, *Uria lomvia*, Greenland

**ABSTRACT**

The thick-billed murre (*Uria lomvia*) is a culturally important seabird species in Greenland and is declining in most areas of Greenland. Scientific studies indicate that at least some of the decline can be linked to drivers in the wintering areas, whereas the role of local breeding conditions is largely unknown. In this study, we collected Local Ecological Knowledge (LEK) about murres in Southwest- (2016, 24 informants) and Northwest Greenland (2018, 24 informants), where locals are holders of valuable information about the areas they move in and the resources they use. We focused on their knowledge about local breeding populations, various aspects of human use of the areas and their view on murre management in West Greenland. The interviews had a semi-structured approach with a series of up to 54 predetermined questions. The survey showed that helicopters, marine traffic, and landslides locally are of concern particularly in Northwest Greenland, while the level of hunting, egging, and disturbances at colonies today generally is considered small and less concerning. In Northwest Greenland some questioned the reasoning behind the regional differences in murre management in West Greenland. Although most considered regulations necessary, many had suggestions to changes. Southwest informants reported that murres nowadays often are farther from the coast during winter. The dissemination level from authorities appears deficient as many seemed uninformed of murre monitoring results and unaware of the biological reasoning behind the management regulations. This study presents valuable perspectives that can be used to direct research and inform management of a valued resource.

**Keywords:** Local Ecological Knowledge, LEK, subsistence hunting, seabird colonies, Arctic, Greenland, *Uria lomvia*, human disturbance, population declines, harvest management

**INTRODUCTION**

Several of the often highly abundant seabird species of the Arctic has been important seasonal resources for Arctic peoples since prehistoric times (Gotfredsen 1997, Gaston et al. 2012). Unlike several other living resources in Greenland today, seabirds are not of substantial commercial importance, but contributes significantly to subsistence and the informal economy that hunting, and country foods in general, constitutes in Greenland (Rasmussen 2005). Traditional foods also have a significant cultural importance (Sowa 2015), and seabirds provides a tasty and welcoming break from the more common year-round available country foods like seal and fish (Pars et al. 2001). Particularly, the numerous and widely distributed thick-billed murre (*Uria lomvia*, hereafter "murre"), which reaches most inhabited areas of Greenland at least at some time period during the year, has been and still is of high countrywide importance (Fabricius 1780, Piniarneq 2019). For some families it is a significant contribution to the household, for others it is more a delicate highlight of the season, served at special occasions (Haastrup 2017).

During the 20th century, the growing number of people combined with firearms becoming more and more common, increasingly faster and larger boats, commercialization of the hunt, and huge bycatches in commercial salmon fisheries, took its toll on the Greenland breeding population of murre (Tull et al. 1972, Falk and Durinck 1992, Kampp et al. 1994). With some delay, legislation with increasingly larger restrictions to mitigate harmful effects were introduced, but with no apparent positive response in the declining colonies, resulting in continued population declines and depleted colonies (Falk and Durinck 1992, Kampp et al. 1994, Merkel et al. 2014). The most pronounced restriction introduced in recent time was when the hunting period after 2001 was restricted to the fall and wintertime in most of Greenland, banning the springtime hunting (Anon 2001). This was considered a breakthrough for a sustainable use of this resource, because the spring hunt was targeting local breeding birds thus taxing heavily on the local breeding populations (Kampp et al. 1994, Falk and Kampp 2002). However, despite the intended and significantly reduced hunting level the following two decades, the breeding population of murre in most Greenland colonies have continued to decline (Merkel et al. 2014).

According to the scientific knowledge, the main drivers currently identified to impact murre population development in the North Atlantic all occur during the non-breeding season and include factors as oceanographic changes, hunting and oil pollution in the wintering area (Descamps et al. 2013, Frederiksen et al. 2019). However, these drivers may not represent the full picture for Greenland. Contrasting population trends have been observed among closely situated colonies, with shared wintering areas, which indicates that local factors in the breeding season also may play a role for the observed population development (Merkel et al. 2014).

Local Ecological Knowledge (LEK), also known as Traditional Ecological Knowledge, is recognized as being able to provide valuable contributions to various fields of science (Huntington 2000, Gilchrist et al. 2005, Born et al. 2011, Laidre et al. 2018). Unlike researchers, who are only present at the colonies in a short period during the chick rearing period, local hunters are spatially more widely present in the areas during longer periods of the seasons and thus, holders of valuable information about local conditions and murres of the area (ibid.).

Here, we present the results of an interview survey collecting LEK about murres in Southwest Greenland in 2016 and Northwest Greenland in 2018. The study is focused on knowledge on local breeding populations, various aspects of human use and management perspectives for murres. The purpose was to make LEK available as a contributing source of information about local factors affecting population trends in Greenland and as a possible tool to improve the current management of murres in Greenland.

## METHODS

### Study area (people, colonies, and hunting periods)

*Northwest region:*

The Upernavik district in Northwest Greenland consist of 10 communities: Upernavik town and 9 settlements (Figure 1). Today there is two relatively large murre colonies in northern Upernavik, *Apparsuit* and *Kippaku*, and two smaller colonies south of Upernavik town, *Kingittoq* and *Timmiakkulussuit* (Table 1, Figure 1). Besides, there are four extinct colonies of the region, which went extinct in the late 1990s or early 2000s. The most noteworthy is *Upernaviup Apparsui*, just south of Upernavik town, which until the 1980s was the largest of the southern Upernavik colonies. In 2018 we visited the two northernmost settlements, Kullorsuaq (Feb 3-6) and Nuussuaq (Feb 7 and 8), and Upernavik town (Feb 10-14) in the southern end of the district (Table 1, Figure 1).

The hunting period has historically mainly been the spring and summer time in the Upernavik district (Evans 1987). Since 2002, the legal hunting period was from September 1 to the end of February, in reality ending in early November, when the last murres leave the area for the winter. In 2017, the year before this study, the open period was changed to last from September 15 to November 15, and a month of spring hunt from April 15 was reintroduced.

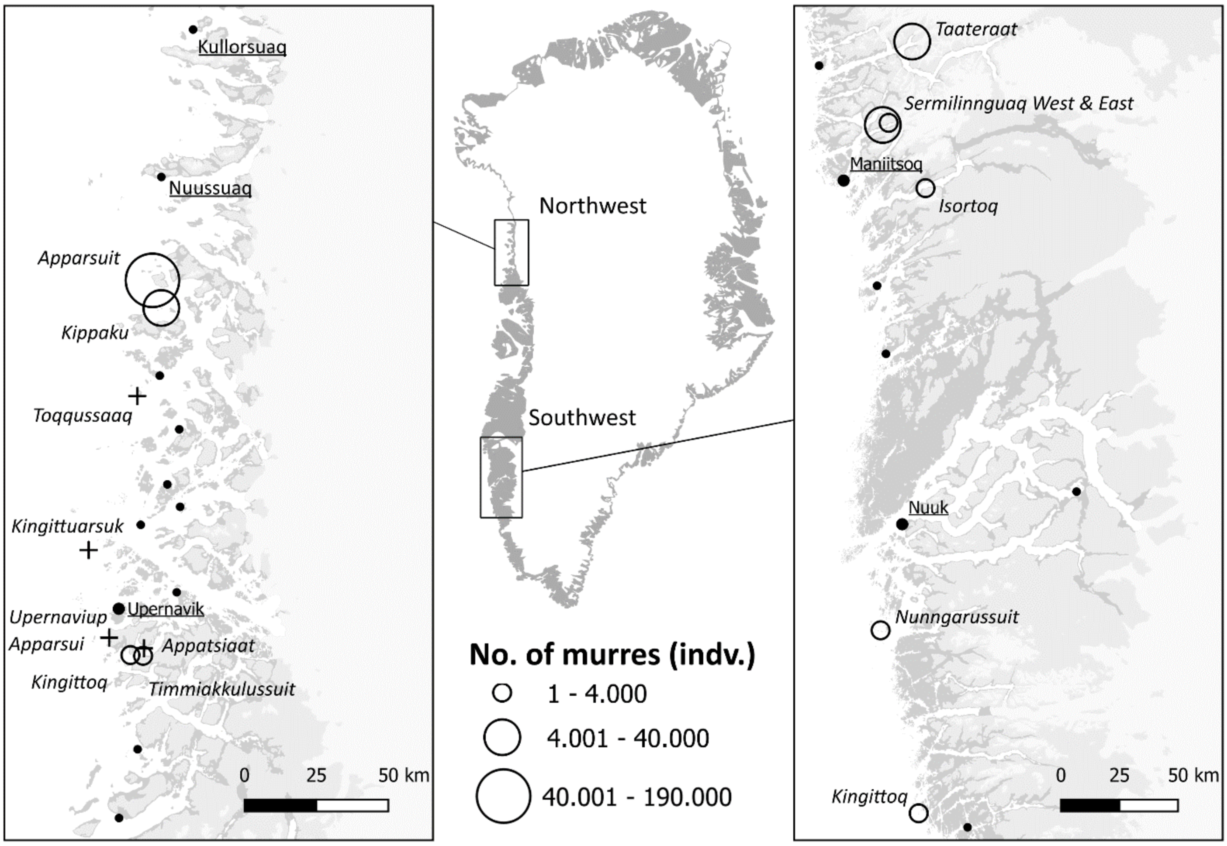



**Figure 1.** Map of Greenland showing the two regions where interview surveys were conducted. All communities (black dots) of the Upernavik and Maniitsoq/Nuuk area are shown, but only communities where interviews were carried out, are named. Location and size of thick-billed murre breeding colonies of the regions are shown, based on the most recent surveys (2014-2017, Greenland Institute of Natural Resources, unpubl.). Colonies that went extinct (+) since the 1990s are also shown.

*Southwest region:*

The Maniitsoq area is the most important murre breeding area south of Upernavik and is also located within the murre winter quarters of Southwest Greenland (Boertmann et al. 2004, Merkel et al. 2014). Thus, murres are present both within and outside the breeding season. Apart from Maniitsoq town there are three settlements within reasonable boating distance to at least one of the 4 colonies of the area, which are situated within three fjords. *Sermilinnguaq West* and *East* are nearest to Maniitsoq, then *Isortoq* and last *Taateraat* furthest away (Table 1, Figure 1).

The Nuuk area about 150 km south of Maniitsoq is a murre hotspot within the Southwest Greenland wintering quarters (Boertmann et al. 2004) and Nuuk is the largest town in Greenland. Hence, it is where the largest market is for murres sold at the local *Kalaalimineerniarfik* – an open market where fresh catches from hunters and fishers are sold (Pars et al. 2001), and it is also where the largest numbers of murres are hunted annually (Piniarneq 2019). However, there is only two minor colonies in the area; *Nunngarussuit* 50 km and *Kingittoq* 135 km south of Nuuk (Table 1, Figure 1), the latter registered for the first time in 2010. The Nuuk area has never been an important breeding area for murres, and they are rare from late spring and all summer. We spend 3 and 4 days respectively on interviews in Nuuk and Maniitsoq, in March 2016.

**Table 1:** Communities visited with number of inhabitants at the time of the interview survey and the nearby murre colonies. Colony size (number of murres), year of the census and the trend of each colony (arrow) is shown and is based on monitoring surveys conducted by the Greenland institute of Natural Resources (Merkel at al. 2014; GINR, unpublished). Extinct colonies are marked with an "x" and year of census is when the colonies were first registered as completely empty. Colonies within each region are sorted according to decreasing proximity to nearby communities (note that both Kullorsuaq and Nuussuaq are situated north of the Northern Upernavik colonies).

| Region | Inhabitants | Colonies in region | Colony size | Year of census | Colony trend |
|---|---|---|---|---|---|
| **Northwest (Feb 2018):** | | | | | |
| **Northern Upernavik** | | *Apparsuit* | 50,500 | 2017 | ↓ |
| **-Kullorsuaq** | 436 | *Kippaku* | 21,400 | 2017 | ↑ |
| **-Nuussuaq** | 186 | *Toqqussaaq* | 0 | 2008 | X |
| **Upernavik town** | 1,067 | *Upernaviup Apparsui* | 0 | 2003 | X |
| | | *Kingittoq* | 2,450 | 2017 | ↓ |
| | | *Timmiakkulussuit* | 890 | 2017 | ↑ |
| | | *Appatsiaat* | 0 | 2007 | X |
| | | *Kingittuarsuk* | 0 | 1998 | X |
| **Southwest (Mar 2016):** | | | | | |
| **Maniitsoq** | 2,567 | *Sermilinnguaq West* | 4,600 | 2017 | ↓ |
| | | *Sermilinnguaq East* | 2,900 | 2017 | ↓ |
| | | *Isortoq* | 1,050 | 2017 | ↓ |
| | | *Taateraat* | 6,700 | 2017 | ↓ |
| **Nuuk** | 17,316 | *Nunngarussuit* | 892 | 2016 | ↓ |
| | | *Kingittoq* | 390 | 2011 | - |

Open hunting period at the time of the interviews: Sep 15 - Nov 15 and Apr 15 - May 15 (Northwest region); Oct 15 - Feb 29 (Southwest region).

Historically the hunting has primarily taken place from October to March in Southwest Greenland (Falk and Durinck 1992). At the time of the interviews, the hunting period was October 15 to the last day of February.

**Preparation and selection of informants**

The interview surveys were advertised prior to our arrival via announcements in the national broadcast radio, posters around the communities, usually with the help of the local KNAPK (association of fishers and hunters in Greenland) representative, and via social media (Facebook). The target group was people with knowledge on murre colonies and/or the murre as a hunting object, including occupational as well as recreational hunters. Hunters in Greenland are registered as either recreational or occupational hunters. Occupational hunters have larger quotas and access to more species than recreational hunters and to earn the rights of an occupational hunting license a minimum of 50% of the income needs to come from hunting or from coastal fisheries.

Informants were often recruited via so called "gate openers" - local key persons, often found via KNAPK, who would put us in contact with others they found relevant. Also, we usually ended each interview by asking for others who were likely to be relevant for the survey, a sampling system often termed chain referral or snowball sampling (Bernard 2011). The visits to the Northwest communities were combined with public meetings with a presentation about murre research and monitoring of the respective areas, where people were encouraged, and some were recruited, to participate in the interview survey. In addition, some informants were recruited by asking around at the local *Kalaalimineerniarfik* (market), the main grocery store or at community facilities.

**Form and contents of interviews**

The semi-structured interviews (Bernard 2011) consisted of a set of up to 54 predetermined questions with minor differences between the Southwest and the Northwest region. Participation was fully voluntary. The informants were interviewed one at a time, except at two occasions when two were interviewed together. We were four people involved in the interview process usually working two and two (Ulunnguaq N. Lyberth (UNL), Sascha Schiøtt, Emma Kristensen and author ALL). All but ALL, who has limited Greenlandic skills, were fluent in West Greenlandic and Danish. The interviews were carried out at a KNAPKs office, the living room of our accommodation, or at communal facilities (community center, or the like). A few were interviewed in their own home.

Apart from taking notes on a printed questionnaire and a map of the local area, each interview was recorded with consent from the informants. All participants were promised anonymity and we obtained their consent to use their anonymized information in various types of publication. The questions were structured with a section of hunting related questions, a section with focus on local breeding colonies and nearby areas, and finally a section about management related issues.

**Analysis of the data**

The essence of all answers was typed into a data matrix by UNL (in Danish), while listening to the recorded interviews. Not all informants had answers to all questions and some results are given for a subset of informants, in which case the sample size is stated for the given question. In case of unclear answers these were excluded from the results. When relevant, responses that were given in free form, were categorized manually into meaningful reoccurring categories, such as “motorboats” or “feeding conditions”, and “more”, “less” or “don’t know”.

Data on community resident numbers at the time of the interviews were retrieved from Statbank Greenland (www.stat.gl) and hunting statistics from *Piniarneq*, a database where licensed hunters are required to report their annual catches (1993-2018, PILU/Piniarneq database, December 2019). Seabird breeding colonies and results from historical as well as recent surveys of breeding seabirds in Greenland are registered in the Greenland Seabird Colony Register (Boertmann et al. 1996, Bakken et al. 2006).

## RESULTS

In total we interviewed 78 informants: 75 men and 3 women (Table 2). The duration of the interviews varied from about 18 min to 1 h 40 min and averaged 48 min (sd = 20 min). Age of the informants ranged from 29 to 81 years of age and the median age was 58 years (mean = 56.2, sd = 10.4, n = 78). The largest age group was the 50-60 years old (44%, n = 34) seconded by the 60-70 years old (28%, n = 22). A minimum of 85% (n =66) had been hunting since childhood or from a young age (17 years or younger). More than half (n = 42) had previously lived somewhere else, however mostly for shorter periods. Two informants had moved to the current location four years earlier, but the remaining had lived there for a minimum of 15 years.

**Table 2:** Number of informants during an interview survey on thick-billed murre in February 2018 (Northwest Greenland) and March 2016 (Southwest Greenland).

| **Region** | **NW Greenland (54)** | | | **SW Greenland (24)** | | |
|---|---|---|---|---|---|---|
| **Community** | **Kullorsuaq** | **Nuussuaq** | **Upernavik** | **Maniitsoq** | **Nuuk** | **Total** |
| **License type:** | | | | | | |
| **-Occupational** | 15 | 5 | 11 | 14 | 6 | **51** |
| **-Recreational** | 2 | 3 | 15 | 4 | 0 | **24** |
| **-None/retired** | | | 3 | | | **3** |
| **Total** | **17** | **8** | **29** | **18** | **6** | **78** |

**Colonies**

*Knowledge of nearby colonies*

All participants in two northern communities of the Northwest region knew of the two northern and nearby colonies (*Apparsuit* and *Kippaku*). In Upernavik town 93% of the 29 informants knew of at least the nearest of the two existing colonies (*Kingittoq*) and, except from two, also of the second colony (*Timmiakkulussuit*). The nearest extinct colony (*Upernaviup Apparsui*) was mentioned by 66% (n = 19) and 28% (n = 8) mentioned the other extinct colony (*Appatsiaat*). At least 59% of the 29 Upernavik informants also mentioned one or both northern colonies (*Apparsuit* and *Kippaku*). The two extinct colonies (*Toqqusaaq* and *Kingittuarsuk*) situated between the northern settlements and Upernavik town were mentioned by 11% and 13% respectively of the 54 Northwest region informants, the latter only by Upernavik town informants. Five mentioned locations that are not registered as murre colonies in the Greenland Seabird Colony Register, of which one location (*Iperaq*) was mentioned twice.

Within the Southwest region, all informants from Maniitsoq (n = 18) knew of murre breeding in the Isortoq fjord just south of Maniitsoq and all, but one, knew of colonies in the Sermilinnguaq fjord just north of Maniitsoq town. The most distant colony (*Taateraat*), 100 km north of Maniitsoq, was mentioned by 33% (n = 6). About 61% (n = 11) marked off more murre colony locations than registered in the Greenland Seabird Colony Register. Three of the six informants from Nuuk could tell the whereabouts of the small colony south of Nuuk (*Nunngarussuit*). Two more knew of a small colony in the area, but were not able point it out or tell the name of the place. Two mentioned the small and relatively new colony further south (*Kingittoq*), however, one of them only knew it as a colony of razorbill (*Alca torda*). The other, confirmed that *Kingittoq* is a new murre colony.

*Observed recent changes and causes of change*

A total of 72 responded to the question if they had experienced population change in nearby colonies within the last 10-15 years (Table 3). Generally, for all areas, more answered “yes” (56-70%) than “no” and “don’t know” (Table 3). All but one of 9 Kullorsuaq and 5 Nuussuaq informants had experienced declines or a mix of decline (*Apparsuit*) and increase (*Kippaku*). In contrast, the majority in Upernavik (11 of 19) experienced increases. Two of these mentioned only the smaller colony furthest away (*Timmiakkulussuit*) in this context and the remaining nine mentioned the nearest and largest *Kingittoq* specifically. Among these, three said that *Kingittoq* started to increase when *Upernaviup Apparsui* went extinct. In Maniitsoq 7 of 11 had experienced increases. The only two who experienced changes at the small colony near Nuuk believed it had increased in recent years.

**Table 3:** Distribution of 72 responses to question: "Have you experienced population change in murre colonies the last 10-15 years?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Yes: declines** | 44% (7) | 38% (3) | 19% (5) | **29% (15)** | 11% (2) | - | **10% (2)** |
| **- increases** | 6% (1) | (0) | 41% (11) | **24% (12)** | 39% (7) | 67% (2) | **43% (9)** |
| **- mixed** | 6% (1) | 25% (2) | - | **6% (3)** | - | - | |
| **- other** | - | - | 11% (3) | **6% (3)** | 11% (2) | - | **10% (2)** |
| **No** | 13% (2) | 38% (3) | 11% (3) | **16% (8)** | 22% (4) | 33% (1) | **24% (5)** |
| **Don't know** | 31% (5) | - | 19% (5) | **20% (10)** | 17% (3) | - | **14% (3)** |
| **N total** | 16 | 8 | 27 | **51** | 18 | 3 | **21** |

Number of informants for each response is in parenthesis. Percentages are rounded to nearest integer.

Ten different causes were mentioned in the Northwest region as contributing to recent declines, where aircrafts (helicopters in particular), motorboats and landslides were the three most frequent causes mentioned (Table 4). That hunting had no influence was mentioned at least twice during the interviews. The only two who suggested a cause for increasing colonies in the Northwest region, mentioned hunting restrictions as a reason.

Causes to declines in the Southwest region were only mentioned twice, whereas four different causes of increases were mentioned (Table 4).

**Table 4:** Number of times that various causes were mentioned when asked about changes in nearby murre breeding colonies in the last 10-15 years (Recent), and changes further back in time (Former) in Northwest and Southwest Greenland, respectively.

| Causes to change | Recent | Former |
|---|---|---|
| **Northwest** | | |
| Declines: | | |
| Aircrafts | 11 | 11 |
| Motorboats | 5 | 5 |
| Landslides | 4 | 1 |
| Climate | 3 | 2 |
| Feeding conditions | 3 | |
| Displacements (moved) | 3 | 6 |
| Shipping | 2 | 1 |
| Traffic | 2 | 3 |
| Egging | (1) | 2 |
| Lice | 1 | 1 |
| Ship horns | | 9 |
| Hunting | | 2 |
| Kittiwake increase | | 1 |
| Bycatch salmon fisheries | | 1 |
| (Not hunting) | 2 | 4 |
| Increases: | | |
| Hunting restrictions | 2 | |
| **Southwest** | | |
| Declines: | | |
| Kittiwake increases | 1 | |
| Feeding conditions | 1 | 1 |
| Bycatch salmon fisheries | | 1 |
| Increases: | | |
| Feeding conditions | 1 | 1 |
| Less hunting | 2 | |
| Less disturbances | 2 | |
| Displacement (moved) | 2 | |

*Changes and causes further back in time*

Of the 78 informants, 48 responded about changes further back in time (Table 5). The majority of these in the Northwest had experienced declines at all three communities (Table 5). Nine from Upernavik mentioned the nearest extinct colony (*Upernaviup Apparsui*) in this context and two others mentioned the extinct colony of *Kingittuarsuk*, a bit north of Upernavik town. One older informant said: *"back then the sky would turn black when shooting a gun at murre colonies"*. Another older informant told about hunting from kayak in murre foraging areas in springtime among abundances of murre that you do not see today.

In the Southwest region only informants from Maniitsoq responded to this and the relatively few responses were somewhat mixed (Table 5). One older respondent from Nuuk was answering at a more general level, referring to much larger abundances in the Nuuk area during autumn and winter, when he was young.

When asked about causes of the changes further back in time in the Northwest region, nine causes were the same as for the recent changes, and four new were mentioned, where disturbances from ship horns was mentioned the most (Table 4). The number of times that disturbances from aircrafts were mentioned, were similar to the recent causes, however, the S-61 helicopter, that was used in the Upernavik area up until the airstrip was completed in year 2000 (Transportkommissionen 2011), was emphasized by several as a reason for former declines in the Upernavik area.

**Table 5:** Distribution of 47 responses to question: "Have you experienced changes in the colonies that goes further back in time?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Declines** | 29% (4) | 86% (6) | 94% (17) | **69% (27)** | 25% (2) | - | **25% (2)** |
| **Increases** | - | - | 6% (1) | **3% (1)** | 25% (2) | - | **25% (2)** |
| **No** | 50% (7) | 14% (1) | - | **21% (8)** | 12% (1) | - | **12% (1)** |
| **Don't know** | 21% (3) | - | - | **8% (3)** | 38% (3) | - | **38% (3)** |
| **N total** | 14 | 7 | 18 | **39** | 8 | | **8** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

*Agreement with scientific data and recommendations for better surveys*

When presented for the results of biological surveys of the colonies in question, the agreement with scientific data was largest in the Northwest region (56% of 54), particularly in Kullorsuaq (71% of 17) and Nuussuaq (75% of 8), and lowest in the Southwest region where 71% of 14 were disagreeing with the presented data (Table 6). Four Upernavik informants, which had experienced increases where biologist had identified declines, were for some reason agreeing with the scientific data, when presented for these.

**Table 6:** Distribution of responses to question: "Do you agree with the scientific data on breeding population sizes obtained by GINR?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Agree** | 71% (12) | 75% (6) | 41% (12) | **56% (30)** | 23% (3) | - | **21% (3)** |
| **Disagree** | - | 25% (2) | 34% (10) | **22% (12)** | 69% (9) | 100% (1) | **71% (10)** |
| **Don't know** | 29% (5) | - | 24% (7) | **22% (12)** | 8% (1) | - | **7% (1)** |
| **N total** | 17 | 8 | 29 | **54** | 13 | 1 | **14** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

When asked about recommendations to when surveys should be carried out 84% of 31 said the breeding period, of which four were more specific and said the incubation (n = 2) or chick rearing (n = 2) period. Two suggested at-sea counts and three others suggested in the spring period, possibly also referring to at-sea occurrences. Three informants mentioned that it was important to involve hunters in the process. One informant from the Northwest region mentioned that it would be nice if biologist saw how many birds there are at sea. Six informants were satisfied with the current system and had trust in the scientific numbers, whereas two stated that it impossible to count birds properly.

*Experience of human and natural disturbances at colonies*

It was a minority in all the areas who believed that human activities were disturbing murre colonies, when asked directly. The largest fraction was found in Upernavik town (43%) (Table 7).
Human activities mentioned as causing disturbances in the Northwest region were (number of times mentioned): motorboats (6), helicopters (6), traffic in general (2), egging (2), gunshots (2), and murre hunting (1). It varied if motorboats were considered disturbing or not. One informant from Kullorsuaq said that hunting at colonies occurred every year. Seven informants mentioned the following human disturbances as belonging to the past specifically: egg collection, ship horns, shootings at colonies, the S-61 helicopter.

The following human disturbances was mentioned once each, by the few responses from the Southwest: egging, seal hunting and creation of noise to make flyouts for the show.

**Table 7:** Distribution of responses to question: "Is it your experience that murre colonies get disturbed by human activities?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Yes** | 19% (3) | 13% (1) | 43% (9) | **29% (13)** | 12% (2) | 33% (1) | **15% (3)** |
| **No** | 81% (13) | 88% (7) | 57% (12) | **71% (32)** | 82% (14) | 67% (2) | **80% (16)** |
| **Don't know** | - | - | - | - | 6% (1) | - | **5% (1)** |
| | | | | | | - | |
| **N total** | 16 | 8 | 21 | **45** | 17 | 3 | **20** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

Natural events causing disturbances was experienced by 60% of 50 informants in the Northwest region where landslides (15), weather (wind, rain and/or storms) (11), feeding conditions (3), falcons (3), climate change (3), gulls (2), sun (1) and insects (1) were mentioned. *Apparsuit* in Northern Upernavik in particular, was mentioned in connection to landslides (n = 9). In the Southwest, 81% of 21 informants had experience of natural events causing disturbances in the form of increased number of eagles and falcons (17), foxes (4), landslides (3), storms (3), rain (2) and climate warming (1).

*Knowledge of egg collection nowadays*

Overall, 75% of 73 informants answered “No” when asked if they knew of egging occurring nowadays (Table 8). Nuussuaq and Nuuk were somehow deviating, however, based on few individuals (Nuuk in particular). One from Upernavik, said that egging had stopped due to camera surveillance at colonies. This could be referring to a camera formerly placed at the nearest extinct colony (*Upernaviup Apparsui*, 1998-2003), or at *Kippaku* in Northern Upernavik (since year 2008) put up for research purposes (Huffeldt and Merkel 2013). Most who answered positive to the occurrence of egging said it was rare and limited. Some had only heard rumors, others had more concrete examples and two said that it happened every year and by people from certain settlements. One of these had heard about quantities so large that some eggs ended up rotting.

**Table 8:** Distribution of responses to question: "Does egging occur nowadays, to your knowledge?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Yes** | 18% (3) | 50% (4) | 22% (6) | **25% (13)** | - | 67% (2) | **10% (2)** |
| **No** | 76% (13) | 38% (3) | 74% (20) | **69% (36)** | 100% (18) | 33% (1) | **90% (19)** |
| **Don't know** | 6% (1) | 13% (1) | 4% (1) | **6% (3)** | - | - | **-** |
| | | | | | | | |
| **N total** | 17 | 8 | 27 | **52** | 18 | 3 | **21** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

*Knowledge on rules at colonies*

When asked if knowing the rules near murre colonies most answered “yes”, and more from the Southwest region (90% of 20) than the Northwest region (82% of 45). A total of 63% of those who answered yes (n = 55), mentioned that there is a distance regulation for nearing the colonies, 29% mentioned the existence of a no-shooting zone and 11% mentioned both the boating and shooting regulation. Ten mentioned an actual distance where 5 said 500m, 2 said 1000m, 2 said they were insecure if the distance was 500 or 1000 m and one mentioned a 5 km distance for helicopters. A minimum of 6 people mentioned that the distance regulations were not followed or were not possible to follow due to official boating routes, especially in bad weather. Some told that they pass closer to the colonies for recreational reasons, however, without disturbing.

**Hunting**

*Hunting frequency and catch numbers*

While a high proportion of the informants from the Northwest region did not hunt murre and among those who did, the most common frequency was 1-5 hunting events annually, all informants of the Southwest were hunting murre regularly and the largest group were hunting weekly or more (Table 9).

**Table 9:** Distribution of responses to question: "How often do you go hunting for murres?"

| | NW | SW |
|---|---|---|
| **Never/not any more** | **27% (14)** | **-** |
| **<1 annually** | **6% (3)** | **-** |
| **1-5 annually** | **60% (31)** | **8% (2)** |
| **5-10 annually** | **6% (3)** | **38% (9)** |
| **10-20 annually** | **2% (1)** | **13% (3)** |
| **weekly or more** | **-** | **42% (10)** |
| **N total** | **52** | **24** |

Number of informants for each response is in parentheses.
Percentages are rounded to nearest integer.

All but 6 informants answered to catch numbers and gave an estimate (range: 0-ca.1800) of how many murre they had caught in the most recent season (Northwest: year 2017, Southwest: winter 2015-2016) (Table 10).

**Table 10:** Sum and average of total hunt of respondents that informed on catches (>0) during the most recent hunting season.

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Occupational** | 115 (8) | 10 (1) | 147 (8) | **272 (17)** | 1801 (14) | 2100 (5) | **3901 (19)** |
| *-average* | *14.4* | *10.0* | *18.4* | ***16.0*** | *128.6* | *420.0* | *205.3* |
| **Recreational** | 0 (0) | 2 (1) | 80 (8) | **82 (9)** | 74 (3) | | **74 (3)** |
| *-average* | | *2.0* | *10.0* | ***9.1*** | *24.7* | | *24.7* |
| **Sum catch** | 115 | 12 | 227 | **354** | 1875 | 2100 | **3975** |
| **N total** | 8 | 2 | 16 | **26** | 17 | 5 | **22** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

A total of 24 informants from the Northwest region had shot no birds and 26 had altogether shot about 354 murre in 2017, of which 191 (54%) were specified as shot in spring. Two from Nuussuaq were not willing to provide an estimate but told only that they catch murre for their own use. All Nuussuaq informants indicated they hunt murres in spring. In Kullorsuaq, 8 of 10 hunted murres in spring and 2 in autumn. In Upernavik 93% of the 27 informants went hunting in autumn. Six of these also hunted during spring or summer, whereas 2 mentioned spring/summer hunting only. Four of the eight from Upernavik who hunted in springtime, pointed out that it was since spring hunting got re-introduced in 2017. Six of the 8 hunters from Kullorsuaq and one from Nuussuaq mentioned spring hunting in connection to narwhale hunting at the ice edge, and some of the Nuussuaq informants told they caught murre when the ice broke up and murre arrived. A

Kullorsuaq informant told that not many people have a shotgun since murre are uncommon for the Kullorsuaq area.

