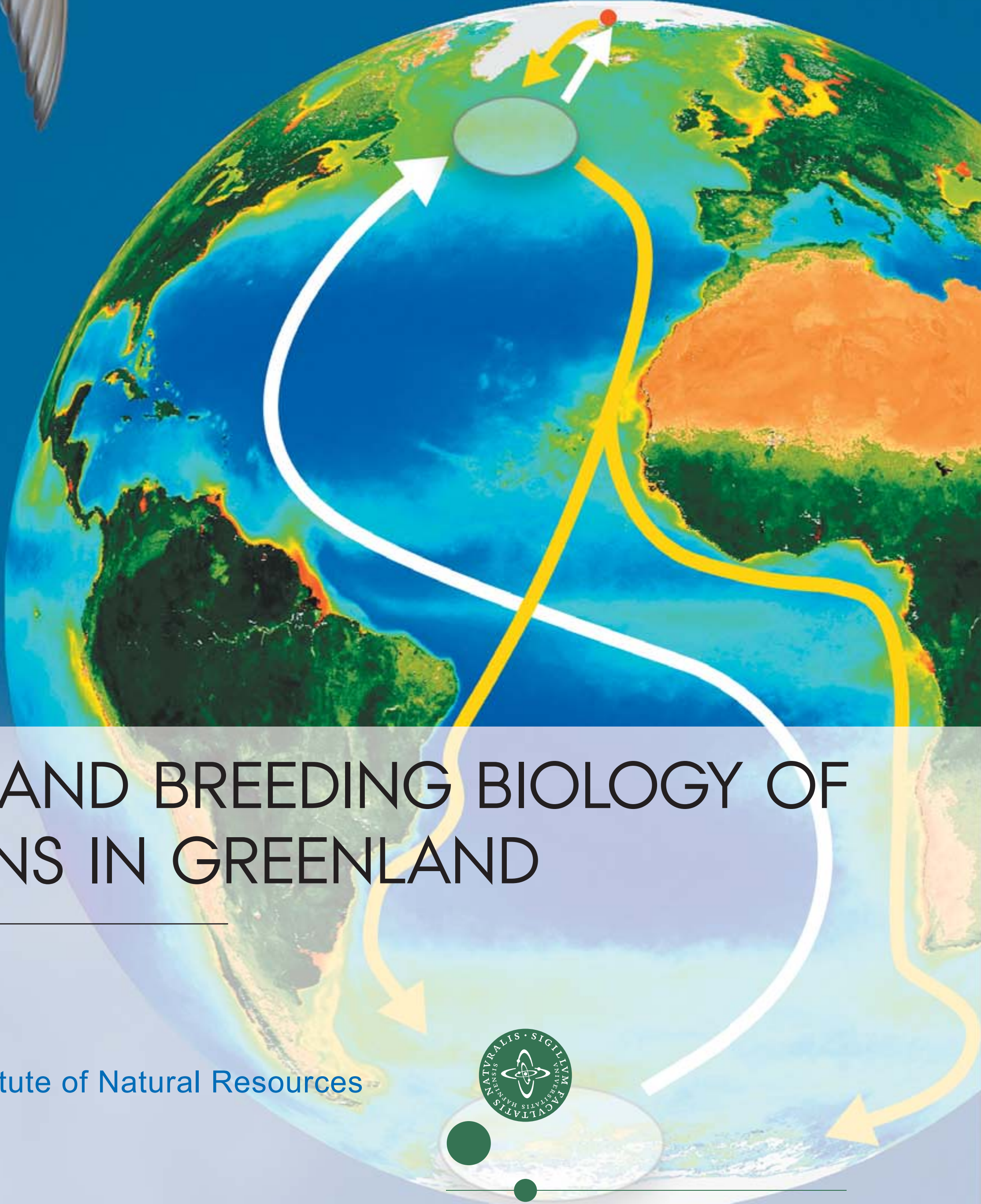

MIGRATION AND BREEDING BIOLOGY OF ARCTIC TERNS IN GREENLAND

PhD Thesis
Carsten Egevang

2010

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Abstract: This thesis presents novel findings for the Arctic tern in Greenland. Included is a study on Arctic tern migration – the longest annual migration ever recorded in any animal. The study documented how Greenland and Iceland breeding terns conduct the roundtrip migration to the Weddell Sea in Antarctica and back. Although the sheer distance (71,000 km on average) travelled by the birds is interesting, the study furthermore showed how the birds depend on high-productive at-sea areas and global wind systems during their massive migration.

Furthermore included is the first quantified estimate of the capacity to produce a replacement clutch in Arctic terns. We found that approximately half of the affected birds would produce a replacement clutch when the eggs were removed late in the incubation period.

At a level of more national interest, the study produced the first estimates of the key prey species of the Arctic tern in Greenland. Although zooplankton and various fish species were present in the chick diet of terns breeding in Disko Bay, Capelin was the single most important prey species found in all age groups of chicks.

The thesis also includes a study on the fluctuating breeding found in Arctic terns. Breeding birds showed a considerable variation in colony size between years in the small and mid sized colonies of Disko Bay. These variations were likely to be linked to local phenomena, such as disturbance from predators, rather than to large-scale occurring phenomena.

Included is also a study that documents the breeding association between Arctic terns and other breeding waterbirds. At Kitsissunnguit a close behavioural response to tern alarms could be identified. These findings imply that the altered distributions of waterbirds observed at Kitsissunnguit were governed by the distribution of breeding Arctic terns.

Included in the thesis are furthermore results with an appeal to the Greenland management agencies. Along with estimates of the Arctic tern population size at the two most important Arctic tern colonies in West Greenland and East Greenland, the study produced recommendations on how a potential future sustainable egg harvest could be carried out, and on how to monitor Arctic tern colonies in Greenland.

Keywords: At-sea hot-spots, Arctic, breeding association, breeding ecology, breeding fluctuation, colony attendance, diet, egg harvest, global wind systems, long-distance migration, nature management, *Sterna paradisaea*, replacement clutch.

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LIST OF PUBLICATIONS/MANUSCRIPTS INCLUDED IN THE THESIS

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Egevang, C., N. Ratcliffe & M. Frederiksen. Sustainable regulation of Arctic tern egg harvesting in Greenland. Manuscript.

Egevang, C., M. W. Kristensen, N. Ratcliffe & M. Frederiksen. Food-related consequences of relaying in the Arctic Tern: Contrasting prey availability within a prolonged breeding season. Manuscript submitted IBIS.

Egevang, C. & M. Frederiksen. Fluctuating breeding of Arctic Terns (*Sterna paradisaea*) in Arctic and High-arctic colonies in Greenland. Manuscript submitted WATERBIRDS.

Jørgensen, P. S., Kristensen, M. W. & **Egevang, C.** 2007. Red Phalarope *Phalaropus fulicarius* and Red-necked Phalarope *Phalaropus lobatus* behavioural response to Arctic Tern *Sterna paradisaea* colonial alarms. Dansk Ornitologisk Forenings Tidsskrift 101 (3): 73-78, 2007.

Preface

This thesis is the result of my PhD conducted at the University of Copenhagen, Center for Macroecology, Evolution and Climate (UC), Greenland Institute of Natural Resources (GINR) and National Environmental Research Institute, Department of Arctic Environment (NERI). The PhD was financially supported by Greenland Institute of Natural Resources (GNIR) and the Commission for Scientific Research in Greenland (KVUG). The principle supervisor was Carsten Rahbek (UC) whereas Morten Frederiksen (NERI) and Norman Ratcliffe (British Antarctic Survey) functioned as external supervisors.

The pre-2002 level of knowledge on the Arctic tern in Greenland was rather low and even rather basic biological information was unavailable for the species. On the other side there's an urgent need for more information in the Greenland management of the living resources and protected areas. This lack of knowledge has been decisive in my choice of study species, study topic and study location at the planning of my PhD. It has been both a strong motivation factor for me throughout my PhD, but also frustrating at times where the lack of information made it difficult to approach topics from a theoretical point of view.

Although my PhD officially started mid 2004, my work on Arctic terns in Greenland is really a continuation of fieldwork conducted in 2002 and 2003. Concurrently with my PhD I have worked as seabird researcher at GNIR, where I have been responsible for monitoring seabirds in Greenland and ad-hoc advising the Greenland Government in a sustainable use of the living resources. For this reason the delivery date of my PhD has been prolonged to March 2010 – more than one year later than first scheduled. Along the course of my PhD the topic included in the PhD got extended. The technology in tracking devices for small-sized seabirds advanced and from dealing only with breeding ecology and censusing methods, my PhD got extended to include migration ecology as well.

During my PhD I have been physically placed in Greenland at GINR until May 2008, where my family and I moved to Denmark and NERI was kind enough to offer me a work seat.

The fieldwork in connection with my PhD was conducted at two very different field sites in Greenland: Kitsissunnguit (Grønne Ejland) during 2002 to 2006 in the southern part of Disko Bay in the Arctic zone in West Greenland and at Sand Island (Sandøen) during 2007 and 2008 in high Arctic Northeast Greenland (see figure 1-3).

During my PhD I have produced papers, reports or book contributions as a spin-off from the work on Arctic terns conducted during my PhD. These are not included in my PhD thesis but are listed here:

Egevang, C. & D. Boertmann 2008. "Ross's Gulls (*Rhodostethia rosea*) breeding in Greenland: A Review, with Special Emphasis on Records from 1979 to 2007." Arctic 61(3): 322-328.

Egevang, C. Kampp, K. & Boertmann D. 2006. ”Declines in breeding waterbirds following a redistribution of Arctic Terns *Sterna paradisaea* in West Greenland” Waterbirds around the World. Eds. G. C. Boere, C. A. Galbraith & D. A. Stroud. The stationery Office, Edinburgh, UK. P. 154 (http://www.jncc.gov.uk/PDF/pub07_waterbirds_part3.3.1.6.pdf).

Egevang, C. , K. Kampp & D. Boertmann 2004 “The Breeding Association of Red Phalaropes (*Phalaropus fulicarius*) with Arctic Terns (*Sterna paradisaea*): Response to a Redistribution of Terns in a Major Greenland Colony” Waterbirds 27 (4): 406-410.

Egevang, C., I. J. Stenhouse, L. M. Rasmussen, M. W. Kristensen and F. Ugarte 2009. ”Breeding and foraging ecology of seabirds on Sandøen 2008”. in Jensen, L.M. & Rasch, M. (eds.) 2009: Zackenberg Ecological Research Operations, 14th Annual Report, 2008. National Environmental Research Institute, Aarhus University, Denmark. 116 pp.

Egevang, C., I. J. Stenhouse, Lars Maltha Rasmussen, Mikkel Willemoes & Fernando Ugarte 2008. “Field report from Sand Island, Northeast Greenland, 2008. http://www.natur.gl/UserFiles/File/feltrapporter/Fieldreport_%20SandIsland_2008_final.pdf.

Egevang, C. 2008. ”Forstyrrelser i grønlandske havfuglekolonier, med speciel fokus på ynglende havterner på Kitsissunnguit (Grønne Ejland), Disko Bugt”. Teknisk rapport nr. 71, Grønlands Naturinstitut, 21 sider. http://www.natur.gl/UserFiles/File/Publlikationer/2008-02_GN_teknisk_rapport_71_final_forstyrrelser_fuglekolonier.pdf

Egevang, C. & Stenhouse, I. J. 2008. Mapping long-distance migration in two Arctic seabird species p. 74-76. In: Klitgaard, A.B. and Rasch, M. (eds.) 2008. Zackenberg Ecological Research Operations, 13th Annual Report, 2007. Danish Polar Center, Danish Agency for Science, Technology and Innovation, Ministry of Science, Technology and Innovation, 2008. http://www.zackenberg.dk/graphics/Design/Zackenberg/Publications/English/Zero%202007.pdf

Egevang, C. & I. J. Stenhouse 2007. ”Field report from Sand Island, Northeast Greenland, 2007”. http://www.natur.gl/UserFiles/File/feltrapporter/Fieldwork_Sand_Island_2007_1.pdf

Egevang, C., D. Boertmann & O. S. Kristensen 2005 ”Monitering af havternebestanden på Kitsissunnguit (Grønne Ejland) og den sydlige del af Disko Bugt, 2002-2004”. Teknisk rapport nr. 62, Grønlands Naturinstitut, 41 p. http://www.natur.gl/filer/Havternemonitering.pdf

The study on the migration of the Arctic tern included novel findings and had appeal to a broad public audience. Therefore I build a web site (www.arctictern.info) especially dedicated to the communication of the results originating from our study.

My thesis deals with an array of different topics within the field of ecology. From small-scale issues, like egg harvesting by local Inuit at the breeding grounds, to large-scale occurring phenomena, such as global wind systems and global marine biological productivity. Although, it may seem like a conflicting cocktail of topics, it is all focused on the same species – the gracious Arctic tern.

Acknowledgements

I owe tremendous thanks to my external supervisor Morten Frederiksen (NERI) who has provided excellent guidance and supervision – not once did I experience that Morten couldn't find the time to support me in technical matters and give me input instantly. Also thanks to Norman Ratcliffe (British Antarctic Survey), my other external supervisor for help modelling the data obtained over the field seasons.

The Greenland Institute of Natural Resource provided the framework to work with my thesis on the Arctic tern – both in Greenland and Denmark. For that I'm most grateful to the director Klaus Nygaard and head of department Fernando Ugarte. Also thanks to Jesper Madsen, head of department and Anders Mosbech, head of section for their willingness to provide me with a disk at the crowed Arctic Environment department at NERI.

Special thanks goes to Scottish friend and colleague Iain Stenhouse (National Audubon Society) who endured cold and stormy days with me in a tent at Sand Island, and gave invaluable language comments to this synopsis.

My thanks goes to the people who assisted me in the field over the years: David Boertmann and Morten Bjerrum (National Environmental Research Institute, Denmark), Anders Tøttrup, Mikkel Willemoes and Peter S. Jørgensen (University of Copenhagen), Lars Maltha Rasmussen, Fernando Ugarte, Ole S. Kristensen, Lars Witting, Kate Skjærbæk Rasmussen and Rasmus Lauridsen (GNIR), Bjarne Petersen, Qasigiannguit and Norman Ratcliffe and Stuart Benn (Royal Society for Protection of Birds). Also thanks to Finn Steffens (Qeqertarsuaq) and Elektriker-it (Aasiaat) for logistic support in Disko Bay, and to the Danish Polar Centre, Zackenberg Ecological Research Operations, POLOG, and Sledge Patrol Sirius and Nette Levermann (Greenland Government) for logistic assistance in Northeast Greenland (Sand Island).

I will also like this opportunity to thank the local inhabitants of Disko Bay. Through arranged meetings in Aasiaat and multiple opportunistic visits at our field camp at Kitsissunnguit, they have thought me another view at harvesting natural resources and the significance of this.

Last, but certainly not least, I would like to thank my family, my wife Inge Thaulow and my two boys Emil and Peter, for patience, understanding and absents during fieldwork – THANKS!

Summary

This PhD thesis presents the results of a study performed on the Arctic tern (*Sterna paradisaea*) in the period 2002-2008. Data in the study were obtained from fieldwork conducted at two study sites in Greenland: Kitsissunnguit (Grønne Ejland), Disko Bay in Arctic West Greenland and Sand Island (Sandøen) in high-Arctic Northeast Greenland.

The level of knowledge of the Arctic tern in Greenland before 2002 was to a large extent poor, with aspects of its biology being completely unknown in the Greenland population. This thesis presents novel findings for the Arctic tern, both on an international scale and on a national scale.

The study on Arctic tern migration (Manus I) – the longest annual migration ever recorded in any animal – is a study with an international appeal. The study documented how Greenland and Iceland breeding terns conduct the roundtrip migration to the Weddell Sea in Antarctica and back. Although the sheer distance (71,000 km on average) travelled by the birds is interesting, the study furthermore showed how the terns depend on high-productive at-sea areas during their massive migration. On the southbound migration, the birds would stop for almost a month (25 days on average) in the central part of the North Atlantic Ocean before continuing south. Close to Equator (~10º N) a divide in the migration path way occurred: seven birds migrated along the coast of Africa, while four birds crossed the Atlantic Ocean to follow the coast of South America. The northbound migration from the winter quarters to the breeding grounds was performed particular fast (520 km per day on average) following a route of favourable wind systems.

Included in this thesis is also the first quantified estimate of the capacity to produce a replacement clutch in Arctic terns (Manus II and III). Although it is often mentioned in the literature that the species willingly relays, this study is the first where the reproductive response of experimentally manipulated breeding pairs is monitored. We found that approximately half (53.3 %) of the affected birds would produce a replacement clutch when the eggs were removed late in the incubation period. Surprisingly, growth and survival rates in chicks from these clutches did not differ from chicks reared four weeks later in the breeding season, although a shift in foraging pattern and prey size was apparent (Manus III).

At a level of more national interest, the study produced the first estimates of the key prey species of the Arctic tern in Greenland. Although zooplankton and various fish species were present in the chick diet of terns breeding in Disko Bay, Capelin (*Mallotus villosus*) was the single most important prey species found in all age groups of chicks (Manus III).

The thesis also includes a study on the fluctuating breeding found in Arctic terns (Manus IV). Although the Arctic tern may show an overall fidelity to the breeding region, our study showed a considerable variation in colony size between years in the small and mid sized colonies of Disko Bay. These variations were likely to be linked to local phenomena, such as disturbance from predators, rather than to large-scale occurring phenomena.

From the long periods spent in Arctic tern colonies it was furthermore possible to document the breeding association between Arctic terns and

Figure 1. An Arctic tern nest at Kitsissunnguit, Disko Bay, Arctic West Greenland where fieldwork was conducted in 2002-2006. Note the lush vegetation surrounding the nest.
Photo: Carsten Egevang.

other breeding waterbirds. In a study conducted on breeding phalaropes (*Phalaropus fulucarius* and *P. lobatus*) at Kitsissunnguit (Manus V) a close behavioural response to tern alarms could be identified. These findings imply that the altered distributions of waterbirds observed at Kitsissunnguit were governed by the distribution of breeding Arctic terns as suggested by Egevang *et al*. (2004).

Included in the thesis are furthermore results with an appeal to the Greenland management agencies. Along with estimates of the Arctic tern population size at the two most important Arctic tern colonies in West Greenland and East Greenland, the study produced recommendations on how a potential future sustainable egg harvest could be carried out (Manus II), and on how to monitor Arctic tern colonies in Greenland (Manus IV).

Dansk resumé

Denne afhandling præsenterer resultater fra studier udført på havterne (*Sterna paradisaea*) i perioden 2002-2008. Data i forbindelse med afhandlingen er indsamlet gennem feltarbejde på to lokaliteter i Grønland: Kitsissunnguit (Grønne Ejland), Disko Bugt i arktisk Vestgrønland samt på Sandøen i høj-arktisk Nordøstgrønland.

Vidensgrundlaget for havternen i Grønland før 2002 var gennemgående ringe, med aspekter af artens ynglebiologi ubeskrevet for den grønlandske bestands vedkommende. Denne afhandling præsenterer ny viden for havternen både på en international skala, såvel som på en national skala.

Først og fremmest er studiet af havternens træk (Manus I) – det længste træk registreret hos noget dyr – et studie med international appel. Studiet dokumenterer hvorledes terner, der yngler i Nordøstgrønland og Island, gennemfører trækket til Weddell Havet ved Antarktis, og tilbage igen. Alene den tilbagelagte distance (gennemsnitlig 71.000 km) er interessant, men studiet kunne også dokumentere, hvordan ternerne under deres lange træk er afhængige af havområder med særlig høj biologisk produktion. På det sydgående træk stopper fuglene trækket og opholder sig i næsten en måned (25 dage i gennemsnit) i den centrale del af Nordatlanten, før de fortsætter mod syd. Tæt ved Ækvator (~10º N) opstår en opdeling af trækvejen: Af 11 mærkede individer fortsætter syv langs Afrikas kyst, mens fire individer krydser Atlanten, for at fortsætte langs østkysten af Sydamerika. Det nordgående træk fra vinterkvarteret til ynglepladserne blev gennemført med særlig høj hastighed (gennemsnitligt 520 km per dag) og fulgte en rute med favorable vindretninger.

Denne afhandling indeholder også det første kvantificerede estimat af havternens evne til at producere et såkaldt omlægskuld – et erstatningskuld hvis første kuld går tabt (Manus II og III). På trods af, at det ofte nævnes i litteraturen at havternen villigt omlægger, er dette studie det første der overvåger det reproduktive respons på eksperimentalt manipulerede ynglepar. Vi fandt, at omtrent halvdelen (53,3 %) af fuglene producerede et omlægskuld, når det første kuld blev fjernet i den sidste del af rugeperioden. Overraskende viste det sig, at vækstrater og overlevelse hos unger fra omlægskuldene ikke var forskellige fra unger opfostret fire uger tidligere, på trods af, at et skifte i både fourageringsmønster og størrelse af byttedyr kunne identificeres (Manus III).

Af mere national interesse producerede studierne i forbindelse med afhandlingen de første undersøgelser af havternens fødevalg i Grønland. På trods af at flere forskellige fiske- og zooplanktonarter var til stede i den føde der blev bragt til ungerne i Disko Bugt, Vestgrønland, viste det sig, at lodde (*Mallotus villosus*) var nøglefødearten for alle aldersgrupper af unger (Manus III).

Afhandlingen omhandler også et studie af den fluktuerende yngleforekomst som forekommer hos havternen (Manus IV). Selv om havternen udviser en overordnet trofasthed mod yngleregionen, viste vores studier, at der forekommer en betydelig variation i antallet af ynglefugle i kolonien mellem sæsonerne i de små og mellemstore kolonier i Disko Bugtområdet. Disse variationer er sandsynligvis koblet til lokalt forekommen-

de fænomener, eksempelvis forstyrrelse fra prædatorer, mere end de er forklaret af forhold der forekommer på større skala.

Gennem de lange perioder, tilbragt i havternekolonierne i forbindelse med feltarbejdet, var det muligt at dokumentere det positive yngleforhold mellem havterner og andre ynglende vandfugle. I et studie udført på ynglende thors- og odinshane (*Phalaropus fulucarius* og *P. lobatus*) på Kitsissunnguit (Manus V), kunne et tæt adfærdsmæssigt respons på havternens advarselskald identificeres. Disse resultater sandsynliggør, at den observerede ændrede fordeling af svømmesnepper på Kitsissunnguit følger havternens udbredelse på øerne, som foreslået af Egevang *et al.* 2004.

Afhandlingen indeholder desuden resultater møntet på de grønlandske forvaltningsmyndigheder. Foruden estimater af ynglebestanden i de to vigtigste havternekolonier i Vest- og Nordøstgrønland, præsenteres anbefalinger til hvordan en fremtidig bæredygtig udnyttelse af havterneægsamling kan tænkes udført (Manus II), og konkrete forslag til hvordan overvågningen af havternekolonierne i Grønland kan udføres (Manus IV).

Figure 2. An Arctic tern nest at the barren Sand Island, High-arctic Northeast Greenland, where fieldwork was conducted in 2007 and 2008.

Eqikkaaneq

Ilisimatuutut allaatigisaq manna imeqqutaallanik (*Sterna paradisaea*) 2002-2008-mi misissuinerit inernerinik saqqummiussivoq. Allaatigisamut atatillugu paasissutissat Kalaallit Nunaanni piffinni marluusuni: Kitsissunnguit, Qeqertarsuup Tunuani Kitaata issittortaani aamma Sandøenimi Tunup avannaani issittorsuarmi, misissuiartornikkut katersorneqarsimapput.

Kalaallit Nunaanni imeqqutaalaq pillugu 2002 sioqqullugu ilisimasanut tunngaviusut annikitsuinnaasimapput, pissuseqatigiit nunatsinni uumasuusut kinguaassiornikkut pissusaat arlalitsigut nassuiarneqarsimanatik. Allaatigisaq manna imeqqutaalaq pillugu paasisanik nutaanik nunap iluani nunallu tamat akornanni nallersuussinnaasunik saqqummiussivoq.

Siullertut pingaarnertullu imeqqutaallap ingerlaartarnera pillugu misissuineq (Manus I) – uumasuni tamani ingerlaarnerit nalunaarsorneqarsimasut tannersaat – misissuineruvoq nunat tamat akornanni soqutiginaateqartussaq. Misissuinerup nassuiarpaa qanoq imeqqutaallat Tunup avannaaniit Islandimiillu, Sikuiuitsumi kujallermiittumut Weddelip Imartaanut, utimullu, ingerlaartarnersut. Ingerlaarnerup takissusaa immini (agguaqatigiissillugu 71.000 km) soqutiginarpoq, misissuinerulli aamma nassuiarpaa, qanoq imeqqutaallat ingerlaarnermi nalaanni imartat immikkut pinngorarfiulluartut pinngitsoorsinnaanngikkaat. Kujammut ingerlaarnerminni timmissat qaammatingajammik (agguaqatigiissillugu ulluni 25-ni) sivisussusilimmik ingerlaarnertik unitsittarpaat Atlantikullu avannaata qiterpasissuani, kujammut ingerlaqqinnginnerminni, uninngaartarlutik. Ækvatorip qanittuani (~10º N) ingerlaarnerup aqqutaani avissaarfeqartarpoq: Nalunaaqutserneqarsimasuni 11-usuni arfineq marluk Afrikap sineriaa atuarlugu ingerlaqqipput, sisamallu Atlantiku ikaarlugu Amerikkap kujalliup sineriaa atuarlugu ingerlaqqiffigalugu. Avannamut ukiivimmiit piaqqisarfimmut ingerlaarneq sukkangaatsiartumik ingerlavoq (agguaqatigiissillugu ullormut 520 km) ingerlaarfillu iluaqutaasunik sammivilinnik anoreqarfiusoq atuarsimallugu.

