Miljøministeriet

Danmarks Miljøundersøgelser

Træk- og overvintrings-strategier hos gæs

Faktorer, der influerer på valg af rasteplads

Jesper Madsen

Miljøministeriet

Danmarks Miljøundersøgelser

Træk- og overvintrings-strategier hos gæs

Faktorer, der influerer på valg af rasteplads

Jesper Madsen
Afdeling for Flora- og Faunaøkologi

Doktordisputats
Faglig rapport fra DMU, nr. 10

Miljøministeriet
Danmarks Miljøundersøgelser
November 1990

Denne afhandling er, i forbindelse med nedenfor anførte tidligere offentliggjorte afhandlinger, af det Naturvidenskabelige Fakultetsråd ved Aarhus Universitet antaget til offentligt forsvar for den naturvidenskabelige doktorgrad.

Aarhus den 12. november 1990

Karl Pedersen
dekan

Forsvaret finder sted den 14. december 1990, kl. 14.15, Auditorium D1, Matematisk Institut, Aarhus Universitet.

Indhold

Forord

Denne afhandling er en sammenfatning og perspektivering af otte udvalgte primærafhandlinger.

Arbejdet er udført i flere sammenhænge. Et basismateriale stammer fra koordineringen af landsdækkende optællinger af gæs, foretaget i et samarbejde mellem Dansk Ornitologisk Forening, Miljøministeriets Fredningsstyrelse (nu Skov- og Naturstyrelsen), Landbrugsministeriets Vildtforvaltning (nu Miljøministeriets Vildtforvaltning) og Zoologisk Museum, København, 1980-1983. Et andet materiale er indsamlet i forbindelse med Grønlands Miljøundersøgelsers baggrundsundersøgelser forud for olieaktivitet i Jameson Land, Østgrønland, 1982-1984. Et tredje materiale er indsamlet i forbindelse med specialestudiet ved Zoologisk Laboratorium, Aarhus Universitet, 1981-84. Endelig er der indsamlet materiale i forbindelse med arbejde på Vildtbiologisk Station (nu Danmarks Miljøundersøgelser, Afd. for Flora- og Faunaøkologi), hvor jeg har været ansat siden 1985, og hvorunder jeg siden 1987 har fungeret som koordinator for gåsearbejdsgruppen i International Waterfowl and Wetlands Research Bureau (IWRB).

Ledetråden i arbejderne har været en sammenkædning af de faktorer, der influerer på valg af habitat og rasteplads hos vilde gæs og svømmeænder på forskellige årstider – grundlagsskabende forskning, som lægger op til en mere økologisk funderet forvaltning og beskyttelse af gåsebestandene og deres levesteder.

Dette arbejde havde ikke været muligt uden bidrag fra en lang række personer. Først og fremmest vil jeg rette en tak til de mere end 100 danske feltornitologer, der har leveret tællinger, samt til mine kolleger, der har været medforfattere til publikationerne og som har støttet arbejdet teknisk. En tak går til Hanne Petersen, Grønlands Miljøundersøgelser for at have givet os frie rammer til at tilrettelægge forskningsaktiviteten i Jameson Land, og kolleger fra Danmarks Miljøundersøgelser, Afd. for Flora- og Faunaøkologi for tilskyndelse undervejs mod denne afhandling.

De otte udvalgte publikationer er i denne sammenfattende afhandling refereret til ved deres numre i indholdsfortegnelsen.

Jesper Madsen
November 1990

SYNOPSIS
Indledning

En årscyklus hos voksne, vilde gæs er groft set fordelt mellem 2-3 måneders yngleaktivitet, inklusiv en fire ugers fældningsperiode, hvor de er ude af stand til at flyve, og en 9-10 måneders periode, hvor de først gradvist bevæger sig mod syd til overvintringsområdet og derefter i modsat retning imod yngleområdet. For ikke-ynglende gæs forlænges træksæsonen af, at svingfjersfældningen foregår på specielle fældningspladser, som oftest ligger fjernt fra yngle- og overvintringsområdet.

For de fleste arter er det karakteristisk, at de uden for ynglesæsonen har en trækstrategi, hvor de optræder i store flokke ofte bestående af tusinder af individer, og at de er i stadig "stepping-stone" lignende bevægelse mellem forskellige rastepladser på trækvejene på vej til og fra overvintringsområdet, der kun benyttes i relativ kort tid (f.eks. St Joseph 1979, Fox, Madsen & Stroud 1983, Owen & Gullestad 1984, Madsen 1984a,b).

Ud over de egentlige trækbevægelser på stor skala foretager gåseflokkene trækbevægelser på mindre skala inden for en lokalitet. For eksempel foretager de flokke af kortnæbbede gæs, der kan overvintre på Tipperhalvøen i Ringkjøbing Fjord, et gradvist skift fra Værnengene i syd til Tipperreservatets enge (Madsen 1985a, Lorenzen & Madsen 1985), hvorfra de i forårets løb fortrækker til fordel for nysåede vårsædsmarker på omkringliggende arealer.

Under indtryk af de massive gåseflokke og deres græsningseffekt på vegetationen fremsatte Drent, Ebbinge & Weijand (1979) hypotesen, at gåseflokkenes trækbevægelser på stor såvel som mindre skala, er dikteret af fødegrundlaget. Med udgangspunkt i teorien om optimal fourageringsstrategi, ifølge hvilken dyr udvælger fourageringssted efter, hvor det er energimæssigt mest profitabelt, d.v.s. størst muligt energetisk udbytte ved mindst mulig indsats (Royama 1970, Charnov 1976), foreslog Drent et al. (1979), at gåseflokkenes trækbevægelser er led i en maximering af det daglige energiindtag. Som eksempel fremdrog de, at gæssene om foråret, hvor de gradvist bevæger sig mod nord, følger en gradient i plantefænologien, der timer udnyttelsen af en føderessource til, at fordøjeligheden af og næringsindholdet i vegetationen er størst.

Owen (1972, 1973) og flere andre forfattere hævder, at forstyrrelsesniveauet er en altafgørende faktor for fordelingen af gåseflokke i landskabet. En alternativ hypotese til forklaring af trækbevægelserne kan således være, at gåseflokkene primært udvælger rastepladser efter, hvor der er mindst risiko for predation samt tilstrækkeligt udsyn (og under forudsætning af, at der er velegnede fødeemner). Da der er få områder, der tilfredsstiller gæssenes krav, medfører det en koncentrering af fuglene. Konsekvensen bliver, at der sker en hurtigere nedgræsning af føderessourcerne, hvorefter flokkene tvinges til at trække videre.

Emnet for denne afhandling er en beskrivelse af nogle af de habitatøkologiske faktorer, der ligger til grund for gæssenes trækstrategi, og en evaluering af implikationer for antal og fordeling af fugle på rastepladserne samt konsekvenser for fremtidig forvaltning. Det vises, at ikke blot fødekvalitet og -mængde er afgørende faktorer for habitatvalget, men at predationsrisiko og i visse situationer konkurrence kan være betydningsfulde.

Konklusionen er, at der bør anvendes en bredere model til forklaring af gæssenes trækbevægelser og habitatvalg, en model, der ikke blot ser snævert på fouragering, men også inkorporerer predationsrisiko, konkurrenceforhold og nogle etologiske forhold relateret til flokdannelse og stedtrofasthed, der reducerer gæssenes plasticitet i ressourceudnyttelse.

Denne model lægger således op til en sammenkobling og udvidelse af de to ovennævnte hypoteser og en udvidelse af teorien om optimal fouragering. Forslaget ligger på linie med andre forsøg, der er gjort på at udvide teorien om optimal fouragering med andre relevante aktiviteter og fitness-komponenter end fouragering og energi, nemlig effekter af fødekonkurrenter (Rosenzweig 1979, Pimm, Rosenzweig & Mitchell 1985) og predationsrisiko (Grubb & Greenwald 1982, Werner et al. 1983) på habitatudnyttelse.

I den anden halvdel af det 20. århundrede har næsten samtlige gåsebestande i Vestpalæarktis været i fremgang (3, Madsen in press). Gæssene benytter i stigende grad kulturprægede habitater som rastepladser, og i medfør heraf forvolder de i visse situationer skader på landbrugsafgrøder (bl.a. Rüger 1985, Lorenzen & Madsen 1986). På den anden side er der et stadigt pres på bestandene og deres levesteder fra menneskelig side, og det omfatter ikke bare aktiviteter i overvintringsområderne, men i stigende omfang også gæssenes sommerkvarterer. I afhandlingens sidste afsnit argumenteres der for, at strategier for forvaltning af bestandene og deres levesteder må tage udgangspunkt i populationsdynamiske analyser og undersøgelser af arternes trækstrategier på en fly-way basis, fremfor som hidtil i konkrete, aktuelle problemstillinger på lokalt plan.

I afhandlingen er habitat defineret bredt som et arealmæssigt sammenhængende, mere eller mindre homogent levested, bestående af et konglomerat af fysiske og biotiske faktorer (Partridge 1978). En habitats bæreevne er udtryk for, hvor mange individer et område kan ernære med en ligevægt mellem områdets produktionsevne og fuglenes eksploitation. Belastning af et område i løbet af en sæson udtrykkes i antal fugledage pr. arealenhed.

I (4) indgår et materiale vedrørende planteædende svømmeænder. Dette er medtaget, da arterne af svømmeænder har mange lighedspunkter med visse gåsearter i habitatspektrum og adfærd, og samtidig indgår de som en komponent, der påvirker gæssenes habitatudnyttelse.

Fødens kvalitet

Udnyttelse af mikrohabitaten

Gæs og visse arter af svømmeænder lever næsten udelukkende af plantefødе, som ofte har lavt indhold af mange essentielle næringsstoffer og højt indhold af strukturstoffer. Gæs har ringe bakteriel nedbrydning af plantecellernes strukturelle kulhydrater (fibre) i tarmen (Mattocks 1971, Buchsbaum, Wilson & Valiela 1986) og er afhængige af mekanisk i kråsen at knuse cellerne og optage mindre, opløste forbindelser. Forskellige plantearters, plantedeles eller vækststadiers fordøjelighed, d.v.s. den andel af føden, som gæssene kan ekstrahere i løbet af tarmpassagen, er således negativt korreleret med fiberindholdet (Nehring & Nerge 1966, Drent et al. 1979, (1)). For at dække deres daglige fødebehov har gæssene et hurtigt turnover af føden i tarmene på bekostning af effektiv fordøjelse. Det bevirker, at gæssene må tilbringe det meste af dagen med fødesøgning (1).

I det brede spektrum af plantearter inden for habitaten er det sandsynligvis primært indholdet af sekundærstoffer, som er afgørende for fødevalget (Buchsbaum, Valiela & Swain 1984), men blandt de plantearter, som gæssene tager, sandsynligvis fordøjeligheden. Forskellige feltundersøgelser og eksperimenter viser, at gæssene er i stand til at selektere plantearter eller plantedele med lavest fiberindhold og højst proteinindhold (Owen, Nugent & Davies 1977, Owen 1979, Prop, van Eerden & Drent 1984, (8)), omend mekanismen for selektionen ikke er klarlagt.

Flere undersøgelser har dokumenteret, at gæssenes gentagne afgræsning af vegetation i vækst kan medvirke til at holde et højt næringsindhold i fødeplanterne, hvorimod næringsværdien hurtigt falder i ugræssede planter (Prins, Ydenberg & Drent (1980), Ydenberg & Prins (1981), (5,8)).

Kvalitetsbestemte habitatskift

Gæs på forårsrastepladser. Boudewijn (1984) demonstrerede, at i kraft af at kulturgræsserne om foråret starter væksten tidligere end strandengsgræsserne, topper fordøjeligheden i kulturgræsserne tidligere end i sidstnævnte. I det hollandske vadehav fouragerede flokke af knortegæs *Branta bernicla* først på kulturgræsenge og siden på saltmarsk. Habitatskiftet var sammenfaldende med tidspunktet for, hvor fordøjeligheden i strandengsgræsserne oversteg kulturgræssernes.

Hos de kortnæbbede gæs, der opholder sig i Danmark om foråret, iagttages visse steder et tilsvarende habitatskift (Madsen 1986). Gæssene har imidlertid radikalt skiftet fourageringsvaner, således at stort set hele bestanden fouragerer på kulturgræsmarker i det tidlige forår for så at skifte til nysåede vårsædsmarker, hvor de tager kernerne i overfladen. Estimater af gæssenes daglige energioptagelse og -forbrug (netto-energiindtaget) i de to typer habitater antydede, at profitabilitet ved fødesøgning kunne forklare det observerede habitatskift (1). Den daglige fourageringstid var 33% kortere og den daglige energioptagelse mere end dobbelt så stor på de nysåede marker i forhold til kulturgræsmarker.

I forårsperioden opbygger gæssene energi- og næringsreserver til den forestående ynglesæson, og de har forhøjet behov for føde med højt proteinindhold (Prop, van Eerden & Drent 1984). Observationerne af, at de kortnæbbede gæs foretog et habitatskift fra fødeemner med relativ højt til føde med lavt proteinindhold var således kontroversiel (Madsen 1984a, (1)). Senere observationer (Madsen upubl.) har dog vist, at gæssene sandsynligvis kompenserer ved at supplere indtaget af kerner med græs, som ædes under lejlighedsvise skift tilbage til græsmarker.

Blisgæs i Vestgrønland. Et fænomen sammenligneligt med det trinvise nordtræk kan imidlertid studeres på et mere begrænset geografisk område med en højdegradient, f.eks. i Vestgrønland, der er yngleområde for den grønlandske blisgås *Anser albifrons flavirostris* (Madsen & Fox 1981, Fox & Madsen 1981).

Gæssenes ankomst i begyndelsen af maj i undersøgelsesåret 1979 var sammenfaldende med det første tøbrud i kærene i dalbundene. I ankomstfasen var gæssene begrænset til denne habitat, og føden bestod af underjordiske plantedele, som blev trukket op af jorden. I løbet af maj forlod gæssene området og trak til højereliggende kær (ca. 200 m.o.h.), som netop var blevet snefrie. Rederne blev anlagt omkring kær i denne højde, og i rugeperioden fouragerede parrene især på stængler og rhizomer og senere nye skud af smalbladet kæruld *Eriophorum angustifolium*. Efter klækningen trak familierne op til plateausøer med omgivende kær (ca. 400-600 m.o.h.), som blev senest snefrie. Ikke-ynglende gæs fældede samtidig i samme habitat.

Blisgæssene foretog således et habitatskift langs en gradient i tøtidspunkt. I starten af sæsonen var de fysisk begrænset til dalbundene, men senere havde de frit valg mellem habitater i forskellig højde. I tråd med Drent, Ebbinge & Weijands (1979) hypotese kan gæssenes habitatskift fortolkes som, at de opsøger den fremspirende vegetation, hvorved de maximerer energiindtaget.

Fældende gæs i Østgrønland. Tilsvarende hypotesen om energioptimering ved nordtrækket om foråret har Owen & Ogilvie (1979) foreslået, at det fældningstræk, som foretages af ikke-ynglende gæs og som næsten udelukkende går i nordlig retning, er en tilpasning til den senere vækststart længere mod nord, hvorved gæssene opsøger den mest næringsrige føde.

I Jameson Land, som er et vigtigt fældningsområde for kortnæbbede gæs fra Island og bramgæs *Branta leucopsis* fra Nordøstgrønland (6,8), kunne det konstateres, at tidspunktet for fuglenes ankomst på fældningspladsen var sammenfaldende med halvgræssernes vækststart, hvilket støtter Owen & Ogilvies (1979) hypotese.

To forhold betyder imidlertid, at man ikke kan udelukke alternative forklaringer. Det er således kontroversielt i forhold til hypotesen, at bramgæssene foretager et fældningstræk, som går fra nordligere yngleområder mod et sydligere fældningsområde. Andre faktorer, f.eks. at fødekonkurrence med ynglefugle driver de ikke-ynglende fugle til områder med få ynglepar kan være en anden mulig forklaring på, at trækket er opstået. I Jameson Land er der en lav tæthed af ynglepar af kortnæbbede gæs og bramgæs (6).

Historisk udvikling i fældningstrækket hos de kortnæbbede gæs er et andet moment, der rejser spørgsmål ved hypotesen. Fældningstrækket fra Island til Østgrønland er først opstået i midten af dette århundrede (bl.a. (6)), samtidig med, at bestanden tog til i antal. Det er derfor nærliggende at tro, at trækket er ikke-ynglende fugles forsøg på at undgå fødekonkurrence med ynglefuglene på Island.

Fødens tilgængelighed

Gæssenes adgangsmuligheder til føderessourcerne kan begrænses af en række biotiske og abiotiske faktorer: overordnet fødemængden (habitatens bæreevne), samt tilstedeværelsen af konkurrerende arter, niveauet af forstyrrelser, tidevand, sne- og isdække, dagslængde og visse adfærdsmæssige aspekter, såsom gæssenes traditionelle brug af bestemte rastepladser.

Fødemængden

Gæssenes muligheder for udnyttelse af habitaten varierer i løbet af træksæsonen. Om vinteren og i det tidlige forår er primærproduktionen på engene på vore breddegrader minimal (bl.a. Lorenzen & Madsen 1985), og gæssene vil gradvist reducere føderessourcerne i et område. Når primærproduktionen sætter igang i løbet af foråret, vil gåseflokkene derimod kunne returnere til det samme område gentagne gange og genfinde en nyfremspiret vegetation. Hvor gæs og ænder fouragerer på frø, hvadenten det er spildsæd, nysået sæd eller frøstande, ligner det vintersituationen på græs: føderessourcerne nedgræsses.

I felten kan et områdes bæreevne for græssende gæs vurderes direkte ved analyse af exploitationsrater, d.v.s. differencen mellem gæssenes konsumption og vegetationens biomasse og nettoprimærproduktion, eller indirekte ved analyse af profitabilitet ved græsning ved forskellig fødetæthed. Vegetationens biomasse kan nå en nedre tærskel, hvor det ikke længere er energetisk profitabelt for gæssene at søge føde, hvorefter de vil skifte til en anden fourageringsplads (Drent & Swierstra 1977, Lorenzen & Madsen 1985).

Habitaters bæreevne for gæs har været behandlet i (4,5,7,8) og for svømmeænder i (4).

Knortegæs i Vadehavet om foråret. Hovedparten af den 150-235.000 individer store bestand af mørkbuget knortegås søger føde på saltmarsk i det hollandske, tyske og danske vadehav fra marts til slutningen af maj. Det er veldokumenteret, at de fleste arktisk ynglende gåsearter udnytter forårsperioden til opbygning af fedt- og næringsreserver til anvendelse i den forestående ynglesæson, og at disse kropsreserver er af vital betydning for yngleresultatet (Ankney & MacInnes 1978, Thomas 1983); således også de mørkbugede knortegæs (Ebbinge et al. 1982, Ebbinge 1989). Forårsperioden har derfor en speciel betydning i gæssenes årscyklus, og saltmarskens bæreevne kan få en kritisk indflydelse på yngleresultatet og ultimativt medvirke til begrænsning af knortegåsbestandens størrelse. På de traditionelle forårsrastepladser i det hollandske vadehav er der indicier for, at bæreevnen er ved at være nået (Ebbinge 1979, Ebbinge & Boudewijn 1984).

På øen Langli i Vadehavet blev knortegæssenes græsning af saltmarskvegetation undersøgt i tre forår med henblik på en estimering af habitatens bæreevne ud fra gæssenes exploitationsrate og en analyse af græsningseffekter på vegetationens produktion (5). Ved at sammenligne græsningsintensiteten på Langli med andre forlandsstrækninger i Vadehavet, ville det være muligt at give en overordnet vurdering af, hvorvidt antallet af knortegæs i Vadehavet om foråret er begrænset af fødemængden. I (7) er det vist, at antallet af knortegæs i Vadehavet om foråret har været relativt stabilt i 1980'erne, hvorimod efterårsbestanden og bestanden som helhed har fluktueret betydeligt. Dette kan være tegn på, at antallet om foråret er begrænset, f.eks. af fødemulighederne.

Forsøgene på Langli viste, at der var stor år-til-år variation i græsningsbelastning og vegetationens (strandannelgræs *Puccinellia maritima*) overjordiske primærproduktion, sandsynligvis forårsaget af vejrmæssigt inducerede forskelle i vækstbetingelser. Exploitationsraten var høj og varierede mellem 85 og 87% af den overjordiske nettoprimærproduktion, hvilket indikerer, at bæreevnen stort set var nået. I de tre forsøgsår var bæreevnen og antallet af gåsedage tilbragt på øen korrelerede, hvilket antyder, at der har foregået en ressourcebegrænsning af antallet af gæs.

På de øvrige undersøgte saltmarske i Vadehavet var græsningsintensiteten betydeligt lavere end på Langli, og muligvis – med undtagelse af mindre delområder – har bæreevnen sandsynligvis ikke været nået (7). På engene på Tipperne var bæreevnen heller ikke nået (Lorenzen & Madsen 1985). Konklusionen er, at der lokalt kan være en antalsregulering som følge af begrænsede ressourcer, men at de danske saltmarske generelt ikke ser ud til at være fuldt belastede. Hvad der er årsagen til det konstante antal i Vadehavet om foråret forbliver endnu ubesvaret. Der er dog visse tegn på, at de øvrige forlandsstrækninger er af ringere kvalitet end marsken på Langli, og dette kan udgøre en del af forklaringen.

Cargill & Jefferies (1984) viste, at snegæs *Anser caerulescens*, der i løbet af sommeren afgræsser saltmarskvegetation i subarktisk Canada, stimulerer græsvæksten betydeligt. En senere undersøgelse (Bazely & Jefferies 1985) viste, at mekanismen først og fremmest var, at tilførslen af ekskrementer gødede vegetationen og accelererede kvælstofomsætningen. En anden mekanisme viste sig at være, at afgræsningen forøgede planternes skudantal (Kotanen & Jefferies 1987).

Ud over Balkenkol et al.'s (1984) påvisning af, at tilførsel af store mængder gåseekskrementer stimulerer græsproduktionen, foreligger der fra vore breddegrader imidlertid ingen realistisk udførte undersøgelser, der har analyseret gåsegræsningens stimulerende effekt på netto-primærproduktionen.

Undersøgelsen på Langli (5) dokumenterede, at gæssenes ekskrementer gøder saltmarskvegetationen, og at gødningseffekten er så hurtig, at gæssene i løbet af foråret selv kan profitere af den forøgede primærproduktion. Effekten må formodes at være så betydelig pga. kvælstofmangel i jorden, og fordi gødningstilskuddet kommer på et tidspunkt, hvor planterne har stort behov for kvælstof til vækst.

Knortegæs og svømmeænder i Vadehavet om efteråret. Om efteråret fouragerer flokke af mørkbugede knortegæs, pibeænder *Anas penelope* og krikænder *Anas crecca* på ålegræsbanker i Vadehavet. I løbet af efteråret forlader svømmeænderne bankerne og søger ind på forlandsarealer for at fouragere på marskvegetationens frøsætning og senere ind i baglandet, mens gæssene stort set forbliver på ålegræsbankerne. I (4) er årsagerne til skiftene forsøgt analyseret med særlig henblik på at belyse den koblede effekt af føderessourcernes størrelse, interspecifik konkurrence og jagtlig forstyrrelse.

Ud fra forsøg med indhegninger af vegetationsafsnit i hhv. et ålegræsbed på Jordsand Flak og i to plantesamfund på Rømødæmningens forland blev det vist, at under uforstyrrede forhold nedgræssede flokkene af andefuglene ressourcerne til en tærskel, hvor det sandsynligvis ikke længere var energetisk profitabelt at søge føde. Begrænsede føderessourcer var således en af mekanismerne bag de observerede habitatskift. Konkurrence om føden og jagtforstyrrelser var imidlertid også en medvirkende faktor (se side 14 og 16).

Interspecifik konkurrence

Konkurrence kan have to fremtrædelsesformer: interferens og exploitativ konkurrence. Den kan være symmetrisk eller asymmetrisk, afhængigt af arternes økologiske og adfærdsmæssige effektivitet og fleksibilitet. Intraspecifikt er interferens et virkningsfuldt redskab til opretholdelse af en hierarkisk struktur i gåseflokken (Boyd 1953, Lamprecht 1986, Black & Owen 1989), og høj status er adgangskort til de bedste føderessourcer og ultimativt forbedret fitness (Teunissen, Spaans & Drent 1985). Interspecifikt vil interferens sandsynligvis have samme resultat som følge af arternes forskellige størrelse, der hos småfugle er en god indikator for dominansforhold (Alatalo & Moreno 1987).

Interspecifik exploitativ konkurrence opstår i situationer, hvor individer af to eller flere økologisk nærtstående arter deles om begrænsede ressourcer, som gradvist ædes op. Denne form for konkurrence er mere usynlig end interferens, og det er normalt blot udkommet og ikke mekanismerne bagved, man observerer.

Oprindeligt har gåsearterne i vinterperioden sandsynligvis været segregerede på habitater med lille geografisk overlap, og morfologisk og fourageringsteknisk tilpasset fødegrundlaget (Owen 1976). For eksempel levede sædgæs *Anser fabalis* i højmoserne, hvor de tog rødder og rhizomer af kærvegetationen, grågæs i sumpområder, hvor føden var rhizomer og skud, bramgæs fouragerede på græsvegetation på små, kystnære holme, og knortegæssene marint på submers vegetation. På ynglepladserne var arterne stort set allopatriske, dog med undtagelse af de nordatlantiske øer, hvor flere arter var sympatriske.

Med stigende kulturpåvirkning konvergerede gåsearterne i habitatudnyttelse, og der kan kun ses få tilfælde af, hvad der menes at være den oprindelige tilpasning (f.eks. knortegæs, der fouragerer marint, og grønlandske blisgæs, der fouragerer i uspolerede irske moser). I dag overvintrer flere arter sympatrisk. På ynglepladserne er der som følge af forøgede, ekspanderende populationer blevet større geografisk overlap i udbredelse. På de arktiske ynglepladser er der ringere diversitet i fødegrundlaget og større lighed i gåsearternes fourageringsteknik og fødevalg i forhold til vintertiden.

Som en følgevirkning af den historiske udvikling med stigende bestande og stort overlap i habitatvalg kan det forventes, at der opstår interspecifik konkurrence på forskellige tidspunkter af året. Konkurrence og mulige konsekvenser deraf har imidlertid kun haft lille bevågenhed. Her fremlægges fire eksempler, hvor det foreslås, at interspecifik konkurrence har haft en effekt på den indbyrdes fordeling af arterne. Eksemplerne antyder, at fænomenet ikke er sjældent, men sandsynligvis overset.

I eksemplerne har der efter al sandsynlighed været tale om exploitativ konkurrence, idet der på intet tidspunkt er bemærket aggression mellem arterne. Hypotesen er, at i tilfælde af at føderessourcerne kommer i underskud, forsøger den ene art at undgå konkurrencen fra den anden (''avoidance'') ved et nicheskift eller ved at forlade området helt.

Rastende gåseflokke i Vestjylland. Analyse af nicheskift, d.v.s. at en art indskrænker sin fourageringsniche i nærvær af en økologisk nærtstående art, og udvider nichen i den anden arts fravær, giver mulighed for at demonstrere eksistensen af interspecifik konkurrence i økologisk tidsperspektiv (Diamond 1978).

På markerne ved Filsø i Vestjylland forekommer der om efteråret flokke af grågæs *Anser anser* og kortnæbbede gæs i tidsmæssig sympatri og allopatri, hvilket giver mulighed for at studere to arters reaktion på hinandens tilstedeværelse (Madsen 1985b). Da grågæssene forekom alene i området (september) foretrak de marker med stub og stub med udlæg (føden er spildsæd). Da arterne forekom sammen (oktober) undgik grågæssene markerne med stub med udlæg, som var den foretrukne habitat hos de kortnæbbede gæs. Da grågæssene havde forladt området (november) foretrak de kortnæbbede gæs fortsat stub med udlæg og stub. I oktober var der kun et lille overlap i udbredelsen af de to arter. Observationerne kunne fortolkes således, at grågæssene, der var de kortnæbbede gæs talmæssigt langt underlegne, foretog et nicheskift i forsøget på at undgå exploitativ konkurrence.

På engene på Tipperhalvøen i Vestjylland forekommer de samme to arter i sympatri i det tidlige forår. De har stort overlap i fødevalg, men er delvis segregerede i arealudnyttelse, idet de kortnæbbede gæs især benytter de centrale dele af fennerne og grågæssene arealerne op mod vejene (Lorenzen & Madsen 1985). De kortnæbbede gæs nedgræsser gradvist engvegetationen, men på grund af deres skyhed forbliver zonerne nærmest vejene imidlertid stort set ugræsset. Segregationen af arterne kan tages som udtryk for, at grågæssene, der er mindre sky, undgår konkurrencen med de kortnæbbede gæs ved at udnytte denne niche.

Fældende gæs i Østgrønland. Et andet eksempel på exploitativ konkurrence mellem gåsearter med konsekvenser for deres indbyrdes udbredelse, er behandlet i (8), som beskriver relationerne mellem to gåsearter i fældningsperioden.

Jameson Land i Østgrønland er fældningsplads for ca. 5000 kortnæbbede gæs og det samme antal bramgæs. Gæssene ankommer til området i slutningen af juni måned – de kortnæbbede gæs fra Island og bramgæssene fra Østgrønland. De slår sig hurtigt ned på egnede fældningspladser, som er søer, elve og kyster med tilstødende kær, hvor de kan fouragere. I 3-4 uger i juli er gæssene ude af stand til at flyve (6).

Gæssene og specielt de kortnæbbede gæs er ekstremt nervøse i fældningsperioden og søger kun føde i umiddelbar nærhed af vandfladen. Bramgæssene bevæger sig kun op til 100 m ind i kærene, mens de kortnæbbede gæs, der har en betydeligt større adræthed (evne til at sprinte), går 200-250 m ind i kærene.

I Jameson Land var stort set alle egnede fældningspladser besat med gæs, og der var en lineær sammenhæng mellem det tilgængelige areal af kær på fældningspladsen og antallet af gæs. Kombineret med at målinger af exploitationsrater på kærvegetationen viste, at gæssene konsumerede en stor del af primærproduktionen, var der belæg for at sige, at områdets bæreevne omtrent var nået.

De to arter var stort set segregerede og optrådte sjældent i blandede flokke. De kortnæbbede gæs var overrepræsenterede langs kysterne, i de større elve og på søer med vidt udsyn, mens bramgæssene især forekom i de mindre elvsystemer og på søer med omkringliggende bakker. I situationer, hvor arterne var segregerede, bestod begge arters føde af halvgræsser og græsser. Hvor de to arter optrådte på samme lokalitet, steg andelen af mos, især i bramgåsens føde. Mos havde lavere næringsværdi end græsser og halvgræsser, og var således en suboptimal fødekilde. Adskilt brugte arterne 40-46% af døgnets timer på græsning og 37-38% på hvile. Hvor de optrådte sammen ændrede de kortnæbbede gæs ikke tidsbudget signifikant, hvorimod bramgæssene forøgede tiden til græsning (til 62% af døgnets timer).

Observationerne antydede, at det var ufordelagtigt for bramgæssene at optræde sammen med de kortnæbbede gæs. Dette hænger sandsynligvis sammen med, at i sympatri måtte bramgæssene forblive i kærzonen omkring vandfladen, som også var afgræsset af de kortnæbbede gæs. Derfor måtte de bruge mere tid på fødesøgning for at dække det daglige energibehov. De kortnæbbede gæs var derimod alene om at udnytte de fjernereliggende kærzoner. Konkurrencen var således asymmetrisk, og det kunne forventes, at bramgæssene ville undgå steder, hvor de kortnæbbede gæs forekom. Segregationen af arterne kan forklares med, at de kortnæbbede gæs pga. deres ekstreme nervøsitet ikke benytter de mindre elvsystemer eller de "lukkede" søer i fældningsperioden. Bramgæssene, der forsøger at undgå konkurrencen med de kortnæbbede gæs, har derved en ledig niche uden konkurrenten.

Herbivore andefugle i Vadehavet. I ålegræsbeddet i det sydlige Vadehav (4) var pibeand og knortegås sympatriske og forekom begge i store koncentrationer. Der var stort overlap i arternes arealudnyttelse, og de gik ofte i blandede flokke. Der blev ikke observeret aggression mellem arterne. Begge levede af ålegræsblade, og i løbet af efteråret nedgræssede de ressourcerne. I takt hermed skiftede knortegæssene gradvist fourageringsmetode; fra næsten udelukkende at have afgræsset blade gik de over til stampefouragering, hvorved de i pytter i beddet stampede rødder og rhizomer frem af sedimentet. Pibeanden havde ikke denne fleksibilitet, og da det sandsynligvis blev energetisk ufavorabelt at fouragere på bladene alene, fortrak arten.

Observationerne sandsynliggør, at der var exploitativ konkurrence mellem arterne, og endvidere at konkurrencen var asymmetrisk, mest kritisk for pibeanden, der ikke kunne skifte fødeemne og fourageringsmetode inden for området.

Forstyrrelser/predationsrisiko

Flokdannelse er en adfærdsform, der øger chancen for at opdage en potentiel predator i tide og reducerer enkeltindividets risiko for predation (Bertram 1978). Flokdannelse reducerer imidlertid også gæssenes plasticitet i udnyttelse af habitater. I kraft af deres flokvise optræden er gæs særlig følsomme over for uro (potentiel predation), og forstyrrelser er en betydningsfuld fordelende faktor i gæssenes habitatvalg (Owen 1972, 1973, Mooij 1982, Madsen 1980, 1982, 1986, Meire, Kuijken & Devos 1988, 2, 4). Defineret som menneskeskabte forskydninger fra normalsituationen i fuglenes antal, fordeling og adfærd, omfatter forstyrrelser både landskabelige elementer (f.eks. hegn, bygninger), som hindrer fugleflokkenes frie udsyn og som kan skjule potentielle predatorer, og uro skabt af menneskelig aktivitet og potentielle predatorer.

Det er sandsynligt, at den første omgivelsesfaktor en gåseflok vurderer et områdes egnethed som rasteplads efter, er predationsrisikoen. Først efter en indledende fase begynder gæssene at vurdere delområdernes fødemuligheder. Det er typisk, at en gåseflok først udnytter de store arealer inden for en rasteplads og først senere bevæger sig ind på mindre delområder (bl.a. Owens 1977), hvilket kan fortolkes derhen, at gæssene først skal opnå fortrolighed med predatormiljøet.

Landskabselementer. I (2) er den forstyrrende effekt af småveje, diger, hegn m.m. over for flokke af kortnæbbede gæs kvantificeret, og gåseflokkenes krav til områdestørrelser vurderet.

Gåseflokkes flugtafstand i forhold til en forstyrrelseskilde er taget som vejledende udtryk for minimum acceptabel områdestørrelse (områdets "radius"). Flugtafstanden er en adfærdsmæssig parameter, afhængig af typen af stimulus, der udløser flugt, frekvensen af stimuli, flokstørrelse og sensitivitet (flugtmulighed, fældning vs. flyvedygtighed). Flugtafstanden er afhængig af flokstørrelse og årstid, som angiver en ændring i frekvensen af stimuli, nemlig jagtlig efterstræbelse som i Danmark ophører 31. december. Både i (2) og (4) er det vist, at jagt medfører forøget skyhed.

Menneskeskabt uro. Hypotesen om at mennskeskabt uro, og specielt jagtudøvelse, påvirker fordelingen af gæs i landskabet, er dokumenteret i en lang række undersøgelser (bl.a. Owen 1972, 1973, Madsen 1980, 1982, 1986, Meire, Kuijken & Devos 1988). Således afspejler fordelingen af kortnæbbede gæs i Danmark forår og efterår effekten af uro i forbindelse med jagt. Om efteråret er gæssene koncentreret på 2-3 lokaliteter, mens de om foråret er spredt på 12-14 lokaliteter langs den jyske vestkyst (Madsen 1982).

Et andet eksempel på stor-skala fordelende effekt af jagtlig forstyrrelse er vinterudbredelsen af de grå gæs *Anser* i Vesteuropa. Grågæssene, der overvintrer i Spanien og Holland, "springer over" Frankrig, på trods af at der er egnede habitater, og andre *Anser* gæs forekommer kun sporadisk. For 15 år siden overvintrede stort set ingen *Anser* gæs i Frankrig og Belgien. I Belgien er der i 1970-erne og 1980-erne skabt flere jagtfredede arealer for gæssene, kulminerende i en jagtfredning af alle arter i 1986. I takt med disse tiltag er bestandene af gæs steget betragteligt, og de har bredt sig over større arealer (Kuijken & Meire 1987).

I Frankrig, hvor der fortsat drives intensiv gåsejagt, er der ikke sket nogen stigning i bestandene (Yesou in press).

Der foreligger imidlertid kun få undersøgelser, der analytisk har forsøgt at vægte effekten af den jagtlige forstyrrelse i forhold til andre faktorer, primært effekten af begrænsende føderessourcer. I (4) er denne vægtning foretaget for to områder i det sydlige Vadehav, der er rasteplads for knortegæs og pibeænder, dels et ålegræsbed dels et forlandsareal.

På vadefladerne på Jordsand Flak drives der jagt på ænder ved lavvande, og på forlandet ud for Ballum drives der trækjagt om aftenen. En del af det undersøgte ålegræsbed på Jordsand Flak er del af et vildtreservat med jagtforbud, og ligeledes er forlandet på Rømødæmningen (i umiddelbar forlængelse af Ballum Forland) jagtfredet. Det var således muligt at se på andefuglenes exploitation af ressourcerne i henholdsvis uforstyrrede og forstyrrede situationer.

På ålegræsvaden betød jagten, at ænder og gæs i dagtimerne på de fleste dage blev fortrængt til den jagtfredede del. Om natten og på de få dage, hvor der ikke blev drevet jagt, søgte fuglene føde i jagtzonen. Konsekvensen var imidlertid, at i den fredede zone blev ålegræsset hurtigt ædt op. På trods af at der stadig var en stor fødemængde tilbage i jagtzonen, fortrak alle pibeænder og de fleste (jagtfredede) knortegæs, sandsynligvis fordi de ikke kunne få dækket deres daglige energibehov. Da pibeænderne var fortrukket, ophørte jagten, og de resterende knortegæs græssede uforstyrret på vaden resten af efteråret.

I den jagtfredede zone på Rømødæmningens forland konsumerede svømmeænderne stort set al tilgængelig frøsætning (se side 12), og de fouragerede primært under højvande i dagtimerne. På Ballum Forland forblev frøressourcerne stort set uudnyttede, og kun sporadisk forekom der andeflokke. Da ænderne havde ædt frøsætningen på Rømødæmningen op, fortrak størstedelen af fuglene. Den resterende del søgte føde på arealer bag digerne, men kun om natten. Om dagen hvilede de på vaden ud for Rømødæmningen. Skiftet til natfouragering må anses for at være en tilpasning til og kompensation for, at der er for megen uro i baglandet i dagtimerne.

Konklusionen på undersøgelsen var, at uroen i forbindelse med jagten bevirkede, at svømmeænderne og størstedelen af knortegæssene måtte forlade området i utide, mens der stadig var føderessourcer til stede.

Uro skabt af naturlige predatorer. Forstyrrende effekter af naturlige predatorer på gåseflokke er sparsomt beskrevet. Madsen (1988) har givet et eksempel på, hvordan en duehøg *Accipiter gentilis* hun optrådte som forstyrrelseskilde. I løbet af en uge dræbte den mindst fire knortegæs ud af en flok på 800, der holdt til på et forland i Vadehavet. Gæssene var ekstremt nervøse, og de fortrak snart til en lokalitet, der normalt ikke huser gæs om foråret.

Tidevand

I tidevandsområder med betydelige tidevandsamplituder kan den daglige tidsperiode, hvor vegetationen på vaderne kan nås af andefuglene, være kritisk for, om fuglene kan nå at få dækket deres energibehov. I (4) er tilpasningen af fourageringen på ålegræsbanker i det sydlige Vadehav hos knortegæs og pibeænder beskrevet. Fuglene kunne nå ålegræsset fra ca. 3 1/2 time før til 3 1/2 time efter lavvande. I lavvandsperioder i dagtimerne fouragerede fuglene næsten uden ophold, og vha. af en lysforstærkende natkikkert blev det konstateret, at de også fouragerede intenst ved natligt lavvande. Natlig fouragering hos gæs er ellers kun bemærket i forbindelse med fuldmåne midt på vinteren (Ebbinge, Canters & Drent 1975, Ydenberg, Prins & Dijk 1984), men intensiteten er aldrig klarlagt. Mayhew (1988) har dokumenteret, at natfouragering har stor betydning for pibeænder, der fouragerer på græsarealer. Den intensive fouragering i lavvandsperioderne i Vadehavet er en tilpasning til tidevandsmiljøet. Estimater af daglig energioptagelse viste, at kun ved at udnytte natlige lavvandsperioder kunne det daglige energibudget balancere (4).

Sne- og isdække

Mid-vinter overvintringsområdet for gæs i Europa ligger generelt syd for 0°C januar-isothermen (Timmerman, Mörzer Bruyns & Philippona 1976), dog med undtagelse af sædgåsen og canadagåsen *Branta canadensis*, der også overvintrer nord for 0°C isothermen, sandsynligvis fordi de pga. deres størrelse er mere kuldetolerante end de mindre arter. I Nordamerika er der omvendt korrelation mellem kropsvægten af canadagæssene (fordelt på otte racer) og januar-isothermen i deres centrale vinterkvarter, hvilket afspejler deres fysiologiske kuldetolerance (Lefebvre & Raveling 1967).

Vinterudbredelsen vil naturligvis betinges af fødens tilgængelighed. Dækkes landjorden af sne og de lavvandede områder af is, umuliggøres gæssenes adgang til føderessoucerne. Eksempler på snedækkets indflydelse ses i Vestjylland, hvor de kortnæbbede gæs i milde vintre uden varsel må fortrække til de hollandske overvintringspladser pga. snefald. Efter få dages tøvejr ankommer flokkene igen sydfra (Madsen 1980). Tilsvarende er store forekomster af sædgæs i det sydøstlige Danmark korreleret med snedække af rastepladserne i Sydsverige (Madsen 1986, Jørgensen & Sørensen 1987).

Isdækket har primært betydning for knortegæssenes fourageringsmuligheder. I tilfælde af, at det sætter ind med hård frost, fryser Mariager Fjord, der er hovedrasteplads for Svalbardbestanden af lysbuget knortegås *Branta bernicla hrota*, hurtigt til. Gæssene fortrækker tværs over Nordsøen til Lindisfarne i det nordøstlige England. Forekomsten der er således korreleret med kuldesummen i Danmark (Madsen 1984b).

Stedtrofasthed

Gæs opfattes som værende meget traditionsbundne i deres valg af rastepladser. Eksempelvis foreligger der data for, at enkeltindivider og par af knortegæs opsøger de samme overvintrings- og forårsrastepladser år efter år, og endog det samme delområde inden for en lokalitet (St Joseph 1979, Prokosch 1984). Traditionen videreføres sandsynligvis gennem generationer, ved at juvenile gæs lærer trækveje og rastepladser af forældrefuglene (familien holder sammen gennem vinteren). Stedtrofasthed kan have den selektive fordel, at fuglen lærer områdets føderessourcer, predationsrisiko m.v. at kende, hvilket kan forøge dens intraspecifikke konkurrenceevne og i sidste ende dens fitness.

Udvikling af stedtrofasthed kan ses som en tilpasning til et relativ forudsigeligt fødegrundlag. Det kan påvirke gæssenes habitatudnyttelse på den måde, at stedtrofasthed giver mindre plasticitet og eksploratorisk evne til at opsøge alternative habitater. Gæssenes strategi står i modsætning til f.eks. granivore svømmeænders, der er særdeles eksploratorisk, tilpasset en temporær, fluktuerende fødekilde.

At gæs imidlertid i en vis udstrækning er eksploratoriske vises bl.a.

af, hvordan de kortnæbbede gæs, der raster i Vestjylland om foråret, har skiftet fødevaner og ekspanderet i udbredelse. I løbet af 1980'erne har bestanden i stigende grad forladt strandenge og kulturgræsarealer til fordel for nysåede kornmarker, hvor de tager kerner i overfladen. I 1970'erne foregik fouragering på nysåede marker stort set kun omkring Vest Stadil Fjord, men i løbet af få år bredte fænomenet sig til næsten alle vestjyske rastepladser (Madsen 1984a). I dag opsøger gåseflokkene nysåede marker langt fra de traditionelle rastepladser (Madsen upubl.).

Diskussion

Der er belæg for, at forskelle i fødekvalitet kan udløse skift i mikrohabitat eller mellem to nærliggende habitater. Der er imidlertid behov for bedre dokumentation for hypotesen om, at gæssenes trinvise, nordgående forårstræk er en tilpasning til plantefænologien. En række undersøgelser har vist, at der eksisterer et alternativ til denne strategi, nemlig at gæssene opnår den samme effekt ved gentagen afgræsning af vegetationen inden for et område (se side 11). En årsag til, at specielt knortegæssene benytter sig af sidstnævnte strategi kan imidlertid være den enkle, at de ikke har flere velegnede rastepladser længere nordpå imod ynglepladserne end Vadehavet og de danske strandenge.

Progressionen i trækket, og specielt det sydgående, kan imidlertid ikke forklares alene ud fra forskelle i plantefænologi. Som vist er der situationer, hvor gåseflokke udøver et højt græsningstryk på vegetationen, og tilsvarende at svømmeænder kan konsumere en stor del af frøsætningen (se også van Eerden 1984). Exploitationsraterne fundet i ålegræsbedet i Vadehavet (4) er højere end rapporteret fra andre undersøgelser (se Thayer et al. 1984), hvorimod afgræsningen af annelgræs på marsken (5) ligner exploitationsraterne fundet i det hollandske vadehav (Prop & Loonen 1989). Dokumentationen efterlader det indtryk, at det ikke er usædvanligt, at gæs og svømmeænder nedgræsser deres fødereressourcer, og at fødemangel kan være en af mekanismerne, der driver flokkene afsted langs trækruten.

Hvorfor bevæger gæssene sig gradvist mod syd, fremfor at fordele sig ud over hele overvintringsområdet straks efter ankomsten fra ynglepladserne?