The annual estimate of murre catches from the Southwest informants ranged from 9 to about 1800, where three numbers (including the highest number reported) were estimates based on the estimated hunting frequency informed at the interviews and the approximate number shot per trip. All Nuuk and Maniitsoq informants hunted in the autumn/wintertime.

When asked about changes in catch numbers compared to 10-15 years ago 68% of 48 Northwest informants and 54% of 24 informants in the Southwest region said that they caught fewer murres today. The reasons mentioned were regulations (12), personal conditions (e.g. job situation, boat availability and age) (9), and a larger focus on fishing (5). Four from the Southwest region mentioned murre being further away from the coast (of which two mentioned it particularly for the same year) as a reason whereas three from the Northwest believed the reason was that fewer murre were available. The proportion of informants not experiencing a change was 25% of the Northwest- and 33% of the Southwest informants. Only 3 in the Southwest said they caught more, all due to change in personal conditions. Three in the Northwest answered, “don’t know”.

When asked about impression of change in numbers shot in the community in general the last 10-15 years, 24 of 42 informants from the Northwest region said that less birds were shot, 4 said “the same” and 12 “don’t know”. Reasons mentioned were regulations (13), fewer murres (5), focus on fishery (3) and that the weather in autumn often is bad (2). Three from Upernavik meant that more got shot and reasons mentioned were that an increased number of boats in Upernavik town and that more young murres came close to the shore in autumn, than earlier. In the Southwest region 8 out of 11 informants said that less murres were shot and 3 said “the same”. Reasons mentioned were that murres were further from the coast (4), focus on fishery (1) regulations (1) and decline in murres (1)

*Catch reporting to Piniarneq*

In the Northwest region 5 of 16 informants from the two northern settlements and all but one of 25 Upernavik informants said they report all their hunt (one said “to the extent possible”) to Piniarneq. Nine from the two northern settlements told that they do not report their murre hunt, due to small catches only for own consumption or because they meant that only larger animals were to be reported. In the Southwest 21 of 24 informants said they report all the murre they catch, two said they reported most, and one said about half.

**Management**

Of 66 informants responding to the question if hunting restrictions were necessary, 80% answered "yes" and more in the Northwest (90% of 48) than in the Southwest (56% of 18) (Table 11). Of those who said that restrictions were irrelevant, some said that weather and ice conditions were protecting animals from over-hunting and others said that hunters, as a principle, did not over-hunt. One said that restrictions were irrelevant because no one respects the rules anyway.

**Table 11:** Distribution of responses to question: "Is it, in your opinion, necessary with hunting seasons and restrictions?"

| | Kull | Nuus | Uper | NW | Mani | Nuuk | SW |
|---|---|---|---|---|---|---|---|
| **Yes** | 88% (14) | 75% (6) | 96% (23) | **90% (43)** | 62% (8) | 40% (2) | **56% (10)** |
| **No** | 13% (2) | 25% (2) | 4% (1) | **10% (5)** | 38% (5) | 40% (2) | **39% (7)** |
| **Don't know** | - | - | - | - | | 20% (1) | **6% (1)** |
| **N total** | 16 | 8 | 24 | **48** | 13 | 5 | **18** |

Number of informants for each response is in parentheses. Percentages are rounded to nearest integer.

Where 8% of 49 Northwest informants were satisfied with the regulations, 75% had 15 different suggestions to improve the regulations. In contrast, 38% of the 13 Southwest informants believed the regulations were fine and 62% had 5 different suggestions to how the regulation could be changed (Table 12).

Where some of the suggested changes would lead to more hunting, others would lead to less or have a neutral (or just non-obvious) effect (Table 12). Some informants had more than one suggestion, but overall, 40% of 45 informants were suggesting actions leading to lesser hunting, 38% to more, and 22% to changes where the result could be either.

**Table 12:** Frequency of which different suggestions for better management were mentioned by informants in two different regions of Greenland (NW - Northwest and SW - Southwest). Frequency in percentage of each suggestion is in relation to the number of informants who had suggestions (NW, N = 37; SW, N = 8).

| Aim | Suggestions | NW | | SW | |
|---|---|---|---|---|---|
| **Less hunting:** | Hunting moratorium | 4 | 11% | | |
| | Stop for sale (only own consumption) | 4 | 11% | | |
| | Better control | 3 | 8% | 2 | 25% |
| | Less restrictions will lead to less overhunting | 3 | 8% | | |
| | Only fall hunting | 2 | 5% | | |
| | Expand eider hunt | 2 | 5% | | |
| | Less birds to recreational hunters | 1 | 3% | | |
| | Annual quota | 1 | 3% | | |
| | **Sum** | **20** | | **3** | |
| **More hunting:** | Adjust season for better hunting | 16 | 43% | 1 | 13% |
| | Larger day quota | 1 | 3% | 1 | 13% |
| | **Sum** | **17** | | **1** | |
| **Other:** | More equality between regions | 6 | 16% | | |
| | More equality occupational/recreational hunters | 4 | 11% | | |
| | Lead better than steel | 2 | 5% | | |
| | No regulations (hunters do not overhunt) | 1 | 3% | | |
| | Better collaboration | | | 3 | 38% |
| | Adjust for climate change | | | 1 | 13% |
| | **Sum** | **13** | | **4** | |
| | **Total count** | **15** | | **5** | |

In the Northwest, 86% of 42 informants had heard about the newly reintroduced spring hunt (one month) in 2017. When asked about their opinion to this, 10% expressed concern for further declines, 19% were neutral, 52% were positive and 19% though it was still too restricted to be useful.

When asked if the information level on regulations in general was satisfying 54% of 65 said "no", 38% "yes" and 8% said "don't know".

## DISCUSSION

The relatively large number of informants, and the amount of information obtained from each informant, revealed a large variation between the two regions with respect to local knowledge about murre colonies, hunting conditions, and murre management perspectives, and to some extent also within the regions. Relatively few informants were interviewed in Nuussuaq, but they were nonetheless a valuable supplement to the group of Northwest region informants. The largest number of informants was from Upernavik town, where the last few informants had limited information and provided no new names in the chain referral process. This could be a sign of saturation – indicating that we had talked with most of the relevant persons available at the time

(Bernard 2011). We seemed to reach a certain level of saturation in Maniitsoq as well, however not as pronounced as in Upernavik town. The Nuuk sample was very limited and should be considered a supplement to the Maniitsoq group as a contrast to the people of the Northwest region. All in all, we feel confident that we managed to collect a large and representative proportion of the available LEK on murres from these two contrasting regions.

**Colony knowledge and population trends**

The informants from the Northwest region knew their colonies well, particularly the two large and very distinct colonies of *Apparsuit* and *Kippaku*. Gilchrist et al. (2005) found that LEK generally is lacking sufficient detail to quantitatively track population change unless the change is of severe decline. This might explain why the observed population changes by informants in most areas were relatively inconsistent. However, the impression of declines at *Apparsuit*, which is a large colony (roughly 5 km long), was very consistent and indicate a certain severity of the decline, which is also supported by scientific data (Merkel et al. 2014). Informants from Upernavik town had a less clear picture of trends in their local colonies. Contrasting population trends at *Kingittoq* and *Timmiakkulussuit* over the past decade, according to the scientific data (Merkel et al. 2014), might have added to an inconsistent impression. A contributing factor could also be that murre hunting is more common in Upernavik town, than in the northern settlements. Informants can be more reluctant to share their knowledge if the species in question constitutes an important resource value or if they believe that the information can be used against them (Anadón et al. 2009).

The Southwest informants from Maniitsoq were also familiar of the local murre colonies, however, several had a more diffuse awareness on the exact locations. This could be due to the large number of seabird colonies in the Maniitsoq area in general and particularly the large number of razorbill, that are easily confused with the murre (Nyeland and Mathæussen 2004). The fact that murres are available during the wintertime, might also cause less attention to be paid at the murre colonies during summer, where other resources are in the focus.

**Causes of decline**

The factors mentioned most as possible causes for both the recent and historical changes were all human related, where various form of transport (aircraft transport, boating etc.) and human disturbances were mentioned as causing declines, and regulations (less disturbance and hunting) were linked to increases.

Several explanations were similar for historical and recent changes, but disturbances at colonies (ship horns and hunting) were mentioned only for historical changes, and displacement of murres to other colonies were mentioned less for recent changes. A few mentioned the former hunting levels as a reason for historical declines, and some mentioned that recent increases were a consequence of hunting restrictions, identifying former hunting levels as having a negative impact on the population level. On the other hand, several said that hunting had no cause in the declines. Hunting as a cause of declining populations is a sensitive topic in public debates in Greenland and hunters often feel they get blamed for all declines (Sejersen 2003). It is somehow peculiar that the extensive bycatch of murres in salmon fisheries in the 1960-70s (Tull et al. 1972) and the former commercial trading during the breeding period in northern settlements, to be sold throughout Greenland (Evans 1987), was mentioned by very few in this study. A larger public awareness of these factors, which according to the scientific literature were contributing significantly to the historical declines, and present-day depleted populations (Tull et al. 1972, Kampp et al. 1994, Falk and Kampp 2002), might contribute to a more balanced and constructive debate.

*Colony disturbances*

Anthropogenic disturbances at murre colonies, in the form of hunting, boat traffic, aerial traffic and the use of ship horns or other loud noises to initiate spectacular fly-outs, have formerly been described as a significant conservation issue in Greenland (Chardine and Mendelhall 1998, Gilchrist 1999, Merkel et al. 1999). The LEK from this study, provides a general impression that the disturbance levels at murre colonies have been markedly reduced compared to a few decades ago, both in the Northwest and the Southwest. Even though relatively few remembered the exact distance limits for boating and shooting near colonies, most were aware of the existence of protection zones against disturbances and were themselves conscious not to disturb when near colonies. However, several also indicated that some disturbances did occur and that some people disrespected the rules. Examples to this was boating, provocation of fly-outs, egging and a single statement about hunting directly at colonies.

*Contrasting trends in neighbor colonies*

The LEK from the Northwest region revealed information that could add to the understanding of contrasting populations trends in the two northern Upernavik colonies – the declining *Apparsuit* and increasing *Kippaku,* situated only 7-10 km apart (Merkel et al. 2014). Several informants expressed concern about disturbances from the helicopter route between the northern settlements and Upernavik town that is passing the two colonies. The problem was considered larger at *Apparsuit*, due to the steep and more than 400 m tall, almost vertical cliff sides that might increase the effect of the helicopter noise and vibrations. In comparison, *Kippaku* is placed on a small and relatively low island (peak 78 m) (Falk and Kampp 1997). The larger frequency of landslides observed by the informants at *Apparsuit* appears to add another disturbance factor to this colony.

**Regional differences in the hunting pattern**

The contrasting hunting opportunities between the two regions were reflected in hunting frequency and catch numbers. Hunting of murres in the Northwest was characterized as relatively limited and largely opportunistic, during narwhale or seal hunting, fishing, or when travelling between communities, whereas the informants from the Southwest region went more frequently on dedicated murre hunting trips and had markedly larger catches. A similar overall difference in the annual hunting levels between the two regions appear from the Piniarneq data, which showed an annual average catch of 18,767 (s.d.= 2,692) murres in the area of Nuuk and Maniitsoq combined, versus 3,499 (s.d. = 1,603) murres in the Upernavik area, for the period 2012 - 2016 (Piniarneq 2019).

The murre availability have always been different between the Northwest and the Southwest region but the regulations introduced in 2002, that put a stop for spring hunting in most of Greenland, had a disproportional impact on people in the Northwest, compared to murre hunters in Southwest Greenland, which is an important wintering area for murres from multiple breeding areas in the North Atlantic (Boertmann et al. 2004, Frederiksen et al. 2016).

Both Piniarneq data and the LEK from this study area indicates that spring- and summer hunting have continued at some level, also before the recent reintroduction of spring hunt in the Northwest region. A limited hunt only for own consumption when murres finally are available in the area after a long winter with no birds, seemed to be somewhat accepted in the communities. Several informants who told that they caught birds in the springtime also told that they considered their catch so small that it was unnecessary to report. That only quota species were to be reported to Piniarneq was also expressed several times, indicating that a small murre hunt for own consumption was considered as insignificant.

Upernavik town deviated somehow from the northern settlements with generally higher murre hunting levels and primarily in the autumn period. This is also the case when looking at Piniarneq data that shows a striking shift from a hunt primarily taking place during the spring up until year 2002, after which the autumn hunting increased. The level of reported murres hunted in autumn peaked in 2013, while it never reached the pre 2002 spring hunting levels (Piniarneq 2019). One said that more recreational hunters in Upernavik town got boats nowadays, and better boats, which gives more opportunities to hunt during autumn where the weather typically is more unstable than in spring. Some also said that murre hunting out of Upernavik town today to a larger extent than earlier was carried out by recreational hunters.

The Southwest informants similarly expressed that they generally were hunting fewer murres nowadays compared to earlier, also in consistence with Piniarneq data. Both Maniitsoq and

Nuuk informants mentioned that murres were far from the coast and difficult to reach in recent years, so that it could hardly pay off to go for murres due to the travel distance and the limited day quota. This was also reported by Haastrup (2017) who did a study on the use of murre in Nuuk in 2016. Several pointed out, that the reason for the offshore distribution of the murres was because their food sources had moved out to sea, rather than an expression of a reduced winter population, and that the murre population was intact. There is no information available about this from the scientific literature, however, considering that some studies have shown a link between winter conditions and population trends (Descamps et al. 2013, Frederiksen et al. 2016), the LEK from this study emphasize the need to study the feeding conditions for murres in the Southwest Greenland wintering quarters.

**Management implications and recommendations**

The thick-billed murre is traditionally and culturally a very important resource in Greenland; as this study as wells as others have shown (Sejersen 2003, Haastrup 2017). The management of murres in Greenland is a balance between allowing harvest of this highly valued resource and sustaining the long-term viability of the species. Doing both is a challenge, when the population is declining and when murres are unevenly distributed between regions, i.e., only present in Northwest when breeding, while present in high abundances during the non-breeding season in the Southwest. The challenge becomes further complicated when biologist argue that spring and summer is a highly unsustainable period for harvest, due to the low reproductive capacity of this species and the age distribution in this period (Evans 1987, Lebreton and Clobert 1991, Kampp et al. 1994). When the management decides to follow this biological advice, there is very little room left for practicing sustainable harvest in the Northwest region. In 2001, the management followed the biological advice when spring hunting was prohibited, making it difficult for people in the Northwest region, particularly in the northern settlements, to continue the traditional use of murres. Even though the majority of the informants from the Northwest region agreed that restrictions were necessary, they were often unsatisfied with the current restrictions and had a range of suggestions to changes. Others disagreed and were frustrated about the limitations and one informant from the Northwest asked: “Why are Inatsisartut [the Greenland parliament] punishing the north? “. Another said: “The regulations are criminalizing hunters since they force hunters, who are brought up with, and desire murre, to hunt murres illegally”.

These statements clearly illustrate that the reasoning behind the management and the apparent preferential treatment of the Southwest region, have not been sufficiently communicated to the hunters. At the same time, the changed management policy in 2017, where the spring harvest was reintroduced in the Northwest region, may have made it worse. Although it probably was appreciated by many, changing course without clearly communicating the reasons for disregarding the biological advice and the associated risk for sustainability, have likely added to the confusion on why spring hunting was prohibited to begin with, and increased the risk of generating mistrust to the managers.

The current study also indicates that biologists to some degree have failed to communicate why they advise so strongly against even a very small level of harvest in spring and why they argue that murre harvest during winter has less population impact. It was clear that many informants had a different opinion, such as the perception that their harvest was too small to report or insignificant because it only served the purpose of their own consumptions, or by the feeling that Inatsisartut is punishing the hunters in the north.

Biological studies have shown that the winter harvest in the Southwest Greenland to a large extent is targeting overwintering murres from other countries, in which many breeding populations also are declining (Descamps et al. 2013, Frederiksen et al. 2016, Frederiksen et al. 2019). This led to a significant shortening of the hunting season in Southwest Greenland (3 months) in December 2016 (Anon 2016), which made the contrasting hunting opportunities between Northwest and Southwest a bit more even. However, not a single informant from the Northwest region mentioned anything about this, which could be an indication of poor communication about the changed regulations. In general, the majority in both regions were unsatisfied with the information level from the authorities.

Likewise, there was a clear indication of a limited awareness of the scientific work on murre population sizes and therefore an apparent need for a higher information level about the murre monitoring program. In addition, biologist should communicate why no at-sea surveys are conducted in the spring or in offshore areas during winter, as some informants advertised for. The same wish is also frequently expressed in public debates.

**Conclusions**

The targeted people of this study clearly knew the whereabouts of the local breeding colonies well, but did not always agree with the scientific data on population trends, especially in the Southwest region. In general, the LEK indicate that human use (hunting and egging) and human disturbances in the breeding areas have been markedly reduced over the past few decades. Although still occurring at a small scale, this was not believed to be a factor for population decline. Instead, there was some concern that mainly helicopters, marine traffic and landslides were contributing to population declines in the Northwest region. The informants generally knew little about the scientific monitoring program and were unaware, or disagreed with biologist, that murres are especially vulnerable during the breeding season. The majority were of the opinion that it is necessary with regulations on the use of murres, and more in the Northwest than in the Southwest. However, many from the Northwest region were not satisfied with the current regulations and had multiple suggestions for improvements. Also, the awareness of regulations in detail and the foundation of the regulations of this much valued resource, was relatively limited. All in all, the study calls for better communications from the authorities, not only on monitoring results, murre natural history and demography, but also about regulation changes and the reasoning behind management decisions. This would likely facilitate a more successful management of the murres in Greenland.

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## REFERENCES


Anadón, J. D., A. Giménez, R. Ballestar, and I. Pérez. 2009. Evaluation of Local Ecological Knowledge as a Method for Collecting Extensive Data on Animal Abundance. Conservation Biology **23**:617-625.

Anon. 2001. Hjemmestyrets bekendtgørelse nr. 38 af 6. december 2001 om beskyttelse af fugle. Greenland Home Rule Government **Executive Order**.

Anon. 2016. Selvstyrets bekendtgørelse nr. 30 af 28. december 2016 om beskyttelse og fangst af fugle. Government of Greenland **Executive Order**.

Bakken, V., D. Boertmann, A. Mosbech, B. Olsen, A. Petersen, H. Strøm, and H. Goodwin. 2006. Nordic Seabird Colony Databases. Results of a Nordic project on seabird breeding colonies in Faroes, Greenland, Iceland, Jan Mayen and Svalbard. Nordic Council of Ministers, Copenhagen.

Bernard, H. R. 2011. Research Methods in Anthropology: Qualitative and Quantitative Approaches. AltaMira Press.

Boertmann, D., P. Lyngs, F. R. Merkel, and A. Mosbech. 2004. The significance of SW Greenland as winter quarters for seabirds. Bird Conservation International **14**:87-112.

Boertmann, D., A. Mosbech, K. Falk, and K. Kampp. 1996. Seabird colonies in western Greenland. NERI Technical Report No. 170, National Environmental Research Institute (NERI), Copenhagen, Denmark.

Born, E., A. Heilmann, L. K. Holm, and K. Laidre. 2011. Polar Bears in Northwest Greenland. An Interview Survey about the Catch and the Climate. Museum Tusculanum Press, University of Copenhagen.

Chardine, J. W., and V. Mendelhall. 1998. Human disturbances in arctic seabird colonies. 2, C. S. W. Group, Akureyri.

Descamps, S., H. Strøm, and H. Steen. 2013. Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre. Oecologia **173**:1271-1282.

Evans, P. G. H. 1987. Project studying ways to reduce the impact of hunting upon the Brünnich's Guillemot Uria lomvia populations of Upernavik district, West Greenland, July 1st – September 8th 1987. Greenland Home Rule, Nuuk.

Fabricius, O. 1780. Fauna Groenlandica - pattedyr og fugle. Det Grønlandske selskabs skrifter VI (translated to Danish by O. Helms), Copenhagen 1929.

Falk, K., and J. Durinck. 1992. Thick-billed Murre hunting in West Greenland. Arctic **45**:167-178.

Falk, K., and K. Kampp. 1997. A manual for monitoring thick-billed murre populations in Greenland. Technical Report 7, Greenland Institute of Natural Resources, Nuuk.

Falk, K., and K. Kampp. 2002. Lomvien i Grønland: Mulige effekter af forskellige bestands-påvirkende faktorer, og praktiske grænser for ressourceudnyttelse. 38, Greenland Institute of Natural Resources, Nuuk.

Frederiksen, M., S. Descamps, K. E. Erikstad, A. J. Gaston, H. G. Gilchrist, D. Grémillet, K. L. Johansen, Y. Kolbeinsson, J. F. Linnebjerg, M. L. Mallory, L. A. McFarlane Tranquilla, F. R. Merkel, W. A. Montevecchi, A. Mosbech, T. K. Reiertsen, G. J. Robertson, H. Steen, H. Strøm, and T. L. Thórarinsson. 2016. Migration and wintering of a declining seabird, the thick-billed murre Uria lomvia, on an ocean basin scale: Conservation implications. Biological Conservation **200**:26-35.

Frederiksen, M., J. F. Linnebjerg, F. R. Merkel, S. I. Wilhelm, and G. J. Robertson. 2019. Quantifying the relative impact of hunting and oiling on Brünnich's guillemots in the North-west Atlantic. Polar Research **38**:1-11.

Gaston, A., M. Mallory, and H. G. Gilchrist. 2012. Populations and trends of Canadian Arctic seabirds. Polar Biology **35**:1221-1232.

Gilchrist, H. G. 1999. Declining Thick-billed Murre *Uria lomvia* colonies experience higher gull predation rates: an inter-colony comparison. Biological Conservation **87**:21-29.

Gilchrist, H. G., M. Mallory, and F. R. Merkel. 2005. Can traditional ecological knowledge contribute to wildlife management? Case studies of migratory birds. Ecology and Society **10**:20.

Gotfredsen, A. B. 1997. Sea bird exploitation on coastal Inuit sites, west and southeast Greenland. International Journal of Osteoarchaeology **7**:271-286.

Huffeldt, N. P., and F. R. Merkel. 2013. Remote Time-lapse Photography as a Monitoring Tool for Colonial Breeding Seabirds: A Case Study Using Thick-billed Murres (Uria lomvia). Waterbirds **36**:330-341.

Huntington, H. P. 2000. Using Traditional Ecological Knowledge in Science: Methods and Applications. Ecological Applications **10**:1270-1274.

Haastrup, A. G. 2017. Appaqanngila? - Ingen lomvie? En analyse af forskellige vidensformer om lomvien og bæredygtighedstanker i Grønland. Masters thesis. University of Copenhagen, Copenhagen.

Kampp, K., D. N. Nettleship, and P. G. H. Evans. 1994. Thick-billed Murres of Greenland: Status and prospects. Pages 133-154 *in* D. N. Nettleship, J. Burger, and M. Gochfeld, editors. Seabirds on Islands. Birdlife International, Cambridge.

Laidre, K. L., A. D. Northey, and F. Ugarte. 2018. Traditional Knowledge About Polar Bears (Ursus maritimus) in East Greenland: Changes in the Catch and Climate Over Two Decades. Frontiers in Marine Science **5**.

Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling.*in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: relevance to conservation and management. Oxford University Press, Oxford.

Merkel, F., A. L. Labansen, D. Boertmann, A. Mosbech, C. Egevang, K. Falk, J. F. Linnebjerg, M. Frederiksen, and K. Kampp. 2014. Declining trends in the majority of Greenland's thick-billed murre (Uria lomvia) colonies 1981–2011. Polar Biology **37**:1061-1071.

Merkel, F. R., A. S. Frich, and P. Hangaard. 1999. Polarlomvien i Disko Bugt og det sydlige Upernavik, 1998. Bestandsopgørelse og grundlag for fremtidig monitering af lomviebestandene. Technical Report 25, Greenland Institute of Natural Resources, Nuuk.

Nyeland, J., and H. Mathæussen. 2004. Monitering af havfuglekolonier i Maniitsoq Kommune, 2003. 87-91214-11-4, Pinngortitaleriffik, Grønlands Naturinstitut, Nuuk.

Pars, T., M. Osler, and P. Bjerregaard. 2001. Contemporary use of traditional and imported food among Greenlandic Inuit. Arctic **54**:22-31.

Piniarneq. 2019. Hunting statistics for Greenland, 1993-2017. Department of Hunting, Fishing and Agriculture. Greenland Self Rule, unpublished data.

Rasmussen, R. O. 2005. Analyse af fangererhvervet i Grønland [Socio-economic analysis of the Greenland hunters]. Unpublished Report, Department of Fisheries and Hunting, Greenland Home Rule, Nuuk.

Sejersen, F. 2003. Grønlands naturforvaltning : ressourcer og fangstrettigheder [Greenland's nature conservation: resources and hunting rights]. Akademisk Forlag, København.

Sowa, F. 2015. Kalaalimernit: The greenlandic taste for local foods in a globalised world. The Polar Record **51**:290-300.

Transportkommissionen. 2011. Transportkommissionen - Betænkning. Greenland Government, Dep. housing, infrastructure and traffic, Nuuk.

Tull, C. E., P. Germain, and A. W. May. 1972. Mortality of Thick-billed Murres in the West Greenland Salmon Fishery. Nature **237**:42-44.

# Paper IV

Huffeldt NP*, **Labansen AL***, Frederiksen M, Linnebjerg JF, Witting L & Merkel FR. Global and local anthropogenic threats to a culturally important food animal.

Manuscript submitted to *Conservation Letters*.

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## Global and local anthropogenic threats to a culturally important food animal

Running title: Threats to a culturally important food animal

(surnames are underlined)

**Nicholas Per Huffeldt***: Greenland Institute of Natural Resources, 3900 Nuuk, Greenland (nph@natur.gl) & Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark (nph@bios.au.dk); Twitter: @nphuffeldt

**Aili Lage Labansen***: Greenland Institute of Natural Resources, 3900 Nuuk, Greenland (aila@natur.gl)

**Morten Frederiksen**: Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark (mfr@bios.au.dk)

**Jannie Fries Linnebjerg**: Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark (jafl@bios.au.dk)

**Lars Witting**: Greenland Institute of Natural Resources, 3900 Nuuk, Greenland (larsw@natur.gl)

**Flemming Ravn Merkel**: Greenland Institute of Natural Resources, 3900 Nuuk, Greenland (flme@natur.gl) & Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark (frm@bios.au.dk)

* denotes joint and corresponding authors: Huffeldt, N.P. (Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark; +45 4630 1200; nph@bios.au.dk) & Labansen, A.L. (Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland; +299 36 12 00; aila@natur.gl)

Keywords (up to 10): Arctic biodiversity loss; cultural continuity; global climate change; human-wildlife interaction; Indigenous Peoples and local communities; microclimate; population dynamics; social-ecological system; *Uria lomvia*; wildlife conservation and management

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**Abstract**

Resources harvested locally often define cultural identities, which is especially pertinent for Indigenous Peoples and societies with locally-based cultures. The loss of biodiversity reverberates across the human-environment interface via valuable wildlife. The identification of the causes of local biodiversity loss is essential for the sustainability of ecosystems and dependent cultures. Here, we show that a seabird of high cultural and food value, *appa(t)* (thick-billed murre(s), *Uria lomvia*), has declining and locally extinct populations in Greenland. High rates of air temperature change and insolation co-occurred with the largest declines in the extant population, while the lowest growth rates that resulted in local extinction occurred when human settlements were nearby. The joint implications of global and local threats to the population viability of appat emphasize the importance of scale for conserving desirable wildlife and dependent cultures and demonstrate how global climate change and biodiversity loss has the potential to degrade cultural continuity.

**Tweetable abstract**

Global climate change and local factors link to declines and local extinction of the culturally important appa *Uria lomvia* in Greenland (associated image, Fig. 2)

## Introduction

Humans are strongly influencing the environment, leading some to proclaim that we have transitioned into a new geological epoch called the Anthropocene (Steffen et al. 2011). A defining characteristic of this transition is a reduction of biodiversity by anthropogenic factors; humans are not immune to this and suffer from the loss of living resources (Dirzo et al. 2014). The negative consequences of declining resources can have disproportionate impacts on Indigenous Peoples and locally-based societies who depend on local resources, not only for food, but also for cultural identity (Golden et al. 2011; Dirzo et al. 2014; Sowa 2015; Sustainable Development Working Group 2018). Both the United Nations and the Arctic Council promote Indigenous Peoples' right to preserve their culture, which is under threat by globalization (UN General Assembly 2007; Arctic Council 2011; Sowa 2015; Sustainable Development Working Group 2018). Food is vital to cultural identity, and insight into the resilience of desirable foods is central to the sustainability of cultures via food sovereignty and food security mechanisms (Sustainable Development Working Group 2018).

Here, we investigated drivers of the population dynamics of a culturally important food animal, the *appa* (a seabird a.k.a. the thick-billed murre, *Uria lomvia*; Fig. 1), that has regionally declining and recently extinct local populations in Greenland (Merkel et al. 2014). The appa breeds in large, dense colonies on rocky cliffs during summer and spend the non-breeding season out at sea. The appa is by far the most popular and culturally important gamebird in Greenland (Haastrup 2017; Piniarneq 2017). Historically, *appat* (plural of appa) were a primary source of sustenance, and they continue to be of high cultural value (Haastrup 2017). Our analysis facilitated a socio-ecological assessment of the population decline of this iconic species. We found that both local and global anthropogenic factors underlie recent changes in the populations of appa breeding colonies, and we discuss briefly their ecological, social, and cultural implications.

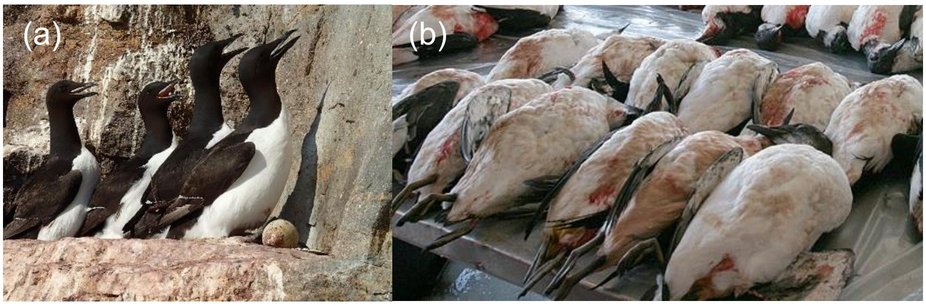


**Figure 1. Appat (thick-billed murres, *Uria lomvia*) in Greenland panting for thermoregulation during the summer breeding season (a) and for sale at a market during winter (b).** Photos © NPH (a) and Carsten Egevang (b).

## Results and discussion

Using linear models and a model selection framework (Burnham et al. 2011; Halsey 2019; see methods section below), we conducted exploratory analyses of potential drivers of the population dynamics of appa breeding colonies from 1983 to 2017 (N = 25). Since 1983, five breeding colonies in Greenland went extinct, and analyses of all colonies with three or more surveys (N = 23) indicated that colonies close to human settlements and the smallest colonies had the lowest population growth rates, "r", (evidence ratio = 74.25, $\Delta$AICc [from the null model] = -8.61, $r^2$ = 0.46; Fig. 2a,b; Supplementary Model Sets). Small appa colonies may be especially vulnerable to Allee effects (*i.e.*, reduced viability at low colony size leading to inverse density dependence) that could be compounded by human exploitation (Stephens & Sutherland 1999).