Allaaserisap massuma aamma imarivaa imeqqutaallap mannilioqqissinnaaneranik – piaqqinerit/manniliornerit siulliit iluatsinngippata mannilioqqissinnaaneq - kisitsisinngorlugu missingersuinerit siullersaat (Manus II aamma III). Naak allaatigisani imeqqutaallat ajornasaaratik mannilioqqittarnerarlugit oqaatiginiarneqartaraluartut, misissuinerup massuma, aappariit piaqqisut misileraatigalugit uukapaatinneqartut kinguaassiornikkut qisuariarnerannik nakkutiginninnerit siullersaraat. Paasivarput, timmissat affaasa missaat (53,3 %) ivanerup naggataata tungaani manniliaat peerneqaraangata mannilioqqittartut. Tupaallannartumik paasinarsivoq, piaqqat mannilioqqinnerniit tukersimasut alliartornerat umaannarsinnaanerallu piaqqanit sapaatit akunnerini sisamani siusinnerusukkut allisarsimasuninngarnit allaanerunngitsut, naak, nerniarnikkut piniagaasalu angissusiisigut allaanerussutit ilisarineqarsinnaasimagaluartut (Manus III).Nunap iluani soqutiginaateqarnertut allaatigisamut atatillugu imeqqutaallat Kalaallit Nunaanni neriniartagaannik misissuinerit siulliit suliarineqarput. Naak aalisakkat uumasuaqqallu ikerinnarsiortut assigiinngitsut arlallit Kitaani, Qeqertarsuup Tunuani piaqqanut apuunneqartartunut ilaagaluartut, paasinarsivoq ammassak (*Mallotus villosus*) piaqqani tamanik angissuseqartuni nerisassat pingaarnersarigaat (Manus III).

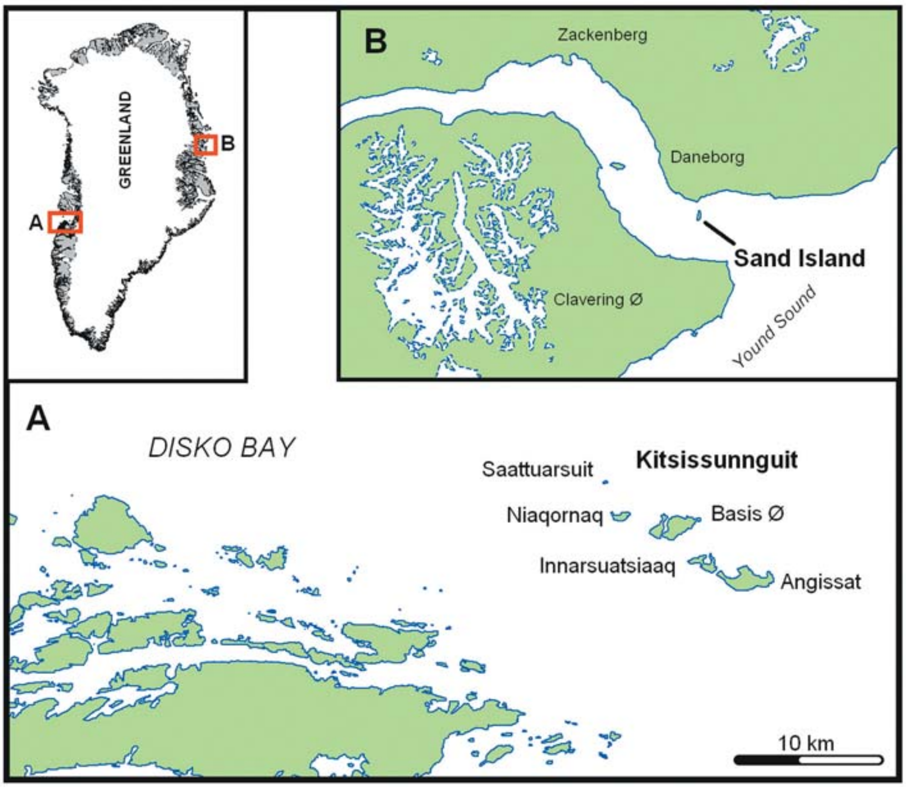

Figure 3. Map of study areas where field work in the thesis were conducted. Inset map in upper left corner shows the location of **A)** Kitsissunnguit in Disko Bay and **B)** of Sand Island in Northeast Greenland. The map scale (lower right corner) applies to both A and B

Allaatigisami aamma sammineqarput imeqqutaallat piaqqiortartut amerlassutsimikkut ilaatigut allanngorartarnerisa, misissuiffigineqarnerat (Manus IV). Naak imeqqutaalaq piaqqisarfimminut amerlanertigut aalajaattaraluartoq, misissuinitta takutippaat, Qeqertarsuup Tunuani piaqqisarfinni minnerni akunnattunilu timmissat piaqqisut piaqqinermiit piaqqinermut malunnaatilimmik allanngorartut. Allanngorarnerit tamakku piffimmi annikitsumi pisunut attuumassuteqarnissaat ilimanaateqarput, assersuutigalugu kiisortunit akornusersorneqarneq, piffimmilu annertunerusumi pisut nassuiaataasinnaanerat ilimanaateqannginnerulluni.

Imeqqutaalaqarfinnut misissuiartortarnerni sivisoqisuni, imeqqutaallat timmissallu naluusillit piaqqisut allat imminnut iluaqusersoqatigiittarneri nalunaarsorneqarsinnaasimapput. Naluumasortut Kajuaqqallu (*Phalaropus fulucarius* aamma *P. lobatus*) piaqqisut Kitsissunnguani misissuiffiginerisigut (Manus V), imeqqutaallat kalerrisaarinerinut qisuariaatit ersarissut ilisarineqarsinnaasimapput. Inernerit taakkua qularnaallisippaat, naluumasortukkut Kitsissunnguani siammarsimaffimmikkut allannguutaasa imeqqutaallat qeqertani sumiinneri malittarigaat, soorlu Egevang *et al.* 2004-mi siunnersuutigineqarsimasoq.

Allaatigisap aamma imarai inernerit Kalaallit Nunaanni oqartussanut saaffiginnittut. Kitaani Tunullu avannaani imeqqutaalaqarfinni pingaarnerpaani piaqqisut amerlassusaannik missingersuinerit saniatigut, siunissami piujuartitsilluni imeqqutaallanik manissarluni atuisinnaanermik inassuteqaatit saqqummiunneqarput (Manus II), Kalaallillu Nunaanni imeqqutaalaqarfiit nakkutigineqarsinnaanerannut tigussaasunik siunnersuuteqartoqarluni (Manus IV).

1 Synopsis

1.1 Introduction

There are several compelling reasons to study the migration and breeding biology of the Arctic tern in Greenland. From a global perspective, the Arctic tern is the very epitome of long-distance migration in birds, and no other animal species connects the two Polar Regions, as the Arctic tern does. Thus, the study of Arctic tern migration is not only an examination of migrating animals at the edge of their physical performance, it is also an exploration of a species moving through a vast proportion of the world's marine areas in a single calendar year, experiencing a rapidly changing environment with altered foraging opportunities on both the breeding and wintering grounds.

At a local scale, no other bird species in Greenland encapsulates the feeling of summer in the Arctic. The cry of the Arctic tern is for many in Greenland the ultimate sign of the end of a long winter and the onset of summer, the return of the sun and warmer temperatures. Although tern eggs are small and may not contribute much as a source of protein, the habit of harvesting Arctic tern eggs in summer has a long tradition in Greenland, and is considered one of the highlights of the summer season. There is no doubt that, to the people of Greenland, the Arctic tern has a special status amongst birds.

From a more scientific point of view, the Arctic tern is interesting to study due to its obvious appearance on the landscape and the placement of its nest directly on the ground. This makes the species relatively easy to study, compared with many other seabird species, where the nest is concealed in a rocky crevice or burrow, or on rocky ledges of high steep cliffs. Furthermore, the Arctic tern is a surface feeder and only capable of foraging in the top half meter of the water column. Theoretically, this two-dimensional feeding niche makes the species more vulnerable to changes in prey availability, and a direct response in breeding performance can be detected within a breeding season.

From an environmental management perspective, the Arctic tern is interesting because of its function as a "biodiversity generator". Smaller species, such as shorebirds, apparently benefit from the agonistic behaviour of the Arctic tern, and increased breeding densities of other species are often found within the boundaries of an Arctic tern colony (Nguyen *et al*. 2006, Egevang *et al*. 2008, Egevang *et al*. 2004, Egevang *et al*. 2006).

The Greenland Institute of Natural Resources generates specific knowledge on the Greenland marine and terrestrial fauna to provide the Greenland Government with management advice on the sustainable use of living resources. In Greenland, there is a long traditional of bird harvesting, and research on seabirds has mainly focused on the two most harvested species, Brünnich's Guillemot (*Uria lomvia*) and Common Eider (*Somateria mollissima*), with little attention directed towards other harvested species, such as the Arctic tern. As monitoring programmes for guillemots and eiders developed over the last decade, opportunities to expanding research activities of GINR (to species like little auks, black-legged kittiwakes, and Arctic terns) arose.

1.2 Objectives

Aim of the thesis: The initial aims of and motivations for my research were to illuminate a number of issues regarding the biology of the Arctic tern in Greenland, particularly from a management perspective. Basic questions, like "What is the current status of the Arctic tern population in Greenland ?", "What is the key prey species for Arctic terns in Greenland ?" and "Do Arctic terns relay in the Arctic ?" were unanswered. Later in the process, technological advances rapidly reduced the mass of geolocators, and allowed the Arctic tern to be targeted as a study subject, and the focus of my research broadened to also include this aspect.

Aim of the synopsis: The aim of this synopsis is to present background information on the biology of the Arctic tern and highlight how the results of this work have contributed to an improved understanding of this species, either globally or specifically in Greenland. In this context, the synopsis also includes results generated during the course of my research, but not presented in the manuscripts – especially those relating to issues specific to Greenland.

1.3 Distribution

The Arctic tern has a circumpolar distribution between the Boreal and High Arctic zones. The breeding range in Greenland is large (more than 350,000 km^2), and the species is found breeding in a variety of habitats.

In Greenland, Arctic terns are found breeding throughout the country. In West Greenland, the Arctic tern shows a patchy distribution with large gaps evident. The core breeding areas are in Disko Bay and in Upernavik District (Boertmann *et al.* 1996, Egevang and Boertmann 2003). In East Greenland, the colonies are fewer, more scattered, and smaller than in West Greenland. Typically, colonies in Greenland are found at small, isolated islets along the coast, and range from a few tens of pairs to a few hundred pairs. Large colonies of more than 2,000 pairs are rare, and even solitary breeding has been recorded in Greenland (Boertmann 1994).

1.4 Population status in Greenland

The total world population of Arctic terns is estimated at 1 to 2 million pairs (Lloyd *et al.* 1991). Global estimates of the Arctic tern population are rough, however, and some large populations (e.g. in Russia and Alaska are difficult to estimate (Wetlands International 2006).

Prior to 2002, there was little effort to monitor the Arctic tern population in Greenland. Counts were opportunistic and only performed in single years. The total Arctic tern population in Greenland is estimated to include at least 65,000 pairs (Egevang and Boertmann 2003), but limited data is available. However, three studies provide information that can be used to address population status: Salomonsen (1950) visited Kitsissunnguit, the largest Arctic tern colony in Greenland, for a short (1½ day) period in 1949, and estimated the population to be 100,000 pairs. This high number of breeding birds has never been encountered again in censuses conducted between 1980 and 2009, where estimates range from 0 to 25,000 pairs (Kampp 1980, Frich 1997, Hjarsen 2000, Egevang *et al.* 2004, Manus IV). Burnham *et al.* (2005) revisited Arctic tern colonies censured in Uummannaq District by Berthelsen (1921) in the period 1905 to 1920, to find that population numbers had declined to less than one-third between counts. Egevang and Boertmann (2003) compared Arctic tern colony counts in the Greenland Seabird Colony Database (GSCD) between 1921 and 2002, and concluded that a long-term decline was present, but the population seemed to stabilize in more recent counts, between 1986 and 2002.

Although the above studies provide only circumstantial evidence of a decline, it seems reasonable to conclude that the Arctic tern population in Greenland has undergone a decline since the middle of the last century. However, the magnitude of this decline is difficult to quantify and attempts to estimate the historical population size should be treated with caution.

The Arctic tern is categorized as “near threatened” in the Greenland Red List (Boertmann 2007).

1.5 Population status at Kitsissunnguit

The Arctic tern population at Kitsissunnguit has been followed with special interest by both managers in Greenland and international, non-government environmental organisations. The archipelago is home to one of the largest Arctic tern colonies in the world, and has been designated both as a Ramsar site, a special protected area for breeding birds in national legislation, and an Important Bird Area (IBA). Despite these designations, there was little effort to monitor the Arctic tern population in a systematic way prior to 2002. The sparse historical information on population size available from Kitsissunnguit indicated a crash in the population, with numbers going from 100,000 pairs in 1949 (Salomonsen 1950) to no breeding birds in 2000 (Hjarsen 2000), and a great concern arose within government and non-governmental institutions.

The Greenland Institute of National Resources introduced a modified distance sampling and line transect method to estimate population size at Kitsissunnguit in 1996 (Frich 1997), and annual counts were performed between 2002 and 2006 (Manus IV). This series of consecutive population estimates showed that the Arctic terns at Kitsissunnguit had not suffered a complete population crash, and found breeding numbers to be relatively stable between 15,000 and 22,000 pairs (Manus IV). Although these estimates are not in the same magnitude as the former estimate by Salomonsen in the mid 20th century, it is within the same magnitude as the estimate of roughly 25,000 pairs by Kampp *et al.* in 1980.

1.6 Fluctuating breeding

The Arctic tern is often referred to as a species with fluctuating colony attendance, large variation in breeding numbers, and years of skipped breeding (Manus IV). Breeding site fidelity at a regional level is high in Arctic terns, but dispersal to neighbouring breeding colonies occurs frequently (Devlin *et al.* 2008, Møller *et al.* 2006, Brindley *et al.* 1999, Ratcliffe

2004). Although poorly understood and documented in the literature, it is important to address whether variations in colony size may be caused by locally occurring phenomena, such as predation and disturbance, or if these variations are linked to large scale events, such as food availability or climatic variations. In order to make sense of counts at Arctic tern colonies where variation occurs, it is important to understand the scale (from within-colony to regional scale) at which variations in colony attendance occur. A particular combination of factors makes it difficult to address population size, status, and trends in Arctic terns (Ratcliffe 2004). This is most pronounced in the Arctic zone where Arctic tern breeding sites may be difficult to access and colonies can be widely distributed.

In addition to estimates of population size from the two study sites, Kitsissunnguit (2002-2006) and Sand Island (2006-2009), it was possible to conduct annual counts in 14 Arctic tern colonies in the southern part of Disko Bay (the Akunnaaq area) in the period 2002-2005 (Manus IV). Considerable fluctuation was found between years in these small and mid-sized colonies (mean CV of individual colonies equalled 117.5%), whereas the colonies at Kitsissunnguit only showed minor annual variation (47.4% at sub-colony level, 14.6% at overall level). When combined, however, the total population size of the Disko Bay colonies (more that 80% of the Artic tern colonies in Disko Bay), varied little (CV 6.7%), indicating local movements between the colonies and that annual variation was linked to locally occurring phenomena.

Variation at high-arctic Sand Island was even more pronounced, with complete breeding failures recorded in two out of four seasons (Manus IV).

1.7 Plausible cause of decline in population size

Arctic tern populations in Greenland are affected by numerous factors regulating population size and the observed long-term decline is likely to be caused by more than one factor. Arctic foxes (*Alopex lagopus*) are known to cause devastating predation when they are able to access a colony (Bianki and Isaksen 2000, Manus IV), and multiple avian predators are known to depredate egg, chicks, and, to a lesser degree, adult Arctic terns (Cramp 1985, Hatch 2002). Although these predators have always been present in Greenland, local Inuit claim that the number of predators in Greenland has increased, causing terns to decline. Although the relationship between food availability and reproductive performance in Arctic terns in Greenland is poorly documented, the study on chick diet and chick survival at Kitsissunnguit (Table 2, Manus III) indicates that productivity is low compared with other studies abroad (Appendix I in Hatch 2002). Food shortage or inaccessibility of suitable prey items can occur in Greenland waters and may affect the ability of Arctic terns to reproduce in some years.

In Greenland, harvesting of Arctic tern eggs for consumption has probably taken place as long as humans have inhabited the country (Manus II). The impact of this harvesting was initially constrained by a small human population size and limited forms of transportation. The human population in Greenland has more than quadrupled since the 1950's (Fægteborg 2000), however, and the number and size of motorized boats has increased rapidly, allowing greater mobility, and likely increasing pressure on the Arctic tern population.

The extent of the annual egg harvest in Greenland remains undocumented, although a few references may provide indications of its magnitude: Salomonsen (1950) estimated the annual harvest at Kitsissunnguit to be as high as 100,000 eggs, while Frich (1997) estimated that 150-200 persons visited the archipelago between 6 and 25 June 1996, and harvested between 3,000 and 6,000 eggs. Since 2002, the level of (illegal) harvesting has declined at Kitsissunnguit (*pers. obs.*).

Conservation concerns for the Arctic tern population in Greenland led to an altered managing of the resource: from an open season for egg harvest until 1 July before 2001, a ban on Arctic tern harvesting was introduced in 2002. Egg harvesting in Greenland is very much a cultural activity, where several generations participate in gathering eggs during summer. The ban on Arctic tern egg harvesting has been met by opposition in Greenland where some even consider it a violation of basic human rights. Since 2002, there has been a considerable pressure on national politicians to re-open the Arctic tern egg harvest season in Greenland.

A harvest of Arctic tern eggs is also carried out in Iceland, and, apparently, this is conducted without an adverse effect on the population. The egg harvest in Iceland differs from the Greenland harvest in several ways: in Iceland the season closes on 15 June, the harvest is only conducted by private landowners, and a high degree of predator control (foxes, gulls, and ravens) takes place (Aevar Petersen *pers. com.*).

The outcome of a model dealing with egg harvesting at Kitsissunnguit (Manus II) indicates that a fairly high number of eggs could be removed from the breeding population each year as long as egg harvesting is only conducted early in season. The model predicted 7 June as a date for harvest closure – the date where 92% of the maximum number of eggs would be available to harvesters, but the impact on productivity would be minor. The highest number of eggs could be harvested on 16 June, whereas harvest until 22 June would negatively affect population productivity. Based on the results of the model, high effort egg harvesting until 1 July (as was the case prior to 2002), is very likely to have placed an unsustainable pressure on the population, and could very well explain the observed decline.

1.8 Renesting in Arctic terns

In order to address the impact of egg harvesting on the Arctic tern population in Greenland, basic parameters of breeding biology are required for the species. Although the Arctic tern is often mentioned as a species that willingly produces a replacement clutch if the first clutch is lost (e.g. depredated or flooded) this is in fact very poorly described in the literature. The only scientific reference to my knowledge relating to relaying in Arctic terns is a paper by Bianki (1967) in Russian, quoted by Cramp (1985) and Hatch (2002), showing that relaying only occurs if eggs are lost during the first 10 days of the incubation period. Cramp (1985) also states (without references) that relaying mainly takes place at lower latitudes, but is “unlikely in the high Arctic”. Population dynamic parameters (such as 1) what proportion of the population will relay, 2) at what stage in the incubation period relaying will occur, and 3) growth and survival rates of chicks originating from replacement clutches), remain largely unknown in Arctic terns.

Renesting in Arctic terns was an important component in the fieldwork at Kitsissunnguit (Manus II and III). By experimentally removing eggs and monitoring the response of the breeding birds, the first estimates of relaying rate, and chick growth and survival rates were obtained for Arctic terns (Manus III). However, this challenge was not without large logistical difficulties. The laying date in Arctic terns breeding in Disko Bay varied (see section "Variation in breeding phenology") by as much as three weeks, making the onset of fieldwork difficult to plan. If breeding terns were to be followed from early incubation, and egg removal experiments allowing the birds to mate, egg formation to take place, an incubation period of 22 days, and chicks were to be followed until fledging, the field season had to be of two to three months in duration. In practice, the demands of such a long field period proved difficult to meet, and not all aspects of renesting in Arctic terns could be covered within the framework of this research.

Despite the fact that eggs were removed in the latter half of incubation, and past the 10 day period suggested by Bianki (1967), at least 16 out of 30 breeding pairs (53.3%) at Kitsissunnguit produced a replacement clutch (Manus III). The clutch size (1.6) at these nests was significantly lower than in control nests (2.1), as was the total Internal Egg Volume (IEV). None of the replacement eggs were relayed in the original nest cup, but were instead placed in a new nest at an average distance of 23.4 meters from the original nest cup.

The results from Kitsissunnguit verify the general perception that Arctic terns do produce a replacement clutch – even if the eggs are removed relatively late in the breeding season. Although the long term impact of relaying, such as the post-fledging survival of chicks, and the extra energy expenditure required of adult females, are not accounted for in this study, it does indicate that the birds are cable of compensating for the loss of eggs to some extent. The findings in Manus III, where chicks from replacement clutches did not differ in their growth and survival (at least to eleven days), further support this conclusion.

1.9 Variation in breeding phenology

The fieldwork at Kitsissunnguit and at Sand Island also revealed that breeding phenology may vary considerably between years, with considerable variation in egg laying between breeding seasons, as also seen in Arctic terns in Shetland (Suddaby and Ratcliffe 1997). At Kitsissunnguit, the majority of eggs hatched in the first week of July (indicating that egg laying took place in mid-June), but in some years early breeding takes place – as was the case in 2004, where eggs hatched three weeks earlier in mid June (Egevang *et al.* 2005). At Sand Island, hatching took place approximately two weeks earlier in 2008 than in 2007, with a broader distribution of hatching dates observed (Egevang *et al.* 2008, Egevang and Stenhouse 2007).

The onset of egg laying is likely correlated with sea ice conditions in Arctic regions (Hatch 2002) and this may explain the observed variation in this study. The variation of up to three weeks difference in egg laying may have implications for population monitoring at Arctic tern colonies. If pair formation is not completed, flush count estimates will underestimate population numbers. In line transect estimates (Manus IV), both the count before (not all pairs will have laid their eggs) and after (eggs will have hatched and chicks not recorded by the observer) the median incubation period will produce underestimates. Before conducting counts in a given year it is recommended that the stage of incubation is addressed – preferably by estimating egg age (Egevang *et al.* 2005).

1.10 Clutch size

From the study in Disko Bay and in Young Sund (Tab. 1) information on average clutch size was obtained. The distribution of one-, two-, and three-egg clutches differed significantly ($\chi^2=126.02$, df = 8, p = < 0.001) between seasons. At high-arctic Sand Island, no 3-egg clutches were observed in the study plots (nor in random observations) during the field seasons in 2007 and 2008, but a difference ($\chi^2=5.99$, df = 1, p = < 0.014) in the proportion of one- and two-egg clutches was identified. The overall clutch size at Sand Island (1.51, SD = 0.50, n = 169) was lower than at Kitsissunnguit (1.84, SD = 0.50, n = 1752), and the distribution of one-, two-, and three-egg clutches differed significantly ($\chi^2=66.45$, df = 2, p = < 0.001).

From the findings in this study from Greenland, it seems reasonable to conclude that investment in a 3-egg clutch only occurs on a regular basis at lower latitudes in the Arctic zone and rarely in the High Arctic. This hypothesis supported by a summary of clutch sizes found in Arctic terns across North America (Hatch 2002, Appendix 1), where 3-egg clutches are absent from locations north of 70° N.

Table 1. Average clutch size (± Standard Deviation) and sample size (n = no. of nests) and the distribution of one-, two-, and three-egg clutches in Arctic tern nests from Kitsissunnguit, western Greenland, 2002-2006, and Sand Island, northeast Greenland, 2007-2008.