En mulig forklaring kan være, at der er en gradient i profitabilitet ved fouragering fra nord mod syd. Sydtrækket udløses af, at den relative værdi af de sydlige områder stiger som følge af gradvis nedgræsning af de nordlige områder. Områderne fyldes op svarende til en "ideal free distribution" (Fretwell 1972). Hos de kortnæbbede gæs, der først fouragerer på spildsæd i Danmark og derpå trækker til Holland og Belgien, hvor de fouragerer på græs, er hypotesen plausibel, men for de mørkbugede knortegæs, hvor der ikke er nogen åbenlys forskel i fødekvalitet, er den ikke.

En anden forklaring kan være, at flokkene forsøger at trække den kortest mulige strækning. Den selektive fordel heraf kan være, at individerne (a) minimerer trækafstanden og derved sparer energi, og (b) bedre kan respondere på variation i vejrforhold og hurtigere returnere til ynglepladserne (se Pienkowski & Evans 1985). Hvis vi antager, at ressourcerne på rastepladserne er begrænsende, vil en delvis test af denne hypotese kunne leveres ved gennemgang af historiske data for, om gæssene som følge af bestandsstigning har bevæget sig hurtigere mod syd og evt. har taget nye, sydligere områder i brug. Specielt den mørkbugede knortegås skulle være velegnet for analyse, idet dens habitatvalg –

som en af de eneste gåsearter – om efteråret stort set har været uforandret siden 1960-erne, og den udnytter den samme fødeplante, ålegræs, fra nord til syd i overvintringsområdet. Fra begyndelsen af 1970-erne til midten af 1980-erne er bestanden næsten fem-doblet. I 1970-erne kulminerede antallet af knortegæs på den franske atlanterhavskyst, der er det sydligste overvintringsområde, i december-januar (Maheo 1979), mens det i 1980-erne kulminerede en måned før (3). Der er således en vis støtte for hypotesen, men der bør foretages en nøjere granskning af data, før vi kan rede trådene ordenligt ud.

Begrænsede ressourcer og stigende gåsebestande øger mulighederne for interspecifik konkurrence, og eksemplerne indikerer, at den kan være en lokal, betydningsfuld faktor for fuglenes fordeling og fænologi. Mekanismen ser primært ud til at være, at der opstår fødeknaphed på et tidligere stadium, end hvis arterne havde været segregerede. Der er ikke belæg for, at interspecifik konkurrence i øjeblikket har nogen større betydning for den overordnede, geografiske fordeling af arterne. Konkurrencen kan imidlertid forventes at få stigende betydning, ikke blot på trækruten, men også på ynglepladserne, f.eks. på de nordatlantiske øer, hvor der er begrænset plads. På Svalbard er der fundet tegn på, at lysbugede knortegæs er kommet i konkurrence med bramgæs, der som følge af en betydelig bestandsstigning har ekspanderet til førstnævntes yngleområde (Madsen, Bregnballe & Mehlum 1989). Der er iagttaget interferens-konkurrence om redepladser, høj exploitationsrate af de foretrukne fødeplanter og et stort overlap i fødevalg (potentiel exploitativ konkurrence). Det er dog endnu uvist, hvor kritisk konkurrencen er for arternes yngleresultat.

Menneskeskabte forstyrrelser medvirker til koncentrering af fuglene og accentuerer nedgræsningen af ressourcerne. Ganske vist kan fuglene til en vis grad kompensere ved at fouragere på andre fødekilder, fouragere på tidspunkter, hvor forstyrrelsen er minimal, eller habituere til forstyrrelser, men i de viste eksempler har forstyrrelsen været at sammenligne med tab af habitat. Eksemplet i (4) antyder, at fødemangel er drivkraften bag trækket, men at den jagtlige forstyrrelse – og den interspecifikke konkurrence "skubber på".

Som det er fremgået af ovenstående er der en række komponenter, hvis kvalitative og kvantitative betydning skal vægtes i en analyse af gåseflokkes træk- og overvintringsstrategi samt udvælgelse af habitat. Det står klart, at det oftest vil være umuligt på basis af en enkelt faktor at fremkomme med en ligefrem forklaring på observerede fordelings- og trækmønstre.

Der er således behov for en bredere model til forklaring af mekanismerne bag gæssenes træk- og habitatskift end de tidligere fremsatte. Det er sandsynliggjort, at udvælgelsen af habitat ikke sker alene på basis af profitabilitet ved fouragering, men at der også indgår andre fitness-komponenter såsom risikoen for at blive prederet samt andre aktiviteter med fitness-værdi end fødesøgning såsom hvile. Risikoen for at blive prederet kan bevirke, at fuglene undgår visse områder, eller at de fouragerer på kortest mulige tid for at kunne tilbringe den resterende tid på et sikkert hvilested med mindre risiko for predation end på fourageringspladsen (især relevant i fældningssituationen).

Denne generelle model inkorporerer således profitabilitet ved fouragering, predationsrisiko, effekt af fødekonkurrenter og en etologisk faktor, der sammenfatter gæssenes sociabilitet og stedtrofasthed, og som reducerer deres fleksibilitet.

Dette forslag er i tråd med en udvidet teori om optimal fourageringsstrategi (Brown 1988), hvori det fremsættes, at i et fouragerende dyrs udvælgelse af habitat indgår en afvejning mellem de fordele, det kan få ved energigevinst, og de omkostninger, der følger af predationsrisiko og fødekonkurrence med andre arter. Brown (1988) foreslår, at måleenheden i denne cost-benefit analyse er den fødetæthed, hvorved det fouragerende dyr opgiver en habitat i forhold til andre ("giving up densities"). Dette mål vil kunne give fingerpeg om styrken af de forskellige komponenter. Med henblik på at få en mere detaljeret beskrivelse af energetikken ved fouragering på forskellige tætheder af ressourcer og fastlæggelse af tærsklen for, hvornår det ikke længere er profitabelt at fouragere, vil det imidlertid også være hensigtsmæssigt at holde fast i måling af netto-energiindtaget som supplement.

Anvendeligheden af modellen i felten forudsætter, at styrken af enkeltkomponenterne kan afprøves i forhold til hinanden, og at "giving up densities" kan måles i forskellige habitater. Eksemplet fra Vadehavet (4) viser, at denne indgangsvinkel er farbar på lokalt niveau. Skal hypotesen eftervises på stor skala, kræver det, at vi kan rangere habitater og "perlekæden" af rastepladser på en relativ skala baseret på egnethed, udledt af cost-benefits ved at befinde sig på et givent sted i forhold til andre, og at omkostninger ved trækket mellem områder kan estimeres. Som det er fremgået af eksemplerne er det mål langtfra nået i praksis. For at nå dertil kræves større internationale samarbejdsprojekter, der inkluderer analyser af fødegrundlaget, exploitationsrater, energiindtag, muligheder for at opsøge alternative fødekilder, samt mulighed for at eksperimentere med forskellig predationsrisiko (f.eks. ved at påføre forstyrrelser). Et vigtigt bidrag vil være at arbejde på individniveau (der foregår med stor succes individuel mærkning af gæs i mange gåsebestande i Europa). Med denne støtte kan der inden for flokkene analyseres for variation i forskellige sociale gruppers fitness ved et bestemt habitatvalg. Med denne vinkel vil der endvidere være bygget en bro til belysning af habitatvalgets konsekvenser for populationsdynamikken.

En supplerende vej at gå er en analyse af historisk udvikling i trækruter og habitatudnyttelse, en mulighed der er udnyttet alt for sjældent. Der er givet flere eksempler i nærværende artikel. Fordelen ved denne indgangsvinkel er, at vi kan få fingerpeg om styrkeforhold mellem komponenterne på stor skala. Problemet er naturligvis testbarheden, idet de historiske data vil kunne levere korrelationer, mens mekanismer og årsagssammenhænge ikke kan udledes med sikkerhed.

Betydning for forvaltning

Inden for landene i Europa, der rummer overvintringsområder for gæs, har forvaltningen af bestandene og deres levesteder været koncentreret om to aspekter: regulering af jagttider som led i beskyttelsen af bestandene og afværgning af skader forvoldt af gæs på landbrugsafgrøder. Forskellige generelle tiltag i retning af biotopsikring (Ramsar-konventionen, EF-fuglebeskyttelsesdirektivet, forskellige bestemmelser i nationale naturfredningslove) er også kommet gæssenes habitater til gode, men der er relativt få tiltag, der specifikt er gjort for at sikre gæssenes habitater.

De fleste forvaltningsmæssige tiltag har været nationale, og der er kun få eksempler på, at der er lavet internationale aftaler om forvaltning af bestandene og deres habitater (f.eks. anbefaling af jagtfredning af knortegæssene). Med EF-fuglebeskyttelsesdirektivet og Bonn-konventionen er der skabt visse lovgivningsmæssige rammer for international intervention.

Generelt er gåsebestandes status tilfredsstillende, men alligevel er de under konstant pres fra det menneskelige samfunds side, specielt i vinterhalvåret, men også i stigende grad i sommertiden (Madsen 1984c). Der er derfor stort behov for langsigtede strategier for forvaltning på en fly-way basis.

Et nødvendigt grundlag for international forvaltning er kendskab til bestandenes geografiske afgrænsning og trækveje (fly-way), deres status, populationsdynamik og økologi samt enkeltlandenes forvaltning af bestandene inden for en fly-way. I (3) er en sådan opdateret dokumentation leveret for fem gåsebestande, der passerer gennem Danmark. Gæssene er velegnede som model-populationer i international forvaltning, fordi 1) bestandene er forholdsvis veldefinerede, 2) bestandsniveau og ynglesucces moniteres årligt for de fleste bestandes vedkommende, og 3) de er økonomisk og rekreativt betydningsfulde og giver forvaltningsmæssige problemer i flere lande.

Den mørkbugede knortegås er et eksempel på en bestand, hvor der er behov for en international forvaltningsplan (3). Siden jagtfredningen af knortegåsen i Danmark i 1972 er bestanden steget fra 40.000 til 235.000 i 1988. Knortegåsen er en af de få arter, der i overvintringsområdet stadig udnytter de naturlige habitater (fladvand, vader, saltmarsk). Bæreevnen af disse habitater er, som det er fremgået ovenfor, tæt på at være nået, og med bestandstilvæksten er gæssene i stigende omfang flyttet over på kulturprægede habitater. Især i England, Holland og Vesttyskland er der opstået problemer, fordi fuglene gør skade på afgrøder eller nedgræsser vegetationen før udsætning af kreaturer eller får. Fra jægerside i Danmark, England og Frankrig er der ønske om at genåbne jagten på bestanden (principielle, internationale aspekter vedrørende dette er diskuteret i (3)).

Spørgsmålet om jagttid og problemerne med knortegæssenes fouragering på dyrkede arealer er forvaltningsmæssigt forbundne. Som demonstreret i (4) kan jagt på ænder på vaderne også have en forstyrrende effekt på knortegæssene. Hvis der indføres jagt på knortegæs i Danmark, hvor gæssene næsten udelukkende udnytter naturlige og seminaturlige habitater (8), vil det sandsynligvis få den utilsigtede effekt, at der sker en reduktion af bærekapaciteten for den naturlige habitat, idet gæssene fordrives mod syd i retning af overvintringskvarteret, med øgede markskadeproblemer som konsekvens. Et tilsvarende eksempel er observeret med kortnæbbede gæs på den dansk-hollandske trækrute (3).

Eksemplerne godtgør, at der er et behov for en international, integreret biologisk og naturpolitisk strategi for forvaltning, der bør tage et overordnet, helhedsorienteret udgangspunkt i bestandenes populationsdynamik, specifikke habitatkrav og følsomhed overfor påførte miljøforandringer, inklusive jagt.

Referencer

Alatalo, R.V. & Moreno, J. 1987. Body size, interspecific interactions, and use of foraging sites in tits (*Paridae*). - Ecology 68: 1773-1777.

Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. - Auk 95:459-471.

Balkenkol, B., Bergmann, H.-H., Holländer, R. & Stock, M. 1984. On the impact of wild goose faeces on meadow vegetation. - Ecol. Birds 6: 223-247.

Bazely, D.R. & Jefferies, R.L. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. - J. Appl. Ecol. 22: 693-703.

Bertram, B.C.R. 1978. Living in groups: predators and prey. I: Krebs, J.R. & Davies, N.B. (red.) Behavioural Ecology - an evolutionary approach. Blackwell Sci. Press., Oxford, pp. 64-96.

Black, J.M. & Owen, M. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. - Anim. Behav. 37: 199-209.

Boudewijn, T. 1984. The role of digestibility in the selection of spring feeding sites by Brent Geese. - Wildfowl 35: 97-105.

Boyd, H. 1953. On encounters between wild Whitefronted Geese in winter flocks. - Behaviour 5: 85-129.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. - Behav. Ecol. Sociobiol. 22: 37-47.

Buchsbaum, R., Valiela, I. & Swain, T. 1984. The role of phenolic compounds and other plant constituents in feeding by Canada geese in a coastal marsh. - Oecologia 63: 343-349.

Buchsbaum, R., Wilson, J. & Valiela, I. 1986. Digestibility of plant constituents by Canada Geese and Atlantic Brant. - Ecology 67: 386-393.

Cargill, S.M. & Jefferies, R.L. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. - J. Appl. Ecol. 21: 669-686.

Charnov, E.L. 1976. Optimal foraging, the marginal theorem. - Theor. Pop. Biol. 9: 129-136.

Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. - Amer. Sci. 66: 322-331.

Drent, R.H., Ebbinge, B. & Weijand, B. 1979. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. orn. Ges. Bayern 23: 239-264.

Drent, R. & Swierstra, P. 1977. Goose flocks and food finding: field experiments with Barnacle Geese in winter. - Wildfowl 28: 15-20.

Eerden, M.R. van 1984. Waterfowl movements in relation to food stocks. I: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (red.) Coastal waders and wildfowl in winter. - Cambridge Univ. Press, pp. 84-100.

Ebbinge, B. 1979. The significance of the Dutch part of the Wadden Sea for *Branta bernicla bernicla*. Pp. 77-87 in: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge.

Ebbinge, B. 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. - Ibis 131: 196-204.

Ebbinge, B. & Boudewijn, T. 1984. Richtlijnen voor het beheer van rotganzen in het Nederlandse waddengebied. - RIN-rapport 84/4, Rijsinst. voor Natuurbeheer, Leersum. 76 pp.

Ebbinge, B., Canters, K. & Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl 26: 5-19.

Ebbinge, B., St Joseph, A., Prokosch, P. & Spaans, B. 1982. The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. - Aquila 89: 249-258.

Fox, A.D. & Madsen, J. 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. Wildfowl 32: 48-54.

Fox, A.D., Madsen, J. & Stroud, D.A. 1983. A review of the summer ecology of the Greenland White-fronted Goose *Anser albifrons flavirostris*. Dansk Orn. Foren. Tidsskr. 77: 43-55.

Fretwell, S.D. 1972. Populations in a seasonal environment. - Princeton Univ. Press, Princeton.

Grubb, T.C. & Greenwald, L. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. - Anim. Behav. 30: 637-640.

Jørgensen, H.E. & Sørensen, B.M. 1987. Gåsetællinger i sydøstlige Danmark. - Fugle 1987,4: 14-15.

Kotanen, P. & Jefferies, R.L. 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. - J. Ecol. 75: 961-975.

Kuijken, E. & Meire, P.M. 1987. Wintering geese in Belgium: a lesson of protection. - De Levende Natuur 88: 213-215.

Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of Bar-headed Geese *(Anser indicus)*. - Behaviour 96: 28-48.

Lefebvre, E.A. & Raveling, D.G. 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. - J. Wildl. Manage. 31: 538-546.

Lorenzen, B. & Madsen, J. 1985. Gåsebestandene på Tipperhalvøen. II: Græsningsøkologi i relation til områdets bæreevne. - Dansk Orn. Foren. Tidsskr. 79: 113-132.

Lorenzen, B. & Madsen, J. 1986. Feeding by geese on the Filsø farmland, Denmark, and the effect of grazing on yield structure of spring barley. - Holarc. Ecol. 9: 305-311.

Madsen, J. 1980. Forekomst, habitatvalg og overnatning hos Kortnæbbet Gås *Anser brachyrhynchus* på Tipperne 1972-1978. - Dansk Orn. Foren. Tidsskr. 74: 45-58.

Madsen, J. 1982. Observations on the Svalbard population of *Anser brachyrhynchus* in Denmark: (a) numbers, distribution and breeding success 1980/81 and (b) Population trends 1931-1980. - Aquila **89:** 133-140.

Madsen, J. 1984a. Numbers, distribution, and habitat selection of Pink-footed Geese *Anser brachyrhynchus* in Denmark 1980-1983. - Nor. Polarinst. Skr. **181:** 19-23.

Madsen, J. 1984b. Status of the Svalbard population of Light-bellied Brent Geese *Branta bernicla hrota* wintering in Denmark 1980-1983. - Nor. Polarinst. Skr. **181:** 119-124.

Madsen, J. 1984c. Study of the possible impact of oil exploration on goose populations in Jameson Land, East Greenland. A progress report. - Nor. Polarinst. Skr. **181:** 141-151.

Madsen, J. 1985a. Gåsebestandene på Tipperhalvøen. I: Forekomst og udvikling 1929-1983. - Dansk Orn. Foren. Tidsskr. **79:** 19-28.

Madsen, J. 1985b. Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. - Ornis Scand. **16:** 140-144.

Madsen, J. 1986. Danske rastepladser for gæs. Miljøministeriet, Fredningsstyrelsen, 114 pp.

Madsen, J. 1988. Duehøg *Accipiter gentilis* forstyrrer og dræber Knortegæs *Branta bernicla* ved specialiseret jagtteknik. - Dansk Orn. Foren. Tidsskr. **82:** 57-58.

Madsen, J. in press. Status and trends of goose populations in the Western Palearctic in the 1980s. Ardea.

Madsen, J., Bregnballe, T. & Mehlum, F. 1989. Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. - Polar Research **7:** 1-21.

Madsen, J. & Fox, A.D. 1981. The summer diet of the Greenland White-fronted Goose. I: Fox, A.D. & Stroud, D.A. (red.) Report on the 1979 Greenland White-fronted Goose Study Expedition to Eqalungmiut Nunaat, west Greenland. - Aberystwyth, pp. 108-115.

Maheo, R. 1979. Conflicts between *Branta bernicla* and agriculture in France. In: Smart, M. (red.) Proceedings, First Techn. Meeting West. Palearc. Migr. Bird Manage. - IWRB, Slimbridge, pp. 146-151.

Mattocks, J.G. 1971. Goose feeding and cellulose digestion. - Wildfowl **22:** 107-113.

Mayhew, P.W. 1988. The daily energy intake of European Wigeon in winter. - Ornis Scand. 217-223.

Meire, P.M., Kuijken, E. & Devos, K. 1988. Numbers and distribution of White-fronted and Pink-footed Geese in Flanders (Belgium), 1981-87 in a North West European context. - Wildfowl **39:** 71-81.

Mooij, J.H. 1982. Die Auswirkungen von Strassen auf die Avifauna einer offenen Landschaft am Unteren Niederrhein (Nordrhein-Westfalen), untersucht am Verhalten von Wildgänsen. - Charadrius **18:** 73-92.

Nehring, K. & Nerge, I. 1966. Die Verdaulichkeit verschiedener Futterstoffe bei Gänsen. - Arch. Geflügelzucht Kleintierk. **15:** 3-21.

Owen, M. 1972. Movements and feeding ecology of white-fronted geese at the New Grounds, Slimbridge. - J. Appl. Ecol. **9:** 385-398.

Owen, M. 1973. The management of grassland areas for wintering geese. - Wildfowl **24:** 123-130.

Owen, M. 1976. Factors affecting the distribution of geese in the British Isles. - Wildfowl **27:** 143-147.

Owen, M. 1979. Food selection in geese. - Verh. orn. Ges. Bayern **23:** 169-176.

Owen, M. & Gullestad, N. 1984. Migration routes of Svalbard Barnacle Geese *Branta leucopsis* with a preliminary report on the importance of the Bjørnøya staging area. - Nor. Polarinst. Skr. **181:** 67-77.

Owen, M., Nugent, M. & Davies, N. 1977. Discrimination between grass species and nitrogen-fertilized vegetation by young Barnacle Geese. - Wildfowl **28:** 21-26.

Owen, M. & Ogilvie, M. 1979. Wing molt and weight of Barnacle Geese in Spitsbergen. - Condor **81:** 42-52.

Owens, N.W. 1977. Responses of wintering Brent Geese to human disturbance. - Wildfowl **28:** 5-14.

Partridge, L. 1978. Habitat selection. I: Krebs, J.R. & Davies, N.B. (red.) Behavioural ecology, an evolutionary approach. - Sinauer, pp. 351-376.

Pienkowski, M.W. & Evans, P.R. 1985. The role of migration in the population dynamics of birds. In: Sibly, R.M. & Smith, R.H. (red.) Behavioural Ecology. Ecological consequences of adaptive behaviour. - Blackwell Sci. Publ., pp. 331-352.

Pimm, S.L., Rosenzweig, M.L. & Mitchell, W. 1985. Competition and food selection: field tests of a theory. - Ecology **66:** 798-807.

Prins, H.H.T., Ydenberg, R.C. & Drent, R.H. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. - Acta Bot. Neërlandica **29:** 585-596.

Prokosch, P. 1984. Population, annual cycle and traditional relationships to feeding areas of the Dark-bellied Brent Goose *(Branta b. bernicla* L. 1758) in the Northfrisian Waddensea - Ecol. Birds **6:** 1-99. (tysk, engelsk resumé).

Prop, J., Eerden, M.R. van & Drent, R.H. 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. - Nor. Polarinst. Skr. **181:** 87-117.

Prop, J. & Loonen, M. 1989. Goose flocks and food exploitation: the importance of being first. - Acta XIX Congr. Int. Ornith.: 1878-1887.

Rosenzweig, M.L. 1979. Optimal habitat selection in two-species competitive systems. - Fortschr. der Zool. **25:** 283-293.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great

Tit (*Parus major*, L.). – J. Anim. Ecol. 39: 619-668.

Rüger, A. (red.) 1985. Extent and control of goose damage to agricultural crops. – IWRB Special Publ. No. 5, Slimbridge, 48 pp.

St Joseph, A.K.M. 1979. The seasonal distribution and movements of *Branta bernicla* in Western Europe. I: Smart, M. (red.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. IWRB, Slimbridge, pp. 45-59.

Thayer, G.W., Bjorndal, K.A., Ogden, J.C., Williams, S.L. & Zieman, J.C. 1984. Role of larger herbivores in seagrass communities. – Estuaries 7: 351-376.

Teunissen, W., Spaans, B. & Drent, R. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. – Ardea 73: 109-119.

Thomas, V.G. 1983. Spring migration: the prelude to goose reproduction and a review of its implications. Pp. 73-81 in: Boyd, H. (ed.) First Western Hemisphere waterfowl and waterbird symp. Can. Wildl. Serv., Ottawa.

Timmerman, A., Mörzer Bruyns, M.F. & Philippona, J. 1976. Survey of the winter distribution of palearctic geese in Europe, Western Asia and North Africa. – Limosa 49: 230-292.

Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Ydenberg, R.C. & Prins, H.H.T. 1981. Spring grazing and the manipulation of food quality by Barnacle Geese. – J. Appl. Ecol. 18: 443-353.

Ydenberg, R.C., Prins, H.H.T. & Dijk, J. van 1984. A lunar rhythm in the nocturnal foraging activities of wintering Barnacle Geese. – Wildfowl 35: 93-96.

Yesou, P. in press. Present status of grey geese *Anser* in France. – Ardea.

1

ORNIS SCANDINAVICA 16: 222–228. Copenhagen 1985

Relations between change in spring habitat selection and daily energetics of Pink-footed Geese Anser brachyrhynchus

Jesper Madsen

Madsen, J. 1985. Relations between change in spring habitat selection and daily energetics of Pink-footed Geese *Anser brachyrhynchus*. – Ornis Scand. 16: 222–228.

During the month prior to spring departure to the breeding grounds the Svalbard population of Pink-footed Geese staging in west Jutland, Denmark shifts from pasture to grain feeding on newly sown fields. This paper compares the daily energy expenditure and net energy intake in the two habitats.
On pastures the geese spent 80% of the feeding day feeding vs 54% on newly sown barley fields, but due to more frequent disturbance flights in the latter habitat, the estimated daily energy expenditure on pastures was lower (1088 kJ vs 1280 kJ). Daily food intake on pastures was estimated at 158.5 g organic matter and on newly sown fields at 229.8 g organic matter, equivalent to a daily net energy intake of 1267 kJ and 2824 kJ, respectively. The net energy intake per peck during a feeding bout was 14 J on pastures and 219 J on newly sown fields.
Thus, from an energetic point of view, feeding on newly sown fields was advantageous compared with feeding on pastures, and the observed habitat shift can be seen as a choice of the most profitable food source. The grain provides sufficient carbohydrates to build up fat reserves for later reproduction, but not sufficient protein.

J. Madsen, Zoological Laboratory, Inst. of Zoology and Zoophysiology, Univ. of Aarhus, Universitetsparken, BIO III, DK-8000 Aarhus C, Denmark. Present address: Game Biology Station, Kalø, DK-8410 Rønde, Denmark.

1. Introduction

The Svalbard population of Pink-footed Geese *Anser brachyrhynchus* wintering in Denmark, the Netherlands and Belgium is concentrated in west Jutland, Denmark from early April to mid May. Formerly, i.e. 30 years ago, the Pinkfeet fed on grasslands throughout spring. Concurrently with changes in farming practises, however, the geese have changed feeding habits, and nowadays newly sown fields have become the most preferred spring habitat. In early spring feeding mainly takes place on pastures, but as soon as sowing of spring cereals commences in west Jutland (usually in early April) the population progressively shifts to the newly sown fields, and from mid April to mid May the majority of the population feed on grain in these fields (Madsen 1984).

The aim of this paper is to compare the daily energy balance of Pinkfeet feeding on two different food sources, pastures and newly sown barley fields, and to examine whether the observed habitat shift can be explained in terms of choice of the most profitable food source. Recent investigations have pointed out the relationship between the accumulation of nutrient reserves (mainly fat and protein) in arctic nesting geese on their spring staging areas and the subsequent breeding success (Ankney 1977, Ankney and MacInnes 1978, Ebbinge et al. 1982); in this paper the potential for accumulation of reserves in the two habitats is discussed.

2. Material and methods

2.1. Study areas

2.1.1. The Tipper peninsula

The area is a grassland and marsh area in Ringkøbing Fjord (55°53'N, 08°13'E), divided in Tipperne (a 450 ha reserve) and Værnengene (600 ha). The area is a tradi-

Accepted 5 February 1985

tional wintering and spring feeding area for up to 4000 Pinkfeet (Madsen 1980). Værnengene, where this study was undertaken, are fertilized pastures whereas Tipperne consist of unfertilized fresh-water meadows. Both areas are cattle-grazed from mid May to mid October. Faecal analysis has revealed that the diet of the Pinkfeet on Værnengene consists of ca. 60% *Alopecurus geniculatus*, 30% *Poa pratensis*, 5% *Agrostris* spp., and 5% other grasses. The geese only graze on green leaves (Lorenzen and Madsen, in press). At night they roost on the surrounding shallow waters.

2.1.2. Filsö

The area is arable land (1300 ha) (55°42′N, 08°13′E) on which spring barley and winter cereals (wheat and rye) are grown. The area is visited by geese in autumn and spring; in the latter season 3000–5000 Pinkfeet are usually seen. After sowing, which takes place from late March (in early years) to the end of April, the geese almost exclusively feed on the newly sown barley fields, where they pick up grain from the soil surface or just beneath it. The geese only visit the fields in the period between sowing and the commencement of germination (up to two weeks after sowing). At night the geese roost on the lake Filsø just north of the fields.

2.2. Field work

The study was undertaken from late March to mid April in 1982 and 1983. During this period goose flocks visit both areas and the accumulation of body reserves has not yet begun. A narrow time interval was necessary, and it was assumed that food demands of the geese in the two habitats were equal (later in spring food demands will change rapidly and might vary with age and social status).

2.3. Energy expenditure

During three days in each habitat a flock of geese (200–800 inds) was kept under observation from the morning departure from the roost until the return flight in the evening. Every 10 min the number of geese engaged in different activities was recorded (following the method of Altmann 1974). Observations were carried out from a car with a telescope (20–45x). Observations were only made during periods when feeding was restricted to daylight hours, i.e. during the dark moon phase or when the sky was overcast. Pecking rates and walking speeds during uninterrupted feeding bouts were timed on a stop watch as the time it took to make 25 pecks and 25 paces, respectively.

2.4. Net energy intake

Estimates of daily food intake were obtained using the marker substance method developed on Red Grouse *Lagopus lagopus scoticus* (Moss and Parkinson 1972) and geese (Ebbinge et al. 1975, Drent et al. 1978/79). In principle the method utilizes the fact that certain food components, which are not digested during gut passage, will be concentrated in the droppings compared with the original food composition:

$$\% \text{ retention} = \left(1 - \frac{\text{konc. of marker in food}}{\text{konc. of marker in droppings}}\right) 100.$$

Drent et al. (1978/79) mention a series of applicable markers. In this study, four different substances were used: neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin, and ash.

For analysis, samples of fresh leaves of grasses from Værnengene were clipped. The species were collected in the same proprotions as they were found in the diet of the geese. Samples of barley grain were taken on the newly sown fields. Fresh droppings were collected in both habitats from sites where the geese were known to have grazed all day. All analyses were done in duplicate.

In order to calculate daily food intake from retention rates, the daily production of droppings was estimated. Geese produce droppings from the time of arrival on the feeding grounds (minus the throughput time) to the depature to the roost where defaecation continues for some time. In both habitats the geese remained on the feeding grounds throughout the day. Throughput time was recorded by watching the abdomen of geese from the arrival in the morning until the first defaecation was observed. Defaecation rate during the day was measured by recording the number of droppings produced by a single goose during an observation period (time was measured on a stop watch). As soon as the goose moved out of sight the observation was stopped. Observations were carried out on more than 100 inds and were evenly distributed over the day.

The number of droppings produced on the roost could not be determined, but Ebbinge et al. (1975) estimated this parameter for wintering Barnacle Geese *Branta leucopsis* in the Netherlands. The ratio between the number of droppings produced during daytime and that produced on the roost was assumed to be equal for the two species (for Barnacle Goose 135:25); from this ratio the nightly defaecation of the Pinkfeet can be calculated when daytime defaecation is known.

The energetic value of the net food intake was calculated from energy contents of pellets of food and droppings (measured with a Gallenkamp bomb calorimeter). All analyses were carried out in duplicate.

2.6. Abdominal profiles

No data have been published on spring weights of Pinkfeet, but Owen (1981) developed a condition index for

Tab. 1. Daily time budgets of Pink-footed Geese on pastures and newly sown barley fields.

Habitat	Date	Time away from roost (min)	Time expenditure (%)				
			Feeding	Walking	Roosting	Alert	Flight
Pastures	27 Mar 1983	816	85.1	2.2	9.6	2.5	0.6
	6 Apr 1982	874	79.8	3.1	12.9	3.2	1.0
	16 Apr 1982	854	75.1	2.4	16.9	2.6	3.1
	Mean	848	80.0	2.6	13.1	2.8	1.6
Newly sown barley fields	27 Mar 1982	768	53.1	3.2	34.7	3.3	5.7
	12 Apr 1983	869	54.6	4.0	34.7	1.5	5.2
	18 Apr 1983	882	55.0	3.0	27.1	4.1	10.8
	Mean	840	54.2	3.4	32.2	3.0	7.2

Barnacle Geese. Thus, the abdominal profiles were correlated with body weights, and a similar index ranging from 1 to 4 (expressing increasing abdominal hanging; see definitions in Owen 1981) was used in this study. As individual birds could not be recognized, average indices of flocks of at least 50 birds were used.

3. Results

3.1. Time and energy expenditure

On the pastures the geese spent on average 80% of the daytime feeding whilst they spent only 54% on the newly sown barley fields (Tab. 1). In both habitats feeding activity varied during the day, with peak activity during morning and evening (Fig. 1). Fruzinski (1977) observed the feeding activity of Pinkfeet in spring in two similar habitat types and found a comparable rhythm. The geese on the newly sown fields spent more time roosting; on the pastures only few individuals were roosting at a time, whereas on the newly sown fields the entire flock often roosted simultaneously (on one occasion they did so for more than one hour). The roosting periods on the newly sown fields usually followed a disturbance and subsequent flight. The farmer at Filsö tried various means to scare the goose flocks away from the fields, and as a result the geese were shyer there than on the pastures at Tipperne. This was reflected by their spending more time in flight compared with those on the pastures. During flight to the feeding grounds in the morning the geese at Filsö spent more time flying around compared with the geese on Værnengene, which was probably also related to their increased wariness.

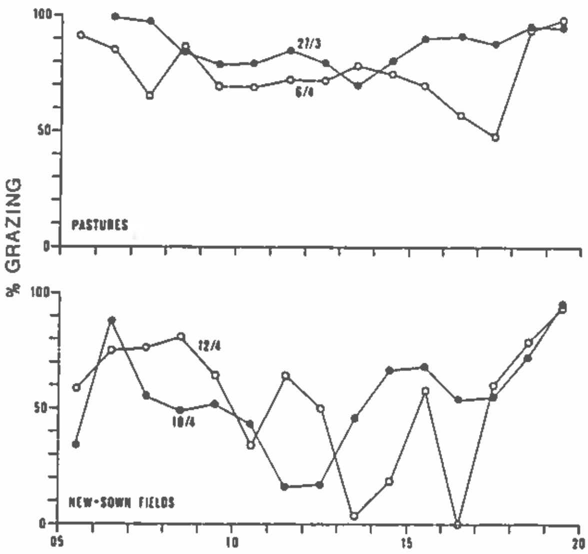


Fig. 1. Grazing activity during daytime (local time) on pastures and newly sown fields. Two examples from each habitat are shown.

Conversion of daily time budgets to daily energy expenditure is shown in Tab. 2. Calculation of basal metabolic rate (BMR) was done using a mean body weight of 2.5 kg (an average of autumn weights (2.6 kg, M. Fog pers. comm.) and winter weights (2.4 kg, Cramp and Simmons 1977). Judged from the abdominal profiles in spring (Fig. 2) the present study took place before the geese put on weight, and therefore it seems reasonable to use the mean of their autumn and winter weights. In Tab. 2 daily energy expenditures of a 2.4 and a 2.6 kg goose are also given. BMR was calculated from the equation for the relationship between body weight and BMR in Aschoff and Pohl (1970). The costs of different activities were taken from studies of Wooley and Owen (1978) and Tucker (1969) (flight). The daily energy expenditures were calculated for the entire 24 h cycle, and it was assumed that the geese roosted all night.

In short, the flocks on the newly sown fields had a higher energy expenditure than the flocks on the pastures, despite a shorter feeding time and more roosting. The increased time spent in flight significantly contributed to this.

Tab. 2. Estimates of daily energy expenditure of an average Pink-footed Goose (2.5 kg) on pastures and newly sown barley fields. Values for time budgets are means of three days, and it is assumed that the geese roost throughout the night.

Activity	Cost of activity[1] (multiple of BMR)	Pastures		Newly sown fields	
		Time budget ($min\ 24\ h^{-1}$)	Energy consumed (kJ)	Time budget ($min\ 24\ h^{-1}$)	Energy consumed (kJ)
Feeding	1.7	678	575	455	386
Walking	1.7	22	19	29	25
Roosting	1.1	702	385	870	478
Alertness	2.1	24	25	25	26
Flight	12.0	14	84	61	365
Daily energy expenditure (kJ)			1088 (1039–1104)[2]		1280 (1222–1297)[2]

1. Sources: Wooley & Owen (1978) and Tucker (1969).
2. Ranges for weights of 2.4 kg and 2.6 kg, respectively.

3.2. Food and net energy intake

The daily defaecation in the two habitats is calculated in Tab. 3. Throughput time was estimated at 45–50 min in both habitats (two observations at each site), which agrees with other studies on geese (Owen 1975). The geese on the pastures defaecated twice as often as the geese on the newly sown fields, and during a 24 h cycle they were estimated to produce more than double the number of droppings compared with those feeding on grain.

The daytime production of droppings on the pastures was also estimated from counts of droppings in the fields. The flocks of Pinkfeet were counted and mapped 1–2 times daily throughout the winter and spring of 1983. In a central field, dropping densities were assessed along transects (the droppings were counted and removed from permanent plots at three wk intervals). The number of goose-days per 4 ha was calculated from

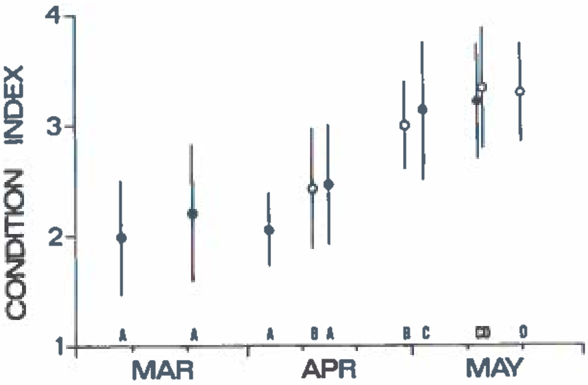


Fig. 2. Development of condition expressed by abdominal profiles on pastures (filled circles) and newly sown barley fields (open circles). Data were obtained at four sites: A: Værnengene/Tipperne, B: Filsö, C: Nissum Fjord, and D: Vest Stadil Fjord. Bars represent one standard deviation.

Tab. 3. Estimates of daily production of droppings, food intake and net energy intake of a Pink-footed Goose on pastures and newly sown barley fields, respectively.

	Pastures	Newly sown fields
Mean time on feeding ground (min)	844	819
Defaecation period during daytime (min)[a]	799	774
Defaecation rate (s)	313[b]	630[c]
Dropping production on feeding ground	153	74
Dropping production on roost[d]	28	14
Total daily dropping production	181	88
Dry weight of dropping (g)	0.727[e]	1.476[f]
Organic contents (g)	0.642	1.094
Daily defaecation (g org. mat.)	116.2	96.3
Retention rate (%)	26.7	58.1
Daily intake (g org. mat.)	158.5	229.8
Energy content of food ($kJ\ g^{-1}$ org. mat.)	19.80	17.67
Energy content of faeces ($kJ\ g^{-1}$ org. mat.)	16.11	12.85
Daily net energy intake (kJ)	1267	2824
Assimilation of energy (%)	40.4	69.5

a. Defaecation period is the time on feeding ground minus throughput time (estimated to be 45 min in both habitats).
b. n = 376 min.
c. n = 325 min.
d. For calculation see text.
e. n = 122.
f. n = 121.

the mappings, and a linear correlation was found between cumulative dropping density and number of goose-days ($r = 0.90$, $n = 23$, $P < 0.001$). One goose-day equals the production of 150 droppings, which is in close accordance with the estimated production of 153 (Tab. 3).

There was a reasonable accordance between the retention rates based on NDF, lignin and ash (Tab. 4), whereas the values based on ADF diverge, probably

Tab. 4. Retention rates of pasture grasses and newly sown barley calculated by the marker substance method.

	NDF[1]	ADF[1]	Lignin[1]	Ash[2]
Pasture grasses	26.6	51.0	29.0	24.4
Barley (ungerminated)	63.5	80.5	52.6	58.1

1. % of organic contents.
2. % of dry weights, silica fraction subtracted from the ash of droppings.

Tab. 5. Comparison of feeding parameters and profitability of feeding on pastures and newly sown barley fields.

	Pastures	Newly sown fields
Pecking rate (s 25 pecks^{-1})	10.9[a]	52.9[b]
Walking speed (s 25 paces^{-1})	42.2[c]	17.1[d]
Daily foraging time (min)	674	455
Daily net energy intake (kJ)	1267	2824
Total number of pecks d^{-1}	92750	12900
Energy intake peck^{-1} (J)	14	219

a. n = 84, SD = 2.0.
b. n = 31, SD = 13.7.
c. n = 30, SD = 11.4.
d. n = 23, SD = 3.8.

due to methological problems in the analysis. Using a mean, and excluding the latter value, it is seen that the barley grain had a digestibility twice that of the pasture grasses. This is expected, because the fibre contents of grass are higher than those of grain (NDF contents are 29.4 and 12.1% of dry weight, respectively), and digestibility is known to be inversely correlated with amount of fibre (Nehring and Nerge 1966).

Due to a higher retention rate, the geese on the newly sown fields had a higher daily food intake. If the water content of grass is assumed to be 80% of fresh weight, food intake on the pastures corresponds to 793 g fresh weight d^{-1}. The estimated intake on the newly sown barley fields corresponds to 4625 barley grains d^{-1} (mean weight of a grain is 0.0487 g dry weight). Due to a higher energy assimilation (Tab. 3), the geese feeding on the newly sown fields double their daily net energy intake compared with pasture feeding geese.

3.3. Feeding profitability

When grazing on pastures, geese pecked faster but walked slower than the geese on the newly sown barley fields (Tab. 5). The pasture vegetation was patchy, and the geese tended to seek out patches with the preferred grasses (especially patches with *Alopecurus geniculatus*) and then slowly traverse that area with a fast pecking rate. On the newly sown fields the food was more evenly distributed, and the geese tended to walk faster to cover the relatively longer distance between the grains, thus giving rise to a slower pecking rate. Pecking rates were seven times higher on pastures than on newly sown fields. Converted into net energy intake per peck, the geese on the newly sown fields had 16 times as high a net intake per peck as the geese on the pastures.

4. Discussion

4.1. Choice of profitable habitat

According to optimal foraging theory an optimal predator (carnivore as well as herbivore) should forage in the most profitable patches or habitats, where food intake per unit foraging time is maximized (Royama 1970, Krebs 1978). When profitability is expressed as net energy intake per peck the Pinkfeet evidently behaved optimally by choosing the newly sown barley fields. Compared with pasture grasses in early spring barley grain is an advantageous food source with high digestibility and a high energy content.

Drent et al. (1978/79) computed net calorific intake per 1000 bites for Barnacle Geese and Brent Geese *Branta bernicla bernicla* feeding on different food sources during the wintering season, and found the habitat utilization to be consistent with the expectations of the profitability hypothesis. Boudewijn (1984) found that spring habitat selection of Brent Geese was correlated to food quality (digestibility) and that the geese changed habitat according to profitability. Charman (1979), in a study of the sequential habitat utilization of Brent Geese in south-east England, also found that the geese first took the most profitable food plants and then made 'a sequential progression down a chain of food preferences'.

4.2. Energy budgets

When the estimated energy expenditures and net energy intakes in the two habitats are compared (Tabs 2 and 3) it is seen that there was an approximate balance in the energy budget on pastures, whereas on newly sown fields the net energy intake of the geese was twice their expenditure. Expenditure was highest on newly sown fields because of an increased amount of flying, but apparently the geese managed to compensate for this by an increased food intake. In a study of the effects of disturbance on time budgets of Pinkfeet wintering in the Netherlands, Schilperoord and Schilperoord-Huisman (1981) likewise found that geese put to flight by disturbance compensated for the lost feeding time (and the higher energy expenditure) by increased time feeding in the hours following the disturbance.

However, it can be roughly calculated that if the Pinkfeet grazing on pastures in west Jutland spent the same daily amount of flying as geese feeding on newly sown fields (one hour) they would not be able to compensate for their energy loss, unless they increased pecking rates or the time spent feeding (e.g., by feeding at night).

The estimated energy budgets should, however, be regarded as rather crude as some of the parameters are insufficiently documented, e.g., energy costs of activity (cost of feeding in the two habitats was regarded as equal), body weights, and defaecation rates at night. Furthermore, in the droppings from the newly sown barley fields, the sand fraction was high and variable, which may have effected the accuracy of the marker concentration measurements.

4.3. Nutritive demands

The so-called 'condition hypothesis' states that nutrient reserves accumulated in spring staging areas are of critical importance to the subsequent reproduction of arctic nesting geese (Ebbinge et al. 1982). As shown by the development of the abdominal profiles, the Pinkfeet rapidly take on weight during the last month before their spring departure (Fig. 2). Judging from the energy budgets there seems to be a significantly better potential for weight increase on the newly sown barley fields than on pastures. A serious constraint is the wariness of the geese, which leads to frequent disturbance flights. Later in spring the flight distance of the geese decreases (Madsen 1985). This might be seen as a behavioural adaptation to meet the increased food demands, improving the opportunity to build up fat reserves.

Also protein reserves accumulated in the spring staging areas are thought to be of critical importance to the egg laying goose (Prop et al. 1984). McLandress and Raveling (1981) showed that Canada Geese *Branta canadensis maxima* changed from a winter diet consisting mainly of maize *Zea mays* to a more diverse and protein-rich diet in spring, and this change coincided with a build up of both protein and fat reserves. The barley grain utilized by the Pinkfeet contains few of the amino acids essential for egg production and the build up of flight muscle (McDonald et al. 1973). The entire population of Pinkfeet changes to the newly sown fields during the month prior to spring departure (Madsen 1984), and at present it is unknown where the geese gain the necessary protein reserves. The following possibilities exist: (1) the geese fly to the pastures for a few hours each day (not the case in this study, but later in spring flocks of geese are seen grazing on pastures); (2) the protein reserves are accumulated prior to the shift to the newly sown fields; or (3) the geese build up the reserves on staging areas in northern Norway during mid May. Wypkema and Ankney (1978) found that Snow Geese *Anser c. caerulescens* were able to supplement their protein reserves on a short-term staging area immediately before their final migration to the breeding grounds (while fat reserves remained stable). However, the Pinkfeet probably only stay in northern Norway for 2–5 d before they migrate to Svalbard (N. Gullestad, unpubl.), which appears to be too short a time to make major supplements to their reserves.

In conclusion it is evident that feeding on newly sown barley fields in spring is advantageous from an energetic point of view compared with feeding on pastures, and the shift from pastures to the newly sown fields can be explained as a choice of the most profitable food source. The newly sown fields provide sufficient carbohydrates to build up fat reserves for spring migration and reproduction, but the geese will have to find a supplementary source of protein in other habitats in order to build up protein reserves.

Acknowledgements – This paper was part of a university dissertation from the University of Aarhus, Denmark. Supervisor was A. Holm Joensen. P. Hald-Mortensen, the National Agency for the Protection of Nature, Monuments and Sites, kindly allowed me to use the facilities at the nature reserve Tipperne. K. Vestergaard Thomsen, the National Institute of Animal Science, kindly carried out the fibre analyses. They are all thanked.