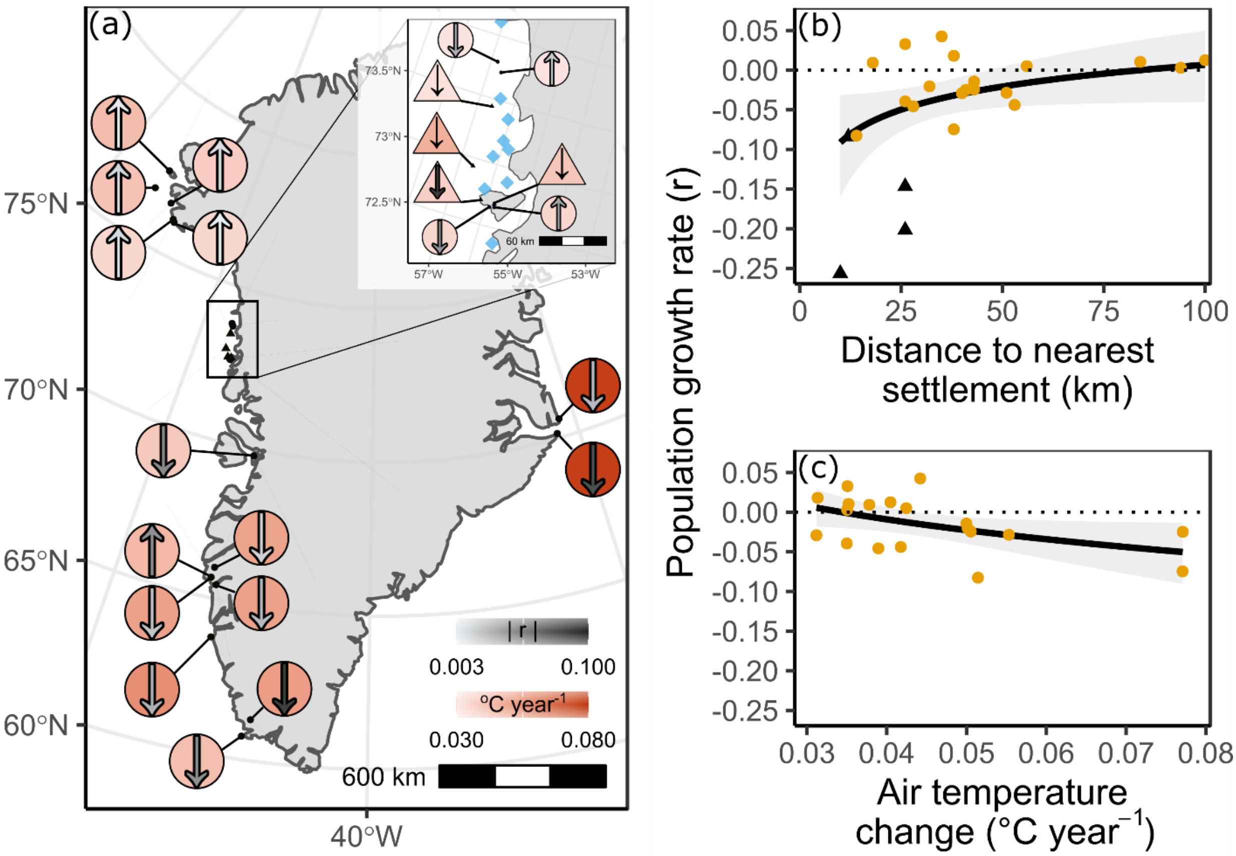


**Figure 2. Local and global threats link to population decline of appat in Greenland.** Map of appa colonies (a), including their colony status (extant = circle, extinct = triangle), rate of air temperature change and population growth rate (arrow direction = growth direction; the three extinct colonies with |r| > 0.1 have only thin black arrows). Within the inset of (a), blue diamonds represent human settlements. The association between population growth rate and distance to the nearest human settlement (b) and air temperature change (c). In (b,c) solid lines and shaded areas represent the back-transformed predicted values and 95% confidence intervals from the top models, respectively including (b) and excluding (c) extinct colonies. Yellow circles and black triangles represent individual extant and extinct colonies, respectively.

The results from this first analysis were driven almost entirely by colonies that went extinct. When we included only extant colonies in the models, rate of air temperature change was exclusively in the top model (evidence ratio = 2.84, ΔAICc = -

2.08, $r^2$ = 0.23; Fig. 2a,c; Supplementary Model Sets). Colonies were growing in the north where the rate of air temperature change was slowest (Fig. 2a). This suggests that appat in Greenland are contracting their breeding range towards its northern limit. Note that two of the four models within two AICc of the top model in this second model selection exercise included distance to the nearest human settlement (Supplementary Model Sets) and that in both model selection exercises insolation exposure (indicated by the primary compass orientation of a colony's breeding cliff(s) [Gabler et al. 2008]) was added to the second-place model (Supplementary Model Sets). Colonies with breeding cliffs facing primarily south and west (indicating more insolation exposure) were generally declining while those facing primarily north and east (indicating less insolation exposure) were generally stable (Fig. 3).

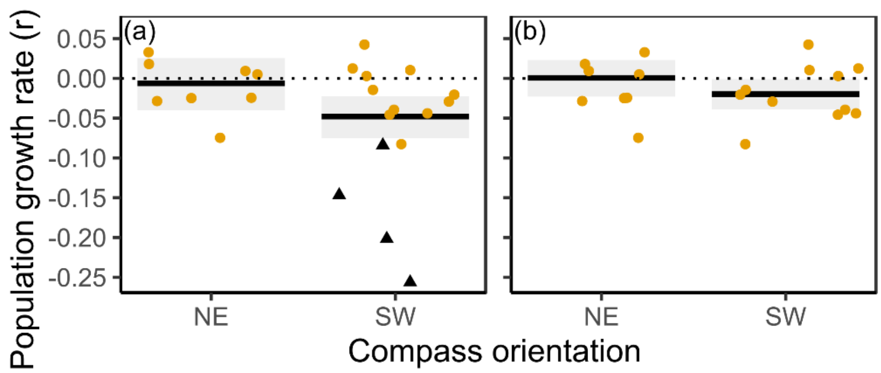


**Figure 3. Microclimate affects population growth rate of appat.** Colonies exposed to more insolation because their breeding cliff(s) faced primarily south or west were generally declining in population when including (a) and excluding extinct colonies (b) in the analyses. Solid lines and shaded areas represent the back-transformed predicted values and 95% confidence intervals from the second-place models. Yellow circles and black triangles represent individual extant and extinct colonies, respectively.

In combination, our results point to local anthropogenic threats as significant drivers of the population decline of appa colonies when access by local communities is easy, and that the global threat of climate change is subjecting appat to an additional anthropogenic-induced challenge.

Globally, climate change has caused declines in biodiversity and the population growth of multiple taxa (Stephens et al. 2016; Trisos et al. 2020; van Klink et al. 2020), and appat, specifically, are challenged by global climate change when breeding (Gaston et al. 2002) and during winter (Descamps et al. 2013). This climatic threat via warming air temperature may be compounded by the microclimate at the breeding colony (Oswald & Arnold 2012; Lembrechts & Nijs 2020) because the amount of insolation breeding appat are exposed to at the colony depends on the compass orientation of the breeding colony (Gabler et al. 2008). In the historically colder climate of the Arctic, higher amounts of insolation at the colony were probably advantageous for snow melt to access breeding sites and for the thermal regulation of individuals, but, under current rates of warming, high amounts of insolation associated with colony-specific microclimates probably increase the risk of heat stress (Gaston et al. 2002; Oswald & Arnold 2012; Levy et al. 2019). The effect of global climate change and associated factors on the population dynamics of extant appat colonies is the most potent risk to their regional viability (Fig 2a,c).

Locally, adoption of technology, unrestricted and commercialized harvest, and bycatch caused severe declines of appat in the 1900s (Tull et al. 1972; Merkel et al. 2014). Currently, the use of faster motorboats that functionally reduce distance is widespread, and human disturbance, egg collecting, and hunting at and near colonies still occur, although at decreasing frequency (personal observations). Even if these latter incidents occur infrequently, small increases in the mortality rate of organisms with slow life-history patterns, like appat, decrease population viability (Lebreton & Clobert 1991). These local factors are the most likely causes to the recent extinction of local appa populations, and they remain a threat to the long-term viability of appat in Greenland (Fig. 2b; Supplementary Model Sets).

The vulnerability and general population decline of appat in Greenland led to a recent call for a decade-long moratorium on their harvest (Pinngortitaleriffik 2013). The Greenlandic Government reacted by shortening the fall and winter hunting season, but, at the same time, the government reopened spring hunting in the northwest (Naalakkersuisut 2017). The fall and winter harvest in Greenland primarily removes appat originating from other countries, while the spring harvest removes appat from the Greenlandic breeding population (Frederiksen et al. 2016). The northwest had four of the five recent colony extinctions, all near settlements (Fig. 2a,b), indicating that previous spring and summer harvests were unsustainable. Combined, this illustrates the immense value of these seabirds for local communities and the political pressure by constituents for access to this resource.

With the identification of the most probable causes for the recent declines (Fig. 2), policymakers will need to balance the conservation of this culturally iconic species for use by future generations against current access and the preservation of local and Indigenous knowledge linked to appat. This dilemma is not unique to Greenland. Meat harvested from the wild constitutes important nutritional (Kuhnlein & Receveur 2007; Golden et al. 2011) and cultural (Sowa 2015; Sustainable Development Working Group 2018) resources, yet both over-exploitation and, paradoxically, the enforcement of existing laws that restrict harvest of these resources threaten the sustainability of less globalized and affluent societies worldwide (Golden et al. 2011). This juxtaposition between ecological and societal interests has the potential to introduce conflict between resource managers and users, and the inclusion of all stakeholders in developing management strategies of highly desirable species may reduce conflict and ensure the sustainability of the resource and the dependent culture.

The loss of biodiversity caused by anthropogenic factors reduces the diversity of ecosystems (Wesche & Chan 2010; Dirzo et al. 2014). This reduction can negatively affect ecosystem processes, such as the transportation of marine nutrients to terrestrial systems by seabirds (Croll et al. 2005), ecosystem services (Dirzo et al. 2014; Stephens et al. 2016; van Klink et al. 2020), and cultural identities via diet, food security, and food sovereignty (Wesche & Chan 2010; Dirzo et al. 2014). Yet, anthropogenic factors can operate at vastly different scales, and this presents challenges to the sustainability of cultures dependent on affected ecosystems. Separate effects at the global and local scale may act synergistically, which could accelerate population declines of valuable species, with potential negative cascades through ecosystems and cultures.

**Conclusions**

Our result---that both local and global threats link to recent declines in the population of the culturally important appa---emphasizes the importance of a broad approach that encompasses different scales when investigating the human-environment interface. Understanding processes at various scales will provide a clearer indication of the socio-ecological effects of biodiversity loss and global climate change and will alleviate the potential for cultural degradation by anthropogenic factors. Additionally, our result highlights the need to resolve local wildlife conflicts to buffer the global threat of climate change and to diminish negative impacts on the continuity of cultures and ecosystems.

**Methods**

Breeding colonies of appat in Greenland (N = 25) were surveyed at irregular intervals from 1983 until 2017 (Supplementary Data), as described previously (Merkel et al. 2014). We excluded zero-counts and then log-transformed the population counts of colonies before further analysis. We included only colonies with at least three colony surveys in our analyses (N = 23). We used *R* version 3.5.1 for all analyses (R Core Team 2018).

All variables used in analyses were limited to the period between the year of the first and the last population survey for each colony and to a radius of 120 km from the colony. A buffer of 120 km represents the maximum foraging-range reported for appat in Greenland (Falk et al. 2002; Mallory et al. 2018). Datasets of monthly-mean air-temperatures ("AT"; CRU TS v. 4.02, Climate Research Unit, University of East Anglia, UK, Harris et al. 2020) and monthly-mean sea-surface temperatures ("SST"; NOAA OI SST V2, *NOAA/OAR/ESRL PSD, Boulder, Colorado, USA,* Reynolds et al. 2002) were cropped and converted to UTM zone 24 before analysis.

Separately for AT and SST, the mean-monthly temperature for each summer month (June, July, and August) was averaged for each colony to obtain a mean summer temperature per colony per year. For each colony the change per year in summer SST ("ΔSST"), change per year in summer AT ("ΔAT"), and change in the transformed population size ("growth rate", "r") were estimated using linear models with year as a continuous predictor variable, similar to Merkel et al. (2014). The resulting coefficients from the linear models, which represented change per year, were then used to assess the influence of ∆SST, ∆AT, and additional predictors on growth rate as described below.

A model selection framework (Burnham et al. 2011; Halsey 2019) and the *MuMIn* package (Barton 2018) were used to assess the influence of the predictor variables on the response variable, growth rate. To meet the assumptions of linear models: one was added to growth rate and then cubed and predictors were log-transformed and then rescaled by subtracting the mean and dividing by two standard deviations using *arm::rescale()* (Gelman & Su 2018; see Supplementary Methods for more detail). Plots of residual vs. fitted values, Q-Q plots, and normalcy of residuals were used to check model assumptions for global and top models (Supplementary Methods). Correlated predictors (correlation coefficient ≥ |0.5|) were not permitted in the same model (Supplementary Methods). We included 13 predictor variables in each model selection exercise. The included predictors were, among others, ∆AT, ∆SST, distance to nearest settlement, colony size, and compass orientation of the colony (see Supplementary Methods for all predictors, their definitions, and motivation for inclusion). The first model selection exercise included extinct and extant colonies, while the second model selection exercise included only extant colonies. All allowed derivative models of a global model were ranked using AICc and the *MuMIn::dredge()* function for each model selection exercise. The evidence ratio of a model to the null model was used to identify the likelihood of the model given our data (Burnham et al. 2011). We also reported the difference in AICc of the top model from the null, or intercept only, model ("∆AICc").

Figures 2b,c and 3 depict back-transformed data, and they were made by calling *ggplot2* (Wickham 2016) from *visreg* (Breheny & Burchett 2017).


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**Data accessibility statement**

Appa data and all R code will be made available either in an established data repository or as supplementary material. This manuscript contains information from CRU TS v. 4.02 (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/), which was made available for use here under the Open Database License (ODbL). *NOAA High Resolution SST data were provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov/.*

**Ethical statement**

All data collection adhered to Greenlandic law and was part of government-sponsored conservation and population monitoring schemes of appat.

**References**


Arctic Council. (2011). Nuuk Declaration (2011). Arctic Council Secretariat.

Barton, K. (2018). MuMIn: Multi-model Inference. *R Package Version 1.42.1*, https://CRAN.R-project.org/package=MuMIn.

Breheny, P. & Burchett, W. (2017). Visualization of regression models using visreg. *R J.*, 9, 56–71.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.*, 65, 23–35.

Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M. & Byrd, G.V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, 307, 1959–1961.

Descamps, S., Strøm, H. & Steen, H. (2013). Decline of an arctic top predator: synchrony in colony size fluctuations, risk of extinction and the subpolar gyre. *Oecologia*, 173, 1271–1282.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Falk, K., Benvenuti, S., Dall'Antonia, L., Gilchrist, G. & Kampp, K. (2002). Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. *Mar. Ecol.-Prog. Ser.*, 231, 293–302.

Frederiksen, M., Descamps, S., Erikstad, K.E., Gaston, A.J., Gilchrist, H.G., Grémillet, D., Johansen, K.L., Kolbeinsson, Y., Linnebjerg, J.F., Mallory, M.L., McFarlane Tranquilla, L.A., Merkel, F.R., Montevecchi, W.A., Mosbech, A., Reiertsen, T.K., Robertson, G.J., Steen, H., Strøm, H. & Thórarinsson, T.L. (2016). Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: conservation implications. *Biol. Conserv.*, 200, 26–35.

Gabler, R.E., Petersen, J.F., Trapasso, L.M. & Sack, D. (2008). *Physical Geography*. 9th edn. Thomson Brooks/Cole, Belmont, CA.

Gaston, A.J., Hipfner, J.M. & Campbell, D. (2002). Heat and mosquitoes cause breeding failures and adult mortality in an Arctic-nesting seabird. *Ibis*, 144, 185–191.

Gelman, A. & Su, Y.-S. (2018). arm: Data analysis using regression and multilevel/hierarchical models. *R Package Version 1.10.1*, https://CRAN.R-project.org/package=arm.

Golden, C.D., Fernald, L.C.H., Brashares, J.S., Rasolofoniaina, B.J.R. & Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proc. Natl. Acad. Sci.*, 108, 19653–19656.

Haastrup, A.G. (2017). *Appaqanngila? Ingen lomvie? En analyse af forskellige vidensformer om lomvien og bæredygtighedstanker i Grønland* (M.Sc. thesis, University of Copenhagen).

Halsey, L.G. (2019). The reign of the p-value is over: what alternative analyses could we employ to fill the power vacuum? *Biol. Lett.*, 15, 20190174.

Harris, I., Osborn, T.J., Jones, P. & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci. Data*, 7, 109.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368, 417–420.

Kuhnlein, H.V. & Receveur, O. (2007). Local cultural animal food contributes high levels of nutrients for Arctic Canadian Indigenous adults and children. *J. Nutr.*, 137, 1110–1114.

Lebreton, J.D. & Clobert, J. (1991). Bird population dynamics, management and conservation: the role of mathematical modelling. In: *Bird Popul. Stud. Relev. Conserv. Manag.* (eds. Perrins, C.M., Lebreton, J.D. & Hirons, G.J.M.). Oxford University Press, Oxford, pp. 105–125.

Lembrechts, J.J. & Nijs, I. (2020). Microclimate shifts in a dynamic world. *Science*, 368, 711–712.

Levy, O., Dayan, T., Porter, W.P. & Kronfeld-Schor, N. (2019). Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecol. Monogr.*, 89, e01334.

Mallory, M.L., Gaston, A.J., Provencher, J.F., Wong, S.N.P., Anderson, C., Elliott, K.H., Gilchrist, H.G., Janssen, M., Lazarus, T., Patterson, A., Pirie-Dominix, L. & Spencer, N.C. (2018). Identifying key marine habitat sites for seabirds and sea ducks in the Canadian Arctic. *Environ. Rev.*, 27, 215–240.

Merkel, F., Labansen, A., Boertmann, D., Mosbech, A., Egevang, C., Falk, K., Linnebjerg, J., Frederiksen, M. & Kampp, K. (2014). Declining trends in the majority of Greenland's thick-billed murre (*Uria lomvia*) colonies 1981–2011. *Polar Biol.*, 37, 1061–1071.

Naalakkersuisut. (2017). januar 2017 om beskyttelse og fangst af fugle. *Selvstyrets Bekendtgør. nr. 1 af 5*, 3–10.

Oswald, S.A. & Arnold, J.M. (2012). Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. *Integr. Zool.*, 7, 121–136.

Piniarneq. (2017). Hunting statistics for Greenland, 1993-2016. Department of Hunting, Fishing and Agriculture. Naalakkersuisut, unpublished data.

Pinngortitaleriffik. (2013). Rådgivning om lomvier, september 2013, 1–8.

R Core Team. (2018). R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna Austria*, URL http://www.R-project.org/.

Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. & Wang, W. (2002). An improved *in situ* and satellite SST analysis for climate. *J. Clim.*, 15, 1609–1625.

Sowa, F. (2015). Kalaalimernit: the Greenlandic taste for local foods in a globalised world. *Polar Rec.*, 51, 290–300.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. *Philos. Trans. R. Soc. Math. Phys. Eng. Sci.*, 369, 842–867.

Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., Strien, A.J. van, Turnhout, C.A.M. van, Vorisek, P. & Willis, S.G. (2016). Consistent response of bird populations to climate change on two continents. *Science*, 352, 84–87.

Stephens, P.A. & Sutherland, W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.*, 14, 401–405.

Sustainable Development Working Group. (2018). *EALLU Abridged Edition 2018*. 2nd Abridged Edition. Arctic Council Secretariat.

Trisos, C.H., Merow, C. & Pigot, A.L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, 580, 496–501.

Tull, C.E., Germain, P. & May, A.W. (1972). Mortality of thick-billed murres in the West Greenland salmon fishery. *Nature*, 237, 42–44.

UN General Assembly. (2007). United Nations declaration on the rights of Indigenous Peoples. *Resolut. 61295*. United Nations, Paris.

Wesche, S.D. & Chan, H.M. (2010). Adapting to the impacts of climate change on food security among Inuit in the Western Canadian Arctic. *EcoHealth*, 7, 361–373.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer, New York.

## Supplementary methods

**Transformations of predictors and the dependent variable for model selection exercises.**

As written in the main text, the response variable growth rate was transformed by adding one to the growth rate and then raising this value to the power of 3 (cubed). Additionally, all continuous predictor in each model selection exercise were log-transformed and then rescaled by subtracting the mean and then dividing by two standard deviations using the *rescale()* function in the *arm* R-package. The transformations were done to improve the distribution of the residuals of the global and top models. The transformation of the response variable and the predictors improved model fit and helped meet the assumptions of linear models.

**Table S1.** Predictor variables of models, their abbreviations, and definitions.

| Predictor | Definition | Type | Abbreviations of transformed predictor | Expected direction of relationship | Associated hypothesis |
|---|---|---|---|---|---|
| $\bar{x}$AT | Mean summer air temperature within 120 km | Continuous | tMAT | - | Warmer summer temperatures increase thermoregulatory costs |
| ΔAT | Summer air temperature change within 120 km | Continuous | tATc | - | Rate of change in summer air temperatures affects thermal regulation of locally adapted populations |
| $\bar{x}$SST | Mean summer SST within 120 km | Continuous | tMSST | +/- | Warmer SST near colonies can effect prey type and availability |
| ΔSST | Summer SST change within 120 km | Continuous | tSSTc | +/- | Rate of change in SST leads to changes in prey availability |
| O | Colony orientation[1] (NE = 292.5°-112.4°, SW = 112.5°-292.4°) | Categorical | tO | - | Colonies facing primarily south or west are exposed to higher levels of solar radiation (insolation) with the potential for increased thermoregulatory costs while at the colony |
| DB | Distance to nearest boat route from colony[2, 3] | Continuous | tDB | - | A decreasing distance to the nearest boating route increases the risk of local anthropogenic effects |
| DS1 | Distance to nearest settlement from colony[3] | Continuous | tDS1 | - | A decreasing distance to the nearest settlement increases the risk of local anthropogenic effects. |
| ADS | Average distance from colony per settlement within 120 km[3] | Continuous | tADS | - | A decreased average distance to settlements within 120 km increases the risk of local anthropogenic effects. |
| ADR | Average distance from colony to settlement per resident within 120 km[3, 4] | Continuous | tADR | - | A decreasing average distance to settlement per resident within 120 km increases the risk of local anthropogenic effects. |
| RS1 | Residents in nearest settlement[4] | Continuous | tRS1 | - | An increasing number of residents in the nearest settlement increase the risk of local anthropogenic effects. |
| SR | Sum of residents within 120 km[4] | Continuous | tSR | - | An increasing number of residents in the nearest settlements increases the risk of local anthropogenic effects. |
| SS | Sum of settlements within 120 km | Continuous | tSS | - | An increasing number of settlements nearby increases the risk of local anthropogenic effects. |
| N | Mean population size of colony during study; *i.e.*, colony size | Continuous | tN | + | Smaller colonies have an increased risk of Allee effects or negative density dependence |

[1] Colony orientation was weighted by the relative abundance of birds on cliffs facing a particular compass direction. This was particularly important for colonies consisting of multiple sub-colonies facing different directions.

[2] Route between two settlements.

[3] Distances were measured using Google Earth Pro (7.3.3.7699 [64-bit]) using the Path function following the most direct boating route for the area confirmed by seamarks, AIS data (https://www.marinetraffic.com [Accessed: October 29, 2019]), and/or local boaters.

[4] The mean number of residents during the study period in the relevant settlements, retrieved from Statistics Greenland (Greenland Statistics [2020] Nuuk: Greenland Statistics. http://bank.stat.gl/pxweb/da/Greenland/Greenland__BE__BE01__BE0120/BEXST4.PX/?rxid=46baea91-559f-4864-a318-87ba275793d8 [Accessed: October 29, 2019]).

**Table S2.** Correlation among predictor variables used in the first model selection exercise using all colonies. Bold values represent correlation coefficients ≥ |0.5|. Predictor definitions provided in Table S1.

| | **tMAT** | **tMSST** | **tATc** | **tSSTc** | **tDB** | **tDS1** | **tADR** | **tN** | **tRS1** | **tSR** | **tSS** | **tADS** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **tMAT** | 1 | | | | | | | | | | | |
| **tMSST** | **0.598166** | 1 | | | | | | | | | | |
| **tATc** | **0.608061** | 0.049405 | 1 | | | | | | | | | |
| **tSSTc** | 0.027164 | **0.504092** | -0.05357 | 1 | | | | | | | | |
| **tDB** | 0.273026 | 0.235201 | -0.0219 | -0.429 | 1 | | | | | | | |
| **tDS1** | 0.193291 | -0.22396 | 0.104704 | -0.43829 | 0.100129 | 1 | | | | | | |
| **tADR** | -0.23338 | -0.16424 | -0.38933 | -0.11256 | 0.039 | **0.589797** | 1 | | | | | |
| **tN** | -0.09188 | -0.34417 | -0.20395 | -0.34959 | -0.10383 | 0.458302 | 0.271352 | 1 | | | | |
| **tRS1** | **0.58488** | **0.563775** | **0.524755** | 0.383902 | -0.06652 | -0.09967 | -0.40106 | -0.48161 | 1 | | | |
| **tSR** | 0.153329 | **0.607058** | 0.070562 | **0.672807** | -0.03337 | -0.30468 | 0.022209 | -0.5111 | **0.649355** | 1 | | |
| **tSS** | **-0.50744** | 0.257202 | **-0.62613** | **0.503995** | -0.1325 | -0.47183 | 0.135801 | -0.39454 | -0.03726 | **0.512562** | 1 | |
| **tADS** | -0.14436 | -0.03561 | -0.39469 | -0.0294 | -0.0148 | **0.614324** | **0.885921** | 0.115745 | -0.13611 | 0.129651 | 0.265102 | 1 |

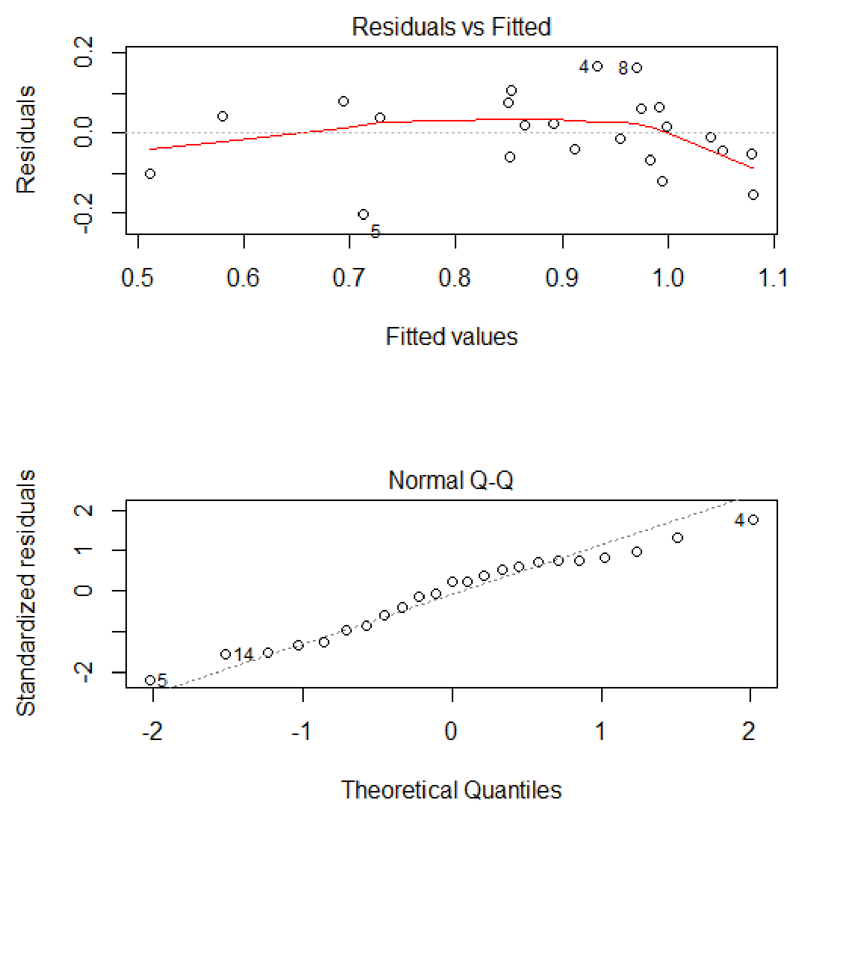



**Figure S1.** Plot of residuals vs. fitted values from the first global model (top) and a Q-Q plot of the residuals (bottom). Residuals from the first global model were normally distributed (Shapiro-Wilks' $W = 0.98$, p = 0.96). For the categorical predictor tO, variance among category levels was homogeneous (Barlett's $K^2_1 = 0.07$, p = 0.80).

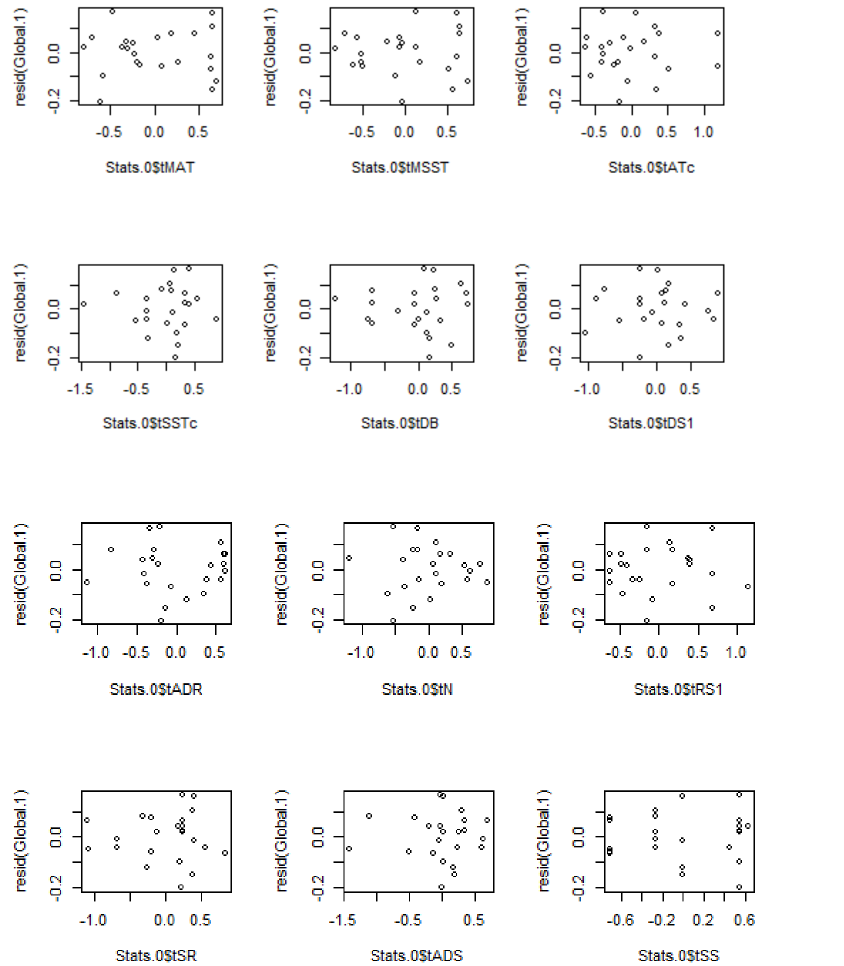



**Figure S2.** Distribution of residuals from the first global model in relation to individual predictors. Predictors are defined in Table S1.