Location	Year	Clutch size (SD)	Clutch size % (n)		
			1	2	3
Kitsissunnguit	2002	1.80 (0.50) n=292	24.3 (71)	72.2 (208)	4.5 (13)
Kitsissunnguit	2003	1.73 (0.45) n=413	26.9 (111)	72.9 (301)	0.2 (1)
Kitsissunnguit	2004	1.76 (0.55) n=446	29.6 (132)	64.6 (288)	5.8 (26)
Kitsissunnguit	2005	1.94 (0.41) n=234	12.0 (28)	82.5 (193)	5.6 (13)
Kitsissunnguit	2006	2.04 (0.49) n=367	9.8 (36)	76.0 (279)	14.2 (52)
Sand Island	2007	1.44 (0.50) n=109	56.0 (61)	44.0 (48)	0
Sand Island	2008	1.65 (0.50) n=60	35.0 (21)	65.0 (39)	0

1.11 Hatching and fledging success

Hatching success (Tab. 2) at Kitsissunnguit did not differ between years ($\chi^2=0.32$, df = 3, p = 0.956), but hatching success at Sand Island in 2008 was significantly lower ($\chi^2=4.04$, df = 1, p = 0.045) than Kitsissunnguit (all years combined). Fledging success in 2002, 2005, and 2006 (2003 data excluded due to short field season) at Kitsissunnguit did not differ between years ($\chi^2=0.19$, df = 2, p = 0.911), whereas fledging success turned out to be significantly higher at Sand Island ($\chi^2=5.06$, df = 1, p = 0.0259).

The highest proportion (14.2 %) of 3-egg clutches was found in 2006 –the same year the highest average chick survival was encountered. Further-

Table 2. Hatching success (proportion of eggs hatched), fledging success (proportion of chicks fledged) and productivity (number of fledglings per nest) from Kitsissunnguit, western Greenland, 2002-2006, and Sand Island, northeast Greenland, 2007-2008.

Location	**Year**	**Hatching success[a]**	**Fledging success[a]**	**Productivity (SD) n**
Kitsissunnguit	2002	0.90 (n=65)	0.37 (n=59)	0.56 (0.50) n=39
Kitsissunnguit	2003	0.93 (n=54)	0.58[b] (n=50)	0.58[b] (0.319) n=24
Kitsissunnguit	2004	*	*	*
Kitsissunnguit	2005	0.91 (n=46)	0.38 (n=42)	0.75 (0.433) n=20
Kitsissunnguit	2006	0.93 (n=73)	0.43 (n=68)	0.85 (0.595) n=46
Sand Island	2007	*	*	*
Sand Island	2008	0.84 (n=85)	0.69 (n=71)	1.04 (0.771) n=48

[a] Productivity and Hatching/Fledging success is not necessary based on measurements in the same eggs/nests.
[b] In 2003 chicks could only be followed to the age of 7-15 days old. Values of fledging success and productivity may not be representative.
* = no data on chick production in 2004 and 2007.

more, the year with the second highest recorded chick production (2005) was also the season with the second highest proportion of 3-egg clutches. Although the few data points in the study may not be sufficient to test if Arctic terns are able to adjust their clutch size to food availability in the current breeding season (Suddaby and Ratcliffe 1997, Kilpi *et al.* 1992), the results suggest that this may in fact the case.

1.12 Growth rate and chick survival

During the course of fieldwork, estimates of hatching success, chick growth and chick survival were obtained. Arctic tern chicks becomes agile and mobile after less than two days and will immediately start running away from the nest site if a land predator (humans included) approaches (Bianki and Isaksen 2000). In order to obtain consistent daily measurements of chick growth and survival, a small enclosure made from chicken wire was set up around Arctic tern nests at the study site. This method has previously been applied (Monaghan *et al.* 1989 *a, b*) in Arctic tern studies, and the birds adapt well to the enclosure after a short habituation period. Nests were found during the incubation period and the nest area was enclosed prior to hatching. As land predators were absent from the study sites during the chick rearing period, and the nest area could easy be approached from the air, it is unlikely that the enclosures induced biased estimates of the level of predation.

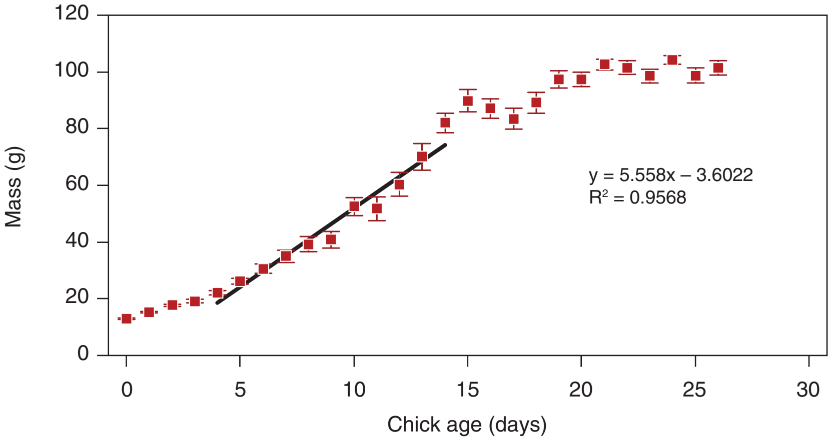

Figure 4. Growth of Arctic tern chicks in 2005 at Kitsissunnguit, Disko Bay, West Greenland. The figure shows average mass and SE bars in chicks (15.2 daily measurements on average) from hatching to fledgling. In the linear growth period (4-14 days) the equation describing daily mass increase is inserted.

Table 3. Table of average growth daily rates (mass and wing) in Arctic tern chicks aged 4-14 days at Kitsissunnguit, West Greenland (see Fig. 4). The number of daily measurements decreases over the season. Average daily measurements are presented in parenthesis.

Year	MASS	WING
2002	5.32 (n=15.5)	7.61 (n=15.5)
2003	5.87 (n=25)	8.05 (n=19)
2005	5.56 (n=15.2)	6.83 (n=15.6)
2006	6.30 (n=39.8)	7.66 (n=34.4)

Arctic tern chick growth rates were measured as the daily increase in mass and wing length. As growth is known to follow a sigmoidal pattern, with little increase in the first 3 days and levelling off after age 15 days (Fig. 4), the linear period between 4 and 14 days was used to compare groups and seasons (Manus II and III, Tab. 3). This period was also used in terns at Shetland (Suddaby and Ratcliffe 1997) to address differences in growth rates between seasons. In Shetland, chick growth varied with year and ranged between 6.9 and 7.8 g per day – the same order of magnitude as recorded at Kitsissunnguit (Tab. 3).

When obtaining measures for chick survival (Tab. 2), the enclosures were an essential tool in keeping track of the chicks from hatching to fledging. As the chicks grow older they become very mobile and difficult to find and information on their fate (alive or dead) becomes almost impossible to achieve without enclosures.

1.13 Feeding

The Arctic tern is an opportunistic, plunge-diving and surface-dipping feeder, with a diet comprising mainly small fish and large zooplankton (Cramps 1985, Hatch 2002). The species shows a high diversity of food items throughout its breeding distribution and during migration. The key prey species of the Arctic tern varies with its distribution, but fish is reported to be important in the diet throughout the breeding range (Hatch 2002). There are no systematic studies on the foraging range of the Arctic tern available, but "most" feeding is reported to take place within a 10 km (Boecker 1967) or 20 km (Pearson 1968) radius of the colony.

The literature on the diet of Arctic Terns in Greenland is very limited (Salomonsen (1950) mentioned zooplankton as important), which makes the results of the fieldwork at Kitsissunnguit and Sand Island relevant in a general context. At Kitsissunnguit, capelin (*Mallotus villosus)* was the single most important prey item over the study period (2002-2006). More detailed studies (Manus III) revealed that capelin accounted for up to 99.9 % of the energy intake of Arctic tern chicks in periods. The study at Kitsissunnguit also revealed variation in diet composition between seasons (Manus III and *unpubl. data*). In some years, other prey items (e.g. Stichaeidae sp. in 2005 and 2006, Wolffish (*Anarhichas* spp.) in 2006) may become important for shorter periods during chick rearing. Even discards from shrimp vessels appear in the chick diet when the commercial catch is sorted close to colony islands. Although these occasional influxes of alternative prey items appear in the diet, the importance of capelin is unquestionable as the key prey species of Arctic terns in Disko Bay, and probably

Figure 5. Arctic tern chick fed with polar cod at Sand Island. Photo: Carsten Egevang.

across most of West Greenland, where capelin constitutes the link between zooplankton and higher trophic levels (Carscadden *et al.* 2002; Friis-Rødel and Kanneworff 2002).

At high-arctic Sand Island, opportunistic observations of prey items carried by adult birds during 2007 and 2008 were conducted, along with systematic observations of chick diet in 2008 (Egevang and Stenhouse 2007, Egevang *et al.* 2008). Polar cod (both larvae and juvenile fish) appeared to be the most important prey species in the chick diet, with crustaceans (especially *Thysanoessa* ssp.) as secondary prey items (Egevang *et al.* 2008).

1.14 Breeding association

The Arctic tern shows a strong antagonistic, anti-predator behaviour towards potential predators within the colony boundaries. Both land mammals and avian predators are fiercely attacked from the air (Hatch 2002). Shorebirds such as purple sandpiper (*Calidris maritima*), semipalmated plover (*Charadrius semipalmatus*), and red phalarope (*Phalaropus fulicarius*) are known to breed in higher densities and with reduced nest predation when found within or close to an Arctic tern colony (Nguyen *et al*. 2006, Smith *et al*. 2007, Summer and Nicoll 2004). In Greenland, Sabine's gulls (*Xema sabini*) breed almost exclusively with Arctic terns (Levermann and Tøttrup 2007), with 21 out of 24 colonies found in association with tern colonies. Ross's gull (*Rhodostethia rosea*) has only been found breeding ten times in Greenland, and nine of these breeding records have been in association with breeding Arctic terns (Egevang and Boertmann 2008). At Kitsissunnguit, there is a strong breeding association between Arctic terns and red-necked phalaropes (*Phalaropus lobatus*) and red phalarope (Egevang *et al.*

2006, Egevang *et al*. 2004). Analysis of the historical and present distribution of breeding terns and phalaropes at Kitsissunnguit showed that phalarope breeding densities are higher on islands where terns breed. In the case of the red phalarope, the breeding association is particularly strong and breeding only occurred where breeding terns are found (Egevang *et al*. 2004). Breeding association and higher breeding densities are also documented for mallards (*Anas platyrhynchos*) and red-breasted mergansers (*Mergus serrator*), while long-tailed ducks (*Clangula hyemalis*) are exclusively found breeding at islands withterns (Egevang *et al*. 2006).

At Kitsissunnguit, where high numbers of Arctic terns breed, the response to predators within the boundaries of the colony is very strong. The presence of an avian predator results in mobbing behaviour of hundreds, sometimes thousands, of terns with intense vocalisation. In order to document the breeding association between phalaropes and terns, we conducted a study (Manus V) on phalarope behavioural response to tern alarm calls. Potential avian predators over-flying the colony and both land and avian predators at the outskirts of the colony do not trigger a response from the terns. As soon as the predator enters an area with breeding terns, alarm calls and mobbing is initiated by the terns. These alarm calls vary, not only in duration, but also in the character of the call (Hatch 2002). Alarm calls in the study were divided into three groups originating from: 1) falcons or gulls, 2) human disturbance, or 3) dreads (false alarms). By recording behavioural response from both red-necked and red phalaropes to tern alarm calls, we were able to document a strong relationship between the species. Phalaropes did not respond differently to alarms caused by a predator compared to false alarms, but extended tern alarms caused stronger phalarope response than short ones. In conclusion, phalaropes benefit from both a higher predator detection rate and aggressive defence in the tern nesting area. This supports the hypothesis (Egevang *et al.* 2004, Egevang *et al.* 2006) of a decline in phalarope numbers and shift in phalarope distribution at Kitsissunnguit, governed by the distribution of breeding Arctic terns (Manus V).

1.15 Migration

The Arctic tern is known to perform the longest annual migration in the animal kingdom. The distance alone, from the breeding colonies at high latitudes of the northern hemisphere to the winter quarters at high latitudes in the southern hemisphere, makes the Arctic tern a candidate for the longest annual roundtrip (Berthold 2001, Newton 2008). There were several early attempts to interpret the migration of the species (Kullenberg 1946, Storr 1958), but the first comprehensive review was presented by Salomonsen (1967). Based on ringing recoveries and observations from the southern seas, Salomonsen suggested that the southbound migration follows the coast of West Europe and later West Africa, with the birds arriving in the waters off South Africa in November. Salomonsen suggested the main wintering areas to be off the southern tip of Africa and South America, and that Arctic terns might circumnavigate the Antarctic continent in early spring before initiating their northbound migration. This hypothesis was later supported by radar and visual observations of terns migrating from the Bellingshausen Sea to the Weddell Sea (Gudmundsson *et al.*1992). It has been suggested that Arctic terns complete the southbound migration in a step-wise fashion, moving between rich feeding grounds (Alerstam 1985). Crossing over land areas and the Greenland inland ice at high altitude was suggested to take place in the migration of the Arctic tern in the mid-1980s using radar observations (Alerstam *et al.* 1986). There was little evidence of the northbound migration of the Arctic tern in spring available for Salomonsen, but a ringing recovery of a Greenland ringed bird from Columbia in the highland of South America, led him to speculate that at least some birds may end up in the Pacific Ocean and cross over land to enter the Atlantic Ocean. However, the major northbound migration was believed to be initiated in March in the Atlantic Ocean and occur more rapidly and over a wider front compared to autumn (Kampp 2001, Bourne and Casement 1996).

Several authors (e.g. Berthold 2001, Newton 2008) have attempted to estimate the total distance travelled during the annual migration of the Arctic tern. As the flight path was largely unknown, these estimates vary, but typically a figure of 40,000 km was quoted as the annual trip from breeding grounds to the wintering grounds, and back.

As advances in technology make devices for mapping animal migration smaller and lighter, the chance of documenting the long migration of the Arctic tern crept closer. The ideal tool for this would be a satellite transmitter with a full year of battery capacity. However, at present, satellite transmitters are still too heavy for birds with a mass under 250 gram to carry on migration. Instead, the less accurate, but much lighter geolocators (miniature archival light loggers), have proven to be an effective tool (Richards *et al.* 2004). By recording and storing ambient light intensity, the geolocators reveal information on sunrise and sunset. When these data are combined with time recordings, two daily geographical positions can be calculated and migration routes can be mapped. The disadvantage of geolocators is that they cannot transmit data, and the tagged bird has to be caught again at the end of the study period – a logistical challenge that normally requires that the bird nest at the same location two years in a row.

Although often quoted in both scientific and popular literature as the longest migration performed by any bird in the world, a study (Shaffer *et al*. 2006) questioned the Arctic tern's status as the longest migrant. Using geolocators, Shaffer *et al*. (2006) were able to document that sooty shearwaters (*Puffinus griseus*) make an annual round trip from New Zealand to the waters in the northern Pacific Ocean and back, of 64,037 (± 9,779) km on average.

Figure 6. An Arctic tern equipped with a geo-locator in 2007 returns to the breeding site at Sand Island in Northeast Greenland the following year, after having completed a round-trip migration of more than 70,000 km.

At Sand Island, we conducted a study (Manus I) which recorded a full year of migration in Arctic terns.

Prior to deploying geolocators on Arctic terns, however, a small-scale dummy test (Egevang 2006) was conducted on terns breeding at Kitsissunnguit in 2006. In order to observe how the birds would respond to objects attached to the leg, eleven arctic terns were equipped with dummies with the approximate mass and physical dimensions as loggers scheduled to be manufactured in 2007. Although some negative behavioural response ("leg-lifting") to the loggers were observed the days following the deployment, the overall conclusion was that very little or no effect could be detected in the chick rearing performed by the tagged adult bird. On the basis of these findings, it was decided to go ahead with a full scale study deploying geolocators on Arctic terns at Sand Island in 2007.

The study on Arctic tern migration revealed the longest migration ever recorded in any animal, with a total annual average distance of 70,900 km (range 59,500-81,600 km) travelled. The study also identified a previously unknown stop-over site in the central part of the North Atlantic Ocean (Fig. 5), where the birds spent on average 24.6 (±6 days) before continuing south. This at-sea hot-spot is located between cold and warm water masses with high eddy variability. Satellite imagery analysis of Chlorophyll *a*. distribution revealed a high biological productivity in this particularly area whereas areas to the south were generally of low productivity. It seems likely that Arctic terns use this area to forage and "fuel up" before conducting their

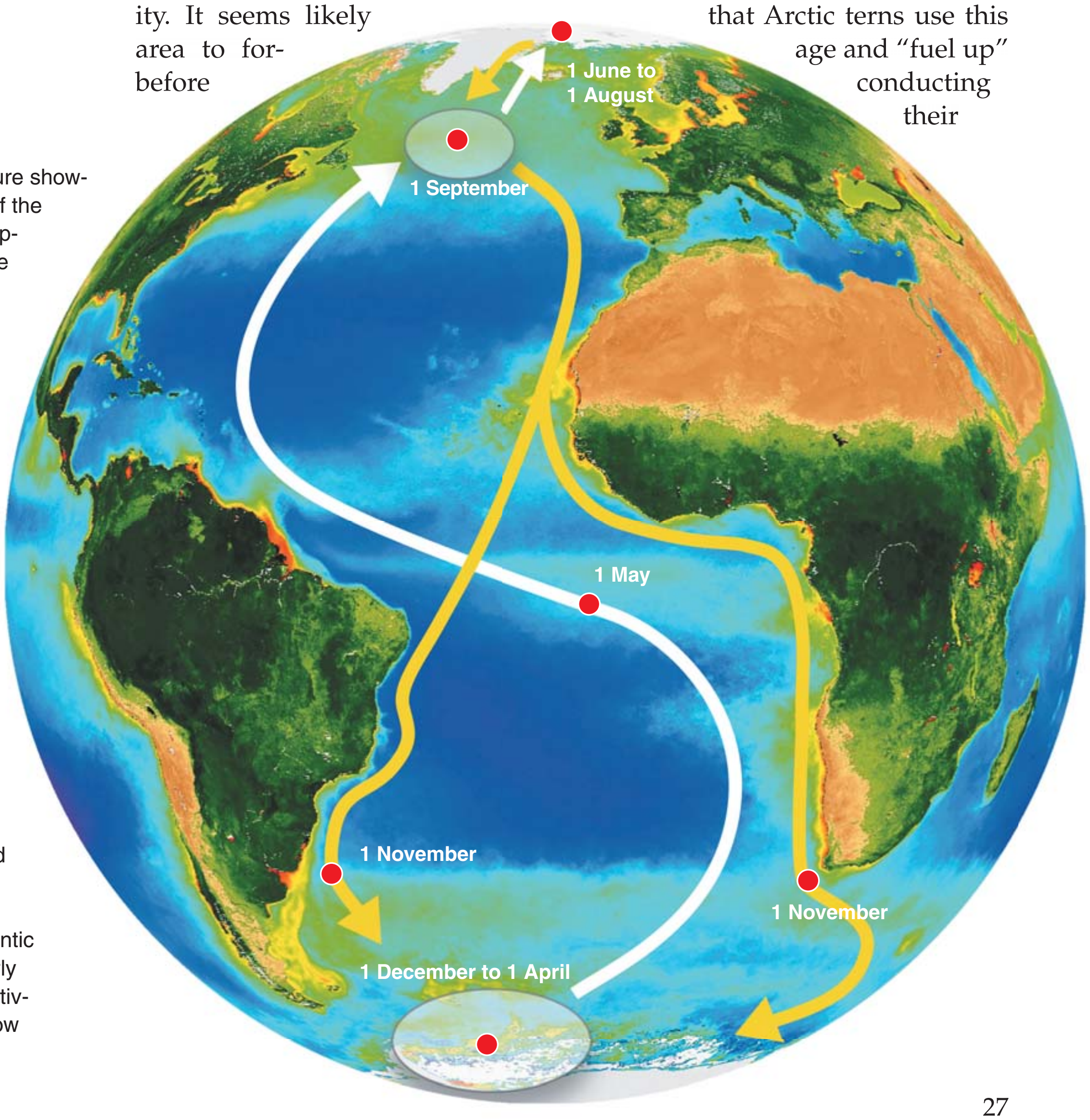

Figure 7. Simplified figure showing migration patterns of the Arctic tern, along with approximate position of the birds each month, from the breeding sites in Greenland and Iceland to the winter grounds at Antarctica. After initiating the southbound migration (yellow line) the birds paused their migration in the central part of the North Atlantic (small circle) for almost a month before they continue towards the wintering sites at Antarctica (large circle). In spring, the northbound migration (white line) is conducted more than twice as fast in a gigantic "S" shaped pattern through the Atlantic Ocean. Areas particularly rich in biological productivity are indicated by yellow and green colours.

migration into tropical marine regions with low productivity and limited food availability. It is likely that this Arctic tern stop-over site may serve as a hot-spot area for other migrating seabirds, e.g. long-tailed skua (Stercorarius longicaudus) has been observed in high densities in this area during ship-based surveys (D. Boertmann pers. com).

The migration study also revealed a divide in the southbound migration of the Arctic tern. Just south (~10° N) of the Cape Verde Island, seven individuals migrated south along the coast of West Africa (as expected from ringing recoveries), while four individuals crossed the Atlantic Ocean to migrate south along the coast of South America. Furthermore, three individuals drifted east along the southern Polar Front and entered the Indian Ocean. Although divides in migratory routes are known in other avian species breeding at a single location, for example ospreys (*Pandion haliaetus*) breeding in Sweden (Hake *et al.* 2001), the study on Arctic tern migration illustrates goal orientation at a global scale. Although the terns travelled through vastly different areas, they all wintered in a relatively restricted geographical area in the Weddell Sea.

The Arctic tern migration study also highlighted differences in the pace of southbound versus northbound migrations. While the migration south to the winter quarters was conducted over a period of three months (average 93 days and an average speed of 330 km per day), the northbound migration back to the breeding sites was much faster. The terns covered the 25,700 km from the winter site north to 60° N in an average of 40 days. This long leg of migration was conducted with average daily distances of 520 km – with some individuals flying up to 670 km per day. Unequal migration speeds of autumn versus spring are known from numerous bird species (Newton 2008) but, in this study, we were able to correlate the fast northbound migration with the prevailing global wind systems.

Most studies on bird migration are performed on land birds and much of our understanding of the mechanism behind migration is based on land bird studies. Seabirds are poorly represented in text books on migration (e.g. Newton 2008, Berthold 2001), even though it is amongst seabirds that the most spectacular migration patterns are found. Even in modern seabird text books seabird migration may be described “as most seabirds migrate exclusively at sea, they have an opportunity to rest or feed whenever they feel like it: not an option for land birds crossing water or deserts” (Gaston 2004). Our study show that the Arctic tern migration in many ways resembles that of land birds with distinct wintering areas and stop-over sites along the migration route, and a high level of synchrony in phenology amongst individuals.

2 Conclusion

In conclusion, the studies performed at Kitsissunnguit and Sand Island elevated the level of knowledge on the Arctic tern in Greenland considerably. From the series of population size estimates in Disko Bay we learned that the breeding population at the largest colony in Greenland, Kitsissunnguit, had not crashed as suggested, but instead numbers were stable over a five year period at 18,500 + 3,500 pairs. Although considerably lower than population size estimates from five or six decades ago, it seems reasonable to conclude that the decline in the Arctic tern population at Kitsissunnguit happened prior to 1980, which may also be the case for the other tern colonies in Greenland. The example from Kitsissunnguit highlights the need for a systematic monitoring plan for Arctic terns, if natural resource managers in Greenland are to address the status of birds like the Arctic tern. However, the fluctuating breeding of the species requires a specially designed monitoring where many colonies are monitored within the same breeding season, or alternatively that large colonies, like Kitsissunnguit are monitored on a regular basis, preferably in consecutive years. The decline in the Greenland Arctic tern population has been linked to an egg harvest of a magnitude beyond what was believed to be a sustainable level. The output of the harvest model (Manus II) indicate that this is very likely to have been the case – egg harvesting beyond mid-June is likely to affect the population severely and should be avoided in future management.

The studies included in this thesis also produced the first estimates of the key prey species of the Arctic tern during the breeding season. In the central parts of West Greenland the capelin proved to be of very high importance. Over the last decade the idea of initiating an industrial fishery for capelin in Greenland has been proposed on several occasions. The identification of the diet of the Arctic tern is simply confirmation of yet another Arctic bird, fish, or mammal species that depends heavily on capelin, making the consequences of opening up a large scale commercial fishery uncertain but nonetheless alarming.

The study at both Kitsissunnguit and Sand Island verified the strong connection between Arctic terns and a number of other avian species that benefit from the protection that terns offer from intruders within the perimeters of the colony. In identifying important natural sites with a high diversity of breeding bird species, one could consider breeding sites of Arctic terns.