5. References

Altmann, J. 1974. Observational study of behaviour: sampling methods. – Behaviour 49: 227–267.

Ankney, C. D. 1977. The use of nutrient reserves by breeding male Lesser Snow Geese *Chen caerulescens caerulescens*. – Can. J. Zool. 55: 1984–1987.

– and MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. – Auk. 95: 459–471.

Aschoff, J. and Pohl, H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. – J. Orn. 111: 38–47.

Boudewijn, T. 1984. The role of digestibility in the selection of spring feeding sites by Brent Geese. – Wildfowl 35: 97–105.

Charman, K. 1979. Feeding ecology and energetics of the Dark-bellied Brent Goose (*Branta bernicla bernicla*) in Essex and Kent. – In: Jefferies, R. L. and Davy, A. J. (eds). Ecological Processes in coastal environments. Blackwell, Oxford, pp. 451–465.

Cramp, S. and Simmons, K. E. L. (eds) 1977. Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic. Vol. I, Oxford.

Drent, R., Ebbinge, B. and Weijand, B. 1978/79. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. – Verh. orn. Ges. Bayern 23: 239–264.

Ebbinge, B., Canters, K. and Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. – Wildfowl 26: 5–19.

– , St. Joseph, A., Prokosch, P. and Spaans, B. 1982. The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. – Aquila 89: 249–258.

Fruzinski, B. 1977. Feeding habits of Pink-footed Geese (*Anser fabalis brachyrhynchus*) in Denmark during the spring passage in April 1975. – Dan. Rev. Game Biol. 10 (6): 1–11.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. – In: Krebs, J. R. and Davies, N. B. (eds). Behavioural Ecology. An evolutionary approach. Blackwell, Oxford, pp. 23–63.

Lorenzen, B. and Madsen, J., in press. The goose populations at the Tipper peninsula, Western Jutland, Denmark. II. Feeding ecology in relation to the carrying capacity of the

area. – Dansk ornithol. Foren. Tidsskr. (In Danish with summary in English.)
Madsen, J. 1980. Occurrence, habitat selection and roosting of the Pink-footed Goose *Anser brachyrhynchus* at Tipperne, western Jutland. – Dan. orn. Foren. Tidsskr. 50: 45–58. (In Danish with summary in English.)
– 1984. Numbers, distribution and habitat utilization of Pink-footed Geese *Anser brachyrhynchus* in Denmark 1980–1983. – Nor. Polarinst. Skr. No. 181: 19–23.
– 1985. Impact of disturbance on field utilization of Pink-footed Geese in West Jutland, Denmark. – Biol. Conserv. 33: 53–63.
McDonald, P., Edwards, R. A. and Greenhalgh, J. F. D. 1973. Animal nutrition. – Oliver & Boyd, Edinburgh.
McLandress, M. R. and Raveling, D. G. 1981. Changes in diet and body composition of Canada Geese before spring migration. – Auk 98: 65–79.
Moss, R. and Parkinson, J. A. 1972. The digestion of heather *Calluna vulgaris* by Red Grouse *Lagopus lagopus scoticus*. – Brit. J. Nutr. 27: 285–298.
Nehring, K. and Nerge, I. 1966. Die Verdaulichkeit verschiedener Futterstoffe bei Gänsen. – Arch. Geflügelzucht Kleintierk. 15: 3–21.
Owen, M. 1975. An assessment of fecal analysis technique in waterfowl feeding studies. – J. Wildl. Manage. 39: 271–279.
– 1981. Abdominal profile – a condition index for wild geese in the field. – J. Wildl. Manage. 45: 227–230.
Prop, J., Eerden, M. R. van and Drent, R. 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. – Nor. Polarinst. Skr. 181: 87–117.
Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (*Parus major* L.). – J. Anim. Ecol. 39: 619–668.
Schilperoord, L. and Schilperoord-Huisman, M. 1981. De invloed van verstoringen op gedrag en dagindeling van de kleine rietgans (*Anser brachyrhynchus*) in Zuidwest Friesland. – Unpubl. M. Sc. report, Univ. of Groningen, Netherlands.
Tucker, V. A. 1969. The energetics of bird flight. – Sci. Amer. 220: 70–78.
Wooley, J. B. and Owen, R. B. Jr. 1978. Energy costs of activity and daily energy expenditure in the Black Duck. – J. Wildl. Manage. 42: 739–745.
Wypkema, R. C. P. and Ankney, C. D. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. Can. J. Zool. 57: 213–219.

2

Biological Conservation 33 (1985) 53–63

Impact of Disturbance on Field Utilization of Pink-footed Geese in West Jutland, Denmark

Jesper Madsen

Zoological Laboratory, Institute of Zoology and Zoophysiology, University of Aarhus, Universitetsparken, BIO III, DK-8000 Aarhus C, Denmark

ABSTRACT

The impact of roads and landscape features on field utilization of pink-footed geese in autumn and spring is examined. Flight distance of goose flocks increases with flock size and is longer in autumn compared to spring. The disturbance distance of roads with traffic volume of more than 20 cars per day is approx. 500 m in autumn, less in spring. Lanes with 0–10 cars per day also have a depressing effect on utilization. Windbreaks, banks, etc. which hinder an open view, have a disturbance distance of approx. 200–300 m. The width of an area (hindrances in more than one direction) must exceed 500 m in order to be acceptable to flocks of pink-footed geese (autumn).

INTRODUCTION

A principal goal for the management of areas for wintering geese, e.g., the design of goose refuges, is to improve the carrying capacity of the areas. Several factors affecting habitat selection of the geese must be considered (Owen, 1973), which can be divided into two categories:

(1) factors influencing the within-habitat (micro-) level, viz. plant community, vegetation height and quality of food plants; and
(2) factors influencing the overall-habitat (macro-) level, viz. biotope, size of the area, openness and disturbance.

Biol. Conserv. 0006-3207/85/$03·30

In this paper I have quantified the impact of some of the factors influencing goose utilization at the macro-habitat level. The study was carried out on the population of pink-footed geese *Anser brachyrhynchus*, staging in West Jutland, Denmark in autumn and spring (Madsen, 1984).

STUDY AREAS

The investigation was carried out in two areas in West Jutland:

(1) The Tipper peninsula (55°53′ N, 08°13′ E), a cattle-grazed grassland, consisting of the nature reserve Tipperne (450 ha of unfertilized, semi-natural grassland) and Værnengene (600 ha of fertilized pastures). The area is a traditional winter and spring haunt for up to 4000 pinkfeet.

(2) Filsø (55°42′ N, 08°13′ E), a 1300 ha farm on which there is a crop rotation of spring barley (the principal crop), winter wheat, rye, rape and seed grass. In autumn the major part of the arable land lies as stubble, which is gradually ploughed, and stubble with undersown seed grass. The area is a traditional haunt for up to 25 000 pinkfeet in autumn and 3000–5000 in spring.

METHODS

Flight distances of goose flocks

The distance at which goose flocks take flight was estimated using a car as a standard stimulus triggering escape flight. The flock size and flight distance was estimated, the latter to the nearest 25 m. The distance from the car to the nearest edge of the flock was often controlled by pacing out or by measuring on a map. The observations were carried out on every possible occasion, on several localities, and in autumn and spring during the seasons 1980/81 to 1982/83.

Effect of landscape features on goose utilization

Two different approaches to the evaluation of the disturbance effect of various landscape features on goose distribution were used. On Filsø the evaluation was based on goose counts and the mapping of flocks, whereas on the Tipper peninsula density of droppings was used as a measure of grazing intensity. The advantage of the former method is that overall distribution factors can be analysed, while the latter gives more detailed information.

Filso

Goose counts and mapping of flocks were carried out at regular intervals (on average every 3 days) in October, from 1980 to 1983. Goose utilization of individual fields has been calculated as the mean number of geese per ha per visit. As utilization is dependent on habitat type, the expression has been calculated only for the years when a field was in a state preferred by the geese. A study of the habitat selection of the geese (Madsen, in press) showed that they preferred the stubble with or without undersown grass. Due to the rotation of crops all fields were in one of these two states in at least one autumn, and most fields for two or three autumns. Distances from field centres to landscape features were measured on a 1:10 000 map. The following parameters were chosen: (1) distance from windbreaks, plantations, banks, etc. which hinder a wide view; (2) distance from roads and country lanes with various traffic volumes: one road with a traffic volume of 20–50 cars or equivalent per day, and several lanes with a traffic volume of less than 10 cars per day; (3) the openness of a field, i.e. the width of a field from banks/windbreaks,

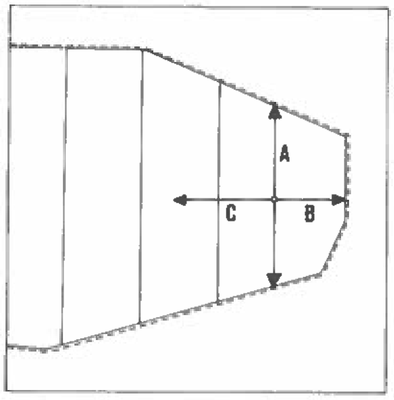


Fig. 1. Definitions of distance to obstruction of open view and width of a field which is enclosed by a bank in more than one direction (broken line). B is the shortest distance from the field centre to the bank; A is the width of the field perpendicular to the direction of the widest view (C). Single lines are water canals.

etc. enclosing the field in more than one direction, measured as the length of the line perpendicular to the direction of the longest view (for visual explanation see Fig. 1).

The Tipper peninsula

As goose utilization is dependent on the plant community the analysis of dropping densities has only been carried out in preferred communities, defined by the highest dropping densities, and only on wide homogeneous swards. Density of droppings was assessed in 20 m^2 circles with 40 m intervals along transects perpendicular to roads and windbreaks. Permanent plots were established in a central pen which was regularly used by the geese. Here droppings were counted and the plots emptied at three-week intervals throughout the period January to June 1983. Transects were chosen so that the effect of the feature being investigated was isolated from other effects, e.g., other roads or plantations.

RESULTS AND DISCUSSION

Flight distances

In both autumn and spring a correlation was found between flight distances and flock size (Spearman's rank correlation, $r_s = 0{\cdot}431$, $p < 0{\cdot}05$, and $r_s = 0{\cdot}384$, $p < 0{\cdot}05$, respectively (Siegel, 1956)). The relationships are, however, not linear but probably concave (Fig. 2).

The interrelation between flight distance, flock size and season has been analysed by a three-way log-linear model (Sokal & Rohlf, 1981), where the flight distance and flock size have been grouped according to the mean distance and size respectively, pooled over the seasonal factor (Table 1). A G-test for goodness of fit yields $G_{ABC} = 7{\cdot}45$ ($p < 0{\cdot}001$), indicating the presence of a three-way interaction between the factors, i.e. flight distance is dependent on both flock size and season.

Generally speaking flocks above 400–600 individuals have a flight distance of 500 m in autumn and 300–400 m in spring. The increased shyness is undoubtedly related to harassment during the shooting season (the open season in Denmark is from 1 September to 31 December). This is also evidenced by the fact that geese staging on Filsø in spring remained as shy as in autumn. Here the farmer regularly fired warning shots at the geese in order to keep them off the newly sown fields (these flocks have been omitted from the three-way analysis).

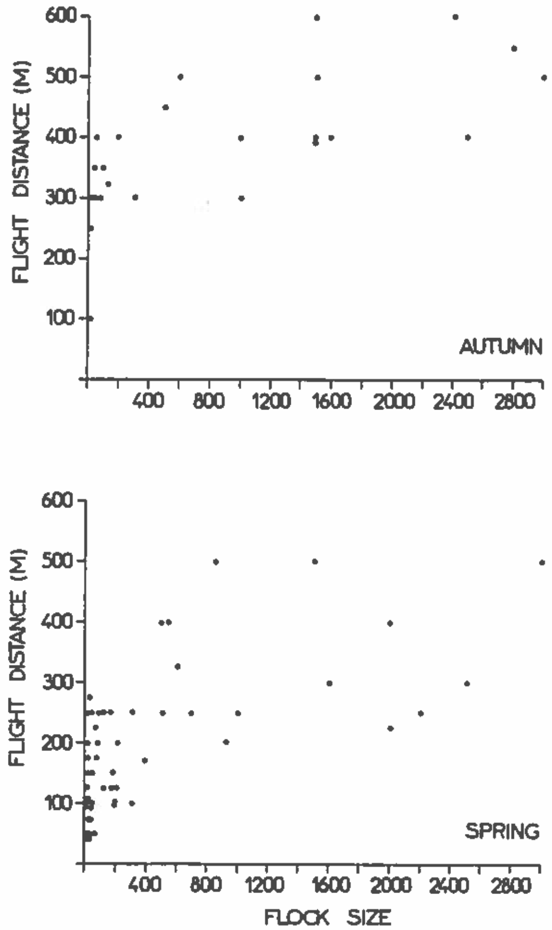


Fig. 2. Flight distances of flocks of pink-footed geese approached by a car in autumn (September–November) and in spring (February–May).

In a study of flight distances of brent geese *Branta bernicla bernicla*, Owens (1977) found a linear relationship between flock size and flight distance. Flight distances should, however, not be expected to increase indefinitely with flock size but rather level off, as the present data suggest.

The disturbing effect of shooting on flight distances of goose flocks has also been reported by Gerdes & Reepmeyer (1983). They found that, in the years following a ban on shooting of white-fronted geese *Anser albifrons* and bean geese *Anser fabalis* in West Germany, the flight distances of wintering flocks of 500–1000 individuals decreased from

TABLE 1

Grouping of Data in a Three-way Analysis of Relation between Flock Size of Pink-footed Geese, Flight distance and Season
(Grouping according to mean size/distance pooled over the season)

Flock size (A)	*Flight distance (B) (m)*	*Season (C)*		*Totals*
		Autumn	*Spring*	
< 590	< 257	2	35	37
	> 257	9	3	12
		11	38	49
> 590	< 257	0	6	6
	> 257	12	7	19
		12	13	25
Totals		23	51	74

generally 500 to 200 m. As a result the geese expanded their feeding grounds to areas close to roads and banks where they previously had been reluctant to go.

Impact of roads

In order to evaluate the impact of roads on goose utilization on Filsø, data have been grouped for fields with a similar distance from a road with similar traffic volume, provided no other landscape features affect utilization. Roads with a traffic volume of 20–50 cars (or equivalent) per day had a serious depressing effect on goose utilization in a range of 0–500 m from the road (Fig. 3A). Even lanes with less than 10 cars per day had a depressing effect, although not as seriously as the more frequented roads. Due to the lack of fields at distances of more than 600–800 m away from the roads, it was not possible to examine the long-distance effect of the roads. However, utilization reached a peak at a distance of 500–600 m from the roads. The disturbance distance, defined as the distance from the road where the geese feed without interruption (modified after van der Zande *et al.*, 1980), is likely to be approximately 500 m. The average flock size of pinkfeet on Filsø in autumn was 1927 individuals, and the disturbance distance corresponds well with the flight distance of bigger flocks in autumn.

The disturbance distance of a road carrying 20–30 cars per day was ca. 240 m on the Tipper peninsula in spring (Fig. 4). Mean flock size of pinkfeet was 362 individuals, and the disturbance distance corresponds

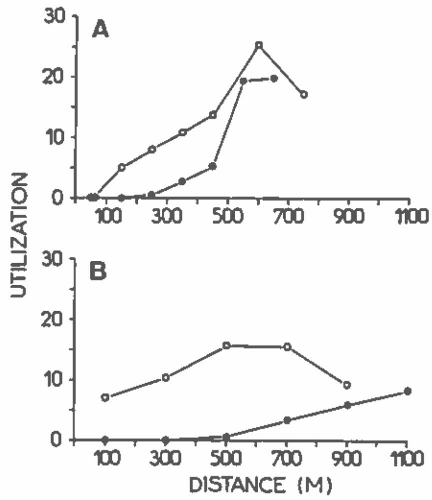


Fig. 3. (A) Relation between utilization (mean number of goose days per ha per visit) and distance from roads on Filsø in autumn. Circles: traffic volume less than 10 cars per day; filled circles: more than 20 cars per day. (B) Utilization related to distance from obstructions to open view (circles) and width of the area (filled circles).

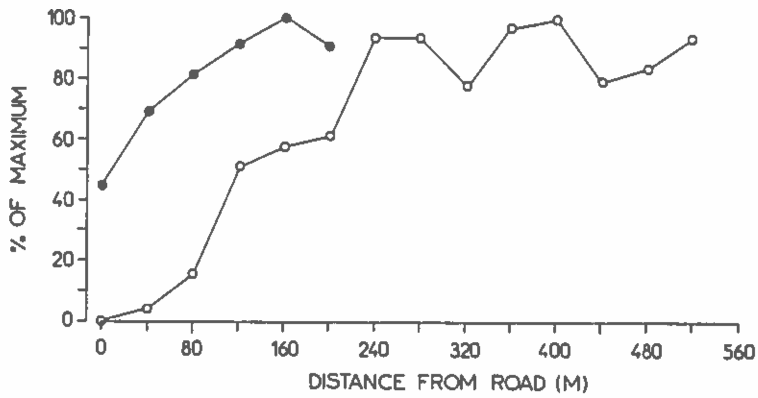


Fig. 4. Relation between goose utilization expressed as percentage of the maximum goose dropping density and the distance from a road on the Tipper peninsula. Circles: traffic volume 20–30 cars per day; filled circles: less than one car per day. Each point represents at least four dropping samples of 20 m^2 in a *Poa pratensis–Alopecurus geniculatus*-dominated grass sward.

well with the flight distance of approximately 200–300 m for that flock size in spring. Even a lane which does not carry cars daily was found to have a depressing effect on utilization (Fig. 4) and a disturbance distance of approx. 100 m. The explanation for this is probably that geese put to flight by disturbance or predators most likely settle in the centre of a field. Only after some time will they reach the field boundaries, and consequently the grazing intensity there is reduced.

The results (Figs 3A and 4) indicate that the relationship between the distance from the road and goose utilization is logistic. The disturbance intensity, i.e. the total loss in goose utilization suffered over the whole disturbance distance (modified after van der Zande *et al.*, 1980) increased with the traffic volume and flight distance. This, again, indicates that the disturbance intensity may be increased in two ways: (1) by increased disturbance distance (which is partly a function of flight distance); and (2) by the movement of the exponential phase of the logistic curve to the right (brought about by increased traffic volume).

This conclusion is partly supported by Mooij (1982), who studied the effect of roads on field utilization by wintering bean geese and white-fronted geese in the Lower Rhine Area of West Germany. Judging from that author's results, there was a logistic relationship between distance from roads and utilization, the disturbance distance being approx. 500–800 m. The longer disturbance distance may be due to the fact that the geese in the Lower Rhine have more space available than in the study areas. Fields far away from potential disturbance sources probably have a higher affinity to geese, and when disturbed from other areas the geese are most likely to fly to safe and undisturbed sites.

Impact of obstructions to open view

The impact of windbreaks, plantations, banks, etc., which hinder the open view of the geese, was analysed for those fields on Filsø where the distance to the central road (carrying more than 20 cars per day) exceeds 600 m. Utilization (U) is correlated with the linear distance from the field centre to an obstruction of the open view (A) and the width (B) of the area (for definition see Fig. 1) by a partial regression analysis (Sokal & Rohlf, 1981). The mutual correlation between A and B is $\tau = 0{\cdot}44$ (Kendall rank correlation coefficient, Siegel, 1956). When the effect of A is eliminated, the partial correlation coefficient is:

$$r_{UB.A} = 0{\cdot}84 \ (p < 0{\cdot}01)$$

When the effect of B is eliminated, the partial correlation coefficient is:

$$r_{UA.B} = 0{\cdot}10 \text{ (non-significant)}$$

This result indicates that an obstruction of the open view on one side of a field has no significant effect on goose utilization, that is, taking the field size on Filsø into account. However, if the field is enclosed by obstructions to open view on more than one side, goose utilization will be affected. As shown in Fig. 3B fields with a width of less than 500 m were not utilized by geese at all, and utilization increased with widths between 500 and 1100 m.

The impact of windbreaks in one direction was analysed on the Tipper peninsula (Fig. 5). A depressing effect on goose utilization was found from 0 m to approx. 150 m proceeding from the windbreak.

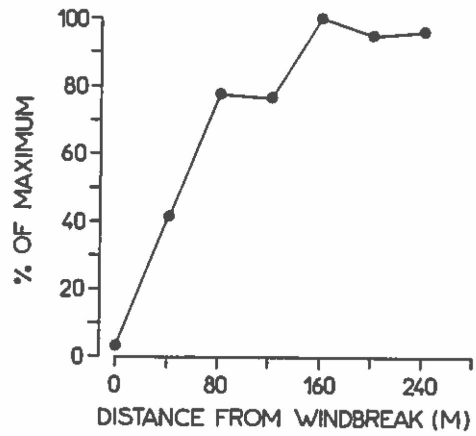


Fig. 5. Goose dropping densities expressed by percentage of maximum value as a function of the distance from a windbreak on the Tipper peninsula. Each point represents at least four dropping samples of 20 m² in a *Poa pratensis–Alopecurus geniculatus*-dominated grass sward.

Karlsson *et al.* (1978) found that bean geese accepted fields with diagonals of 250 m × 250 m, but these workers did not quantify the relationship between intensity of utilization and field size, and the 250 m × 250 m is a minimum acceptable field size. As indicated above, the minimum width accepted by the pinkfeet was 500 m. Although not directly comparable with Karlsson *et al.*'s (1978) results, the minimum acceptable field size for pinkfeet appears to be larger than for bean geese.

CONCLUSIONS

It is concluded that disturbance, broadly defined as both actual, which puts geese to flight (e.g., human beings, cars, aircraft) as well as potential, which may hide predators (landscape features), is a very important factor affecting overall goose utilization. Owen (1972, 1973) reached the same conclusion on the basis of studies of wintering white-fronted geese and barnacle geese *Branta leucopsis* in Britain. Other authors have emphasized how disturbance may modify goose distribution both within sites and between sites (Kuyken, 1969; Göransson & Karlsson, 1976; Owens, 1977; Gerdes *et al.*, 1978; Madsen, 1980, 1982; Gerdes & Reepmeyer, 1983; Mooij, 1982).

A primary goal for management policies for goose habitats is thus to reduce disturbance. How big a goose-managed area has to be will, however, depend on several factors, e.g., species, size of the population, shyness, and proximity to other goose areas.

The pinkfoot is an extremely wary goose and other species occurring in West Jutland, particularly the greylag goose *Anser anser*, are less shy and less demanding with regard to field size (Madsen, in prep). Flight distance gives an indication of the minimum acceptable size of an area, but this changes with shooting regulations. It can be concluded that the following requirements on the macro-habitat level should be fulfilled to make an area acceptable for, say, at least 1000 pinkfeet:

(1) extensive feeding grounds at a distance of 500 m away from roads with traffic volumes of above 20 cars should be available;
(2) traffic on lanes should be regulated, as even less than one car per day has a depressing effect on goose utilization; and
(3) the width of the area should exceed 1 km; and windbreaks, plantations, etc. should not be established within the area.

ACKNOWLEDGEMENTS

This paper was part of a final dissertation from the University of Aarhus. Dr phil. A. Holm Joensen, Natural History Museum, Aarhus, was supervisor. A. P. Møller commented on an earlier draft of this manuscript.

REFERENCES

Gerdes, K., Hess, D. & Reepmayer, H. (1978). Räumliche und zeitliche Verteilungsmuster der Gänse (*Anser fabalis*, *A. albifrons* und *A. anser*) im Bereich des Dollart (1971–1977). *Vogelwelt*, **99**, 81–116.

Gerdes, K. & Reepmayer, H. (1983). Zur räumlichen Verteilung überwinternder Saat- und Blessgänse (*Anser fabalis* und *A. albifrons*) in Abhängigkeit von naturschutzschädlichen und fördernden Einflüssen. *Vogelwelt*, **104**, 54–67.

Göransson, G. & Karlsson, J. (1976) Störningseffekter på djur—med exempel från gåsjakten i Skåne. *Anser*, **16**, 119–24.

Karlsson, J., Lones, J. & Manson, M. (1978). Storlek och form på sädgässens betesmarker under hösten i Skåne. *Anser*, **17**, 146–53.

Kuyken, E. (1969). Grazing of wild geese on grasslands at Damme, Belgium. *Wildfowl*, **20**, 47–54.

Madsen, J. (1980). Occurrence, habitat selection, and roosting of the pink-footed goose at Tipperne, Western Jutland, Denmark, 1972–1978. *Dansk orn. Foren. Tidsskr.*, **74**, 45–58. (Danish with English summary.)

Madsen, J. (1982). Observations on the Svalbard population of *Anser brachyrhynchus* in Denmark. *Aquila*, **89**, 133–40.

Madsen, J. (1984). Numbers, distribution and habitat utilization of pink-footed geese in Denmark 1980–1983. *Norsk Polarinstitutt Skrifter*, **181**, 19–23.

Madsen, J. (In press). Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. *Ornis Scand.*

Mooij, J. H. (1982). Die Auswirkungen von Strassen auf die Avifauna einer offenen Landschaft am Unteren Niederrhein (Nordrhein-Westfalen), untersucht am Verhalten von Wildgänsen. *Charadrius*, **18**, 73–92.

Owen, M. (1972). Movements and feeding ecology of white-fronted geese at the New Grounds, Slimbridge. *J. appl. Ecol.*, **9**, 385–98.

Owen, M. (1973). The management of grassland areas for wintering geese. *Wildfowl*, **24**, 123–30.

Owens, N. W. (1977). Responses of wintering brent geese to human disturbance. *Wildfowl*, **28**, 5–14.

Siegel, S. (1956). *Nonparametric statistics for the behavioural sciences*. London, McGraw-Hill.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. San Francisco, Freeman.

van der Zande, A. N., Keurs, W. J. & van der Weijden, W. J. (1980). The impact of roads on the densities of four bird species in an open field habitat—evidence of a long-distance effect. *Biol. Conserv.*, **18**, 299–321.

3

DANISH REVIEW OF GAME BIOLOGY Vol. 12 No. 4

Status and Management of Goose Populations in Europe, with Special Reference to Populations Resting and Breeding in Denmark

by
JESPER MADSEN

Med et dansk resumé:
Status og forvaltning
af gåsebestande i Europa,
og især bestande,
der raster og yngler i Danmark

Резюме на русском языке:
Состояние популяций гусей в Европе и
заведование ими, особенно популяций,
обитающих и гнездующих в Дании

ISSN 0374-7344

COMMUNICATION NO. 211 FROM VILDTBIOLOGISK STATION
Vildtbiologisk Station, Kalø, 8410 Rønde, Denmark
1987

Abstract

Madsen, J. 1987. Status and Management of Goose Populations in Europe, with Special Reference to Populations Resting and Breeding in Denmark. – Dan. Rev. Game Biol. Vol. 12, No. 4.

This paper reviews the status, ecology and management of goose populations in Europe. The development of populations within the 20th century is summarized, and factors determining their size discussed. Crop damage by geese, and its possible solution, is discussed. Proposals to future management and research are given.

Five populations passing through Denmark are used as examples, viz. *Anser fabalis fabalis*, the Svalbard *Anser brachyrhynchus*, the northwest European *Anser anser*, *Branta bernicla bernicla*, and the Svalbard *Branta bernicla hrota*. The five populations have in common, together with most of the other 16 populations occurring in Europe, that within this century they have increased in numbers and have changed feeding habits. In populations where the dynamics are known, the increase has been attributed to a better survival, and relaxation of shooting pressure seems to be the major causal factor. Many species have, during part of the winter season, changed from feeding in natural habitats or extensively farmed land to feeding on arable land or improved pastures. This has been attributed partly to the destruction of the former habitats (development, reclamation), and partly to better feeding conditions on the farmland. In *Branta b. bernicla* the population increase has led to an earlier exhaustion of the natural food resources on the mudflats, and consequently to the shift to pastures and winter cereal fields. The combination of changed habits and the increase in numbers has given rise to damage on crops. The best solution to the problems is to create refuges with alternative feeding areas, and a better protection and management of mudflats and marshes, which are traditional haunts. An international strategy for the management of the European goose populations is needed. It should be based on knowledge of dynamics and ecological requirements of the populations. Research on the breeding ecology is needed in most populations, however, especially in those breeding in Siberia. Studies of population dynamics are missing for some populations.

Contents

(Continued next page)

Introduction

At some stage in their annual cycle, the European subcontinent harbours a total of 21 wild goose populations. Throughout this paper a population is defined as a group which is more or less discrete with little interchange of individuals with any other group of the same species. The populations total between 1,329,000 and 1,569,000 geese (Table 1), of which the bulk breeds in arctic regions outside Europe. With a few exceptions the populations have increased markedly during the second half of the 20th century, and the total number of geese wintering in Europe today is probably higher than ever before.

In the course of the last two centuries environmental conditions in Europe have altered considerably, especially due to the intensification of farming and the development of urban societies and industry. In Denmark for example, the uncultivated area, viz. heathlands, moorlands, meadows and saltmarshes, was reduced by 80-85% from 1850 to 1950, and the trend has been continuing since (FERDINAND 1980). Many of the traditional goose feeding sites have been changed into agricultural lands, and the geese have to a large extent changed their feeding habits. Thus, nowadays, at least 16 of the 21 goose populations rely partly or mostly on feeding habitats in cultivated lands during their stay in Europe.

The shift to the farmland has, combined with the increase in goose numbers given rise to conflicts with the farming community. Especially since the 1970s the farmers have shown a growing intolerance towards the geese.

This development has raised the question among wildlife administrators and nature conservationists of how to alleviate the conflicts and how to manage the goose populations and their habitats on an international as well as a national basis. So far the international efforts have been concerned only with the management of the Brent Goose (see SMART 1979, SCOTT & SMART 1982), and the only initiative has been an agreement of not to reopen the shooting season in countries where a ban was imposed.

In this paper the status and management of goose populations in Europe, and especially those passing through and breeding in Denmark is reviewed. The selected populations are:

Taiga Bean Goose *(Anser fabalis fabalis)*

Svalbard population of Pink-footed Goose *(Anser brachyrhynchus)*

Northwest European population of Greylag Goose *(Anser anser anser)*

Dark-bellied Brent Goose *(Branta bernicla bernicla)*

Svalbard population of Light-bellied Brent Goose *(Branta bernicla hrota)*

The purpose of the paper is:

1) to review the status of the five goose populations, including the distribution and number of geese, their ecology, past history, management and population development in all the range states,
2) to provide management and research recommendations for the populations,
3) to summarise and discuss in general trends in goose populations in Europe, factors determining population levels, and goose damage and possible solutions.

Without the international goose counts organized through the International Waterfowl Research Bureau (IWRB), it would not be possible to review the relatively detailed population and distributional

Table 1. Goose populations wintering and breeding in Europe. Most population estimates are based on data from 1980-1984.

Population	Breeding range	Winter range	Population size	Source
Bean Goose				
Anser fabalis fabalis	N Scandinavia, W Siberia	W Europe	60,000	VAN DEN BERGH (1985)
Anser fabalis rossicus	N Siberia	Central and W Europe	200,000-250,000	FOG (1982a)
Pink-footed Goose				
Anser brachyrhynchus	Iceland, E Greenland	British Isles	120,000	OGILVIE (1977-1985)
Anser brachyrhynchus	Svalbard	Denmark, Netherlands	25,000	MADSEN (1984a)
White-fronted Goose				
Anser albifrons albifrons	Siberia	Central and W Europe	300,000-400,000	NETHERLANDS GOOSE WORKING GROUP (unpubl.)
Anser albifrons flavirostris	W Greenland	British Isles	18,000	GREENLAND WHITE-FRONTED GOOSE STUDY (unpubl.)
Lesser White-fronted Goose				
Anser erythropus	N Scandinavia, Siberia	SE Europe, Asia Minor	25,000-50,000 (?)	TIMMERMAN et al.(1976)
Greylag Goose				
Anser anser	Iceland	Scotland	80,000	OGILVIE (1977-1985)
Anser anser	Outer Hebrides, Scotland	N Scotland	2,000	OGILVIE (1984)
Anser anser	W and NW Europe	Spain, Netherlands	130,000	PRESENT PAPER
Anser anser	Central and NE Europe	N Africa	20,000	HUDEC (1984)
Anser anser	E Europe	Balkan Peninsula	20,000-30,000 (?)	HUDEC (1984)
Canada Goose				
Branta canadensis	British Isles	British Isles	20,000	OGILVIE (1977)
Branta canadensis	Sweden	Baltic Basin	20,000	(NILSSON 1984a, MADSEN 1986)
Barnacle Goose				
Branta leucopsis	N Siberia, Gotland	Netherlands	60,000	EBBINGE (1982, unpubl.)
Branta leucopsis	E Greenland	Scotland, Ireland	25,000	OGILVIE (1983)
Branta leucopsis	Svalbard	Caelaverock, Scotland	10,000	OWEN (1984, unpubl.)
Brent Goose				
Branta bernicla bernicla	N Siberia	W Europe	150,000-200,000	IWRB BRENT GOOSE RESEARCH GROUP (unpubl.)
Branta bernicla hrota	NE Canada, N Greenland	Ireland	18,000	OGILVIE (1977-1985)
Branta bernicla hrota	Svalbard, Franz Josef Land	Denmark, England	4,000	MADSEN (1984c)
Red-breasted Goose				
Branta ruficollis	N Siberia	SE Europe, Caspian Sea	22,000-27,000	VINOKUROV (1982)

data. Partly due to the IWRB, partly to nationally organized counts, population sizes, proportion of juveniles and family group sizes are monitored each winter in most goose populations in Europe. From this basic work many more detailed investigations have originated, especially ringing and colour ringing programmes, from which much new information about population dynamics, life histories, migration patterns and behavioural ecology has emerged.

Acknowledgements

I express my gratitude to the goose working groups in the various countries and to the IWRB Goose Research Groups. Special thank is due to the following persons for allowing me access to unpublished data and manuscripts and for fruitful discussions during the preparation of the manuscript: J. AMAT, B. EBBINGE, W. KNIEF, R. MAHEO, M. METAIS, M. A. OGILVIE, M. OWEN, J.-Y. PIROT, P. PROKOSCH, J. ROOTH and L. SCHILPEROORD. The manuscript benefitted much from the criticism by M. OWEN. P. HARTMANN produced the histograms, and J. ALEXANDERSEN and E.-M. NIELSEN typed the manuscript.

Taiga Bean Goose *Anser fabalis fabalis* (with remarks on *Anser fabalis rossicus)*

Two subspecies of Bean Goose regularly winter in western Europe: the slenderbilled *Anser fabalis fabalis*, also called Taiga Bean Goose, and the shorter- and deeper-billed *Anser fabalis rossicus*, also called Tundra Bean Goose. Intermediate forms occur, and some authors (e.g. OGILVIE 1978) tend to consider the two forms to be intergrading, while others (ROSELAAR 1977, HUYSKENS 1977, 1979, VAN IMPE 1980a, 1980b, VAN DEN BERGH 1985) consider them as subspecies, as they have been shown to diverge in both morphology and ecology.

From the point af view of population management the two forms ought to be identified as separate entities, and in the present review this has been done. As the Bean Geese passing through Denmark solely belong to the *fabalis* population, special attention will be paid to this, while the *rossicus* population will only be mentioned briefly.

The *rossicus* population breeds in north Siberia, partly overlapping with *fabalis* (Fig. 1, after DELACOUR 1951 and later corrections), and is by far the most numerous of the two populations wintering in Europe. Recent counts in the wintering quarters have indicated that the population probably exceeds 200,000-250,000 geese (FOG 1982a). In autumn the population migrates south of the Baltic and has its main autumn haunts in the German Democratic Republic (GDR) and Poland (LITZBARSKI 1979). Depending on the severity of the winter, geese move on to the Netherlands and the western part of the Federal Republic of Germany (FRG) or into central Europe and as far as France and Spain (Fig. 2). Neck-banding carried out in the GDR (LITZBARSKI 1979) has revealed that there is some connection between the western and central European wintering grounds. Bean Geese wintering in the Netherlands may thus reappear in central Europe later in winter (VAN DEN BERGH 1985, LITZBARSKI unpubl.).

The *fabalis* population breeds in north Scandinavia, north Russia and west Siberia and has a more northwesterly wintering distribution, including Sweden, Denmark, the GDR and the Netherlands (Fig. 3). The population probably numbers more than 60,000 geese. Much new information concerning the migration pattern and ecology

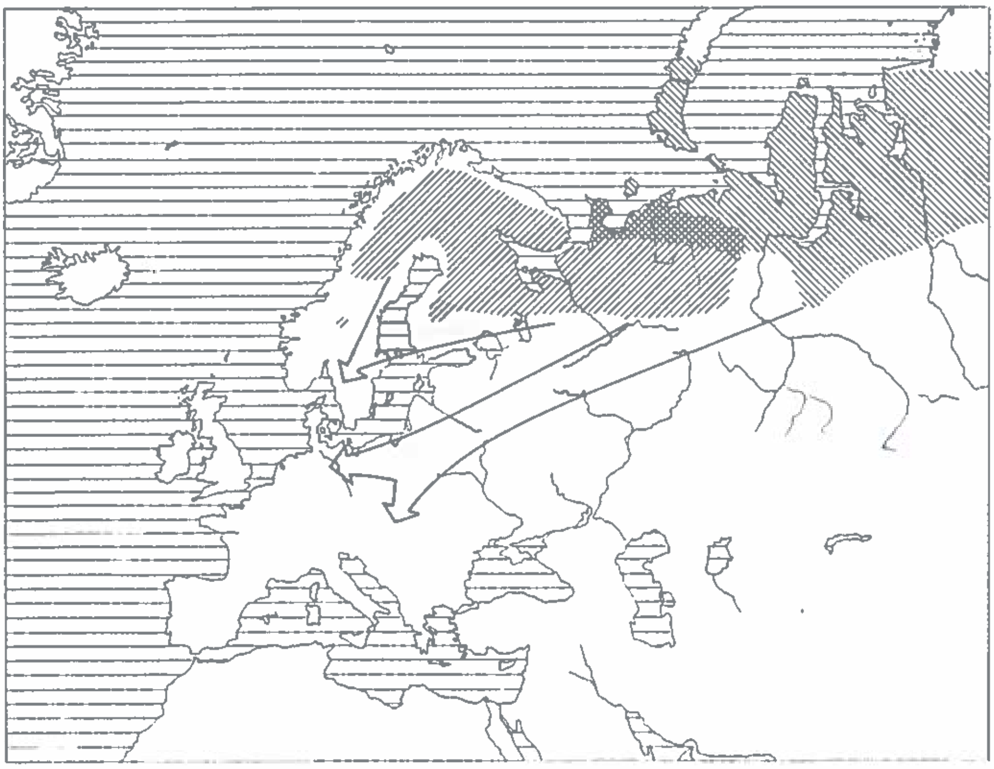


Fig. 1. Breeding distribution and migration routes of Bean Goose populations: To the west *Anser fabalis fabalis*, to the east *A. f. rossicus*. The extension of the range of *fabalis* into Siberia is not well known (After DELACOUR 1951, with later corrections).

of the population has arised from a Scandinavian study sponsored by the Nordic Council for Wildlife Research (NILSSON & FOG 1984).

Breeding grounds and breeding ecology

The number of breeding pairs in the Scandinavian countries and the Soviet Union is unknown. Only in Finland is it estimated that more than 1,000 pairs nest (PIRKOLA & KALINAINEN 1984), but the centre of gravity probably lies in the Soviet part of the breeding range, and on the southeast Kola peninsula breeding density is high (FILCHAGOV et al. 1985). In Finland the population has been increasing in the last decades, whereas in Sweden and Norway it has been decreasing over this century (MELLQUIST & VON BOTHMER 1982, 1984, HAFTORN 1971).

In Scandinavia and possibly also in the Soviet Union the preferred nesting habitat is the minerotrophic type of forest mire with *Carex*, *Eriophorum* and *Trichophorum* spp. (PIRKOLA & KALINAINEN 1984). Pairs usually nest solitarily or in small, loose colonies in scrub within the mires and feed either in fields cut for hay or in the mires (PIRKOLA & KALINAINEN 1984, MELLQUIST & VON BOTHMER 1984). The main food plants are sedges and grasses, *Equisetum* spp. and in summer various berries (PIRKOLA & KALINAINEN 1984, FILCHAGOV et al. 1985).

The phenology of the breeding season is poorly known. In Finland and on the Soviet part of the Kola peninsula the Bean Geese arrive on their breeding grounds from the second half of April to mid May (LAMPIO 1984, FILCHAGOV et al. 1985).

Moulting grounds are found in Finnmark in north Norway (TVEIT 1984), probably harbouring 1,100-2,300 geese (TVEIT unpubl.), and at the Kola peninsula in the Soviet Union (BIANKI cited in PIRKOLA & KALINAINEN 1984). Moulting concentrations are also known from south Novaya Zemlya and areas to the east (USPENSKI 1965), but are probably mainly used by the *rossicus* population.

Management measures and problems. In Scandinavia the breeding habitats have seriously deteriorated in various ways, of which forestry drainage and peat digging seem to be the most negative interferences (PIRKOLA & KALINAINEN 1984). The traditional hay-cutting in the mires has ceased in many areas, causing a change in the plant communities and a decrease in the Bean Goose population (MELLQUIST & VON BOTHMER 1982, 1984).

In Sweden the Swedish Sportsmen's Association together with the World Wildlife Fund have attempted to reintroduce Bean Geese to former breeding grounds where the vegetation is now managed to the benefit of the geese (MELLQUIST & VON BOTHMER 1982).

Wintering grounds

The wintering range of the *fabalis* population includes the countries Sweden, Denmark, the GDR and the Netherlands. Some *fabalis* flocks possibly also occur in Po-

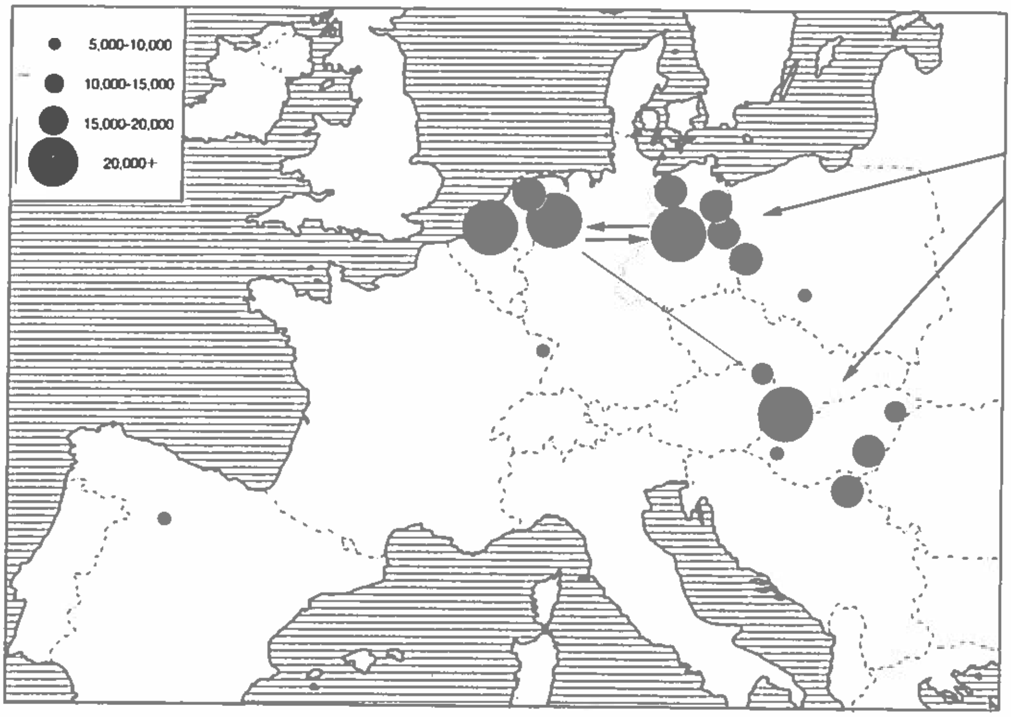


Fig. 2. Midwinter distribution of Tundra Bean Geese *Anser fabalis rossicus* in Europe. Arrows indicate directions of movements (After VAN DEN BERGH 1985).

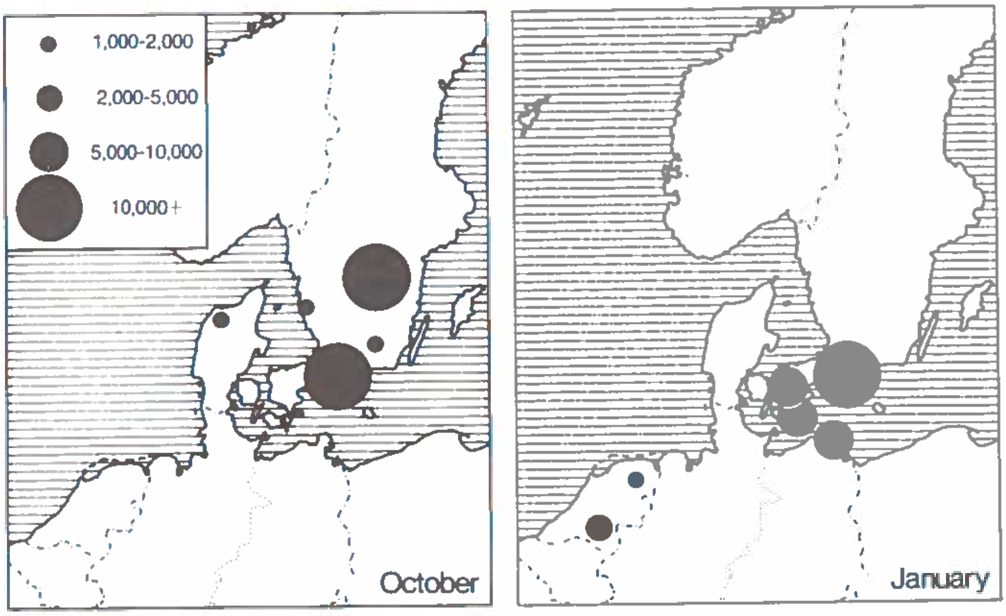


Fig. 3. Distribution of Taiga Bean Geese *Anser fabalis fabalis* in October and January. Sources, see text.

land, and few hundred reach southeast England. Spring staging areas are found in Denmark, Sweden and Finland. The pattern of occurrence in Sweden, Denmark and the Netherlands is shown in Fig. 4.