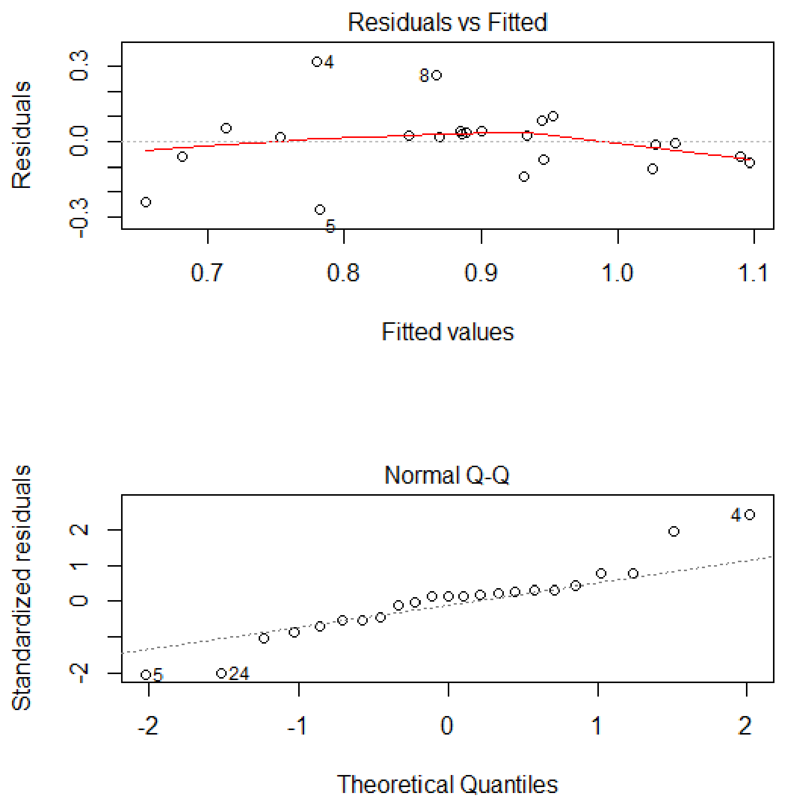



**Figure S3.** Residuals plotted against fitted values from the top model resulting from the first model selection exercise (top) and a Q-Q plot of the residuals (bottom). Residuals from the top model from the first modelling exercise were normally distributed (Shapiro-Wilks' $W = 0.93$, $p = 0.13$).

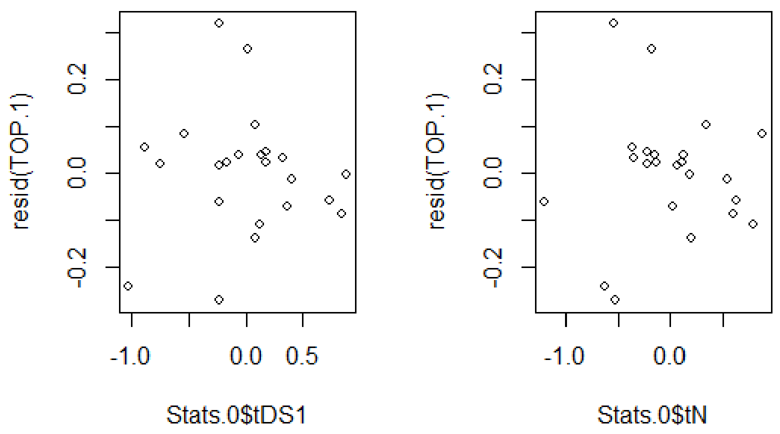



**Figure S4.** Distribution of residuals in relation to predictors in the top model from the first model selection exercise using all colonies. Predictor definitions provided in Table S1.

**Table S3.** Correlation among predictor variables used in the second model selection exercise using only extant colonies. Bold values represent correlation coefficients ≥ |0.5|. Predictor definitions provided in Table S1.

| | tMAT | tMSST | tATc | tSSTc | tDB | tDS1 | tADR | tN | tRS1 | tSR | tSS | tADS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **tMAT** | 1 | | | | | | | | | | | |
| **tMSST** | **0.629555** | 1 | | | | | | | | | | |
| **tATc** | **0.597266** | 0.041156 | 1 | | | | | | | | | |
| **tSSTc** | 0.092738 | **0.528352** | 0.016981 | 1 | | | | | | | | |
| **tDB** | 0.341654 | 0.288452 | -0.10421 | -0.37033 | 1 | | | | | | | |
| **tDS1** | -0.04978 | -0.34995 | -0.09056 | -0.42325 | -0.10092 | 1 | | | | | | |
| **tADR** | -0.30604 | -0.18285 | -0.4146 | -0.09998 | -0.05914 | **0.747976** | 1 | | | | | |
| **tN** | **-0.53564** | **-0.58066** | -0.4181 | -0.4905 | -0.18304 | 0.265354 | 0.26466 | 1 | | | | |
| **tRS1** | **0.654403** | **0.603076** | **0.534293** | 0.428065 | 0.022634 | -0.15228 | -0.35731 | **-0.63674** | 1 | | | |
| **tSR** | 0.265384 | **0.639662** | 0.118989 | **0.688004** | 0.003832 | -0.25663 | 0.053389 | **-0.55149** | **0.68851** | 1 | | |
| **tSS** | -0.38281 | 0.359509 | **-0.64131** | **0.530098** | -0.05113 | -0.26417 | 0.260136 | -0.10197 | -0.07591 | 0.491168 | 1 | |
| **tADS** | -0.1757 | -0.04359 | -0.40938 | -0.04181 | -0.01174 | **0.786627** | **0.912963** | 0.097258 | -0.12712 | 0.140762 | 0.340803 | 1 |

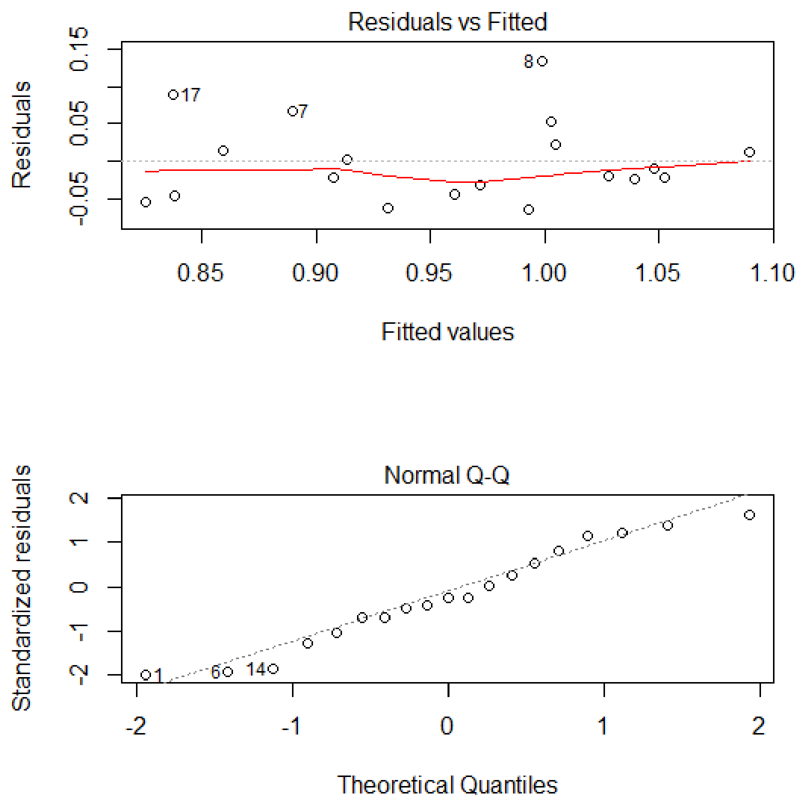



**Figure S5.** Plot of residuals vs. fitted values from the second global model of only extant colonies (top) and a Q-Q plot of the residuals (bottom). Residuals from the second global model were normally distributed (Shapiro-Wilks' $W$ = 0.91, p = 0.07). For the categorical predictor tO, variance among category levels was homogeneous (Barlett's $K^2_1$ = 0.02, p = 0.89).

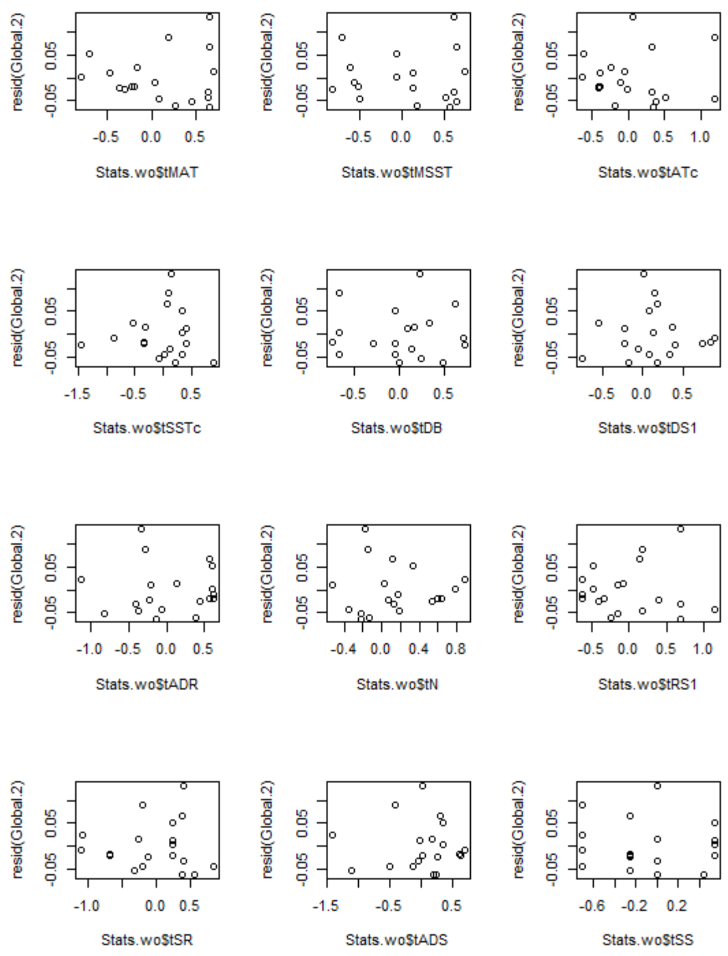
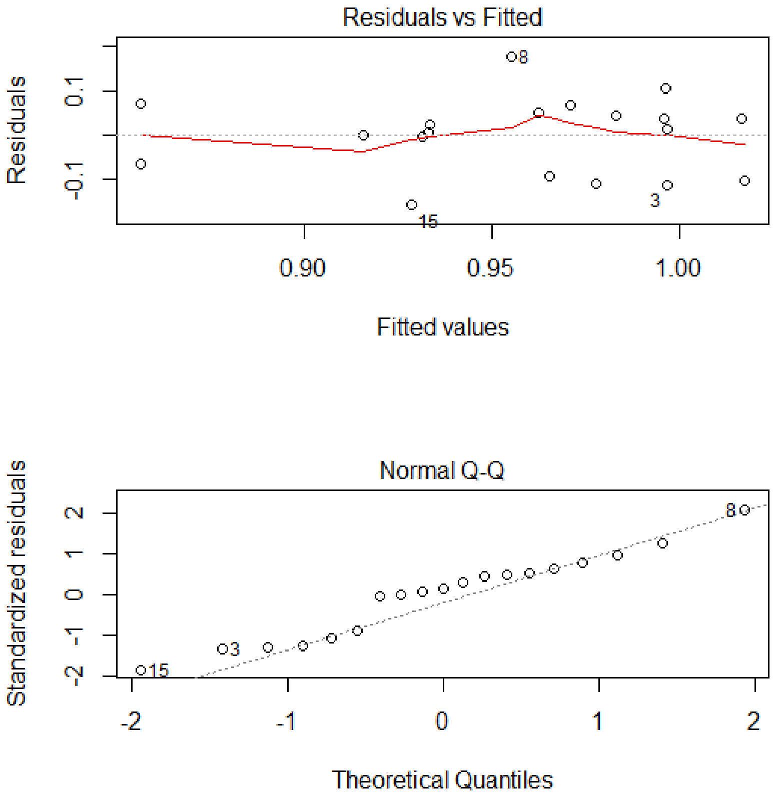



**Figure S6.** Distribution of residuals from the second global model of only extant colonies in relation to individual predictors. Predictors defined in Table S1.



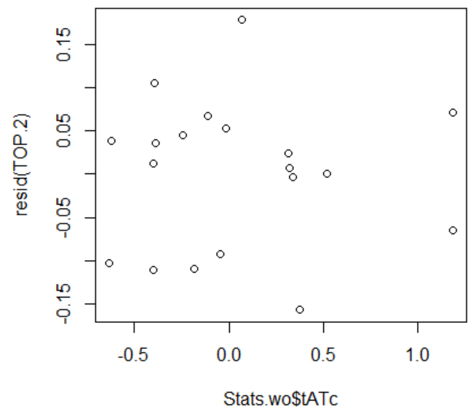




**Figure S7.** Plot of residuals vs. fitted values from the top model resulting from the second model selection exercise including only extant colonies (top) and a Q-Q plot of the residuals (bottom). Residuals from the top model from the first modelling exercise were normally distributed (Shapiro-Wilks' $W = 0.96$, p = 0.50).

**Figure S8.** Distribution of residuals in relation to the predictor tATc from the top model resulting from the second model selection exercise using only extant colonies. Predictor definitions provided in Table S1.

## Supplementary model sets

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel

Global and local anthropogenic threats to a culturally important food animal

Supplementary Model Sets

Supplementary Model Set 1 Page 2

Supplementary Model Set 2 Page 9

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel. Global and local anthropogenic threats to a culturally important food animal
Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 145 | | | | | + | | | + | | | | | | -18.46969072 | 0 | -8.61484395 | 0.047418717 | 74.24882668 |
| 2 | 465 | | | | | + | | + | + | + | | | | | -18.0272191 | 0.44247162 | -8.17237233 | 0.038007413 | 59.51248754 |
| 3 | 401 | | | | | + | | | + | + | | | | | -17.86559328 | 0.604097443 | -8.010746508 | 0.035056754 | 54.89230935 |
| 4 | 657 | | | | | + | | | + | | + | | | | -17.49296299 | 0.976727724 | -7.638116226 | 0.029097526 | 45.56127453 |
| 5 | 177 | | | | | + | + | | + | | | | | | -17.28597943 | 1.183711285 | -7.431132665 | 0.026236757 | 41.08184649 |
| 6 | 161 | | | | | | + | | + | | | | | | -17.28194675 | 1.187743965 | -7.427099985 | 0.026183908 | 40.99909498 |
| 7 | 209 | | | | | + | | + | + | | | | | | -16.96160559 | 1.508085128 | -7.106758823 | 0.022308649 | 34.93116503 |
| 8 | 129 | | | | | | | | + | | | | | | -16.80752299 | 1.66216773 | -6.952676221 | 0.020654499 | 32.34107552 |
| 9 | 419 | | + | | | | + | | + | + | | | | | -16.78339183 | 1.686298892 | -6.928545059 | 0.020406788 | 31.95320629 |
| 10 | 417 | | | | | | + | | + | + | | | | | -16.75846779 | 1.711222927 | -6.903621023 | 0.020154056 | 31.55747579 |
| 11 | 641 | | | | | | | | + | | + | | | | -16.73881153 | 1.730879187 | -6.883964763 | 0.01995695 | 31.24884394 |
| 12 | 433 | | | | | + | + | | + | + | | | | | -16.60121434 | 1.868476379 | -6.746367572 | 0.018630105 | 29.1712544 |
| 13 | 17 | | | | | + | | | | | | | | | -16.4465024 | 2.023188315 | -6.591655636 | 0.017243286 | 26.9997557 |
| 14 | 273 | | | | | + | | | | + | | | | | -16.36760081 | 2.102089908 | -6.512754042 | 0.016576269 | 25.95533098 |
| 15 | 385 | | | | | | | | + | + | | | | | -16.21507778 | 2.254612943 | -6.360231007 | 0.015359137 | 24.0495312 |
| 16 | 913 | | | | | + | | | + | + | + | | | | -15.87672632 | 2.592964404 | -6.021879547 | 0.012968649 | 20.30647445 |
| 17 | 4241 | | | | | + | | | + | | | | | + | -15.86063707 | 2.60905365 | -6.0057903 | 0.01286474 | 20.14377183 |
| 18 | 1169 | | | | | + | | | + | | | + | | | -15.74578388 | 2.723906839 | -5.890937111 | 0.012146774 | 19.01957203 |
| 19 | 153 | | | | + | + | | | + | | | | | | -15.58442072 | 2.885269996 | -5.729573955 | 0.011205246 | 17.54531526 |
| 20 | 449 | | | | | | | + | + | + | | | | | -15.3903606 | 3.079330119 | -5.535513832 | 0.010169082 | 15.92287757 |
| 21 | 163 | | + | | | | + | | + | | | | | | -15.22897451 | 3.24071621 | -5.374127741 | 0.009380743 | 14.68848525 |
| 22 | 2193 | | | | | + | | | + | | | | + | | -15.2249183 | 3.244772423 | -5.370071528 | 0.009361737 | 14.65872562 |
| 23 | 897 | | | | | | | | + | + | + | | | | -15.17447689 | 3.295213832 | -5.319630119 | 0.00912858 | 14.29364538 |
| 24 | 149 | | | + | | + | | | + | | | | | | -15.16614506 | 3.303545664 | -5.311298287 | 0.00909063 | 14.23422311 |
| 25 | 4497 | | | | | + | | | + | + | | | | + | -15.14501202 | 3.324678696 | -5.290165254 | 0.008995079 | 14.08460881 |
| 26 | 387 | | + | | | | | | + | + | | | | | -15.0211915 | 3.448499215 | -5.166344735 | 0.00845508 | 13.23907081 |
| 27 | 649 | | | | + | | | | + | | + | | | | -14.97982056 | 3.489870162 | -5.124973788 | 0.008281979 | 12.96802736 |
| 28 | 193 | | | | | | | + | + | | | | | | -14.92090065 | 3.548790072 | -5.066053878 | 0.008041551 | 12.5915624 |
| 29 | 277 | | | + | | + | | | | + | | | | | -14.80775652 | 3.661934194 | -4.952909756 | 0.007599253 | 11.89900613 |
| 30 | 469 | | | + | | + | | + | + | + | | | | | -14.7847177 | 3.684973022 | -4.929870928 | 0.007512216 | 11.76272301 |
| 31 | 2177 | | | | | | | | + | | | | + | | -14.74963312 | 3.7200576 | -4.89478635 | 0.007381584 | 11.55817727 |
| 32 | 137 | | | | + | | | | + | | | | | | -14.70790308 | 3.761787637 | -4.853056313 | 0.007229163 | 11.3195142 |
| 33 | 665 | | | | + | + | | | + | | + | | | | -14.69255869 | 3.77713203 | -4.837711921 | 0.007173911 | 11.23300096 |
| 34 | 405 | | | + | | + | | | + | + | | | | | -14.61320124 | 3.856489484 | -4.758354466 | 0.006894833 | 10.79601661 |
| 35 | 1425 | | | | | + | | | + | + | | + | | | -14.58465616 | 3.885034557 | -4.729809394 | 0.006797125 | 10.64302446 |
| 36 | 451 | | + | | | | | + | + | + | | | | | -14.56594506 | 3.903745663 | -4.711098288 | 0.006733831 | 10.5439174 |
| 37 | 409 | | | | + | + | | | + | + | | | | | -14.49791901 | 3.971771706 | -4.643072245 | 0.006508644 | 10.1913174 |
| 38 | 131 | | + | | | | | | + | | | | | | -14.45623773 | 4.01345299 | -4.60139096 | 0.006374404 | 9.981121714 |
| 39 | 643 | | + | | | | | | + | | + | | | | -14.43518354 | 4.034507181 | -4.580336769 | 0.006307652 | 9.87660061 |
| 40 | 337 | | | | | + | | + | | + | | | | | -14.29901072 | 4.170679995 | -4.444163956 | 0.00589248 | 9.226520294 |
| 41 | 2449 | | | | | + | | | + | + | | | + | | -14.2986551 | 4.17103562 | -4.44380833 | 0.005891433 | 9.224879847 |
| 42 | 169 | | | | + | | + | | + | | | | | | -14.22165268 | 4.248038037 | -4.366805914 | 0.005668916 | 8.876461136 |
| 43 | 49 | | | | | + | + | | | | | | | | -14.15699156 | 4.312699155 | -4.302144795 | 0.005488568 | 8.594069718 |
| 44 | 133 | | | + | | | | | + | | | | | | -14.11959571 | 4.350095013 | -4.264748937 | 0.005386897 | 8.434871389 |
| 45 | 162 | + | | | | | + | | + | | | | | | -14.11835253 | 4.351338194 | -4.263505757 | 0.00538355 | 8.429629985 |
| 46 | 4273 | | | | | + | + | | + | | | | | + | -14.11124682 | 4.358443902 | -4.256400048 | 0.005364457 | 8.399733877 |
| 47 | 1153 | | | | | | | | + | | | + | | | -14.094568 | 4.375122723 | -4.239721227 | 0.005319906 | 8.329976321 |
| 48 | 1185 | | | | | | + | | + | | | + | | | -14.06269486 | 4.406995861 | -4.207848089 | 0.005235797 | 8.198277281 |
| 49 | 2065 | | | | | + | | | | | | | + | | -13.98231674 | 4.487373983 | -4.127469968 | 0.005029548 | 7.875329175 |
| 50 | 4257 | | | | | | + | | + | | | | | + | -13.97603397 | 4.493656744 | -4.121187206 | 0.005013773 | 7.850628585 |
| 51 | 899 | | + | | | | | | + | + | + | | | | -13.97500286 | 4.494687856 | -4.120156095 | 0.005011188 | 7.846582191 |
| 52 | 2513 | | | | | + | | + | + | + | | | + | | -13.9451038 | 4.524586917 | -4.090257033 | 0.004936831 | 7.730151927 |
| 53 | 305 | | | | | + | + | | | + | | | | | -13.92062979 | 4.549060931 | -4.065783019 | 0.004876787 | 7.636134423 |
| 54 | 4753 | | | | | + | | | + | | + | | | + | -13.9059791 | 4.563711623 | -4.051132327 | 0.004841193 | 7.580401477 |
| 55 | 1201 | | | | | + | + | | + | | | + | | | -13.89311862 | 4.576572096 | -4.038271855 | 0.004810163 | 7.531814087 |
| 56 | 418 | + | | | | | + | | + | + | | | | | -13.86026316 | 4.609427564 | -4.005416387 | 0.004731788 | 7.409094212 |
| 57 | 130 | + | | | | | | | + | | | | | | -13.85054578 | 4.619144941 | -3.99569901 | 0.004708854 | 7.373183044 |
| 58 | 4225 | | | | | | | | + | | | | | + | -13.84901902 | 4.620671697 | -3.994172253 | 0.004705261 | 7.367556663 |
| 59 | 473 | | | | + | + | | + | + | + | | | | | -13.8263988 | 4.64329192 | -3.971552031 | 0.004652343 | 7.284698231 |
| 60 | 21 | | | + | | + | | | | | | | | | -13.79344438 | 4.676246343 | -3.938597608 | 0.004576314 | 7.1656502 |
| 61 | 2705 | | | | | + | | | + | | + | | + | | -13.78829043 | 4.681400286 | -3.933443664 | 0.004564536 | 7.147208294 |
| 62 | 81 | | | | | + | | + | | | | | | | -13.78473693 | 4.68495379 | -3.92989016 | 0.004556433 | 7.134520751 |
| 63 | 642 | + | | | | | | | + | | + | | | | -13.72782603 | 4.741864688 | -3.872979263 | 0.004428605 | 6.934366014 |
| 64 | 2689 | | | | | | | | + | | + | | + | | -13.71122629 | 4.758464426 | -3.856379524 | 0.004392 | 6.87704987 |
| 65 | 393 | | | | + | | | | + | + | | | | | -13.68504568 | 4.78464504 | -3.830198911 | 0.004334882 | 6.787613827 |
| 66 | 185 | | | | + | + | + | | + | | | | | | -13.68040598 | 4.789284743 | -3.825559207 | 0.004324838 | 6.771885821 |
| 67 | 4249 | | | | + | + | | | + | | | | | + | -13.63809134 | 4.831599375 | -3.783244576 | 0.004234297 | 6.630115918 |
| 68 | 4737 | | | | | | | | + | | + | | | + | -13.63619263 | 4.833498084 | -3.781345866 | 0.004230279 | 6.623824573 |
| 69 | 4113 | | | | | + | | | | | | | | + | -13.60135766 | 4.868333057 | -3.746510893 | 0.004157236 | 6.509453121 |
| 70 | 1041 | | | | | + | | | | | | + | | | -13.58800148 | 4.881689241 | -3.733154709 | 0.004129566 | 6.466127222 |
| 71 | 25 | | | | + | + | | | | | | | | | -13.53306631 | 4.936624412 | -3.678219538 | 0.004017681 | 6.290935382 |
| 72 | 529 | | | | | + | | | | | + | | | | -13.50161095 | 4.968079771 | -3.646764179 | 0.003954986 | 6.192767566 |
| 73 | 2257 | | | | | + | | + | + | | | | + | | -13.42485628 | 5.044834442 | -3.570009508 | 0.00380608 | 5.95960828 |
| 74 | 217 | | | | + | + | | + | + | | | | | | -13.37574425 | 5.093946467 | -3.520897484 | 0.003713756 | 5.815046264 |
| 75 | 4369 | | | | | + | | | | + | | | | + | -13.31523877 | 5.154451944 | -3.460392006 | 0.003603087 | 5.641759602 |
| 76 | 213 | | | + | | + | | + | + | | | | | | -13.24580296 | 5.223887756 | -3.390956194 | 0.003480142 | 5.449250613 |
| 77 | 1297 | | | | | + | | | | + | | + | | | -13.21602483 | 5.253665892 | -3.361178059 | 0.00342871 | 5.368717373 |
| 78 | 341 | | | + | | + | | + | | + | | | | | -13.21524002 | 5.254450694 | -3.360393256 | 0.003427365 | 5.366611094 |
| 79 | 425 | | | | + | | + | | + | + | | | | | -13.2148064 | 5.25488432 | -3.35995963 | 0.003426622 | 5.365447669 |
| 80 | 4529 | | | | | + | + | | + | + | | | | + | -13.20906507 | 5.260625648 | -3.354218303 | 0.003416799 | 5.350067359 |

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel. Global and local anthropogenic threats to a culturally important food animal
Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 81 | 2433 | | | | | | | | + | + | | | + | | -13.11804424 | 5.351646476 | -3.263197474 | 0.003264785 | 5.112040999 |
| 82 | 281 | | | | + | + | | | | + | | | | | -13.08669669 | 5.382994025 | -3.231849926 | 0.003214012 | 5.032540685 |
| 83 | 2321 | | | | | + | | | | + | | | + | | -13.06687019 | 5.402820527 | -3.212023424 | 0.003182308 | 4.98289831 |
| 84 | 1441 | | | | | | + | | + | + | | + | | | -13.06649577 | 5.403194954 | -3.211648997 | 0.003181712 | 4.981965533 |
| 85 | 785 | | | | | + | | | | + | + | | | | -13.0640516 | 5.405639117 | -3.209204833 | 0.003177826 | 4.975880882 |
| 86 | 4513 | | | | | | + | | + | + | | | | + | -13.06260396 | 5.407086764 | -3.207757187 | 0.003175527 | 4.972280527 |
| 87 | 1409 | | | | | | | | + | + | | + | | | -13.06004835 | 5.409642373 | -3.205201577 | 0.003171472 | 4.96593098 |
| 88 | 386 | + | | | | | | | + | + | | | | | -13.05270794 | 5.416982782 | -3.197861169 | 0.003159853 | 4.947738406 |
| 89 | 4481 | | | | | | | | + | + | | | | + | -12.92593635 | 5.543754368 | -3.071089582 | 0.002965779 | 4.643854772 |
| 90 | 389 | | | + | | | | | + | + | | | | | -12.91670785 | 5.552982873 | -3.061861077 | 0.002952126 | 4.622476214 |
| 91 | 2241 | | | | | | | + | + | | | | + | | -12.90565406 | 5.564036662 | -3.050807288 | 0.002935855 | 4.596998746 |
| 92 | 2179 | | + | | | | | | + | | | | + | | -12.89681925 | 5.572871466 | -3.041972484 | 0.002922915 | 4.576736741 |
| 93 | 905 | | | | + | | | | + | + | + | | | | -12.8370651 | 5.632625622 | -2.982218329 | 0.002836878 | 4.442019717 |
| 94 | 1443 | | + | | | | + | | + | + | | + | | | -12.74012994 | 5.729560782 | -2.885283169 | 0.00270266 | 4.23185988 |
| 95 | 427 | | + | | + | | + | | + | + | | | | | -12.68027164 | 5.789419084 | -2.825424867 | 0.002622971 | 4.107080491 |
| 96 | 4515 | | + | | | | + | | + | + | | | | + | -12.60522714 | 5.864463581 | -2.750380369 | 0.002526374 | 3.955828989 |
| 97 | 1457 | | | | | + | + | | + | + | | + | | | -12.58773238 | 5.881958341 | -2.732885609 | 0.002504372 | 3.921376753 |
| 98 | 1177 | | | | + | + | | | + | | | + | | | -12.55648088 | 5.913209844 | -2.701634107 | 0.002465543 | 3.860578541 |
| 99 | 4505 | | | | + | + | | | + | + | | | | + | -12.50316931 | 5.966521413 | -2.648322538 | 0.00240069 | 3.759031216 |
| 100 | 441 | | | | + | + | + | | + | + | | | | | -12.44940182 | 6.020288896 | -2.594555054 | 0.002337011 | 3.659320693 |
| 101 | 921 | | | | + | + | | | + | + | + | | | | -12.42274397 | 6.046946744 | -2.567897206 | 0.002306067 | 3.610869504 |
| 102 | 651 | | + | | + | | | | + | | + | | | | -12.37677543 | 6.092915284 | -2.521928666 | 0.002253669 | 3.528822807 |
| 103 | 195 | | + | | | | | + | + | | | | | | -12.24319619 | 6.226494528 | -2.388349422 | 0.002108064 | 3.300832506 |
| 104 | 898 | + | | | | | | | + | + | + | | | | -12.23970495 | 6.229985773 | -2.384858177 | 0.002104387 | 3.295075524 |
| 105 | 201 | | | | + | | | + | + | | | | | | -12.1577542 | 6.311936519 | -2.302907431 | 0.002019902 | 3.162787363 |
| 106 | 4245 | | | + | | + | | | + | | | | | + | -12.15366009 | 6.316030632 | -2.298813318 | 0.002015771 | 3.15631958 |
| 107 | 2961 | | | | | + | | | + | + | + | | + | | -12.12861503 | 6.341075691 | -2.27376826 | 0.001990686 | 3.117040924 |
| 108 | 450 | + | | | | | | + | + | + | | | | | -12.11259661 | 6.357094105 | -2.257749846 | 0.001974806 | 3.092175606 |
| 109 | 395 | | + | | + | | | | + | + | | | | | -12.10384169 | 6.365849029 | -2.248994922 | 0.00196618 | 3.078669308 |
| 110 | 2435 | | + | | | | | | + | + | | | + | | -12.09255455 | 6.377136171 | -2.237707779 | 0.001955115 | 3.061343554 |
| 111 | 2185 | | | | + | | | | + | | | | + | | -12.04098286 | 6.428707857 | -2.186136094 | 0.001905345 | 2.983413298 |
| 112 | 139 | | + | | + | | | | + | | | | | | -12.03623561 | 6.43345511 | -2.181388841 | 0.001900828 | 2.976340186 |
| 113 | 1173 | | | + | | + | | | + | | | + | | | -12.03100664 | 6.438684077 | -2.176159874 | 0.001895865 | 2.968568758 |
| 114 | 5009 | | | | | + | | | + | + | + | | | + | -12.00886054 | 6.46083018 | -2.15401377 | 0.001874987 | 2.935878964 |
| 115 | 2497 | | | | | | | + | + | + | | | + | | -11.99941284 | 6.47027788 | -2.144566071 | 0.001866151 | 2.922043018 |
| 116 | 457 | | | | + | | | + | + | + | | | | | -11.97909423 | 6.490596489 | -2.124247462 | 0.001847288 | 2.892507378 |
| 117 | 135 | | + | + | | | | | + | | | | | | -11.96095693 | 6.508733787 | -2.106110164 | 0.001830612 | 2.866394826 |
| 118 | 197 | | | + | | | | + | + | | | | | | -11.92411579 | 6.545574927 | -2.069269024 | 0.001797199 | 2.814077536 |
| 119 | 2201 | | | | + | + | | | + | | | | + | | -11.88986907 | 6.579821644 | -2.035022306 | 0.001766687 | 2.766301289 |
| 120 | 157 | | | + | + | + | | | + | | | | | | -11.87759443 | 6.592096291 | -2.022747659 | 0.001755878 | 2.749375595 |
| 121 | 1161 | | | | + | | | | + | | | + | | | -11.76577065 | 6.703920068 | -1.910923882 | 0.001660397 | 2.599871293 |
| 122 | 453 | | | + | | | | + | + | + | | | | | -11.73071319 | 6.738977529 | -1.875866421 | 0.001631546 | 2.55469594 |
| 123 | 171 | | + | | + | | + | | + | | | | | | -11.73046857 | 6.739222147 | -1.875621803 | 0.001631347 | 2.554383497 |
| 124 | 141 | | | + | + | | | | + | | | | | | -11.72900963 | 6.740681086 | -1.874162864 | 0.001630157 | 2.552520831 |
| 125 | 4233 | | | | + | | | | + | | | | | + | -11.7246464 | 6.745044323 | -1.869799627 | 0.001626605 | 2.546958274 |
| 126 | 194 | + | | | | | | + | + | | | | | | -11.61497125 | 6.854719474 | -1.760124477 | 0.001539807 | 2.411049762 |
| 127 | 2499 | | + | | | | | + | + | + | | | + | | -11.59299649 | 6.876694234 | -1.738149716 | 0.001522981 | 2.384703644 |
| 128 | 2691 | | + | | | | | | + | | + | | + | | -11.58396248 | 6.885728239 | -1.729115712 | 0.001516118 | 2.373956223 |
| 129 | 4993 | | | | | | | | + | + | + | | | + | -11.54672155 | 6.922969172 | -1.691874779 | 0.001488148 | 2.330161059 |
| 130 | 650 | + | | | + | | | | + | | + | | | | -11.53594392 | 6.933746795 | -1.681097156 | 0.00148015 | 2.317638033 |
| 131 | 1187 | | + | | | | + | | + | | | + | | | -11.50932008 | 6.960370637 | -1.654473313 | 0.001460577 | 2.286990261 |
| 132 | 4259 | | + | | | | + | | + | | | | | + | -11.50895845 | 6.960732273 | -1.654111677 | 0.001460313 | 2.286576769 |
| 133 | 2178 | + | | | | | | | + | | | | + | | -11.49327302 | 6.976417698 | -1.638426252 | 0.001448905 | 2.268713943 |
| 134 | 2945 | | | | | | | | + | + | + | | + | | -11.46827467 | 7.001416049 | -1.613427902 | 0.001430908 | 2.240533374 |
| 135 | 391 | | + | + | | | | | + | + | | | | | -11.41919527 | 7.050495446 | -1.564348504 | 0.001396221 | 2.186220496 |
| 136 | 138 | + | | | + | | | | + | | | | | | -11.4133711 | 7.056319617 | -1.558524333 | 0.001392161 | 2.179863296 |
| 137 | 4373 | | | + | | + | | | | + | | | | + | -11.3946952 | 7.074995523 | -1.539848427 | 0.001379222 | 2.159602579 |
| 138 | 4501 | | | + | | + | | | + | + | | | | + | -11.35796281 | 7.11172791 | -1.503116041 | 0.001354122 | 2.120300917 |
| 139 | 4483 | | + | | | | | | + | + | | | | + | -11.32562975 | 7.14406097 | -1.47078298 | 0.001332406 | 2.086298598 |
| 140 | 4761 | | | | + | + | | | + | | + | | | + | -11.32348015 | 7.146210568 | -1.468633382 | 0.001330975 | 2.084057451 |
| 141 | 2697 | | | | + | | | | + | | + | | + | | -11.3216171 | 7.148073616 | -1.466770334 | 0.001329736 | 2.082117005 |
| 142 | 1411 | | + | | | | | | + | + | | + | | | -11.30079547 | 7.168895247 | -1.445948704 | 0.001315964 | 2.060552914 |
| 143 | 4745 | | | | + | | | | + | | + | | | + | -11.2877624 | 7.181928317 | -1.432915633 | 0.001307416 | 2.047168905 |
| 144 | 1155 | | + | | | | | | + | | | + | | | -11.26230128 | 7.20738944 | -1.407454511 | 0.001290878 | 2.021272483 |
| 145 | 907 | | + | | + | | | | + | + | + | | | | -11.25115155 | 7.218539173 | -1.396304777 | 0.001283701 | 2.01003551 |
| 146 | 1301 | | | + | | + | | | | + | | + | | | -11.16071936 | 7.308971361 | -1.30587259 | 0.00122695 | 1.921173688 |
| 147 | 4227 | | + | | | | | | + | | | | | + | -11.14926302 | 7.320427695 | -1.294416256 | 0.001219942 | 1.910200342 |
| 148 | 2129 | | | | | + | | + | | | | | + | | -11.14896337 | 7.320727346 | -1.294116605 | 0.001219759 | 1.909914167 |
| 149 | 1073 | | | | | + | + | | | | | + | | | -11.12417447 | 7.345516249 | -1.269327701 | 0.001204734 | 1.886387927 |
| 150 | 285 | | | + | + | + | | | | + | | | | | -11.09758248 | 7.372108239 | -1.242735712 | 0.001188822 | 1.861472527 |
| 151 | 1157 | | | + | | | | | + | | | + | | | -11.08337024 | 7.386320479 | -1.228523472 | 0.001180404 | 1.848291568 |
| 152 | 4739 | | + | | | | | | + | | + | | | + | -10.96563611 | 7.504054606 | -1.110789345 | 0.001112923 | 1.742628616 |
| 153 | 4145 | | | | | + | + | | | | | | | + | -10.90719018 | 7.562500543 | -1.052343408 | 0.001080871 | 1.692440726 |
| 154 | 2243 | | + | | | | | + | + | | | | + | | -10.8963552 | 7.573335523 | -1.041508428 | 0.001075031 | 1.683296737 |
| 155 | 57 | | | | + | + | + | | | | | | | | -10.84980844 | 7.619882277 | -0.994961673 | 0.0010503 | 1.644573099 |
| 156 | 85 | | | + | | + | | + | | | | | | | -10.83762856 | 7.632062158 | -0.982781792 | 0.001043923 | 1.634588182 |
| 157 | 134 | + | | + | | | | | + | | | | | | -10.83456437 | 7.635126353 | -0.979717597 | 0.001042325 | 1.632085751 |
| 158 | 4229 | | | + | | | | | + | | | | | + | -10.82158597 | 7.648104746 | -0.966739204 | 0.001035583 | 1.621529115 |
| 159 | 1433 | | | | + | + | | | + | + | | + | | | -10.81055793 | 7.659132792 | -0.955711159 | 0.001029889 | 1.612612572 |
| 160 | 1154 | + | | | | | | | + | | | + | | | -10.80854389 | 7.661146831 | -0.953697119 | 0.001028852 | 1.610989456 |