3 Future research

The study on the long-distance migration of the Arctic tern (Manus I) revealed a number of new facts not previously known about the impressive annual migration and verified existing knowledge obtained from ringing recoveries. This study also raises some new questions that would be interesting to pursue in future studies: 1) at the breeding areas, the Arctic tern is known to be on the wing most of the time. When it rests, it sits on the ground or alternatively on an iceberg. Unlike most other seabirds, the Arctic tern rarely rests on the water and only in very calm weather. The geolocators used in the migration study also record dry or wet condition during the period of deployment, which can be used to indicate the individual's behaviour during migration (Guilford *et al.* 2009). From a both physiological and energetic perspective it could be interesting to investigate whether Arctic terns manage the long stretches of migration between the polar areas without long periods of resting on the water; 2) The migration study identified a divide into two different southbound routes. This divide could be coincidental, where wind systems drive the birds to take a western or eastern route. This would mean that the same individual may migrate south by either of the two different routes each year. An alternative explanation would be that the route may be genetically coded or learned in the individual and the same bird will choose the same route each year. The geolocators have the capacity to log for two years and are cable of storing data for up to ten years. In theory, loggers applied in 2007 and not retrieved in 2008 (potentially up to 40 loggers) should contain data on two round trips which could help shed light on which of the two hypotheses is most plausible. An attempt to retrieve loggers at Sand Island was made in 2009, but was unsuccessful due to a year of breeding failure. Hopefully, an attempt in 2010 will prove to have more success; 3) The migration study identified an area in the central part of the Atlantic Ocean to be of high importance for the terns on their southbound migration. It seems likely that this area may be important for other surface feeding seabirds as an at-sea foraging hot-spot, and it could be interesting to expand the number of study species in a migration study using geolocators. Such a study could prove to be an efficient tool to identify at-sea areas of high biodiversity otherwise difficult or cost-prohibitive to obtain.

Although the study on relaying in Arctic terns (Manus III) did produce estimates of the species' ability to produce a replacement clutch when the first clutch was removed, additional detailed information is needed in order to address the impact of harvesting and relaying at the population level. However, large logistical difficulties are associated with a study of this kind. Relaying Arctic terns may easily move within or even well out of the colony to place their new nest. The chances of detection of the new nest site, and establishing an accurate estimate of what proportion of the population will relay, decreases with distance from the original nest site. Unless devices, such as radio transmitters, that are able to track the location of the bird in a study are used, it will be difficult to obtain accurate estimates of relaying in Arctic terns.

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Manus I

TRACKING OF ARCTIC TERNS *STERNA PARADISAEA* REVEALS LONGEST ANIMAL MIGRATION

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Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration

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The study of long-distance migration provides insights into the habits and performance of organisms at the limit of their physical abilities. The Arctic tern *Sterna paradisaea* is the epitome of such behavior; despite its small size (<125 g), banding recoveries and at-sea surveys suggest that its annual migration from boreal and high Arctic breeding grounds to the Southern Ocean may be the longest seasonal movement of any animal. Our tracking of 11 Arctic terns fitted with miniature (1.4-g) geolocators revealed that these birds do indeed travel huge distances (more than 80,000 km annually for some individuals). As well as confirming the location of the main wintering region, we also identified a previously unknown oceanic stopover area in the North Atlantic used by birds from at least two breeding populations (from Greenland and Iceland). Although birds from the same colony took one of two alternative southbound migration routes following the African or South American coast, all returned on a broadly similar, sigmoidal trajectory, crossing from east to west in the Atlantic in the region of the equatorial Intertropical Convergence Zone. Arctic terns clearly target regions of high marine productivity both as stopover and wintering areas, and exploit prevailing global wind systems to reduce flight costs on long-distance commutes.

at-sea hotspot | global wind systems | geolocator | trans-equatorial migration

Developments in tracking technologies in the last three decades have revolutionized our understanding of movements of wide-ranging marine predators during both the breeding and nonbreeding periods (1–4). Until recently, minimum device sizes restricted deployments on seabirds to albatrosses, large petrels, and shearwaters (>400 g) (3–7), neglecting smaller species which, arguably, have even greater migratory capabilities and are potentially more sensitive indicators of the status of marine ecosystems (8, 9). These include a species long regarded as the classic exponent of long-distance migration in vertebrates, the Arctic tern (*Sterna paradisaea*).

The Arctic tern exhibits a circumpolar breeding distribution at high latitudes of the northern hemisphere and winters at high latitudes in the southern hemisphere (10, 11). The species nests on the ground, and is an opportunistic plunge-diving and surface-dipping feeder, with a diet comprising mainly small fish and large zooplankton (12, 13). There were several early attempts to infer its movements (14, 15), but the first comprehensive review (16) was presented by Salomonsen in 1967. He suggested that the main wintering areas were most likely to be off the southern tip of Africa and South America, and that Arctic terns might circumnavigate the Antarctic continent in early spring before initiating their northbound migration. This appeared to be supported by subsequent radar and visual observations of terns migrating from the Bellingshausen Sea to the Weddell Sea (17). It has been suggested that Arctic terns complete the southbound migration in a step-wise fashion, moving between rich feeding grounds, and may use high altitude migration flights to cross large expanses of land, such as the Greenland ice sheet (18, 19). Until now, there was little information on the northward return to the colony, but it was generally believed to start in March and occur more rapidly and over a wider front (20, 21). Several authors (10, 11) have attempted to estimate the total distance traveled during this impressive annual migration, typically quoting a figure of 40,000 km.

Although many (but not all) of these suppositions have subsequently proved correct, they were based on limited banding recoveries and at-sea observations, and hence inevitably reflected a range of potential biases (including, respectively, spatial and temporal variability in recovery effort, and lack of information on provenance, age, and status of individuals). Nor could they provide information on variation among individuals and populations in the phenology of migration, flight paths, or preferred wintering habitats. With the aim of providing much greater detail on individual movement patterns, we developed miniature (1.4-g) archival light loggers (geolocators) similar to those used in a recent study of passerines (22), for deployment on Arctic terns at two Arctic colonies.

Results and Discussion

With an accuracy of ∼185 km in flying seabirds (23), the geolocators were used to document the migration routes, stopover sites, and wintering areas of Arctic terns from colonies in high-Arctic Greenland ($n = 10$) and Arctic Iceland ($n = 1$). At the end of the breeding season, tagged birds traveled southwest to a stopover region of deep water in the eastern portion of the Newfoundland Basin and the western slope of the mid-North Atlantic Ridge between 41–53° N and 27–41° W, in which they remained for an average ± SD of 24.6 ± 6 days (Fig. 1). This previously unknown oceanic hotspot for terns was located at the junction between cold, highly productive northern water and warmer, less-productive southern water, and was characterized by high *Chl. a* concentrations and high eddy variability (24, 25). Between 5 and 22 September 2007, all 11 birds continued their migration southeast toward the West African coast. South of the Cape Verde Islands (∼10° N), however, migration routes diverged: seven birds continued to fly south parallel to the African coast, whereas four others crossed the Atlantic to follow the east coast of Brazil. Birds in both groups ceased their directed southbound transits at ∼38–40° S, and shifted to a pattern of predominantly east–west movements. Three birds then traveled east into the Indian Ocean (one as far as 106° E). All birds subsequently moved south, spending the austral summer (December–March) south of 58° S and between 0 and 61° W in the Atlantic sector of the Southern Ocean. This region, which includes the Weddell Sea, is particularly productive, and supports higher densities of a key prey

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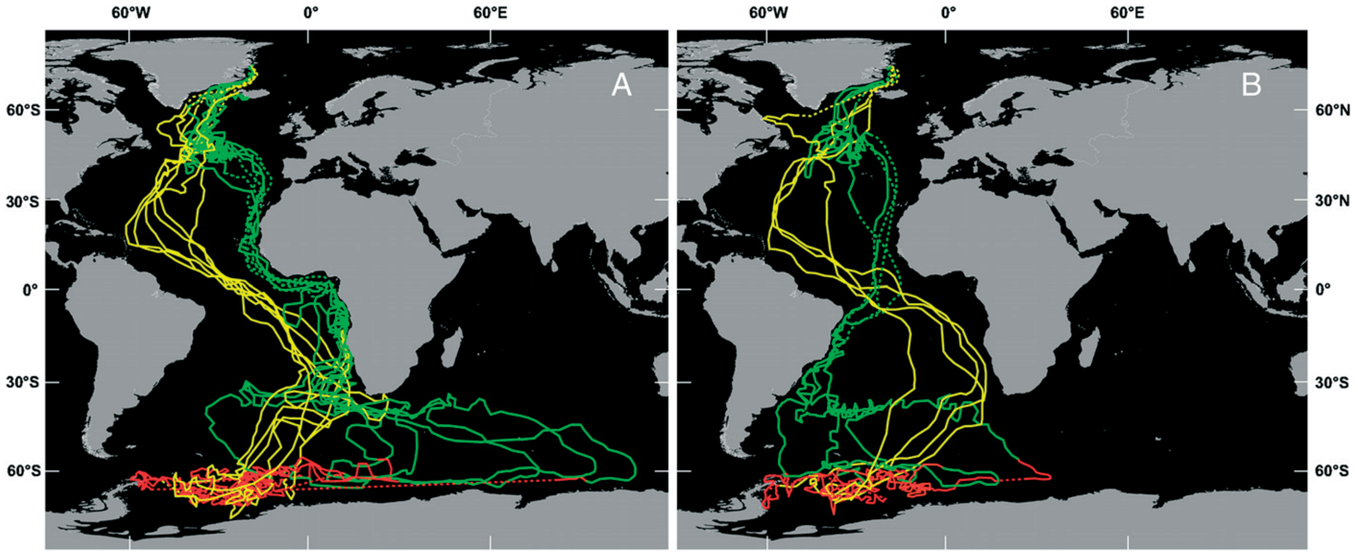

Fig. 1. Interpolated geolocation tracks of 11 Arctic terns tracked from breeding colonies in Greenland ($n = 10$ birds) and Iceland ($n = 1$ bird). Green = autumn (postbreeding) migration (August–November), red = winter range (December–March), and yellow = spring (return) migration (April–May). Two southbound migration routes were adopted in the South Atlantic, either (*A*) West African coast ($n = 7$ birds) or (*B*) Brazilian coast. *Dotted lines* link locations during the equinoxes.

for many seabirds, Antarctic krill (*Euphausia superba*), than elsewhere in the Southern Ocean (26).

All birds began the return migration to breeding colonies in early–mid April, always traveling over deep water at considerable distance from continental shelf margins, and taking a sigmoidal route, counterclockwise around the South Atlantic and clockwise around the North Atlantic gyres. Upon return in late May to the same general stopover region in the North Atlantic used during the southbound migration, two individuals transited rapidly west through the area, three remained there for 3–6 days before continuing to the north, and the remaining five birds appeared not to pause or deviate from their general course. Thus, there was little indication that the area was particularly important for northbound terns. Although the Arctic tern from Iceland began its outbound and return migration earlier than the Greenland-breeding birds (Table 1), there was no obvious difference in migration routes between this individual and some of the terns from Greenland. Thus, the emerging pattern for transequatorial migrants is of a high degree of mixing of birds from different breeding populations in wintering areas, as evident in this study and previous ones (5, 7, 27). This contrasts with the dominant strategies of southern hemisphere albatrosses, which, despite a similar capacity for long-distance migration and hence overlap, nevertheless tend to show a high degree of between-population segregation in nonbreeding distributions (28).

The Greenlandic birds exhibited clear synchrony in timing of migration, all reaching the North Atlantic stopover site, departing the wintering area and crossing the Equator within a few days of each other (Table 1), but there was no indication that they traveled together in the same flocks. Similarly, at-sea observations suggest that flock sizes of migrating terns are typically very small (<15 birds) (17), and recent results (7) from studies of other migrant seabirds also indicate high levels of synchrony in timing of passage through restricted flyways and no evidence of persistent associations between individuals (including members of a pair).

The routes used for both the southbound and northbound migrations showed a high level of congruence with parts of those taken by Manx shearwater (*Puffinus puffinus*) and Cory's shearwater (*Calonectris diomedea*), which also winter in the South Atlantic, albeit considerably farther north than Arctic terns (5, 6). It would appear, therefore, that the terns' small size is no handicap to exploiting the prevailing global wind systems (clockwise in the North, and counter clockwise in the South Atlantic), in a similar way to that of shearwaters (27), and confirms similar suggestions made several decades ago for terns (29). The efficiency of tern flight paths is illustrated by the return

Table 1. Phenology of migration stages of Arctic terns from colonies in Greenland (n = 10) and Iceland (n = 1)

	Greenland birds (n = 10)	Iceland bird (n = 1)
Arrival at North Atlantic stopover site	22 Aug (16–27 Aug)	16 Aug
Time spent at North Atlantic stopover site	24.6 Days (10–30 days)	16 days
Departure from North Atlantic stopover site	15 Sep (5–22 Sep)	1 Sep
Arrival in wintering region	24 Nov (25 Oct–30 Nov)	5 Nov
Time spent in wintering region	149 Days (139–173 days)	151 days
Departure from wintering region	16 Apr (12–19 Apr)	3 Apr
Date passing Equator on northbound migration	3 May (25 Apr–7 May)	13 Apr
Duration of northbound migration	40 Days (36–46 days)	41 days
Duration of southbound migration	93 Days (69–103 days)	80 days

Arrival and departure dates and durations are given as mean with range in parentheses.

Table 2. Summary of distances traveled during migration stages of Arctic terns (Greenland and Iceland birds combined, $n = 11$)

Migration segment	Distance traveled
Total distance traveled on migration	70,900 km (59,500–81,600 km)
Distance traveled on southbound migration	34,600 km (28,800–38,500 km)
Distance traveled per day on southbound migration	330 km·day^{-1} (280–390 km·day^{-1})
Distance traveled on northbound migration	25,700 km (21,400–34,900 km)
Distance traveled per day on northbound migration	520 km·day^{-1} (390–670 km·day^{-1})
Distance traveled within winter site	10,900 km (2,700–21,600 km)

migration from Antarctica to south Greenland (c. 60° N), an average distance of 24,270 km (range 20,070–27,790 km) covered in only 40 days (range 36–46 days), with average travel distances of 520 km·day^{-1} (range 390–670 km·day^{-1}). As birds seem to have been exploiting favorable winds, travel (ground) speed will be higher than air speed. Nevertheless these flight speeds are of the same order as the maximum range speed (9.7 ms^{-1}) calculated from aerodynamics theory, and mean groundspeeds observed using radar (11.3 ms^{-1}) (17), which would correspond to 838 and 976 km·day^{-1}, respectively, if birds were to fly nonstop (which is, of course, unlikely). Overall, the northbound migration took less than half the time (40 vs. 93 days), despite being three quarters the length (25,700 vs. 34,600 km) of the southbound journey. Indeed, the average annual distance traveled, from departing the breeding site in August to return in late May/early June (i.e., excluding movements within the breeding season) was 70,900 km (range 59,500–81,600 km). This is the longest round-trip animal migration ever recorded electronically (3, 5, 7). As our estimates of travel distance, and hence speed, were affected by the fractal dimension of the flight path (i.e., the step length for the distance measurements) (30), and by the considerable errors inherent in geolocation (23), they are not directly comparable with previous studies. Nevertheless, the tracked birds were considered to travel nearly twice the total distance generally cited for the annual Arctic tern migration. As Arctic terns can live for more than 30 years (31), the total distance traveled in a lifetime may exceed 2.4 million km, equivalent to approximately three return journeys to the Moon.

Our study demonstrated heterogeneity in migration routes within a population, yet clear migratory connectivity between populations. We confirmed that the main wintering region was the marginal ice zone around Antarctica, which agrees with at-sea observations (ref. 18 and references therein). Given that the highest densities of Arctic terns in the Southern Ocean have been observed in the Weddell Sea (17), and that a very high (likely >50%) proportion of the worlds Arctic terns breed in Greenland and Iceland (13), the wintering areas used by our tracked birds may well be typical of the majority of the North Atlantic population. Thus, the long-term changes in duration and extent of winter sea ice, and declines in abundance of Antarctic krill in this region (26, 32) should be viewed with considerable concern.

Material and Methods

We fitted miniature archival light loggers (Mk14 geolocators, mass 1.4 g; British Antarctic Survey), attached to plastic leg rings (mass of logger, ring, tape, and cable tie: 2.0 g, ~1.9% of adult body mass), to 50 breeding Arctic terns in July 2007 at Sand Island (74° 43′ N, 20° 27′ W), Young Sound, Northeast Greenland. An additional 20 geolocators were deployed on Arctic terns at Flatey Island (65° 22′N; 22° 55′W), Breiðafjörður, Iceland, in June 2007. The following season, a minimum of 21 birds equipped with loggers (>42%) were observed at Sand Island, but only 10 loggers (20%) were retrieved. At Flatey Island, four birds were resighted (20%), and one (5%) logger was retrieved. All recaptured birds were in good physical condition and no significant difference ($t = -1.57$, $P = 0.133$, df = 18, $n = 10$) could be detected in their body mass between the 2 years (mean ± SD in 2007 and 2008: 106.0 g ± 6.3 and 110.3 ± 6.0, respectively). The average clutch size of breeding pairs in 2008 at Sand Island equipped with loggers was 1.3 (± 0.43, $n = 8$), whereas clutch size in control birds the same year was 1.7 (±0.48, $n = 60$). Although poor in power of analysis because of low sample size in the logger group, a one-sided Fisher's exact test indicated no statistical difference ($P = 0.038$) between the two groups. Not all birds observed at colonies in 2008 could be recaptured; some birds were clearly breeding, but the nest could not be located or the targeted bird would not enter the trap; others were likely to be nonbreeders or failed breeders, which are very difficult to capture. In one case (Iceland), the nest of an equipped bird was abandoned after being trampled by domestic sheep before the bird could be trapped.

Although fidelity at the regional level is high in nesting Arctic terns (33), dispersal to neighboring breeding colonies occurs frequently (33–36) and is likely driven by food availability, presence of predators, disturbance, or changing climatic conditions. The only study to apply modern capture–mark–recapture techniques to adult Arctic terns showed a low reencounter probability, ranging from 0.12 to 0.74, depending on colony and year (33).

Ten of the 11 loggers retrieved were downloaded successfully, providing a full year of migration data (July 2007 to July 2008). Six months of migration data were extracted from the remaining logger. Light data were processed following the approach of Phillips et al. (23). Times of sunrise and sunset were calculated from light records and converted to location estimates using TransEdit and BirdTracker (British Antarctic Survey) using thresholds of 10, an angle of elevation of −4.7°, and applying the compensation for movement. Locations were unavailable at periods of the year when birds were at very high latitudes and experiencing 24 h daylight. In addition, only longitudes were available around equinoxes, when day length is similar throughout the world. Overall, after omitting periods with light level interference and periods around equinoxes, the filtered data sets contained between 166 and 242 days of locations for each individual (mean = 207.2 days, SD = 20.58, $n = 10$). The data set contained two daily positions, after fitting points to a smooth line, travel distances were calculated in ArcMap (ESRI) using great circle distances (Table 2). A straight-line path was assumed between the preceding and succeeding valid fix around periods when locations were unavailable (discussed above). The only exceptions were during the autumn migration around the west African coast, where it was assumed that birds did not cross land and the projected route was altered to follow the coast, and for movement north and south to the breeding colonies in Greenland and Iceland from 60° N. As positions obtained from geolocators exhibit a relatively low accuracy, we used a conservative approach when calculating distances and speed, and hence values presented here should be regarded as minimum estimates. Great-circle distances were calculated using the mean of the two daily positions, interpolating between adjacent valid locations across periods when data were unavailable because of proximity to the equinox or light level interference. Stopover sites were identified following the approach of Guilford et al. (6); where latitudinal movements were <0.8° over a 0.5-day period, they smoothed over 3 days.

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Manus II

SUSTAINABLE REGULATION OF ARCTIC TERN EGG HARVESTING IN GREENLAND

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Manuscript

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Abstract

The Arctic tern population in West Greenland is likely to have undergone a severe decline since mid 20th century. This decline has been suggested to be a consequence of an unsustainable egg harvest conducted by local Inuit. In this study we model breeding parameters obtained over a five year period at the largest Arctic tern colony in Greenland, Kitsissunnguit to predict the impact of harvest on the local population. The model incorporates estimates of nest and chick survival to fledging, clutch size in both "normal" and replacement nests to predict how harvest size and the impact on reproduction varies with harvest effort, duration and start date. Model output indicates the least impact on the Arctic tern population if harvest is conducted early in the season. Effort (man hours spent harvesting) governs the total number of eggs removed from the population whereas duration of the harvest only has a minor impact. A Impact- Harvest Ratio helped us determine a time period where egg were available to harvesters but where the harvest would only have minor impact as the birds were allowed to relay. Based on model output, we recommend that an Arctic tern egg harvest at Kitsissunnguit with the least impact should be conducted early in the breeding season preferably with 1) a stopping date before 10 June or 2) a harvest carried out during one day. An opening of egg harvest at Kitsissunnguit should be followed by monitoring of population size and fledging success at both affected and unaffected islands in the archipelago. In the context of the model output, the former closing date (1 July) in the Greenland Arctic tern harvest has probably caused high impact on reproduction and it seems plausible that this may have caused a population decline.

Key words: Seabirds, Arctic Tern, *Sterna paradisaea*, Arctic, Greenland, egg harvest, model, sustainable use, regulation.

Introduction

Harvesting of seabird eggs, chicks and adults is widespread across most parts of the world. Seabirds are harvested for subsistence, income and recreation, which can cause additive mortality and population declines (Moller 2006, Nettleship *et al.* 1994). Seabird life histories are characterized by high adult survival, low annual reproductive rates and delayed maturation (Croxall *et al.* 1984, Furness and Monaghan 1987). This makes seabirds as a group particularly vulnerable to overexploitation. Furthermore, seabirds often aggregate at high densities in predictable colony locations which make harvesting of a large proportion of the population easier than would be the case in dispersed or mobile species (Coulson 2002). The remoteness of many seabird colonies also means that monitoring, and enforcement of regulations, is difficult to conduct.

In the past, the collection of seabird products, such as eggs, chicks and adults for food and feathers for insulation was fundamental to the survival of indigenous human communities. Today, reliance on seabirds as a resource has lessened, yet harvesting is still valued by indigenous people as part of their cultural heritage and ethnic identity. This has led to conflicts between conservationists and indigenous people, but their aspirations are not mutually exclusive provided harvests are managed in a sustainable manner. Achieving this can be a major challenge owing to compensatory demographic mechanisms that can buffer populations against harvesting mortality. Designing sustainable harvesting regulations therefore requires estimation of key demographic parameters and simulation modelling of various management options.

In modern Greenland, seabird harvesting is still important with approximately 150,000 birds, mainly Brünnich's guillemots (*Uria lomvia*) and common eider (*Somateria mollissima*) shot annually during winter (Merkel and Barry 2008). Before new harvest regulations were introduced in 2002, the seabird harvest level caused concern and strong criticism from conservationists and non-government environmental organisations (Hansen 2002).

The Arctic tern (*Sterna paradisaea*) is a wide-spread breeder in Greenland with a patchy distribution. It is usually found breeding on skerries, inlets and islands in colonies varying from few pairs to tens of thousands pairs (Boertmann 2004). Harvesting of tern eggs has probably taken place as long as humans have inhabited the country, and is even today considered an important activity during summer. Although historical censuses of Greenland Arctic tern colonies are scarce, there is evidence that the population has suffered a decline since mid 20th century (Burnham *et al.* 2005, Egevang *et al.* 2004, Salomonsen 1950). This decline has been associated with an increase in egg harvesting, as both human population size and mobility through better boats with larger engines, have increased in the same period (Hansen 2002). The concern for the Greenland Arctic tern population led to a ban on Arctic tern egg harvesting from 2002 and onwards. Before 2002, egg harvesting was allowed with a closing date at July 1st.The new regulations have led to protests from local people who view this as an infringement of their cultural heritage, and so there is pressure for the ban to be lifted. Conservationists are sympathetic to these pleas but maintain that any future harvesting should be conducted in a sustainable manner. The challenge for conservation biologists was to identify the suite of management prescriptions that will allow this.

There is little written documentation of the Greenland Arctic tern harvest. Salomonsen (1950) estimated the annual number of eggs harvested to be as high as 100,000, while Frich (1997) estimated that 150-200 persons visited the archipelago between 6 and 25 June 2006, and harvested between 3,000 and 6,000 eggs with a harvesting rate of 20-30 eggs per day per person. The first year after the ban on egg harvesting, 42 persons were recorded in illegal egg harvesting activities between 18 and 24 June 2002. On 27 June 2002 two families were caught with a total of 398 boiled Arctic tern eggs – collected in less than 24 hours. Since 2002, the level of illegal harvesting has declined at Kitsissunnguit (*pers. obs.*).

In this study we combine breeding parameters on Arctic terns obtained from Greenland in a model to predict whether a sustainable egg harvest can be practiced in Greenland. The goal of this study is to see if a balance could be found between conflicting interests of egg harvest by indigenous people and preserving wildlife as applied in similar studies, e.g. sooty terns (*Sterna fuscata*) and Glaucous-winged gulls (*Larus glaucescens*) (Feare 1976; Feare 1976; Zador *et al.* 2006). The aim is to produce recommendations for managers on how enforceable regulations can secure that egg harvesting is still possible for local Inuit with minimum impact on the Arctic tern population.

Methods and material

Study site

The study was conducted between 2002 and 2006 at Kitsissunnguit (Grønne Ejland), the largest Arctic tern colony in Greenland. The archipelago contains four major islands and a small number of skerries and islets, and is located in the southern part of Disko Bay, West Greenland (68°50’N, 52°00’W). Arctic terns breed at relatively low densities throughout the interior parts of the islands on habitat comprising dwarf scrub heath.