Sweden

Numbers and distribution. In autumn the Bean Geese arrive on the Swedish staging areas in late September, and usually peak numbers of 40,000 to 60,000 are reached in October (NILSSON & PERSSON 1984, NILSSON 1981, 1984a). The geese remain until the winter weather forces them to leave; in mild winters up to 25,000 stay. Spring migration starts in March and lasts until end of April. Numbers are usually lower than in autumn, and the passage seems to be rapid.

During autumn migration two staging areas dominate: Tåkern adjacent to lake Vättern, and southwest Skåne (NILSSON & PERSSON 1984). The Tåkern area is used only in autumn and deserted in November, while Skåne is also a wintering area. In spring the same areas are used as in autumn, but in addition, Bean Geese stage along the coast of north Sweden, where they are not seen in autumn.

Ecology. In autumn most geese feed on agricultural lands, especially waste grain in stubble fields, sugar beet, waste potatoes and winter cereals, whereas grasslands are only used to a minor extent. In winter the geese turn to winter cereal fields and grassland, while in spring they concentrate on grassland (NILSSON & PERSSON 1984). In winter the geese spend on average 78% of the active day feeding, and the feeding activity increases inversely with temperatures (EBENMAN et al. 1976).

Past history. In November 1956 and 1958 the first counts were organized in Skåne (MATHIASSON 1963), and 16,800 and 12,800 Bean Geese were found, respectively. In comparison, the November counts between 1977 and 1980 varied between 17,900 and 28,700 individuals (NILSSON & PERSSON 1984). NILSSON & PERSSON, (1984) estimate that over the last two decades (1960 to 1980) the total autumn population has increased from about 20,000 to 40,000-60,000 geese. However, within the Swedish haunts the geese have redistributed. Thus, the importance of Tåkern has increased markedly during the last decades, whereas numbers in Skåne have remained more or less constant.

Legal status. In Norrbotten the open season extends from 1 to 15 September, in Skåne from 1 to 21 November. About 3,000 Bean Geese are bagged annually (THELANDER 1982).

Management measures and problems. Crop damage caused by grazing Bean Geese and Canada Geese has only been documented for winter rape (JÖNSSON 1982a), whereas damage to winter cereals is nonexistent or negligible (MARKGREN 1963, EBENMAN et al. 1976, JÖNSSON 1982a).

Plans to create goose refuges in order to alleviate conflicts with agriculture have been suggested (HAMILTON 1982, JÖNSSON 1982b).

Finland

Numbers and distribution. Having left Skåne in Sweden in spring, flocks of Bean Geese move on to Finland on their way to the breeding grounds. Major staging areas are found in the districts of Lumijoki, Liminka and Tyrnävä at the northeast corner of the Gulf of Bothnia (LAMPIO 1984). The first geese arrive along the west coast in the first half of April, and numbers peak in the last week of April/early May with more than 10,000 staging Bean Geese. The geese move on shortly after.

No information exists on autumn gathering places or their relative importance.

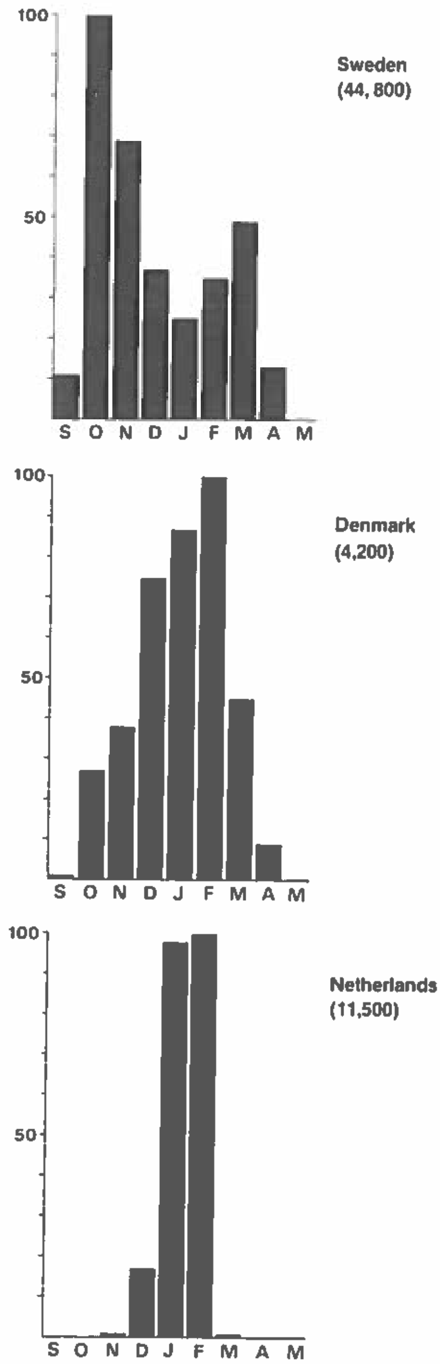


Fig. 4. Phenology of Taiga Bean Geese in three of the winter range states. Data from 1980-1984. Numbers in brackets give average maximum (= 100%). Sources, see text.

Ecology. In spring the Bean Geese feed mainly in pastures and stubble fields which are ploughed late in spring after the departure of the geese (LAMPIO 1984).

Legal status. The open season extends from 20 August to 30 November, except for southern and western districts where it starts on 1 September. 4,000 to 5,000 Bean Geese are bagged annually (ERMALA & VIKBERG 1982).

Denmark

Numbers and distribution. In Denmark two groups of *fabalis* seem to stage and winter. In northwest Jutland Bean Geese arrive in the beginning of October, dispersed over 4-5 haunts. Numbers peak in November with 2,000-3,000 individuals; in mild winters some of the geese remain, while in cold winters they leave the region totally and reappear from March to April. In southeast Denmark another group arrives in December, and numbers peak in January and February. In 1980-83 up to 6,000 geese were counted in this region (MADSEN 1986), but in the winter 1985/86 up to 17,000 have been counted (H. E. JØRGENSEN pers. comm.). The highest numbers are recorded in cold winters, when the Bean Geese leave Skåne in Sweden and migrate further south. If the cold weather continues for longer periods, the geese also leave the Danish haunts.

Ecology. In northwest Jutland most of the geese feed on grasslands, but also on winter cereal fields and stubble fields. In southeast Denmark they feed primarily on winter cereals and to a minor degree on grasslands and sugar beet (MADSEN 1986). Some of the major Danish haunts are former or partly intact peatlands. Sometimes the geese are found roosting here; elsewhere the geese roost along the coasts or on lakes.

Past history. In northwest Jutland the numbers in autumn have declined much in this century, probably due to agricultural changes, but also to drainage of peatlands which were traditional Bean Goose haunts.

Legal status. The open season extends from 1 September to 31 December. According to FOG (1977) about 300 to 600 geese were bagged annually in the 1960s.

Management measures and problems. In two of the remaining peatlands where Bean Geese are staging, drainage and reclamation continue and threaten the original habitat.

German Democratic Republic

Numbers and distribution. The information is very scant, but according to LITZBARSKI (1979) Bean Geese from Sweden *(fabalis)* stay along the Baltic coast in winter. The rossicus population is mainly distributed in the central regions of the country. No exact figures on *fabalis* numbers have been published.

Legal status. The open season extends from mid August to 31 January (LAMPIO 1983).

The Netherlands

Numbers and distribution. The *fabalis* population has nine regular wintering sites distributed in the provinces Drenthe, Friesland, Overijssel, Noord-Brabant and Limburg. The haunts are separated from the haunts of the *rossicus* population. In mild winters up to 2,000 *fabalis* reach the Netherlands, in colder winters up to 17,000-18,000 (VAN DEN BERGH 1985, NETHERLANDS GOOSE WORKING GROUP 1983, 1984a, 1984b, in press). In colder winters more sites are used, and some mixing with the *rossicus* geese occurs. Usually the first *fabalis* geese arrive in late October/early November, and numbers peak in January and February. By the end of February most geese have left the country.

Ecology. The *fabalis* geese occur in the few remaining peatlands where they mainly feed in meadows. Only in severe winters do they visit arable land feeding on winter cereals, waste potatoes and sugar beet (VAN IMPE 1980b, VAN DEN BERGH 1985). In contrast to the *fabalis,* the *rossicus* geese typically feed on arable lands on waste potatoes and sugar beet, and gradually change to grasslands as the winter proceeds. In some places the *fabalis* roost in the peatlands or on adjacent lakes, whereas the *rossicus* roost on shallow waters along the coast or on lakes and rivers.

Past history. According to references in VAN DEN BERGH (1985) the *fabalis* was formerly the more common of the two subspecies in the Netherlands, but the wintering population has declined over the present century.

Legal status. The open season extends from 1 September to 31 January, but shooting is only allowed from 30 minutes before sunrise to 10.00 a.m.

Management measures and problems. Since 1970 some of the feeding grounds have deteriorated due to drainage and development, and the goose numbers in those areas have declined (VAN DEN BERGH 1985). Most of the present roosts are refuges, while only a few of the feeding grounds are protected.

Population development

The most reliable estimate of the size of the *fabalis* population is presented by the Swedish autumn counts reviewed above. In October, when peak numbers are reached in Sweden, only less than 2,000 Bean Geese occur in Denmark. According to the counts the population has increased from about 20,000 in 1960 to 40,000-60,000 in 1977-1982 (NILSSON & PERSSON 1984, NILSSON 1981, 1984a). The increase has been reflected in the breeding population in Finland (PIRKOLA & KALINAINEN 1984), but not in the Swedish and Norwegian populations which have declined (MELLQUIST & VON BOTHMER 1982, HAFTORN 1971).

Discussion

A possible reason for the population increase is the spring shooting ban in the Soviet Union in the 1960s (PIRKOLA & KALINAINEN 1984), but other unknown factors may well have been operating.

Summarising the migration pattern of the *fabalis* population, Sweden is the principal autumn and spring staging area. In mild winters a high proportion of the population remains in Skåne, but usually most geese move on, first to Denmark, then to the Netherlands and probably the GDR. In mild winters the Netherlands are only reached by less than 2,000 birds, which may be the flocks staging in northwest Denmark until late autumn.

The population has to some extent retained its former adaptation to the mire habitat in the wintering areas. Although the geese are gradually changing habits, some flocks still feed on grasslands associated with peatlands, especially in the Netherlands, but also in Denmark and Sweden.

Management needs. In the breeding range the conservation of forest mire habitats is of vital importance for the future wellbeing of the *fabalis* population, and more efforts should be put into this matter. On the wintering grounds the *fabalis* is still associated with the peatland habitat, and the conservation of these sites is important to

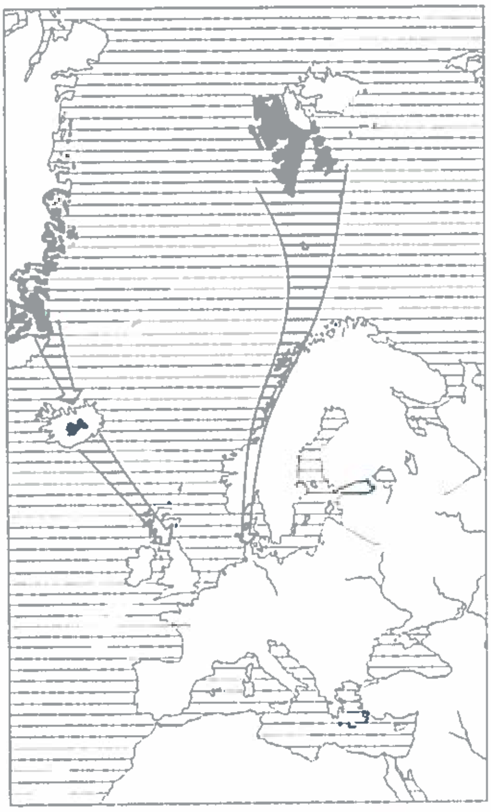


Fig. 5. Breeding distribution and migration routes of Pink-footed Geese. Sources, see text.

maintain the peculiar adaptation of this goose population.

Research needs. Very little is known about the situation of the Bean Geese and their racial distribution and ecology in the Soviet Union, and studies are badly needed.

Although a picture of the migration route of the *fabalis* population is emerging (NILSSON 1984b), more information is needed about the occurrence of the subspecies in the GDR.

Virtually nothing is known about the population dynamics of the *fabalis* subspecies. One way to get more information would be to carry out age counts and counts of family group sizes in Sweden in autumn, when most of the population is concentrated there.

Pink-footed Goose *Anser brachyrhynchus* (Svalbard population)

There are two separate populations of Pink-footed Geese in the world, one breeding in Svalbard and wintering in Denmark, the Netherlands and Belgium, another breeding in Iceland and east Greenland and wintering in the British Isles (Fig. 5). The former numbers at present about 25,000 individuals (MADSEN 1984a), the latter about 120,000 (OGILVIE 1982a, 1977-1985, unpubl.). Despite the nearness of the wintering ranges, ringing recoveries have shown that there is only a slight interchange and no net immigration or emigration of individuals between the two populations (EBBINGE et al. 1984, WILDFOWL TRUST unpubl. data).

In the following only the Svalbard population of Pink-footed Goose will be treated.

Breeding grounds and breeding ecology

According to LOVENSKIOLD (1963) and NORDERHAUG (1970) most Pink-footed Geese breed in western Svalbard, although many areas, especially in the eastern islands, are still unexplored. Compared to the other two breeding species, Barnacle Goose *Branta leucopsis* and Light-bellied Brent Goose *Branta bernicla hrota,* which are mainly concentrated to islets when breeding, the Pink-footed Geese have the widest distribution. Nesting habitats range from islets to inland tundras; lowland cliff sides beneath grassy slopes, especially close to sea bird colonies, seem to be a favourite nest site (NYHOLM 1965, NORDERHAUG et al. 1964, F. MEHLUM pers. comm.). The wider distribution of the Pink-footed Geese is probably related to their ability to protect the nest from predation by Arctic Foxes *Alopex lagopus*, an ability the two smaller species do not share (e.g. LØVENSKIOLD 1963, EKKER 1981, MELTOFTE et al. 1981). The remains of adult Pink-footed Geese are, however, sometimes found at Arctic Fox dens (M. OWEN, pers. comm.).

The Pink-footed Geese usually arrive to Svalbard during the last 10 days of May when there is still extensive snow cover, and egg laying commences from the first days of June (LØVENSKIOLD 1963). In years of late snow melt, many birds are either breeding later or are prevented from breeding at all. In those years few juveniles are brought to the wintering grounds (Table 2). Hatching usually takes place during the first half of July. Autumn migration extends throughout September into October (LØVENSKIOLD 1963). As shown for the Barnacle Geese (PROP et al. 1984), the time of mass emigration probably depends on the time of heavy snow fall.

Besides some information about breeding biology (BLURTON JONES & GILLMOR 1959, LØVENSKIOLD 1963, NYHOLM 1965, EKKER 1981) and densities (NORDERHAUG 1970, PROKOSCH 1984a), there is very little published information about the summer ecology of the Svalbard population of Pink-footed Goose. This is in contrast to the intensive studies of the breeding ecology of the Svalbard population of Barnacle Goose carried out by a team of Dutch and British scientists (PROP et. al. 1981, 1984).

Table 2. Proportion (in %) of juveniles in the Svalbard breeding goose populations, as recorded on the wintering grounds (data from M. OWEN, M.A. OGILVIE, L. SCHILPEROORD, J. MADSEN unpubl.).

Year	Pink-footed Goose	Barnacle Goose	Light-bellied Brent Goose
1980	24.2	22.7	16.5-24.2[1]
1981	5-10[2]	3.2	1.5
1982	21.8	12.0	18.3
1983	10-12[3]	8.0	5.5-8.0[1]
1984	24.7	26.2	18.3
Mean	17.8	14.4	13.0

Notes: *1:* Variation between Danish and English estimates, *2:* Variation between Danish and Dutch estimates, *3:* Only small sample.

Legal status. The open season starts 21 August, previously 1 September with a possibility of shortening in years of late spring (F. MEHLUM pers. comm.). Since 1975 the Pink-footed Goose has been protected in spring. No bag statistics exist, but probably only a few hundred are bagged annually (F. MEHLUM pers. comm.).

Management measures and problems. Fifteen small bird sanctuaries are situated on the west coast of Svalbard, however, only a few pairs of Pink-footed Geese breed there (PRESTRUD & BØRSET 1984). On Svalbard human activities, i.e. industrial and touristic, are increasing. In the forthcoming years 15-20 oil exploration companies and groups are expected to be operating (F. MEHLUM pers. comm.), which will undoubtedly cause much disturbance to breeding and moulting geese and increase their susceptibility to Arctic Fox predation, especially due to heavy helicopter traffic (see MADSEN 1984b).

Migration routes and staging areas

Until recently the migration routes of the Pink-footed Geese from their Danish spring haunts to Svalbard, and the reverse autumn routes were unknown. However, goose flocks passing through central Norway (Fig. 5) from 5 to 25 May have been identified as Pink-footed Geese (FRENGEN 1977, BOLLINGMO 1981). Most geese seem to reach the northern Atlantic coastline at

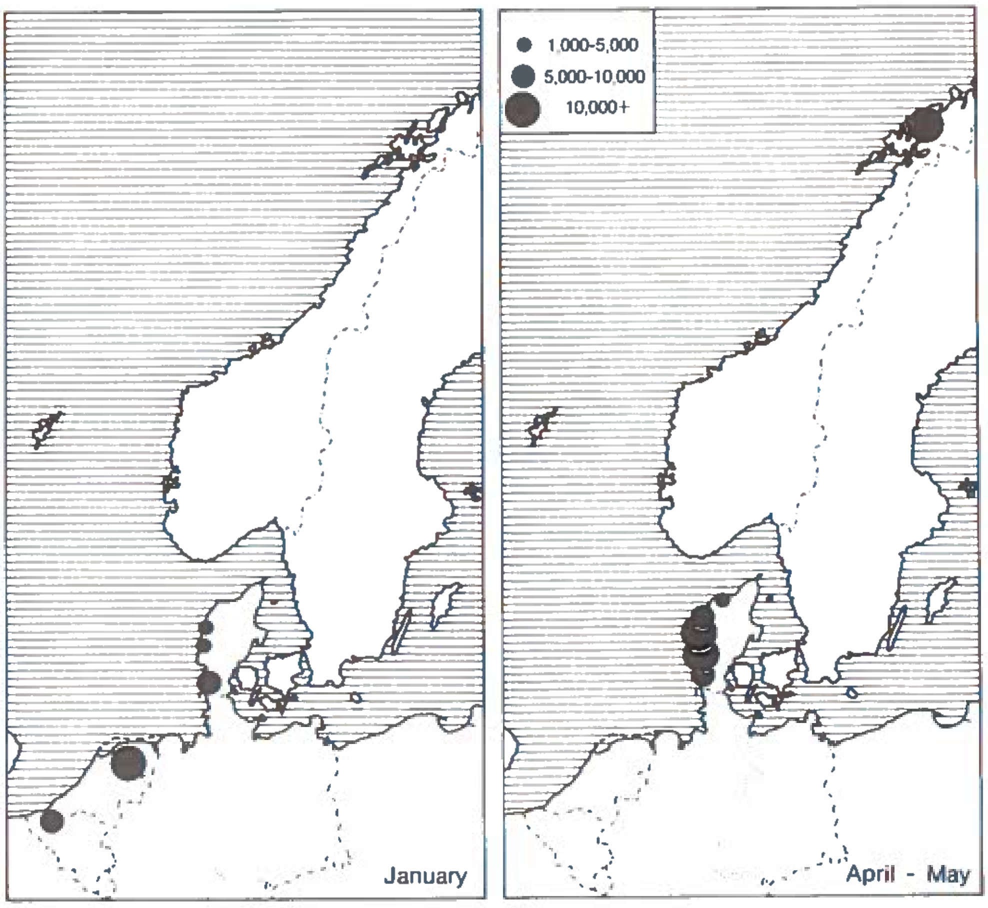


Fig. 6. Midwinter and spring distribution of the Svalbard Pink-footed Geese. Sources, see text.

Trondheim, from where they follow the coast.

A regular spring staging area has been found on the islands Andøya and Grunnfør in Nordland. Here up to 10,000 Pink-footed Geese have been recorded in mid May, and probably the entire population stops for 3-5 days (RIKARDSEN 1982, N. GULLESTAD pers. comm.). The geese leave the islands between 16 and 20 May.

The exact route from Nordland to Svalbard is still unknown, and it is also unknown whether the geese make a short stop on Bear Island or by-pass it. However, Bear Island is largely snow-covered in May, so the Pink-footed Geese probably, as do the Barnacle Geese, fly straight to Svalbard (M. OWEN pers. comm.). In autumn it is now known that flocks of Pink-footed Geese stop on Bear Island for a short time from mid September to early October (OWEN et al. 1985). The autumn migration route through Norway has not yet been described, but probably the geese follow the same path as in spring, though only stopping in Nordland for a short period (N. GULLESTAD pers. comm.).

Habitat selection. On Andøya in Nordland the geese graze in saltmarshes and fens, and only to a little extent on agricultural land (RIKARDSEN 1982, N. GULLESTAD pers. comm.). In autumn they graze the short coastal tundra on Bear Island and grub for roots in heathy habitats behind the cliffs (M. OWEN pers. comm.).

Legal status. Open season extends from 21 August to 23 December (Norway in general) (LAMPIO 1983).

Management measures and problems. There are no protected feeding and resting areas.

Wintering grounds

The wintering grounds normally range from northwest Jutland in Denmark, over FRG, the Netherlands to northwest Belgium (Fig. 6). In cold winters the range can be extended to sites in northern France (HOLGERSEN 1958, ROUX 1962). The Pinkfoot is a rare visitor in south Sweden (NILSSON & PERSSON 1982).

Below a national review of the present and past situation of the Pink-footed Goose is given. The relative distribution in the various countries through the winter season is presented in Fig. 7.

Denmark

Numbers and distribution. 12-14 sites situated in a narrow corridor along the west coast of Jutland are used by the Pink-footed Geese.

In autumn the first flocks arrive from 15-25 September (MADSEN 1980), and the staging population builds up to a peak around mid October, when the entire Svalbard population can be concentrated in the Danish haunts. Owing to shooting disturbance the geese are concentrated in only two farmland areas, holding 93% of all goose-days spent in the country in autumn, viz. Filsø and Vest Stadil Fjord (MADSEN 1986). However, in the autumns since 1981 their occurrence has changed quite dramatically. In the main haunt, Filsø, farming practice has changed; before 1980 winter crops were little used, but in the 1980s the areas of winter cereals and rape have increased (MADSEN 1986), and the stubble area, which is preferred by the geese (MADSEN 1985a) has declined. Due to the farmer's fear of damage to the winter cereals, the geese are driven off the farmland by intensified shooting pressure, resulting in an abrupt decrease in the autumn staging population. The geese now move on directly to the Netherlands, flying across the North Sea, and thus by-passing FRG. As a result the Pink-footed Geese now leave Denmark earlier than mid October, and in November only a few thousand geese remain.

As long as daily mean temperatures in winter remain below 0°C only few Pink-footed Geese winter in Denmark. However, from mid December flocks arrive from the south following 1-2 days of thaw. The geese make use of two haunts especially, in Ballum Enge with up to 16,000 individuals recorded in January and the Tipper peninsula with up to 6,000 (MADSEN 1985c, 1986). The geese probably come directly from the Netherlands.

From the end of March to the beginning of May the whole population is concentrated in Denmark. The geese make use of up to 14 sites on a chain along the west coast. Most sites are only used for a relatively short period, and there is much movement between them within short intervals (MADSEN 1984a).

Ecology. In autumn almost all geese feed on spilt grain in stubble fields (MADSEN 1984a); leaves of winter cereals are only grazed to a small extent. In winter and early spring, feeding is concentrated on grasslands, which are rough pastures and saltmarshes. Primary production on the grasslands starts at the end of March/beginning

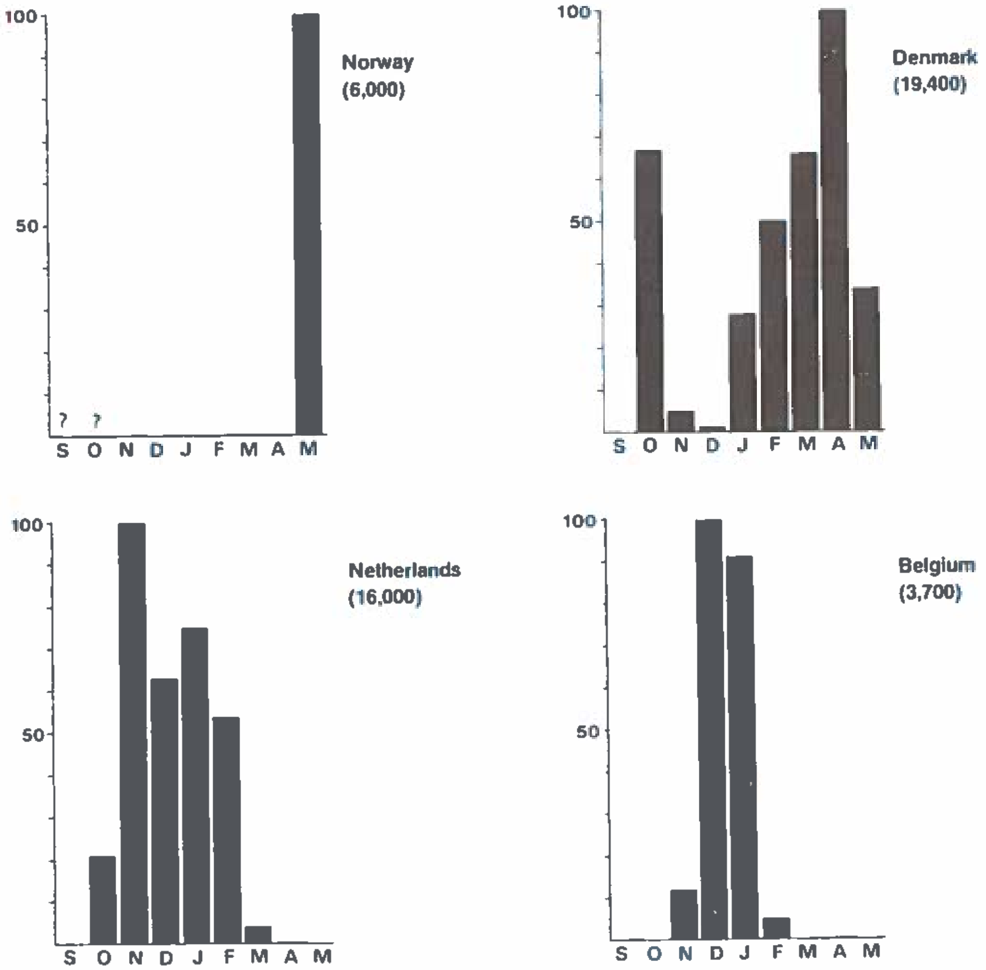


Fig. 7. Phenology of Svalbard Pink-footed Geese in the winter range states and on the migration route, expressed in percentage of peak month. Data from 1980-1985. Numbers in brackets give the average maximum (= 100%). Sources, see text.

of April, and the wintering goose flocks gradually deplete the food resources, which are not replenished (LORENZEN & MADSEN 1985). In Værnengene (the Tipper peninsula) the goose flocks have a systematic foraging routine, revisiting the same fields at intervals, until a threshold green biomass of approx. 40 g dry weight per m^2 is reached, whereupon the flocks shift to other, previously ungrazed areas. LORENZEN & MADSEN (1985) concluded that the carrying capacity of Værnengene in winter was reached at about 150,000 goose-days, or about 1,000 goose-days/ha.

As sowing of spring cereals in west Jutland commences from end of March, the goose flocks gradually shift to the newly sown fields where they pick up grain from the surface. An analysis of daily energy balance of Pink-footed Geese feeding on grassland and newly sown fields, respectively, revealed that from an energetic point of view it is of great advantage to feed in the latter habitat (MADSEN 1985b). From mid April to mid May the majority of geese feed on newly sown fields or are baited at Vest Stadil Fjord.

Past history. Before 1955 spring shooting of Pink-footed Goose was legal. The population only had few haunts in Denmark, the most important being Tipperne, where probably the entire Svalbard population could be concentrated in autumn and spring (LIND 1956, MADSEN 1980). Other known haunts were Filsø and some saltmarsh areas in the Danish Wadden Sea. In spring the geese fed entirely on grasslands, and in autumn also on stubble fields in Filsø. Following the spring shooting ban the geese gradually dispersed to other sites in west Jutland. In the late 1950s Vest Stadil Fjord, a former shallow lagoon with adjacent reed swamps, was reclaimed for agricultural land. Soon the Pink-footed Geese started to utilize the farmland, and this was the first place where they were observed to feed on the newly sown fields in spring (FOG 1982b). In the course of the 1970s a massive shift to the newly sown fields happened in many areas of west Jutland, and nowadays flocks of Pink-footed Geese are seen widely dispersed on fields even far inland, where they were unknown only five years ago (MADSEN 1984a).

Before 1979 the saltmarshes at Højer adjacent to the West German border were important staging areas for up to 3-5,000 Pink-footed Geese. However, since the marshes have been diked in 1979 most geese have abandoned the area, probably due to increased human activity and deterioration of the feeding grounds (GRAM 1982).

Legal status. The open season extends from 1 September to 31 December. Based on a questionnaire to Danish hunters, FOG (1977) estimated that 400-700 Pink-footed Geese were bagged annually in the 1960s; today the annual bag is believed to be about 1,500, based on contact with hunters in west Jutland (MADSEN unpubl.).

Management measures and problems. Due to claims of goose damage to newly sown oat fields and pastures at Vest Stadil Fjord in the early 1970s, an experiment was carried out, with the aim to keep the geese off the potentially damaged areas by means of baiting with grain (FOG 1982b). Since 1973 the Danish Game Foundation has paid for purchase and scattering of barley grain every spring; the geese have concentrated on the fields with bait, and claims of damage have almost stopped.

Claims of damage to newly sown cereal fields have also recently come from other sites, e.g. Filsø. Here the effect of goose feeding on yield structure of spring barley has been analysed in two consecutive years. A reduction of 7-20% in yield expressed in grain weight was estimated for central areas. However, much of the damage could probably be avoided by more careful drilling of the seed barley (LORENZEN & MADSEN 1986).

In only two Pink-footed Goose haunts, Tipperne and Vejlerne, are the feeding grounds and roosts protected areas, and shooting is not allowed. In four other places the feeding grounds are protected, but without shooting restrictions (MADSEN 1986).

In the 1960s the grasslands in Tipperne were overgrown, due to lack of cattle-grazing and cutting. Since 1972 a management programme was started by the Nature Conservancy Council to restore the original short-grazed habitat. During the period 1972-1978 the goose-grazed area was increased three-fold following reintroduced cattle-grazing and cutting (MADSEN 1980). However, due to the spring shift to the newly sown fields the population of Pink-footed Goose in Tipperne has declined despite the management programme.

Federal Republic of Germany

Past history. Formerly the Pink-footed Geese used sites along the German North Sea coastline (e.g., HOLGERSEN 1960, HUMMEL 1980). Four sites were important, all of which were saltmarshes and rough pastures: Emsland with maximum numbers of 2-3,000 geese, Föhr with 8-10,000, Jadebusen with up to 10,000, and Rodenäs-Vorland with up to 12,000 geese (see review by PROKOSCH 1984b). However, today none of these areas hold Pink-footed Geese in significant numbers, and in autumn and spring the geese by-pass the German haunts. On Föhr ploughing up of the goose-grazed pastures, settlement of human population, and probably increased shooting pressure in the 1950s was responsible for the population decrease; in Emsland drainage and reclamation in the 1950s; in Jadebusen increased human activity in the 1970s, and on Rodenäs-Vorland building of a seawall and subsequent increase in human activities since 1979 (see also p. 44) (PROKOSCH 1984b).

Today less than 1,000 Pink-footed Geese stay in FRG at any time during winter.

Legal status. Total protection since 1977.

The Netherlands

Numbers and distribution. Only one large area south of the town of Sneek in southwest Friesland is used by the Pink-footed Geese.

The first large flocks arrive in the second half of October; peak numbers are usually reached in November (TIMMERMAN 1977, ROOTH et al. 1981) with up to 18,000 recorded in the 1980s (SCHILPEROORD 1984). The geese have, however, since 1982 arrived about two weeks earlier (SCHILPEROORD 1984 and pers. comm.), because of the increased shooting pressure at the Danish autumn haunts. Numbers remain relatively constant until December, whereupon flocks move southwards to Belgium, and in mild winters northwards to Denmark. Normally all geese have left Friesland after the first week of February, though flocks may return later in February in response to adverse snow and frost conditions in Denmark (SCHILPEROORD 1984, MADSEN 1984a).

Ecology. Virtually all Pink-footed Geese are concentrated on grasslands, which are wet, fertilized pastures, intensively used in summer for cattle grazing and hay cutting (SCHILPEROORD 1984).

Past history. Pink-footed Geese have been known to winter in the province of Zeeland as far back as 1900. However, in around 1920 the geese abandoned the area (LEBRET 1959), and until the winter 1955/56 virtually no Pink-footed Geese occurred in the Netherlands. Then, rather abruptly, the wintering population in Friesland built up from a few hundred to about 12,000 geese (TIMMERMAN 1977); this happened in parallel with the decrease in the wintering populations in Emsland and Jadebusen in FRG. The peak number of 12,000 geese remained quite constant until the 1980s when numbers have reached a maximum of 18,000 (SCHILPEROORD 1984).

Legal status. Since 1976 the Pink-footed Goose is a protected species in the Netherlands. However, an unknown number, probably hundreds, are still shot due to misidentification by hunters (SCHILPEROORD pers. comm.).

Management measures and problems. Only a small part of the feeding grounds is protected, and there are no shooting restrictions, so disturbance from shooting restricts the available feeding grounds. In the near future the central part of the area will be reclaimed and developed as agricultural land, probably having a deleterious effect on the goose habitat (SCHILPEROORD 1984).

The earlier arrival since 1982 has caused conflicts with farming interests, because the geese graze on grasslands meant for a late hay cut (SCHILPEROORD pers. comm.).

Belgium

Numbers and distribution. One area around the small town of Damme in northwest Belgium is a regular wintering ground (KUYKEN 1969, 1985).

The Pink-footed Geese usually arrive in mid November, and numbers peak around the turn of the year. In the 1980s the annual maximum has been around 3-4,000, though in 1981/82, which was a hard winter, 11,000 individuals were recorded. The geese leave the area by the beginning of February.

Ecology. The geese graze on wet pastures grazed by cattle from April to November (KUYKEN 1969).

Past history. The first Pink-footed Geese were recorded at Damme in the winter of 1958/59 (VANDEKERKHOVE et al. 1960), coinciding with the creation of a goose reserve with no shooting. In the 1960s up to 1,000 geese wintered (KUYKEN 1969), and since then the population has increased to 3-4,000 individuals (KUYKEN 1983, 1985).

Legal status. Since 1960 there has been local protection of the geese at Damme, and since 1968/69 local, legal prohibition of goose shooting. Since 1981/82 goose shooting in Belgium has been completely banned.

Management measures and problems. Local shooting prohibition at Damme and surrounding polders has increased the available goose feeding grounds (KUYKEN 1985). Goose numbers have increased, but the geese have dispersed over wider areas, resulting in a reduction of goose grazing pressures in the traditional haunt. Claims of damage in the 1960s were shown to be groundless (KUYKEN 1969).

Population development

Only since 1980 have coordinated population counts and age counts been performed (MADSEN 1982, 1984a, JEPSEN unpubl.). In an attempt to reconstruct the population development in the 20th century, MADSEN (1982) used the annual maximum figures recorded in Denmark in spring and autumn. With some reservations these figures are believed to reflect population trends, since the geese only make use of few haunts, especially pronounced before 1955 when spring shooting was legal. In Fig. 8 a reconstruction of the population trend is depicted.

The population seems to have increased in two steps in this century:

1) from approximately 10-12,000 geese in the 1930s-1950s to 15-18,000 geese in the 1960s-mid 1970s and
2) from 15-18,000 to 21-27,000 geese in the 1980s.

In the 1980s the population has been relatively stable at about 25,000 individuals on average.

Discussion

It has been suggested (MADSEN 1982) that the first increase in the Pink-footed Goose population was caused by the spring shooting ban in Denmark, both directly because of lowered mortality, and indirectly because more feeding area became available. Our knowledge about other influencing factors is, however, too scarce to make firm conclusions.

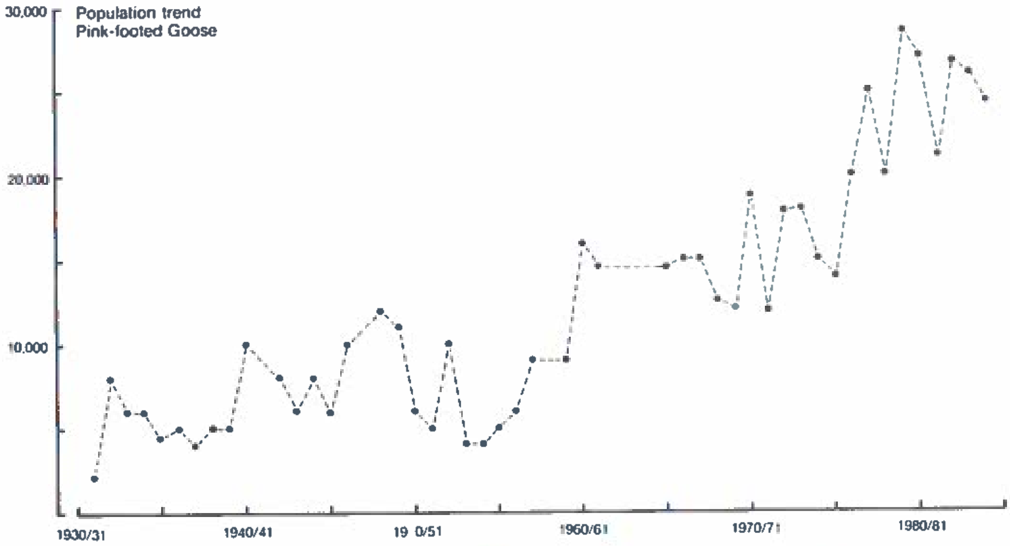


Fig. 8. Population development of the Svalbard population of Pink-footed Goose, 1930-1984 (After MADSEN 1982, 1984 and unpubl.).

The second increase may have occurred for several reasons: 1) baiting of geese at Vest Stadil Fjord in Denmark since 1973 may have improved the condition of the potential breeders, ultimately resulting in a higher recruitment to the population, 2) a spring shooting ban in Svalbard in 1975, a ban in the Netherlands in 1976 and in FRG in 1977 may have resulted in a lowered mortality. EBBINGE et al. (1984) have, on basis of ringing recoveries and goose captures in the Netherlands, calculated that the proportion of juveniles did not change significantly between the periods 1955-74, 29%, and 1975-83, 25%, whereas mortality in the two periods fell from 29% to 15%. These data suggest that the better protection of the population has been the factor causing the increase in the 1970s, whereas spring baiting seems to have played a minor role, if any.

The history of the Svalbard Pink-footed Goose in the 20th century is characteristic of many goose populations with regard to: 1) changes of wintering grounds, 2) changed feeding habits, and 3) increases in population size.

Changes of wintering grounds have taken place both within and between countries in the wintering quarters. In each case of change the reason has been attributed to human interference, either in the form of agricultural or urban/industrial development, or because shooting practices have changed. Shooting has been and still is a highly significant factor determining the winter distribution of Pink-footed Geese.

In the last decades changes in spring distribution also reflect a shift in feeding habits. This has been caused by changed farming practices in west Jutland, opening up a new habitat with an energetically favourable food resource in the form of grain. The shift to the newly sown fields has happened quite abruptly, and it cannot be ignored that – albeit alleviating a local damage problem – the baiting at Vest Stadil Fjord has accelerated the process, accustoming the population to feed on grain in spring, also producing artificially large concentrations so that all birds are quickly exposed to the habit (MADSEN 1984a). The shift would probably have happened without baiting but at a slower rate.

Problems of goose damage can be identified in autumn in Denmark and the Netherlands and in spring in Denmark. In autumn the amount of damage in Denmark is undoubtedly exaggerated (LORENZEN & MADSEN 1986). However, the tolerance of the farmer at Filsø in Denmark to the geese has lessened due to the introduction of more vulnerable crops, a problem which also applies to other damage problems. Problems in autumn have been exacerbated by increased shooting disturbance in Denmark. This has caused the large concentrations of geese in the Filsø area. Damage problems in the Netherlands also relate to the shooting pressure in Denmark.

Management needs. Both from the point of view of recreational, shooting and agricultural interests, it is desirable that a solution to the autumn situation of the Pink-footed Goose in Denmark is found. A possibility is to regulate shooting pressures in certain traditional autumn haunts, where the geese do not cause damage, e.g., Vest Stadil Fjord. A dispersal of the population over large areas will give a lower grazing pressure overall, a model used with success in Belgium (KUYKEN 1985). A goose reserve with improved grasslands is planned in the Filsø area (JEPSEN 1984). This new feeding ground will, however, not be able to hold more than a small proportion of the population, due to the relatively small size of this reserve (MADSEN 1985d).

Solutions to the spring damage problems in Denmark are not so straightforward as those in autumn. It is believed that inevitably whatever management measure is taken, the geese will to some extent continue to feed on newly sown fields. However, the present situation is not sustainable, primarily due to a growing intolerance to the geese among farmers. Some of the agricultural lands visited by geese are already marginal with respect to quality and economics, and the farmers tend to believe that the goose feeding is the factor hampering a positive economic balance. Even if experiments show that the damage is exaggerated (e.g., LORENZEN & MADSEN 1986), the farmers will probably not tolerate the presence of the geese. In a recent meeting (November 1985) arranged by the Danish Wildlife Administration with farmers and hunting clubs in west Jutland, damage problems were discussed. It was agreed that a long term solution to the problems should be sought, and that the only possibility was to establish reserves for geese. The reserves should be on managed grasslands, so that the geese would have an alternative to the newly sown fields. This should be combined with some effective scaring devices in the most vulnerable fields. The baiting at Vest Stadil Fjord has solved some local short-term problems, but as long as this continues the geese will be acquainted with grain feeding. Baiting should only be used as a last resort, if the other devices should fail. Therefore, other solutions to the problems at Vest Stadil Fjord should be tried as soon as possible.

The wintering grounds in the Netherlands are to some extent threatened by development, and there seems to be an urgent need for the protection of the central feeding grounds. Recently, more Pink-footed Geese have moved on to Belgium in winter, probably as a result of the shooting ban there. If this situation should be permanent, steps to protect the Belgian sites ought to be taken very soon.

The spring staging areas in Norway have no protection, but it is unknown if threats to the areas exist.

Research needs. At present, the knowledge of the whereabouts of the Pink-footed

Part of a flock of Pink-footed Geese on the Filsø farmland, western Denmark, autumn 1978. Due to the farmer's fear of damage to winter cereals, the majority of the geese are now driven off the area in autumn. (Photo: E. Thomsen.)

Geese through the year is patchy (see also OGILVIE 1984). Especially in late autumn and in winter a high proportion of the population is missing in the international counts (SCHILPEROORD 1984). Migration routes through Norway are being tracked, but still the importance of the staging areas is little known. To enable proper management of the population throughout the annual cycle, more international cooperation of counts and research is needed. An individual marking programme would provide the best answers to many questions concerning migration routes, the importance of the different haunts and countries, and detailed population dynamics.

There is a great need for more information on the summer ecology of the Pink-footed Geese. NORDERHAUG (1970) predicted that a limit to the population would be reached at 12-13,000 individuals due to saturation of the breeding grounds. With hindsight this has proved not to hold true, but it should be expected that the situation on Svalbard means that further population growth may be limited at a level near the present 25,000-30,000 individuals. A study of breeding biology and habitat ecology along the lines of the Barnacle Goose studies in Svalbard (PROP et al. 1981, 1984) would provide much insight to the importance of the breeding grounds in determining population levels. Again, an individual marking programme would be a very useful tool.

Much ecological work has been done recently in Denmark, whereas only little has been done in Norway, the Netherlands and Belgium. The concentration of the geese in a few places offers a good opportunity to test the 'condition hypothesis' put forward by ANKNEY & MACINNES (1978) and later by EBBINGE et al. (1982), that the body condition of geese in spring is an important factor determining breeding success. This project would need the cooperation of Danish, Dutch and Norwegian researchers.

To evaluate the effect of various shooting practices on the staging geese, a project in Denmark in autumn should be set up. This study should be aimed at giving some practical devices for limiting shooting to tolerable levels, where the geese are still enabled to use the haunts.

Greylag Goose
Anser anser anser
(northwest European population)

The breeding range of the Greylag Goose extends from Iceland in the west to the eastern coast of the Soviet Union in the east. In the western Palearctic it has a disjunct breeding distribution in northwest and central Europe and in Iceland (Fig. 9). Five populations can be identified (HUDEC 1984, OGILVIE 1982b):

1) the Icelandic breeding population wintering in Scotland with about 80,000 geese (OGILVIE 1977-1985);
2) a resident population in northwest Scotland of 2,000-2,500;
3) the northwest European breeding population wintering in southern Spain and the Netherlands, about 130,000 geese (J. ROOTH pers. comm.), here referred to as northwest European population;
4) the central and northeast European breeding population wintering in north Africa, about 20,000, here referred to as the central European population, and
5) the west Soviet Union breeding population wintering in the south of the Balkan peninsula and the western part of Asia Minor, possibly about 20,000-30,000 geese.