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel. Global and local anthropogenic threats to a culturally important food animal
Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 161 | 1429 | | | + | | + | | | + | + | | + | | | -10.79221679 | 7.677473933 | -0.937370018 | 0.001020487 | 1.597891598 |
| 162 | 2049 | | | | | | | | | | | | + | | -10.71289065 | 7.756800064 | -0.858043886 | 0.000980804 | 1.535754733 |
| 163 | 2073 | | | | + | + | | | | | | | + | | -10.69697397 | 7.772716753 | -0.842127198 | 0.000973029 | 1.523581173 |
| 164 | 2577 | | | | | + | | | | | + | | + | | -10.67789484 | 7.791795882 | -0.823048069 | 0.000963791 | 1.509115978 |
| 165 | 413 | | | + | + | + | | | + | + | | | | | -10.66835724 | 7.801333481 | -0.81351047 | 0.000959206 | 1.501936439 |
| 166 | 1193 | | | | + | | + | | + | | | + | | | -10.63943244 | 7.830258282 | -0.784585668 | 0.000945433 | 1.480371151 |
| 167 | 4281 | | | | + | + | + | | + | | | | | + | -10.62233352 | 7.847357201 | -0.767486749 | 0.000937385 | 1.467768727 |
| 168 | 459 | | + | | + | | | + | + | + | | | | | -10.62097693 | 7.848713787 | -0.766130163 | 0.000936749 | 1.466773487 |
| 169 | 4265 | | | | + | | + | | + | | | | | + | -10.61867515 | 7.851015566 | -0.763828385 | 0.000935672 | 1.465086364 |
| 170 | 2385 | | | | | + | | + | | + | | | + | | -10.60884977 | 7.860840949 | -0.754003001 | 0.000931086 | 1.457906497 |
| 171 | 345 | | | | + | + | | + | | + | | | | | -10.60535612 | 7.864334595 | -0.750509355 | 0.000929461 | 1.455362015 |
| 172 | 1329 | | | | | + | + | | | + | | + | | | -10.60255829 | 7.86713243 | -0.74771152 | 0.000928162 | 1.453327508 |
| 173 | 170 | + | | | + | | + | | + | | | | | | -10.6008352 | 7.868855524 | -0.745988427 | 0.000927363 | 1.452075937 |
| 174 | 4117 | | | + | | + | | | | | | | | + | -10.59848382 | 7.871206898 | -0.743637052 | 0.000926273 | 1.450369753 |
| 175 | 2713 | | | | + | + | | | + | | + | | + | | -10.57762205 | 7.892068668 | -0.722775282 | 0.000916661 | 1.435319742 |
| 176 | 1045 | | | + | | + | | | | | | + | | | -10.5541498 | 7.915540921 | -0.699303029 | 0.000905966 | 1.418573111 |
| 177 | 4226 | + | | | | | | | + | | | | | + | -10.5438752 | 7.925815523 | -0.689028428 | 0.000901324 | 1.411304161 |
| 178 | 29 | | | + | + | + | | | | | | | | | -10.52504345 | 7.944647274 | -0.670196677 | 0.000892877 | 1.398077863 |
| 179 | 2457 | | | | + | + | | | + | + | | | + | | -10.50892705 | 7.960763669 | -0.654080281 | 0.000885711 | 1.386857145 |
| 180 | 89 | | | | + | + | | + | | | | | | | -10.48275352 | 7.9869372 | -0.627906751 | 0.000874195 | 1.368825914 |
| 181 | 2051 | | + | | | | | | | | | | + | | -10.46214479 | 8.007545927 | -0.607298023 | 0.000865233 | 1.354793456 |
| 182 | 4121 | | | | + | + | | | | | | | | + | -10.45342789 | 8.016262831 | -0.598581119 | 0.000861471 | 1.348901503 |
| 183 | 1186 | + | | | | | + | | + | | | + | | | -10.44451382 | 8.025176894 | -0.589667056 | 0.00085764 | 1.342902784 |
| 184 | 2690 | + | | | | | | | + | | + | | + | | -10.44004766 | 8.029643062 | -0.585200889 | 0.000855726 | 1.339907316 |
| 185 | 4489 | | | | + | | | | + | + | | | | + | -10.41375835 | 8.055932365 | -0.558911585 | 0.000844552 | 1.322409951 |
| 186 | 455 | | + | + | | | | + | + | + | | | | | -10.40793597 | 8.061754753 | -0.553089197 | 0.000842097 | 1.318565758 |
| 187 | 4258 | + | | | | | + | | + | | | | | + | -10.39969458 | 8.069996138 | -0.544847812 | 0.000838634 | 1.313143533 |
| 188 | 4401 | | | | | + | + | | | + | | | | + | -10.35991871 | 8.109772013 | -0.505071937 | 0.00082212 | 1.287285797 |
| 189 | 1049 | | | | + | + | | | | | | + | | | -10.32622987 | 8.14346085 | -0.4713831 | 0.000808388 | 1.265783819 |
| 190 | 4625 | | | | | + | | | | | + | | | + | -10.29426766 | 8.175423057 | -0.439420893 | 0.000795572 | 1.245715977 |
| 191 | 4738 | + | | | | | | | + | | + | | | + | -10.25255435 | 8.217136372 | -0.397707578 | 0.00077915 | 1.220003575 |
| 192 | 537 | | | | + | + | | | | | + | | | | -10.24319363 | 8.226497089 | -0.388346861 | 0.000775512 | 1.214306863 |
| 193 | 1417 | | | | + | | | | + | + | | + | | | -10.20956078 | 8.260129937 | -0.354714013 | 0.00076258 | 1.194057303 |
| 194 | 313 | | | | + | + | + | | | + | | | | | -10.20682468 | 8.262866044 | -0.351977907 | 0.000761537 | 1.192424886 |
| 195 | 2947 | | + | | | | | | + | + | + | | + | | -10.06818814 | 8.401502584 | -0.213341366 | 0.000710537 | 1.112567807 |
| 196 | 2441 | | | | + | | | | + | + | | | + | | -10.06053468 | 8.409156042 | -0.205687909 | 0.000707823 | 1.108318447 |
| 197 | 394 | + | | | + | | | | + | + | | | | | -10.05975953 | 8.409931189 | -0.204912762 | 0.000707549 | 1.107888976 |
| 198 | 477 | | | + | + | + | | + | + | + | | | | | -9.966268823 | 8.503421897 | -0.111422054 | 0.000675235 | 1.057292111 |
| 199 | 397 | | | + | + | | | | + | + | | | | | -9.965315694 | 8.504375026 | -0.110468925 | 0.000674914 | 1.056788363 |
| 200 | 4995 | | + | | | | | | + | + | + | | | + | -9.859357261 | 8.610333458 | -0.004510492 | 0.000640088 | 1.002257791 |
| 201 | 1 | | | | | | | | | | | | | | -9.854846769 | 8.61484395 | 0 | 0.000638646 | 1 |
| 202 | 1209 | | | | + | + | + | | + | | | + | | | -9.852206527 | 8.617484192 | 0.002640242 | 0.000637803 | 0.99868075 |
| 203 | 257 | | | | | | | | | + | | | | | -9.806923335 | 8.662767385 | 0.047923434 | 0.000623525 | 0.976323086 |
| 204 | 4377 | | | | + | + | | | | + | | | | + | -9.772643792 | 8.697046927 | 0.082202977 | 0.000612929 | 0.959731723 |
| 205 | 426 | + | | | + | | + | | + | + | | | | | -9.725221094 | 8.744469625 | 0.129625675 | 0.000598566 | 0.937242864 |
| 206 | 2307 | | + | | | | | | | + | | | + | | -9.696681416 | 8.773009303 | 0.158165353 | 0.000590086 | 0.923963531 |
| 207 | 2187 | | + | | + | | | | + | | | | + | | -9.690142155 | 8.779548564 | 0.164704614 | 0.000588159 | 0.920947445 |
| 208 | 4514 | + | | | | | + | | + | + | | | | + | -9.682921497 | 8.786769222 | 0.171925272 | 0.00058604 | 0.917628517 |
| 209 | 4881 | | | | | + | | | | + | + | | | + | -9.67435473 | 8.795335989 | 0.180492039 | 0.000583535 | 0.913706368 |
| 210 | 1442 | + | | | | | + | | + | + | | + | | | -9.648534123 | 8.821156596 | 0.206312646 | 0.00057605 | 0.901985962 |
| 211 | 2434 | + | | | | | | | + | + | | | + | | -9.632730741 | 8.836959978 | 0.222116028 | 0.000571516 | 0.894886831 |
| 212 | 259 | | + | | | | | | | + | | | | | -9.576104365 | 8.893586354 | 0.278742403 | 0.000555561 | 0.869905058 |
| 213 | 1305 | | | | + | + | | | | + | | + | | | -9.521359503 | 8.948331216 | 0.333487265 | 0.000540561 | 0.846416577 |
| 214 | 4253 | | | + | + | + | | | + | | | | | + | -9.505132912 | 8.964557807 | 0.349713857 | 0.000536193 | 0.839577132 |
| 215 | 2249 | | | | + | | | + | + | | | | + | | -9.441832326 | 9.027858393 | 0.413014442 | 0.000519488 | 0.813420388 |
| 216 | 1410 | + | | | | | | | + | + | | + | | | -9.430197152 | 9.039493567 | 0.424649617 | 0.000516474 | 0.808701982 |
| 217 | 1315 | | + | | | | + | | | + | | + | | | -9.428765612 | 9.040925107 | 0.426081157 | 0.000516105 | 0.808123344 |
| 218 | 199 | | + | + | | | | + | + | | | | | | -9.421336746 | 9.048353973 | 0.433510023 | 0.000514191 | 0.805127192 |
| 219 | 2329 | | | | + | + | | | | + | | | + | | -9.370479404 | 9.099211315 | 0.484367364 | 0.000501281 | 0.78491199 |
| 220 | 793 | | | | + | + | | | | + | + | | | | -9.368658162 | 9.101032557 | 0.486188606 | 0.000500825 | 0.784197558 |
| 221 | 4482 | + | | | | | | | + | + | | | | + | -9.354574616 | 9.115116103 | 0.500272153 | 0.00049731 | 0.778694814 |
| 222 | 906 | + | | | + | | | | + | + | + | | | | -9.35061457 | 9.119076149 | 0.504232199 | 0.000496327 | 0.777154506 |
| 223 | 2833 | | | | | + | | | | + | + | | + | | -9.350545867 | 9.119144852 | 0.504300902 | 0.00049631 | 0.77712781 |
| 224 | 1413 | | | + | | | | | + | + | | + | | | -9.343412188 | 9.126278531 | 0.51143458 | 0.000494542 | 0.774360857 |
| 225 | 2242 | + | | | | | | + | + | | | | + | | -9.33506711 | 9.13462361 | 0.519779659 | 0.000492483 | 0.771136538 |
| 226 | 390 | + | | + | | | | | + | + | | | | | -9.332310233 | 9.137380487 | 0.522536536 | 0.000491805 | 0.770074306 |
| 227 | 2265 | | | | + | + | | + | + | | | | + | | -9.296741763 | 9.172948956 | 0.558105006 | 0.000483136 | 0.756500184 |
| 228 | 143 | | + | + | + | | | | + | | | | | | -9.252908359 | 9.21678236 | 0.601938409 | 0.000472662 | 0.740100564 |
| 229 | 4485 | | | + | | | | | + | + | | | | + | -9.211519282 | 9.258171437 | 0.643327486 | 0.000462981 | 0.724941916 |
| 230 | 4521 | | | | + | | + | | + | + | | | | + | -9.189781663 | 9.279909056 | 0.665065106 | 0.000457976 | 0.717105325 |
| 231 | 221 | | | + | + | + | | + | + | | | | | | -9.169431747 | 9.300258973 | 0.685415022 | 0.00045334 | 0.709845803 |
| 232 | 2521 | | | | + | + | | + | + | + | | | + | | -9.158584906 | 9.311105813 | 0.696261862 | 0.000450888 | 0.706006432 |
| 233 | 291 | | + | | | | + | | | + | | | | | -9.137459708 | 9.332231012 | 0.717387061 | 0.000446151 | 0.698588415 |
| 234 | 349 | | | + | + | + | | + | | + | | | | | -9.129664464 | 9.340026255 | 0.725182305 | 0.000444415 | 0.69587088 |
| 235 | 4537 | | | | + | + | + | | + | + | | | | + | -9.123510653 | 9.346180066 | 0.731336116 | 0.00044305 | 0.693733042 |
| 236 | 203 | | + | | + | | | + | + | | | | | | -9.086661003 | 9.383029716 | 0.768185766 | 0.000434961 | 0.681068165 |
| 237 | 1449 | | | | + | | + | | + | + | | + | | | -9.052954784 | 9.416735935 | 0.801891985 | 0.000427692 | 0.669686228 |
| 238 | 2050 | + | | | | | | | | | | | + | | -8.900009086 | 9.569681633 | 0.954837683 | 0.000396205 | 0.620382633 |
| 239 | 5017 | | | | + | + | | | + | + | + | | | + | -8.871869309 | 9.59782141 | 0.98297746 | 0.000390669 | 0.611715038 |
| 240 | 2305 | | | | | | | | | + | | | + | | -8.862299515 | 9.607391204 | 0.992547254 | 0.000388805 | 0.608795036 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 241 | 205 | | | + | + | | | + | + | | | | | | -8.790684828 | 9.679005891 | 1.064161941 | 0.000375129 | 0.587381374 |
| 242 | 5001 | | | | + | | | | + | + | + | | | + | -8.708236434 | 9.761454285 | 1.146610334 | 0.000359979 | 0.563659368 |
| 243 | 2953 | | | | + | | | | + | + | + | | + | | -8.642259293 | 9.827431426 | 1.212587475 | 0.000348297 | 0.545368406 |
| 244 | 33 | | | | | | + | | | | | | | | -8.641406709 | 9.82828401 | 1.213440059 | 0.000348149 | 0.54513597 |
| 245 | 4235 | | + | | + | | | | + | | | | | + | -8.637532647 | 9.832158072 | 1.217314121 | 0.000347475 | 0.544081047 |
| 246 | 2699 | | + | | + | | | | + | | + | | + | | -8.589550553 | 9.880140166 | 1.265296216 | 0.000339238 | 0.531183306 |
| 247 | 1283 | | + | | | | | | | + | | + | | | -8.570099733 | 9.899590986 | 1.284747036 | 0.000335955 | 0.52604237 |
| 248 | 289 | | | | | | + | | | + | | | | | -8.540922753 | 9.928767967 | 1.313924016 | 0.000331089 | 0.518423912 |
| 249 | 1163 | | + | | + | | | | + | | | + | | | -8.512761092 | 9.956929628 | 1.342085677 | 0.00032646 | 0.511175227 |
| 250 | 4237 | | | + | + | | | | + | | | | | + | -8.486600962 | 9.983089757 | 1.368245807 | 0.000322218 | 0.504532559 |
| 251 | 2498 | + | | | | | | + | + | + | | | + | | -8.444629103 | 10.02506162 | 1.410217666 | 0.000315526 | 0.494054802 |
| 252 | 2443 | | + | | + | | | | + | + | | | + | | -8.439004585 | 10.03068613 | 1.415842184 | 0.00031464 | 0.492667344 |
| 253 | 202 | + | | | + | | | + | + | | | | | | -8.43809144 | 10.03159928 | 1.416755329 | 0.000314496 | 0.492442457 |
| 254 | 1165 | | | + | + | | | | + | | | + | | | -8.411995908 | 10.05769481 | 1.442850861 | 0.00031042 | 0.486058919 |
| 255 | 1025 | | | | | | | | | | | + | | | -8.406400496 | 10.06329022 | 1.448446273 | 0.000309552 | 0.484700969 |
| 256 | 4491 | | + | | + | | | | + | + | | | | + | -8.387589159 | 10.08210156 | 1.46725761 | 0.000306654 | 0.480163406 |
| 257 | 1181 | | | + | + | + | | | + | | | + | | | -8.359993987 | 10.10969673 | 1.494852781 | 0.000302452 | 0.473583805 |
| 258 | 2969 | | | | + | + | | | + | + | + | | + | | -8.347002616 | 10.1226881 | 1.507844153 | 0.000300494 | 0.470517523 |
| 259 | 2186 | + | | | + | | | | + | | | | + | | -8.33690992 | 10.1327808 | 1.517936849 | 0.000298982 | 0.468149109 |
| 260 | 1159 | | + | + | | | | | + | | | + | | | -8.329173804 | 10.14051691 | 1.525672964 | 0.000297827 | 0.466341779 |
| 261 | 198 | + | | + | | | | + | + | | | | | | -8.267222261 | 10.20246846 | 1.587624507 | 0.000288743 | 0.452117918 |
| 262 | 4231 | | + | + | | | | | + | | | | | + | -8.261649075 | 10.20804164 | 1.593197693 | 0.00028794 | 0.450859803 |
| 263 | 1281 | | | | | | | | | + | | + | | | -8.233671465 | 10.23601925 | 1.621175304 | 0.00028394 | 0.444596721 |
| 264 | 258 | + | | | | | | | | + | | | | | -8.216386036 | 10.25330468 | 1.638460733 | 0.000281496 | 0.440770756 |
| 265 | 4747 | | + | | + | | | | + | | + | | | + | -8.178664514 | 10.29102621 | 1.676182255 | 0.000276237 | 0.432535391 |
| 266 | 4994 | + | | | | | | | + | + | + | | | + | -8.145963007 | 10.32372771 | 1.708883761 | 0.000271757 | 0.425520616 |
| 267 | 4097 | | | | | | | | | | | | | + | -8.136336578 | 10.33335414 | 1.718510191 | 0.000270452 | 0.423477415 |
| 268 | 458 | + | | | + | | | + | + | + | | | | | -8.123456997 | 10.34623372 | 1.731389772 | 0.000268716 | 0.420759071 |
| 269 | 3 | | + | | | | | | | | | | | | -8.109681187 | 10.36000953 | 1.745165581 | 0.000266872 | 0.417870881 |
| 270 | 1162 | + | | | + | | | | + | | | + | | | -8.103646642 | 10.36604408 | 1.751200127 | 0.000266068 | 0.416611951 |
| 271 | 2946 | + | | | | | | | + | + | + | | + | | -8.08686243 | 10.38282829 | 1.767984339 | 0.000263844 | 0.413130329 |
| 272 | 399 | | + | + | + | | | | + | + | | | | | -8.061354733 | 10.40833599 | 1.793492036 | 0.0002605 | 0.407894785 |
| 273 | 4523 | | + | | + | | + | | + | + | | | | + | -8.048465471 | 10.42122525 | 1.806381298 | 0.000258827 | 0.405274506 |
| 274 | 4234 | + | | | + | | | | + | | | | | + | -8.019313154 | 10.45037756 | 1.835533614 | 0.000255082 | 0.399410005 |
| 275 | 142 | + | | + | + | | | | + | | | | | | -8.017557167 | 10.45213355 | 1.837289602 | 0.000254858 | 0.39905948 |
| 276 | 1451 | | + | | + | | + | | + | + | | + | | | -7.994341872 | 10.47534885 | 1.860504897 | 0.000251917 | 0.394454118 |
| 277 | 2505 | | | | + | | | + | + | + | | | + | | -7.98829515 | 10.48139557 | 1.866551619 | 0.000251156 | 0.393263342 |
| 278 | 4509 | | | + | + | + | | | + | + | | | | + | -7.914337579 | 10.55535314 | 1.94050919 | 0.000242038 | 0.378986538 |
| 279 | 1419 | | + | | + | | | | + | + | | + | | | -7.901457402 | 10.56823332 | 1.953389367 | 0.000240485 | 0.376553673 |
| 280 | 454 | + | | + | | | | + | + | + | | | | | -7.900790347 | 10.56890037 | 1.954056422 | 0.000240404 | 0.376428103 |
| 281 | 1465 | | | | + | + | + | | + | + | | + | | | -7.870893153 | 10.59879757 | 1.983953615 | 0.000236837 | 0.370842881 |
| 282 | 2113 | | | | | | | + | | | | | + | | -7.851662204 | 10.61802851 | 2.003184565 | 0.000234571 | 0.367294139 |
| 283 | 2561 | | | | | | | | | | + | | + | | -7.824326116 | 10.6453646 | 2.030520653 | 0.000231387 | 0.362308099 |
| 284 | 290 | + | | | | | + | | | + | | | | | -7.816900683 | 10.65279004 | 2.037946086 | 0.000230529 | 0.360965446 |
| 285 | 2057 | | | | + | | | | | | | | + | | -7.806540562 | 10.66315016 | 2.048306206 | 0.000229338 | 0.359100458 |
| 286 | 461 | | | + | + | | | + | + | + | | | | | -7.800064246 | 10.66962647 | 2.054782522 | 0.000228597 | 0.357939514 |
| 287 | 2 | + | | | | | | | | | | | | | -7.723450019 | 10.7462407 | 2.131396749 | 0.000220005 | 0.34448719 |
| 288 | 4267 | | + | | + | | + | | + | | | | | + | -7.612365256 | 10.85732546 | 2.242481512 | 0.000208119 | 0.325875212 |
| 289 | 4353 | | | | | | | | | + | | | | + | -7.565643751 | 10.90404697 | 2.289203017 | 0.000203313 | 0.318350753 |
| 290 | 261 | | | + | | | | | | + | | | | | -7.543670128 | 10.92602059 | 2.31117664 | 0.000201092 | 0.314872237 |
| 291 | 1195 | | + | | + | | + | | + | | | + | | | -7.524698718 | 10.944992 | 2.33014805 | 0.000199193 | 0.311899573 |
| 292 | 1057 | | | | | | + | | | | | + | | | -7.51092248 | 10.95876824 | 2.343924289 | 0.000197826 | 0.309758554 |
| 293 | 2698 | + | | | + | | | | + | | + | | + | | -7.459486401 | 11.01020432 | 2.395360368 | 0.000192803 | 0.301893738 |
| 294 | 2137 | | | | + | + | | + | | | | | + | | -7.431151239 | 11.03853948 | 2.423695529 | 0.000190091 | 0.29764679 |
| 295 | 2115 | | + | | | | | + | | | | | + | | -7.430659254 | 11.03903146 | 2.424187514 | 0.000190044 | 0.29757358 |
| 296 | 1081 | | | | + | + | + | | | | | + | | | -7.404621731 | 11.06506899 | 2.450225038 | 0.000187586 | 0.293724649 |
| 297 | 9 | | | | + | | | | | | | | | | -7.395177709 | 11.07451301 | 2.45966906 | 0.000186702 | 0.292340947 |
| 298 | 1158 | + | | + | | | | | + | | | + | | | -7.365270995 | 11.10441972 | 2.489575774 | 0.000183931 | 0.288001991 |
| 299 | 1313 | | | | | | + | | | + | | + | | | -7.354560086 | 11.11513063 | 2.500286683 | 0.000182949 | 0.286463732 |
| 300 | 4746 | + | | | + | | | | + | | + | | | + | -7.333511783 | 11.13617894 | 2.521334986 | 0.000181034 | 0.283464753 |
| 301 | 4381 | | | + | + | + | | | | + | | | | + | -7.321241208 | 11.14844951 | 2.53360556 | 0.000179926 | 0.281730939 |
| 302 | 2306 | + | | | | | | | | + | | | + | | -7.295383393 | 11.17430733 | 2.559463376 | 0.000177615 | 0.278111911 |
| 303 | 4487 | | + | + | | | | | + | + | | | | + | -7.244250819 | 11.2254399 | 2.610595949 | 0.000173132 | 0.271091745 |
| 304 | 65 | | | | | | | + | | | | | | | -7.225956561 | 11.24373416 | 2.628890208 | 0.000171555 | 0.26862334 |
| 305 | 513 | | | | | | | | | | + | | | | -7.223486953 | 11.24620377 | 2.631359815 | 0.000171344 | 0.268291848 |
| 306 | 5 | | | + | | | | | | | | | | | -7.217102141 | 11.25258858 | 2.637744628 | 0.000170797 | 0.267436717 |
| 307 | 4153 | | | | + | + | + | | | | | | | + | -7.204963561 | 11.26472716 | 2.649883208 | 0.000169764 | 0.265818481 |
| 308 | 1415 | | + | + | | | | | + | + | | + | | | -7.20277201 | 11.26691871 | 2.652074758 | 0.000169578 | 0.265527364 |
| 309 | 2059 | | + | | + | | | | | | | | + | | -7.197995011 | 11.27169571 | 2.656851757 | 0.000169173 | 0.264893908 |
| 310 | 2563 | | + | | | | | | | | + | | + | | -7.158534335 | 11.31115638 | 2.696312433 | 0.000165868 | 0.259718684 |
| 311 | 4230 | + | | + | | | | | + | | | | | + | -7.12543786 | 11.34425286 | 2.729408909 | 0.000163146 | 0.255456164 |
| 312 | 93 | | | + | + | + | | + | | | | | | | -7.118620476 | 11.35107024 | 2.736226293 | 0.000162591 | 0.254586875 |
| 313 | 35 | | + | | | | + | | | | | | | | -7.088300389 | 11.38139033 | 2.76654638 | 0.000160145 | 0.250756435 |
| 314 | 4125 | | | + | + | + | | | | | | | | + | -7.021983338 | 11.44770738 | 2.83286343 | 0.000154922 | 0.242578062 |
| 315 | 265 | | | | + | | | | | + | | | | | -7.009490984 | 11.46019974 | 2.845355785 | 0.000153957 | 0.241067599 |
| 316 | 2585 | | | | + | + | | | | | + | | + | | -6.980315954 | 11.48937476 | 2.874530814 | 0.000151727 | 0.237576546 |
| 317 | 769 | | | | | | | | | + | + | | | | -6.972336547 | 11.49735417 | 2.882510222 | 0.000151123 | 0.236630575 |
| 318 | 2371 | | + | | | | | + | | + | | | + | | -6.962478964 | 11.50721176 | 2.892367805 | 0.00015038 | 0.235467141 |
| 319 | 1309 | | | + | + | + | | | | + | | + | | | -6.954549275 | 11.51514144 | 2.900297494 | 0.000149785 | 0.234535399 |
| 320 | 321 | | | | | | | + | | + | | | | | -6.931036216 | 11.5386545 | 2.923810553 | 0.000148034 | 0.231794222 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 321 | 4355 | | + | | | | | | | + | | | | + | -6.883921967 | 11.58576875 | 2.970924801 | 0.000144588 | 0.22639763 |
| 322 | 1053 | | | + | + | + | | | | | | + | | | -6.872518434 | 11.59717229 | 2.982328335 | 0.000143766 | 0.225110437 |
| 323 | 2507 | | + | | + | | | + | + | + | | | + | | -6.861138481 | 11.60855224 | 2.993708287 | 0.00014295 | 0.223833201 |
| 324 | 1314 | + | | | | | + | | | + | | + | | | -6.861001985 | 11.60868873 | 2.993844784 | 0.00014294 | 0.223817925 |
| 325 | 2251 | | + | | + | | | + | + | | | | + | | -6.854879808 | 11.61481091 | 2.99996696 | 0.000142504 | 0.223133846 |
| 326 | 34 | + | | | | | + | | | | | | | | -6.841176074 | 11.62851464 | 3.013670694 | 0.00014153 | 0.221610189 |
| 327 | 4129 | | | | | | + | | | | | | | + | -6.760826317 | 11.7088644 | 3.094020452 | 0.000135957 | 0.212883497 |
| 328 | 1027 | | + | | | | | | | | | + | | | -6.757096678 | 11.71259404 | 3.097750091 | 0.000135704 | 0.212486877 |
| 329 | 4633 | | | | + | + | | | | | + | | | + | -6.736637334 | 11.73305339 | 3.118209435 | 0.000134323 | 0.210324287 |
| 330 | 323 | | + | | | | | + | | + | | | | | -6.565497559 | 11.90419316 | 3.289349209 | 0.000123307 | 0.193075378 |
| 331 | 5003 | | + | | + | | | | + | + | + | | | + | -6.525960239 | 11.94373048 | 3.32888653 | 0.000120893 | 0.189296016 |
| 332 | 2955 | | + | | + | | | | + | + | + | | + | | -6.515915842 | 11.95377488 | 3.338930927 | 0.000120288 | 0.188347717 |
| 333 | 4266 | + | | | + | | + | | + | | | | | + | -6.490382689 | 11.97930803 | 3.364464079 | 0.000118762 | 0.185958446 |
| 334 | 1194 | + | | | + | | + | | + | | | + | | | -6.475639431 | 11.99405129 | 3.379207338 | 0.000117889 | 0.184592669 |
| 335 | 1282 | + | | | | | | | | + | | + | | | -6.456749147 | 12.01294157 | 3.398097621 | 0.000116781 | 0.182857373 |
| 336 | 267 | | + | | + | | | | | + | | | | | -6.45195372 | 12.017737 | 3.402893048 | 0.000116501 | 0.182419459 |
| 337 | 2393 | | | | + | + | | + | | + | | | + | | -6.426856618 | 12.0428341 | 3.427990151 | 0.000115049 | 0.180144662 |
| 338 | 1337 | | | | + | + | + | | | + | | + | | | -6.401947732 | 12.06774299 | 3.452899037 | 0.000113625 | 0.177914974 |
| 339 | 1059 | | + | | | | + | | | | | + | | | -6.398692071 | 12.07099865 | 3.456154698 | 0.00011344 | 0.177625594 |
| 340 | 263 | | + | + | | | | | | + | | | | | -6.395800534 | 12.07389018 | 3.459046234 | 0.000113276 | 0.177368974 |
| 341 | 1437 | | | + | + | + | | | + | + | | + | | | -6.325084935 | 12.14460578 | 3.529761834 | 0.000109341 | 0.171207173 |
| 342 | 771 | | + | | | | | | | + | + | | | | -6.303063109 | 12.16662761 | 3.551783659 | 0.000108143 | 0.169332367 |
| 343 | 4490 | + | | | + | | | | + | + | | | | + | -6.291814117 | 12.1778766 | 3.563032652 | 0.000107537 | 0.168382631 |
| 344 | 4493 | | | + | + | | | | + | + | | | | + | -6.205777281 | 12.26391344 | 3.649069488 | 0.000103009 | 0.161292669 |
| 345 | 4387 | | + | | | | + | | | + | | | | + | -6.162085754 | 12.30760496 | 3.692761014 | 0.000100783 | 0.157807316 |
| 346 | 4409 | | | | + | + | + | | | + | | | | + | -6.159184784 | 12.31050594 | 3.695661985 | 0.000100637 | 0.157578585 |
| 347 | 4099 | | + | | | | | | | | | | | + | -6.07801227 | 12.39167845 | 3.776834498 | 9.66342E-05 | 0.151311107 |
| 348 | 4385 | | | | | | + | | | + | | | | + | -6.070880503 | 12.39881022 | 3.783966266 | 9.62903E-05 | 0.15077251 |
| 349 | 1026 | + | | | | | | | | | | + | | | -6.047094022 | 12.4225967 | 3.807752747 | 9.51518E-05 | 0.148989958 |
| 350 | 1418 | + | | | + | | | | + | + | | + | | | -6.032130703 | 12.43756002 | 3.822716066 | 9.44426E-05 | 0.147879425 |
| 351 | 2315 | | + | | + | | | | | + | | | + | | -6.024001123 | 12.4456896 | 3.830845645 | 9.40595E-05 | 0.147279546 |
| 352 | 2819 | | + | | | | | | | + | + | | + | | -6.002890758 | 12.46679996 | 3.851956011 | 9.30719E-05 | 0.145733159 |
| 353 | 2442 | + | | | + | | | | + | + | | | + | | -5.994404212 | 12.47528651 | 3.860442557 | 9.26778E-05 | 0.145116084 |
| 354 | 1421 | | | + | + | | | | + | + | | + | | | -5.993119931 | 12.47657079 | 3.861726838 | 9.26183E-05 | 0.145022929 |
| 355 | 2114 | + | | | | | | + | | | | | + | | -5.90639199 | 12.56329873 | 3.948454779 | 8.86879E-05 | 0.138868562 |
| 356 | 463 | | + | + | + | | | + | + | + | | | | | -5.887719624 | 12.5819711 | 3.967127145 | 8.78637E-05 | 0.137578093 |
| 357 | 2369 | | | | | | | + | | + | | | + | | -5.865074345 | 12.60461637 | 3.989772424 | 8.68745E-05 | 0.136029132 |
| 358 | 207 | | + | + | + | | | + | + | | | | | | -5.862553627 | 12.60713709 | 3.992293142 | 8.6765E-05 | 0.135857794 |
| 359 | 398 | + | | + | + | | | | + | + | | | | | -5.846524125 | 12.62316659 | 4.008322644 | 8.60724E-05 | 0.13477328 |
| 360 | 41 | | | | + | | + | | | | | | | | -5.700759935 | 12.76893078 | 4.154086834 | 8.00224E-05 | 0.125300125 |
| 361 | 2817 | | | | | | | | | + | + | | + | | -5.691799641 | 12.77789108 | 4.163047128 | 7.96647E-05 | 0.124740018 |
| 362 | 4889 | | | | + | + | | | | + | + | | | + | -5.672215357 | 12.79747536 | 4.182631412 | 7.88884E-05 | 0.123524507 |
| 363 | 1058 | + | | | | | + | | | | | + | | | -5.669405134 | 12.80028558 | 4.185441634 | 7.87777E-05 | 0.123351063 |
| 364 | 4239 | | + | + | + | | | | + | | | | | + | -5.653239845 | 12.81645087 | 4.201606924 | 7.81435E-05 | 0.122358079 |
| 365 | 1033 | | | | + | | | | | | | + | | | -5.628766914 | 12.8409238 | 4.226079854 | 7.71931E-05 | 0.120869971 |
| 366 | 2562 | + | | | | | | | | | + | | + | | -5.623928642 | 12.84576208 | 4.230918127 | 7.70066E-05 | 0.120577924 |
| 367 | 2058 | + | | | + | | | | | | | | + | | -5.622638673 | 12.84705205 | 4.232208095 | 7.6957E-05 | 0.120500178 |
| 368 | 2313 | | | | + | | | | | + | | | + | | -5.612886983 | 12.85680374 | 4.241959786 | 7.65826E-05 | 0.119914068 |
| 369 | 4098 | + | | | | | | | | | | | | + | -5.582214685 | 12.88747603 | 4.272632083 | 7.54171E-05 | 0.118089078 |
| 370 | 1285 | | | + | | | | | | + | | + | | | -5.522629425 | 12.94706129 | 4.332217344 | 7.32034E-05 | 0.114622785 |
| 371 | 1029 | | | + | | | | | | | | + | | | -5.454569128 | 13.01512159 | 4.40027764 | 7.07542E-05 | 0.110787778 |
| 372 | 299 | | + | | + | | + | | | + | | | | | -5.417858024 | 13.0518327 | 4.436988745 | 6.94673E-05 | 0.108772757 |
| 373 | 4354 | + | | | | | | | | + | | | | + | -5.413711157 | 13.05597956 | 4.441135612 | 6.93234E-05 | 0.108547457 |
| 374 | 11 | | + | | + | | | | | | | | | | -5.375962663 | 13.09372806 | 4.478884106 | 6.80272E-05 | 0.106517919 |
| 375 | 2250 | + | | | + | | | + | + | | | | + | | -5.320608523 | 13.1490822 | 4.534238245 | 6.61703E-05 | 0.103610239 |
| 376 | 322 | + | | | | | | + | | + | | | | | -5.272267442 | 13.19742328 | 4.582579326 | 6.45901E-05 | 0.101135946 |
| 377 | 1323 | | + | | + | | + | | | + | | + | | | -5.260556294 | 13.20913442 | 4.594290474 | 6.4213E-05 | 0.100545468 |
| 378 | 297 | | | | + | | + | | | + | | | | | -5.236798924 | 13.23289179 | 4.618047844 | 6.34547E-05 | 0.099358186 |
| 379 | 4101 | | | + | | | | | | | | | | + | -5.223798658 | 13.24589206 | 4.631048111 | 6.30436E-05 | 0.098714439 |
| 380 | 4609 | | | | | | | | | | + | | | + | -5.221928721 | 13.247762 | 4.632918048 | 6.29847E-05 | 0.098622187 |
| 381 | 1414 | + | | + | | | | | + | + | | + | | | -5.213915682 | 13.25577504 | 4.640931087 | 6.27328E-05 | 0.098227846 |
| 382 | 7 | | + | + | | | | | | | | | | | -5.207699012 | 13.26199171 | 4.647147757 | 6.25381E-05 | 0.097922995 |
| 383 | 1167 | | + | + | + | | | | + | | | + | | | -5.204185135 | 13.26550558 | 4.650661633 | 6.24284E-05 | 0.097751101 |
| 384 | 4105 | | | | + | | | | | | | | | + | -5.179057596 | 13.29063312 | 4.675789172 | 6.16489E-05 | 0.096530661 |
| 385 | 67 | | + | | | | | + | | | | | | | -5.174473646 | 13.29521707 | 4.680373123 | 6.15078E-05 | 0.096309669 |
| 386 | 2841 | | | | + | + | | | | + | + | | + | | -5.156836539 | 13.31285418 | 4.69801023 | 6.09678E-05 | 0.095464091 |
| 387 | 515 | | + | | | | | | | | + | | | | -5.153177714 | 13.31651301 | 4.701669055 | 6.08563E-05 | 0.095289607 |
| 388 | 4486 | + | | + | | | | | + | + | | | | + | -5.139091833 | 13.33059889 | 4.715754936 | 6.04292E-05 | 0.094620846 |
| 389 | 262 | + | | + | | | | | | + | | | | | -5.136296944 | 13.33339377 | 4.718549824 | 6.03448E-05 | 0.094488711 |
| 390 | 4522 | + | | | + | | + | | + | + | | | | + | -5.06945026 | 13.40024046 | 4.785396509 | 5.83612E-05 | 0.091382777 |
| 391 | 1289 | | | | + | | | | | + | | + | | | -5.066495812 | 13.40319491 | 4.788350957 | 5.82751E-05 | 0.091247884 |
| 392 | 266 | + | | | + | | | | | + | | | | | -5.035234783 | 13.43445594 | 4.819611986 | 5.73713E-05 | 0.089832721 |
| 393 | 1291 | | + | | + | | | | | + | | + | | | -5.007200993 | 13.46248973 | 4.847645776 | 5.65728E-05 | 0.088582329 |
| 394 | 4357 | | | + | | | | | | + | | | | + | -4.999061875 | 13.47062884 | 4.855784894 | 5.6343E-05 | 0.088222571 |
| 395 | 10 | + | | | + | | | | | | | | | | -4.94748852 | 13.5222022 | 4.907358249 | 5.49087E-05 | 0.085976685 |
| 396 | 770 | + | | | | | | | | + | + | | | | -4.92134491 | 13.54834581 | 4.933501859 | 5.41956E-05 | 0.084860128 |
| 397 | 1450 | + | | | + | | + | | + | + | | + | | | -4.906375125 | 13.56331559 | 4.948471643 | 5.37914E-05 | 0.08422733 |
| 398 | 1287 | | + | + | | | | | | + | | + | | | -4.882081825 | 13.58760889 | 4.972764944 | 5.3142E-05 | 0.083210439 |
| 399 | 4131 | | + | | | | + | | | | | | | + | -4.86214412 | 13.6075466 | 4.992702649 | 5.26149E-05 | 0.082385047 |
| 400 | 6 | + | | + | | | | | | | | | | | -4.782612292 | 13.68707843 | 5.072234477 | 5.05637E-05 | 0.079173214 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 401 | 514 | + | | | | | | | | | + | | | | -4.779831177 | 13.68985954 | 5.075015591 | 5.04934E-05 | 0.079063196 |
| 402 | 66 | + | | | | | | + | | | | | | | -4.768962791 | 13.70072793 | 5.085883977 | 5.02197E-05 | 0.078634717 |
| 403 | 4386 | + | | | | | + | | | + | | | | + | -4.646929148 | 13.82276157 | 5.207917621 | 4.72471E-05 | 0.073980124 |
| 404 | 206 | + | | + | + | | | + | + | | | | | | -4.611776025 | 13.85791469 | 5.243070744 | 4.64239E-05 | 0.072691169 |
| 405 | 5002 | + | | | + | | | | + | + | + | | | + | -4.586408775 | 13.88328194 | 5.268437994 | 4.58388E-05 | 0.071775004 |
| 406 | 2121 | | | | + | | | + | | | | | + | | -4.566354075 | 13.90333664 | 5.288492694 | 4.53815E-05 | 0.071058887 |
| 407 | 2569 | | | | + | | | | | | + | | + | | -4.561784262 | 13.90790646 | 5.293062507 | 4.52779E-05 | 0.07089671 |
| 408 | 2954 | + | | | + | | | | + | + | + | | + | | -4.531762692 | 13.93792803 | 5.323084076 | 4.46033E-05 | 0.069840442 |
| 409 | 73 | | | | + | | | + | | | | | | | -4.526672429 | 13.94301829 | 5.32817434 | 4.44899E-05 | 0.069662915 |
| 410 | 2370 | + | | | | | | + | | + | | | + | | -4.496656895 | 13.97303382 | 5.358189873 | 4.38272E-05 | 0.068625236 |
| 411 | 13 | | | + | + | | | | | | | | | | -4.458687783 | 14.01100294 | 5.396158985 | 4.3003E-05 | 0.067334705 |
| 412 | 521 | | | | + | | | | | | + | | | | -4.458417007 | 14.01127371 | 5.396429761 | 4.29972E-05 | 0.06732559 |
| 413 | 4130 | + | | | | | + | | | | | | | + | -4.43329073 | 14.03639999 | 5.421556038 | 4.24604E-05 | 0.06648506 |
| 414 | 325 | | | + | | | | + | | + | | | | | -4.432783269 | 14.03690745 | 5.4220635 | 4.24496E-05 | 0.066468193 |
| 415 | 269 | | | + | + | | | | | + | | | | | -4.376144676 | 14.09354604 | 5.478702093 | 4.12644E-05 | 0.064612264 |
| 416 | 69 | | | + | | | | + | | | | | | | -4.289561162 | 14.18012956 | 5.565285607 | 3.95161E-05 | 0.061874768 |
| 417 | 4238 | + | | + | + | | | | + | | | | | + | -4.28735485 | 14.18233587 | 5.567491919 | 3.94725E-05 | 0.061806548 |
| 418 | 4361 | | | | + | | | | | + | | | | + | -4.260716466 | 14.20897425 | 5.594130303 | 3.89502E-05 | 0.060988793 |
| 419 | 4865 | | | | | | | | | + | + | | | + | -4.25880935 | 14.21088137 | 5.596037419 | 3.89131E-05 | 0.060930664 |
| 420 | 1065 | | | | + | | + | | | | | + | | | -4.204763474 | 14.26492724 | 5.650083294 | 3.78757E-05 | 0.059306187 |
| 421 | 1166 | + | | + | + | | | | + | | | + | | | -4.196359938 | 14.27333078 | 5.65848683 | 3.77168E-05 | 0.059057519 |
| 422 | 298 | + | | | + | | + | | | + | | | | | -4.118418957 | 14.35127176 | 5.736427812 | 3.62753E-05 | 0.056800287 |
| 423 | 4495 | | + | + | + | | | | + | + | | | | + | -3.890723359 | 14.57896736 | 5.964123409 | 3.23718E-05 | 0.050688222 |
| 424 | 777 | | | | + | | | | | + | + | | | | -3.808610092 | 14.66108063 | 6.046236677 | 3.10697E-05 | 0.048649277 |
| 425 | 43 | | + | | + | | + | | | | | | | | -3.792949687 | 14.67674103 | 6.061897082 | 3.08273E-05 | 0.04826983 |
| 426 | 329 | | | | + | | | + | | + | | | | | -3.738960164 | 14.73073056 | 6.115886605 | 3.00063E-05 | 0.046984228 |
| 427 | 2506 | + | | | + | | | + | + | + | | | + | | -3.725211164 | 14.74447956 | 6.129635605 | 2.98007E-05 | 0.046662343 |
| 428 | 2123 | | + | | + | | | + | | | | | + | | -3.713775613 | 14.75591511 | 6.141071156 | 2.96308E-05 | 0.046396299 |
| 429 | 1035 | | + | | + | | | | | | | + | | | -3.65301023 | 14.81668049 | 6.201836539 | 2.87441E-05 | 0.045007854 |
| 430 | 1321 | | | | + | | + | | | + | | + | | | -3.63767908 | 14.83201164 | 6.217167688 | 2.85246E-05 | 0.044664162 |
| 431 | 1031 | | + | + | | | | | | | | + | | | -3.629887612 | 14.83980311 | 6.224959157 | 2.84137E-05 | 0.044490501 |
| 432 | 2314 | + | | | + | | | | | + | | | + | | -3.604273072 | 14.86541765 | 6.250573697 | 2.80521E-05 | 0.043924332 |
| 433 | 2818 | + | | | | | | | | + | + | | + | | -3.599082472 | 14.87060825 | 6.255764297 | 2.79794E-05 | 0.043810483 |
| 434 | 4137 | | | | + | | + | | | | | | | + | -3.597933994 | 14.87175672 | 6.256912774 | 2.79633E-05 | 0.043785333 |
| 435 | 42 | + | | | + | | + | | | | | | | | -3.534368884 | 14.93532184 | 6.320477885 | 2.70886E-05 | 0.042415605 |
| 436 | 2571 | | + | | + | | | | | | + | | + | | -3.479474159 | 14.99021656 | 6.375372609 | 2.63552E-05 | 0.04126724 |
| 437 | 4359 | | + | + | | | | | | + | | | | + | -3.316815951 | 15.15287477 | 6.538030817 | 2.42966E-05 | 0.038043866 |
| 438 | 462 | + | | + | + | | | + | + | + | | | | | -3.305878705 | 15.16381201 | 6.548968064 | 2.41641E-05 | 0.037836387 |
| 439 | 1423 | | + | + | + | | | | + | + | | + | | | -3.258081286 | 15.21160943 | 6.596765482 | 2.35934E-05 | 0.036942865 |
| 440 | 4867 | | + | | | | | | | + | + | | | + | -3.181676009 | 15.28801471 | 6.67317076 | 2.27091E-05 | 0.035558168 |
| 441 | 4363 | | + | | + | | | | | + | | | | + | -3.174335153 | 15.29535557 | 6.680511615 | 2.26259E-05 | 0.035427894 |
| 442 | 327 | | + | + | | | | + | | + | | | | | -3.035667898 | 15.43402282 | 6.819178871 | 2.11103E-05 | 0.033054769 |
| 443 | 331 | | + | | + | | | + | | + | | | | | -2.933466113 | 15.53622461 | 6.921380655 | 2.00586E-05 | 0.031408073 |
| 444 | 1034 | + | | | + | | | | | | | + | | | -2.900463454 | 15.56922727 | 6.954383315 | 1.97304E-05 | 0.03089405 |
| 445 | 4611 | | + | | | | | | | | + | | | + | -2.892394462 | 15.57729626 | 6.962452307 | 1.96509E-05 | 0.03076966 |
| 446 | 1286 | + | | + | | | | | | + | | + | | | -2.883137177 | 15.58655354 | 6.971709591 | 1.95602E-05 | 0.030627567 |
| 447 | 271 | | + | + | + | | | | | + | | | | | -2.846400988 | 15.62328973 | 7.00844578 | 1.92042E-05 | 0.030070132 |
| 448 | 1290 | + | | | + | | | | | + | | + | | | -2.840550389 | 15.62914033 | 7.014296379 | 1.91481E-05 | 0.029982296 |
| 449 | 4103 | | + | + | | | | | | | | | | + | -2.801483427 | 15.66820729 | 7.053363341 | 1.87777E-05 | 0.029402321 |
| 450 | 1030 | + | | + | | | | | | | | + | | | -2.796843635 | 15.67284708 | 7.058003134 | 1.87342E-05 | 0.029334189 |
| 451 | 4107 | | + | | + | | | | | | | | | + | -2.776038458 | 15.69365226 | 7.07880831 | 1.85403E-05 | 0.02903062 |
| 452 | 779 | | + | | + | | | | | + | + | | | | -2.755419299 | 15.71427142 | 7.099427469 | 1.83501E-05 | 0.028732864 |
| 453 | 2379 | | + | | + | | | + | | + | | | + | | -2.751477032 | 15.71821369 | 7.103369736 | 1.8314E-05 | 0.028676283 |
| 454 | 1322 | + | | | + | | + | | | + | | + | | | -2.74101074 | 15.72867998 | 7.113836029 | 1.82184E-05 | 0.028526608 |
| 455 | 1067 | | + | | + | | + | | | | | + | | | -2.678735586 | 15.79095513 | 7.176111182 | 1.76599E-05 | 0.027652045 |
| 456 | 4610 | + | | | | | | | | | + | | | + | -2.528561527 | 15.94112919 | 7.326285242 | 1.63824E-05 | 0.025651772 |
| 457 | 4393 | | | | + | | + | | | + | | | | + | -2.514143824 | 15.9555469 | 7.340702945 | 1.62647E-05 | 0.025467517 |
| 458 | 1037 | | | + | + | | | | | | | + | | | -2.327510512 | 16.14218021 | 7.527336257 | 1.48156E-05 | 0.023198489 |
| 459 | 4106 | + | | | + | | | | | | | | | + | -2.277450131 | 16.19224059 | 7.577396638 | 1.44494E-05 | 0.022625033 |
| 460 | 4102 | + | | + | | | | | | | | | | + | -2.276668602 | 16.19302212 | 7.578178167 | 1.44437E-05 | 0.022616194 |
| 461 | 2122 | + | | | + | | | + | | | | | + | | -2.185832192 | 16.28385853 | 7.669014577 | 1.38024E-05 | 0.021611984 |
| 462 | 4395 | | + | | + | | + | | | + | | | | + | -2.171532823 | 16.2981579 | 7.683313945 | 1.37041E-05 | 0.021458017 |
| 463 | 2377 | | | | + | | | + | | + | | | + | | -2.151781309 | 16.31790941 | 7.70306546 | 1.35694E-05 | 0.021247145 |
| 464 | 75 | | + | | + | | | + | | | | | | | -2.144309288 | 16.32538143 | 7.710537481 | 1.35188E-05 | 0.021167914 |
| 465 | 15 | | + | + | + | | | | | | | | | | -2.133599198 | 16.33609152 | 7.721247571 | 1.34466E-05 | 0.021054862 |
| 466 | 523 | | + | | + | | | | | | + | | | | -2.069096174 | 16.40059455 | 7.785750595 | 1.30198E-05 | 0.020386644 |
| 467 | 2825 | | | | + | | | | | + | + | | + | | -2.017410517 | 16.4522802 | 7.837436252 | 1.26877E-05 | 0.019866545 |
| 468 | 4358 | + | | + | | | | | | + | | | | + | -1.975856727 | 16.49383399 | 7.878990042 | 1.24268E-05 | 0.019458038 |
| 469 | 1066 | + | | | + | | + | | | | | + | | | -1.960754869 | 16.50893585 | 7.8940919 | 1.23333E-05 | 0.019311665 |
| 470 | 2570 | + | | | + | | | | | | + | | + | | -1.936648265 | 16.53304245 | 7.918198504 | 1.21856E-05 | 0.019080293 |
| 471 | 71 | | + | + | | | | + | | | | | | | -1.927399413 | 16.54229131 | 7.927447356 | 1.21293E-05 | 0.018992261 |
| 472 | 1293 | | | + | + | | | | | + | | + | | | -1.923869542 | 16.54582118 | 7.930977227 | 1.21079E-05 | 0.018958771 |
| 473 | 4109 | | | + | + | | | | | | | | | + | -1.917607414 | 16.5520833 | 7.937239355 | 1.20701E-05 | 0.018899503 |
| 474 | 4617 | | | | + | | | | | | + | | | + | -1.915046471 | 16.55464425 | 7.939800298 | 1.20546E-05 | 0.018875318 |
| 475 | 4866 | + | | | | | | | | + | + | | | + | -1.863075427 | 16.60661529 | 7.991771342 | 1.17454E-05 | 0.018391151 |
| 476 | 326 | + | | + | | | | + | | + | | | | | -1.845162613 | 16.62452811 | 8.009684156 | 1.16407E-05 | 0.018227168 |
| 477 | 2827 | | + | | + | | | | | + | + | | + | | -1.829496629 | 16.64019409 | 8.025350139 | 1.15499E-05 | 0.018084952 |
| 478 | 4362 | + | | | + | | | | | + | | | | + | -1.696825613 | 16.77286511 | 8.158021156 | 1.08086E-05 | 0.016924203 |
| 479 | 74 | + | | | + | | | + | | | | | | | -1.672169761 | 16.79752096 | 8.182677008 | 1.06761E-05 | 0.016716843 |
| 480 | 522 | + | | | + | | | | | | + | | | | -1.662455458 | 16.80723526 | 8.192391311 | 1.06244E-05 | 0.016635844 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 481 | 14 | + | | + | + | | | | | | | | | | -1.659531418 | 16.8101593 | 8.195315351 | 1.06089E-05 | 0.016611539 |
| 482 | 330 | + | | | + | | | + | | + | | | | | -1.590145729 | 16.87954499 | 8.26470104 | 1.02472E-05 | 0.01604512 |
| 483 | 270 | + | | + | + | | | | | + | | | | | -1.534448551 | 16.93524217 | 8.320398217 | 9.96572E-06 | 0.015604451 |
| 484 | 4494 | + | | + | + | | | | + | + | | | | + | -1.507901859 | 16.96178886 | 8.34694491 | 9.83432E-06 | 0.015398696 |
| 485 | 70 | + | | + | | | | + | | | | | | | -1.479716704 | 16.98997402 | 8.375130065 | 9.6967E-06 | 0.015183211 |
| 486 | 778 | + | | | + | | | | | + | + | | | | -1.331747711 | 17.13794301 | 8.523099058 | 9.00519E-06 | 0.014100436 |
| 487 | 4139 | | + | | + | | + | | | | | | | + | -1.310511896 | 17.15917882 | 8.544334873 | 8.91008E-06 | 0.013951511 |
| 488 | 4365 | | | + | + | | | | | + | | | | + | -1.278481065 | 17.19120965 | 8.576365704 | 8.76852E-06 | 0.013729852 |
| 489 | 77 | | | + | + | | | + | | | | | | | -1.237393809 | 17.23229691 | 8.61745296 | 8.59022E-06 | 0.013450668 |
| 490 | 1422 | + | | + | + | | | | + | + | | + | | | -1.21797519 | 17.25171553 | 8.636871579 | 8.50721E-06 | 0.013320704 |
| 491 | 4138 | + | | | + | | + | | | | | | | + | -0.922042496 | 17.54764822 | 8.932804273 | 7.33713E-06 | 0.011488576 |
| 492 | 1295 | | + | + | + | | | | | + | | + | | | -0.817890272 | 17.65180045 | 9.036956497 | 6.96482E-06 | 0.010905607 |
| 493 | 333 | | | + | + | | | + | | + | | | | | -0.782333171 | 17.68735755 | 9.072513598 | 6.84209E-06 | 0.010713434 |
| 494 | 4394 | + | | | + | | + | | | + | | | | + | -0.718816404 | 17.75087431 | 9.136030365 | 6.62821E-06 | 0.010378539 |
| 495 | 4873 | | | | + | | | | | + | + | | | + | -0.540738388 | 17.92895233 | 9.314108381 | 6.06355E-06 | 0.00949439 |
| 496 | 2378 | + | | | + | | | + | | + | | | + | | -0.298027671 | 18.17166305 | 9.556819098 | 5.37061E-06 | 0.008409363 |
| 497 | 1039 | | + | + | + | | | | | | | + | | | -0.124429592 | 18.34526113 | 9.730417176 | 4.9241E-06 | 0.00771022 |
| 498 | 2826 | + | | | + | | | | | + | + | | + | | 0.585038127 | 19.05472885 | 10.4398849 | 3.45357E-06 | 0.00540764 |
| 499 | 1038 | + | | + | + | | | | | | | + | | | 0.761939873 | 19.23163059 | 10.61678664 | 3.16122E-06 | 0.004949873 |
| 500 | 4619 | | + | | + | | | | | | + | | | + | 0.827132667 | 19.29682339 | 10.68197944 | 3.05983E-06 | 0.004791127 |
| 501 | 4367 | | + | + | + | | | | | + | | | | + | 0.893563411 | 19.36325413 | 10.74841018 | 2.95987E-06 | 0.004634601 |
| 502 | 4111 | | + | + | + | | | | | | | | | + | 0.912004355 | 19.38169507 | 10.76685112 | 2.9327E-06 | 0.004592065 |
| 503 | 4875 | | + | | + | | | | | + | + | | | + | 1.026944255 | 19.49663497 | 10.88179102 | 2.76891E-06 | 0.004335599 |
| 504 | 335 | | + | + | + | | | + | | + | | | | | 1.111570809 | 19.58126153 | 10.96641758 | 2.6542E-06 | 0.004155973 |
| 505 | 4618 | + | | | + | | | | | | + | | | + | 1.191859865 | 19.66155058 | 11.04670663 | 2.54975E-06 | 0.003992438 |
| 506 | 1294 | + | | + | + | | | | | + | | + | | | 1.234015307 | 19.70370603 | 11.08886208 | 2.49657E-06 | 0.003909167 |
| 507 | 4110 | + | | + | + | | | | | | | | | + | 1.441244952 | 19.91093567 | 11.29609172 | 2.25084E-06 | 0.003524397 |
| 508 | 79 | | + | + | + | | | + | | | | | | | 1.504315037 | 19.97400576 | 11.35916181 | 2.18097E-06 | 0.003414989 |
| 509 | 78 | + | | + | + | | | + | | | | | | | 2.029875629 | 20.49956635 | 11.8847224 | 1.67697E-06 | 0.002625822 |
| 510 | 4366 | + | | + | + | | | | | + | | | | + | 2.239958871 | 20.70964959 | 12.09480564 | 1.50976E-06 | 0.002363994 |
| 511 | 334 | + | | + | + | | | + | | + | | | | | 2.343387967 | 20.81307869 | 12.19823474 | 1.43366E-06 | 0.002244848 |
| 512 | 4874 | + | | | + | | | | | + | + | | | + | 2.353493017 | 20.82318374 | 12.20833979 | 1.42644E-06 | 0.002233535 |