Data collection

Study plots were defined with the tern colony, and all nests laid within these through the season were located by intensive searching. The clutch size of each nest was recorded and the egg length, breadth and mass was recorded using Vernier callipers and electronic scale with 0.1 g accuracy. Laying date were determined by backtracking hatching dates by 22 days (Cramp 1985, Hatch 2002). Nests were enclosed within a 5-8 meter diameter, 25 cm high fence of chicken wire, with shelter for the chick being provided in the form of piled rocks, peat or driftwood. Nests were then checked every 1-2 days to determine their fate. Once the chicks hatched they were fitted with a metal ring and had their wing and weight measured on every visit. In the small number of instances where chicks were missing from their enclosure, watches were stationed on vantage points overlooking the adult’s territory. Any chicks seen walking around nearby or being fed by adults were recaptured, and returned to the enclosure if their ring number indicated they belonged there.

Renesting

Estimates of the replacement period in Arctic terns were obtained by experimentally removing clutches of 30 breeding pairs within a study plot during 2006. Before removing the eggs in the nest, one of the adult birds in the pair was caught and dyed with picric acid. After removal, picric marked birds in the study plot and surrounding area were observed from a blind each day. When these birds were observed incubating their nests were located and treated as described above.

Population size

The high number of breeding birds combined with the fact that terns at Kitsissunnguit breed scattered at low densities over extensive areas meant that complete colony counts usually employed for tern censuses were not applicable. Instead, densities of Arctic tern nests were sampled along a line transect (Buckland *et al.* 2001). North-south oriented lines 250-m apart were used in the field with data subsequent analysed using the software Distance version 5.0 (Thomas *et al.* 2006). Transects were always conducted by two people: an observer and a navigator. The observer would walk along a transect line at an equal pace, searching for nests and measuring the distance between the nest and the transect line with a measuring tape. The navigator would walk approximately 15 meters behind the observer and give directions to keep them on the track line. The line transect counts were conducted between 18 June and 3 July in 2002-2006 at a time in the breeding cycle when the majority of the colony had stopped laying eggs but prior to the eggs hatching.

Harvest efficiency

When egg harvesting takes place at Kitsissunnguit, participants walk side by side searching the ground for Arctic tern nests. When a nest is found, all eggs in the clutch are collected (own observations). The Inuit way of searching for eggs in the colony resembles the method used under line transect population estimation. As input in the harvest model, an estimate of harvest efficiency (eggs encountered per time unit) could be obtained from the line transect.

Parameter estimation

Nest survival and chick survival were estimated separately using the Stephens method described in Rotella *et al.* (2004), implemented in SAS. This uses a non-linear mixed model with a binomial error distribution and logit link to estimate daily survival probability. We fitted a number of models containing pertinent covariates and conducted model selection by comparing AIC values. The most parsimonious model was that with the lowest AIC value, unless a competing model with fewer parameters differed from this by less than two AIC units. In the case of nest survival the covariates were calendar date and whether the nest was a first or a relay clutch. In the case of chicks the covariates were calendar date, chick age, hatch order and whether the brood was from a first attempt or a relay.

The likelihood of a clutch containing two eggs was modelled using a generalised linear model with a logit link and binomial error distribution, with two eggs clutches adopting a value of one and single egg clutches a value of zero. The covariate fitted to the model was whether the clutch was a first or relay nesting attempt. The rate of egg inviability (defined as the likelihood of an egg that fails to hatch at the end of the incubation period owing to infertility, early embryo death or exhaustion during hatching) was estimated using a similar model, in which the response variable was the number of inviable eggs in the clutch and the binomial denominator was the total clutch size. Covariates fitted to the model were calendar date and whether the eggs were in a first or relay clutch. Model selection in both cases was conducted using likelihood ratio tests. Both these models were implemented in SAS.

Incubation and fledging periods and their ranges were taken from the literature (Cramp 1985). SDs were estimated by generating random normal distributions from the published mean and iteratively varied SD values until the maximum and minimum values matched the published range in values. The mean replacement period and its SD were estimated from the intervals between clutch removal and relaying in the experimental study plot.

The start date (average date upon which individuals laid their first clutch) and the stop date (the average date after which individuals would not initiate further relay clutches) and their SD were estimated by iteratively varying these values in a simulation model of the laying season (see below for details). The resulting estimated frequency distribution of nest initiation dates were compared with those observed in the experimental study plot. The values that minimised the sum of the squared deviations between observed and expected values were those used in further simulation models (Green 1988, Ratcliffe *et al.* 2005).

Simulation model

A simulation models that allowed for re-nesting (Beintema and Müskens 1987; Green 1988; Green *et al.* 1997; Ratcliffe *et al.* 2005) was used to estimate productivity and number of nesting attempts made by Arctic terns, and the numbers of eggs that were harvested by humans, under a range of harvest management options. Options involved variations in the date harvesting started, the number of days the harvest remained open and the amount of harvesting effort (spread equally over the open period) in terms of man hours. We also only allowed one of the islands in the archipelago, Basisø, to be open to harvesting, although the model has the flexibility to include variation in the area open for harvest.

Breeding pairs were randomly allocated to a management zone by generating a random probability: if this was less than the proportion of pairs occupying Basisø then the pair was at risk of harvesting, otherwise they bred on another island where only natural mortality occurred. Breeding pairs were also randomly allocated incubation, fledging and replacement periods and a start and stop date, all of which were drawn randomly from a normal distribution with the mean and standard deviation appropriate to each parameter. Clutch size was two unless a randomly generated probability exceeded the estimated proportion of two egg clutches, in which case it was one. The laying period was calculated as the clutch size minus 1 day, on the basis of one egg being laid per day and incubation started the day the last egg was laid.

During each day of the laying and incubation periods, the clutch was subjected to a likelihood of natural failure by testing whether a random probability exceeded the date-specific daily nest survival rate until the incubation period elapsed or the nest failed. On those days when harvesting occurred, nests on Basisø were further subjected to a likelihood of being harvested in the same way. The daily likelihood of harvest-induced failure was calculated by multiplying the effort on that day by the probability of a nest being encountered per man hour. A tally of the number of eggs harvested from the population during the season was kept.

Pairs that lost eggs during the laying period were allowed to continue to lay eggs until clutch completion. Those that failed during incubation were allowed to relay if the date of failure plus the replacement period was earlier than the stop date, otherwise they would give up breeding for the season and simulations for that pair ceased. A tally of the number of nesting attempts made by the population during the season was kept.

If the nest survived to the end of the incubation period, a random likelihood was generated for each egg in the clutch: if this was lower than the likelihood of egg inviability the egg failed to hatch, otherwise it produced a chick. Each chick that hatched was subjected to an age- and hatching order-specific daily mortality rate until its fledging period elapsed or it died. In the unlikely event of an A-chick dying before its sibling, the B-chick would thereafter be exposed to the lower mortality rates experienced by A-chicks. A tally of the number of chicks that fledged from the population during the season was kept.

This procedure was repeated for each of 300 pairs in each season simulated. This number of pairs was sufficiently large to avoid demographic stochasticity, but small enough to allow reasonably rapid processing times. The number of chicks fledged and the number of nesting attempts were each divided by the number of pairs to estimate productivity and nesting attempts per pair. These values were estimated 999 times for each harvest management option, and the mean and SD (equivalent to SE) of these bootstrapped replicates were calculated. Numbers of eggs harvested were treated similarly, but values were scaled up according to the actual number of pairs in the harvested area before the average and SD were calculated. A bespoke program written in Microsoft Visual Basic 6·0 was used to perform the simulations.

Population model

In order to evaluate the potential impact of egg harvesting on population growth rate, we constructed a simple matrix model in ULM (Legendre and Clobert 1995). Matrix models provide a simple and flexible tool for exploring how variation in demographic parameters affects population growth (Caswell 2001). Little demographic information is available for the Arctic tern, and the model parameters were therefore mainly based on best guesses. The model had 3 age classes; adult survival was set to 0.9 (Devlin *et al.* 2008), age of recruitment to 3 years (Hatch 2002), and first-second- and third-year survival to 0.5, 0.8 and 0.85 respectively.

Parameter estimates are given ± 1 Standard Error or with 95% confidence intervals when noted. Parameters of the nest survival and chick survival models are given on the logit scale.

Results

Model input

The average clutch size at Kitsissunnguit in 2002-2006 equalled 1.84 (±0.012, n=1752) expressed as a 0.921 (95% CI 0.850-0.960) probability of a two egg clutch in first nesting attempt. Clutch size (1.6 eggs, ±0.13, n=16) in replacement nests was significantly lower ($\chi2=16.8$, $p=0.0002$, df=2) than non-manipulated nests (2.04±0.026, n=367) in 2006 and expressed as a probability of 0.654 (95% CI 0.483-0.792) in the model. Daily nest survival (egg harvest excluded) varied over the course of the breeding season, and daily chick survival varied with chick age (slope 0.067±0.021, $p=0.0013$) and with hatching order (Fig. 1). Egg inviablity probability was estimated to 0.035 (95% CI 0.020-0.058).

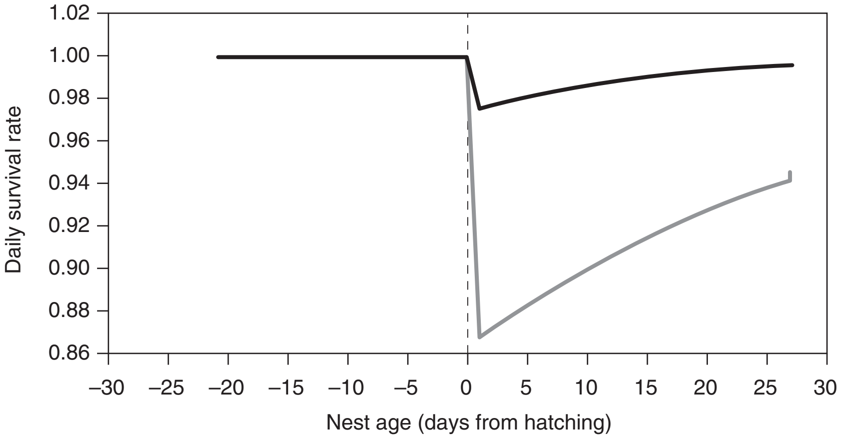


Figure 1. Daily survival rates in relation to age and hatch order for a breeding attempt initiated at the average day of first clutch initiation (day 34). Age is expressed in days to or from hatching (where day zero is the hatching date). The black line represents the survival rate of eggs and the A-chick, and the grey line the survival rate of the B-chick.

The incubation period was set to 22 days and the period from hatching to fledging to 27 days (Cramp 1985, Hatch 2002) whereas the replacement period (period between a nest is harvested and a replacement nest produced) was set to 9.5 days (±0.23, n=16).

The population estimates for Kitsissunnguit based on transects varied between 15,354 and 21,760 pairs (Egevang and Frederiksen 2010) with an average of 18,465 (±1,023) pairs used in the simulation model. The land area (Basisø) exposed to harvesting equals 38.0% (3.21 vs. total of 8.43 km^2) of the total land area whereas 80.4% (14,845±1,136) of the total Kitsissunnguit population numbers (average 2002-2006) is found at Basisø.

The line transect also produced estimates of nest encounter probability, which can be used as an expression of harvest efficiency as search for nests in the two situations resemble each other. In 2004, 555 minutes of effective searching over 6,360 meters of line resulted in 415 found eggs originating from 234 nests. These results were used to calculate a probability that an individual nest was encountered person hour^{-1}: 234[nests found]/(9.25 [hours search time]×18,465[nests, total])=0.001370

Model output

Model output consisted of predicted harvest size (number of eggs harvested) and productivity (number of chicks fledging per nest) under various harvest scenarios (Figs 2 and 3, A and B). An Harvest-Impact Ratio (HIR) is presented in Figure 2 C and Figure 3 C, and was calculated as:

$(HIR = Nh/(P0\text{-}Ph))$,

where Nh is the number of eggs harvested, P0 is productivity when no eggs are harvested (unaffected productivity value equals 0.9 chick per nest) and Ph is productivity under harvest.

The variation of harvesting and breeding parameters is most marked in relation to season (Fig. 2 and 3). Harvests increased through the first half of the season owing to the cumulative increase in the proportion of birds that have laid eggs, but then decline later in the season owing to hatching. The impact of harvesting on productivity increases through time as losses are too late in the season to be replaced. This is evident from the relationship between timing of harvests and number of nesting attempts per pair. Increasing effort clearly results in greater harvests, and a linear increase in impact when controlling for season. Duration has relatively little effect, with only a subtle decrease in impact during the middle of the season owing to eggs having the opportunity to hatch before being harvested at a given level of effort.

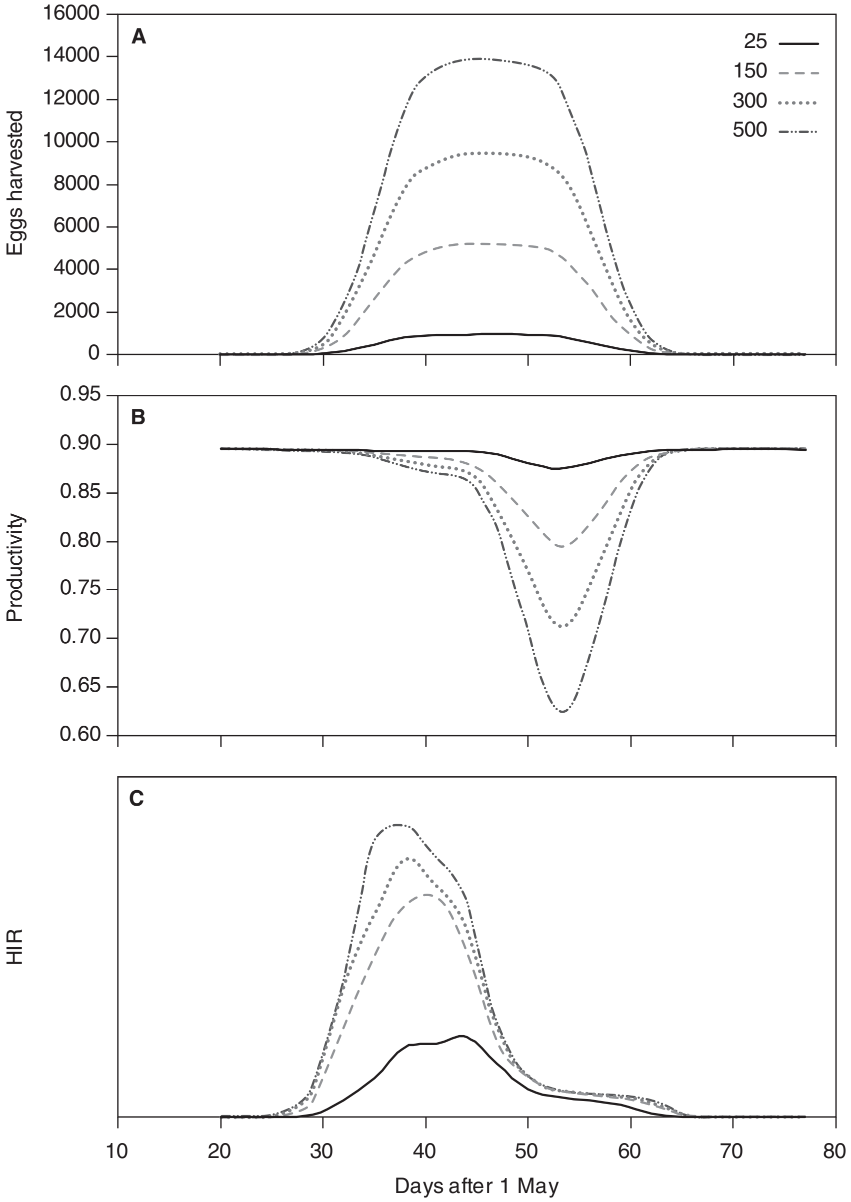
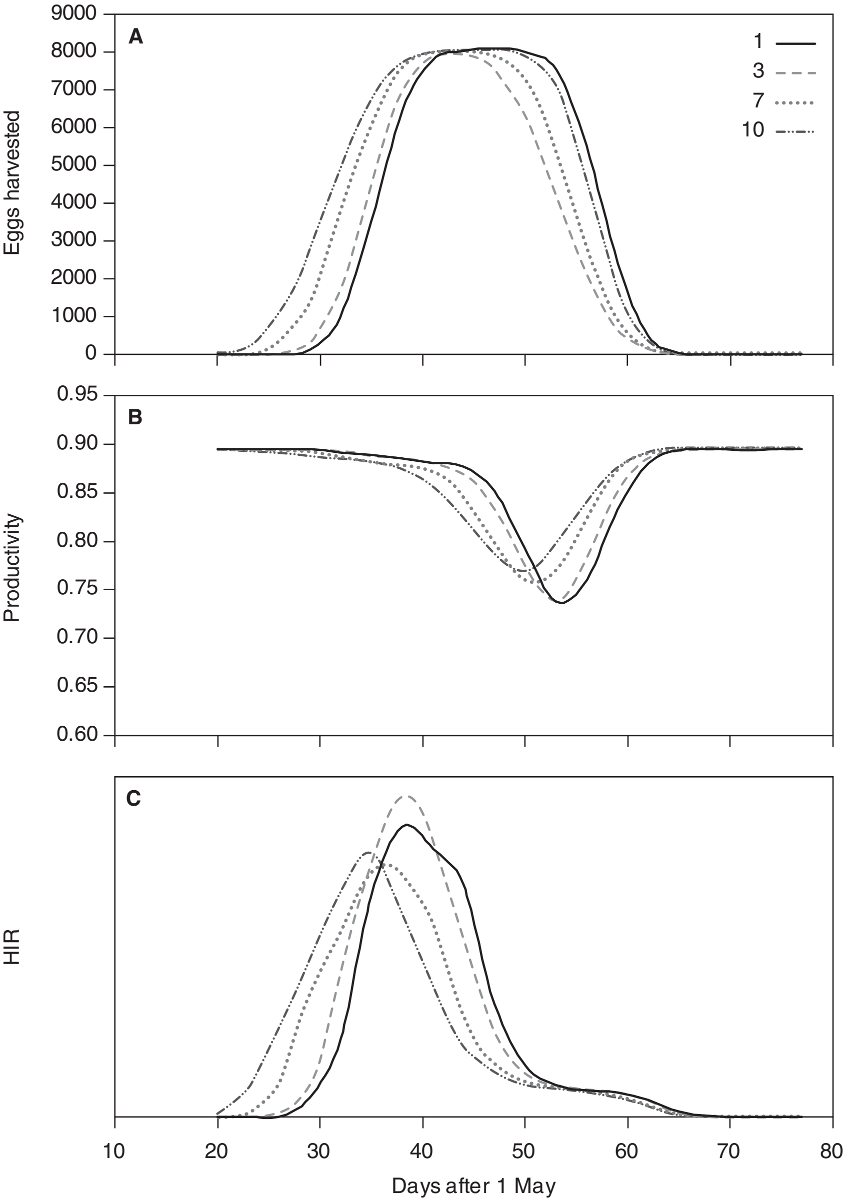


Figure 2. **A)** Harvest (number of eggs), **B)** productivity (fledglings produced per nest) and **C)** HIR (Harvest-Impact Ratio – see text) of simulated Arctic terns egg harvest plotted against harvest start (days after May 1st) over the breeding season with constant duration of harvest season (2 days) and an effort of 25, 150, 300 and 500 man hours.

Figure 3. **A)** Harvest (number of eggs), **B)** productivity (fledglings produced per nest) and **C)** HIR (Harvest-Impact Ratio – see text) of simulated Arctic terns egg harvest plotted against harvest start (days after May 1st) over the breeding season with constant effort (250 man hours) and a duration of harvest season of one, three, seven or ten days.



At constant effort (Fig. 3C) a peak in HIR occurred between 4 and 8 June defining the day where harvest can be carried out with minimum effect on the overall productivity relative to harvest size. Harvest was high during this period (Fig. 3A), although the peak in harvest occurred a bit later (9-21 June).

The model can help identifying periods in the breeding season when egg harvesting is possible/optimal (harvesters will encounter a significant number of egg during a visit in the colony) but where the number of eggs removed will have a minimum impact at population level. The model predicts that the highest number of eggs can be harvested at day 47 (from 1 May = 16 June) whereas the greatest reduction in productivity (due to harvesting) will appear at day 53 (22 June). The Harvest-Impact Ratio (HIR) predicts the highest value to occur at day 38 (7 June, i.e. the day with least impact on productivity relative to harvest size). Although this is nine days away from the peak harvesting date, harvest size on day 38 are on average 92.2% (±0.0048) of that on day 47.

At constant duration (Fig. 2) the overall pattern repeats. Highest values of HIR (Fig. 2 C) are found around 4 to 8 June (day 35-39) although low effort (25 man hours) peaked somewhat later. Highest number of eggs harvested (Fig. 2A) also took place in the period around 9-21 June.

With a breeding success of 0.9 chicks per nest, the matrix model projected the population to grow at 4% per year. Reducing breeding success to 0.6 chicks per nest, similar to the impact of the most intensive harvest scenario simulated (Fig. 2B), led to a 4% decline in growth rate so that the population was stable. Given the limited data available on Arctic tern demography, these values should be taken as indicative. Varying the input values for the model led to somewhat different projected growth rates, but for all realistic values a decline in breeding success from 0.9 to 0.6 caused a 3-4% decline in population growth rate.

Discussion

The harvest model applied in the study provides an effective tool to evaluate the effects of egg harvesting at Kitsissunnguit. Although a useful tool to design future management initiatives, the predictions derived from the model must interpreted with caution as these are only as robust as the data and parameter estimates upon they are based (review in Bassinger 1998).

As in other studies (Zador *et al.* 2006, Feare 1976) exploring modelling of a sustainable egg harvest, our main findings suggest that harvesting should be conducted as early in the season as possible allowing the birds to relay and minimize the impact at population level. The clutch size in replacement nests were lower, as found in several *Larid* species (Golet *et al.* 2004, Wood *et al.* 2009), and delayed fledging dates significantly. Despite this, Arctic terns at Kitsissunnguit were cable to compensate for the lost of the first clutch early in the season by relaying and maintaining a production of similar magnitude as non-harvested nests. Although, early breeding individuals in bird populations are reported to be more productive that late ones (Lack 1966, Perrins 1970), studies has shown that late breeding in seabirds may be possible without a decline in productivity (de Forest and Gaston 1996, Hipfner *et al.* 1999, Harris and Wanless 2004) or even beneficial in some cases (Brown and Morris 1996).

The aim of this study was to produce management advice on how a sustainable egg harvest could be carried out in Greenland. The overall goal is to ensure that egg harvesters will be rewarded when visiting the colony, while the impact at population level is kept at a minimum allowing the birds to relay and produce a significant number of fledglings. In practice, there are three management scenarios which could help insure this: 1) introduction of a closing date – a fixed date during the breeding season where harvesting will stop, 2) a bag limit – a fixed number of eggs allowed to be harvested over the season or 3) restrictions in effort – a fixed amount of harvesting man hours allowed during the season.

The harvest model predicts the largest potential harvest to take place six days earlier (22 June vs. 16 June) than the date where the highest impact was identified, but the date with highest Harvest-Impact Ratio falls nine days earlier (7 June) with the numbers of eggs available for harvesters in the colony being almost (92%) as high as in the peak period. A simple population model furthermore predicts that high effort harvesting can result in a 4% per annum decline in growth rate of the Arctic tern population.

A closing date (scenario 1) in egg harvesting around 7 June would ensure that locals visiting the colony would collect high numbers of eggs. At the same time, the proportion of eggs removed from the population would only have a minor impact, as most birds would be able to produce a replacement clutch. Moreover, early season harvests will be more palatable to people as the eggs have not yet developed, although some older Inuit prefer the ripe taste of eggs containing partially developed embryos.

The model helps to predict a theoretical optimal closing date by comparing potential harvest versus productivity, but the actual impact on productivity would obviously depend on harvest effort. Although the overall goal of sustainability in egg harvest also could be reached by management scenario 2 or 3, the logistic challenges of enforcing bag numbers or man hours spent egg harvesting seems an overwhelming task in rural Greenland. The risk of under- or non-reporting of the number of eggs harvested is high, and can result in inverse density dependence in a declining population owing to a fixed harvest representing an increased proportion impact. Monitoring accumulated egg numbers harvested in the current breeding season would furthermore introduce a high level of bureaucracy into the management system.

Another option would be to regulate effort by opening up for harvesting on a single day (a "harvest day") and otherwise keep the colony closed for the public. Under the supervision of the hunting officer or another local designated authority harvest could be allowed to take place at Basisø. This would represent an enforceable scenario with well-defined dates where access to the island was allowed and no public access otherwise. More importantly, an effort restricted scenario is positively density dependent, so if the population density declines so does the harvest. Long-term changes in the population size or years with low breeding numbers will thus result in a low proportion of harvested eggs and limited negative impact at population level.

A disadvantage of the introduction of a closing date is that the breeding phenology of Arctic terns breeding in Arctic regions may vary considerably between years, potentially correlated with sea ice break-up (Hatch 2002). At Kitsissunnguit the majority of the eggs hatch in the first week of July (indicating that egg laying took place in mid-June), but in some years early breeding takes place – as the case in 2004 where eggs hatched three weeks earlier in mid June. This means that in some years a fixed closing date will be "off synch" with egg laying, resulting in years with either a higher impact on breeding productivity than predicted ("early" years) or in "late years" with reduced or absent egg harvest before the closing date. Ideally, the stage (laying date) of the breeding cycle should be addressed early in a current year before a closing date or a harvesting period is determined. However, the amount of time acquired to obtain on-site estimates of laying date, validate data and communicate an closing date/harvest date to the scatted settlements in the Disko Bay, mean that this would not be realistic within the time frame available.