During the present century Greylag Geese have been introduced in several parts of Europe, and today most of these are not possible to distinguish from the wild stock. Whereas the British populations seem to be discrete, the dividing lines between the con-

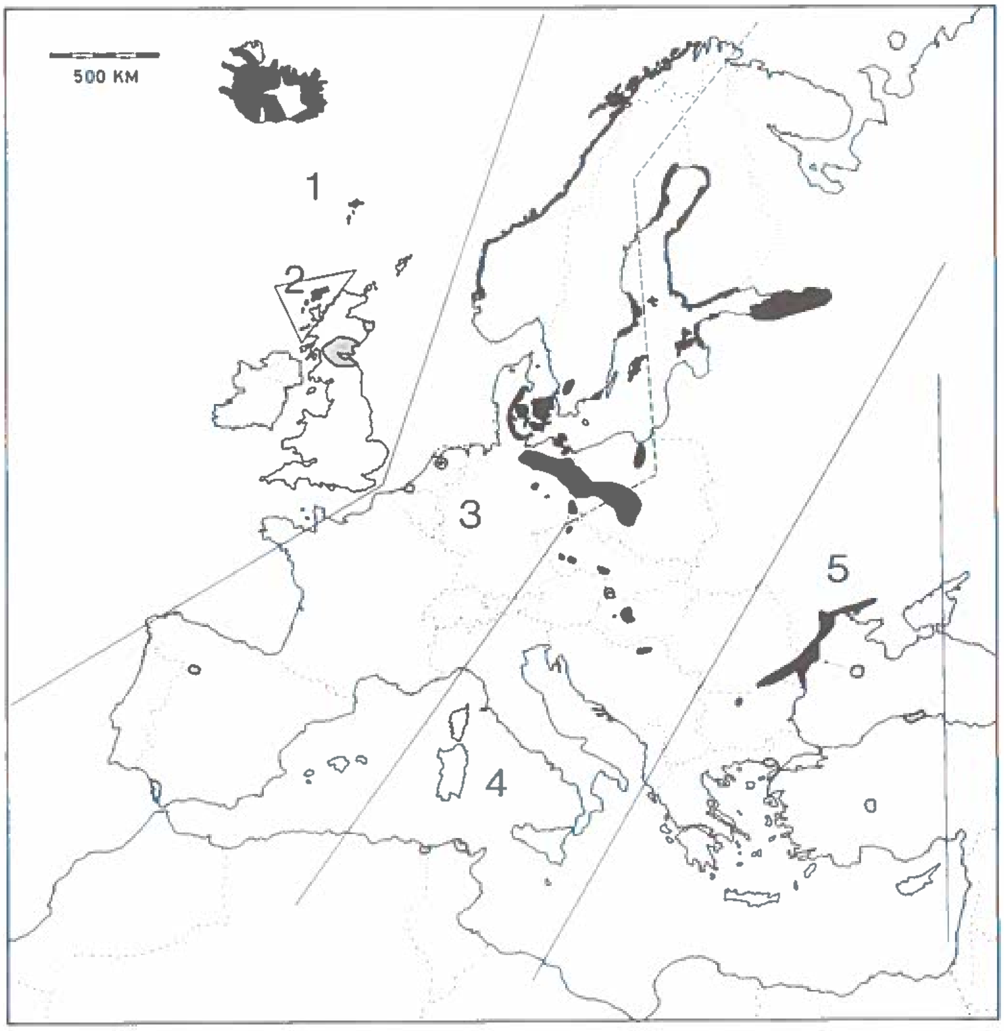


Fig. 9. Populations of Greylag Geese in Europe. 1: the Icelandic/Scottish population, 2: the north Scotland population, 3: the northwest European population, 4: the central European population, and 5: the east European population. Breeding areas are black, wintering areas hatched. Punctuated lines indicate that the border lines between flyways are not well known. (After HUDEC 1984, with a few amendments).

tinental populations are not quite clear, and ringing recoveries show that some mixing occurs. Thus, non-breeding individuals from the central European population move to moulting grounds in the range of the northwest European population (PALUDAN 1965, VON ESSEN & BEINERT 1982, GROMADZKI & MAJEWSKI 1984).

Ringing schemes which are presently under operation in Scandinavia under the auspices of the Nordic Council for Wildlife Research and in central Europe by East German, Polish, Czechoslovakian and Austrian biologists will hopefully throw more light on the movement patterns of populations in the near future. Much of the present knowledge of population dynamics and migration of the European Greylag Geese has been compiled by HUDEC & RUTSCHKE (1982, 1984).

In the present review only the status and management of the northwest European population will be treated, including the states of Norway, Sweden, Denmark, GDR, FRG, Poland, the Netherlands and Spain. The population breeds in all these states, except Spain, and winters in Spain, the Netherlands and in small numbers in Norway, FRG and Denmark. Besides these countries an introduced population of approx. 300 birds breeds and winters in Belgium (LIPPENS 1971). Generally a few hundred to 2,000 stay in France during autumn and winter (ROUX 1962, C. RIOLS, unpubl.), and a few hundred winter in Portugal (OGILVIE 1978).

Breeding grounds and breeding ecology

The center of gravity of the breeding area of the Greylag Goose lies in the southern Baltic, viz. Denmark, Schleswig-Holstein in the FRG, north GDR and southwest Sweden (Fig. 3). The estimated size of the breeding population in the various range states is given in Table 3. The total for the population is thus estimated at 12,050 to 12,800 pairs. It must be noted, however, that the estimates are rough, as the assessment of the breeding geese is difficult due to their dispersed nesting, and furthermore because the estimates stem from different years. From Norway there exists no information about the total population size, but OGILVIE (1978) thought that it must be in the order of at least 2,000 pairs, which does not seem unrealistic and is probably an underestimate. The Norwegian Greylag Geese breed on small islands along the North Atlantic coastline, and are thus almost impossible to count. In several of the countries Greylag Geese have been introduced, and this category of breeders is very difficult to distinguish from the wild breeding population and is inevitably included in the figures. In Table 3 the total estimated breeding stock of Poland is included, although new data have shown that the Greylag Geese breeding in southern Poland seem to belong to the central European population (GROMADZKI & MAJEWSKI 1984). At present it is not known how many of the Polish birds move south to Central Europe. From ringing recoveries it is now evidenced that Estonian Greylag Geese belong to the central European population (KUMARI 1984).

Table 3. Estimate of the breeding pair numbers in the northwest European population of Greylag Goose.

Country	Breeding pairs	Source
Norway	(2,000)	OGILVIE 1978
Sweden	1,700-2,200	NILSSON 1982
Denmark	2,850-3,000	FOG et al. 1984
Poland	1,150	GROMADZKI & WIELOCH 1983
GDR	3,000	RUTSCHKE et al. 1982
FRG	1,000-1,100	HUMMEL 1982
Netherlands	320	DUBBELDAM & POORTER 1982
Belgium	30	LIPPENS 1971
TOTAL	12,050-12,800	

The breeding biology of the Greylag Geese has been described in detail by HUDEC & ROOTH (1970). Apart from the major phenological events, breeding will not be given much space here.

The adult Greylag Geese arrive on the breeding grounds in Denmark from the end of February to mid March (JENSEN 1977, MØLLER 1978), while the younger birds lag up to one month behind. In the FRG the first geese arrive from the end of January to the end of March (HAACK 1968), in the GDR from the beginning of February to the beginning of March (LITZBARSKI

1982), whereas in Norway the arrival is about one month later than in the GDR (HAFTORN 1971). Major stopping places between the wintering and breeding grounds are known from the Netherlands (ROOTH et al. 1981) and from the Wadden Sea coastline of the FRG (HUMMEL 1982).

The most frequently used nesting habitat is eutrophic fresh water with dense emergent vegetation, mostly reedbeds, with ready access to feeding grounds constituting meadows and pastures. In Norway and Sweden islets are common breeding habitats.

In Denmark and the GDR egg-laying usually commences from mid March (N. O. PREUSS pers. comm., HAUFF 1982, JØRGENSEN 1986). Peak hatching is in the last week of April, peak fledging in the end of June to mid July. The timing of egg-laying is, however, highly dependent on ice conditions on the nesting grounds (KUX & HUDEC 1970, PREUSS pers. comm.). In Norway eggs hatch during the last week of May, and young fledge during the first week of August (FOLKESTAD 1983).

Moult migration and moulting grounds

In the first half of the breeding season non-breeding Greylag Geese gather in small assemblages on the breeding grounds. In the GDR the non-breeders move away from most breeding grounds from mid March to end April and aggregate in a few traditional sites where they stay until end of May (RUTSCHKE 1982, LITZBARSKI 1982). In the GDR thus between 8,000 and 10,000 non-breeders are counted in mid May. From Holstein in the FRG similar May assemblages have been described (HAACK 1968).

In the course of May most non-breeders migrate to moulting centres situated in Norway, Sweden, Denmark, the Netherlands and Poland. The moult migration pattern is rather complex, and the northwest European moulting centres do not only receive geese from the northwest European population, but also from the central European population (PALUDAN 1965, HAACK & RINGLEBEN 1972, VON ESSEN & BEINERT 1982, GROMADZKI & MAJEWSKI 1984). The pattern is furthermore complicated by the fact that within the past decades some moulting areas have lost their value while others have been newly colonised or have increased in importance (see below).

Arrival on the moulting grounds in Denmark, the Netherlands and Sweden takes place in the second half of May (PALUDAN 1965, LEBRET & TIMMERMAN 1968, VON ESSEN & BEINERT 1982), and most geese seem to start to shed remiges by the end of May or the beginning of June, regaining the powers of flight 25-30 days later. In Ranafjord in Norway the geese do not regain

Table 4. Major moulting grounds for Greylag Geese in northern Europe.

Site and Country	Number of Geese	Year	Source
Oostvaarderplassen, Netherlands	20,000	1980-83	ROOTH pers. comm.
Vejlerne and Saltbækvig, Denmark	5,000	1980-83	MADSEN 1986
Gotland, Sweden[1]	3,300-5,400	1974-79	VON ESSEN & BEINERT 1982
Ranafjord etc., Norway	19,000	1985	FOLLESTAD et al. 1986
Słońsk, Poland	2,000	1980 (?)	GROMADZKI & MAJEWSKI 1984

Note: 1: Numbers have decreased to less than 2,000 since 1979.

flight before the second half of July (LUND 1965).

As a rule the moulting grounds are only used by the non-breeding Greylag Geese for a short period. Shortly after having regained the powers of flight most geese leave the areas, probably mostly in the direction of their homeland – from Scandinavia towards the southeast, and from the Netherlands towards the northeast and east. Neckbanding in the GDR has shown that 90% of the non-breeders leaving in May return to the country in July and August (LITZBARSKI 1982).

Below an outline of the present situation and the past history of the major moulting centres is given. In Table 4 the number of geese visiting the moulting grounds in the respective countries is shown.

Norway. Three islands on the coast of northwest Norway are known to be moulting grounds: Vega with 2,000 individuals, Vikna 500 and Smøla 100 (LUND 1965, 1971). From 1961-63 to 1971 the number of moulting geese around Vega doubled. In 1985 much of the Norwegian coastline has been searched, and 19,000 moulting Greylag Geese have been found (FOLLESTAD et al. 1986).

Denmark. Two moulting grounds exist at present: Vejlerne holds up to 1,000 individuals and Saltbækvig 2,000-3,000 (MADSEN 1986 and unpubl.). In the 1950s probably more than 3,000 non-breeding Greylag Geese moulted in Vejlerne, but since 1959 numbers declined sharply (PALUDAN 1965). Since the end of the 1960s, birds have been using Vejlerne again, although in smaller numbers.

Sweden: At present Greylag Geese moult around Gotland in the Baltic. In the 1970s up to 5,400 were recorded, but since 1979 numbers have declined (VON ESSEN & BEINERT 1982). Gotland was colonised in the 1950s, possibly in connection with the decrease in the Vejlerne population. Besides Gotland only two minor moulting grounds exist. During the 19th century the island of Hallands Väderö off northwest Skåne was a moulting ground for some hundreds of Greylag Geese (ANDERSSON 1969), but the geese had abandoned the area by the turn of the century, probably due to a heavy shooting pressure.

The Netherlands. Nowadays moulting Greylag Geese are found only in Oostvaarderplassen in Southern Flevoland (ROOTH pers. comm.). Southern Flevoland was reclaimed in 1968, but 5,000 ha of reed swamp and shallow lakes were maintained as a nature reserve. Since the 1970s Greylag Geese have been moulting here in increasing numbers, in 1974 more than 2,000 individuals (DUBBELDAM 1978), in 1980 6,000 (DUBBELDAM & POORTER 1982), and in 1984 20,000 (ROOTH pers. comm.). On their arrival the Greylag Geese feed on grass and during moult on *Phragmites* leaves and stems (DUBBELDAM & POORTER 1982).

Simultaneously with the increase in numbers in Oostvaarderplassen, two other moulting grounds fell into disuse, Steile Bank in Gaasterland and the Haringvliet in the Delta region, where up to 2,000-5,000 and 1,300 geese, respectively, moulted in the 1960s (LEBRET & TIMMERMAN 1968, OUWENEEL 1969, DUBBELDAM & POORTER 1982). Steile Bank was colonised for the first time in 1960, coinciding with the decrease in the Danish Vejlerne population.

Poland. A moulting ground at the Warta and Odra river confluence in the Słońsk region in west Poland receives between 1,400 and 2,500 Greylag Geese (GROMADZKI & MAJEWSKI 1984). These birds seem to originate mainly from the central European breeding grounds.

Autumn staging areas and wintering grounds

Following the fledging of the young and the regained powers of flight of adults in July the Greylag Geese gradually move to autumn gathering haunts (see RUTSCHKE 1982) where they remain until the emigration to the wintering grounds. Most non-breeders seem to return to their homeland from the moulting centres and join the family parties on the autumn haunts. The distribution in September is shown in Fig. 10, the known mid September concentrations in Table 5. In Fig. 11 the seasonal phenology in six range states is presented.

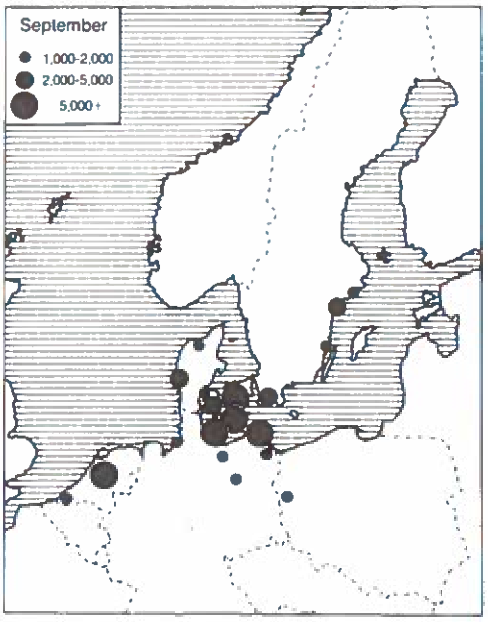


Fig. 10. September distribution of Greylag Geese in northwest Europe (northwest European population). Sources, see text.

Norway

Numbers and distribution. No autumn staging areas are known from the literature, but some probably exist along the Atlantic coast. However, shooting disturbance is thought to cause many Greylag Geese to leave the breeding and gathering grounds prematurely in August (FOLKESTAD 1983). Southerly migrating flocks are seen at Jæren in southwest Norway from September to November (BYRKJEDAL & ELDØY 1981).

Table 5. The estimated size of the mid September population of the northwest European Greylag Geese. Most data stem from the late 1970s or early 1980s.

Country	Mid September number	Source
Norway	> 1,000	no reference
Sweden	11,000-13,000	ANDERSSON 1982
Denmark	19,000-29,000	MADSEN 1986
Poland	> 1,000	MAJEWSKI 1983
GDR	35,000-40,000	RUTSCHKE et al. 1982
FRG	6,000-8,000	HUMMEL 1982
Netherlands	20,000	ROOTH pers. comm.
TOTAL	93,000-112,000	

The Norwegian data seem to be conflicting, but goose flocks may leave the country unnoticed before September.

At Jæren, and also in other sites in southern Norway, flocks of few hundred Greylag Geese stay through the winter, favoured by the relatively mild Atlantic weather conditions (BYRKJEDAL & ELDØY 1981).

Ecology. In autumn the geese feed on pastures (HAFTORN 1971) and probably also on saltmarshes.

Legal status. The open season ranges from 21 August to 23 December (LAMPIO 1983).

Management measures and problems. On the island of Smøla the season has been opened from 10 August, mainly to avoid crop damage (FOLKESTAD 1983). At this time not all goslings have fledged and not all adults have completed moult of remiges.

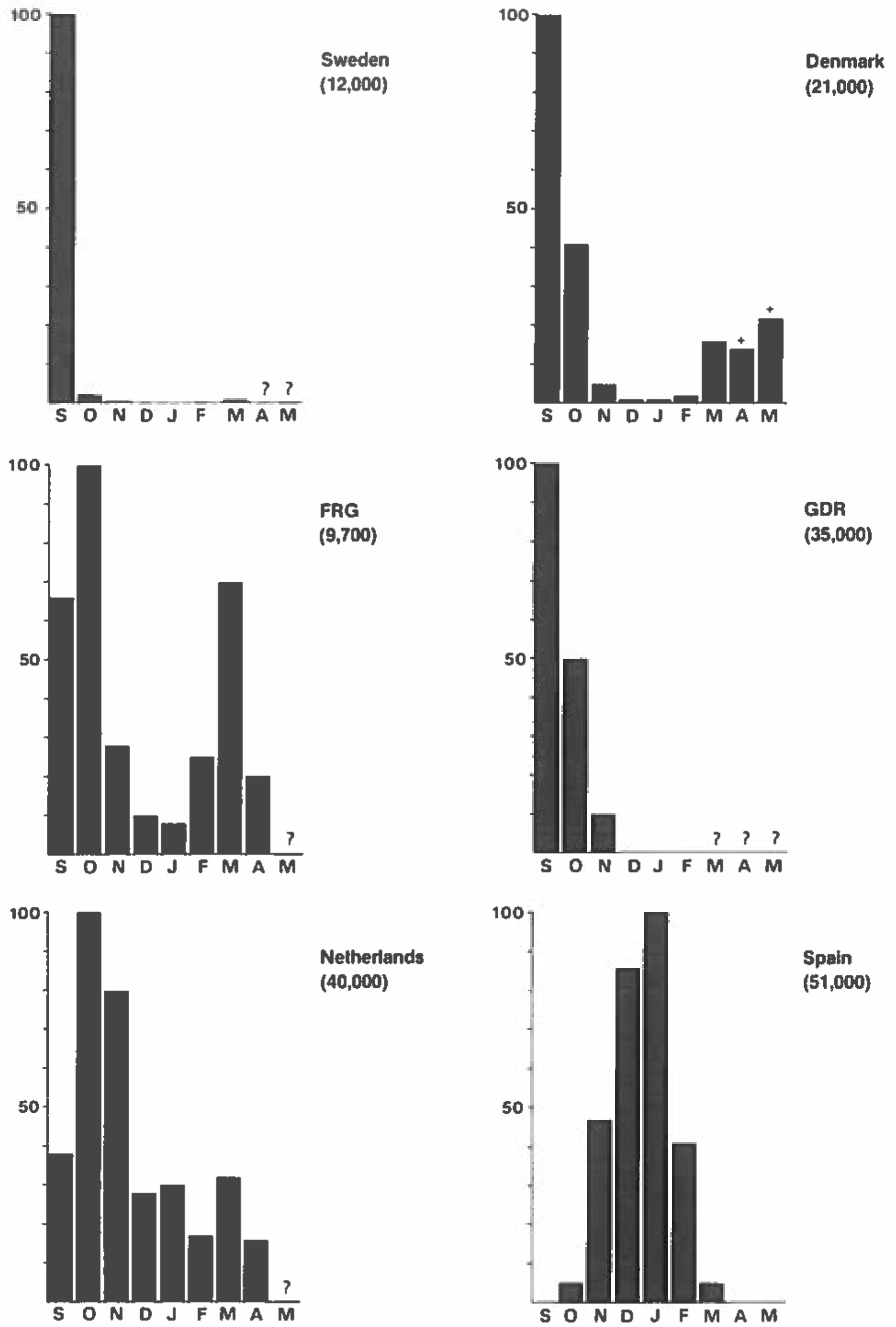


Fig. 11. Phenology of Greylag Geese in six range states of the northwest European population, expressed in percentage of peak month. Numbers in spring have been underestimated in the breeding range states. Most data from 1980-1984. Numbers in brackets give average maximum (= 100%). Sources, see text.

Sweden

Numbers and distribution. In early autumn 12,000 to 20,000 Greylag Geese gather in Götaland and Svealand in south Sweden (ANDERSSON 1982, GREYLAG GOOSE PROJECT OF THE NORDIC COUNCIL FOR WILDLIFE RESEARCH unpubl.). The geeese arrive from the breeding grounds in July, and numbers reach their peak in September. Emigration takes place quickly after mid September, and in mid October only a few hundred are left in the country (NILSSON 1984a).

Ecology. The Greylag Geese feed on saltmarshes, stubbles, rape and clover fields (EHRLÉN & WAHLÉN 1979). The diurnal rhythm is diphasic, feeding occurring mainly in the morning and evening.

Past history. From the late 1960s to 1981 the number of Greylag Geese in most of the gathering places has increased by more than a three-fold (ANDERSSON 1982, EHRLÉN 1983).

Legal status. The Greylag Goose is protected in all counties except Kalmar, where there is an open season from 20 July to 31 August to avoid goose damage to crops (THELANDER 1982). About 1,000 Greylag Geese are bagged there annually.

Management measures and problems. In some areas grazing by Greylag Geese on clover fields causes damage (PETTERSON 1985).

Denmark

Numbers and distribution. From the end of July to the beginning of August the Greylag Geese move from the widely dispersed breeding grounds to the autumn gathering grounds (MADSEN 1986). The autumn peak numbers are reached in mid September with 20,000 to 30,000 geese (MADSEN 1986, GREYLAG GOOSE PROJECT OF THE NORDIC COUNCIL FOR WILDLIFE RESEARCH unpubl.). From the beginning of October numbers decline, and by mid November usually less than 1,000 Greylag Geese remain. Usually almost no geese winter, but in mild seasons a few hundred may stay at Tipperne in west Jutland (MADSEN 1985c).

Ecology. In autumn most Greylag Geese feed on stubble fields, followed by pastures and meadows. Winter cereals and sugar beet are used to a small extent. In July and August flocks may feed on ripening cereals (MADSEN 1986). The usual diurnal pattern is that the Greylag Geese feed around dawn and dusk and roost on lakes or lagoons during day and at night.

Past history. Within the last decade the autumn staging population has doubled. In the 1960s and 1970s 11,000 to 18,000 geese were counted in September, in the 1980s up to 32,000 (FOG 1977, MADSEN 1986, GREYLAG GOOSE PROJECT OF THE NORDIC COUNCIL FOR WILDLIFE RESEARCH unpubl.). In the same period the breeding population has increased considerably (FOG et al. 1984). Based on ringing recoveries PREUSS (1982) estimated an annual increase of approximately 9% in the Danish breeding population in the 1970s.

Legal status. The season is open from 1 August to 31 December. In the 1960s it was estimated that at least 1,500 to 1,700 Greylag Geese were bagged annually (FOG 1977). Today probably more than 5,000 geese are shot each year.

Management measures and problems. In most autumn haunts shooting is regulated by means of game reserves or privately (MADSEN 1986). However, in some haunts the staging Greylag Goose populations have recently decreased due to intensified shooting disturbance.

Greylag Geese feeding on ripening cereals in summer cause local damage to crops. From 1972 to 1981 a total of 25 farmers have received licenses to shoot Greylag Geese to avoid the damage. However, according to J. FOG (1982), probably less than 100 geese have been shot during the whole period.

German Democratic Republic

Numbers and distribution. After return of the non-breeding geese from the moulting grounds and the fledging of young a summer migration takes place to the 20-25 traditional gathering places. By mid August 25,000 geese are in the country (LITZBARSKI 1982). In the second half of August flocks of Scandinavian and east European Greylag Geese move to the GDR, and in mid September a peak number of 35,000 to 40,000 is reached. Most of the geese from the central GDR move to autumn gathering grounds along the coast. From mid September to mid November the geese leave the country, and only few geese are wintering there.

Ecology. In summer and early autumn most geese feed in stubble fields and on pastures. Only to a small extent do the Greylag Geese feed on winter cereal fields (RUTSCHKE et al. 1982).

Past history. Within the last decades the breeding population has increased considerably (HAUFF 1982, NAACKE 1982). The autumn population has increased accordingly, although this has not been quantified.

Legal status. The open season extends from 16 July to 31 January. In the 1970s on average 360 Greylag Geese were bagged annually (RUTSCHKE et al. 1982).

Management measures and problems. Most of the gathering places are protected areas with shooting regulations or prohibition. According to RUTSCHKE et al. (1982) damage problems are not severe.

Poland

Numbers and distribution. Only a small amount of information exists. According to GROMADZKI & MAJEWSKI (1984) Greylag Geese stay in the country until October or November, and virtually no geese winter. Based on data presented by MAJEWSKI (1983) there seems to be an autumn population of about 1,000 geese in the Słońsk area alone, and the total for the country is probably much higher.

Past history. The breeding population has increased considerably during the last decades (GROMADZKI & WIELOCH 1983, MAJEWSKI 1983).

Legal status. The open season extends from 20 August to 10 February in the western part of Poland, and from 20 August to 30 April in the eastern and northern parts (GROMADZKI & WIELOCH 1983).

Federal Republic of Germany

Numbers and distribution. The most important autumn gathering grounds are situated in east Schleswig-Holstein and north Lower Saxony (HAACK 1968, HUMMEL 1982, 1977-1984, KNIEF pers. comm.). The flocks gradually concentrate in few places, reaching a peak of up to 12,000 individuals in October. Most of the geese in Schleswig-Holstein leave during October, whereas in Lower Saxony the geese stay until the onset of frost in November. Up to 1,000 Greylag Geese winter at the Elbe Estuary and along the East Friesian coast.

In cold winters the geese move on to the Netherlands (HUMMEL 1982).

Ecology. In summer and autumn Greylag Geese mainly feed on pastures, in stubble fields and to some degree in ripening cereal fields (HAACK 1968, KNIEF 1985, BRUNS & VAUK 1985-1986).

Past history. From 1974 to 1980 the autumn population has been steadily increasing (HUMMEL 1977-1984), and in Warder Lake in Holstein the population tripled from less than 500 to 1,500 geese from 1960 to 1967 (HAACK 1968).

Legal status. The open season is divided into two periods: 1-31 August and 1 November-15 January from half an hour before sunrise to 10.00 a.m. In Schleswig-Holstein the season is further restricted, and in Lower Saxony the Greylag Goose is protected throughout the year (HUMMEL 1982).

Management measures and problems. In Schleswig-Holstein the Greylag Geese cause damage to ripening cereals and cattle-grazed pastures. In the bird-sanctuary Wallnau on the island of Fehmarn Greylags have been baited with grain to alleviate local crop damage. Some compensation is paid to farmers (KNIEF 1985), in Schleswig-Holstein amounting to 7,500-25,000 DM annually (1980-1983), in the Dümmer in Lower Saxony 67,000 DM (total amount from 1976-1981).

The Netherlands

Numbers and distribution. The autumn population gradually builds up from August onwards, to reach peak in October and November of between 21,000 and 51,000 geese (ROOTH et al. 1981, NETHERLANDS GOOSE WORKING GROUP 1983, 1984a, 1984b, in press). Ringing recoveries have shown that most of the autumn staging geese come from the Scandinavian breeding grounds (ROOTH 1971). From mid November numbers decline, but 10,000 to 13,000 remain the whole winter.

In autumn most Greylag Geese stay in Oostvaarderplassen in Southern Flevoland, whereas the main winter concentrations are found further south in the Haringvliet area in the Delta region.

Ecology. In the Oostvaarderplassen both breeding, moulting and autumn staging geese feed on *Typha latifolia* and *Phragmites autralis* green parts and rhizomes (DUBBELDAM 1978, DUBBELDAM & POORTER 1982). By virtue of their feeding activity the Greylag Geese have been found to play a major role in the maintenance of the ecosystem of the open *Phragmites* marsh. In autumn when high numbers are present, flocks also make feeding flights to adjacent farmland fields of winter rape, and in winter to pastures and winter cereal fields.

Before the construction of the barrage in the Haringvliet in 1970 the wintering Greylag Geese there fed on *Scirpus* and pasture grasses (ZWARTZ 1972, OUWENEEL 1981), but since the tidal movements were nullified and the water became fresh the *Scirpus* areas disappeared. The geese now feed on fields with sugar beet and pastures in autumn and on pastures in winter (OUWENEEL 1981).

Past history. During the last two decades the Greylag Geese have been increasing greatly in numbers. In the 1960s 8,000 to 12,000 geese stayed in autumn and about 2,000 in mid January (ROOTH 1971), in the 1970s 21,000 to 38,000 geese stayed in autumn and about 10,000 in winter (ROOTH et al. 1981), and now up to 51,000 in autumn and 13,000 in winter.

Concurrently with the successive drainage of the Ijsselmeer polders from the

1940s to the 1970s, the Greylag Geese have moved considerably between sites, making use of the temporarily created marshlands which were – apart from the Oostvaarderplassen – later turned into farmland (ROOTH et al. 1981).

Legal status. The open season ranges from 10 October to 31 January from half an hour before sunrise to 10 a.m.

Management measures and problems. No severe crop damage by Greylag Geese has been reported. The Oostvaarderplassen has been preserved as a waterfowl reserve, and the water levels are managed to optimize the conditions for the breeding and resting birds.

Spain

Numbers and distribution. The Marismas (marshes) of the Guadalquivir River in south Spain are the main wintering area of the Atlantic flyway of Greylag Geese (SANCHEZ et al. 1977, AMAT 1986b). The wintering population has increased greatly, and in the 1980s 60,000 to 75,000 geese or about 70% of the flyway population winter in the Marismas. In the winters of 1980/81, 1981/82 and 1982/83 severe droughts occurred, and in 1980/81 about 10,000 Greylags died, mainly from starvation.

The first Greylag Geese arrive in the Marismas in September and numbers peak in December and January. By mid March almost all the geese have migrated north.

Greylag Geese started to winter in the salinas of Villáfafila in the Zamora province in northwest Spain in the late 1970s, and so far numbers have increased to more than 5,000 geese (counts by the Spanish Ornithological Society, submitted by J. AMAT).

In the winter of 1983/84 the population in Spain was estimated at 120,000 Greylag Geese (J. CASTROVIEJO pers. comm. to J. ROOTH).

Ecology. In winters with normal hydrological conditions in the Marismas the Greylag Geese concentrate just after arrival on flooded areas of *Scirpus littoralis.* Later, when other marsh zones become flooded, the geese move to areas of *Scirpus maritimus,* whose rhizomes constitute the main diet of the geese. They pull out the plants from the watersoftened ground with their bills (SANCHEZ et al. 1977, AMAT 1986a, b).

The feeding sites are usually within 100-500 m of the roost. The geese feed in the morning and late afternoon, roosting during most of the daytime (AMAT 1986b).

Under drought conditions the geese are unable to pull the *Scirpus* plants from the dry, hardened ground, and they have to spend more time feeding and with a reduced energetic return (AMAT 1986a). In the winters of 1980/81 to 1982/83 the geese made increasing use of other habitat types, such as winter cereal fields, stubble rice and pastures situated 1-5 km from the roosts (AMAT 1986b).

In the winters of 1983/84 and 1984/85, when the hydrological conditions were normal, the geese have probably as a result of the population increase in the Marismas also been using pastures, which is unusual in rainy seasons. This may indicate that the carrying capacity of the *Scirpus* habitats has been reached (AMAT 1986b).

Past history. Counts are available from the Marismas since the middle of this century. BERNIS (1964) stated, probably referring to the 1940s-1960s, that 5,000 to 10,000 Greylag Geese spent the winter there. In the winter of 1967/68 19,000 Greylag Geese were counted (BERNIS & VALVERDE 1972) (from the same season ROOTH (1971) gives the number of 25,000 geese); in the first half of the 1970s about 20,000 (SANCHEZ et al. 1977), and in the second half up to 75,000 geese (AMAT 1986b).

Legal status. The open season extends from mid September to the beginning of February. In years of severe drought (e.g., 1980/1981) the season may be closed. SANCHEZ et al. (1977) estimated that in years of flooding 1,500 to 2,000 geese were bagged in the Marismas, in drought years 6,000 to 7,000. Since 1981/82 shooting in the Donana National Park has been banned, probably resulting in a reduced kill. AMAT (1986b) writes that within the last two decades shooting pressure in the Marismas has declined considerably.

Management measures and problems. Part of the Marismas is a national park with restrictions on traffic and shooting. To the north of the national park the Marismas have been drained for agricultural purposes and the water contaminated with pesticides. As a consequence of these transformations the Marismas have suffered serious pertubations in the water inflow regime (AMAT 1986b). This has accentuated the problems in years with severe droughts. The national park area is entirely depending on its water supply from several rivers, but today only one flows into the area. A 'Water Supply Regeneration Plan' has now been initiated, aimed at increasing the water inflow and securing flooded marshlands under drought conditions.

Population development

Based on the results of mid-winter counts from Spain, the Netherlands and the FRG since 1967/68, a population trend as depicted in Fig. 12 is derived. It is, however, uncertain whether the graph gives a proper picture of the trend. In years with drought (1980-83) the Greylag Geese disperse over wider areas in the Marismas and it is therefore likely that some flocks have not been counted. The figures from the winters 1980/81, 1981/82 and 1982/83 are thus believed to be underestimates.

The trend is indicating an exponential growth over the last two decades, and within the last decade the population has increased by a four-fold, equivalent to an annual rate of increase of 13%. As it has been shown above, the development has been reflected simultaneously in all range states.

Discussion

The impressive growth in the Greylag Goose population has taken place despite the deterioration of the conditions in the Guadalquivir Marismas, where the droughts within a single season caused the death of 10,000 Greylag Geese. It cannot at present be said what has been the decisive factors causing the increase. Three factors have to be considered:

1) *A net immigration of geese from the other populations.* As shown above there is no clear-cut borderline between the northwest European and central European populations, and some mixing seems to occur. However, if there had been an immigration from the latter to the former, it would have been apparent from the intensive ringing schemes operating in both ranges. This has not been observed, and therefore this factor seems not to have been significant.
2) *A lowered mortality.* The harvest of the Greylag Geese along the migration route has been considerable. The annual bag in the 1970s probably exceeded 10,000 geese, and a relaxation of the shooting pressure may have caused the increase. In south Spain the shooting pressure has decreased over the last decades (AMAT 1986b), in Poland spring shooting has been banned since 1976 (MAJEWSKI 1983) and, possibly most significantly, an increasing proportion of the autumn population has been attracted to the Oostvaarderplassen refuge in the

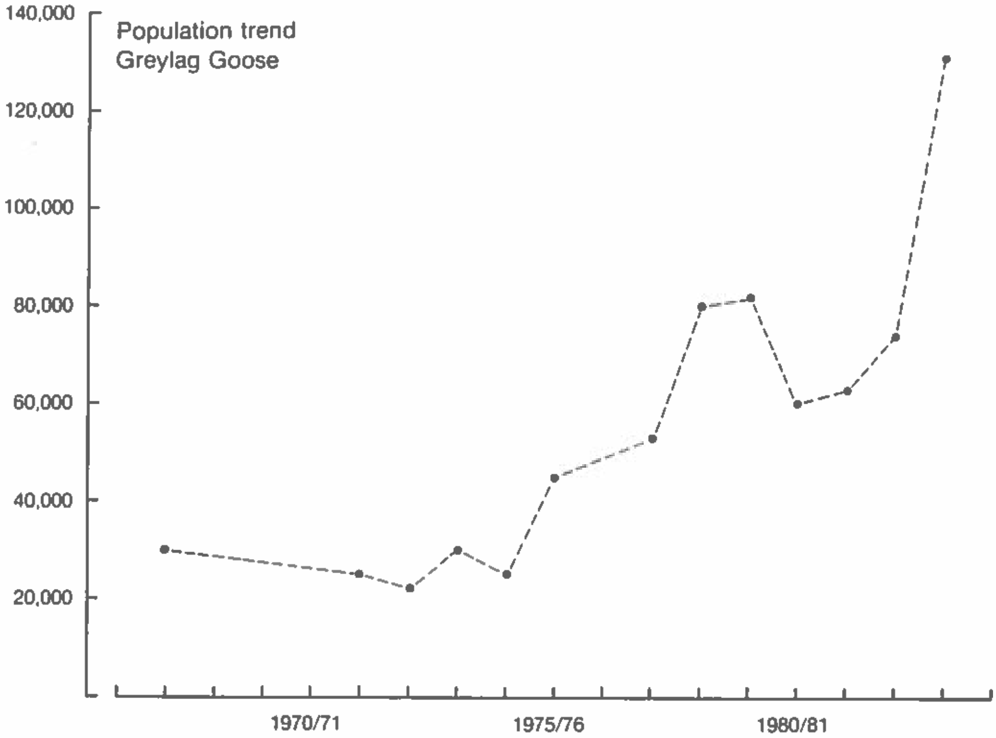


Fig. 12. Development of the northwest European population of Greylag Goose, 1967-1983. Sources, see text.

Netherlands, where the geese are virtually out of reach of hunters.

3) *An increased recruitment.* From various parts of the breeding range (e.g., MAJEWSKI 1983, BRUNS & VAUK 1985-1986) it has been recorded that within the last decades the breeding Greylag Geese have changed habits, adapting themselves to areas with human activity. This change may have increased the breeding capacity and the recruitment rate of population.

The evidence for especially the two latter hypotheses is, however, not firm. At present too little is known about population dynamics and interplaying density-dependent factors. In this context analyses of ringing data are much needed. As it is discussed later (see p. 59) the most likely explanation for the increase is, however, lowered mortality. No other goose population in Europe has demonstrated improvements in breeding success.

The story of the Greylag Geese in this century resembles that of the other goose populations in west Europe, in that they have been markedly increasing and have changed feeding habitats and partially migration patterns. The Greylag Geese still rely heavily on their traditional and natural food source, the *Scirpus* and other *Cyperaceae* as well as grasses. Feeding on these food plants is especially prevalent in Spain and the Netherlands, but also in other parts of the range during the breeding and moulting periods. The Greylag Goose of the Atlantic flyway has, however, throughout its range increasingly been feeding on pastures and arable land, and possibly due to this flexibility in habitat selection the population has enabled itself to compensate for the negative effects of habitat deterioration, and has – although there is not necessarily a causal relationship – even increased in numbers.

Management needs. Nowadays in northwest Europe the Greylag Geese feed in a range of habitats. Crop damage is not a large-scale problem and is solved locally. Although autumn shooting is allowed in all range states, the geese seem to find enough refuges to sustain the shooting pressure and disturbance. Only in France does shooting seem to be so intensive that the geese have not a single, regular refuge. There, some refuge systems ought to be established, especially as they may act as alternative wintering sites to the Guadalquivir Marismas in drought years.

The situation in the Marismas, which was alarming in 1980 to 1983, can be solved to the benefit of the geese and other water birds breeding and wintering there, if present plans of improving the water supply are carried through with determination.

Research needs. To establish better population monitoring, more detailed and extensive observations of the numbers and distribution of Greylag Geese are needed especially in Poland and Norway. Ringing schemes should be expanded, so that the border lines between the northwest European and central European populations and the interrelation between them can be deciphered.

Ringing data have been compiled in several range states, primarily aimed at analysing the migration pattern of the Greylag Geese, but there are only a few analyses of population dynamics, a prerequisite for the future international management of the population. The analysis should contain both an overall and a national break-down of the ringing data, so that the condition of the entire population and its subpopulations can be studied. This project calls for international co-operation. Another possibility would be to organize age-ratio counts on autumn staging areas in northwest Europe. Although ageing in Greylag Goose is not easy, the excellent results from Britain show that it is indeed possible.

In this connection it must be stressed that future ringing schemes should be based on catching of breeding birds and goslings of known origin, and not as it has been practised in several studies on mass ringing of moulting birds, whose origin is not known. Furthermore, it cannot be ignored that the disturbance caused by the ringing actions on the moulting grounds has been the reason for the abandonment of some Danish and Swedish sites as suggested by LEBRET & TIMMERMAN (1968).

At present no studies have focused on body reserve dynamics and correlates with breeding success in the Greylag Goose, as it has been done for some af the arctic nesting populations. Here lies a challenge for international cooperation among goose biologists to make an integrated, comparative study which will contribute with valuable results to the future management of the population.

Dark-bellied Brent Goose *Branta bernicla bernicla*

The nominate race of the Brent Goose breeds in north Siberia and winters along the west European coastlines from Denmark to France (Fig. 13). In addition a few hundred geese occur in spring on the coast of the GDR (NEHLS 1979). The population has undergone tremendous changes in the present century. In the 1930s there was a dramatic decline in the Brent Goose population simultaneously with the die-off of its principal food *Zostera marina* all over Europe. After a period of protection by most

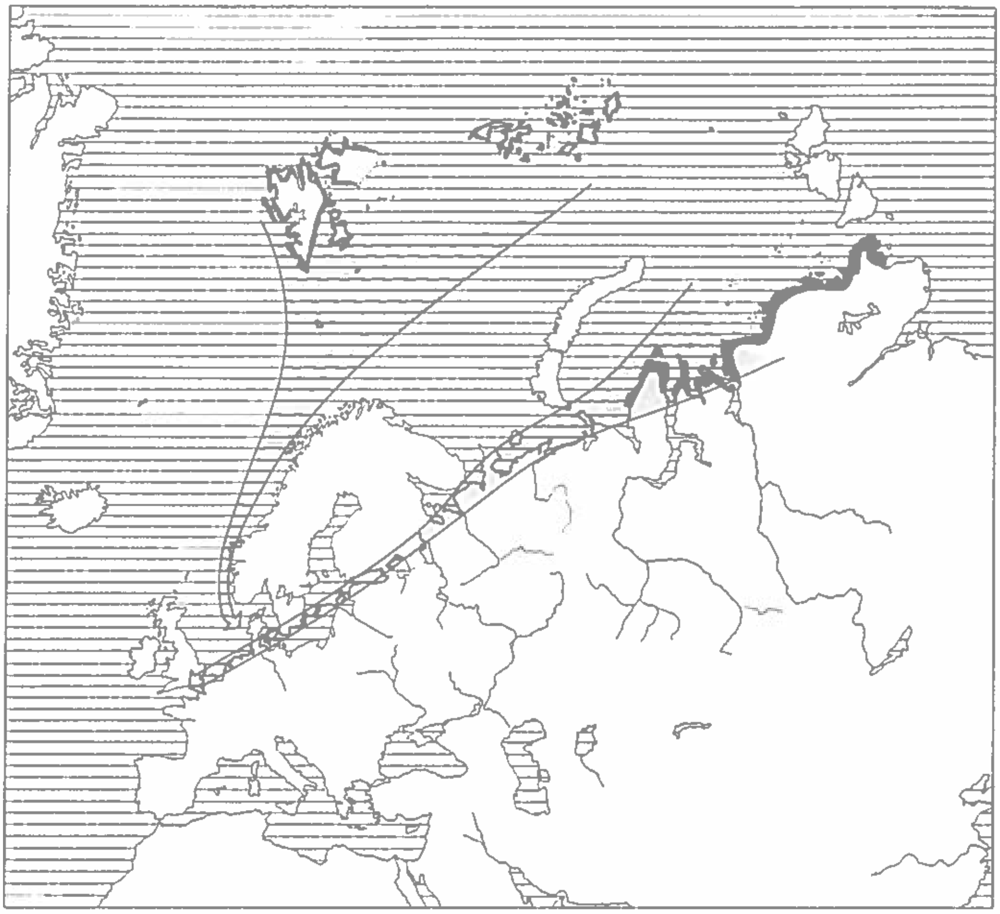


Fig. 13. Breeding distribution and migration routes of Light-bellied Brent Geese (west) and Dark-bellied Brent Geese (east). The extension of the breeding ranges are not well documented. Sources, see text.

countries throughout its range, the Brent Goose population has recovered from 16,000 in the 1950s to a present level fluctuating between 150,000 and 200,000, depending on breeding success (IWRB BRENT GOOSE RESEARCH GROUP, unpubl.).

The status and management of the Brent Goose has been much discussed in the last few decades. In parallel with the population increase, conflicts with agriculture have arisen in some countries, and there are some pressures from hunting organizations to re-open the season. With this background an international 'Technical Meeting on Western Palearctic Migratory Bird Management' was held in Paris in 1977 at the invitation of the International Council for Game and Wildlife Conservation (CIC) and the IWRB to present and discuss the status of the Brent Goose (see SMART 1979), and a second Technical Meeting in Paris in 1979 at the invitation of the International Foundation for the Conservation of Game (IGF) and the IWRB (see SCOTT & SMART 1982).

The present review is primarily based on the contributions from the proceedings of the two meetings as well as on more recent publications and unpublished information collected by the IWRB Brent Goose Research Group. Much of the recent knowledge stems from an intensive colour-marking project of the research group, initiated by a study of the implications of a third London airport and carried out by ST JOSEPH in England beginning in 1972/73.

Breeding grounds and breeding ecology

The breeding range of the Brent Goose is situated along the north Siberian coastline (Fig. 13) including the west Kolguev Island, northern half of the Yamal peninsula, islands in the Kara Sea, north Taimyr peninsula and east to Severnaya Zemlya (USPENSKI 1960, KISTCHINSKI & VRONSKI 1979). However, ornithological surveys have not been made there in recent years, and in the main breeding area, the Taimyr, not since 1949. USPENSKI (1960) states that moulting Brent Geese are found on Novaya Zemlya, along the north Taimyr and probably also in the rest of the breeding range.

Virtually nothing is known about the breeding biology of the subspecies. The geese usually arrive at the breeding areas between 10-20 June, and depart from the middle of August to the beginning of September (USPENSKI 1960).

Migration routes and staging areas

On migration from the breeding grounds in north Siberia to the wintering grounds in west Europe the Brent Geese cross the Kanin peninsula in the Barents Sea and pass through the White Sea across Onega Bay between the second half of September and the first half of October (Fig. 13) (USPENSKI 1960, BIANKI 1979). The geese fly via Lake Ladoga and maybe Lake Onega in the USSR to the Gulf of Finland, entering through the Bay of Vyborg, where they are observed from the first half of September to early October with a peak in the second half of September (LAMPIO 1979). The passage is also observed along the coast of Estonia with peak numbers in October (KUMARI 1979). Usually only a few Brent Geese are observed in the GDR (NEHLS 1979), and most flocks seem to pass the Swedish coastline. They pass through Kalmarsund, southeast Sweden, mainly in October (EDELSTAM 1972) and flocks also pass overland through Skåne (ALERSTAM 1976, LINDELL 1977). The geese usually reach Danish waters by the end of September with peak arrival in October (FOG 1972, MELTOFTE 1973). The flocks pass overland from the Baltic Sea to the Wadden Sea across southern Jutland and northern Schleswig (SCHMIDT 1976).