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Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | | | + | | | | | | | | | | | -32.9029 | 0 | -2.084317615 | 0.066600031 | 2.835331347 |
| 2 | 261 | | | + | | | | | | + | | | | | -31.88439 | 1.01851403 | -1.065803585 | 0.040022749 | 1.703869417 |
| 3 | 21 | | | + | | + | | | | | | | | | -31.50529 | 1.397614243 | -0.686703372 | 0.033112072 | 1.409664434 |
| 4 | 4101 | | | + | | | | | | | | | | + | -31.18619 | 1.716715874 | -0.367601741 | 0.028228923 | 1.20177649 |
| 5 | 277 | | | + | | + | | | | + | | | | | -30.90314 | 1.99975909 | -0.084558525 | 0.024503734 | 1.043185761 |
| 6 | 69 | | | + | | | | + | | | | | | | -30.82257 | 2.080337081 | -0.003980534 | 0.023536126 | 1.001992249 |
| 7 | 1 | | | | | | | | | | | | | | -30.81859 | 2.084317615 | 0 | 0.023489329 | 1 |
| 8 | 13 | | | + | + | | | | | | | | | | -30.5962 | 2.306706432 | 0.222388818 | 0.021017424 | 0.894764782 |
| 9 | 3 | | + | | | | | | | | | | | | -30.40436 | 2.498548502 | 0.414230887 | 0.019095082 | 0.812925797 |
| 10 | 7 | | + | + | | | | | | | | | | | -30.33364 | 2.569261038 | 0.484943423 | 0.018431746 | 0.784685945 |
| 11 | 17 | | | | | + | | | | | | | | | -29.89305 | 3.009857784 | 0.925540169 | 0.01478741 | 0.629537356 |
| 12 | 263 | | + | + | | | | | | + | | | | | -29.88198 | 3.020925711 | 0.936608096 | 0.014705803 | 0.626063141 |
| 13 | 1029 | | | + | | | | | | | | + | | | -29.84056 | 3.062345164 | 0.978027549 | 0.014404382 | 0.61323088 |
| 14 | 6 | + | | + | | | | | | | | | | | -29.694 | 3.208903509 | 1.124585894 | 0.013386588 | 0.569900812 |
| 15 | 33 | | | | | | + | | | | | | | | -29.69203 | 3.21087478 | 1.126557165 | 0.0133734 | 0.569339374 |
| 16 | 133 | | | + | | | | | + | | | | | | -29.68745 | 3.215453356 | 1.131135741 | 0.013342819 | 0.568037483 |
| 17 | 4357 | | | + | | | | | | + | | | | + | -29.53481 | 3.36808971 | 1.283772095 | 0.012362407 | 0.526298863 |
| 18 | 41 | | | | + | | + | | | | | | | | -29.43727 | 3.465630404 | 1.381312789 | 0.011773954 | 0.501246945 |
| 19 | 4097 | | | | | | | | | | | | | + | -29.22712 | 3.675780916 | 1.591463301 | 0.010599582 | 0.451250956 |
| 20 | 29 | | | + | + | + | | | | | | | | | -29.17829 | 3.724609265 | 1.64029165 | 0.010343936 | 0.440367433 |
| 21 | 9 | | | | + | | | | | | | | | | -29.12277 | 3.780129402 | 1.695811787 | 0.010060736 | 0.428310922 |
| 22 | 269 | | | + | + | | | | | + | | | | | -29.10359 | 3.79931105 | 1.714993435 | 0.009964707 | 0.424222704 |
| 23 | 2 | + | | | | | | | | | | | | | -29.08152 | 3.821381906 | 1.737064291 | 0.009855346 | 0.419566961 |
| 24 | 77 | | | + | + | | | + | | | | | | | -29.0677 | 3.835205283 | 1.750887668 | 0.009787464 | 0.416677043 |
| 25 | 65 | | | | | | | + | | | | | | | -29.04535 | 3.857552023 | 1.773234408 | 0.009678714 | 0.41204727 |
| 26 | 513 | | | | | | | | | | + | | | | -28.83564 | 4.067268667 | 1.982951052 | 0.008715218 | 0.371028824 |
| 27 | 259 | | + | | | | | | | + | | | | | -28.62274 | 4.280163516 | 2.195845901 | 0.007835176 | 0.333563192 |
| 28 | 4229 | | | + | | | | | + | | | | | + | -28.55783 | 4.345076489 | 2.260758874 | 0.007584956 | 0.322910709 |
| 29 | 57 | | | | + | + | + | | | | | | | | -28.5381 | 4.364807481 | 2.280489866 | 0.007510494 | 0.319740697 |
| 30 | 11 | | + | | + | | | | | | | | | | -28.51129 | 4.39161875 | 2.307301135 | 0.007410483 | 0.315482973 |
| 31 | 325 | | | + | | | | + | | + | | | | | -28.4984 | 4.404499687 | 2.320182072 | 0.00736291 | 0.313457644 |
| 32 | 129 | | | | | | | | + | | | | | | -28.47773 | 4.425177926 | 2.340860311 | 0.007287176 | 0.310233464 |
| 33 | 4099 | | + | | | | | | | | | | | + | -28.42142 | 4.48148403 | 2.397166415 | 0.007084881 | 0.301621244 |
| 34 | 1285 | | | + | | | | | | + | | + | | | -28.408 | 4.494901754 | 2.410584139 | 0.007037508 | 0.299604481 |
| 35 | 35 | | + | | | | + | | | | | | | | -28.40325 | 4.499654775 | 2.41533716 | 0.007020803 | 0.298893314 |
| 36 | 262 | + | | + | | | | | | + | | | | | -28.39194 | 4.510959664 | 2.42664205 | 0.006981231 | 0.297208601 |
| 37 | 1025 | | | | | | | | | | | + | | | -28.37217 | 4.530736251 | 2.446418636 | 0.006912538 | 0.294284198 |
| 38 | 49 | | | | | + | + | | | | | | | | -28.35213 | 4.550774167 | 2.466456552 | 0.006843628 | 0.291350498 |
| 39 | 4117 | | | + | | + | | | | | | | | + | -28.32841 | 4.574492589 | 2.490174974 | 0.006762947 | 0.287915718 |
| 40 | 25 | | | | + | + | | | | | | | | | -28.30277 | 4.600137434 | 2.515819819 | 0.006676783 | 0.284247509 |
| 41 | 257 | | | | | | | | | + | | | | | -28.24167 | 4.661229769 | 2.576912154 | 0.006475917 | 0.275696108 |
| 42 | 67 | | + | | | | | + | | | | | | | -28.22058 | 4.68232045 | 2.598002835 | 0.006407985 | 0.272804074 |
| 43 | 85 | | | + | | + | | + | | | | | | | -28.21214 | 4.690763428 | 2.606445813 | 0.00638099 | 0.271654862 |
| 44 | 2049 | | | | | | | | | | | | + | | -28.20022 | 4.702684079 | 2.618366464 | 0.006343071 | 0.270040527 |
| 45 | 389 | | | + | | | | | + | + | | | | | -28.18576 | 4.717147101 | 2.632829486 | 0.006297366 | 0.26809477 |
| 46 | 285 | | | + | + | + | | | | + | | | | | -28.13665 | 4.766257633 | 2.681940018 | 0.006144616 | 0.261591799 |
| 47 | 4103 | | + | + | | | | | | | | | | + | -28.0925 | 4.810400795 | 2.72608318 | 0.00601048 | 0.255881306 |
| 48 | 149 | | | + | | + | | | + | | | | | | -28.09187 | 4.811036498 | 2.726718883 | 0.00600857 | 0.255799987 |
| 49 | 73 | | | | + | | | + | | | | | | | -28.02963 | 4.873272887 | 2.788955272 | 0.005824473 | 0.247962529 |
| 50 | 1027 | | + | | | | | | | | | + | | | -27.99339 | 4.909515579 | 2.825197964 | 0.005719877 | 0.243509583 |
| 51 | 515 | | + | | | | | | | | + | | | | -27.77041 | 5.132495358 | 3.048177743 | 0.005116432 | 0.217819428 |
| 52 | 1045 | | | + | | + | | | | | | + | | | -27.7611 | 5.141806649 | 3.057489034 | 0.005092667 | 0.216807695 |
| 53 | 4109 | | | + | + | | | | | | | | | + | -27.76039 | 5.142518732 | 3.058201117 | 0.005090854 | 0.216730516 |
| 54 | 71 | | + | + | | | | + | | | | | | | -27.74182 | 5.161083512 | 3.076765897 | 0.005043818 | 0.214728047 |
| 55 | 43 | | + | | + | | + | | | | | | | | -27.70919 | 5.193713233 | 3.109395618 | 0.004962196 | 0.211253212 |
| 56 | 15 | | + | + | + | | | | | | | | | | -27.67245 | 5.230451721 | 3.146134106 | 0.004871877 | 0.207408074 |
| 57 | 4129 | | | | | | + | | | | | | | + | -27.53666 | 5.366240231 | 3.281922616 | 0.004552083 | 0.193793657 |
| 58 | 131 | | + | | | | | | + | | | | | | -27.51284 | 5.390065507 | 3.305747892 | 0.004498177 | 0.19149876 |
| 59 | 2065 | | | | | + | | | | | | | + | | -27.48857 | 5.414331363 | 3.330013748 | 0.004443931 | 0.189189358 |
| 60 | 4102 | + | | + | | | | | | | | | | + | -27.43789 | 5.46501351 | 3.380695895 | 0.004332732 | 0.184455332 |
| 61 | 529 | | | | | + | | | | | + | | | | -27.22343 | 5.679471414 | 3.595153799 | 0.00389218 | 0.16569991 |
| 62 | 273 | | | | | + | | | | + | | | | | -27.21885 | 5.68405496 | 3.599737345 | 0.00388327 | 0.165320598 |
| 63 | 10 | + | | | + | | | | | | | | | | -27.20758 | 5.695327881 | 3.611010266 | 0.003861444 | 0.164391396 |
| 64 | 2051 | | + | | | | | | | | | | + | | -27.14883 | 5.754073212 | 3.669755597 | 0.003749672 | 0.159633008 |
| 65 | 70 | + | | + | | | | + | | | | | | | -27.065 | 5.83790638 | 3.753588765 | 0.003595747 | 0.153080036 |
| 66 | 1037 | | | + | + | | | | | | | + | | | -27.05794 | 5.844964519 | 3.760646904 | 0.00358308 | 0.152540758 |
| 67 | 405 | | | + | | + | | | + | + | | | | | -27.0566 | 5.846299147 | 3.761981532 | 0.00358069 | 0.152439 |
| 68 | 75 | | + | | + | | | + | | | | | | | -27.02653 | 5.8763767 | 3.792059085 | 0.003527244 | 0.150163656 |
| 69 | 81 | | | | | + | | + | | | | | | | -27.02084 | 5.882068355 | 3.79775074 | 0.00351722 | 0.149736923 |
| 70 | 4113 | | | | | + | | | | | | | | + | -27.01976 | 5.883140164 | 3.79882255 | 0.003515335 | 0.1496567 |
| 71 | 1031 | | + | + | | | | | | | | + | | | -26.98612 | 5.916783173 | 3.832465558 | 0.003456697 | 0.147160305 |
| 72 | 14 | + | | + | + | | | | | | | | | | -26.95313 | 5.949769428 | 3.865451813 | 0.003400153 | 0.144753077 |
| 73 | 34 | + | | | | | + | | | | | | | | -26.94725 | 5.955654115 | 3.8713365 | 0.003390163 | 0.14432779 |
| 74 | 4098 | + | | | | | | | | | | | | + | -26.92581 | 5.977090353 | 3.892772738 | 0.003354021 | 0.142789128 |
| 75 | 4359 | | + | + | | | | | | + | | | | + | -26.84241 | 6.060491052 | 3.976173437 | 0.003217033 | 0.136957213 |
| 76 | 141 | | | + | + | | | | + | | | | | | -26.83953 | 6.063375932 | 3.979058317 | 0.003212396 | 0.136759802 |
| 77 | 521 | | | | + | | | | | | + | | | | -26.83874 | 6.064168227 | 3.979850612 | 0.003211124 | 0.136705636 |
| 78 | 4373 | | | + | | + | | | | + | | | | + | -26.82527 | 6.077635299 | 3.993317684 | 0.003189574 | 0.135788216 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