In conclusion, based on the findings in this study future management of the Arctic tern population at Kitsissunnguit could include a limited egg harvest. This should be restricted to only one island in the archipelago

(Basisø) and include either a) a closing date between 7-10 June or b) introduction of a harvest day in the same period. It is however important that an opening of egg harvest at Kitsissunnguit is followed by a monitoring programme to assess the impact of the harvest to allow fine tuning of the harvest model. We recommend monitoring productivity and population size of birds in closed and open areas of the archipelago so that the model input parameters can be adjusted. It would furthermore be especially valuable to study fledging success of replacement clutches in situations where a large proportion of the colony relays.

The output of the harvest model can furthermore be used to address the cause of the observed historical decline in Arctic tern population size. The finding of an optimal harvest period in early June and a severe impact on productivity predicted during late June puts the pre-2002 closing date of 1 July into perspective. Combining this with the outcome of the simple population model with high effort harvest of a 4% decline in annual growth rate (equals a 62.5% decline over 25 years if the population would otherwise be stable), it seems plausible that a high effort historical harvest conducted late in the breeding season could have accounted for the observed decline in the Greenland Arctic tern.

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Manus III

FOOD-RELATED CONSEQUENCES OF RELAYING IN THE ARCTIC TERN: CONTRASTING PREY AVAILABILITY WITHIN A PROLONGED BREEDING SEASON

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Manuscript submitted IBIS

Food-related consequences of relaying in the Arctic Tern:

Contrasting prey availability within a prolonged breeding season

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Key words: Arctic Tern, *Sterna paradisaea*, seabird, replacement clutch, Arctic, diet, Greenland, Capelin, *Mallotus villosus,* egg harvesting, intraspecific kleptoparasitism.

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Abstract

Egg harvesting may affect seabird population dynamics at several levels. The rate of renesting is one of the most important single factors influencing annual reproductive success in harvested populations. However, those birds that do renest may face additional costs since late season declines in prey availability may result in elevated chick mortality owing to starvation compared to birds hatching their first clutch. Such costs are likely to be most pronounced at higher latitudes where windows of opportunity for successful breeding are at their narrowest.

We experimentally removed entire clutches from 30 Arctic Tern nests. Subsequently we monitored chick diet, provisioning rate, growth and survival in both the replacement nests and a control group.

The experimental egg removal resulted in 16 replacement nests (53.3 %) located at an average distance of 23.4 m (± 7.65) from the original nest site. The replacement clutches were four weeks (± 3 days) delayed in the breeding cycle compared to non-manipulated breeding pairs and clutch size in replacement nests (1.6 eggs, ± 0.13, n = 16) was significantly lower than in the control group (2.1 eggs, ± 0.08, n = 46).

This late breeding season for replacement clutches resulted in a different foraging situation compared to controls. Feeding in control nests was characterised by long feeding trips and a low feeding rate, large Capelin as the principal prey item and a high incidence of kleptoparasitism. Feeding of chicks from replacement nests was characterised by short feeding trips/high feeding rate, fish larvae as principal prey and an absence of kleptoparasitism. In both groups, Capelin was the single most important prey species.

Despite the altered food availability, the energetic provisioning rate, chick growth and chick survival did not differ between the two groups. The parent birds in replacement nests switched to low quality prey items and compensated for this by significantly increasing feeding rate.

Introduction

The ability to produce a replacement clutch may be an important adaptation to increase an individual's annual reproductive success. This is particularly the case in avian species that are prone to the loss of offspring due to stochastic events such as flooding or to a high risk of nest predation (Brown and Morris 1996; Wendeln *et al.* 2000). However, the production of an additional clutch of eggs requires a costly investment in terms of energy, and only females of "high quality" (older, experienced with high fitness) in a population may be able to allocate the needed energy into a replacement clutch (Hegyi and Sasvari 1998; Hipfner *et al.* 1999). Furthermore, the delay in the breeding cycle may result in altered, sub-optimal conditions for chick rearing compared with chick rearing earlier in the season owing to deteriorating food availability (Hipfner 2001; Perrins 1970).

In Greenland the Arctic Tern (*Sterna paradisaea*) has a widespread, patchy distribution with the largest colonies found in central West Greenland (Boertmann 1994). The Arctic Tern in Greenland has traditionally been subject to intensive exploitation by local

Inuit in terms of egg harvesting (Salomonsen 1950), which most likely has caused a general decline in the population over the last decades (Boertmann *et al.* 1996; Egevang *et al.* 2004). Although egg harvesting has never been economically important in Greenland, the harvesting of tern eggs has always been a popular recreational activity, often carried out by several generations in family groups. Egg harvesting would usually take place during early incubation, but especially the older Inuit generation favour the ripe taste of tern eggs in late development state, and harvesting could continue until late incubation. Arctic Tern egg harvesting was prohibited in 2002 in Greenland and now only occurs illegally at far lower levels (Egevang *et al.* 2004). Although Arctic Terns may produce a replacement clutch to compensate for the harvested eggs, it is unlikely that all affected individuals will invest in a second clutch that season. The likelihood of relaying may also be related to the stage of the incubating period of which egg loss occurs, as found by Feare (1976) in Sooty Terns (*Onychoprion fuscatus*). Furthermore, egg harvesting may create a mismatch between food demand and food availability due to the delay in breeding season.

Surface-feeding seabirds are only capable of feeding in a 2-dimensional space whereas diving species exploit a 3-dimensional feeding area. The general perception is that this makes surface feeders particularly prone to breeding failure during years of poor food availability, a dependency that is particularly pronounced when birds rely on few or a single prey species (Regehr and Rodway 1999, Furness and Tasker 2000). Reproductive success of Arctic Terns is known to vary greatly with the food availability, which has been documented on several occasions in the Boreal zone where Lesser Sandeel (*Ammodytes marinus*) is the key food species (Monaghan *et al.* 1989; Monaghan *et al.* 1992; Suddaby and Ratcliffe 1997). Although literature on the diet of

Arctic Terns in Greenland is very limited (Salomonsen 1950 mentioned zooplankton as important), it is likely that Capelin (*Mallotus villosus*) and invertebrates are the main components of the diet. In southern and central West Greenland, Capelin is regarded as the key seabird prey species (Carscadden *et al.* 2002; Friis-Rødel and Kanneworff 2002), but the link between seabird breeding success and Capelin abundance has not yet been quantified.

In this paper, we study the effect of simulated harvesting of Arctic Tern eggs on a) chick growth and reproductive success, and b) chick diet and foraging strategies within the species' core distribution area in West Greenland. The study furthermore presents the first estimate of renesting rates in Arctic Terns along with the first detailed description of Arctic Tern chick diet in West Greenland.

Materials and Methods

Study site

Fieldwork was conducted in the period 16 June to 30 July 2006 at the archipelago Kitsissunnguit (Grønne Ejland) in the southern part of Disko Bay (68˚50'N, 52˚00'W), West Greenland (Figure 1). Kitsissunnguit holds the largest Arctic Tern breeding site in Greenland with approximately 20,000 pairs, with 17,000 of the pairs breeding at Basis Ø – the location of the fieldwork conducted in 2006. The terns breed scattered over most of the island, usually with at least 2-4 meters between nests, and only few areas have no nests. The total area with breeding terns was estimated to be 3.12 km^2 in 2006, with a low overall breeding density of 5,400 nests per km^2 (0.005 pairs per m^2).

Arctic Terns arrive in this region during the second half of May, and egg laying takes place in early June. The first fledglings are usually seen around mid July, and colony exodus happens at the end of July. In early August only few birds are found in the colony. Although hatching is well synchronized within large sections of the archipelago, a tendency towards later hatching is found when moving from the central part of the islands towards the outskirts of the colony. This tendency is even more pronounced (with up to two week delay in hatching date) when moving W from Basis Ø towards the more exposed skerries, Saattuarsuit, in the archipelago (*Pers. obs. Kitsissunnguit 2002-2006*).

Study plots

Two study plots were established within the first week of the field season: a control plot (46 nests; size app. 13,000 m^2) and a plot where clutches were experimentally removed, designated the “relay plot” (30 nests; size app. 8,200 m^2) hereafter. Well-drained, flat heather sections at the edge of large continuous areas of breeding Arctic Terns comprised the habitat in both study plots, with a distance to the shoreline of approximately 200 and 100 m, respectively. Daily measurements of hatching stage, chick mass (to the nearest 0.1 g) and wing length (to the nearest 1mm) were conducted in both plots in order to quantify chick age, growth rate and survival. The chicks in both study plots were kept in enclosures (chicken wire, mesh size 25 mm, height 25 cm, diameter app. 5 m), which ensured consistent measurements up to the age of fledging. Chicks in the control plot were monitored with daily measurements to the day of fledging while the last day of measurements in the relay plot was 30 July, when A-chicks had an age of 9-11 days (day of hatching = day 0).

In the relay plot one parent at each nest was caught using *Kieler*-traps, and biometric measurements, including bill length, were taken. The adult bird was dyed with picric acid on the right or left cheek and upper rump and fitted with a metal ring and coloured darvic ring before it was released. To ensure that no nests were abandoned due to the handling of the bird, the marked adult bird in each of 30 nests was observed incubating before the eggs were removed. On 19 June, the eggs of the nests in the relay plot were collected and the reproductive behaviour of the adult birds closely monitored in the 4-28 days post removal. The combination of marks used ensured that individual identification could be made from a distance of up to 30 meters using a 20-60x spotting scope. The search for replacement nests was conducted within the relay plot and in a 100m strip around the plot.

Feeding observations

Observations of food provisioning by the adult birds to the enclosed chicks were conducted in both the control plot and the relay nests from a hide positioned 10-25 meters from the nests. Variables recorded during the feeding observations included: time of the prey delivery, which chick was fed when the brood comprised two chicks, prey identity (to the highest taxonomic resolution possible), prey size (in relation to the bill of the adult bird) and the outcome of the prey delivery (successful or kleptoparasitised by other adult birds). In the relay plot, the provisioning (marked or unmarked) adult was also recorded. In order to minimise bias originating from individual prey preferences in a parent bird, the hide was relocated on a regular basis to avoid long periods of observations on the same nests. The relocation of the hide was always done at least 20 hours prior to feeding observations to allow birds to habituate to its presence. Feeding observations was conducted by three observers doing 3-hour sessions, where feeding observations during and 10 minutes after changing shifts were omitted from data analysis. Total duration of observation periods varied between three and twelve hours, involving 3-4 nests at a time. Feeding observations were conducted between 08:30 and 22:00 local time (GMT minus 3 hours) on clear days. The weather during chick rearing in both the control and relay group was generally good and did not include severe weather systems preventing the birds from foraging. Furthermore, on days with strong wind, heavy rain or thick fog, feeding observations were not conducted, to avoid bias from reduced foraging performance in the adult bird (Hatch 2002).

Data analysis

The data on feeding observations from both study plots were subdivided into three age-classes according to chick age: 0-3 days, 4-7 days and 8-11 days. When comparing chick diet between the two groups, feeding observations were pooled into “nest hours” (i.e. four hours of observation on three nests equals twelve nest hours). When comparing feeding rates between the two groups, observations were pooled into 5-hour periods.

The first hatched chick (the A-chick) is superior in competition with siblings for food brought to the nest due to larger size and higher mobility (Langham 1972). In the current analysis, chick rank is included as a prediction when comparing diet and growth rates in control versus relay chicks.

Conversions of food item size from bill length to mm were done using the average culmen length of the adults caught and measured in the relay plot. Food items were scored in relation to the total bill length in the field, so in order to achieve an estimate of prey item size, a factor of 0.25 was added to culmen length. Conversion factors from length to weight and calorific content were taken from Weslawski *et al.* (1994), Finley *et al. (*1990), Bradstreet (1980), Harris and Hislop (1978) and Wigley *et al.* (2003). Wet weights of both fish and fish larvae were converted to dry weight by dividing by 4.35 (Payne *et al.* 1999).

In the comparison of means with equal variances and normal error distribution, t-tests were used. Data not normally distributed were normalized with an arcsinh-transformation. To test for difference in variances, F-tests were used, and differences in means were tested using Welch's approximate t (Zar 1999). All tests were two-tailed, and $\alpha = 0.05$ was taken as the threshold for significance. Estimates are presented as means with one standard error throughout the text. Daily chick survival probability was estimated using known-fate models in MARK (White and Burnham 1999), and between-group differences were evaluated using likelihood ratio tests. These models allow for right-censoring, i.e. the fact that chicks in the experimental nests were only followed until they were 9-11 days old.

Calculations of area size were performed in GIS software MapInfo 8.5. The Internal Egg Volume (IEV) of the Arctic Tern egg was estimated as $IEV = 0.00048\ LB^2$, where egg length (L) and breadth (B) were measured with electronic callipers.

Results

Relaying

Of the 30 pairs whose clutches were removed, 16 pairs (53.3 %) were observed to produce a replacement clutch. All embryos in the collected eggs in the relay plot were in the last half of their development stage (estimated 2-9 days from hatching), with expected hatching dates between 21 and 28 June. Eggs in the control plot hatched between 20 June and 3 July (median hatching date 23 June). The first replacement nests were observed in the plot 28 June, and replacement eggs hatched between 19 July and 22 July. A backwards calculation using a 22 day incubation period (Hatch 2002, Cramp 1985) showed that replacement eggs were laid between 27 and 30 June – eight to eleven days post egg collection. Hence, the removal of eggs at the end of incubation delayed the nesting season of experimental nests by approximately four weeks (28 ± 3 days) compared to the original hatching date.

The mean clutch size (Table 3) of the control plot was 2.1 (± 0.08, n = 46), similar to the relay plot where clutch size was 2.1 eggs (± 0.07, n = 30) before egg removal. The mean clutch size (1.6 eggs, ± 0.13, n = 16) in replacement nests was significantly lower (χ^2 = 16.8, p = 0.0002, df = 2) than in control nests and nests with experimentally removed eggs (pooled data). Total clutch volume (expressed as Internal Egg Volume) equalled 35.4 ml (± 8.68, n = 42) on average per nest in the control plot, whereas IEV in relay nests (27.8 ml, ± 8.76, n = 11) was significantly lower (t = 2.53, df = 51, p = 0.014). However, IEV of A-eggs in relay nests (17.34 ml, n = 11) were not different (F = 0.58, P = 0.45) from A-eggs in the control plot (17.69 ml, n = 55). B-eggs in relay nests (16.373 ml, n = 7) were near-significant smaller (F = 3.56 P = 0.06) compared with B-eggs from the control group (17.24 ml, n = 51), consistent with the smaller clutch size.

Hatching rate in the relay plot (84.0%, ± 37.4, n = 25) was lower, but not significantly different ($\chi^2 = 0.6$, p = 0.433, df = 1), than hatching in the control plot (91.8%, ± 27.7, n = 97). The lower hatching rate in the relay plot was caused by higher nest abandonment with two nests (both with two eggs) out of 16 nests (12.5%) abandoned before hatching. In the control plot only a single case (2.2%) of nest abandonment was observed.

There were no instances where the same nest scrapes were reused, and replacement nests were located between 6.0 and 100.6 m (mean 23.4 ± 7.65) from the original nest.

Chick production and growth rate

It is very rare that B-chicks (or C-chicks) survive to the age of fledging in Disko Bay (*pers. obs*. Kitsissunnguit 2002-2005), but the 2006-season had a "high" proportion of B-chicks that survived to fledgling. In the control plot, where the fate of chicks from 2-egg clutches was known in 37 nests, five of the pairs (13.5%) fledged two chicks. This was not different ($\chi^2 = 0.15$, df = 1, p = 0.7) from the relay plot where one (11.1%) of nine two-egg clutches produced two chicks beyond the age of 11 days.

Daily chick survival varied with age, and this variation could parsimoniously be modelled with four age groups: 0-1 days, 2-5 days, 6-10 days, and 11 days and over. These age groups were based on post-hoc examination of estimates from a model with full daily variation in survival and thus to some extent arbitrary, but the main conclusions in the following were unchanged when using other models for age variation (constancy, full daily variation, quadratic trend). Survival differed between A, B, and C chicks ($\chi^2 = 20.5$, df = 2, $P < 0.0001$), but there was no difference between control and experimental chicks ($\chi2 = 0.033$, df = 1, $P = 0.85$). Estimated daily survival was very high from 0-1 days (0.996, 0.986, and 0.964 for A, B and C chicks, respectively), low from 2-5 days (0.947, 0.836, and 0.658), higher from 6-10 days (0.982, 0.939, and 0.852), and very high after 11 days (0.998, 0.992, and 0.979). Estimated overall survival to fledging was 0.691 (± 0.066) for A chicks, 0.293 (± 0.073) for B chicks and 0.050 (± 0.081) for C chicks.

The daily growth rate (Table 3), from day four to eleven of the control group (6.39 g ± 0.62) did not differ significantly ($t = 0.01$; df = 58, $p = 0.992$) from that of chicks hatched from experimental clutches (6.61 g ± 0.82). Similarly, growth rate of wing length did not differ between the two groups (control 7.66 mm ± 1.55 vs. relay 7.66 mm ± 0.67; test: $t = 0.31$; df = 58, $p = 0.761$).

Diet

A total of nine different prey species were identified from 1237 prey deliveries to the A-chick (summarized in Table 1) in the control and the relay plot combined, originating from 203 and 155 nest hours of observation, respectively (Table 2). Unidentified prey items comprised approximately 7 % of the total number of observed feeds. The majority (>90%) of these feeds were unidentified fish larvae. The most numerous prey species was Capelin, accounting for 20.0-77.6 % of prey numbers in the three age groups and between 97.1 and 99.9 % of the corresponding energy (fish and fish larvae combined) in the control group. In the relay group only one feed with a juvenile Capelin (i.e. older than 0-group but not spawning) was observed. Still, Capelin larvae accounted for between 47.7 and 73.7 % by numbers and between 37.1 and 51.4 % of the energy brought to replacement chicks. The size of Capelin larvae (0-group) averaged 29 mm estimated from an average observed prey size of 0.74 (± 0.005, n = 627) bill length when applying the average bill size (culmen = 31.6 mm, n = 26, ± 0.255) found in the adult birds at Kitsissunnguit.

The only other post-larval fish observed in the chick diet was two successful deliveries with Polar Cod (*Boreogadus saida*) to replacement chicks (Table 1). Two other fish larvae were recorded in the diet: Stichaeidae sp. and Wolffish (*Anarhichas* spp.) with 362 and 91 successful deliveries, respectively and only found in the diet of replacement chicks. Other prey species identified in the diet was *Gammarus* spp. (46 deliveries), shrimp *Pandalus* ssp. (2 deliveries) – from trawler discard and butterfly (*Lepidoptera* spp.) larvae (2 feeds). These did not, however, contribute significantly to energy provision within the three age groups (<1%). Feeding with spiders (arachnids) was also observed in the control plot (youngest age group) accounting for 2.3 % of the energy; a single adult individual provided 82.1 % of the arachnid deliveries.

Feeding rate and kleptoparasitism

The mean feeding rates (Table 2) of the youngest age group did not differ significantly between nests in the control and relay plots, expressed as the numbers of deliveries (Welch's approximate t =1.13, df = 3, P = 0.333) or as the amount of energy brought to the chick (t = 0.22, df = 12, P = 0.816). In the 4-7 days old chicks, the mean number of deliveries was significantly higher for relay chicks than controls (Welch's approximate t = 3.71, df = 12, P = 0.003), whereas there was no significant difference between groups in the mean amount of energy brought to the chicks (t = 1.26, df = 30, P = 0.219). The oldest chicks showed the same pattern, with the number of feeds being significantly higher in replacement chicks than in the control chicks (Welch's approximate t = 2.42, df = 7, P = 0.046), while the amount of energy was not (t = 1.01, df = 24, P = 0.111). Kleptoparasitism was only observed in the control plot, where 30 of 81 Capelin feeds (37.0 %) were stolen by other adult birds before a successful delivery to the chick in the nest. Significant differences in kleptoparasitism between experimental and control plot could be detected in the two oldest age groups (4-7 days: $\chi^2 = 146.67$, df = 1; 8-11 days: $\chi^2 = 39.64$, df =1). The only prey species targeted by kleptoparasites was large Capelin. Stolen fish (10.28 cm ± 3.54, n = 29) were significantly larger (t = 2.677, df = 78, P = 0.007) than Capelin fed to the chick (8.82 cm ± 2.11, n = 51).

Discussion

The study at Kitsissunnguit reveals a striking difference in diet composition between non-manipulated nests and nests with simulated egg harvesting within the same breeding season. The predominant prey during the first chick-rearing period, juvenile Capelins, was virtually absent with only one delivery observed in the relay group versus 81 (51 successful) Capelin deliveries in the control group. During the four-week delay in the breeding cycle, it is likely that a shift in available food items in the upper layers of the water column have taken place. The parent birds switched to an alternative prey and hence altered the duration of the feeding trips from long to short trips. In the two older age groups (4-11 days), this shift resulted in 10-15 times higher item provisioning rate in the relay group, however Capelin fish larvae contain less than 2% of the energy of a 10 cm Capelin and so the total amount of energy brought to the relay chicks did not differ from that of the control group.

Surprisingly, despite the altered food availability, survival and growth of chicks hatched from replacement eggs were similar to those in the control group up to the age of 11 days at least. Thus, the adult birds were able to compensate for the low quality diet by increasing the feeding rate significantly without adverse effects on chick growth or survival. However, the fate of the replacement chicks could only be monitored to the age of nine to eleven days, whereas the control group could be followed to the day of fledging. Chick mortality due to starvation usually occurs within the first three to eight days for chicks hatched from first nesting attempts, and we assumed that survival to day 11 was equivalent to fledging. However, starvation of near-fledged tern chicks has been documented in Shetland (Monaghan *et al.* 1989), probably owing to vertical migration of prey fish, and this could have affected terns chicks hatched from replacement nests in Kitsissunnguit after the study ceased.

Another behavioural feature associated with feeding that differed between the two groups of chicks was the absence of intraspecific kleptoparasitism in the relay group. Steele and Hockey (1995) found that prey representing long handling times was most likely to be stolen by conspecific individuals. Other investigators (Hopkins and Wiley 1972; Ratcliffe *et al.* 1997; Stienen *et al.* 2001; Dies and Dies 2005) found that larger fish stand a higher risk of kleptoparasitism. This was also the situation at Kitsissunnguit, where only larger fish and not fish larvae were kleptoparasitised, and stolen fish on average were 16.5% larger than those fed to chicks. Kleptoparasitism may also influence chick feeding in other ways than the actual chance of losing the fish. Handling time when delivering a fish was very high due to other adults pursuing the feeder, hence reducing provisioning rate even if the prey was delivered to the chick.

Potential predators on Arctic Tern eggs and chicks, such as Glaucous Gull (*Larus hyperboreus*), Great Black-backed Gull (*Larus marinus*), Common Raven (*Corvus corax*) and Arctic Skua (*Stercorarius parasiticus*) were observed close to or sometimes within the borders of the colony. The presence of avian predators along the shoreline did not cause a response from the many breeding birds, but when the predator moved into the air space above areas with nests, large numbers (usually hundreds) of terns would join in an effective, mutual mobbing of the intruder. There were no incidents of egg predation within the study plots (n = 121 eggs) and amongst the hatched eggs (n = 108), 52 chicks survived to fledging (or presumed fledging (n = 13) in the relay plot), 51 chicks died from starvation and five chicks “disappeared” from the enclosures and could not be found again – it is likely that these five chicks were predated. No chick predation was observed in the relay plot. Predation from Peregrine Falcons (*Falco peregrinus*) was regularly observed on fledglings and adult birds. Overall, the predation level at Kitsissunnguit must be considered low compared to other studies (Hatch 2002, Cramp 1985).

A weakness of the study at Kitsissunnguit is that we could not obtain information on survival beyond day 11 in replacement chicks. However, the high survival rate of chicks older that 11 days within the control group in the same breeding season, combined with low observed predation rate and an equal growth rate amongst replacement chicks and control chicks, makes it very likely that these chicks would in fact survive to fledging. Another weakness is the estimate of the proportion of relaying breeding pairs. Although considerate observation time was spent in the relay plot, at the surroundings and in the colony in general, we can not completely rule out the possibility that more replacement nests may have occurred. The estimate in this study, where approximately half of the birds relayed, should be regarded as a low-end estimate. This estimate should furthermore be seen in a context of variation of favourable feeding conditions between years that may affect the ability to relay, and more importantly, that removal of eggs earlier in the season may have induced a higher degree of relaying, as found by Feare (1976) in Sooty Terns.

When summarizing the results of this study regarding the potential effects of egg harvesting, the equal growth rate and chick survival in the two groups combined with the absence of kleptoparasitism in the relay group may indicate only a minor negative effect of harvesting. However, only 53.3 % of breeding pairs produced a replacement clutch, which in itself reduced the reproductive outcome of the current breeding season substantially. Also, clutch size was lower in the breeding pairs that did produce a replacement clutch. Furthermore, the long-term effects on the adult birds of the markedly higher feeding rates found in replacement nests may be an important aspect at the individual level.