In spring the same route seems to be followed. A major migration through Kalmarsund is seen in the last ten days of May, in the Gulf of Finland and Estonia from late April to early June with peak numbers in late May (LAMPIO 1979, KUMARI 1979). The geese seem to pass the Kanin peninsula in the first half of June (BIANKI 1979).

Ecology. On the White Sea coasts in the autumn, the Brent Geese stop for a short period and feed on *Zostera* in shallow waters (BIANKI 1979). In Finland, Estonia and Sweden the geese usually do not stop (LAMPIO 1979, KUMARI 1979, FREDGA 1979), whereas thousands stay and feed on *Zostera* and green algae in shallow waters of the Danish Baltic Sea (MADSEN 1986).

Legal status. The Brent Goose is protected along the whole migration route.

Past history. In Finland, Sweden and the GDR an increase in numbers of geese has been recorded in parallel with the general population development since the 1960s. In

Fig. 14. Midwinter and spring distribution of Dark-bellied Brent Geese. Sources, see text.

the GDR the Brent Goose was considerably more abundant in the 1920s than at present (NEHLS 1979), reflecting the population decline in the 1930s.

Management measures and problems. There are no reports of feeding on farmland along the autumn and spring migration route.

Wintering grounds

The Dark-bellied Brent Goose winters from Denmark in the northeast, through FRG, the Netherlands, south and southeast England to the west coast of France (Fig. 14). In midwinter the population is mainly distributed in France, England and the southern part of the Netherlands; in mild winters, however, also in other parts of the winter range. In spring the population moves to the Netherlands, FRG and Denmark (Fig. 14) (ST JOSEPH 1979a, 1982). The phenology in the five winter range states is shown in Fig. 15.

Denmark

Numbers and distribution. The most important site of the Brent Goose is in the Wadden Sea, holding about 75% of the goose-days spent in Denmark (MADSEN 1986). Other important sites are in Ringkøbing Fjord, in the archipelago south of Funen and on the islands in the Kattegat. The Brent Goose arrives in Denmark by the end of September, and numbers peak in October with 11,000 to 40,000 individuals in 1980-1983 (MADSEN 1986). The geese usually leave by the end of November, and in winter only a few hundred remain, except for mild seasons where up to 5,000 may stay. From March to May a spring population of 14,000 to 23,000 geese is built up, representing 10-12% of the entire population (MADSEN 1986). The geese depart for the breeding grounds between 20-30 May (MADSEN 1985c, MØLLER 1978).

Ecology. In autumn the Brent Goose is almost exclusively confined to shallow waters

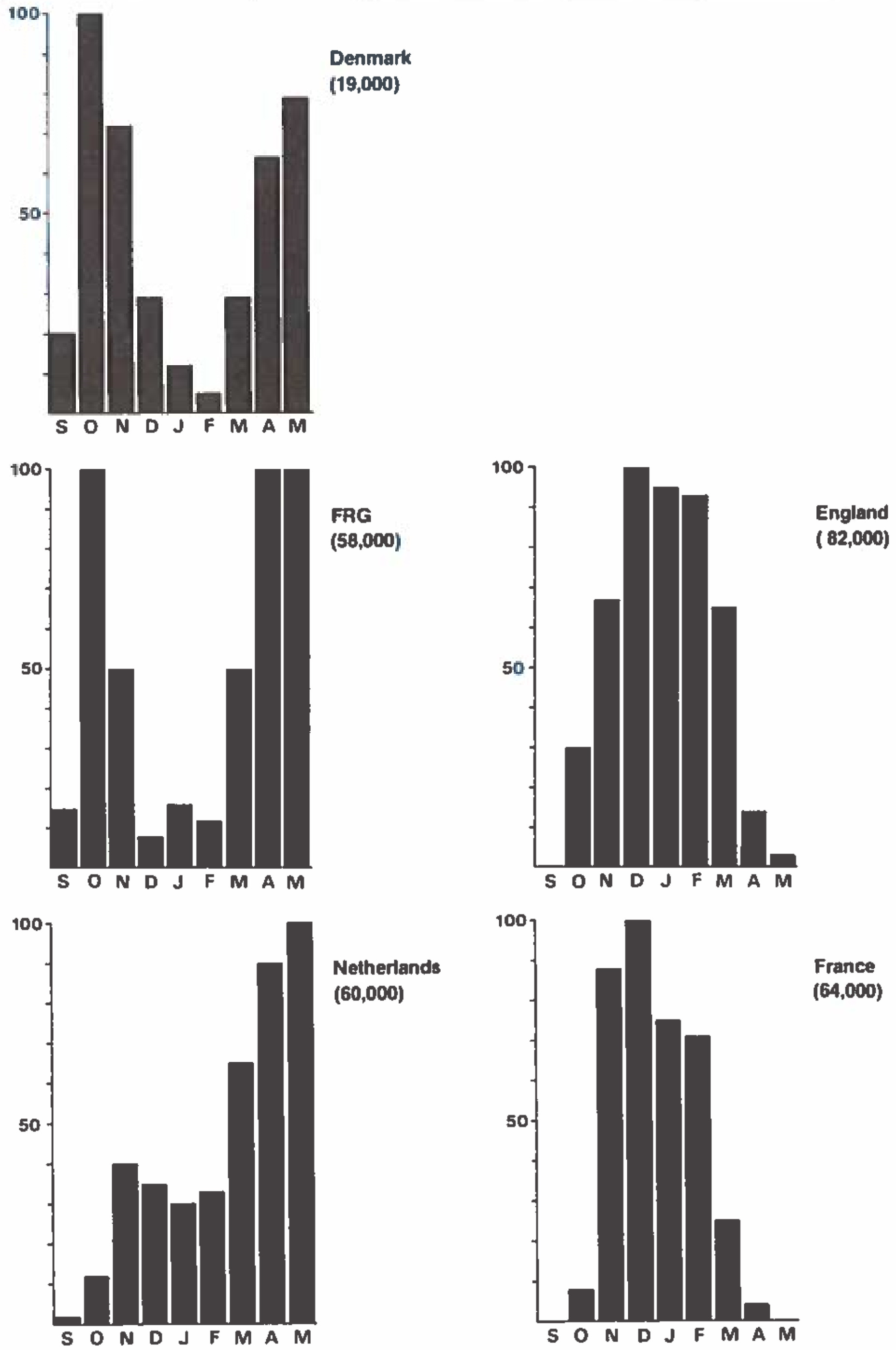


Fig. 15. Phenology of Dark-bellied Brent Geese in five winter range states, expressed in percentage of peak month. Most data are from 1980-1984 (data from FRG from 1975-1979). Numbers in brackets give average maximum (=100%). Sources, see text.

and mudflats feeding on *Zostera* and green algae, and only in few sites in the Wadden Sea flocks graze on saltmarshes created by land reclamation (MADSEN 1986). In spring the geese shift to saltmarshes. In Tipperne in Ringkøbing Fjord the geese graze on fresh water marshes and pastures (MADSEN 1985c, LORENZEN & MADSEN 1985).

Past history. The population decline in the first half of the century was also significant in Danish waters (MØLLER 1978), although the information is sparse, and the reduction cannot be quantified. Very soon after the die-off of the *Zostera marina* in 1932-33 flocks of Brent Geese were seen feeding on saltmarshes in spring (CHRISTIANSEN 1936). However, in contrast to the general downward trend, the spring population around Tipperne increased from approximately 1,000 in 1929-1931 to 2,000-4,000 in the mid 1930s (LIND 1956, MADSEN 1985c). Here the geese found an alternative diet consisting primarily of *Ruppia spp.*

From the 1960s to the 1980s the increase in the spring and autumn population in Denmark has been substantial, viz. approximately 4,000 to 11,000-40,000 (FOG 1972, MADSEN 1986).

Legal status. Total protection since 1972. In three years in the 1960s the annual bag was estimated at 1,200 to 3,000, 4-8% of the total population before shooting (FOG 1972).

Management measures and problems. Apart from an isolated case where usually not more than few hundred Brent Geese feed on winter wheat in October (MADSEN 1986), there are no reports of regular farmland feeding in Denmark (FOG 1977).

Since 1978 the dense submerged macrophyte stands in Ringkøbing Fjord suffered a die-off due to hyper-eutrofication of the water, and the 2,000-4,000 Brent Geese, which used to feed on these plants in spring were forced to shift to fresh water marshes (MADSEN 1985c).

Federal Republic of Germany

Numbers and distribution. The Brent Goose occurs along the German Wadden Sea coastline with the highest concentrations in the Northfriesian part (PROKOSCH 1984d, unpubl.). In the autumns of 1979-84, 50,000-60,000 and around 5,000 geese have been recorded in the Northfriesian and Lower Saxonian Wadden Sea, respectively; in spring 50,000-80,000 representing 35-49% of the total population and 10,000-15,000 representing 8-10% of the total population, respectively. In midwinter the population varies between 0 and 8,000 Brent Geese, dependent on the severity of the winter.

The geese arrive from mid September to the beginning of October, and numbers peak in October; by the end of November most geese have moved on to England and France (PROKOSCH 1984d). Based on sightings of colour-marked individuals it has been shown that the geese stage for a relatively short period, ranging from few days to four weeks. The geese may return in January, but most usually arrive in March, and spring staging numbers peak in April and May. In spring the geese stage for about two months, and they are strikingly faithful to their haunts from year to year (PROKOSCH 1984d). The geese depart in late May.

One of the major spring haunts, Rodenäs Foreshore, adjacent to the Danish border was diked in 1979-82 (for diking plans, see PROKOSCH 1979). Here up to 18,000 Brent Geese stayed prior to the diking. The population has gradually declined since; in 1983 down to 4,000 individuals (PROKOSCH 1984e). Sightings of colour-marked individuals have shown that most of the displaced geese have moved to the islands of Sylt, where they have colonised a hitherto unimportant site, as well as Föhr and Langeness.

Ecology. In autumn most Brent Geese feed on intertidal mudflats, mainly on the extensive *Zostera* beds in the Northfriesian Wadden Sea (PROKOSCH 1984d). Only to a small extent do they make use of saltmarshes. From March onwards the geese are concentrated on saltmarshes grazed by cattle and sheep on the halligs and along the coastline. Only a small percentage of birds feed on the mudflats. In recent years flocks have been observed feeding on winter cereal fields inside the sea walls (PROKOSCH pers. comm.).

Based on observations of consecutive years with stable goose numbers in the traditional saltmarsh feeding grounds it is believed that the carrying capacity of these areas to Brent Geese has been reached (PROKOSCH pers. comm.). A registered increase in goose numbers in recent years has coincided with goose flocks using new, probably sub-optimal saltmarshes.

Past history. Before this century the Brent Geese were reported to be numerous in the Northfriesian Wadden Sea (see review by PROKOSCH 1984d). Following the die-off of the *Zostera marina* beds in 1932 it is known that the geese switched to saltmarshes. However, there are no reports quantifying the population decrease. In the springs of 1965 and 1966 when the first counts were arranged, 12,000-18,000 geese were counted representing 50-65% of the total population. Since then numbers in spring have increased, though at a lower rate than the total population (PROKOSCH 1984d). In the Wadden Sea of Lower Saxony the population has also increased considerably (PROKOSCH unpubl.).

Legal status. The Brent Goose was protected in Lower Saxony in 1977; in Schleswig-Holstein the season is open from 1 November to 15 January. It is estimated that up to 2,000 Brent Geese are bagged annually (PROKOSCH pers. comm.).

Management measures and problems. Since the 1970s the goose grazing on saltmarshes in spring has caused severe conflicts with cattle-holding farmers on the halligs in the Northfriesian Wadden Sea. Compensation for goose damage has been paid since 1973 (SCHWARZ & RÜGER 1979). Since 1980 270,000 to 300,000 DM have been paid annually by the Ministry of Agriculture and the County of Schleswig-Holstein (KNIEF 1985, PROKOSCH pers. comm.). The goose damage is especially severe on the small halligs with a large proportion of saltmarsh area, less severe on the larger halligs where the areas grazed are smaller. Assessment of damage is done *ad hoc* by a 'Brent Goose Committee', roughly estimating goose grazing pressure from dropping densities and vegetation height.

In a new 'Hallig-programme' presented by the Ministry of Agriculture the halligs will be subsidised for the conservation of the saltmarsh habitat and farming practice, and the geese will be included among the natural but manageable hazards of farming, and compensation for damage will therefore not be paid (PROKOSCH pers. comm.).

In 1982 the diking of 550 ha of saltmarsh on the Rodenäs Foreshore was concluded, and in 1986 the diking of another important spring feeding area for Brent Geese, Nordstrand Bay, will be finished with 845 ha of saltmarsh being diked (PROKOSCH 1979). In Rodenäs the diked saltmarsh has become a nature reserve with sheep grazed grasslands, and in spring flocks of geese now feed behind the sea wall, although it is only a quarter of the numbers which made use of the former foreshore.

With a recent proclamation of the German Wadden Sea as a national park, including the part in Lower Saxony, but excluding the halligs, further diking should be brought to an end, and the feeding habitats of the Brent Geese secured.

The Netherlands

Numbers and distribution. Within the Netherlands two distinct Brent Goose areas can be described: The Wadden Sea in the north, and the Delta area in the southwest. Whereas the Wadden Sea is primarily a spring staging area, the Delta region is mainly a wintering site (ROOTH et al. 1981, NETHERLANDS GOOSE WORKING GROUP 1983, 1984a, 1984b, in press).

In the Wadden Sea the Brent Geese arrive in October, and numbers peak in October and November with between 10,000 and 29,000 geese (EBBINGE & BOUDEWIJN 1984). Usually less than 10,000 winter, though up to 22,000 have been observed in mild winters, representing on average 9% of the world population. By March the geese return from the wintering areas in England and France, and they stay until 20-25 May. In April and May 48,000 to 85,000 geese, or 33-42% of the world population stay here, with peak numbers recorded along the Friesian coast and on the islands of Terschelling and Texel (EBBINGE & BOUDEWIJN 1984).

In the Delta area the Brent Geese winter from October to April with peak numbers of 10,000 to 12,000, representing on average 7% of the total population reached in midwinter (NETHERLANDS GOOSE WORKING GROUP 1983). In the Delta area the numbers are hardly affected by cold spells.

Colour-marking has revealed that geese occurring in the Dutch Wadden Sea in spring winter in both England and France without tendency of preference of one of the two countries (EBBINGE & BOUDEWIJN 1984), as was previously suggested by ST JOSEPH (1979a).

Ecology. In the Wadden Sea a seasonal shift in habitat preference is observed (EBBINGE & BOUDEWIJN 1984; see also BILT & HELMING 1978). In autumn most Brent Geese feed on intertidal mudflats where the green algae *Enteromorpha* and *Ulva* constitute the major part of the diet (DIJKSTRA & DIJKSTRA-DE VLIEGER 1977). The *Zostera* beds, which had an extensive distribution before 1932, have hardly recovered since the die-off in 1932 (VAN DEN HOEK et al. 1979), and are therefore of little importance for the Brent Geese today (but see JACOBS et al. 1981). In late autumn the wintering stock of Brent Geese moves to improved grasslands bordering the Wadden Sea. From March onwards, the geese start feeding on natural saltmarshes and grazed saltmarshes created by land reclamation works. In spring some feeding also takes place on developing *Enteromorpha* and on diatoms (CADÉE 1972).

It has been shown that until mid April the digestibility of the pasture grasses is higher than that of the saltmarsh grasses, whereafter the digestibility of the later growing saltmarsh vegetation overtakes that of the pasture grasses (BOUDEWIJN 1984), explaining the shift in habitat preference of the Brent Geese in spring. On the saltmarshes *Plantago maritima* is a highly preferred food plant together with *Festuca* and *Puccinellia* (EBBINGE 1979). The repeated grazing of *Plantago* by the geese has been shown to keep the plants in an active stage of growth with high nutritive quality (PRINS et al. 1980).

In the Delta area the Brent Geese feed on *Zostera* and green algae in autumn (WOLFF et al. 1967), but change to improved inland grasslands later in autumn (NETHERLANDS GOOSE WORKING GROUP 1984a).

Past history. According to the review by MÖRZER BRUYNS & TIMMERMAN (1968) the number of Brent Geese in the Netherlands decreased catastrophically by an order of 90% or more shortly after 1932. The authors were convinced that it was directly caused by the disappearence of the *Zostera marina*, the staple food of the Brent Goose. In the years following the *Zostera* disease the geese were found feeding on inland grassland and winter wheat fields.

The first organized counts in the Netherlands in May 1960 recorded 2,600 to 3,000 Brent Geese, and in midwinter 1966/67 4,300 (MÖRZER BRUYNS & TIMMERMAN 1968). Since then the spring population has increased by more than a tenfold, the winter population by a threefold.

Legal status. Total protection since 1950.

Management measures and problems. The increased numbers of geese feeding inland on improved grasslands have caused conflicts with farmers who either produce hay or keep sheep or cattle. Damage problems are especially pronounced in spring (PFEIFFER 1979). So far there is little published information on damage assessment; however, direct compensation is paid to farmers from a fund created by a levy on hunting licenses. In 1979 more than half a million Dfl. were paid for all damage by geese in the Netherlands (DEN UIL et al. 1982), increasing to over one million Dfl. in the 1980s (VAN WELIE 1985). Texel, an island with very little saltmarsh left, has had most serious problems, because even in May there is no alternative feeding for the geese. Here a 110 ha farm, Zeeburg, has been turned into a Brent Goose reserve by the Dutch government in 1976 to alleviate the local damage problems (PFEIFFER 1979, PEERAER 1982). By scaring the geese from other farmland areas to the goose reserve, most of the damage problems have now been solved. Up to 10,000 Brent Geese feed within the reserve in spring (EBBINGE pers. comm.).

On Terschelling, where up to 15,000 Brent Geese stay in spring, most geese feed in a saltmarsh reserve, but there is also a considerable number visiting the polder grasslands. To solve the damage problems on the polders a scaring experiment was set up. By different scaring techniques, such as very pistols, rockets fired over flocks, shotguns fired over the flocks, geese killed by shotgun, the number of geese in the polder was reduced, but on the saltmarsh reserve numbers also went down. Counts on the neighbouring island and along the mainland coast, as well as an increase in the assessed goose damage in these areas showed that the displaced geese had settled there. It was thus concluded that, although solving the local conflicts on Terschelling, the problem itself was only relocated (THISSEN & BRUGGEMAN 1982).

On basis of analyses of grazing intensity on the saltmarshes in the Dutch Wadden Sea EBBINGE & BOUDEWIJN (1984) have estimated that with their present management, the saltmarshes cannot support significantly more Brent Geese. Thus, if numbers of Brent Geese continue to increase, an overspill to grassland is unavoidable and will increase. In addition to the saltmarsh area 1,200 ha of improved grasslands are needed to meet the food requirements of the present spring staging population. If the saltmarshes are better managed than today by use of intensified sheep grazing on the marshes created by land reclamation, the area of improved grassland necessary will be reduced. If scaring of geese from the polders is successful, alternative feeding grounds must be at hand, either on the saltmarshes or on the improved grasslands.

England

Numbers and distribution. The south and southeast coast of England, together with the west coast of France, constitute the central wintering ground of the Brent Goose (ST JOSEPH 1979a, 1982). In midwinter the

British population has varied between 66,500 and 92,600 birds in the 1980s (OGILVIE 1977-1985), representing 45-51% of the world population.

The first Brent Geese arrive at the end of September. Sites in Essex and Kent, especially Maplin Sands/Foulness Island receive birds early in the season, and the wintering population usually peaks in November and December. In contrast the peak on the south coast occurs later, in January and February (PRATER 1981). Numbers begin to diminish by the end of February and especially during March when the geese move on to the Wadden Sea. Since the late 1970s the Wash has become a regular spring staging area with up to 5,000 Brent Geese (PRATER 1981).

Ringing and sighting of colour-marked geese shows that the Brent Geese have a strong faithfulness to their wintering grounds in subsequent seasons. They do not only return to the same estuary, but also to the same section of coast within it (ST JOSEPH 1979a).

Ecology. The traditional winter feeding habitat of the Brent Goose is the intertidal flat with *Zostera* beds and green algae, which constitute the main food items (RANWELL & DOWNING 1959). Today the feeding habits have partly changed, and the geese make use of a wider range of habitats covering mudflats, saltmarshes and farmland areas, which are used in succession (CHARMAN 1979, TUBBS & TUBBS 1982). In autumn almost all Brent Geese feed on *Zostera.* At first the undisturbed mudflats are exploited, and later when these are depleted, the geese move into more disturbed areas and become partly habituated to human activity (OWENS 1977). When the *Zostera* beds have been depleted, and it is no longer profitable to feed there, the geese turn to *Enteromorpha.* From November onwards an increasing number changes to saltmarshes, feeding on *Puccinellia* and *Spergularia* (CHARMAN & MACEY 1978), and later on to farmland with winter cereals, improved grasslands and even onto playing fields. Before 1974 inland feeding was only found in isolated sites in Essex, but from 1973/74 the number of birds feeding inland as well as the number of inland sites have increased tremendously (ST JOSEPH 1979b, ROUND 1982). WHITE-ROBINSON (1982) compared the time budgets of Brent Geese feeding on inland pasture with time budgets on saltmarsh, and he found that pastures supported higher densities of geese, and having the choice of the two habitats, a flock spent almost 90% of its feeding time on pastures. However, certain individuals exclusively grazed on saltmarsh.

The number of geese feeding inland is correlated with the number of birds present along the coast, and the development has undoubtedly been caused by the population increase and the following faster depletion of the traditional food sources. In the 1980s more than 40,000 Brent Geese feed inland in late winter, and they now range up to 9 km from the water (OGILVIE pers. comm.) and have developed overland migration routes, too (HARRISON 1979). The inland feeding habit has spread along the south and southeast coast of England.

Past history. The known history of the Brent Geese in England has been reviewed by ATKINSON-WILLES & MATTHEWS (1960) and by OGILVIE & ST JOSEPH (1976). Information about numbers of the Dark-bellied Brent Goose in the period before 1930 is extremely scarce, and it is not possible from the English counts – as SALOMONSEN (1958) claimed – to give an exact estimate of the former population size, nor of the magnitude of the population decline in the 1930s. However, undoubtedly the former population decreased massively and possibly by the order of 75% (ATKINSON-WILLES & MATTHEWS 1960). In the mid

1950s the midwinter population amounted to 7,400 birds. In the 1960s the English population had increased to a mean of 16,000 birds, on average representing 63% of the total population (calculated from data in OGILVIE & ST JOSEPH 1976). In the 1970s the wintering population was steadily increasing, averaging 37,000 geese or 47% of the total population (calculated from data in OGILVIE 1979, 1977-1985), indicating that since the 1960s a higher proportion of geese wintered outside the English haunts.

Legal status. Fully protected since 1954. 300-400 geese are shot annually under license (see below). ST JOSEPH (cited in PROKOSCH 1984d) estimates that 1,000-2,000 Brent Geese are shot annually, either illegally or under license.

Management measures and problems. The inland feeding has given rise to conflicts with farmers complaining of goose damage on winter cereals. One big problem giving rise to increased damage is that farmers are growing cereals in more and more marginal areas because of price guarantees by the EEC. Wheat is now being grown right up to the sea wall, where there used to be a buffer of wet grazing land of little interest to the farmer in winter and which the geese could use (M. OWEN pers. comm.) Assessment of the damage has only been carried out in few cases, but the published examples of extreme cases have shown that the goose grazing can have a considerable negative effect on yields of winter wheat (ST JOSEPH 1979b, DEANS 1979). Various means of scaring have been tried but most have proved to be rather inefficient, unless pursued with a great deal of effort (ST JOSEPH 1979b). Since 1982/83 Brent Geese have been allowed to be shot under license (NUGENT 1985). In 1984/85 which is typical for recent years, 50-60 licenses were granted to farmers complaining of damage. A limit of 723 kills was set, but only 368 Brent Geese were actually killed (OGILVIE pers. comm.). Since the start of licensed shooting conflicts have levelled off. There exists no legal mechanism for direct compensation for damage. So far no special goose reserves have been created to lessen the conflicts. However, a saltmarsh area in Essex has just been protected by a non-government organisation mainly with the aim of establishing an undisturbed managed feeding ground where the Brent Geese will not cause damage (OGILVIE pers. comm.).

France

Numbers and distribution. Together with England, France is the principal wintering area for the Brent Goose. In mid January 1979-1984 the French wintering grounds harboured a total of 41,000-65,000 geese (MAHEO 1984 and unpubl.), representing on average 33% of the total population. The geese are found in estuaries from the western part of the English Channel south to the Bassin d'Arcachon near Bordeaux.

The Brent Geese start to arrive in October, and during November numbers rapidly increase, usually reaching a peak in December. From late January numbers begin to decline, and by the end of March most geese have left the country.

Along the French coast there is a temporal difference in site usage. The Golfe du Morbihan and nearby sites receive early arrivals by the end of October; numbers peak in November and December with 15,000-23,000 individuals (MAHEO 1984), and the geese already start leaving the area in December. From the Golfe du Morbihan the geese move on to the main wintering sites, of which Charente Maritime and Bassin d'Arcachon in the southwest range are the most important. Here the peak is usually a month later than at the Golfe du Morbihan.

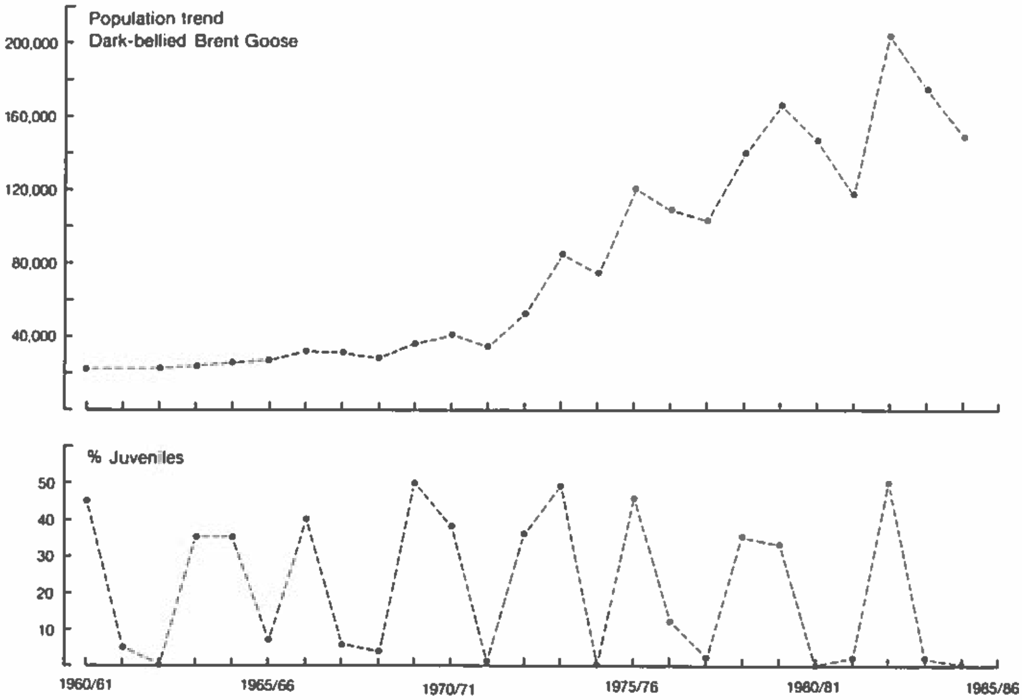


Fig. 16. Population development and percentage of juveniles in wintering flocks in Dark-bellied Brent Goose, 1960-1984 (IWRB BRENT GOOSE RESEARCH GROUP, unpubl.).

Ecology. The Brent Geese are almost completely restricted to the seashore, feeding on intertidal *Zostera marina* and *noltii* beds, and also on *Enteromorpha* and *Ulva*. Only to a small extent do the geese feed on saltmarshes (MAHEO 1979). Inland feeding only occurs in a single site, Baie de Bourgneuf, where usually a few hundred geese feed on improved grassland and winter cereal fields (BAVOUX et al. 1985).

Past history. Brent Geese have been counted in France since 1960-1961, when 6,000 to 7,000 were recorded. Later in the 1960s up to 11,500 individuals were counted, or on the average 32% of the total population (calculated from MAHEO 1984), and in the 1970s up to 65,000, or on average 36% of the total population. Numbers prior to 1960 are not known, but MAHEO (1976) mentions that the Brent Geese were probably much more numerous in the Golfe du Morbihan around 1930 than they are today.

In the 1960s and 1970s Golfe du Morbihan was the most important wintering area in France (MAHEO 1976), but since the late 1970s the site has primarily functioned as a pre-wintering site.

Legal status. Fully protected since 1966. In the Golfe du Morbihan MAHEO (1976) estimated that 300-500 geese were illegally killed each winter.

Management measures and problems. Only in the Baie de Bourgneuf are there conflicts with agriculture. Complaints by farmers of damage to winter cereals have caused the geese to be scared off the fields by various devices by the Ministry of Environment (BAVOUX et al. 1985).

Population development

It was shown by SALOMONSEN (1958) that the Brent Goose was much more numerous in the latter half of the 19th century, and that numbers decreased thereafter, reaching a low point in the 1950s. However, most of the evidence stems from the Svalbard Light-bellied Brent Goose population, and the numerical documentation from the literature concerning the Dark-bellied Brent Goose is, as it has been shown above, more fragmentary and anecdotal. Nevertheless, it is evident that the population underwent a drastic decline in the 1930s.

The population development since 1955 is well documented by internationally co-ordinated counts by the IWRB (Fig. 16). It was not until the 1960s that signs of recovery in the population size were recorded. From the beginning of the 1970s the population increased exponentially, reaching a record peak of 203,000 geese in 1982/83.

The high-arctic breeding Brent Geese are liable to high annual population fluctuations due to the variable conditions on the breeding grounds, and the number of juveniles brought to the wintering grounds varies between 0 and 53% of the total autumn population. Out of 28 years (1955-1982) only 13 were successful (i.e. more than 33% juveniles), and 12 with breeding failures (i.e. less than 7% juveniles) (PROKOSCH 1984d).

Discussion

The decrease in the Dark-bellied Brent Goose population in the 1930s happened simultaneously with the 'wasting disease' of *Zostera marina* along the Atlantic coastline in 1932, most probably caused by a series of mild winters combined with the virulence of the amoeboid parasite *Labyrinthula macrocystis* (see RASMUSSEN 1977 for a review). Whether it was the disappearance of the principal food source or other factors such as shooting pressure, or factors in combination, which were responsible for the decline in the Brent Goose population has been much questioned (VIERECK 1951, SALOMONSEN 1958, OGILVIE 1979). Direct starvation in the years following the die-off of the *Zostera* was not reported (SALOMONSEN 1958), but in the Dutch Wadden Sea geese were reported to be in very poor condition, some weighing only 0.5 kg instead of the usual 1.5 kg (MÖRZER BRUYNS & TIMMERMAN 1968). In fact at least to some extent the geese were able to switch to other food sources as the *Zostera marina* disappeared, mainly *Zostera noltii* which was not affected by the disease, green algae and saltmarsh vegetation (VIERECK 1951, SALOMONSEN 1958). However, the disappearance of *Zostera marina* may have caused the geese to become more vulnerable to shooting, both because of their poor condition, and because they were forced to seek food in areas where hunters had easier access to the birds. This was in fact what happened to the North American Light-bellied Brent Goose in 1971/72 when its principal food *Ulva* was scarce and it had to turn to saltmarshes rather than open bays. In that winter 70,700 geese were estimated to have been bagged, the highest ever recorded (ROGERS 1979). With the combination of a poor breeding season in the summer 1972, the population was reduced from 151,000 in January 1971 to 40,700 geese in January 1973. A similar coincidence of negative factors may have caused the depression of the Dark-bellied Brent Goose population, rather than the *Zostera* disease in itself.

The increase from the 1960s to the 1980s has been shown to be caused by a lowered annual mortality rate which decreased from an average of 22.1% (1963-1971) to 13.3% (1972-1982), whereas the proportion of juveniles did not change on the average 22.2% and 22.3%, respectively. Biologists analysing the population dynamics have almost exclusively concluded that the relaxation in hunting pressure on the wintering grounds was responsible for the increase (OGILVIE 1979, PROKOSCH 1984d, EBBINGE 1985), and especially the shooting ban in Denmark since 1972.

It is known that *Zostera marina* recovered over most of its former range in western Europe from the 1940s, excluding the Dutch Wadden Sea, but the Brent Goose population did not increase accordingly (VIERECK 1951). Hence, it seems not to have been altered food conditions that has caused the increase.

The future population development of the Dark-bellied Brent Goose will, as long as shooting is banned over most of its range, be dependent on the carrying capacity of the breeding and wintering grounds. EBBINGE (1985) has shown that at higher population levels in the 1970s, the proportion of successful breeding pairs has been reduced, indicating that some density-dependent effects are operating on reproduction. At which stage in the life cycle this pressure lies is so far unknown. As there seems to be no ongoing Soviet studies on the breeding grounds, an early answer can hardly be expected.

Research in the Dutch and German Wadden Sea has shown that the acquisition of sufficient body reserves on the spring staging areas is a prerequisite for successful breeding (EBBINGE et al. 1982, PROKOSCH 1984d), and thus the conservation and management of the spring staging areas in the Wadden Sea are of vital importance for the well-being of the Brent Goose population. As indicated in the Dutch and Northfriesian Wadden Sea the carrying capacity of the saltmarshes in their present state has possibly been reached (EBBINGE & BOUDEWIJN 1984, PROKOSCH 1984d and pers. comm.). At the level of foraging goose flocks there has been shown to be much competition for preferred food patches, and a highly differing feeding efficiency among individuals, the most efficient birds also being the most successful breeders (DRENT & VAN EERDEN 1980, TEUNISSEN et al. 1985). Together, these works indicate that the spring staging areas do not offer an infinite scope for population growth, but rather that a density-dependent factor here could be acting on the reproductive capacity of the population. If the spring is the 'bottle neck' limiting population growth, further increase will depend on the possibility of the geese to make use of inland pastures to build up body reserves, a question which is presently being investigated in the Dutch Wadden Sea.

Conditions on the English and French wintering grounds do not appear to be limiting at present. The carrying capacity of the intertidal habitats in England has been exceeded, but by adapting themselves to inland feeding the geese have opened the doors to a new habitat which can - if the farming communities allow and/or sufficient reserves are created - support vast numbers of geese.

Management needs. At the two technical meetings in Paris the need for managing the Brent Goose population was highlighted (DE KLEMM 1979, SWIFT & HARRISON 1979, SMART 1979, ST JOSEPH 1982). At the time of the meetings (1977, 1979) the population was in an exponential growth phase, and conflicts with agriculture in Britain, the Netherlands and the FRG had sharpened. Since then the increase has levelled off, and although the solutions are not complete in the long term, ways of solving the damage problems have been found or are prepared in most cases. The strategy for alleviation of conflicts has not been internationally coordinated.

Licensed shooting as practised in England will not solve the conflicts with agriculture in the long term, because the problems are only relocated. As suggested by

ST JOSEPH (1982, unpubl.) and WHITE-ROBINSON (1982), a possible solution will be to develop scattered alternative feeding sites bordering the sea wall in the 'home range' of the goose flocks, accompanied by licensed shooting over vulnerable crops. This would probably be the cheapest solution and would prevent the massive concentration of geese in few large refuges.

EBBINGE & BOUDEWIJN (1984) advocate that to prevent damage along the Dutch Wadden Sea, the saltmarsh areas should be more effectively managed by summer grazing to raise the carrying capacity. Geese scared from susceptible grasslands would then have alternative refuge areas with sufficient resources.

If a shooting season should be reopened, several aspects should be addressed in an international forum before its eventual implementation.

First, the Brent Geese are liable to irregular breeding success, which results in an unequal age-cohort representation in the population. Population size is not an indicator of its resilience (KIRBY et al. 1985). A shooting system should therefore be finely-tuned with a harvest quota, derived from an annual assessment of population size and breeding success, and ideally, from a knowledge of population demography (as proposed by KIRBY et al. 1985).

Second, recognizing that the Brent Goose is a migratory species distributed over several countries, range states should jointly agree on a shooting system and on the setting of annual quotas in the respective countries. This implies that those states agree on a desirable population level and for guidelines on whether to have shooting and, if so, how much (see DE KLEMM 1979).

Third, a desirable population level should be defined, either by the North American concept of 'threshold level' which is a rather arbitrary level set as a guideline for shooting, or by the concept of a population level related to habitat carrying capacity. However, the application of the latter concept is a difficult affair, because it implies a coupling not only of shooting levels with the size of the natural resources, but also with agricultural damage problems, reserve policies and habitat management. This is not an easy pathway to handle which is illustrated by the example of the diking of Rodenäs Foreshore in the German Wadden Sea. The carrying capacity of the saltmarsh areas there has been reduced considerably, and the risk of damage to other more susceptible areas has increased accordingly. Not many would accept it as good management to depress the Brent Goose population to a level fitting the new capacity by shooting. It is more sensible to delay a decision on a reopened shooting season until the eventual levelling off of the population, which is predicted in the near future.

Research needs. As recommended at the technical meetings in Paris (SMART 1979, SCOTT & SMART 1982), studies of the breeding and moulting population of Brent Goose have the highest priority in the international efforts of research. At present virtually nothing is known about the population from June to mid September.

In the wintering quarters a great deal of work has been and is currently being done on assessment of food resources and exploitation rates by the Brent Geese. However, more information on food exploitation rates and carrying capacity of the *Zostera* beds and green algae shallows would be useful especially from France in order to get a more precise picture of how close to the ceiling of the capacity of the natural resources the population is and to analyse factors determining population movements within the wintering range (see DRENT et al. 1979).

Light-bellied Brent Goose
Branta bernicla hrota
(Svalbard population)

Two populations of Light-bellied Brent Goose winter in western Europe. One breeds in Svalbard and Franz Josef Land (Fig. 13) and winters in Denmark and England, the other breeds in northwest Canada and north Greenland and winters in Ireland. The Svalbard population which is treated in this review is one of the smallest goose stocks of the world, at present amounting to approximately 4,000 individuals (MADSEN 1984c), while the north Canadian population numbers around 18,000 (OGILVIE 1977-1985). A third population breeds in northern Canada and winters along the north American Atlantic coast, and counts at present around 130,000 individuals (KIRBY et al. 1985).

Breeding grounds and breeding ecology

The Light-bellied Brent Goose is a scattered breeder in Svalbard, and a rare breeder on Franz Josef Land. Before 1969 less than 100 breeding pairs could be accounted for in Svalbard (NORDERHAUG 1970), but many parts had only been visited by ornithologists once or not at all. In 1969 600-750 Brent Geese (including goslings, but the number of breeding pairs not estimated) were found on Tusenøyane in southeast Svalbard (NORDERHAUG 1974), and recently it has been confirmed that this archipelago is the main breeding area of the population. Thus the total population there in July/August 1985 was estimated at 1,200-2,000 geese, representing around 50% of the entire Light-bellied Brent Goose stock, of which 30-50% were breeding (F. MEHLUM pers. comm.). In Franz Josef Land very few pairs are known to breed (GORBUNOV 1932, TOMKOVICH 1984).

Very little is known about the breeding biology of the Brent Goose in Svalbard. According to LØVENSKIOLD (1963) they arrive during the last few days of May and the first days of June, indicating that they go almost non-stop from Denmark to Svalbard. From the middle of August the Brent Geese start to assemble, and southward movements begin by the end of August and last until the third week of September. Eggs have been found from 9 June and newly hatched goslings from 6 July. Most pairs nest on islands where Arctic Foxes usually do not have access, and more rarely Brent Geese breed on small islands in rivers (LØVENSKIOLD 1963). The Glaucous Gull *Larus hyperboreus* seems to be a heavy predator on Brent Goose eggs and goslings (NYHOLM 1965). The diet of the Brent Geese is reported to consist of grasses, mosses, algae, *Oxyria, Ranunculus* and other dicotyledons (LE ROI 1911, NYHOLM 1965).

Past history. LØVENSKIOLD (1963) states that the Brent Goose formerly, probably referring to the beginning of this century, was the most numerous of the goose species breeding in Svalbard. Brent Geese were breeding in large numbers on the islands along the coasts of Spitsbergen, but in the 1950s the population there was almost exterminated due to nest robbing by fishermen and whalers collecting eggs and down from Eider *Somateria mollissima* and Brent Goose nests. NORDERHAUG (1970) also concluded that the population had been heavily reduced in the first half of the century, but that it had then stabilized since the 1950s.

Legal status. Fully protected in Svalbard in 1955. Since 1963 when the Eider was protected, eggs of Brent Geese have not been gathered either (NORDERHAUG 1970).

Management measures and problems. In the bird sanctuaries in Svalbard less than 30 pairs of Brent Geese breed (PRESTRUD & BØRSET 1984). Tusenøyane are part of the Southeast Svalbard Nature Reserve with protection from all technical interference, but with no restrictions on landing on the islands (NORWEGIAN MINISTRY OF ENVIRONMENT).

Migration routes and staging areas

In spring the Light-bellied Brent Geese migrate from northwest Denmark to southwest Norway, west of Kristiansand to Jæren, where the passage culminates 20-26 May (HAFTORN 1971, BYRKJEDAL & ELDØY 1981). The northerly migration along the Norwegian west coast is seldom seen as the geese usually fly far from land, possibly directly to the breeding grounds (SALOMONSEN 1958). To what degree they stop on Bear Island is unknown, but as for the Pink-footed Geese, they probably by-pass.

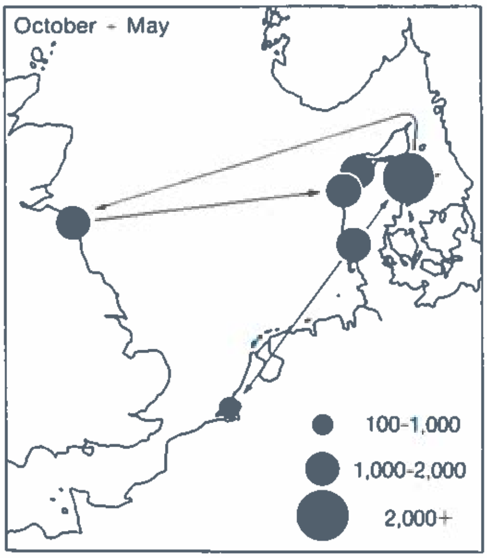


Fig. 17. Distribution of the Svalbard Light-bellied Brent Geese in the wintering quarters. Arrows indicate directions of movements. (After MADSEN 1984c).

In autumn at least part of the population stops on Bear Island on the southerly migration from Svalbard. In 1984 OWEN et al. (1985) recorded passage of flocks between 7-18 September with a maximum of 350 geese. The migration along the north Norwegian coast probably occurs far at sea. Flocks are regularly seen from Utsira to Jæren. In the latter place some flocks may rest before the passage to Denmark (SALOMONSEN 1958, BYRKJEDAL & ELDØY 1981). Most flocks pass Jæren in the first half of September.

Ecology. No published information exists. In 1984 J. M. BLACK (pers. comm.) saw flocks of Brent Geese grazing on the headland of Bear Island together with Barnacle Geese.

Legal status. Total protection in Norway.

Wintering grounds

The main wintering quarters are situated in Denmark and northeast England (Fig. 17). Very few individuals are seen in the West German Wadden Sea among the Dark-bellied Brent Geese (PROKOSCH 1984c). In the Netherlands up to 200 birds are seen in cold winters (LAMBECK 1981, VAN DEN BERGH 1984), probably displaced from the Danish Wadden Sea because of bad weather conditions, and few individuals are seen among the Dark-bellied Brent Geese in the Dutch Wadden Sea area (LAMBECK 1977).

The phenology in Denmark and England is shown in Fig. 18.

Denmark

Numbers and distribution. The population has five regular haunts which are used in succession: the Danish part of the Wadden Sea, Mariager and Randers Fjords, Nissum

Bredning, Agerø and Nissum Fjord (MADSEN 1984c).

The Light-bellied Brent Goose is the earliest among the arctic nesting geese to arrive in Denmark. On their way from Norway to the Wadden Sea peak numbers pass Blåvandshuk in southwest Jutland before mid September (MELTOFTE 1973), around two weeks ahead of the Dark-bellied Brent Geese. In September the Light-bellied Brent Geese are only seen in the Wadden Sea, though usually in small numbers. Larger flocks of up to 1,100 individuals have been recorded, and give rise to the suspicion that the majority of the population stays there in September and October. They may well be overlooked, due to the vastness of the area and to mixing with the more numerous Dark-bellied Brent Geese (MADSEN 1984c).

From the end of November most of the population is concentrated in Mariager Fjord. If the winter is mild, and the shallow waters not frozen, the geese remain there until March. However, in cold winters where Mariager Fjord becomes icebound an increasing proportion of the population is displaced to Lindisfarne in northeast England. Hence, the number of Brent Geese in Lindisfarne is negatively correlated with mean temperatures in Denmark in January and February (MADSEN 1984c). From March to the end of May the population gathers in two sites, Nissum Fjord and around the small island Agerø in northwest Jutland. Nissum Bredning is irregularly used. The geese leave the spring haunts between 20 to 31 May.