| | Top model | Models with delta AICc =< 2 | | | Null model | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
| 79 | 137 | | | | + | | | | + | | | | | | -26.78291 | 6.119997539 | 4.035679924 | 0.003122726 | 0.132942316 |
| 80 | 145 | | | | | + | | | + | | | | | | -26.78213 | 6.120778697 | 4.036461082 | 0.003121506 | 0.132890401 |
| 81 | 271 | | + | + | + | | | | | + | | | | | -26.74186 | 6.161044041 | 4.076726426 | 0.00305929 | 0.130241714 |
| 82 | 1041 | | | | | + | | | | | | + | | | -26.73219 | 6.170715225 | 4.08639761 | 0.003044533 | 0.129613439 |
| 83 | 2113 | | | | | | | + | | | | | + | | -26.68219 | 6.220718165 | 4.13640055 | 0.002969359 | 0.126413086 |
| 84 | 258 | + | | | | | | | | + | | | | | -26.61927 | 6.28363615 | 4.199318535 | 0.0028774 | 0.12249816 |
| 85 | 66 | + | | | | | | + | | | | | | | -26.60131 | 6.301591328 | 4.217273713 | 0.002851683 | 0.121403344 |
| 86 | 135 | | + | + | | | | | + | | | | | | -26.59328 | 6.309619841 | 4.225302226 | 0.002840259 | 0.120916977 |
| 87 | 1301 | | | + | | + | | | | + | | + | | | -26.5406 | 6.362304699 | 4.277987084 | 0.002766416 | 0.117773317 |
| 88 | 1057 | | | | | | + | | | | | + | | | -26.53509 | 6.367816169 | 4.283498554 | 0.002758803 | 0.117449212 |
| 89 | 289 | | | | | | + | | | + | | | | | -26.53055 | 6.372350936 | 4.288033321 | 0.002752555 | 0.117183211 |
| 90 | 341 | | | + | | + | | + | | + | | | | | -26.52662 | 6.376279233 | 4.291961618 | 0.002747154 | 0.116953272 |
| 91 | 4105 | | | | + | | | | | | | | | + | -26.49976 | 6.403144769 | 4.318827155 | 0.002710499 | 0.11539277 |
| 92 | 2081 | | | | | | + | | | | | | + | | -26.43506 | 6.467846407 | 4.383528792 | 0.002624215 | 0.111719457 |
| 93 | 267 | | + | | + | | | | | + | | | | | -26.37942 | 6.523486094 | 4.439168479 | 0.002552216 | 0.108654274 |
| 94 | 1026 | + | | | | | | | | | | + | | | -26.33364 | 6.569260458 | 4.484942843 | 0.002494466 | 0.106195725 |
| 95 | 4485 | | | + | | | | | + | + | | | | + | -26.30896 | 6.59394846 | 4.509630845 | 0.002463864 | 0.104892903 |
| 96 | 1033 | | | | + | | | | | | | + | | | -26.30037 | 6.602532091 | 4.518214476 | 0.002453312 | 0.104443686 |
| 97 | 1287 | | + | + | | | | | | + | | + | | | -26.2951 | 6.607805112 | 4.523487497 | 0.002446852 | 0.104168682 |
| 98 | 4609 | | | | | | | | | | + | | | + | -26.23467 | 6.668231831 | 4.583914216 | 0.00237403 | 0.101068466 |
| 99 | 514 | + | | | | | | | | | + | | | | -26.19451 | 6.708397548 | 4.624079933 | 0.002326829 | 0.099058968 |
| 100 | 4353 | | | | | | | | | + | | | | + | -26.1787 | 6.724201134 | 4.639883519 | 0.002308515 | 0.098279309 |
| 101 | 2057 | | | | + | | | | | | | | + | | -26.17181 | 6.731094536 | 4.646776921 | 0.002300572 | 0.097941153 |
| 102 | 1283 | | + | | | | | | | + | | + | | | -26.17116 | 6.731741765 | 4.64742415 | 0.002299828 | 0.097909463 |
| 103 | 265 | | | | + | | | | | + | | | | | -26.16366 | 6.739239527 | 4.654921912 | 0.002291222 | 0.097543099 |
| 104 | 1030 | + | | + | | | | | | | | + | | | -26.15683 | 6.746077157 | 4.661759543 | 0.002283402 | 0.097210187 |
| 105 | 42 | + | | | + | | + | | | | | | | | -26.14545 | 6.757453239 | 4.673135624 | 0.002270451 | 0.096658821 |
| 106 | 130 | + | | | | | | | + | | | | | | -26.03998 | 6.86291926 | 4.778601645 | 0.002153825 | 0.091693772 |
| 107 | 4225 | | | | | | | | + | | | | | + | -26.0095 | 6.89340377 | 4.809086155 | 0.002121245 | 0.090306749 |
| 108 | 769 | | | | | | | | | + | + | | | | -26.00867 | 6.894230255 | 4.80991264 | 0.002120369 | 0.090269439 |
| 109 | 93 | | | + | + | + | | + | | | | | | | -25.99775 | 6.905157058 | 4.820839443 | 0.002108816 | 0.089777605 |
| 110 | 134 | + | | + | | | | | + | | | | | | -25.98874 | 6.914165919 | 4.829848305 | 0.002099338 | 0.089374117 |
| 111 | 4355 | | + | | | | | | | + | | | | + | -25.98299 | 6.919916239 | 4.835598624 | 0.002093311 | 0.089117522 |
| 112 | 2121 | | | | + | | | + | | | | | + | | -25.97884 | 6.924063955 | 4.83974634 | 0.002088974 | 0.088932896 |
| 113 | 3073 | | | | | | | | | | | + | + | | -25.9748 | 6.928099543 | 4.843781928 | 0.002084763 | 0.088753629 |
| 114 | 2050 | + | | | | | | | | | | | + | | -25.87429 | 7.028611297 | 4.944293682 | 0.001982581 | 0.084403464 |
| 115 | 321 | | | | | | | + | | + | | | | | -25.82612 | 7.076782229 | 4.992464614 | 0.0019354 | 0.082394853 |
| 116 | 4137 | | | | + | | + | | | | | | | + | -25.82546 | 7.077444724 | 4.993127109 | 0.001934759 | 0.082367564 |
| 117 | 4131 | | + | | | | + | | | | | | | + | -25.78636 | 7.116543314 | 5.032225699 | 0.001897303 | 0.080772974 |
| 118 | 333 | | | + | + | | | + | | + | | | | | -25.76408 | 7.138826476 | 5.054508861 | 0.001876281 | 0.07987803 |
| 119 | 2561 | | | | | | | | | | + | | + | | -25.75623 | 7.14667307 | 5.062355455 | 0.001868935 | 0.079565259 |
| 120 | 297 | | | | + | | + | | | + | | | | | -25.73095 | 7.171958285 | 5.08764067 | 0.001845455 | 0.078565679 |
| 121 | 771 | | + | | | | | | | + | + | | | | -25.73093 | 7.171973199 | 5.087655584 | 0.001845441 | 0.078565093 |
| 122 | 2073 | | | | + | + | | | | | | | + | | -25.71308 | 7.189819371 | 5.105501757 | 0.001829048 | 0.077867168 |
| 123 | 2089 | | | | + | | + | | | | | | + | | -25.7116 | 7.191301834 | 5.106984219 | 0.001827692 | 0.077809472 |
| 124 | 327 | | + | + | | | | + | | + | | | | | -25.70813 | 7.194775013 | 5.110457399 | 0.001824521 | 0.077674466 |
| 125 | 1065 | | | | + | | + | | | | | + | | | -25.70798 | 7.194927774 | 5.110610159 | 0.001824382 | 0.077668533 |
| 126 | 1035 | | + | | + | | | | | | | + | | | -25.67685 | 7.22605337 | 5.141735755 | 0.001796209 | 0.076469151 |
| 127 | 89 | | | | + | + | | + | | | | | | | -25.66404 | 7.238865199 | 5.154547584 | 0.001784739 | 0.075980862 |
| 128 | 385 | | | | | | | | + | + | | | | | -25.60897 | 7.293937395 | 5.20961978 | 0.001736265 | 0.073917188 |
| 129 | 291 | | + | | | | + | | | + | | | | | -25.60571 | 7.297198477 | 5.212880862 | 0.001733436 | 0.073796761 |
| 130 | 79 | | + | + | + | | | + | | | | | | | -25.58675 | 7.316150816 | 5.231833202 | 0.001717088 | 0.073100754 |
| 131 | 2177 | | | | | | | | + | | | | + | | -25.53962 | 7.363284252 | 5.278966637 | 0.001677095 | 0.07139815 |
| 132 | 4365 | | | + | + | | | | | + | | | | + | -25.52491 | 7.377995143 | 5.293677528 | 0.001664804 | 0.070874912 |
| 133 | 391 | | + | + | | | | | + | + | | | | | -25.51624 | 7.386668243 | 5.302350628 | 0.0016576 | 0.070568224 |
| 134 | 139 | | + | | + | | | | + | | | | | | -25.49946 | 7.403444696 | 5.319127081 | 0.001643754 | 0.069978758 |
| 135 | 523 | | + | | + | | | | | | + | | | | -25.46712 | 7.435779872 | 5.351462257 | 0.001617392 | 0.068856467 |
| 136 | 1281 | | | | | | | | | + | | + | | | -25.45072 | 7.452181407 | 5.367863792 | 0.001604183 | 0.0682941 |
| 137 | 387 | | + | | | | | | + | + | | | | | -25.42931 | 7.473593305 | 5.389275691 | 0.0015871 | 0.067566847 |
| 138 | 2305 | | | | | | | | | + | | | + | | -25.39038 | 7.512521906 | 5.428204291 | 0.001556507 | 0.066264422 |
| 139 | 4107 | | + | | + | | | | | | | | | + | -25.34571 | 7.557198316 | 5.472880701 | 0.001522123 | 0.064800604 |
| 140 | 4358 | + | | + | | | | | | + | | | | + | -25.30428 | 7.598624583 | 5.514306968 | 0.001490919 | 0.063472186 |
| 141 | 323 | | + | | | | | + | | + | | | | | -25.28647 | 7.61643287 | 5.532115255 | 0.001477703 | 0.062909529 |
| 142 | 281 | | | | + | + | | | | + | | | | | -25.22858 | 7.674322391 | 5.590004777 | 0.001435544 | 0.061114728 |
| 143 | 74 | + | | | + | | | + | | | | | | | -25.20979 | 7.693111731 | 5.608794116 | 0.001422121 | 0.060543264 |
| 144 | 4245 | | | + | | + | | | + | | | | | + | -25.20756 | 7.695341711 | 5.611024096 | 0.001420536 | 0.060475797 |
| 145 | 537 | | | | + | + | | | | | + | | | | -25.20302 | 7.69987935 | 5.615561735 | 0.001417317 | 0.060338744 |
| 146 | 270 | + | | + | + | | | | | + | | | | | -25.1341 | 7.768807993 | 5.684490378 | 0.001369302 | 0.058294636 |
| 147 | 1059 | | + | | | | + | | | | | + | | | -25.04567 | 7.857238535 | 5.77292092 | 0.001310077 | 0.055773275 |
| 148 | 1293 | | | + | + | | | | | + | | + | | | -25.03301 | 7.869891877 | 5.785574262 | 0.001301815 | 0.05542153 |
| 149 | 2321 | | | | | + | | | | + | | | + | | -24.99439 | 7.908511128 | 5.824193513 | 0.001276918 | 0.054361627 |
| 150 | 153 | | | | + | + | | | + | | | | | | -24.93552 | 7.967384047 | 5.883066432 | 0.001239878 | 0.052784736 |
| 151 | 157 | | | + | + | + | | | + | | | | | | -24.90532 | 7.997581733 | 5.913264118 | 0.001221298 | 0.051993734 |
| 152 | 305 | | | | | + | + | | | + | | | | | -24.89856 | 8.004340183 | 5.920022568 | 0.001217178 | 0.051818332 |
| 153 | 4145 | | | | | + | + | | | | | | | + | -24.88827 | 8.01463078 | 5.930313165 | 0.001210931 | 0.051552396 |
| 154 | 2307 | | + | | | | | | | + | | | + | | -24.88482 | 8.01808072 | 5.933763106 | 0.001208844 | 0.051463547 |
| 155 | 2083 | | + | | | | + | | | | | | + | | -24.8659 | 8.036999752 | 5.952682137 | 0.001197463 | 0.050979022 |
| 156 | 4125 | | | + | + | + | | | | | | | | + | -24.85538 | 8.047520559 | 5.963202944 | 0.00119118 | 0.050711556 |

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Predictor abbreviations defined in Supplementary Methods, Table S1.

| | Top model | Models with delta AICc =< 2 | | | Null model | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Model_rank** | **Model_ID** | **tADR** | **tADS** | **tATc** | **tDB** | **tDS1** | **tMAT** | **tMSST** | **tN** | **tO** | **tRS1** | **tSR** | **tSS** | **tSSTc** | **AICc** | **Delta AICc from the top model** | **Delta AICc from the null model** | **Weight** | **Evidence ratio** |
| 157 | 1053 | | | + | + | + | | | | | | + | | | -24.80552 | 8.097384834 | 6.013067219 | 0.001161849 | 0.049462839 |
| 158 | 2097 | | | | | + | + | | | | | | + | | -24.79173 | 8.111172524 | 6.026854909 | 0.001153867 | 0.049123023 |
| 159 | 4611 | | + | | | | | | | | + | | | + | -24.78876 | 8.114145172 | 6.029827557 | 0.001152153 | 0.049050064 |
| 160 | 2059 | | + | | + | | | | | | | | + | | -24.75337 | 8.149538565 | 6.06522095 | 0.001131943 | 0.048189676 |
| 161 | 397 | | | + | + | | | | + | + | | | | | -24.71898 | 8.18392381 | 6.099606195 | 0.001112648 | 0.04736825 |
| 162 | 78 | + | | + | + | | | + | | | | | | | -24.69735 | 8.205555239 | 6.121237624 | 0.001100679 | 0.04685869 |
| 163 | 4227 | | + | | | | | | + | | | | | + | -24.66802 | 8.234879196 | 6.150561581 | 0.001084659 | 0.046176661 |
| 164 | 4231 | | + | + | | | | | + | | | | | + | -24.66782 | 8.235087829 | 6.150770214 | 0.001084546 | 0.046171844 |
| 165 | 2129 | | | | | + | | + | | | | | + | | -24.65454 | 8.248361457 | 6.164043842 | 0.001077372 | 0.045866425 |
| 166 | 2115 | | + | | | | | + | | | | | + | | -24.63249 | 8.270409045 | 6.186091431 | 0.00106556 | 0.045363579 |
| 167 | 1049 | | | | + | + | | | | | | + | | | -24.63091 | 8.271988829 | 6.187671214 | 0.001064719 | 0.045327761 |
| 168 | 1073 | | | | | + | + | | | | | + | | | -24.59464 | 8.308262656 | 6.223945041 | 0.001045582 | 0.044513066 |
| 169 | 4121 | | | | + | + | | | | | | | | + | -24.54648 | 8.356428054 | 6.272110439 | 0.001020702 | 0.043453876 |
| 170 | 4153 | | | | + | + | + | | | | | | | + | -24.47494 | 8.427966024 | 6.343648409 | 0.000984838 | 0.041927045 |
| 171 | 3075 | | + | | | | | | | | | + | + | | -24.44508 | 8.457823943 | 6.373506329 | 0.000970245 | 0.041305766 |
| 172 | 3089 | | | | | + | | | | | | + | + | | -24.43517 | 8.467738049 | 6.383420434 | 0.000965447 | 0.041101518 |
| 173 | 313 | | | | + | + | + | | | + | | | | | -24.41896 | 8.483948172 | 6.399630557 | 0.000957654 | 0.040769734 |
| 174 | 1286 | + | | + | | | | | | + | | + | | | -24.37167 | 8.531234568 | 6.446916953 | 0.000935277 | 0.039817113 |
| 175 | 266 | + | | | + | | | | | + | | | | | -24.36351 | 8.539391279 | 6.455073664 | 0.000931471 | 0.039655056 |
| 176 | 2105 | | | | + | + | + | | | | | | + | | -24.27703 | 8.625870271 | 6.541552656 | 0.000892053 | 0.037976933 |
| 177 | 329 | | | | + | | | + | | + | | | | | -24.27416 | 8.628741448 | 6.544423833 | 0.000890773 | 0.037922453 |
| 178 | 326 | + | | + | | | | + | | + | | | | | -24.2486 | 8.654306365 | 6.56998875 | 0.000879459 | 0.037440796 |
| 179 | 1081 | | | | + | + | + | | | | | + | | | -24.23774 | 8.665159953 | 6.580842338 | 0.000874699 | 0.037238163 |
| 180 | 4130 | + | | | | | + | | | | | | | + | -24.21013 | 8.69276911 | 6.608451495 | 0.000862708 | 0.036727637 |
| 181 | 785 | | | | | + | | | | + | + | | | | -24.20704 | 8.695866244 | 6.611548629 | 0.000861373 | 0.036670806 |
| 182 | 4230 | + | | + | | | | | + | | | | | + | -24.20385 | 8.699050038 | 6.614732423 | 0.000860003 | 0.036612476 |
| 183 | 2577 | | | | | + | | | | | + | | + | | -24.18336 | 8.719545836 | 6.635228221 | 0.000851234 | 0.036239191 |
| 184 | 4237 | | | + | + | | | | + | | | | | + | -24.17403 | 8.728876232 | 6.644558617 | 0.000847272 | 0.036070522 |
| 185 | 299 | | + | | + | | + | | | + | | | | | -24.14132 | 8.761583579 | 6.677265964 | 0.000833529 | 0.035485434 |
| 186 | 4111 | | + | + | + | | | | | | | | | + | -24.13775 | 8.765153589 | 6.680835974 | 0.000832043 | 0.035422149 |
| 187 | 390 | + | | + | | | | | + | + | | | | | -24.1021 | 8.800807195 | 6.716489581 | 0.000817341 | 0.03479628 |
| 188 | 2563 | | + | | | | | | | | + | | + | | -24.01689 | 8.886009987 | 6.801692372 | 0.000783253 | 0.033345042 |
| 189 | 1034 | + | | | + | | | | | | | + | | | -24.01043 | 8.892473372 | 6.808155757 | 0.000780726 | 0.033237455 |
| 190 | 138 | + | | | + | | | | + | | | | | | -23.94449 | 8.958417015 | 6.8740994 | 0.000755403 | 0.032159425 |
| 191 | 2193 | | | | | + | | | + | | | | + | | -23.90974 | 8.993166992 | 6.908849377 | 0.000742392 | 0.031605482 |
| 192 | 4106 | + | | | + | | | | | | | | | + | -23.90214 | 9.000762102 | 6.916444488 | 0.000739578 | 0.031485686 |
| 193 | 522 | + | | | + | | | | | | + | | | | -23.85019 | 9.052716862 | 6.968399247 | 0.000720613 | 0.030678303 |
| 194 | 4385 | | | | | | + | | | + | | | | + | -23.84437 | 9.058532755 | 6.97421514 | 0.00071852 | 0.030589222 |
| 195 | 4354 | + | | | | | | | | + | | | | + | -23.81611 | 9.086791926 | 7.002474311 | 0.000708439 | 0.030160048 |
| 196 | 2137 | | | | + | + | | + | | | | | + | | -23.8083 | 9.094602244 | 7.010284629 | 0.000705678 | 0.030042498 |
| 197 | 1039 | | + | + | + | | | | | | | + | | | -23.7671 | 9.135801129 | 7.051483514 | 0.00069129 | 0.029429969 |
| 198 | 2091 | | + | | + | | + | | | | | | + | | -23.75945 | 9.143451041 | 7.059133426 | 0.000688651 | 0.029317616 |
| 199 | 2179 | | + | | | | | | + | | | | + | | -23.75686 | 9.146039416 | 7.061721801 | 0.00068776 | 0.029279698 |
| 200 | 4369 | | | | | + | | | | + | | | | + | -23.72987 | 9.173030032 | 7.088712417 | 0.000678541 | 0.028887214 |
| 201 | 401 | | | | | + | | | + | + | | | | | -23.67092 | 9.231984359 | 7.147666744 | 0.000658832 | 0.028048128 |
| 202 | 3081 | | | | + | | | | | | | + | + | | -23.60153 | 9.301377722 | 7.217060107 | 0.000636364 | 0.027091641 |
| 203 | 4625 | | | | | + | | | | | + | | | + | -23.5824 | 9.320505046 | 7.236187431 | 0.000630308 | 0.026833781 |
| 204 | 1297 | | | | | + | | | | + | | + | | | -23.58156 | 9.321343834 | 7.237026219 | 0.000630043 | 0.026822529 |
| 205 | 290 | + | | | | | + | | | + | | | | | -23.5778 | 9.325104346 | 7.240786731 | 0.00062886 | 0.026772143 |
| 206 | 337 | | | | | + | | + | | + | | | | | -23.5754 | 9.327499953 | 7.243182338 | 0.000628107 | 0.026740095 |
| 207 | 1067 | | + | | + | | + | | | | | + | | | -23.56394 | 9.338968685 | 7.25465107 | 0.000624515 | 0.026587196 |
| 208 | 777 | | | | + | | | | | + | + | | | | -23.55529 | 9.347611794 | 7.263294179 | 0.000621822 | 0.026472546 |
| 209 | 1282 | + | | | | | | | | + | | + | | | -23.53589 | 9.367014957 | 7.282697342 | 0.000615819 | 0.026216962 |
| 210 | 2058 | + | | | + | | | | | | | | + | | -23.52575 | 9.37715644 | 7.292838825 | 0.000612704 | 0.026084359 |
| 211 | 393 | | | | + | | | | + | + | | | | | -23.49834 | 9.404559952 | 7.320242337 | 0.000604366 | 0.025729395 |
| 212 | 2185 | | | | + | | | | + | | | | + | | -23.49121 | 9.411689819 | 7.327372204 | 0.000602216 | 0.025637835 |
| 213 | 4139 | | + | | + | | + | | | | | | | + | -23.48286 | 9.420040789 | 7.335723174 | 0.000599706 | 0.025531007 |
| 214 | 1291 | | + | | + | | | | | + | | + | | | -23.43679 | 9.466112598 | 7.381794983 | 0.000586049 | 0.0249496 |
| 215 | 4110 | + | | + | + | | | | | | | | | + | -23.41495 | 9.487948841 | 7.403631226 | 0.000579686 | 0.024678679 |
| 216 | 1058 | + | | | | | + | | | | | + | | | -23.37547 | 9.527429398 | 7.443111783 | 0.000568355 | 0.024196292 |
| 217 | 2569 | | | | + | | | | | | + | | + | | -23.32409 | 9.578818547 | 7.494500932 | 0.000553937 | 0.023582498 |
| 218 | 143 | | + | + | + | | | | + | | | | | | -23.30772 | 9.595186031 | 7.510868416 | 0.000549422 | 0.023390292 |
| 219 | 2114 | + | | | | | | + | | | | | + | | -23.30419 | 9.598711721 | 7.514394106 | 0.000548455 | 0.023349095 |
| 220 | 4241 | | | | | + | | | + | | | | | + | -23.27807 | 9.624833651 | 7.540516036 | 0.000541338 | 0.023046116 |
| 221 | 770 | + | | | | | | | | + | + | | | | -23.27142 | 9.631482325 | 7.54716471 | 0.000539541 | 0.02296963 |
| 222 | 331 | | + | | + | | | + | | + | | | | | -23.26908 | 9.633822427 | 7.549504812 | 0.00053891 | 0.02294277 |
| 223 | 2123 | | + | | + | | | + | | | | | + | | -23.23675 | 9.66614943 | 7.581831815 | 0.00053027 | 0.022574916 |
| 224 | 4617 | | | | + | | | | | | + | | | + | -23.22997 | 9.672931027 | 7.588613412 | 0.000528475 | 0.022498498 |
| 225 | 2082 | + | | | | | + | | | | | | + | | -23.20649 | 9.696416947 | 7.612099332 | 0.000522305 | 0.022235845 |
| 226 | 4610 | + | | | | | | | | | + | | | + | -23.2043 | 9.698600147 | 7.614282532 | 0.000521735 | 0.022211585 |
| 227 | 322 | + | | | | | | + | | + | | | | | -23.18959 | 9.713309776 | 7.628992161 | 0.000517912 | 0.022048822 |
| 228 | 413 | | | + | + | + | | | + | + | | | | | -23.17745 | 9.725457593 | 7.641139978 | 0.000514776 | 0.021915306 |
| 229 | 4226 | + | | | | | | | + | | | | | + | -23.16949 | 9.733410611 | 7.649092996 | 0.000512733 | 0.021828332 |
| 230 | 3329 | | | | | | | | | + | | + | + | | -23.14629 | 9.756615011 | 7.672297396 | 0.000506818 | 0.021576539 |
| 231 | 386 | + | | | | | | | + | + | | | | | -23.13133 | 9.771569381 | 7.687251766 | 0.000503043 | 0.021415809 |
| 232 | 4233 | | | | + | | | | + | | | | | + | -23.09956 | 9.803340119 | 7.719022504 | 0.000495115 | 0.021078299 |
| 233 | 395 | | + | | + | | | | + | + | | | | | -23.07751 | 9.825395529 | 7.741077915 | 0.000489685 | 0.020847131 |
| 234 | 349 | | | + | + | + | | + | | + | | | | | -23.06477 | 9.838131518 | 7.753813903 | 0.000486577 | 0.020714798 |