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Table 1. The number of successful prey deliveries (n = 1237), prey group and corresponding energy (% of total energy within the age group) fed to Arctic tern A-chicks at Kitsissunnguit 2006. Observations are subdivided into three age groups for both control chicks (203 nest hours) and replacement chicks (155 nest hours). The prey group "Fish larvae" covers three "0-group" fish species whereas "Others" covers both marine (Gammarus spp., Pandalus ssp.) and terrestrial (Lepidoptera spp., Arachnids) species (see Results for details).

		Control		**Relay**	
Chick age	**Species/group**	**Number (%)**	**Energy (%)**	**Number (%)**	**Energy (%)**
0-3 days	Capelin	4 (7.3)	84	1 (1.5)	22
	Fish larvae	7 (12.7)	11	65 (98.5)	78
	Others	44 (80.0)	5	0	0
4-7 days	Capelin	24 (28.2)	99	0	0
	Fish larvae	15 (17.7)	1	648 (99.7)	100
	Others	46 (54.1)	0	2 (0.3)	0
8-11 days	Capelin	22 (44.9)	98	0	0
	Arctic cod	0	0	2 (0.6)	13
	Fish larvae	16 (32.7)	2	329 (99.4)	87
	Others	11 (22.5)	0	0	0

Table 2. Feeding rate (numbers and energy), prey size and kleptoparasitism in control and replacement nests of Arctic Tern, Kitsissunnguit 2006 divided into age groups (days). Numbers (n) of five-hour periods are presented under each age group and values are listed as mean (+ SE) except for kleptoparasitism (frequency and proportion presented). The number of 5-hour periods in feeding rate observations are indicated by "n =" while "n =" in prey size indicate the number of prey items recorded. P-value from statistic tests (t-test and Chi square for *kleptoparasitism*) is shown for each group.

	Age group	**Control**	**Experimental nests**	**P value**
Mean feeding rate (feedings/5 hours)	0-3 (n = 4/10)	13.8 (6.2)	6.6 (1.3)	0.333
	4-7 (n = 19/13)	4.5 (0.9)	49.2 (12.0)	0.003
	8-11 (n = 18/8)	2.7 (0.5)	41.0 (15.8)	0.046
Mean feeding rate (kj/5 hours)	0-3 (n = 4/10)	8.8 (3.7)	10.0 (3.0)	0.816
	4-7 (n = 19/13)	27.2 (7.9)	32.1 (7.4)	0.219
	8-11 (n = 18/8)	21.3 (5.3)	37.1 (9.0)	0.111
Mean prey size (dw in mg)	0-3 (n = 55/66)	26.3 (11.4)	61.3 (14.9)	0.077
	4-7 (n = 85/651)	238.6 (51.0)	26.5 (1.2)	< 0.001
	8-11 (n = 49/331)	306.8 (70.8)	37.1 (4.9)	< 0.001
Frequency of kleptoparasitism (proportion stolen)	0-3	2%(1/56)	0	0.928
	4-7	19% (20/105)	0	< 0.001
	8-11	18% (11/60)	0	< 0.001

Table 3. Summary of the findings in replacement nests and control nests in Arctic terns at Kitsissunnguit 2006.

	Control	*N*	**Relay**	*n*
Clutch size	2.1 ± 0.08 [1]	*76*	1.6 ± 0.13	*16*
Internal Egg Volume (ml) per nest	35.4 + 1.34 [1]	*42*	27.8 ± 2.64	*11*
Nests with 3 eggs (%)	7 (15.2%) [1]	*46*	0 (0%)	*16*
Hatching success	90.6%	*96*	84.0%	*25*
Reproductive outcome (chicks per nest)	0.85 ± 0.088	*46*	0.88 ± 0.125 [2]	*16*
Daily wing growth rate (age 4-11 days)	7.66 mm ± 1.55	*35* [3]	7.66 mm ± 0.67	*13* [4]
Daily mass increase (age 4-11 days)	6.39 g ± 0.62	*35* [3]	6.61 g ± 0.82	*13* [4]

[1]: Collected eggs from the relay plot included. [2]: Survival in relay chicks only measured until chick age 9-11 days. [3]: Number of daily measurements varied between 38 and 28 chicks, [4]: Number of daily measurements varied between 15 and 9 chicks

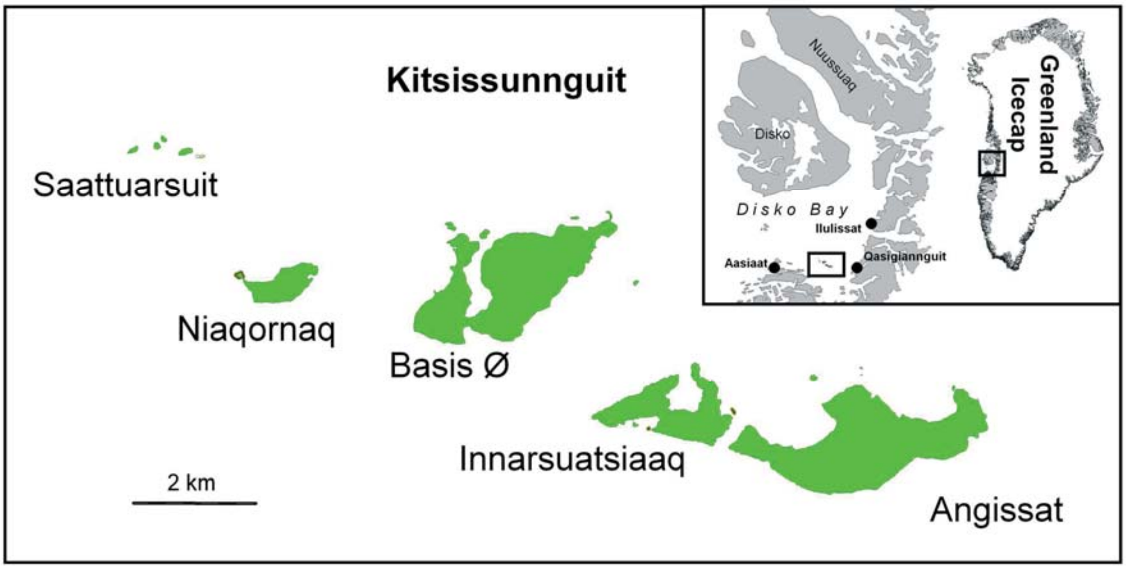

Figure 1: Map of the archipelago Kitsissunnguit with field work location, Basis Ø. Inset map in the right upper corner indicates location of Disko Bay.

Manus IV

FLUCTUATING BREEDING OF ARCTIC TERNS (*STERNA PARADISAEA*) IN ARCTIC AND HIGH-ARCTIC COLONIES IN GREENLAND

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Fluctuating breeding of Arctic Terns (*Sterna paradisaea*) in Arctic and High-arctic colonies in Greenland

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Abstract

The Arctic Tern is regarded as a species showing large variations in colony attendance between breeding seasons. This makes comparable counts of colony size complicated, and reliable population status estimates are difficult to obtain.

In this study, three different areas in two different regions with breeding Arctic Terns were surveyed in consecutive breeding seasons. Both small, mid and large sized colonies were surveyed over a four to five year period in Arctic and High-arctic Greenland. Colony size was estimated with simple direct counts or line transects to estimate nest density.

A considerable between-year variation in population size was found in the small and mid sized Arctic Tern colonies in Disko Bay, West Greenland (mean CV of individual colonies 117.5%, CV of total 49.6%). In the largest colony in Greenland, Kitsissunnguit, overall colony size only showed minor variations (CV 14.6%), but variation in breeding density was pronounced at sub-colony level (mean CV 47.4%). When combining the surveyed colonies in Disko Bay, the total population size varied only little (CV 6.7%). This amount of variation was smaller than expected if colonies fluctuated independently ($P= 0.023$), indicating that local movements between the colonies took place and that annual variation was linked to local phenomena rather than to large-scale phenomena. At High-arctic Sand Island in Northeast Greenland, Arctic Terns returned to the colony at the start of each season, but complete breeding failure, likely caused by the presence of Arctic Fox in the colony, was recorded in two out of four seasons.

Based on the results of this study, we recommend future Greenland Arctic Tern colony surveys to 1) survey multiple colonies within the same season covering adjoining colonies over a larger area, or 2) survey one large, representative colony in multiple years.

Keywords: Arctic Tern, seabirds, survey methods, breeding, *Sterna paradisaea*, Arctic, Greenland.

Running head: Arctic Tern colonies in Greenland

To obtain sustainable use of natural resources or to identify a need for conservation actions, wildlife managers around the world depend on reliable population status estimates. Whether ecosystem-based management or conservation issues of important natural sites are the focus, the assessment of population size development form counts is a key tool.

Seabirds as a group are generally characterised by long life expectancy with a relatively small annual investment in reproductive outcome, often breeding in large colonies with a high degree of site fidelity (Coulson 2002; Weimerskirch 2002). Colonial breeding at predictable sites makes seabirds ideal for monitoring and survey schemes, monitoring not only the status of seabird populations, but also as indicators for the state of the marine environment (Piatt *et al.* 2007; Parsons *et al.* 2008).

Arctic Terns perform the longest known annual roundtrip migration in any animal (Egevang *et al.* 2010) and are surface-feeders that plunge-dive or surface-dip for small fish or invertebrates (Cramp 1985; Bianki and Isaksen 2000; Hatch 2002). The Arctic Tern (*Sterna paradisaea*) usually breeds in land predator-free environments, such as islands and skerries, and is particularly good at defending the colony against avian predators. Arctic Tern breeding ground requirements are simple and the nest, with one, two or more rarely three eggs, is placed on the ground in a large variety of substrates and habitats. The annual reproductive outcome of Arctic Terns fluctuates widely, with breeding failure over large areas reported (Avery *et al.* 1992; Boertmann *et al.* 1996). Furthermore, colony desertion within the breeding season and high chick mortality from starvation (Monaghan *et al.* 1989; Monaghan *et al.* 1992; Suddaby and Ratcliffe 1997) seem to occur on a more regular basis than in most other seabirds.

Although site fidelity at a regional level is high in nesting Arctic Terns, dispersal to neighbouring breeding colonies occurs frequently (Devlin *et al.* 2008, Møller *et al.* 2006, Brindley *et al.* 1999, Ratcliffe 2004). This means that large variation in colony attendance between seasons is observed at some Arctic Tern colonies. Although poorly understood, it is important to address whether these variations may be caused by locally occurring phenomena, such as predation and disturbance, or whether they are linked to large-scale events such as food shortage linked to e.g. climatic variations. When interpreting counts of Arctic Tern colonies where variation occurs, it is furthermore important to address the scale (from within-colony to regional scale) at which the variations in colony attendance occur.

A combination of these factors makes it particularly difficult to address population size, population status and trends in Arctic Terns (Ratcliffe 2004). This is specifically the case in the Arctic zone where breeding sites may be difficult to access and colonies can be far apart.

In Greenland, the Arctic Tern is a widespread breeder with its core distribution in West Greenland between 68° and 74°N (Boertmann *et al.* 1996; Egevang and Boertmann 2003). Although no systematic monitoring schedule of Arctic Tern colonies has been initiated in Greenland, opportunistic counts during the last five to six decades indicate a decline in the population (Salomonsen 1950; Egevang *et al.* 2004; Burnham *et al.* 2005). This decline is assumed to be linked to non-sustainable egg harvesting, which has been a popular recreative activity carried out by local family groups. Arctic Tern egg harvesting was officially banned in 2002, and although some illegal harvesting still takes place in the Disko Bay area, the magnitude of tern egg harvesting seems to have decreased markedly (own observations). Due to the lack of systematic counts, fluctuations in colony size are poorly documented in Greenland, although years with non-breeding and breeding failure have been noted by several authors (Salomonsen 1950, Boertmann *et al.* 1996, Levermann and Tøttrup 2007, GSCD 2009). Although breeding failure (1992 – the summer following the Mount Pinatubo eruption) over a large scale has been documented on one occasion in Greenland (Boertmann *et al.* 1996), the scale and reasons for fluctuating breeding are largely undocumented.

In this paper we present the results of Arctic Tern colony surveys from four to five consecutive seasons conducted in both small, mid and large sized colonies in two different regions of Greenland. In conclusion, a number of recommendations for future monitoring of Arctic Tern colonies in Greenland are listed.

METHODS

Study area

Arctic Tern surveys were conducted in three study areas located in two different regions and climate zones of Greenland.

1. Kitsissunnguit (Grønne Ejland) is located in the southern part of Disko Bay, West Greenland (68.85° N, 52.00° W). The site consists of four major islands (size: 0.44-3.55 km^2) and many islets and skerries (Fig. 1A). Kitsissunnguit holds the largest Arctic Tern colony in Greenland and probably one of the largest in the World (Cramp 1985, Bianki and Isaksen 2000, Hatch 2002). The archipelago furthermore holds large diversity (by Arctic standards) and high densities of other breeding waterbirds, likely a result of breeding association between Arctic Terns and other waterbirds (Egevang *et al.* 2004; Jørgensen *et al.* 2007; Egevang and Boertmann 2008). The coast of Kitsissunnguit is mostly rocky, whereas the interior is made up of large consecutive areas covered by dwarf scrub heath with Crowberry (*Empetrum nigrum*) and mosses (*Bryophyta*) as the dominant species.
2. The "Akunnaaq area" is located in the southern part of Disko Bay, West Greenland (approximately 20 km southwest of Kitsissunnguit) between the town Aasiaat and the settlement of Akunnaaq (68.72-68.80° N, 52.20-52.73° W). The study area consists of numerous skerries and small islands (Fig. 1A), of which many hold breeding Arctic Terns. Fourteen colonies on islets between 0.002 and 0.2 km^2 in size (Tab. 1, Fig 1A) were counted annually between 2002 and 2005. The colonies were all low-lying with rocky coasts and dwarf bush heath found in the central parts of islets.
3. Sand Island (Sandøen) is located within the high-arctic zone of Northeast Greenland, at the mouth of Young Sound (74.26° N, 20.16° W, Fig. 1B). The small island (0.22 km^2) peaks at only three meters above sea level, with a habitat consisting of mostly sand and gravel with vegetation being extremely sparse. The surroundings of the island are highly influenced by sea ice. Break-up of the ice-covered fjord occurs in early July, but drift ice in varying amounts may be present throughout the breeding season.

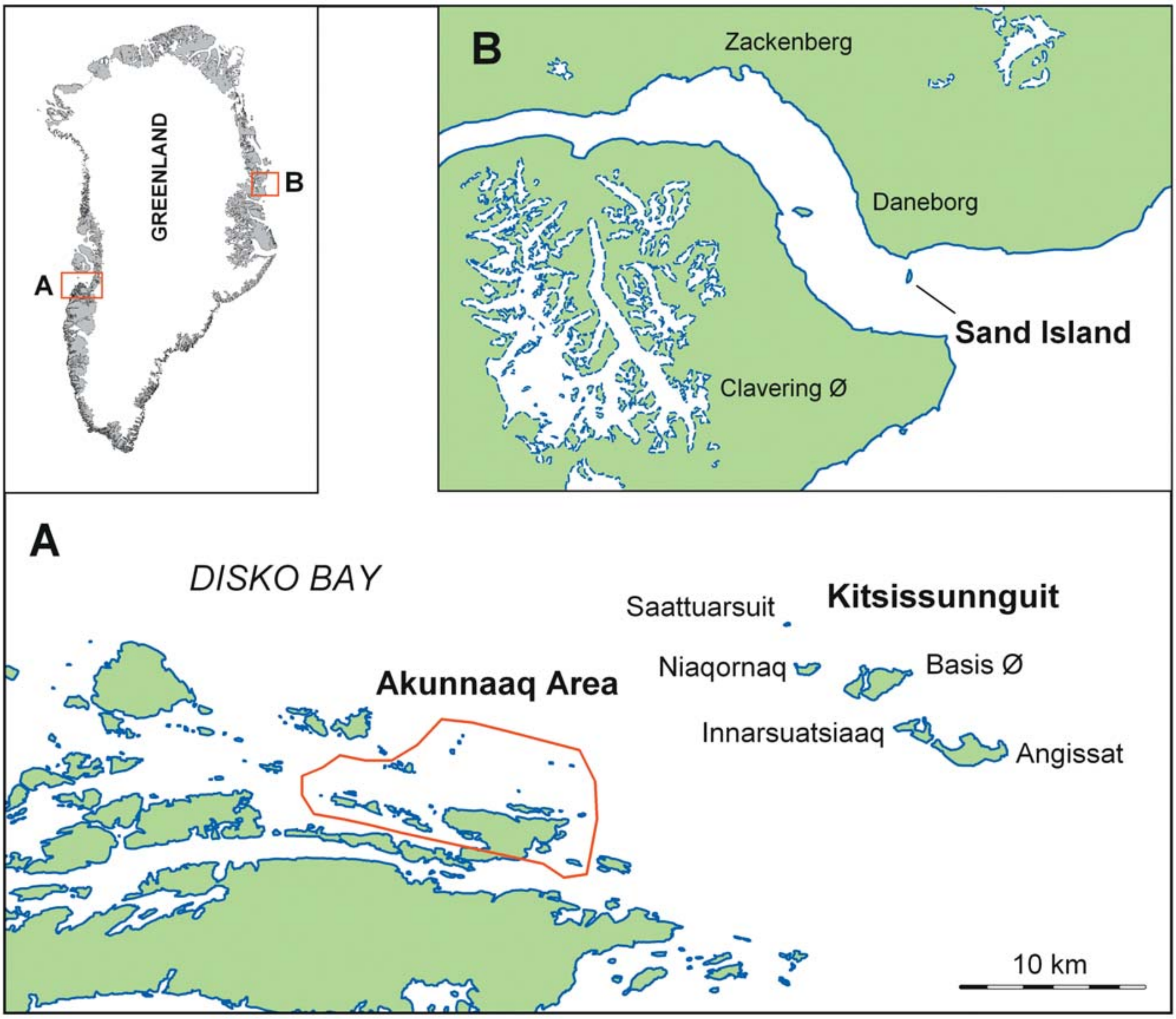

Figure 1. Map of study areas. Inset map in upper left corner shows the location of **A)** Kitsissunnguit and the Akunnaaq Area in Disko Bay and **B)** of Sand Island in Northeast Greenland. The map scale (lower right corner) applies to both A and B.

Table 1. Colony size (individuals) at 14 Arctic Tern colonies in the southern part of Disko Bay in 2002-2005. Colony code refers to the Greenland Seabird Colony Database (GSCD 2009). Asterisk (*) indicates “dog islands” – sites where sledge dogs are located through the summer.

Colony code	2002 (18 June)	2003 (17 June)	2004 (19 June)	2005 (18 June)	CV 2002 to 2005 (%)
68013	2,000	0	650	1,800	85.4
68142	10	30	0	0	141.4
68155	600	0	600	1,050	76.6
68166	30	0	0*	12	135.0
68167	1,000	0	520	330	90.3
68174	80	0	40	200	108.0
68175	0*	0	0	0*	–
68188	30	0	0	650	188.4
68189	55	0	260	0	156.9
68190	300	0	400	50	103.0
68191	200	0	140	400	89.7
68192	100	0	1,000	300	128.8
68193	300	0	0	100	141.4
68194	0	1,200	430	950	83.2
Total	**4,705**	**1,230**	**4,040**	**5,842**	**49.6**

Both Kitsissunnguit and the Akunnaaq area are situated within the core distribution area for Arctic Tern in Greenland, and neighbouring Arctic Tern colonies (not included in neither of the study sites) are few kilometres away. In contrast, Sand Island is more isolated and the nearest tern colony is more than 50 km away.

Predators at all three study areas included Arctic Fox (*Alopex lagopus*), Glaucous Gull (*Larus hyperboreus*), Great Black-backed Gull (*L. marinus*), Common Raven (*Corvus corax*), Peregrine Falcon (*Falco peregrinus*), Gyrfalcon (*Falco rusticolus*) and occasionally Lesser Black-backed Gull (*L. fuscus*), Parasitic Jaeger (*Stercorarius parasiticus*) and Long-tailed Jaeger (*S. longicaudus*).

Methods

Due to differences in colony area and population size at the study sites two different methods were applied when estimating population size.

1. The high number of breeding birds combined with the fact that terns at Kitsissunnguit breed scattered over a large consecutive area called for special census methods. Line transects (Buckland *et al.* 2001) recording the nest of Arctic Terns were applied on the major islands. North-south oriented lines 250 m apart were used in the field with data subsequently analysed using the software Distance ver. 5.0 (Thomas *et al.* 2006). Counts were always conducted by two persons: an observer and a navigator. The observer would walk along a transect line at an equal pace, searching for nests and measuring the distance between the nest and the transect line with a measuring tape. The navigator would walk approximately 15 meters behind the observer and using a GPS directing the observer to stay on the line. The line transect counts were conducted between 18 June and 3 July in 2002 -2006 at a time in the breeding cycle when the majority of the colony had stopped laying eggs but prior to the start of hatching.
2. Direct counts were applied at the Akunnaaq area and at Sand Island. We used flush counts to estimate colony size, and the number of birds present at the colony was transformed into breeding pairs by dividing with a factor of 1.5 (Bullock and Gomersall 1981). The colonies were located on small islands that could be surveyed from the sea, and counts were performed with a boat as platform. The counts in the Akunnaaq area were conducted within a narrow time window (17-19 June), which correspond to mid incubation (Table 1). Roosting terns (i.e. larger flocks aggregated at the shoreline) were ignored in the population size estimate. Islands with sledge dogs (“dog islands”) were recorded on the same occasion.

Counts at Sand Island were conducted between 20 and 26 July (mid-late incubation). The island was divided into segments that were counted (flush counts) separately by walking through the colony on foot.

We used permutation tests to evaluate whether regional annual total nest counts were less variable than expected if colonies fluctuated independently, which would indicate between-colony movements. Within each colony, annual counts were permuted randomly 9,999 times, simulated regional annual totals and their variance (or equivalently CV) were calculated, and a one-tailed P value determined as the proportion of simulated totals having lower variance than the observed regional annual totals.

RESULTS

The overall population size at Kitsissunnguit (all islands combined) showed little variation (CV=13.9 %) between years with a population size between 15,400–21,800 pairs in 2002-2006 (Table 2, details in Appendix I). However, at individual islands a more pronounced variation (Tab. 2) was recorded with differences of almost a factor three in breeding population (e.g. Niaqornaq 2002 vs. 2003). Furthermore, the island Innarsuatsiaaq showed two years without terns followed by two years with low densities of breeding terns. The breeding density at Kitsissunnguit (all years and all islands combined) averaged 4,823 pairs/km^2 (+1,483). At a smaller scale (comparing between the islands), breeding densities varied between 7,213 and 629 pairs/km^2 (Appendix I).

The fourteen colonies in the Akunnaaq area showed considerable differences in population size between years, with coefficient of variation ranging from 76.6 % to 188.4 % (Table 1), whereas CV of the colonies combined was lower at 49.6 %. Only one site (68175) did not include breeding terns in any of the surveyed years, whereas the other thirteen colonies had breeding terns in at least two of surveyed years. All of the colonies experienced years without breeding terns (most of them in 2003), and the largest absolute variation in colony size was found in the largest colony (68013), ranging from 0 to 2,000 individuals (Tab. 1). When ignoring years without breeding terns (0-years) the average difference in maximum and minimum individuals in the colonies were 372 (SD = 387) with two colonies varying by as much as a factor 10 (68192) or 20 (68188) between years.

The permutation test showed no evidence of lower regional variation within each of the two regions (Kitsissunnguit $P = 0.20$, Akunnaaq $P = 0.90$), but when the two regions were pooled to form an overall Disko Bay total, variance and thus CV were lower than expected if individual colonies fluctuated independently ($P = 0.023$).

At Sand Island, variation in breeding numbers was more pronounced. Both 2006 and 2009 were years with total breeding failures, whereas the breeding population in 2007 and 2008 was estimated at between 700 and 1000 pairs, based on counts varying between 1150 and 1500 individuals. In the two years with breeding failure, birds returned to the colony at the start of the season, but egg-laying was either postponed or laid eggs depredated, until breeding was eventually abandoned.

Table 2. Arctic Tern population size (pairs) at Kitsissunnguit (Grønne Ejland) in 2002-2006. Population size was estimated using line transects. Details on estimates are found in Appendix I.

	2002	2003	2004	2005	2006	CV 2002-2005 (%)	CV 2002-2006 (%)
Angissat	0	0	0	0	0	–	–
Innarsuatsiaaq	0	0	776	600[1]	800[1]	68.7	93.0
Basis Ø	11,525	17,626	15,901	12,112	17,060	15.8	19.1
Niaqornaq	3,159	1,245	1,984	2,346	2,500[1]	27.7	31.3
Saattuarsuit	670[1]	670[1]	530[1]	1,420[1]	1,400[1]	46.9	46.3
Total	**15,354**	**19,541**	**19,191**	**16,478**	**21,760**	**11.6**	**13.9**

[1] Estimate from direct counts

Although the breeding numbers in 2007 and 2008 were similar, the distribution of tern nests differed between the two seasons. In 2007 birds bred scattered over most of the island, whereas in 2008 the majority (estimated 80%) of the terns bred at the elevated central part of the island (Egevang & Stenhouse 2008, Egevang *et al.* 2009). In 2007/2008 the breeding density equalled 2,574-3,676 pairs per km^2 on Sand Island.