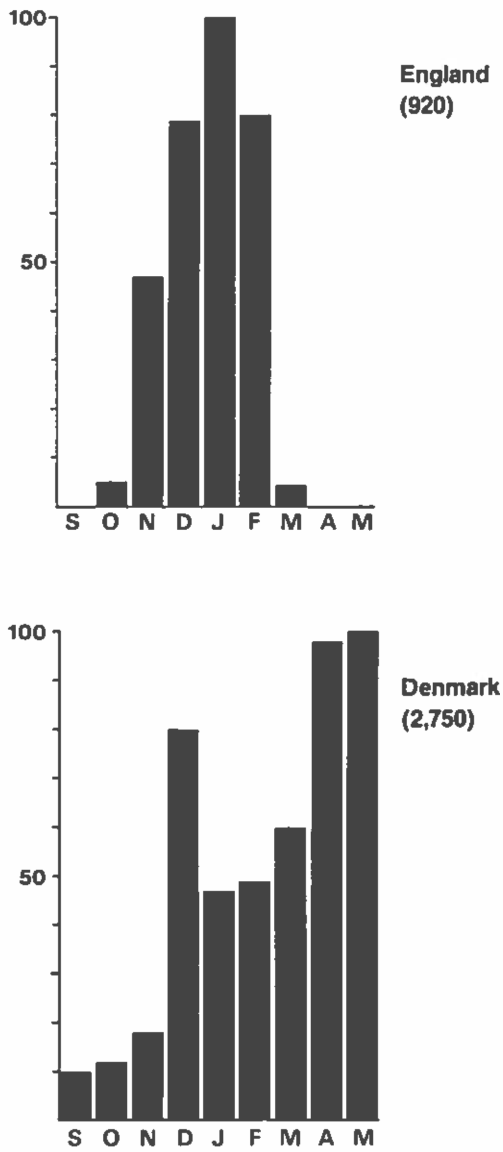


Fig. 18. Phenology of Light-bellied Brent Geese in the winter range, expressed in percentage of peak month. Data are from 1980-1984. Numbers in brackets give average maximum (=100%). Sources, see text.

Ecology. In autumn and winter the Brent Geese feed on mudflats and shallow water. From March to May the geese gradually shift to saltmarshes and to lesser extent pastures (MADSEN 1984c).

Past history. In the beginning of this century Light-bellied Brent Geese were numerous in the shallow-watered fjords, Limfjorden, Nissum Fjord and Mariager Fjord, but declined drastically in numbers in the first half of the century (SALOMONSEN 1958, FOG 1972). In the 1960s the spring population was confined to Nissum Fjord and Nissum Bredning, but since the mid 1970s an increasing part of the geese has stayed around the island Agerø in Limfjorden. Nissum Bredning was formerly an important spring haunt, but has now lost its value, probably due to pollution of the shallow waters.

Legal status. Total protection since 1972. Before the ban it was estimated that approximately 220 birds were bagged annually (Fog 1967), representing about 10% of the population.

Management measures and problems. The feeding grounds on saltmarshes are protected areas. However, apart from minor parts, none of the haunts are reserves with shooting regulations (Madsen 1986). A general threat posed on the haunts is the increasing hypereutrofication and pollution of the shallow waters of the fjord systems. In Nissum Fjord the submerged macrophyte vegetation has almost died-out recently (Jepsen 1984), as it has over large parts of Nissum Bredning.

England

Numbers and distribution. Only one site, Lindisfarne in Northumberland is used regularly by the Light-bellied Brent Geese.

The Brent Geese usually arrive in November, and numbers peak in January, although depending on the severity of the winter in Denmark (Madsen 1984c). When the winters are mild in Denmark numbers remain below 1,000, but in cold winters the majority of the population is gathered at Lindisfarne, in January 1985 reaching a record maximum figure of 3,000 (Ogilvie 1977-1985). The geese leave Lindisfarne before mid March.

Ecology. The Brent Geese feed on beds of *Zostera* spp. on shallow waters and mudflats (Smith cited in Evans & Dugan 1984).

Past history. Prior to the population decrease in the first half of this century large numbers wintered in Moray Basin and other sites in east Scotland. The origin of these flocks is unknown, and they may have been Canadian birds (Owen pers. comm.). Flocks were also seen south to Essex (Salomonsen 1958, Atkinson-Willes & Matthews 1960).

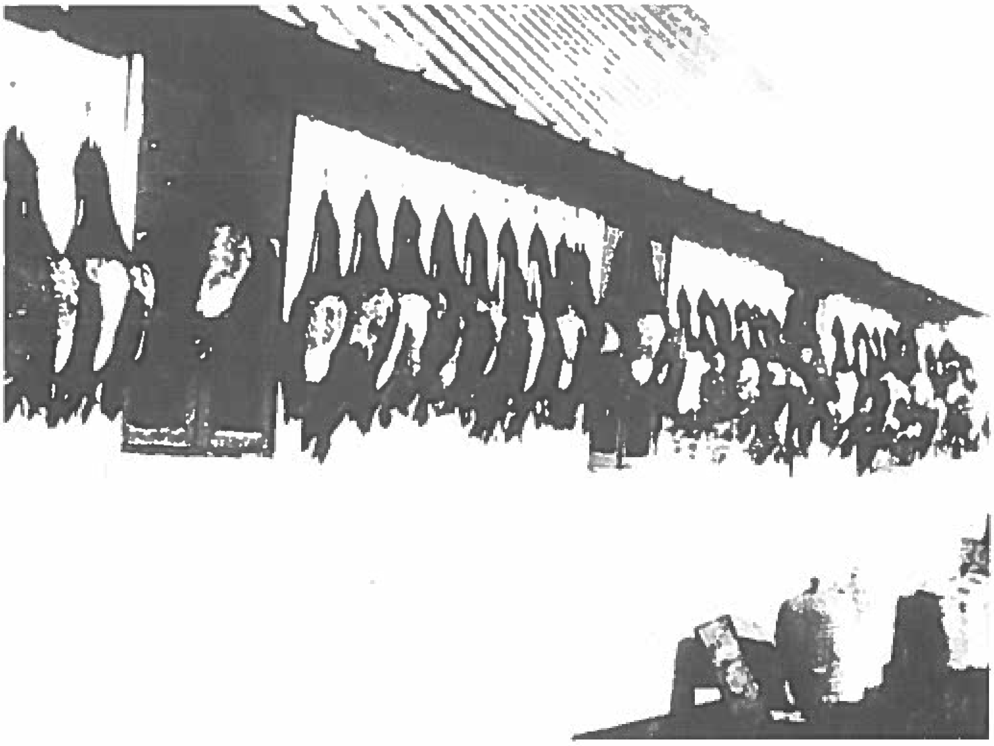
Legal status. Total protection since 1954.

Management measures and problems. The Lindisfarne area is a national nature reserve with some shooting restrictions, however, not over the central feeding grounds (Nature Conservancy Council unpubl.).

Population development

The fragmentary information that exists on the population trends of the Svalbard Light-bellied Brent Geese gives the impression of a population decline in parallel with that of the Dark-bellied population. Based on observations of the number of geese passing south Norway in autumn Salomonsen (1958) estimated that in the latter part of the 18th century the Svalbard population numbered at least 25,000 (Salomonsen made a wrong calculation in his paper, erroneously writing 250,000), and in the latter part of the 19th century at least 40,000-50,000 geese. Accordingly, Løvenskiold (1963) notes that the Brent Goose was breeding in 'immense' numbers on the islands around Svalbard.

However, it was not until the middle of the present century when counts started in Britain and Denmark that it was identified how serious the population decline had been. Salomonsen (1958) estimated that the population did not exceed 4,000 indivi-



A wall full of bagged Light-bellied Brent Geese, western Limfjord, Denmark, in the 1940s. Despite the population decline in the 1930s, a fair number of Brent Geese was apparently shot in the following decade. This supports the theory that factors other than the die-back of the seagrass *Zostera marina*, e.g. overshooting, contributed to the decline. (Photographer unknown.)

duals in the 1950s, and from the breeding grounds it was correspondingly reported that most of the former breeding grounds were empty of Brent Geese (LØVENSKIOLD 1963, NORDERHAUG 1970). When counts in Denmark and England were coordinated in the late 1960s it was estimated that the population had dropped further to 1,600-2,000 individuals (FOG 1972). In the 1980s the population has recovered a little, now reaching around 4,000 geese (MADSEN 1984c). Breeding success expressed by the proportion of juveniles in the winter flocks shows that the population has a low average reproductive success (Table 2), which is lower than that of the other Svalbard goose populations.

Discussion

The reasons for the decline of the Svalbard population of Light-bellied Brent Goose in the first half of this century are probably the same as for the Dark-bellied Brent Goose population. The 'wasting disease' of the *Zostera* food supplies in the wintering quarters probably also affected the Light-bellied Brent Goose population as it was probably almost exclusively feeding on *Zostera marina* in autumn and winter. It is known that shooting pressure on the population in both autumn and spring was considerable (FOG 1972), and this may likewise have had a negative effect on the population level. Egg collection and associated disturbance on the breeding islands of the Brent Geese may, in addition to the factors on the wintering grounds, have had a critical impact on the breeding success of the population.

It has been suggested that the Brent Goose and the Barnacle Goose compete for nest sites and food during the breeding season (Owen & Norderhaug 1977), and that the increase of the Barnacle Goose population may have caused that the Brent Goose was forced out of some of the breeding areas. However, the decrease of the Brent Goose happened before the increase of the Barnacle Goose, but possibly the now densely breeding Barnacle Geese along the coasts of Spitsbergen may prevent the Brent Geese from re-establishing there.

Whilst the population of Dark-bellied Brent Goose has tripled in numbers since the shooting ban in Denmark in 1972, the Light-bellied Brent Goose population has shown only modest signs of recovery. An annual kill of approximately 220 birds in Denmark prior to 1972 (Fog 1967) may well have been the factor controlling population size, and a decreased shooting mortality can have been the reason for the positive development recorded since 1970.

Because the population of Svalbard Light-bellied Brent Goose is so small and often concentrated in one or two haunts, it is highly vulnerable to environmental perturbations or deterioration, as for example the die-off of the macrophyte vegetation in Nissum Fjord in Denmark. A single event of this character may affect the welfare of a major part of the population.

The reproductive rate in the population since 1980 has on average been low and not exceeded 25% of juveniles in the wintering flocks (Table 2). This feature is common to the other Svalbard goose populations, but in contrast to the Dark-bellied Brent Goose which has an average reproductive rate twice as high as the Light-bellied Brent Goose (see p. 50). In the Svalbard Barnacle Goose it has been concluded that at present the breeding success is limited by factors operating on the breeding grounds (Owen 1984). In the Light-bellied Brent Goose there is so far no evidence as to the factors limiting the population growth.

Management needs. As long as the population has not recovered more than at present, highest possible priority should be given to protect the stock and its haunts. A reserve in the major Danish haunt, Mariager Fjord and Randers Fjord, to reduce disturbance is much needed. However, site protection will only be effective if the habitats are also preserved. This implies action against pollution of the coastal shallow waters.

If the shooting season of the Dark-bellied Brent Goose should be re-opened in Denmark, it should of course not include areas where Light-bellied Brent Geese occur. However, it must be emphasized that there does not exist a complete map of the whereabouts of the population in the winter range. For example it is not known how important the Wadden Sea is to the population. Before an eventual decision about reopening the season, this basic information should be at hand.

At present only a small proportion of the population breeds in sanctuaries in Svalbard. The identification of Tusenøyane as the central breeding area of the population should be followed up by an analysis of needs for sanctuaries in the area.

Research needs. To make a proper management of the population and its sites, an inventory and monitoring scheme on several aspects of the ecology of the population should be initiated. First, virtually nothing is known about breeding ecology, and still there are many gaps in our knowledge of the breeding distribution. Second, there are times of the year (September, November, March) where we do not know the whereabouts of a major part of the population. Third, little is known about factors determining population levels. As part of the latter the influence of spring feeding conditions on the build-up of body reserves ought to be studied. To enable these studies, a part of the population should be individually marked with plastic leg rings.

General discussion and conclusions

Population trends and regulation

One critical question in population management is what regulates the size of goose populations. In order to unravel this question the published population reviews are examined.

All five goose populations reviewed here, and most other populations wintering in Europe, have increased during the last decades. In six of the best monitored populations the possible reasons for the increasing trends have been analysed on basis of population parameters and life histories: Icelandic Pink-footed Goose (OGILVIE & BOYD 1976, EBBINGE 1985), Svalbard Pink-footed Goose (EBBINGE et al. 1984), European Whitefronted Goose (EBBINGE 1985), Svalbard Barnacle Goose (OWEN & NORDERHAUG 1977, OWEN 1984), Siberian Barnacle Goose (EBBINGE 1982), and Dark-bellied Brent Goose (PROKOSCH 1984c, EBBINGE 1985). Without any exceptions these six populations have increased.

A common feature in all six populations is that the increases have not been brought about by better reproduction. Annual recruitment has either been constant or has even decreased. The increases have on the other hand been attributed to a marked decrease in mortality. As the highest mortality in general is found in the wintering quarters and not on the breeding grounds, it seems that the releasing factors should be sought on the wintering grounds. In the six populations the increases have coincided with a better protection, and in all studies it is currently believed that restriction of shooting in Europe has been the prime releasing factor. Shooting has seemingly largely been an additive mortality factor, and not compensatory.

Changes in agricultural practice on the wintering grounds may have benefitted the geese in providing a more secure winter forage, leading to a better survival. In most cases, however, the population increases have been started abruptly over few years, suggesting that they were caused by action of a quick change in a single significant factor, e.g., shooting pressure, rather than a more gradual change, as for example the better feeding conditions changing over a longer span of years (EBBINGE 1985).

On the whole, conditions have probably been constant on the arctic breeding grounds. Only on Svalbard have bird sanctuaries provided a better protection to the Barnacle Geese.

In conclusion, the analyses of population dynamics of the six populations provide circumstantial evidence for the hypothesis that goose populations wintering in Europe have been – and some populations probably still are – regulated by shooting.

How far the goose populations will develop will depend on the ceiling of the habitat capacity of their environment. Density-dependent regulating mechanisms have been documented in some populations, and so far it has especially affected reproduction and not so much adult mortality (Icelandic Pink-footed Goose: OGILVIE & BOYD 1976, EBBINGE 1985; Icelandic Greylag Goose: BOYD & OGILVIE 1972; Greenland Barnacle Goose: OGILVIE 1978, CABOT & WEST 1983; Svalbard Barnacle Goose: OWEN 1984: Dark-bellied Brent Goose: EBBINGE 1985). This has for example been

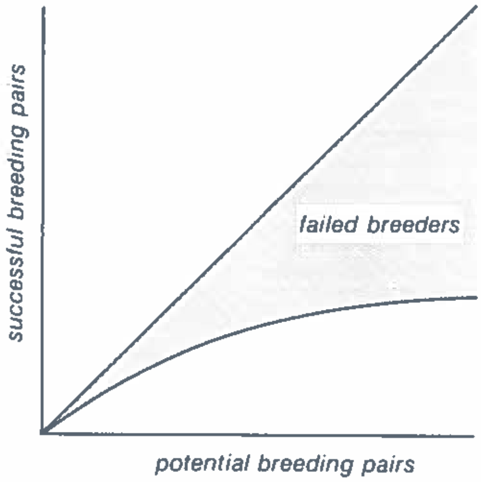


Fig. 19. Generalized trend found in several goose populations: the proportion of successful breeders is reduced at higher population levels (After EBBINGE 1985).

shown by the finding that the number of successful breeding pairs levels off with increased population size (Fig. 19).

The density-dependent effect can be brought about at various stages during prebreeding and breeding:

1) By increased competition on spring staging areas. During this period, where the geese put on weight and which is vital to the breeding potential, food competition may affect the breeding outcome. This may be the case in the Dark-bellied Brent Goose, which is concentrated on saltmarshes in the Wadden Sea, where there is a limited capacity (see p. 46), and possibly also in other populations.
2) Through competition for nest sites, including density effects on nesting success. This can be pronounced in populations where breeding is restricted to islets or cliffs, e.g., the Svalbard Barnacle Goose (OWEN 1984).
3) By increased competition for food during the nesting and fledging period. For the Svalbard Barnacle Goose it has been indicated that food resources during nesting and post-nesting limit breeding success (PROP et al. 1984), and likewise for the Pink-footed Goose breeding in central Iceland (GARDARSSON 1976). However, generally very little is known about the habitat capacity of the Arctic breeding grounds.

As it appears from the above discussion, the various predictions point in the direction that in the future the density-dependent factors will operate on the breeding grounds or the spring staging areas, but not on the wintering grounds. This is probably contrary to the original situation, where the goose populations supposedly were regulated by limited food resources on the wintering grounds (OWEN 1980a). Because of the shift to the agricultural lands, which has taken place in many goose populations over the last decades, potential food resources seem not to be limiting.

The hypothesis that populations will be regulated by factors on the breeding grounds, does primarily apply to those breeding in the north Atlantic and possibly those breeding along the north Siberian coastline. This, probably, does not apply to the Whitefronted Geese breeding over the vast expanses of the Siberian tundra or to the Greylag Geese breeding in west and central Europe, which still have the possibility of expanding their breeding range.

Goose damage and possible solutions

In January 1984 goose damage in west Europe was the theme of an IWRB meeting with participating biologists and wildlife administrators from eight countries. The aim of the meeting was to map the extent of damage and to discuss possible solutions.

The following discussion is partly based on the conclusions from the meeting (see RÜGER 1985).

In relation to national farm output the amount of goose damage in west Europe is negligible, but the income of individual farmers may be hampered seriously. The critical cases are when geese compete directly for food with sheep or cattle, e.g., Brent Geese in the Wadden Sea. Furthermore, damage can occur locally where geese graze winter cereals or take seeds in newly sown fields or ripening cereals. The extent of damage has increased over the last decade because the farmers increasingly make use of crops which are vulnerable to goose grazing, e.g., winter cereals and fertilized pastures. Assessment of the damage has, however, only been carried out in relatively few cases, and it is believed that the farmers often are prone to exaggerate the losses.

It is anticipated that goose damage to crops to some extent will occur as long as geese feed on farmlands. The question is then, how to alleviate the damage. Should it be done by scaring, by direct compensation to the farmers, or indirectly by purchase of land to create managed goose refuges?

Scaring devices, e.g., very pistols or dummies, only have a short-term effect, and can only be used with limited success in cases where the problem is isolated, but cannot be advocated generally. Either the geese will habituate to the deviceds, or the problems are only relocated to other potentially damaged areas. Licensed shooting over vulnerable crops may have some effect, as the English example with the Brent Geese feeding inland has shown (see p. 48). The relative success is more due to the psychological effect, which the farmer obtains by the legal possibility of doing something, rather than to the scaring effect.

Payment of direct compensation is practised in the Netherlands, FRG and on a small scale in Sweden. The Dutch example (see p. 46) shows, however, how easily the problems can be inflated, and it ought to discourage the application of that method.

The indirect way of compensation by purchase of alternative feeding grounds to draw geese from nearby farmland where they are accused of damage has been used with some success on Texel in the Dutch Wadden Sea, and it is planned to be used in the German Wadden Sea as well. Recently this method has been practiced on Islay in Scotland, where a goose refuge has been established in an area where Barnacle Geese cause damage to grass crops (NUGENT 1985).

At the IWRB goose damage meeting it was the general opinion that this form was the only possible long-term solution to the conflicts with the farming community. The refuges are, however, costly to establish and to manage, probably overriding the level of crop damage. Another problem is that big refuges will possibly attract so many geese that damage problems in the surrounding farmland are exacerbated (OWEN 1977, 1980b). A network of smaller refuges will probably alleviate that effect in some goose species, e.g. Brent Goose, as suggested by ST JOSEPH (unpubl.), but not in others. However, in planning future policies it is essential that our thinking is radical and flexible, to suit the particular situation and the needs of the particular species.

As a further complication the damage by Pink-footed Geese in Denmark and the Netherlands in autumn shows that the problem need not only be caused by the attraction of the geese to farmland areas, but may also be caused by shooting disturbance or other human activities, concentrating disproportionally large numbers of geese in a few areas (see p. 22). This indicates that solutions should often integrate other aspects than just the isolated damage problem.

For the Dark-bellied Brent Goose especially, it has been proposed, that one way to reduce the damage would be to control the population size (SWIFT & HARRISON 1979, ST JOSEPH unpubl.). This argument is adduced because a correlation has been found between the population increase in the 1970s and the number of geese feeding inland in England. Today the problems have been reduced by the more pragmatic solution of licensed shooting (see p. 48), which is perhaps not a sustainable long-term solution, but it does on the other hand not imply any philosophy of how to manage bird populations in Europe. Population limitation seems to be a dangerous track to follow, if the basis is to regard the birds as hazards to the human society. According to that argument the habitat capacity should set the population levels. However, as various examples in this review have shown, the habitat capacity concept is difficult to handle, because the capacity is hard to measure and a variable parameter. The capacity will be highly dependent on human impact on the habitats, and as the natural and semi-natural habitats are decreasing in area all the time, solutions to damage problems should be based on the conservation and management of natural habitats rather than on population control.

Future management strategies

Although most populations are in a healthy state, they are under constant pressure from human impact, especially in the winter quarters, but also increasingly on the breeding grounds. Therefore, there is a great need for strategies for the long-term management of the geese all along their migration routes. It is important that we recognize the populations as international natural resources, and that strategies are based upon integrated knowledge of population dynamics and the ecological requirements of the geese. A shooting system should be based on and concerned with population parameters only. An important aim of a strategy is the restoration of endangered goose stocks, in Europe especially the Light-bellied Brent Goose from Svalbard and the Lesser Whitefronted Goose. A restoration plan should aim at habitat preservation and regulation of shooting and disturbance in key areas.

Dansk resumé

Status og forvaltning af gåsebestande i Europa, og især bestande, der raster og yngler i Danmark

I denne oversigt gøres der status over gåsebestandene, deres økologi og forvaltning i Europa. Bestandenes udvikling i det 20. århundrede resumeres, og det diskuteres, hvilke faktorer der bestemmer deres størrelse. Markskadeproblemer og deres mulige løsning diskuteres, og der gives forslag til fremtidig forvaltning og forskning. Specielt fem bestande, der trækker gennem Danmark eller yngler herhjemme, beskrives.

Skovsædgås (*Anser fabalis fabalis*)

Skovsædgåsen, der er en race af Sædgåsen, yngler i Nordskandinavien og Vestsibirien i delvis geografisk overlapning med Tundra Sædgås (*A. f. rossicus*) (Fig. 1). Den overvintrer i Sydsverige, Danmark, Østtyskland og Holland (Fig. 3 & 4), i de tre sidstnævnte lande især i kolde vintre, mens *rossicus*-bestanden overvintrer i Centraleuropa og Holland (Fig. 2). *Fabalis*-bestanden

tæller ca. 60.000 gæs, mens *rossicus*-bestanden tæller ca. 250.000. Der er normalt ikke blanding af de to bestande i overvintringsområdet. På overvintringspladserne har *fabalis*-bestanden en speciel tilknytning til moseområder og fouragerer på tilstødende græsarealer. Store dele af bestanden fouragerer i dag også på vintersæd, sukkerroer og andre landbrugsafgrøder. Der er ikke særlige markskadeproblemer. Bestanden er tredoblet fra 1960 til 1980. Af særlige trusler mod bestanden fremhæves ødelæggelsen af ynglebiotopen, skovmoserne, på grund af afvandinger og tørvegravning samt opgivelsen af høslæt omkring moserne. Der savnes viden om bestandens populationsdynamik, om antallet i Østtyskland og om yngleforholdene i Sovjetunionen.

Kortnæbbet Gås (*Anser brachyrhynchus*) (Svalbardbestanden)

Bestanden af Kortnæbbet Gås yngler på Svalbard og overvintrer i Danmark, Holland, Belgien og tidligere også i Vesttyskland (Fig. 5, 6 & 7). Under trækket i maj måned stopper bestanden kortvarigt i Nordnorge. Hovedparten af bestanden opholder sig i Vestjylland i oktober, og fra marts til maj forekommer hele bestanden her. I vintermånederne opholder hovedparten af de Kortnæbbede Gæs sig i Holland og Belgien, i milde vintre dog også i Sydvestdanmark.

Om efteråret fouragerer gæssene mest på stubmarker og lidt på vintersæd, om vinteren og tidligt forår på græsarealer, og i april-maj hovedsageligt på nysåede kornmarker i Vestjylland. Om efteråret forekommer der markskader på Filsø i Vestjylland, hvor gæssene i de senere år har fourageret på vintersæd. Gæssene fordrives og flyver til Holland, hvor de på grund af den tidlige ankomst gør skade på et sent høslæt. Markskadeproblemet forværres af, at gæssene samles på Filsø, fordi de fordrives fra Vest Stadil Fjord på grund af jagt. På Vest Stadil Fjord forvolder gæssene ellers ingen markskader om efteråret. Fourageringen på de nysåede marker om foråret har spredt sig langs den jyske vestkyst. Om foråret fodres gæssene på Vest Stadil Fjords marker med udlagt korn for at afbøde skaderne.

Fra 1955 til 1980 er bestanden fordoblet (Fig. 8), forårsaget af formindsket dødelighed, sandsynligvis som følge af formindsket jagttryk.

Langtidsløsninger på problemerne i Vestjylland er nødvendige. Der bør oprettes reservater for gæssene langs vestkysten med gode fourageringsmuligheder. Fodringen af gæs bør opgives for om muligt at vænne gæssene af med at fouragere på nysåede marker. Om efteråret bør gæssene spredes på flere lokaliteter, f.eks. ved jagtreguleringer.

Der vides for lidt om populationsdynamiske forhold og yngleøkologien hos bestanden.

Grågås (*Anser anser anser*) (den nordvesteuropæiske bestand)

Bestanden af Grågås yngler i Nordvest-Europa og overvintrer i Sydspanien og Holland, med nogen overlapning til den central-europæiske bestand, der overvintrer i Nordafrika (Fig. 9).

Ynglebestanden tæller mindst 12.000 par (Tabel 3) og hele bestanden ca. 130.000 gæs. Ikke-ynglende gæs i bestanden fælder svingfjer på specielle fældningspladser, især Oostvaarderplassen-reservatet i Holland, mindre antal langs Norges vestkyst, ved Gotland, i Danmark og Polen (Tabel 4).

I august-september samles gæssene på rastepladser især i det sydlige Østersøområde (Fig. 10 & 11, Tabel 5). Fra oktober sker trækket mod overvintringspladserne. Om efteråret fouragerer gæssene især på stubmarker og græsarealer, i mindre grad på kogleaks *Scirpus* spp. i flodlejer og sumpe. Om vinteren i Sydspanien tager gæssene især rodstængler og kogleaks i oversvømmede flodlejer i Coto Donana reservatet ved Guadalquivir floden. I vintrene 1980/81 til 1982/83 var der tørke i området, som forårsagede massedødsfald blandt gæssene på grund af fødemangel. Forholdene er i dag forbedrede, idet der nu ledes mere vand gennem reservatet.

På trods af tørken er bestanden firedoblet de sidste 10-12 år (Fig. 12). Årsagen hertil er sandsynligvis formindsket jagt på bestanden og muligvis forbedrede ynglevilkår. Markskader forårsaget af Grågæs er lokale og ikke alvorlige.

Der savnes populationsdynamiske undersøgelser af bestanden og bedre kendskab til udvekslingen mellem Grågås-bestandene i Europa.

Mørkbuget Knortegås (*Branta bernicla bernicla*)

Den Mørkbugede Knortegås yngler i Nordsibirien og overvintrer langs kysterne af Vesteuropa (Fig. 13, 14 & 15). Bestanden tæller ca. 150.000 gæs. Om efteråret opholder de fleste Knortegæs sig i Vadehavsområdet (Holland-Danmark). Om vinteren er bestanden koncentreret i England og Frankrig, og fra marts til maj i Vadehavsområdet. Om efteråret og vinteren fouragerer gæssene hovedsageligt på vadeflader, hvor de æder ålegræs *Zostera* spp. og grønalger. Om foråret skifter de over til af afgræsse strandenge. Gæssene er i stigende grad også begyndt at fouragere på græsmarker bag digerne i både England og Holland, hvilket hænger sammen med, at de nedgræsser ressourcerne på vaderne.

Siden begyndelsen af 1970erne er bestanden femdoblet (Fig.16), hvilket primært anses at skyldes jagtfredningen i Vesteuropa og specielt Danmark. I England, Holland og Vesttyskland forvolder gæssene markskader ved at konkurrere om græsset med får og kreaturer, men problemerne er delvis løst ved henholdsvis licensjagt, oprettelse af reservater og økonomisk kompensation til de ramte landmænd. Langtidsløsninger på problemerne savnes dog stadig. Digebyggerier i det tyske Vadehav har forværret problemerne, fordi græsningsarealerne er blevet formindsket. Genåbning af jagttid bør ske efter et internationalt kvotesystem baseret på viden om knortegæssenes populationsdynamik. Det foreslås, at man venter en årrække for at se, hvordan bestanden videre udvikler sig.

Der savnes viden om bestandens yngleøkologi.

Lysbuget Knortegås (*Branta bernicla hrota*) (Svalbardbestanden)

Bestanden af Lysbuget Knortegås yngler på småøer omkring Svalbard og Franz Josef Land og overvintrer i Danmark og Østengland (Fig. 13, 17 & 18). Bestanden tæller kun 4.000 gæs. Bestanden har 4-5 rastepladser i Danmark, hvoraf Mariager Fjord/Randers Fjord er overvintringspladsen, Nissum Fjord og Sydvestmors forårsrastepladserne. Det er uvist, hvor bestanden opholder sig om efteråret, men sandsynligvis i det danske Vadehav. I strenge vintre flytter det meste af bestanden til Lindisfarne i England. Om efteråret og vinteren fouragerer gæssene på vadeflader og fladvand, hvor de æder ålegræs og grønalger, og om foråret afgræsser de især strandenge. Siden 1970 er bestanden omtrentligt fordoblet. Forurening i Nissum Fjord har ødelagt det meste af fjordvegetationen, der var vigtig fødekilde for knortegæssene, og forureningen af de indre danske farvande er også en trussel mod fjordvegetationen i Mariager Fjord.

Det foreslås, at der oprettes vildtreservat i Mariager Fjord, samt at der foretages bedre beskyttelse af det vigtigste yngleområde på Svalbard.

Der savnes viden om populationsdynamik, yngleøkologi og bestandens trækmønster.

I alt forekommer der 21 gåsebestande i Europa, der tilsammen tæller ca. 1,5 mill. gæs (Tabel 1). Næsten samtlige bestande er gået frem de sidste årtier. Populationsdynamiske analyser af seks bestande har samstemmende vist, at bestandene først og fremmest er gået frem på grund af formindsket dødelighed. Hovedansvarlig herfor anses at være, at jagttrykket generelt er blevet reduceret. Jagten har således en additiv effekt til de naturlige dødsårsager. I dag ses der i nogle bestande tæthedsafhængig regulering af reproduktionen, hvilket tyder på, at forhold på ynglepladserne i fremtiden vil begrænse bestandene (Fig. 19).

Gåseskader på landbrugsafgrøder er steget, dels fordi bestandene i høj grad har slået over på landbrugsjorden, dels fordi bestandene har været i fremgang, og dels fordi landbruget i stigende grad benytter afgrøder, der er følsomme over for gåsegræsning, f.eks. vintersæd, fremfor vårsæd.

Markskadeproblemerne vil bedst løses ved at oprette gåsereservater med græsarealer og en bedre beskyttelse og pleje af vader og fladvand, strandenge og enge, der er traditionelle gåserastepladser.

Der er behov for en international strategi for forvaltning af de europæiske gåsebestande. Strategien bør baseres på kendskab til bestandenes dynamik og økologiske behov. Jagten bør indrettes efter disse principper. Endvidere bør der sættes kræfter ind på at retablere de små bestande.

Резюме на русском языке:

Состояние популяций гусей в Европе и заведование ими, особенно популяций, обитающих и гнездующих в Дании

В этой обзорной статье дается отчет о популяциях гусей, их экологии, и заведовании ими в Европе. Резюмируется развитие популяций в 20 столетии, и обсуждаются условия, определяющие их численность. Обсуждаются проблемы вреда, причиняемого гусями на полях, и их возможные разрешения, и даются предложения о заведовании ими и исследовании их в будущем. В особенности описываются пять популяций, перелетающих через Данию и гнездующих там.

Гуменник (Anser fabalis fabalis)

Гуменник гнездует в северной Скандинавии и Западной Сибири, географически часто совпадая с тундровым гуменником (A. fabalis rossicus) (Фиг. I). Он зимует в Южной Швеции, Дании, Восточной Германии и Голландии (Фиг. 3 и 4). В трех последних странах этот вид особенно встречается в суровые зимы. Популяция fabalis составляет прибл. 60.000 гусей, а популяция rossicus прибл. 250.000. В районах зимовки эти две популяции нормально не смешиваются. На местах зимовки популяция fabalis предпочитает болотистые местности, и фуражирует на соседних с болотами травостойных лугах. Значительная часть популяции нынче также фуражирует на полях озимого хлеба, сахарной свеклы и других земледельческих культур. Вред, причиняемый полям, не представляет серьёзных проблем. С I960 по I980 г. популяция возросла втрое. Из особенных опасностей, грозящих популяции, придается значение порче биотопа гнездования, т. е. лесных болот вследствие осушения, раскапывания торфа и покидания сенокосных угодий вокруг болот. Не имеется достаточных сведений о популяционной динамике, о численности популяции в Восточной Германии и об условиях гнездования в Советском Союзе.

Короткоклювый гуменник (Anser brachyrynchus) (Шпицбергенская популяция)

Популяция короткоклювого гуменника гнездует на Шпицбергене и зимует в Дании, Голландии и Бельгии, а прежде также зимовала в Западной Германии (Фиг. 5, 6 и 7). На перелете в мае месяце популяция кратковременно останавливается в Северной Норвегии. Главная часть популяции в октябре находится в Западной Ютландии, а с марта по май там встречается вся популяция. В зимние месяцы наибольшая часть короткоклювых гуменников находится в Голландии и Бельгии, а в мягкие зимы также в Югозападной Дании. Осенью гуси главным образом фуражируют на жнивах, и немного на озимых культурах, зимой и ранней весной на травостойных лугах, а в апреле - мае на недавно засеянных нивах в Западной Ютландии. Осенью случаются повреждения полей на Фильсё в Западной Ютландии, где гуси за последние годы фуражировали на озимых культурах. Гусей угоняют, они улетают в Голландию, и вследствие раннего прибытия туда вредят поздним сенокосным лугам. Проблема вреда на полях обостряется тем, что охота угоняет гусей из Стадиль-Фиорда, где они иначе не причиняют вреда. Фуражирование весной на недавно засеянных нивах распространилось вдоль западного берега Ютландии. На полях у Западного Стадиль-Фиорда гусей для предотвращения вреда кормят выложенным зерном.

С I955 по I980 г. популяция возросла вдвое (Фиг. 8), вероятно благодаря пониженной заинтересованности охотников.

Требуются долгосрочные решения проблем в Западной Ютландии. Рекомендуется устроить для гусей заповедники вдоль западного берега с хорошими альтернативными возможностями фуражирования. Кормление гусей следует прекратить, чтобы отучить их от фуражирования на недавно засеянных полях. Осенью гусей следует рассредоточить на несколько местностей, напр. регулированием охоты.

О популяционной динамике и экологии размножения не имеется достаточных сведений.

Серый гусь (Anser anser anser)
(Популяция Северозападной Европы)

Популяция серого гуся гнездует в Северозападной Европе, а зимует в Испании и Голландии, с некоторым совпадением с популяцией Центральной Европы, зимующей в Северной Африке (Фиг. 9). Гнездующая популяция составляет по меньшей мере 12.000 пар (Табл. 3), а вся популяция прибл. 130.000 гусей. Линька маховых перьев негнездующих гусей популяции происходит на специальных местах линьки, в особенности в заповеднике Оостваарденплассен в Голландии, а меньшее число их линяет вдоль западных берегов Норвегии, у острова Готланда, в Дании и в Польше (Табл. 4).

В августе – сентябре гуси собираются на местах привала, особенно в южной части Балтийского Моря (Фиг. 11 и 12). С октября происходит перелет на места зимовки. Осенью гуси в особенности фуражируют на жнивах и травостойных лугах, в меньшей степени камышем Scirpus spp. в руслах рек и болотах. Зимой, в Южной Испании, гуси в особенности питаются корневыми стеблями и камышем в наводненных руслах рек в заповеднике Коте Донана у реки Гвадалквивира. В зимах 1980/81 и 1982/83 в этом районе была засуха, и она вызвала массовую гибель гусей вследствие недостатка пищи. Ныне условия улучшились, так как теперь через заповедник проводится больше воды. Несмотря на засуху, популяция за последние 10 – 12 лет возросла в 4 раза (Фиг. 12). Это вероятно объясняется понижением заинтересованности охотников, а может быть также улучшением условий размножения. Вред на полях, причиняемый серыми гусями, только местный и несерьёзный. Не имеется исследований популяционной динамики и достаточных знаний об обмене между популяциями Европы.

Темнобрюхая черная казарка (Branta bernicla bernicla)

Темнобрюхая черная казарка гнездится в Северной Сибири и зимует вдоль берегов Западной Европы (Фиг. 13, 14 и 15). Численность популяции составляет прибл. 150.000 гусей. Осенью большинство казарок обитает в районе морских отмелей (от Голландии до Дании), зимой популяция концентрируется в Англии и Франции, а с марта по май в районе морских отмелей. Осенью и зимой гуси главным образом фуражируют на пространствах отмелей, где они питаются водяной травой Zostera spp. и водорослями. Весной они переходят к фуражированию на прибрежных лугах. Как в Англии, так и в Голландии, гуси в возрастающей степени также начали фуражировать на травостойных лугах за плотинами, что объясняется истощением ресурсов травы на отмелях. С начала 1970-х годов популяция увеличилась в 5 раз, что главным образом считается результатом запрета охоты в Западной Европе, в особенности в Дании. В Англии, Голландии и Западной Германии гуси причиняют вред на пастбищах, конкурируя из-за травы с овцами и коровами, но эти проблемы отчасти разрешены, соответственно введением лицензий на охоту, учреждением заповедников и возмещением убытков пострадавшим земледельцам. Однако, всё еще нет долгосрочных решений этих проблем. У морских отмелей Германии проблемы обострились строительством плотин, так как этим сокращена площадь пастбищ. Если снова будет разрешена охота в определенные периоды, это следует организовать по международной системе квот, основанной на знании популяционной динамики. Предлагается обождать несколько лет, пока не выяснится дальнейшее развитие популяции.

Светлобрюхая черная казарка (Branta bernicla hrota) (Шпицбергенская популяция)

Популяция светлобрюхой черной казарки гнездится на островках вокруг Шпицбергена и Земли Франца Иосифа, а зимует в Дании и Восточной Англии (Фиг. 13, 17 и 18). Численность популяции составляет только 4.000 гусей. В Дании эта популяция имеет 4 – 5 мест привала, из которых Мариагер-Фиорд и Рандерс-Фиорд служат для зимовки, а Ниссум-Фиорд и югозападная часть острова Морс для обитания весной. Где популяция обитает осенью, точно не известно – вероятно на датских морских отмелях. В суровые зимы большинство популяции перелетает на остров Линдисфарн в Англии. Осенью и зимой гуси фуражируют на морских отмелях и других мелких водах, питаясь морской травой и водорослями, а весной главным образом съедают траву с прибрежных лугов. С 1970 г. популяция возросла приблизительно вдвое. В Ниссум-Фиорде наибольшая часть растительности уничтожена загрязнением. Она была важнейшей пищей казарок, и загрязнение внутренних датских вод также угрожает водяной растительности в Мариагер-Фиорде.

Предлагается устроить заповедники в Мариагер-Фиорде и у югозападной части острова Морс, и улучшить защиту важнейшего района гнездования на Шпицбергене.

О популяционной динамике, экологии гнездования и ходе перелетов нет достаточных сведений.

В общем, в Европе встречаются 2I популяция гусей, общей численности около I,5 милл. особей. Почти все популяции за последнее десятилетие увеличились.

Анализы популяционной динамики шести популяций показали, что их рост главным образом произошел благодаря пониженной смертности, и что это прежде всего является результатом пониженной заинтересованности охотников. Следовательно, охота оказывала эффект, добавочный к естественным причинам смерти. Нынче у некоторых из популяций наблюдается регулирование воспроизведения, зависимое от плотности, и это указывает на то, что условия на местах гнездования в будущем ограничат численности популяций.

Вред, причиняемый гусями на полях, повысился, отчасти потому, что популяции ь высокой степени перешли на посевные участки земли, отчасти вследствие роста популяций, а также потому, что земледельцы всё чаще сеют культуры, особенно чувствительные к фуражированию гусей, напр. переходять с ярового хлеба на озимый.

Проблемы вреда на полях лучше всего можно разрешить учреждением для гусей заповедников с травостойными пространствами, а также усиленной охраной и борьбой с загрязнением морских отмелей и других мелководных пространств, являющихся традиционными местами привала.

Требуется международная стратегия по заведыванию европейскими популяциями гусей. Эта стратегия должна быть основана на знании динамики и экологических потребностей этих популяций. Охоту следует организовать по этим принципам. Следует также принять меры для восстановления малочисленных популяций.

References

ALERSTAM, T., 1976: The autumn highway of Brent Goose migration across Skåne? - Anser 15: 281-284 (In Swedish with an English summary).

AMAT, J. A., 1986a: Some aspects of the foraging ecology of a wintering Greylag Goose *Anser anser* population. - Bird Study 33: 74-80.

AMAT, J. A., 1986b: Numerical trends, habitat use, and activity of Greylag Geese wintering in Southwestern Spain. - Wildfowl 37: 35-45.

ANDERSSON, Å., 1969: Hallands Väderö, a moulting area for the greylag goose *Anser anser* during the 19th century. - Vår Fågelv. 28: 116-123 (In Swedish with an English summary).

ANDERSSON, Å., 1982: Sensommar - och höstkoncentrationer av grågäss i Sverige. - Vår Fågelv. Suppl. 9: 39-44.

ANKNEY, C. D. & MACINNES, C. D., 1978: Nutrient reserves and reproductive performance of female Lesser Snow Geese. - Auk 95: 459-471.

ATKINSON-WILLES, G. L. & MATTHEWS, G. V. T., 1960: The past status of the Brent Goose. - Brit. Birds 53: 352-357.

BAVOUX, C., BREDIN, D. & METAIS, M., 1985: Frequentation des polder de la Baie de Bourgneuf par la Bernache Cravant. Hivers 1981-82 à 1983-84. - Unpubl. report, Ligue Francaise pour la Protection des Oiseaux. 34pp.

BERGH, A. B. VAN DEN, 1984: Influx of Pale-bellied Brent Goose *Branta bernicla hrota* in the winter 1981/82. - Limosa 57: 129-132 (In Dutch with an English summary).

BERGH, L. M. J. VAN DEN, 1984: Movements of Bean Geese *Anser fabalis* between West and Central European wintering areas. - Limosa 57: 116-118 (In Dutch with an English summary).

BERGH, L. M. J. VAN DEN, 1985: Occurrence of the European Bean Goose *Anser fabalis fabalis* in the Netherlands. - Limosa 58: 17-22 (In Dutch with an English summary).

BERNIS, F., 1964: La invernada y migracion de nuestros ansares *(Anser anser* y *Anser faba-*

lis). – Ardeola 9: 67-109.

BERNIS, F. & VALVERDE, J. A., 1972: El censo español de aves acuaticas del invierno 1967-68. – Ardeola 17/18: 105-126.

BIANKI, V. V., 1979: Status of *Branta bernicla bernicla* in White Sea passage areas, USSR. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 21-24.

BILT, E. VAN DER & HELMING, B., 1978: The winter ecology of the Brent Goose *Branta bernicla* on Terschelling. – Limosa 51: 31-40 (In Dutch with an English summary).

BLURTON JONES, N. G. & GILLMOR, R., 1959: Some observations on wild geese in Spitsbergen. – Wildfowl Trust Ann. Rep. 10: 118-132.

BOLLINGMO, D. O.., 1981: Spring migration of Pink-footed Geese. – Vår Fuglefauna 4: 174-175 (In Norwegian with an English summary).

BOUDEWIJN, T., 1984: The role of digestibility in the selection of spring feeding sites by Brent Geese. – Wildfowl 35: 97-105.

BOYD, H. & OGILVIE, M. A., 1972: Icelandic Greylag Geese wintering in Britain in 1960-71. – Wildfowl 23: 64-82.

BRUNS, H. A. & VAUK, G. 1985-1986: Wildgänse am Dümmer (1)-(5). – Niedersächsischer Jäger 1985: 1217-1219, 1264-1267, 1986: 66-70, 184-187, 291-293.

BYRKJEDAL, I. & ELDØY, S., 1981: The occurrence of geese at Jæren, SW Norway: wintering populations in the period 1963/64-79/80, and seasonal variations. – Stavanger Mus. Årbok 1980: 31-40 (In Norwegian with an English summary).

CABOT, D. & WEST, B., 1983: Studies on the Population of Barnacle Geese, *Branta leucopsis,* wintering on the Inishkea Islands, Co. Mayo. – Irish Birds 2: 318-336.

CADÉE, G. C., 1972: Diatoms as Brent Goose food. – De levende Natuur 75; 119-120 (In Dutch with an English summary).

CHARMAN, K., 1979: Feeding ecology and energetics of the Dark-bellied Brent Goose *(Branta bernicla bernicla)* in Essex – Kent. In: Jefferies, R. L. & Davy, A. J. (eds.) Ecological Processes in Coastal Environments. – Blackwell Sci. Publ., Oxford, pp. 451-465.

CHARMAN, K., 1979: The seasonal pattern of food utilization by *Branta bernicla* on the coast of southeast England. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 64-76.

CHARMAN, K. & MACEY, A., 1978: The winter grazing of saltmarsh vegetation by Dark-bellied Brent Geese. – Wildfowl 153-162.

CHRISTIANSEN, A., 1936: Knortegæssene, *Branta b. bernicla,* og sygdommen i Bændeltangen. – Dansk Orn. Foren. Tidsskr. 30: 41-46.

DEANS, I. R., 1979: Feeding of Brent geese on cereal fields in Essex and observations on the subsequent loss of yield. – Agro-Ecosystems 5: 283-288.

DELACOUR, J., 1951: Taxonomic notes on the Bean Goose, *Anser fabalis* Lath. – Ardea 39: 135-142.

DIJKSTRA, L. & DIJKSTRA-DE VLIEGER, R., 1977: Voedseloecologie van de Rotgans. – PhD Thesis, Univ. Groningen. 110 pp.

DRENT, R., EBBINGE, B. & WEIJAND, B., 1979: Balancing the energy budgets of arctic-breeding geese throughout the annual cycle – a progress report. – Verh. Orn. Ges. Bayern 23: 239-264.

DRENT, R. & EERDEN, M. R. VAN, 1980: Goose flocks and food exploitation: how to have your cake and eat it. – Acta XVII Congr. Int. Ornithol.: 800-806.