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel. Global and local anthropogenic threats to a culturally important food animal
Predictor abbreviations defined in Supplementary Methods, Table S1.

| | Top model | Models with delta AICc =< 2 | | Null model | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
| 235 | 2369 | | | | | | | + | | + | | | + | | -23.04174 | 9.86116328 | 7.776845665 | 0.000481005 | 0.020477617 |
| 236 | 3074 | + | | | | | | | | | | + | + | | -23.0293 | 9.873608751 | 7.789291136 | 0.000478022 | 0.020350586 |
| 237 | 2306 | + | | | | | | | | + | | | + | | -23.02538 | 9.87751953 | 7.793201916 | 0.000477088 | 0.020310832 |
| 238 | 4501 | | | + | | + | | | + | + | | | | + | -23.0065 | 9.896403014 | 7.812085399 | 0.000472604 | 0.020119964 |
| 239 | 779 | | + | | + | | | | | + | + | | | | -22.99281 | 9.910091818 | 7.825774203 | 0.000469381 | 0.019982726 |
| 240 | 4361 | | | | + | | | | | + | | | | + | -22.98212 | 9.920788628 | 7.836471013 | 0.000466877 | 0.019876135 |
| 241 | 1309 | | | + | + | + | | | | + | | + | | | -22.97431 | 9.928593326 | 7.844275711 | 0.000465059 | 0.019798723 |
| 242 | 4381 | | | + | + | + | | | | + | | | | + | -22.95608 | 9.946826351 | 7.862508736 | 0.000460838 | 0.019619048 |
| 243 | 2313 | | | | + | | | | | + | | | + | | -22.92329 | 9.979615326 | 7.895297711 | 0.000453345 | 0.019300026 |
| 244 | 2329 | | | | + | + | | | | + | | | + | | -22.91985 | 9.983052551 | 7.898734936 | 0.000452566 | 0.019266885 |
| 245 | 1289 | | | | + | | | | | + | | + | | | -22.90876 | 9.994140569 | 7.909822954 | 0.000450064 | 0.019160365 |
| 246 | 1313 | | | | | | + | | | + | | + | | | -22.90277 | 10.00013811 | 7.915820495 | 0.000448716 | 0.019102993 |
| 247 | 3105 | | | | | | + | | | | | + | + | | -22.84722 | 10.05568582 | 7.971368208 | 0.000436425 | 0.01857973 |
| 248 | 1038 | + | | + | + | | | | | | | + | | | -22.83259 | 10.07031423 | 7.985996619 | 0.000433245 | 0.018444329 |
| 249 | 4865 | | | | | | | | | + | + | | | + | -22.78652 | 10.11638295 | 8.032065334 | 0.000423379 | 0.018024332 |
| 250 | 2337 | | | | | | + | | | + | | | + | | -22.78261 | 10.12029862 | 8.03598101 | 0.000422551 | 0.017989078 |
| 251 | 2817 | | | | | | | | | + | + | | + | | -22.61753 | 10.28537689 | 8.201059279 | 0.000389075 | 0.0165639 |
| 252 | 142 | + | | + | + | | | | + | | | | | | -22.56864 | 10.33426822 | 8.249950606 | 0.000379679 | 0.016163894 |
| 253 | 4487 | | + | + | | | | | + | + | | | | + | -22.54361 | 10.35929498 | 8.27497737 | 0.000374958 | 0.015962889 |
| 254 | 3331 | | + | | | | | | | + | | + | + | | -22.52995 | 10.37295558 | 8.28863796 | 0.000372405 | 0.015854229 |
| 255 | 4481 | | | | | | | | + | + | | | | + | -22.50355 | 10.39935587 | 8.31503826 | 0.000367522 | 0.015646326 |
| 256 | 2562 | + | | | | | | | | | + | | + | | -22.49254 | 10.41036721 | 8.32604959 | 0.000365504 | 0.01556042 |
| 257 | 1295 | | + | + | + | | | | | + | | + | | | -22.47637 | 10.42653788 | 8.342220267 | 0.000362561 | 0.015435116 |
| 258 | 4363 | | + | | + | | | | | + | | | | + | -22.43975 | 10.46315692 | 8.378839301 | 0.000355983 | 0.015155078 |
| 259 | 2433 | | | | | | | | + | + | | | + | | -22.439 | 10.46390042 | 8.379582803 | 0.00035585 | 0.015149445 |
| 260 | 2178 | + | | | | | | | + | | | | + | | -22.38142 | 10.52147995 | 8.437162337 | 0.000345752 | 0.014719514 |
| 261 | 335 | | + | + | + | | | + | | + | | | | | -22.36896 | 10.53393882 | 8.449621209 | 0.000343604 | 0.014628105 |
| 262 | 4387 | | + | | | | + | | | + | | | | + | -22.26643 | 10.6364779 | 8.552160285 | 0.000326432 | 0.01389703 |
| 263 | 4367 | | + | + | + | | | | | + | | | | + | -22.23128 | 10.67162512 | 8.58730751 | 0.000320745 | 0.013654942 |
| 264 | 3097 | | | | + | + | | | | | | + | + | | -22.15448 | 10.74842375 | 8.664106138 | 0.000308662 | 0.013140541 |
| 265 | 1315 | | + | | | | + | | | + | | + | | | -22.04788 | 10.85502336 | 8.770705745 | 0.000292642 | 0.012458491 |
| 266 | 2315 | | + | | + | | | | | + | | | + | | -22.04081 | 10.86209 | 8.77777238 | 0.000291609 | 0.012414549 |
| 267 | 298 | + | | | + | | + | | | + | | | | | -22.03568 | 10.86722133 | 8.782903711 | 0.000290862 | 0.012382738 |
| 268 | 3345 | | | | | + | | | | + | | + | + | | -21.91831 | 10.98459151 | 8.900273891 | 0.000274284 | 0.011676968 |
| 269 | 2122 | + | | | + | | | + | | | | | + | | -21.90776 | 10.99513933 | 8.91082172 | 0.000272841 | 0.011615547 |
| 270 | 4867 | | + | | | | | | | + | + | | | + | -21.88297 | 11.01993871 | 8.93562109 | 0.000269479 | 0.011472407 |
| 271 | 4138 | + | | | + | | + | | | | | | | + | -21.88115 | 11.0217517 | 8.937434081 | 0.000269235 | 0.011462012 |
| 272 | 2090 | + | | | + | | + | | | | | | + | | -21.84835 | 11.05455672 | 8.970239101 | 0.000264855 | 0.011275539 |
| 273 | 1066 | + | | | + | | + | | | | | + | | | -21.83949 | 11.06341068 | 8.979093066 | 0.000263685 | 0.011225733 |
| 274 | 2585 | | | | + | + | | | | | + | | + | | -21.82675 | 11.0761561 | 8.991838487 | 0.00026201 | 0.011154422 |
| 275 | 2201 | | | | + | + | | | + | | | | + | | -21.81821 | 11.08469318 | 9.000375567 | 0.000260894 | 0.011106911 |
| 276 | 793 | | | | + | + | | | | + | + | | | | -21.68951 | 11.21339228 | 9.129074668 | 0.000244634 | 0.010414697 |
| 277 | 4483 | | + | | | | | | + | + | | | | + | -21.66859 | 11.23431597 | 9.149998353 | 0.000242088 | 0.010306308 |
| 278 | 2377 | | | | + | | | + | | + | | | + | | -21.64847 | 11.25443406 | 9.17011644 | 0.000239665 | 0.010203156 |
| 279 | 3083 | | + | | + | | | | | | | + | + | | -21.59608 | 11.30682748 | 9.22250986 | 0.000233468 | 0.009939337 |
| 280 | 399 | | + | + | + | | | | + | + | | | | | -21.58424 | 11.31866656 | 9.234348949 | 0.00023209 | 0.009880675 |
| 281 | 4393 | | | | + | | + | | | + | | | | + | -21.48706 | 11.41584177 | 9.331524155 | 0.000221083 | 0.009412073 |
| 282 | 345 | | | | + | + | | + | | + | | | | | -21.46394 | 11.43896877 | 9.354651159 | 0.000218542 | 0.009303863 |
| 283 | 1321 | | | | + | | + | | | + | | + | | | -21.38782 | 11.51508721 | 9.430769593 | 0.00021038 | 0.008956419 |
| 284 | 2819 | | + | | | | | | | + | + | | + | | -21.36175 | 11.5411579 | 9.456840285 | 0.000207656 | 0.008840427 |
| 285 | 409 | | | | + | + | | | + | + | | | | | -21.36096 | 11.54194076 | 9.457623143 | 0.000207574 | 0.008836967 |
| 286 | 2345 | | | | + | | + | | | + | | | + | | -21.35763 | 11.54527671 | 9.460959093 | 0.000207228 | 0.008822239 |
| 287 | 4486 | + | | + | | | | | + | + | | | | + | -21.35154 | 11.55136089 | 9.46704328 | 0.000206599 | 0.008795442 |
| 288 | 3113 | | | | + | | + | | | | | + | + | | -21.33117 | 11.57173683 | 9.487419216 | 0.000204505 | 0.008706289 |
| 289 | 2339 | | + | | | | + | | | + | | | + | | -21.27265 | 11.63024946 | 9.545931843 | 0.000198609 | 0.008455265 |
| 290 | 4619 | | + | | + | | | | | | + | | | + | -21.26746 | 11.63544216 | 9.551124547 | 0.000198094 | 0.008433341 |
| 291 | 2833 | | | | | + | | | | + | + | | + | | -21.2168 | 11.68610156 | 9.601783947 | 0.000193139 | 0.00822241 |
| 292 | 4235 | | + | | + | | | | + | | | | | + | -21.21203 | 11.69087863 | 9.606561015 | 0.000192678 | 0.008202794 |
| 293 | 2187 | | + | | + | | | | + | | | | + | | -21.13941 | 11.76349629 | 9.679178674 | 0.000185808 | 0.007910302 |
| 294 | 4493 | | | + | + | | | | + | + | | | | + | -21.12717 | 11.77573363 | 9.691416017 | 0.000184674 | 0.007862049 |
| 295 | 2435 | | + | | | | | | + | + | | | + | | -21.1177 | 11.78520262 | 9.700885006 | 0.000183802 | 0.007824914 |
| 296 | 2353 | | | | | + | + | | | + | | | + | | -21.08628 | 11.81662489 | 9.732307277 | 0.000180937 | 0.007702937 |
| 297 | 2571 | | + | | + | | | | | | + | | + | | -21.08262 | 11.82028147 | 9.735963853 | 0.000180606 | 0.007688866 |
| 298 | 2371 | | + | | | | | + | | + | | | + | | -21.07835 | 11.82455692 | 9.74023931 | 0.000180221 | 0.007672447 |
| 299 | 330 | + | | | + | | | + | | + | | | | | -21.03738 | 11.86552383 | 9.781206215 | 0.000176567 | 0.007516888 |
| 300 | 2385 | | | | | + | | + | | + | | | + | | -20.99009 | 11.9128183 | 9.828500686 | 0.00017244 | 0.007341219 |
| 301 | 4633 | | | | + | + | | | | | + | | | + | -20.95897 | 11.94392923 | 9.859611615 | 0.000169779 | 0.007227907 |
| 302 | 1305 | | | | + | + | | | | + | | + | | | -20.9557 | 11.94720142 | 9.862883803 | 0.000169501 | 0.007216091 |
| 303 | 2449 | | | | | + | | | + | + | | | + | | -20.92388 | 11.97902513 | 9.894707511 | 0.000166825 | 0.007102178 |
| 304 | 4377 | | | | + | + | | | | + | | | | + | -20.85516 | 12.04774357 | 9.963425955 | 0.000161191 | 0.006862298 |
| 305 | 334 | + | | + | + | | | + | | + | | | | | -20.75329 | 12.1496105 | 10.06529288 | 0.000153186 | 0.006521529 |
| 306 | 4401 | | | | | + | + | | | + | | | | + | -20.73936 | 12.16354234 | 10.07922472 | 0.000152123 | 0.006476258 |
| 307 | 1290 | + | | | + | | | | | + | | + | | | -20.73134 | 12.17156515 | 10.08724753 | 0.000151514 | 0.006450331 |
| 308 | 4249 | | | | + | + | | | + | | | | | + | -20.70471 | 12.19818908 | 10.11387146 | 0.00014951 | 0.006365034 |
| 309 | 3107 | | + | | | | + | | | | | + | + | | -20.66748 | 12.23542013 | 10.15110252 | 0.000146753 | 0.006247641 |
| 310 | 4366 | + | | + | + | | | | | + | | | | + | -20.60002 | 12.30288532 | 10.2185677 | 0.000141885 | 0.006040407 |
| 311 | 394 | + | | | + | | | | + | + | | | | | -20.58152 | 12.32138393 | 10.23706632 | 0.000140579 | 0.005984795 |
| 312 | 3121 | | | | | + | + | | | | | + | + | | -20.51906 | 12.38383924 | 10.29952163 | 0.000136257 | 0.005800792 |

Huffeldt, N.P., A.L. Labansen, M. Frederiksen, J.F. Linnebjerg, L. Witting, F.R. Merkel. Global and local anthropogenic threats to a culturally important food animal
Predictor abbreviations defined in Supplementary Methods, Table S1.

Top model | Models with delta AICc =< 2 | Null model

| Model_rank | Model_ID | tADR | tADS | tATc | tDB | tDS1 | tMAT | tMSST | tN | tO | tRS1 | tSR | tSS | tSSTc | AICc | Delta AICc from the top model | Delta AICc from the null model | Weight | Evidence ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 313 | 1329 | | | | | + | + | | | + | | + | | | -20.51461 | 12.38828959 | 10.30397198 | 0.000135954 | 0.005787899 |
| 314 | 778 | + | | | + | | | | | + | + | | | | -20.42708 | 12.47582548 | 10.39150787 | 0.000130132 | 0.005540038 |
| 315 | 1294 | + | | + | + | | | | | + | | + | | | -20.38016 | 12.52274037 | 10.43842276 | 0.000127115 | 0.005411595 |
| 316 | 4362 | + | | | + | | | | | + | | | | + | -20.30388 | 12.59901994 | 10.51470233 | 0.000122358 | 0.005209084 |
| 317 | 3337 | | | | + | | | | | + | | + | + | | -20.29211 | 12.61079451 | 10.52647689 | 0.00012164 | 0.005178507 |
| 318 | 2314 | + | | | + | | | | | + | | | + | | -20.20528 | 12.69762393 | 10.61330632 | 0.000116472 | 0.004958494 |
| 319 | 3082 | + | | | + | | | | | | | + | + | | -20.20191 | 12.70099352 | 10.6166759 | 0.000116276 | 0.004950147 |
| 320 | 3330 | + | | | | | | | | + | | + | + | | -20.16758 | 12.73532353 | 10.65100592 | 0.000114297 | 0.004865903 |
| 321 | 4253 | | | + | + | + | | | + | | | | | + | -20.16499 | 12.73791283 | 10.65359521 | 0.000114149 | 0.004859607 |
| 322 | 4386 | + | | | | | + | | | + | | | | + | -20.1248 | 12.77810528 | 10.69378767 | 0.000111878 | 0.004762922 |
| 323 | 398 | + | | + | + | | | | + | + | | | | | -19.95562 | 12.94728635 | 10.86296874 | 0.000102803 | 0.004376595 |
| 324 | 2441 | | | | + | | | | + | + | | | + | | -19.9521 | 12.95079913 | 10.86648152 | 0.000102623 | 0.004368914 |
| 325 | 4881 | | | | | + | | | | + | + | | | + | -19.85135 | 13.05155859 | 10.96724097 | 9.75808E-05 | 0.004154262 |
| 326 | 2186 | + | | | + | | | | + | | | | + | | -19.74086 | 13.1620392 | 11.07772159 | 9.23366E-05 | 0.003931003 |
| 327 | 4234 | + | | | + | | | | + | | | | | + | -19.65884 | 13.24406289 | 11.15974527 | 8.86263E-05 | 0.003773046 |
| 328 | 4409 | | | | + | + | + | | | + | | | | + | -19.65454 | 13.24836329 | 11.16404568 | 8.8436E-05 | 0.003764942 |
| 329 | 4618 | + | | | + | | | | | | + | | | + | -19.65406 | 13.24884625 | 11.16452864 | 8.84146E-05 | 0.003764033 |
| 330 | 2825 | | | | + | | | | | + | + | | + | | -19.64871 | 13.25419872 | 11.1698811 | 8.81783E-05 | 0.003753973 |
| 331 | 2361 | | | | + | + | + | | | + | | | + | | -19.64371 | 13.25919018 | 11.17487257 | 8.79585E-05 | 0.003744616 |
| 332 | 2570 | + | | | + | | | | | | + | | + | | -19.55056 | 13.3523443 | 11.26802669 | 8.39556E-05 | 0.003574202 |
| 333 | 1314 | + | | | | | + | | | + | | + | | | -19.52387 | 13.37903207 | 11.29471446 | 8.28428E-05 | 0.003526825 |
| 334 | 1323 | | + | | + | | + | | | + | | + | | | -19.51873 | 13.38417317 | 11.29985556 | 8.26301E-05 | 0.003517771 |
| 335 | 4239 | | + | + | + | | | | + | | | | | + | -19.49733 | 13.40557347 | 11.32125586 | 8.17506E-05 | 0.003480331 |
| 336 | 4866 | + | | | | | | | | + | + | | | + | -19.49676 | 13.40614798 | 11.32183037 | 8.17272E-05 | 0.003479331 |
| 337 | 4482 | + | | | | | | | + | + | | | | + | -19.43404 | 13.46885906 | 11.38454145 | 7.92043E-05 | 0.003371928 |
| 338 | 4497 | | | | | + | | | + | + | | | | + | -19.4089 | 13.49400541 | 11.40968779 | 7.82147E-05 | 0.003329797 |
| 339 | 3353 | | | | + | + | | | | + | | + | + | | -19.33206 | 13.57084203 | 11.48652442 | 7.52668E-05 | 0.003204298 |
| 340 | 1337 | | | | + | + | + | | | + | | + | | | -19.29487 | 13.60803807 | 11.52372045 | 7.38799E-05 | 0.003145255 |
| 341 | 2370 | + | | | | | | + | | + | | | + | | -19.28638 | 13.61652802 | 11.53221041 | 7.3567E-05 | 0.003131932 |
| 342 | 4873 | | | | + | | | | | + | + | | | + | -19.25169 | 13.65121866 | 11.56690104 | 7.23019E-05 | 0.003078076 |
| 343 | 2393 | | | | + | + | | + | | + | | | + | | -19.25151 | 13.6513917 | 11.56707409 | 7.22957E-05 | 0.00307781 |
| 344 | 3339 | | + | | + | | | | | + | | + | + | | -19.23848 | 13.66441889 | 11.58010128 | 7.18263E-05 | 0.003057827 |
| 345 | 2338 | + | | | | | + | | | + | | | + | | -19.19777 | 13.70513446 | 11.62081685 | 7.03789E-05 | 0.002996206 |
| 346 | 2347 | | + | | + | | + | | | + | | | + | | -19.15193 | 13.75097459 | 11.66665698 | 6.87841E-05 | 0.002928314 |
| 347 | 4489 | | | | + | | | | + | + | | | | + | -19.13335 | 13.76955293 | 11.68523531 | 6.81481E-05 | 0.002901238 |
| 348 | 3129 | | | | + | + | + | | | | | + | + | | -19.10169 | 13.80121492 | 11.7168973 | 6.70778E-05 | 0.00285567 |
| 349 | 4395 | | + | | + | | + | | | + | | | | + | -19.09572 | 13.80718288 | 11.72286527 | 6.68779E-05 | 0.002847162 |
| 350 | 2818 | + | | | | | | | | + | + | | + | | -19.06744 | 13.83545995 | 11.75114233 | 6.5939E-05 | 0.00280719 |
| 351 | 3106 | + | | | | | + | | | | | + | + | | -19.03146 | 13.8714424 | 11.78712479 | 6.47633E-05 | 0.002757137 |
| 352 | 4238 | + | | + | + | | | | + | | | | | + | -19.02204 | 13.88086491 | 11.7965473 | 6.44589E-05 | 0.002744178 |
| 353 | 2434 | + | | | | | | | + | + | | | + | | -19.01915 | 13.88375097 | 11.79943336 | 6.4366E-05 | 0.002740221 |
| 354 | 3361 | | | | | | + | | | + | | + | + | | -18.86809 | 14.0348117 | 11.95049408 | 5.96834E-05 | 0.002540874 |
| 355 | 2379 | | + | | + | | | + | | + | | | + | | -18.67413 | 14.22876959 | 12.14445198 | 5.41672E-05 | 0.002306034 |
| 356 | 3115 | | + | | + | | + | | | | | + | + | | -18.58276 | 14.32014147 | 12.23582386 | 5.17482E-05 | 0.002203051 |
| 357 | 2457 | | | | + | + | | | + | + | | | + | | -18.5221 | 14.38080505 | 12.29648744 | 5.02021E-05 | 0.002137232 |
| 358 | 2841 | | | | + | + | | | | + | + | | + | | -18.42712 | 14.47578681 | 12.39146919 | 4.78737E-05 | 0.002038105 |
| 359 | 2443 | | + | | + | | | | + | + | | | + | | -18.06467 | 14.83823416 | 12.75391655 | 3.99386E-05 | 0.001700287 |
| 360 | 4491 | | + | | + | | | | + | + | | | | + | -17.89638 | 15.00652623 | 12.92220862 | 3.67154E-05 | 0.001563069 |
| 361 | 4875 | | + | | + | | | | | + | + | | | + | -17.85987 | 15.04303636 | 12.95871874 | 3.60513E-05 | 0.001534794 |
| 362 | 2827 | | + | | + | | | | | + | + | | + | | -17.85024 | 15.05266729 | 12.96834968 | 3.58781E-05 | 0.001527421 |
| 363 | 3363 | | + | | | | + | | | + | | + | + | | -17.37202 | 15.53087891 | 13.4465613 | 2.82479E-05 | 0.001202586 |
| 364 | 4509 | | | + | + | + | | | + | + | | | | + | -17.12094 | 15.78196846 | 13.69765085 | 2.49152E-05 | 0.001060701 |
| 365 | 1322 | + | | | + | | + | | | + | | + | | | -17.01653 | 15.88637396 | 13.80205635 | 2.36479E-05 | 0.00100675 |
| 366 | 4394 | + | | | + | | + | | | + | | | | + | -16.95425 | 15.94865453 | 13.86433691 | 2.29228E-05 | 0.000975882 |
| 367 | 2378 | + | | | + | | | + | | + | | | + | | -16.94527 | 15.95763323 | 13.87331562 | 2.28201E-05 | 0.000971511 |
| 368 | 4889 | | | | + | + | | | | + | + | | | + | -16.92946 | 15.97344736 | 13.88912975 | 2.26404E-05 | 0.00096386 |
| 369 | 2346 | + | | | + | | + | | | + | | | + | | -16.8718 | 16.03110321 | 13.9467856 | 2.19971E-05 | 0.00093647 |
| 370 | 3338 | + | | | + | | | | | + | | + | + | | -16.82398 | 16.0789285 | 13.99461088 | 2.14773E-05 | 0.000914342 |
| 371 | 3377 | | | | | + | + | | | + | | + | + | | -16.75178 | 16.15112005 | 14.06680243 | 2.07159E-05 | 0.000881927 |
| 372 | 3114 | + | | | + | | + | | | | | + | + | | -16.67871 | 16.2241933 | 14.13987568 | 1.99726E-05 | 0.000850286 |
| 373 | 4505 | | | | + | + | | | + | + | | | | + | -16.66011 | 16.24279857 | 14.15848095 | 1.97877E-05 | 0.000842413 |
| 374 | 4495 | | + | + | + | | | | + | + | | | | + | -16.39096 | 16.51194243 | 14.42762481 | 1.72962E-05 | 0.000736345 |
| 375 | 3369 | | | | + | | + | | | | | + | + | | -16.21377 | 16.68913278 | 14.60481517 | 1.58298E-05 | 0.000673914 |
| 376 | 2442 | + | | | + | | | | + | + | | | + | | -15.83837 | 17.06453567 | 14.98021806 | 1.31207E-05 | 0.000558582 |
| 377 | 2826 | + | | | + | | | | | + | + | | + | | -15.49275 | 17.4101552 | 15.32583759 | 1.10384E-05 | 0.000469934 |
| 378 | 4490 | + | | | + | | | | + | + | | | | + | -15.41424 | 17.48866717 | 15.40434956 | 1.06135E-05 | 0.000451843 |
| 379 | 4874 | + | | | + | | | | | + | + | | | + | -15.33313 | 17.56977614 | 15.48545853 | 1.01917E-05 | 0.000433886 |
| 380 | 4494 | + | | + | + | | | | + | + | | | | + | -15.14025 | 17.76265648 | 15.67833886 | 9.25471E-06 | 0.000393996 |
| 381 | 3362 | + | | | | | + | | | + | | + | + | | -15.02177 | 17.88113205 | 15.79681443 | 8.7224E-06 | 0.000371335 |
| 382 | 3385 | | | | + | + | + | | | + | | + | + | | -13.58749 | 19.31541042 | 17.23109281 | 4.25781E-06 | 0.000181266 |
| 383 | 3371 | | + | | + | | + | | | + | | + | + | | -13.35419 | 19.54871422 | 17.4643966 | 3.789E-06 | 0.000161307 |
| 384 | 3370 | + | | | + | | + | | | + | | + | + | | -10.89916 | 22.00374042 | 19.91942281 | 1.11026E-06 | 4.72664E-05 |

# Makin' some noise - A study on anthropogenic threats to thick-billed murre (appa, *Uria lomvia*) in Greenland

The thick-billed murre (*Uria lomvia*) is the culturally most important seabird species in Greenland. It is declining in most areas of Greenland and have shown local extinctions. Recent research indicates that at least some of the population decline can be linked to drivers in the wintering areas, whereas the role of local breeding conditions largely is unknown. We used a suite of different methods to investigate local drivers during the breeding period, suspected to play a role for the population decline in Greenland. The first part of this thesis provides a brief introduction to historical and current challenges for the murre population in Greenland and describes the research questions. The second part consists of four scientific papers. We investigated the effects of gunshots with an experimental approach and show that there was large variation in the distance of first reaction, and that most responded at distances greater than the current no-disturbance zone allow. We also quantified marine traffic using underwater acoustics, which proved to be a promising tool to study vessel activity. Marine traffic near a declining colony was five times larger, compared to at a stable nearby colony. Local ecological knowledge indicates and confirms the assumption that human disturbances are far less common today than 2-3 decades ago, but that they still occur. A need for a higher information level from authorities was also identified. Lastly, statistical analyses on the impact of various local drivers on murre population trends in Greenland showed that both local human factors and the local climate, derived from global warming, have had an impact on population development in Greenland. Drivers linked to global climate change are difficult to mitigate, which make management measures to diminish negative effects of local anthropogenic drivers even more important.

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