DISCUSSION

The information obtained from comparing surveys in this study shows that a high degree of variation in population size between years. The highest coefficient of variation was found at colony level, whereas lower variation was found for the two study areas, Kitsissunnguit and the Akunnaaq Area (Tab. 1 and 2). When combining the two study areas, which include more than 80 % (GSCD 2009) of the Arctic Tern population in Disko Bay, to address annual population size variations at a large scale, a CV of only 6.7% was found with the grand total ranging between 20,000 and 23,000 pairs (Tab. 3), a level of variation that was smaller than expected if colonies fluctuated independently. This led us to conclude that year-to-year variation in the Arctic Tern population in Disko Bay is not governed by large scale phenomena. Instead, the switching of colonies between seasons is more likely driven by more locally occurring phenomena, such as predation or disturbance. However, in 2003 it seems likely that mesoscale movements from the southern colonies (Akunnaaq area) to Kitsissunnguit may have taken place.

Variation was also found among colonies in the distribution and density of the breeding birds. The highest and most pronounced variation was found amongst the smaller and midsized colonies in the Akunnaaq area. Here colonies with up to 2,000 breeding individuals one year could be followed by years without or with very few pairs breeding. However, tern colonies are located densely in the southern part of Disko Bay, and it is likely that the local terns may shift between suitable nesting grounds. Even in 2003, which seemed to be a poor overall breeding season in the Akunnaaq area, a site (Pullat, code 68148) less than 10 km outside the Akunnaaq study area held 3,000 breeding Arctic Terns. Although direct evidence that the same individuals move around between colonies from year to year in the (southern) Disko Bay area is difficult to obtain, the circumstantial evidence of this study indicates that this is in fact the case.

At the high-arctic Sand Island, the short summer leaves only a brief window of opportunity for completing the breeding cycle. The four years of data included in this study indicate that complete breeding failure takes place at a regular basis (two out of four seasons). When the birds arrive to breed between late June and early July, sea ice still covers the surroundings of the island connecting it with the mainland. From here, Arctic Foxes are able to access the island and cause considerable nest predation. The time for ice break-up and isolation of the island from land predators may vary between years, but usually takes place in early July (ZERO 1997-2009). The presence of a predator on the island in egg–laying period seemed to make the birds postpone their egg laying, as suggested by Levermann and Tøttrup (2007), or more likely to postpone the decision of investing in a replacement clutch after having the first clutch depredated early in the season.

Table 3. Grand total (from table 1 and 2) and coefficient of variation (CV) from Arctic colony censuses in Disko Bay 2002-2005.

	2002	2003	2004	2005	CV (%)
Kitsissunnguit	15,354	19,541	19,191	16,478	11.6
Akunnaaq area	4,705	1,230	4,040	5,842	49.6
Grand Total	**20,059**	**20,771**	**23,231**	**22,320**	**6.7**

The fluctuating occurrence of Arctic Terns between breeding seasons stressed by this study clearly emphasises the need for a specialized monitoring programme for this species. Monitoring of Arctic Terns in single colonies conducted in single years does not provide a reliable estimate of the population status, as Arctic Terns show a lesser degree of site fidelity compared with most other Arctic seabird species. The use of counts of breeding birds or nests in fixed study plots for later extrapolation is furthermore questionable, as within-colony movements of the location of nest along with variation in breeding density between years seems to occur at a regular basis.

Future monitoring of Arctic Tern populations in Greenland is recommended to apply one of the following two approaches (or ideally a combination of both): 1) Survey of multiple colonies within the same season covering adjoining colonies over a larger area, or 2) survey of one large, representative colony in multiple years. However, since logistics in Greenland are both expensive and time consuming, the first approach seems most cost effective and likely to produce a suitable estimate for managing purposes.

In terms of the survey method, this will probably be determined by the size, structure and breeding density of the colony. Smaller and mid-sized colonies up to 2,000 birds breeding on skerries and islets that can be surveyed from the sea are best counted using a boat as platform. Large colonies with higher number of birds are recommended to be surveyed by counts in subdivisions of the colony (preferably delimited by easily recognisable, natural boundaries in the field). Large colonies with high breeding numbers and nests evenly distributed at low or medium densities should be surveyed using line transects or a similar approach.

The period for conducting surveys should be timed to coincide with late incubation. As timing of egg laying may vary considerably between seasons and locations, it is important to address the state of the breeding cycle before conducting the counts. This is particularly the case for line transects, where recording of tern nests need to be conducted when the majority of the birds have started incubation but before eggs starts hatching and chicks can move away from the nest area.

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Appendix I

Detailed results from line transect counts conducted on Kitsissunnguit, 2002 to 2006. Data on search effort from the islands in the archipelago are joint (pooled data) while point estimates of density (pairs per km^2) with standard error (SE), confidence variance (CV) and confidence interval (CI) are given for each of the individual islands. Data were analysed using software Distance 5.0 (Thomas *et al.* 2006) applying a half normal cosine detection function with a 3% right truncation.

	2002	**2003**	**2004**	**2005**	**2006**
Pooled data					
ESW[1] (SE)	1.9–(0.12)	2.3–(0.14)	3.0–(0.11)	3.3–(0.18)	2.6–(0.15)
f (0)[2] (SE)	5.23–(0.319)	4.37–(0.270)	3.28–(0.126)	3.03–(0.169)	3.75–(0.213)
Effort[3] L(n)	8.6–(11)	9.4–(12)	17.8–(26)	8.9–(11)	7.7–(8)
Observations (nests)	139	228	433	232	227
Basis Ø West (0.90 km^2)					
Density (SE)	4199–(1253.1)	6587–(1690.9)	4049–(2195.8)	3600–(1233.7)	5746–(2097.9)
Population size (SE)	3785–(1129.4)	5938–(1524.1)	3650–(1979.0)	3244–(1111.6)	5177–(1890.0)
CV (%)	29.84	25.67	54.22	34.27	36.51
95% CI	177–81101	2791-12635	732-18198	1158-9084	1731-15487
Basis Ø East (2.22 km^2)					
Density (SE)	3483–(518.8)	5261–(651.1)	5514–(964.4)	3989–(322.4)	5345–(853.7)
Population size (SE)	7740–(1152.8)	11688–(1446.6)	12251–(2142.7)	8868–(716.7)	11883–(1897.7)
CV (%)	14.89	12.38	17.49	8.08	15.97
95% CI	5368-11160	8561-15958	8264-18163	7422-10596	7627-18513
Niaqornaq (0.45 km^2)					
Density (SE)	7040–(2795.0)	2665–(1119.7)	4420–(1466.2)	5213–(1502.1)	
Population size (SE)	3159–(1254.1)	1245–(523.1)	1984–(658.0)	2346–(503.3)	
CV (%)	39.70	42.01	33.17	28.81	
95% CI	965-10342	356-4357	721-5461	562-5425	
Innersuatsiaaq (1.23 km^2)					
Density (SE)			629–(340.8)		
Population size (SE)			776–(420.1)		
CV (%)			54.14		
95% CI			242-2494		

[1] Effective strip width (m)
[2] Probability density function (10^{-3})
[3] Effort = length (L) of lines (in km) and numbers (n) of lines

Manus V

RED PHALAROPE *PHALAROPUS FULICARIUS* AND RED-NECKED PHALAROPE *PHALAROPUS LOBATUS* BEHAVIOURAL RESPONSE TO ARCTIC TERN *STERNA PARADISAEA* COLONIAL ALARMS

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Red Phalarope *Phalaropus fulicarius* and Red-necked Phalarope *Phalaropus lobatus* behavioural response to Arctic Tern *Sterna paradisaea* colonial alarms

PETER SØGAARD JØRGENSEN, MIKKEL WILLEMOES KRISTENSEN and CARSTEN EGEVANG

(Med et dansk resumé: Thorshanes og Odinshanes respons på alarmer i en havternekoloni)

Abstract The breeding association between Arctic Terns and Red and Red-necked Phalaropes has been mentioned several times in the ornithological literature, though mostly anecdotally. The present study, conducted at the Kitsissunnguit archipelago in western Greenland, investigates phalarope behavioural response to Arctic Tern colonial alarms, specifically the relationship between type and duration of tern alarms and phalarope response type. The majority of tern alarms elicited a visible response from the phalaropes. No difference in phalarope response type was detected between true alarms (tern responses to the presence of gulls, falcons or humans) and dreads (false alarms). Tern alarms to which the phalaropes reacted were of longer duration than alarms that caused no change in phalarope behaviour, whereas no relationship was found between tern alarm duration and phalarope response type (passive vs active). In conclusion, phalaropes respond strongly to tern alarms, but do not differentiate between predator-related alarms and dreads. These findings support the view that phalaropes, where possible, take advantage from Arctic Tern colonies, and that this relationship – fulfilling the criteria of both the *information parasitism* and the *defence parasitism hypotheses* – explains the high densities of phalaropes at Kitsissunguit.

Introduction

Beneficial breeding associations are well known in multi-species colonies of birds. Many examples are known among colonial waterbirds (e.g., Alberico et al. 1991). Typically, such relationships form between a semi-aggressive, bold species (often a larid) and a more timid species of waterbird, where the latter benefits from the strong colony defence of the bold species. In most of these cases, however, the details of the relationship are unknown and the mechanism through which the timid species benefits from the breeding association has not been documented.

In order to obtain a higher individual survival and reproductive output, a timid species can benefit from breeding associations with more aggressive

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species if the bold species provides a higher predator detection rate and/or predator detection at a greater distance, giving the timid species more time to react (the *information parasitism hypothesis*, Nuechterlein 1981); or if the bold species aggressively defends the surroundings of its nest and thereby indirectly provides protection to the timid species (*defence parasitism hypothesis*, Dyrcz et al. 1981).

Arctic Terns *Sterna paradisaea* have been known to associate with high breeding densities of several species of shorebirds, including Red-necked Phalarope *Phalaropus lobatus* and Red Phalarope *Phalaropus fulicarius* (Løvenskiold 1964, Hildén & Voulanto 1972, Cramp & Simmons 1983, Egevang et al. 2004), Ruddy Turnstone *Arenaria interpres* (Brearey & Hildén 1985) and Purple Sandpiper *Calidris maritima* (Summers & Nicoll 2004).

The present study focuses on the association between Arctic Terns and phalaropes in a major Arctic Tern colony in western Greenland. Using relatively simple observations of phalarope response to tern alarms and dreads (false alarms), we investigate whether phalaropes use information parasitism to benefit from the terns, and which behavioural responses they express.

Study area and methods

Fieldwork was conducted at the Kitsissunnguit (Grønne Ejland) archipelago in the southern part of Disko Bay, West Greenland (68˚50'N, 52˚00'W) in the period 2-28 July, 2006. Kitsissunnguit is the largest Arctic Tern colony in Greenland with 16000-22000 estimated breeding pairs in 2002-2006 (Egevang et al. 2004; this study). By Arctic standards, the site holds a rich avifauna with 25 breeding species recorded, some of them rare in West Greenland (e.g., Red Phalarope, Long-tailed Skua *Stercorarius longicaudus*, Ross's Gull *Rhodostethia rosea*, cf. Kampp & Kristensen 1980, Kampp 1982, Frich 1997). The major avian predators are Glaucous Gull *Larus hyperboreus*, Great Black-backed Gull *Larus marinus*, Gyrfalcon *Falco rusticolus*, Peregrine Falcon *Falco peregrinus* and Raven *Corvus corax*. Arctic fox *Alopex lagopus* also occur at the archipelago where it occasionally breeds, and although Arctic Terns and foxes may co-exist at Kitsissunnguit for a few years (Kampp 1982), the terns probably avoid the easternmost island in the archipelago because foxes have been established there for decades (Egevang et al. 2004). The coasts of the islands are generally rocky, whereas the inland is covered by dwarf scrub heath with willow *Salix* spp., dwarf birch *Betula nana* and crowberry *Empetrum nigrum* as the dominant plant species. There are many moist areas, ponds and small lakes with sedge *Carex* spp. and cotton grass *Eriophorum* spp.

The current study was conducted at Basisø, a fox-free island of approximately 3.5 km^2. In 2006 there were 45 pairs of Red-necked Phalaropes and 7 of Red Phalaropes on the island, which numbers may underestimate the actual number of nests because females may be polyandrous (Cramp & Simmons 1983).

Observations of phalarope and tern behaviour were conducted from the edge of two small ponds. All phalarope individuals present at the ponds during an observation period were kept under observation. The three main behaviours performed by phalaropes outside tern alarm periods were feeding, resting and preening. Observation periods varied from one to three hours, in total covering 30 hours, and were evenly distributed over the study period. Initially the phalaropes preferred a pond of c. 2500 m^2, but after the first week the behaviour of the birds changed and, apparently as a result of the fledging of the chicks, they began to frequent a new pond adjacent to the first. Both sites offered a good view of the water surface and the brinks. Apart from the phalaropes and a high number of Arctic Terns, the breeding species in the surrounding area were Mallard *Anas platyrhynchos*, Long-tailed Duck *Clangula hyemalis*, and Red-breasted Merganser *Mergus serrator*.

Both phalarope species were included in the study but no distinction between them were made, due to their very similar behaviour and response to aerial predators. The dataset mainly includes local breeders but, as the season advanced, these became mixed with migrants and with local juveniles.

The following behavioural patterns were recorded:

Tern alarms. The duration of tern alarms, defined as mass up-flight by at least half of the terns in the study area, was recorded. The type of alarm was categorized as a) originating from disturbance from gull or falcon, b) originating from human disturbance, or c) dreads (false alarms).

Phalarope response to tern alarms. During tern alarms the behavioural response of the phalaropes was recorded. Six different types of response were identified: 1) no response (no change in behaviour), 2) tucking to water surface (*Tucking*), 3) stopping ongoing behaviour and/or looking up (*Stop/looking up*), 4) take-off from pond (*Upflight*), and 5)

Table 1. Behavioural response of Red Phalarope and Red-necked Phalarope to Artic Tern alarms during 30 hours of observation at Kitsissunnguit in 2006. Arctic Tern alarms were caused by present gulls/falcons or humans, or were dreads (false alarms). The six different types of phalarope behavioural responses were: 1) No reaction (i.e. no change in behaviour); 2) Tucking (i.e. tucking to water surface); 3) Stop/looking up (i.e. stopping ongoing behaviour and/or looking up); 4) Upflight (i.e. take off from pond; 5) Swim surface (i.e. swimming out on pond surface), and; 6) Swim brink (i.e swimming to the brink).

Adfærdsrespons fra Thorshane og Odinshane på havternealarmer under 30 observationstimer på Kitsissunnguit i 2006. Havternealarmerne var fordelt på måger/falke, mennesker og falske alarmer (henholdsvis 2., 3. og 1. kolonne). De seks typer af adfærdsrespons var: 1) Ingen reaktion (ingen ændring i adfærd); 2) Trykkende (til vandfladen); 3) Stop/kig op (stopper igangværende adfærd og/eller kigger op); 4) Opflyvning (letter fra dam); 5) Svømmer ud på vandfladen; 6) Svømmer ind til brinken.

	Tern Alarm Type			Total
	Dreads	Gull/Falcon	Human	
1) No reaction	6	4	1	11
2) Tucking	1	1	-	2
3) Stop/look up	28	8	-	36
4) Upflight	8	4	1	13
5) Swim surface	2	-	-	2
6) Swim brink	5	1	-	6
Total	50	18	2	70

swimming out on pond surface or 6) to the brink (*Swim surface/brink*). Phalarope response during each tern alarm sometimes included more than one of these types, but only the predominant one was included in the statistical analysis.

Response types 2) and 3) were classified as *passive*, types 4), 5) and 6) as *active*.

The frequency distributions of phalarope responses were statistically tested using χ^2-tests. Mann-Whitney U-tests were used to test the difference in duration of tern alarms grouped on basis of phalarope response.

Results

The terns responded strongly to predators within the boundaries of the colony, and the presence of aerial predators resulted in fierce mobbing behaviour involving hundreds, on a few occasions thousands of birds. The type and intensity of the vocalisation of the terns varied somewhat, depending on the predator species, so that at least three types of alarm calls (falcon, gull, human) could be distinguished in the field. The mean duration of gull/falcon alarms was 30.3 s (n=17), which is longer than the mean duration of dreads (23.0 s, n=44) (Mann-Whitney U-test, U=239.5, P<0.05).

The mean number ± SD of phalaropes observed in each period was 16.8 ± 10.5. We recorded 70 alarms in total, and their types and the corresponding phalarope behaviours are shown in Table 1. The mean frequency ± SD of tern upflights was 2.6 ± 1.3 hour^{-1}. The frequency of gull/falcon alarms was 0.26 hour^{-1}, while dreads comprised 71% of all alarms. The phalaropes never reacted to an intruding predator before the terns alarmed, and in the few cases where a gull was observed close to the colony without releasing alarm from the terns, no anti-predator behaviour was observed from the phalaropes.

Phalaropes responded visibly to most of the tern alarms, 59 out of 70 (Table 1; $\chi_1^2 = 31.56$, Yates-correction, $P<0.001$). The most common responses were Upflight and Stop/look up. No difference in the distribution between missing, active and passive responses to dreads or gull/falcon/human alarms could be detected ($\chi_2^2 = 1.98$, $P = 0.37$). The most common form of response in both cases was the passive response behaviour (dreads: 58%, n=50; gull/falcon/human: 45%, n=20).

Tern alarms to which phalaropes reacted visibly were of longer duration (26.5 s, n=52) than alarms eliciting no response from the phalaropes (16.1 s, n=9) (Mann-Whitney U-test, U=110.5, P<0.05). No difference was found between the duration of tern alarms to which phalaropes responded passively (23.3 s, n=36) and actively (33.8 s, n=16), respectively (Mann-Whitney U-test, U=226, P>0.05).

Discussion

The study on phalarope behavioural response to Arctic Tern alarms at Kitsissunnguit reveals a close association between the species. The phalaropes reacted instantly to tern alarms in 84% of the recorded alarms, indicating a one-way transfer of information from terns to phalaropes, as implied by the *information parasitism hypothesis*. At large Arctic Tern colonies (such as Kitsissunnguit) a predator will be detected at a considerable distances, and the intensity of the alarm will increase as the predator travels through the colony. This provides terns and other birds in the colony with an early warning system, passing on information on direction, distance and species of the approaching predator. This early warning gives the breeding birds the time necessary to perform anti-predator behaviour and warn offspring to seek cover.

Spontaneously occurring dreads without an obvious cause are common in tern colonies. The reason is not known; among the proposed causes is that it may contribute to the maintainance of pair bonds (Cullen 1960), and irrespective of the underlying cause the dreads may serve as an indicator of the frequency of predator visits to the colony (Meehan & Nisbet 2002). In the present study more than two thirds of the recorded alarms were dreads. The fact that phalaropes did not show any difference in behavioural response to dreads versus alarms involving predators indicates that the phalaropes react to tern alarms before they have visually identified a potential predator.

Tern alarm intensity and duration depends on the predator species, but also on how close the predator is to a given part of the colony and of the behaviour exhibited by the predator. For example will low hunting flights result in much more intense alarms from the terns than straight transits above the colony. These factors may also contribute to explaining why phalaropes apparently do not differentiate between real tern alarms and dreads, even though predatory alarms on average last longer than dreads, and phalaropes respond more frequently to longer alarms.

The dominance of passive responses to active ones may serve to lower depredation on eggs or chicks, since it allows the phalarope to stay in its territory, whereas the upflight response means that it has to leave, even in the case of a false alarm (Alberico et al. 1991).

The mean frequency of tern upflights (2.6 hour^{-1}) is comparable to the mean rate of 2 hour^{-1} quoted by Cramp (1985); it may, however, vary through the breeding period (Cramp l.c.). The frequency of gull/falcon alarms at Kitsissunnguit (0.26 hour^{-1}) is lower than the about 4 hour^{-1} – caused by Herring Gull alone – found during the hatching and chick rearing stage in a small (505 pairs) mixed tern colony in Canada (Whittam & Leonard 1999). This may indicate that predator numbers are relatively low at Kitsissunnguit. The many terns in the colony form an effective defence towards intruders such as Ravens, gulls and skuas. However, falcons are able to outfly the terns and are less affected by their mobbing (Egevang et al. 2005).

Egevang et al. (2004) documents that a marked decline in phalarope numbers took place after Arctic Terns abandoned the easternmost island in the Kitsissunnguit archipelago, Angissat. In addition, they discuss whether the unusually high breeding density of Red-necked Phalarope – and the presence of the rare Red Phalarope – at Kitsissunnguit is a direct result of the presence of a major tern colony, i.e., if the distribution of terns determines the distribution of phalaropes, or if both terns and phalaropes simply prefer a fox-free environment so that the presence or absence of foxes determines the distribution of both terns and phalaropes. The results of the present study verify the strong behavioural response of phalaropes to tern alarms, showing that the relationship between the species fulfils the criteria of both the *information parasitism* and the *defence parasitism hypothesis*, and thereby strengthen the first hypothesis, without being able to reject the second.

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Resumé

Thorshanes og Odinshanes respons på alarmer i en havternekoloni

Den positive ynglerelation mellem svømmesnepperne Thorshane *Phalaropus fulicarius* og Odinshane *P. lobatus* på den ene side, og Havternen *Sterna paradisaea* på den anden, er velkendt, men er oftest behandlet rent anekdotisk i den ornitologiske litteratur. Fra den 2. til 28. juli 2006 undersøgte vi de to svømmesneppers adfærdsrespons på kollektive havternealarmer på øgruppen Kitsissunnguit (Grønne Ejland) i Disko Bugt i Grønland. Undersøgelsen blev foretaget ved relativt simple observationer af typen

Phalaropes breeding in tern colonies use tern alarms (upflights and calls) as warning signals indicating the presence of predators, but are unable to distinguish between true and false alarms. Photo: Mikkel Willemoes Kristensen.

og længden af havternealarmerne og typen af svømmesneppernes respons herpå.

Hyppigheden af havternealarmer på hvilke svømmesnepperne responderede var signifikant højere end alarmer uden respons. Der blev ikke fundet nogen forskel mellem falske ternealarmer og ternealarmer forårsaget af måger, falke eller mennesker hvad angår hyppighed og fordeling af manglende respons, passiv respons, og aktiv respons. Alarmer af den sidstnævnte type var dog af signifikant længere varighed end falske alarmer. Ternealarmer med svømmesneppe-respons varede i gennemsnit længere end alarmer uden respons, mens der ikke var nogen tilsvarende signifikant forskel på længden af ternealarmer med henholdsvis aktiv og passiv svømmesneppe-respons.

Resultaterne viser, at svømmesnepperne reagerer markant på ternealarmer, og at de i deres respons ikke skelner mellem rovdyrsrelaterede alarmer og falske alarmer. Resultaterne understøtter formodningen om, at den høje yngletæthed af Odinshane – og tilstedeværelsen af Thorshane – på Kitissunnguit skyldes at ynglende svømmesnepper tiltrækkes af havternekolonier.

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MIGRATION AND BREEDING BIOLOGY OF ARCTIC TERNS IN GREENLAND

This thesis presents novel findings for the Arctic tern in Greenland.

Included is a study on Arctic tern migration– the longest annual migration ever recorded in any animal. The study documented how Greenland and Iceland breeding terns conduct the roundtrip migration to the Weddell Sea in Antarctica and back. Although the sheer distance (71,000 km on average) travelled by the birds is interesting, the study furthermore showed how the birds depend on high-productive at-sea areas and global wind systems during their massive migration.

Furthermore included is the first quantified estimate of the capacity to produce a replacement clutch in Arctic terns. We found that approximately half of the affected birds would produce a replacement clutch when the eggs were removed late in the incubation period.

At a level of more national interest, the study produced the first estimates of the key prey species of the Arctic tern in Greenland. Although zooplankton and various fish species were present in the chick diet of terns breeding in Disko Bay, Capelin was the single most important prey species found in all age groups of chicks.

The thesis also includes a study on the fluctuating breeding found in Arctic terns. Breeding birds showed a considerable variation in colony size between years in the small and mid sized colonies of Disko Bay. These variations were likely to be linked to local phenomena, such as disturbance from predators, rather than to large-scale occurring phenomena.

Included is also a study that documents the breeding association between Arctic terns and other breeding waterbirds. At Kitsissunnguit a close behavioural response to tern alarms could be identified. These findings imply that the altered distributions of waterbirds observed at Kitsissunnguit were governed by the distribution of breeding Arctic terns.

Included in the thesis are furthermore results with an appeal to the Greenland management agencies. Along with estimates of the Arctic tern population size at the two most important Arctic tern colonies in West Greenland and East Greenland, the study produced recommendations on how a potential future sustainable egg harvest could be carried out, and on how to monitor Arctic tern colonies in Greenland.

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