DUBBELDAM, W., 1978: The Greylag Goose *Anser anser* in Flevoland in 1972-1975. – Limosa 51: 6-30 (In Dutch with an English summary).

DUBBELDAM, W. & POORTER, E. P. R., 1982: Short communications on *Anser anser* in the Netherlands, 1970-1980, with special reference to Oostvaarderplassen. – Aquila 89: 73-76.

EBBINGE, B., 1979: The significance of the Dutch part of the Wadden Sea for *Branta bernicla bernicla.* In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 77-87.

EBBINGE, B., 1982: The status of *Branta leucopsis* in 1980-81. – Aquila 89: 151-161.

EBBINGE, B. S., 1985: Factors determining the population size of arctic-breeding geese, wintering in Western Europe. – Ardea 73: 121-128.

EBBINGE, B. S. & BOUDEWIJN, T., 1984: Richtlijnen voor het beheer van rotganzen in het Nederlandse waddengebied. – RIN-rapport

84/4, Rijksinstituut voor Natuurbeheer, Leersum. 76 pp.

EBBINGE, B. S., MEULEN, H. T. VAN DEN & SMIT, J. J., 1984: Changes in winter distribution and population size of Pink-footed Geese breeding in Svalbard. - Nor. Polarinst. Skr. 181: 11-17.

EBBINGE, B., ST JOSEPH, A., PROKOSCH, P. & SPAANS, B., 1982: The importance of spring staging areas for arctic-breeding geese, wintering in Western Europe. - Aquila 89: 249-258.

EBENMAN, B., PERSSON, H. & NILSSON L., 1976: Food-seeking activity and time-budgets of wintering and resting bean geese *Anser fabalis* in Skåne, South Sweden. - Anser 15: 185-194 (In Swedish with an English summary).

EDELSTAM, C., 1972: The visible migration of birds at Ottenby. - Vår Fågelv. Suppl. 7 (In Swedish with an English summary). 360 pp.

EHRLÉN, J., 1983: Roosting by Greylag Goose *Anser anser* in the area of Mörkö-Tullgarn. - Fåglar i Sörmland 16: 11-14 (In Swedish with an English summary).

EHRLÉN, J. & WAHLÉN, L., 1979: Grågåsen som rastare i Mörkö Tullgarn-området 1968-1979. - Fåglar i Sörmland 12: 45-51.

EKKER, Å. T., 1981: The Pink-footed Goose on Spitzbergen. - Vår Fuglefauna 4: 104-108 (In Norwegian with an English summary).

ERMALA, A. & VIKBERG, P., 1982: Gåsjakten i Finland. - Vår Fågelv. Suppl. 9: 93-96.

ESSEN, L. VON & BEINERT, R., 1982: Moulting *Anser anser* along the Gotland coast. - Aquila 89: 27-37.

EVANS, P. R. & DUGAN, P. J., 1984: Coastal birds: Numbers in relation to food resources. In: Evans, P. R., Goss-Custard, J. D. & Hale, W. G. (eds.) Coastal waders and wildfowl in winter. - Cambridge Univ. Press, Cambridge, pp. 8-28.

FERDINAND, L. 1980: Fuglene i landskabet. - Danish Ornithological Society, Copenhagen, 351 pp.

FILCHAGOV, A. V., BIANKI, V. V. & MIKHAILOV, K. T., 1985: Bean Goose *(Anser fabalis)* on the Kola peninsula. - Ornitologica 20: 26-32 (In Russian with an English summary).

FOG, J., 1982: Markskader forvoldt af gæs i Danmark. - Vår Fågelv. Suppl. 9: 79-82.

FOG, M., 1967: An investigation on the Brent Goose *(Branta bernicla)* in Denmark. - Dan. Rev. Game Biol. 5. 40 pp.

FOG, M., 1972: Status for Knortegåsen (Branta bernicla). - Report, Game Biology Station, Kalø. 105 pp.

FOG, M., 1977: Geese, goose research and goose problems in Denmark. - Die Vogelwelt 98: 121-141 (In German with an English summary).

FOG, M., 1982a: Number of Bean Goose *(Anser fabalis sp.)* in the wintering areas. - Aquila 89: 123-125.

FOG, M., 1982b: Baiting as a means of preventing crop damage by Pink-footed Geese *Anser brachyrhynchus* at Vest-Stadil Fjord, Denmark. In: Scott, D. A. (ed.) Managing Wetlands and their Birds. - IWRB, Slimbridge, England, pp. 233-234.

FOG, M., LAMPIO, T., MYRBERGET, S., NILSSON, L., NORDERHAUG, M. & RØV, N., 1984: Breeding distribution and numbers of Greylag Geese *Anser anser* in Denmark, Finland, Norway and Sweden. - Swedish Wildlife Res. 13 (1): 187-212.

FOLKESTAD, O., 1983: Moulting stage and body weight in Greylag Geese shot during an early hunting season at Smøla, Møre and Romsdam, W. Norway, 1982. - Vår Fuglefauna 6: 75-87 (In Norwegian with an English summary).

FOLLESTAD, A., LARSEN, B. H., & NYGÅRD, T., 1986: Sjøfuglundersøkelser langs kysten av Sør- og Nord-Trøndelag og sørlige deler av Nordland. - Viltrapport 41, Norwegian Directorate for Wildlife and Freshwater Fish (112 pp.).

FREDGA, S., 1979: Status of *Branta bernicla bernicla* on passage in Sweden. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 30-32.

FRENGEN, O., 1977: Trekkende gjess over sentrale deler av Trøndelag i mai. - Trøndersk Natur 4: 9-13.

GARDARSSON, A., 1976: Population and production of the Pink-footed Goose *(Anser brachyrhynchus)* in Thjórsárver, 1971-1974. - Univ. of Iceland, Reykjavik (In Icelandic with an English summary).

GORBUNOV, G., 1932: Die Vögel von Franz-

Joseph Land. – Trans. Arct. Inst. IV: 1-244 (In Russian with a German summary).
GRAM, I., 1982: Forekomsten af Kortnæbbet Gås *(Anser brachyrhynchus)* i Tøndermarsken. In: Madsen, J. & Lund, T. (eds.) Annual report of the Goose Working Group of the Danish Ornithological Soc., pp. 50-58.
GROMADZKI, M. & MAJEWSKI, P., 1984: The migrations of Greylag Goose *Anser anser* in Poland. – Acta Sc. Nat. Brno 18: 4-14.
GROMADZKI, M. & WIELOCH, M., 1983: Distribution and number of the grey-lag goose *Anser anser* in Poland in the years 1977-1979. – Acta Ornith. 19: 155-178.
HAACK, W., 1968: Zum Jahresvorkommen der Graugans, *Anser anser,* in Ostholstein 1958-1967. – Corax 2: 180-194.
HAACK, W. & RINGLEBEN, H., 1972: Über den Mauserzug nicht brütender Graugänse *(Anser anser)* im nord- und mitteleuropäischen Raum. – Vogelwarte 26: 257-276.
HAFTORN, S., 1971: Norges fugler. – Universitetsforlaget, Oslo. 862 pp.
HAMILTON, G., 1982: Klingavälsåns naturreservat i Malmöhus län – ett gåsreservat? – Vår Fågelv. Suppl. 9: 111-116.
HARRISON, J. G., 1979: A new overland migration route of *Branta bernicla bernicla* in southeast England in autumn. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 60-63.
HAUFF, P., 1982: Bestandsentwicklung und Brutbiologie der Graugans *Anser anser,* im NSG Kuhlrader Moor und Röggeliner See. – Beitr. Vogelkd. 28: 48-58.
HOEK, C. VAN DEN, ADMIRAAL, W., COLIJN, F. & JONGE, V. N. DE, 1979: The role of algae and seagrasses in the ecosystem of the Wadden Sea: a review. In: Wolff, W. J. (ed.) Ecology of the Wadden Sea, Vol. 3. – Balkema, Rotterdam, pp. 9-118.
HOLGERSEN, H., 1958: The effect of the cold weather of February 1956 on the distribution of Pink-footed Geese in North-West Europe. – Wildfowl Trust Ann. Rep. 9: 170-174.
HOLGERSEN, H., 1960: Wanderungen und Winterquartiere der Spitzbergen Kurzschnabel Gänse. – Proc. XIIth Int. Orn. Congr. Helsinki 1958: 310-316.
HUDEC, K., 1984: Migrational movements of the Greylag Goose *Anser anser* in Europe: a Synopsis. – Acta Sc. Nat. Brno 18 (1): 33-55.
HUDEC, K. & ROOTH, J., 1970: Die Graugans. – Die Neue Brehm-Bücherei. Wittenberg Lutherstadt. 148 pp.
HUDEC, K. & RUTSCHKE, E. (eds.) 1982: The Greylag Goose *Anser anser* in Europe (I.). – Acta Sc. Nat. Brno 16 (12): 1-49.
HUDEC, K. & RUTSCHKE, E. (eds.), 1984: The Greylag Goose *Anser anser* in Europe (II.). – Acta Sc. Nat. Brno 18 (1): 1-55.
HUMMEL, D., 1977-1984: Das Auftreten von Wildgänsen in der Bundesrepublik Deutschland. – Ber. Dtsch. Sekt. Int. Rat Vogelschutz 16-24 (Annual reports).
HUMMEL, D., 1980: Durchzug und Überwinterung der Kurzschnabelgans *(Anser brachyrhynchus)* im Bereich der Nordseeküste (1974-1977). – Die Vogelwelt 101: 121-131.
HUMMEL, D., 1982: The Greylag Goose *Anser anser* in the Federal Republic of Germany. – Acta Sc. Nat. Brno 16 (12): 15-20.
HUYSKENS, G., 1977: De verspreiding van *Anser fabalis fabalis* en *Anser fabalis rossicus* in Europa buiten het broedseizoen. – Watervogels 2: 69-75.
HUYSKENS, G., 1979: De Europese rietganzen *Anser fabalis fabalis/Anser fabalis rossicus* ondersoiken of sorten di of niet skadelijk. – Meus en Vogel 17: 204-208.
IMPE, J. VAN, 1980a: Etude de deux populations de l'Oie des Moissons *Anser fabalis.* – Alauda 48: 1-20.
IMPE, J. VAN, 1980b: Ecologie et ethologie des Oies des Moissons *Anser fabalis fabalis* et *Anser fabalis rossicus.* – Le Gerfaut 70: 499-558.
JACOBS, R. P. W. M., HARTOG, C. DEN, BRASTER, B. F. & CARRIERE, F. C., 1981: Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). – Aquat. Bot. 10: 241-259.
JENSEN, H., 1977: Greylag studies 5: Arrival of the population. – Danske Fugle 29: 109-123 (In Danish with an English summary).
JEPSEN, P. U., 1984: Protection and management of arctic goose populations in Denmark. – Nor. Polarinst. Skr. 181: 153-160.
JÖNSSON, B., 1982a: Gässkador inom lantbruket i Skåne. – Vår Fågelv. Suppl. 9: 71-74.
JÖNSSON, B., 1982b: Förslag om gåserefugiet i

Skåne. – Vår Fågelv. Suppl. 9: 117-118.

JORGENSEN, H. E., 1986: Ungeproduktion hos Grågås *Anser anser* i Danmark. – Dansk Orn. Foren. Tidsskr. 80: 58-64.

KIRBY, R. E., BARRY, T. W., KERBES, R. H. & OBRECHT III, H. H., 1985: Population dynamics of North American Light-bellied Brent Geese as determined by productivity and harvest surveys. – Wildfowl 36: 49-52.

KISTCHINSKI, A. A. & VRONSKI, N. V., 1979: On the summer distribution of *Branta bernicla bernicla*. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 19-20.

KLEMM, C. DE, 1979: A strategy for the international conservation and management of *Branta bernicla bernicla*. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 176-184.

KNIEF, W., 1985: Goose damage in the Federal Republic of Germany. In: Rüger, A. (ed.) Extent and Control of Goose damage to agricultural crops. – IWRB Special Publ. No. 5, Slimbridge, pp. 35-38.

KUMARI, E. E., 1979: Status of *Branta bernicla bernicla* on passage in Baltic USSR. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, p. 25.

KUMARI, E. 1984: Recent developments in the Greylag Goose populations in the eastern part of the Baltic Basin. – Ardeola 31: 27-32.

KUX, Z. & HUDEC, K., 1970: Der Legebeginn bei der Graugans *(Anser anser L.)* in der Tschechoslowakei. – Acta Mus. Moraviae 55: 233-246.

KUYKEN, E., 1969: Grazing of wild geese on grasslands at Damme, Belgium. – Wildfowl 20: 47-55.

KUYKEN, E., 1983: Aantallen en verspreiding van overwinterende ganzen in de oostkustpolders: seizoen 1981/82. – Veldornithologisch Jaarboek van Noord-West-Vlaanderen 1981-1982: 41-46.

KUYKEN, E., 1985: The effects of shooting ban on wintering geese in NW-Flandern (Belgium), in relation to agriculture. – Trans. 17th Congr. Int. Union Game Biol., Brussels, Sept. 17-21, 1985, p. 567 (abstract).

LAMBECK, R. H. D., 1977: The occurrence of Brent Goose *Branta bernicla* subspecies in the Dutch Wadden Sea area during spring 1976. – Limosa 50: 92-97 (In Dutch with an English summary).

LAMBECK, R. H. D., 1981: Pale-bellied Brent Geese *Branta bernicla hrota* in the Delta area in winter 1978/79. – Limosa 54: 47-51 (In Dutch with an English summary).

LAMPIO, T., 1979: Status of *Branta bernicla bernicla* in Finland. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, pp. 26-28.

LAMPIO, T., 1983: Waterfowl hunting in Europe, North America and some African and Asian countries in 1980-81. – IWRB Spec. Publ. no. 3, Slimbridge. 35 pp.

LAMPIO, T., 1984: On the spring migration of the Bean Goose, *Anser fabalis*, in Finland. – Swedish Wildlife Res. 13 (1): 59-72.

LEBRET, T., 1959: The decrease in the Pink-footed Goose *(Anser brachyrhynchus)* in the province of Zeeland, Netherlands. – Limosa 32: 191-193.

LEBRET, T. & TIMMERMAN, A., 1968: A concentration of Greylag Geese *(Anser anser)* in wing moult in the Netherlands. – Limosa 41: 2-17 (In Dutch with an English summary).

LIND, H. 1956: The movement of geese at Tipperne, W. Jutland. – Dansk Orn. Foren. Tidsskr. 50: 90-124 (In Danish with an English summary).

LINDELL, L., 1977: Migrating Brent Geese *Branta bernicla* in South Sweden on 25 September 1976. – Anser 16: 146-147 (In Swedish with an English summary).

LIPPENS, L. 1971: Reintroducing the Greylag in Belgium. – WAGBI Rep. & Year Book 1970-71: 62-66.

LITZBARSKI, H., 1979: Erste Ergebnisse der Beringung und farbigen Kennzeichnung von Saatgänsen, *Anser fabalis*, in der Deutschen Demokratischen Republik. – Beitr. Vogelkd. 25: 101-123.

LITZBARSKI, H., 1982: Populationsstruktur und Zugverhalten der Graugänse, *Anser anser*, in der DDR. – Beitr. Vogelkd. 28: 107-128.

LORENZEN, B. & MADSEN, J., 1985: The goose populations at the Tipper peninsula, Western Jutland, Denmark. II: Grazing ecology in relation to the carrying capacity of the area. – Dansk Orn. Foren. Tidsskr. 79: 113-132 (In

Danish with an English summary).
Lorenzen, B. & Madsen, J., 1986: Feeding by geese on the Filsø farmland, Denmark, and the effect of grazing on yield structure of spring barley. - Holarc. Ecol. 9: 305-311.
Lund, H. M.-K., 1965: Marking of 240 Greylags *(Anser a. anser L.)* in Norway. - Trans. VI Congr. Int. Union Game Biol., pp. 267-269.
Lund, H. M.-K., 1971: Ringing of *Anser anser* in Norway. - Sterna 10: 247-250 (In Norwegian with an English summary).
Løvenskiold, H. L., 1963: Avifauna Svalbardensis. - Nor. Polarinst. Skr. 129: 1-460.
Madsen, J., 1980: Occurrence, habitat selection and roosting of the Pink-footed Goose *Anser brachyrhynchus* at Tipperne, Western Jutland. - Dansk Orn. Foren. Tidsskr. 50: 45-58 (In Danish with an English summary).
Madsen, J., 1982: Observations on the Svalbard population of *Anser brachyrhynchus* in Denmark. - Aquila 89: 133-140.
Madsen, J., 1984a: Numbers, distribution and habitat utilization of Pink-footed Geese *Anser brachyrhynchus* in Denmark 1980-1983. - Nor. Polarinst. Skr. 181: 19-23.
Madsen, J., 1984b: Study of the possible impact of oil exploration on goose populations in Jameson Land, East Greenland. A progress report. - Nor. Polarinst. Skr. 181: 141-151.
Madsen, J., 1984c: Status of the Svalbard population of Light-bellied Brent Geese *Branta bernicla hrota* wintering in Denmark 1980-1983. - Nor. Polarinst. Skr. 181: 119-124.
Madsen, J., 1985a: Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. - Ornis Scand. 16: 140-144.
Madsen, J., 1985b: Relations between change in spring habitat selection and daily energetics of Pink-footed Geese *Anser brachyrhynchus*. - Ornis Scand. 16: 222-228.
Madsen, J., 1985c: The goose populations at the Tipper peninsula, Western Jutland. I: Occurrence and population trends, 1929-1983. - Dansk Orn. Foren. Tidsskr. 79: 19-28 (In Danish with an English summary).
Madsen, J., 1985d: Impact of disturbance on field utilization of Pink-footed Geese in West Jutland, Denmark. - Biol. Conserv. 33: 53-63.
Madsen, J., 1986: Status of the staging goose populations and their haunts in Denmark, 1980-1983. - National Agency for the Protection of Nature, Monuments and Sites, Ministry of Environment, Copenhagen (In Danish with an English summary). 114 pp.
Maheo, R., 1976: The Brent Geese of France, with special reference to the Golfe du Morbihan. - Wildfowl 27: 55-62.
Maheo, R., 1979: Conflicts with agriculture in France. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 146-151 (In French with an English summary).
Maheo, R., 1984: Bernache cravant. Rapport de Synthese. - Secretariat Fauna Flore, Muséum National d'Histoire Naturelle. 9 pp.
Majewski, P., 1983: Some remarks on the situation of *Anser anser* in Poland. - Aquila 90: 15-18.
Markgren, G., 1963: Migrating and wintering geese in southern Sweden. Ecology and behaviour studies. - Acta Vertebratica 2: 297-418.
Mathiasson, S., 1963: The Bean Goose, *Anser fabalis* (Latham), in Skåne, Sweden, with remarks on occurrence and migration through northern Europe. - Acta Vertebratica 2: 419-533.
Mellquist, H. & Bothmer, R. von, 1982: Sädgåsen son häckfågel i Sverige. - Vår Fågelv. Suppl. 9: 23-28.
Mellquist, H. & Bothmer, R. von, 1984: Effects of haymaking on Bean Goose, *Anser fabalis*, breeding habitats in Sweden. - Swedish Wildlife Res. 13 (1): 40-58.
Meltofte, H., 1973: The migration of geese *Anserinae* at Blåvandshuk, W. Jutland, 1963-1971. - Dansk Orn. Foren. Tidsskr. 67: 35-41 (In Danish with an English summary).
Meltofte, H., Elander, M., Hjort, C., 1981: Ornithological Observations in Northeast Greenland between 74°30' and 76°00' N. lat., 1976. - Meddr. Grønland, Biosci. 3. 53 pp.
Mulder, T., 1976: Bijgeloof, domesticatie en vangst. In: Lebret, T., Mulder, T., Philippona, J. & Timmerman, A.: Wilde ganzen in Nederland. - Thieme, Zutpen, pp. 141-147.
Møller, A. P. (ed.), 1978: Nordjyllands Fugle - deres yngleudbredelse og trækforhold. - Scandinavian Science Press, Klampenborg. 372 pp.
Mörzer Bruyns, M. F. & Timmerman, A.,

1968: On the occurrence of the dark-breasted brent goose in the Netherlands. - Limosa 41: 90-106 (In Dutch with an English summary).

NAACKE, J., 1982: Effects of various factors on the size of the breeding and resting stock of the Greylag Goose, *Anser anser L.* in the German Democratic Republic. - Aquila 89: 57-66.

NEHLS, H. W., 1979: Passage of *Branta bernicla bernicla* on the coast of the German Democratic Republic. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 33-36.

NETHERLANDS GOOSE WORKING GROUP, 1983: Geese counts in the Netherlands in 1980/81. - Limosa 56: 9-17 (In Dutch with an English summary).

NETHERLANDS GOOSE WORKING GROUP, 1984a: Geese counts in the Netherlands in 1981/82. - Limosa 57: 7-16 (In Dutch with an English summary).

NETHERLANDS GOOSE WORKING GROUP, 1984b: Geese counts in the Netherlands in 1982/83. - Limosa 57: 147-152 (In Dutch with an English summary).

NETHERLANDS GOOSE WORKING GROUP, in press: Geese counts in the Netherlands and Flanders (Belgium) in 1983/84. - Limosa (In Dutch with an English summary).

NILSSON, L., 1981: Goose counts in Sweden in October-April 1979/80 and 1980/81. - Anser 20: 221-226 (In Swedish with an English summary).

NILSSON, L., 1982: Det häckende grågåsbeståndets storlek och utbredning i Sverige. - Vår Fågelv., Suppl. 9: 33-38.

NILSSON, L., 1984a: Counts of geese in Sweden in October-April 1981/82 and 82/83. - Anser 23: 101-108 (In Swedish with an English summary).

NILSSON, L., 1984b: Migrations of Fennoscandian Bean Geese *Anser fabalis.* - Swedish Wildlife Res. 13 (1): 83-106.

NILSSON, L. & FOG, M. (eds.), 1984: Studies on Fennoscandian population of Bean Goose *(Anser fabalis)*, Greylag Goose *(Anser anser)* and lesser white-fronted Goose *(Anser erythropus)*. - Swedish Wildlife Res. 13 (1).

NILSSON, L. & PERSSON, H., 1982: The occurrence of Pinkfeet *Anser brachyrhynchus* in Sweden in 1977/78-1980/81. - Anser 21: 25-30 (In Swedish with an English summary).

NILSSON, L. & PERSSON, H., 1984: Non-breeding distribution, numbers and ecology of Bean Goose *Anser fabalis* in Sweden. - Swedish Wildlife Res. 13 (1); 107-170.

NORDERHAUG, M., 1970: The present status of the Brent Goose *(Branta bernicla hrota)* in Svalbard. - Nor. Polarinst. Årbok 1968: 7-23.

NORDERHAUG, M., 1971: The present status of the Pink-footed Goose *(Anser fabalis brachyrhynchus)* in Svalbard. - Nor. Polarinst. Årbok 1969: 55-69.

NORDERHAUG, M., 1974: Studies of Brent Geese *(Branta bernicla hrota)* on Tusenøyane, East Svalbard. - Nor. Polarinst. Årbok 1972: 89-98 (In Norwegian with an English summary).

NORDERHAUG, M., OGILVIE, M. A. & TAYLOR, R. J. F., 1964: Breeding success of geese in West Spitsbergen. - Wildfowl Trust Ann. Rep. 16: 106-110.

NUGENT, M. J., 1985: Goose damage in Great Britain. In: Rüger, A. (ed.). Extent and Control of Goose damage to agricultural crops. - IWRB Special Publ. No. 5, Slimbridge, pp. 13-24.

NYHOLM, E. S., 1965: Ecological observations on the geese of Spitsbergen. - Ann. Zool. Fenn. 2: 197-207.

OGILVIE, M. A., 1977-1985: Numbers of geese in Britain and Ireland. - Wildfowl 28-35.

OGILVIE, M. A., 1977: The numbers of Canada Geese in Britain, 1976. - Wildfowl 28: 27-34.

OGILVIE, M. A., 1978: Wild Geese. - Poyser, Berkhamsted. 206 pp.

OGILVIE, M. A., 1979: General introduction to *Branta bernicla bernicla* with particular reference to the wintering areas. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 10-18.

OGILVIE, M. A., 1982a: The status of the Pink-footed Goose *Anser brachyrhynchus.* - Aquila 89: 127-131.

OGILVIE, M. A., 1982b: The Greylag Goose *Anser anser* in the British Isles. - Acta Sc. Nat. Brno 16 (12): 7-10.

OGILVIE, M. A., 1983: The numbers of Greenland Barnacle Geese in Britain and Ireland. - Wildfowl 34: 77-88.

OGILVIE, M. A., 1984: Summary and conclusions at Arctic Geese Symposium in Oslo, Norway, 24-26 October 1983. – Nor. Polarinst. Skr. 181: 165-168.

OGILVIE, M. A. & BOYD, H., 1976: The numbers of Pink-footed and Greylag Geese wintering in Britain: observations 1969-75 and predictions 1976-80. – Wildfowl 27: 63-75.

OGILVIE, M. A. & ST JOSEPH, A. K. M., 1976: Dark-bellied Brent Geese in Britain and Europe, 1955-76. – Brit. Birds 69: 422-439.

OUWENEEL, G. L., 1969: Moulting Greylag Geese *(Anser anser)* in the Haringvliet in the summer of 1969. – Limosa 42: 206-223 (In Dutch with an English summary).

OUWENEEL, G. L., 1981: Aantalsveranderingen bij de Grauwe Gans *(Anser anser)* langs het Hollands Diep-Haringvliet. – Watervogels 6: 13-18.

OWEN, M., 1977: The role of wildfowl refuges on agricultural land in lessening the conflict between farmers and geese in Britain. – Biol. Conserv. 11: 209-222.

OWEN, M., 1980a: Wild Geese of the World. – Batsford, London. 236 pp.

OWEN, M., 1980b: The role of refuges in wildfowl management. – Proc. Brit. Crop Protection Council Symp., London, pp. 44-61.

OWEN, M., 1984: Dynamics and age structure of an increasing goose population – the Svalbard Barnacle Goose *Branta leucopsis*. – Nor. Polarinst. Skr. 181: 37-47.

OWEN, M. & NORDERHAUG, M., 1977: Population dynamics of Barnacle Geese breeding in Svalbard, 1948-1976. – Ornis. Scand. 8: 161-174.

OWEN, M., GULLESTAD, N., BLACK, J. & PERCIVAL, S., 1985: Bear Island Expedition 1984. – Report, Wildfowl Trust, Slimbridge. 12 pp.

OWENS, N. W., 1977: Responses of wintering Brent Geese to human disturbance. – Wildfowl 28: 5-14.

PALUDAN, K., 1965: Migration and moult-migration of *Anser anser*. – Danske Vildtundersøgelser 12 (In Danish with an English summary). 54 pp.

PALUDAN, K., 1973: Migration and survival of *Anser anser* (Aves) ringed in Denmark. – Vidensk. Meddr. Dansk Naturh. Foren. 136: 217-232.

PEERAER, A. M., 1982: Brent Geese with their 'golden feet'. In: Scott., D. A. & Smart, M. (eds.) Proc. Second Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 35-39.

PERSSON, H., 1982: Sädgässens fältval i Skåne. – Vår Fågelv. Suppl. 9: 75-78.

PETTERSON, J.-O., 1985: Goose damage in Sweden. In: Rüger, A. (ed.). Extent and Control of Goose damage to agricultural crops. – IWRB Special Publ. No. 5, Slimbridge, pp. 45-48.

PFEIFFER, J. W. G., 1979: Problems with *Branta bernicla bernicla* in the Netherlands. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 126-131.

PIRKOLA, M. K. & KALINAINEN, P., 1984: The status, habitats and productivity of breeding populations of Bean Goose, *Anser fabalis fabalis*, in Finland. – Swedish Wildlife Res. 13 (1): 9-48.

PRATER, A. J., 1981: Estuary Birds of Britain and Ireland. – Poyser, Calton. 440 pp.

PRESTRUD, P. & BØRSET, A., 1984: Status of the goose populations in the bird sanctuaries in Svalbard. – Nor. Polarinst. Skr. 181: 129-133.

PREUSS, N. O., 1982: Grågæssenes farlige rejse frem og tilbage mellem yngleplads og vinterkvarter. In: Madsen, J. & Lund, T. (eds.) Annual report of the Goose Working Group of the Danish Ornithological Soc., pp. 59-61.

PRINS, H. H. T., YDENBERG, R. C. & DRENT, R. H., 1980: The interaction of Brent Geese, *Branta bernicla*, and Sea Plantain, *Plantago maritima*, during spring staging: field observations and experiments. – Acta Bot. Neerl. 29: 585-596.

PROKOSCH, P., 1979: Plans for the diking-in of feeding habitat of *Branta bernicla bernicla* in Schleswig-Holstein, Federal Republic of Germany. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 106-120.

PROKOSCH, P., 1984a: Breeding sites and distribution of geese in the northwest Isfjord area, Svalbard, 1982. – Nor. Polarinst. Skr. 181: 135-139.

PROKOSCH, P., 1984b: The wintering sites of Svalbard Pink-footed Geese *Anser brachyrhynchus* in Germany – present situation. –

Nor. Polarinst. Skr. 181: 25-28.
PROKOSCH, P., 1984c: The occurrence of *Branta bernicla hrota* in Brent Goose flocks in the German Wattenmeer. - Nor. Polarinst. Skr. 181: 125-127.
PROKOSCH, P., 1984d: Population, annual cycle and traditional relationship to feeding areas of the Dark-bellied Brent Goose *(Branta b. bernicla,* L. 1758) in the Northfriesian Waddensea. - Ecol. Birds 6: 1-99 (In German with an English summary).
PROKOSCH, P., 1984e: Ringelgans-Rundbrief 12. - WWF - Wattenmeerstelle Schleswig-Holstein, Kiel. 24 pp.
PROP, J., EERDEN, M. R. VAN, DAAN, S., DRENT, R. H., TINBERGEN, J. M. & ST JOSEPH, A. K. M., 1981: Ecology of Barnacle Goose *(Branta leucopsis)* during the breeding season. Preliminary Results from Expeditions to Spitsbergen in 1977 and 1978. - Proc. Norwegian-Netherlands Symp. on Svalbard, Arctic Centre, Groningen, pp. 50-112.
PROP, J., EERDEN, M. R. VAN & DRENT, R. H., 1984: Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. - Nor. Polarinst. Skr. 181: 87-117.
RANWELL, D. S. & DOWNING, B. M., 1959: Brent Goose *(Branta bernicla* (L.)) winter feeding pattern and Zostera resources at Scott Head Island, Norfolk. - Anim. Behav. 7: 42-56.
RASMUSSEN, E., 1977: The wasting disease of Eelgrass *(Zostera marina)* and its effects on environmental factors and fauna. In: McRoy, C. P. & Helffenick, C. (eds.) Seagrass Ecosystems: A Scientific Perspective. - Dekker, New York, pp. 1-51.
RIKARDSEN, F., 1982: Migration studies of Pink-footed Geese *Anser brachyrhynchus* on Andøya, Nordland. - Vår Fuglefauna 5: 163-168 (In Norwegian with an English summary).
ROGERS, J. P., 1979: *Branta bernicla hrota* in the USA - a management review. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 198-207.
ROI, O. LE, 1911: Avifauna Spitsbergensis. - Bonn.
ROOTH, J., 1971: The occurrence of the Greylag Goose *Anser anser* in the western parts of its distribution area. - Ardea 59: 17-27.
ROOTH, J., EBBINGE, B., HAPEREN, A. VAN, LOK, M., TIMMERMAN, A., PHILIPPONA, J. & BERGH, L. VAN DEN, 1981: Numbers and distribution of wild geese in the Netherlands, 1974-1979. - Wildfowl 32: 146-155.
ROSELAAR, C. S., 1977: De geographische variate van de Rietgans. - Watervogels 2: 61-68.
ROUND, P., 1982: Inland feeding by Brent Geese *Branta bernicla* in Sussex, England. - Biol. Conserv. 23: 15-32.
ROUX, F., 1962: The migration of wild geese in France. - Wildfowl Trust Ann. Rep. 13: 74-78.
RÜGER, A. (ed.), 1985: Extent and Control of Goose damage to agricultural crops. - IWRB Special Publ. No. 5, Slimbridge. 48 pp.
RUTSCHKE, E., 1982: Stability and dynamics in the social structure of the Greylag Goose *(Anser anser).* - Aquila 89: 39-55.
RUTSCHKE, E., NAACKE, J. & LITZBARSKI, H., 1982: Die Graugans *Anser anser* in der DDR. - Acta Sc. Nat. Brno 16 (12): 21-49.
SALOMONSEN, F., 1958: The present status of the Brent Goose in Western Europe. - Vidensk. Medd. Dansk Naturh. Foren. 120: 43-80.
SANCHEZ, A., CASTROVIEJO, J. & DELIBES, M., 1977: On the wintering of Greylag Geese in the Marismas of the Guadalquivir (Southwestern Spain). - Proc. Int. Congr. Game Biol. 13: 65-76.
SCHILPEROORD, L., 1984: The status of the Pink-footed Goose *Anser brachyrhynchus* in Southwest Friesland (the Netherlands) and the movements over Western Europe. - Nor. Polarinst. Skr. 181: 29-36.
SCHMIDT, G. A. J., 1976: The overland migration of waterfowl over Schleswig-Holstein. In: Kumari, E. (ed.) Bird Migration. - Acad. of Science of the Estonian SSR, Tallin, pp. 87-99.
SCHWARZ, R. & RÜGER, A., 1979: Conflicts with agriculture in Schleswig-Holstein. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge, pp. 122-125.
SCOTT, D. A. & SMART, M. (eds.), 1982: Second Techn. Meeting Western Palearctic Migr. Bird Management. - IWRB, Slimbridge. 228 pp.
SMART, M. (ed.), 1979: Proc. First Techn.

Meeting Western Palearctic Migr. Bird Management. – IWRB, Slimbridge. 228 pp.

ST JOSEPH, A. K. M., 1979a: The seasonal distribution and movements of *Branta bernicla* in Western Europe. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 45-59.

ST JOSEPH, A. K. M., 1979b: The development of inland feeding by *Branta bernicla bernicla* in southeastern England. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 132-145.

ST JOSEPH, A. K. M., 1982: Review of the status of *Branta bernicla bernicla*. In: Scott, D. A. & Smart, M. (eds). Proc. Second Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 16-25.

SWIFT, J. A. & HARRISON, J. G., 1979: Shooting of *Branta bernicla* in Europe. In: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge, pp. 152-165.

TEUNISSEN, W., SPAANS, B. & DRENT, R., 1985: Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. – Ardea 73: 109-119.

THELANDER, B., 1982: Gåsjakten i Sverige: Historik, nuvarande förhållanden, jaktmetoder, omfattning och avskjutning. – Vår Fågelv. Suppl. 9: 85-92.

THISSEN, J. B. M. & BRUGGEMAN, J. H., 1982: Effecten van verjaging van rotganzen vit de Terschellinger polder in het voorjaar van 1982. – RIN-rapport 82/10, Rijksinstituut voor Natuurbeheer, Leersum. 58 pp.

TIMMERMAN, A., 1977: The winter occurrence of the Pink-footed Goose *Anser brachyrhynchus*. –Limosa 50: 71-91 (In Dutch with an English summary).

TIMMERMAN, A., MÖRZER BRUYNS, M. F. & PHILIPPONA, J., 1976: Survey of the winter distribution of Palearctic geese in Europe, western Asia and North Africa. – Limosa 49: 230-292.

TOMKOVICH, P. S., 1984: The birds of Graham Bell Island, Franz Josef Land. – Ornitologica 19: 13-21 (In Russian with an English summary).

TUBBS, C. R. & TUBBS, J. M., 1982: Brent Goose *Branta bernicla bernicla* and their food in the Solent, southern England. – Biol. Conserv. 23: 33-54.

TUBBS, C. R. & TUBBS, J. M., 1983: The distribution of *Zostera* and its exploitation by wildfowl in the Solent, southern England. – Aquatic Botany 15: 223-239.

TVEIT, G., 1984: Autumn migration, wintering areas and survival of Bean Geese *Anser fabalis* marked on the moulting grounds in Finnmark, north Norway. – Swedish Wildlife Res. 13 (1): 73-82.

UIL, G. DEN, LEBRET, T. & PHILIPPONA, J., 1982: Goose shooting and prevention of damage. – Aquila 89: 281-283.

USPENSKI, S. M., 1960: The Brent Goose *(Branta bernicla L.)* in the Soviet Union. – Wildfowl Trust Ann. Rep. 11: 80-93.

USPENKI, S. M., 1965: Die Wildgänse Nordeurasiens. – Die Neue Brehms-Bücherei No. 352, Wittenberg Lutherstadt. 80 pp.

VANDEKERKHOVE, J., BUYSSE, R., KUYKEN, E. & BURGGRAEVE, G., 1960: De ganzen te Damme. – Wielewaal 26: 336-338.

VIERECK, H. V., 1951: Über die Ursachen für die Abnahme der Ringelgans *(Branta bernicla)* in den Winterquartieren. – Die Vogelwarte 16: 18-22.

VINOKUROV, A. A., 1982: Present status of the *Branta ruficollis* population and measures for its conservation. – Aquila 89: 115-122.

WELIE, H.W.M. VAN, 1985: Compensation for goose damage in the Netherlands. In: Rüger, A. (ed.). Extent and control of Goose damage to agricultural crops. – IWRB Special Publ. No. 5, Slimbridge, pp. 29-33.

WHITE-ROBINSON, R., 1982: Inland and saltmarsh feeding of wintering Brent Geese in Essex. – Wildfowl 33: 113-118.

WOLFF, W. F., KOEIJER, P. DE, SANDEE, A. J. J. & WOLF, L. DE, 1967: The distribution of brent geese in the Delta-area in relation to the distribution of their food. – Limosa 40: 163-174 (In Dutch with an English summary).

ZWARTZ, L., 1972: The Grey Lag Geese *Anser anser* of the brackish tidal habitat the Veutjagersplaten, Holland. – Limosa 45: 119-134 (In Dutch with an English summary).

4

DANISH REVIEW OF GAME BIOLOGY Vol. 13 No. 4

Autumn Feeding Ecology of Herbivorous Wildfowl in the Danish Wadden Sea, and Impact of Food Supplies and Shooting on Movements

by

JESPER MADSEN

Med et dansk resumé:
Fødeøkologi hos planteædende andefugle
i Vadehavet om efteråret,
og fødemængdens og jagtens effekt
på flokkenes træk

Резюме на русском языке:
Экология питания травоядных утиных на
датских морских отмелях осенью, и эффект
наличного количества пищи и охоты на
перелеты стай.

ISSN 0374-7344

COMMUNICATION NO. 217 FROM VILDTBIOLOGISK STATION
Vildtbiologisk Station, Kalø, 8410 Rønde, Denmark
1988

Abstract

Madsen, J. 1988: Autumn Feeding Ecology of Herbivorous Wildfowl in the Danish Wadden Sea, and Impact of Food Supplies and Shooting on Movements. - Dan. Rev. Game Biol. 13 (4).

The southern part of the Danish Wadden Sea is an important autumn staging area for Brent Geese (peak numbers 6,000), Wigeon (15,000) and Teal (3,500). In autumn 1985 and 1986 their ecology and movements were studied in relation to food availability and shooting activity. In September-October the wildfowl fed in the tidal zones on a 138 ha *Zostera* bed. Due to the tide they could only feed from 3 hours before to 3 hours after low tide, and to fulfill their daily energy demands the birds also fed during nightly low water periods. During autumn the above-ground *Zostera* resources were reduced from 39 tons to 1 ton, the grazing by wildfowl accounting for the major part of the losses. In consequence, feeding efficiency of Brent Geese and Wigeon was hampered. Brent Geese switched to below-ground parts of *Zostera*, Wigeon abandoned the area. Interspecific exploitative competition became acute, with Brent Goose as the best coping species of the two.

In 1985 duck shooting on the mud flats was moderate; in 1986, however, it was intensified, displacing the ducks and geese to the southern part of the *Zostera* bed, which is part of a non-shooting zone. This zone was soon depleted for resources, and the majority of the wildfowl were forced to leave the area earlier than in 1985 even though food was still available in the shooting zone. At night the birds fed in the shooting zone. When the ducks had abandoned the area, shooting ceased, and the protected Brent Goose could remain undisturbed for the rest of the autumn.

In October a concentration of ducks built up in the non-shooting zone at the Rømø barrage. Here the ducks consumed ripening *Suaeda* and *Atriplex* seeds in the salt marshes. Ducks were actively feeding around high tide, during both day and night.

In the course of October the seed stock was heavily reduced due to ducks foraging, natural fall-off and wave action, whereupon the majority of the ducks left the area. The remaining ducks rested throughout daytime and flew into the adjacent hinterland at night to feed. The adjacent salt marshes of which parts are shooting zones were not used during daytime, and only irregularly at night.

It is concluded that the number of wildfowl was limited by the food resources, and that switching between habitats was linked to depletion of food stocks. Shooting modified movements and caused birds to leave the area prematurely.

Contents

Introduction

The question of how many waterfowl a given foraging area along the migration route can support, i.e. the habitat capacity, has important implications for the understanding of the dynamics of the migration, as well as for the management of the key areas. Many waterfowl habitats, and especially wetlands, are today threatened by development and human disturbance. At that point when the bird numbers - or rather the number of bird-days - have reached the ceiling of the habitat capacity, human interference can be expected to have a negative impact on the status of the site.

Waterfowl movements have only recently been analysed in relation to the size of food supplies in the staging and wintering areas. For a Dutch staging area VAN EERDEN (1984) demonstrated that herbivorous wildfowl removed a considerable part of the available *Salicornia* spp. seed stock, and also that switching between food sources and areas was related to the depletion of the local food supplies. Likewise, in various goose studies, it has been demonstrated that shifts between habitats were linked to the depletion of the vegetation and impaired feeding profitability (DRENT & SWIERSTRA 1977, CHARMAN 1979, DRENT et al. 1978, LORENZEN & MADSEN 1985). Thus, there is evidence that in the absence of disturbance, foraging waterfowl make optimum use of their feeding grounds.

Substantial evidence has demonstrated the effect of disturbance, particularly shooting, on the distribution of waterfowl in potential staging and wintering areas (see review by MELTOFTE 1982, ARCTANDER et al. 1984, MADSEN 1986). However, less information exists regarding the ecological and behavioural consequences of disturbance (OWENS 1977, JOENSEN & MADSEN 1985, JAKOBSEN 1986). A central question is whether or not the birds can compensate for the lost feeding time, or whether behavioural constraints hinder exploitation of the food resources.

The Danish Wadden Sea is an important staging area for herbivorous dabbling ducks and Brent Geese *Branta bernicla*. In October-November when peak numbers are reached, up to 20,000 Dark-bellied Brent Geese *Branta b. bernicla*, 57,000 Wigeon *Anas penelope*, and 17,000 Teal *Anas crecca* can be present at one time (LAURSEN & FRIKKE in prep.). The three species feed mainly in intertidal mudflats and in saltmarshes, though at some stage in late autumn duck-flights into the hinterlands can also be observed.

The aim of this study was three-fold:

1) to describe the feeding ecology of herbivorous wildfowl and their spatial and temporal distribution in a part of the Danish Wadden Sea;

2) to analyse the impact of wildfowl grazing on food supplies, and to evaluate the extent to which bird numbers were food-limited and its possible influence on movements between habitats;

3) to analyse whether human activity, especially hunting, was modifying site usage and bird movements.

The project was part of a research programme by the Game Biology Station, evaluating the importance of the Danish Wadden Sea as a waterfowl staging area and the influence of human interference on bird numbers and distribution.

Acknowledgements

The Coast Authority (Kystinspektoratet) and the Directory of Agriculture (Jordbrugsdirektoratet) are thanked for permitting access to the Rømø Foreshore; the Royal Danish Army Air Corps (HFT) is thanked for helicopter assistance to erect the observation tower. John Frikke and Ebbe Bøgebjerg are thanked for assistance in the field. Karsten Laursen, Myrfyn Owen, John Frikke and Janice Mather kindly commented on the manuscript.

Study area

The study was carried out in the southern part of the Danish Wadden Sea (Fig. 1), part of the Nature and Wildlife Reserve Vadehavet. The study area comprised two major waterfowl feeding areas in the Danish Wadden Sea, i.e. the tidal flats at Koldby Leje, and the salt marshes along the barrage connecting Rømø with the mainland and Ballum Foreshore.

Koldby Leje, Jordsand Flak

This area is an intertidal mudflat, part of which is covered with seagrass *Zostera* spp. It is a major feeding ground for herbivorous wildfowl, especially Brent Geese and Wigeon. At high water the birds roost around the small island of Jordsand, some Brent Geese also roosting in the southern Ballum Foreshore. In 1985 and 1986, the *Zostera* bed covered 138 ha. *Zostera noltii* was the dominant species over most of the bed, showing highest densities on elevations 5-10 cm above the low water line. In shallow depressions where water was retained at low tide, however, *Z. noltii* was interspersed with *Z. marina,* though the latter never reached the densities of the former. *Z. marina* did not seem to overwinter, had an underdeveloped rhizome compared to *Z. noltii,* and was probably dependent on sexual reproduction. *Z. noltii,* on the other hand, had a well-developed rhizome, this being indicative of a high degree of vegetative reproduction.

The southern third of the flats is part of the non-shooting zone in the southern part of the Danish Wadden Sea. North of the zone, shooting of wildfowl is allowed from 16 September to 29 February.

The Rømø barrage and Ballum Foreshore

These salt marshes have been created by means of land reclamation work and are currently grazed by sheep. The marsh areas south of the barrage and most parts of Ballum Foreshore are dominated by a vegetation of *Puccinellia maritima,* and in certain regions by *Festuca rubra.* Over large areas *Atriplex litoralis* and *Suaeda maritima* occur in dense stands, *Suaeda* especially in low-lying regions. In the marsh north of the barrage, *Suaeda* occurs in extremely high densities. In the low-lying regions, especially the marsh south of the barrage, *Salicornia europaea* forms a dense vegetation. In October the salt marshes are visited by large flocks of dabbling ducks, especially Wigeon and Teal. Crop contents of collected birds demonstrated that the ducks feed primarily on seeds of *Suaeda* and *Atriplex.*

The Rømø barrage and adjoining salt marshes are non-shooting zones. In Ballum Foreshore, shooting is allowed in a zone

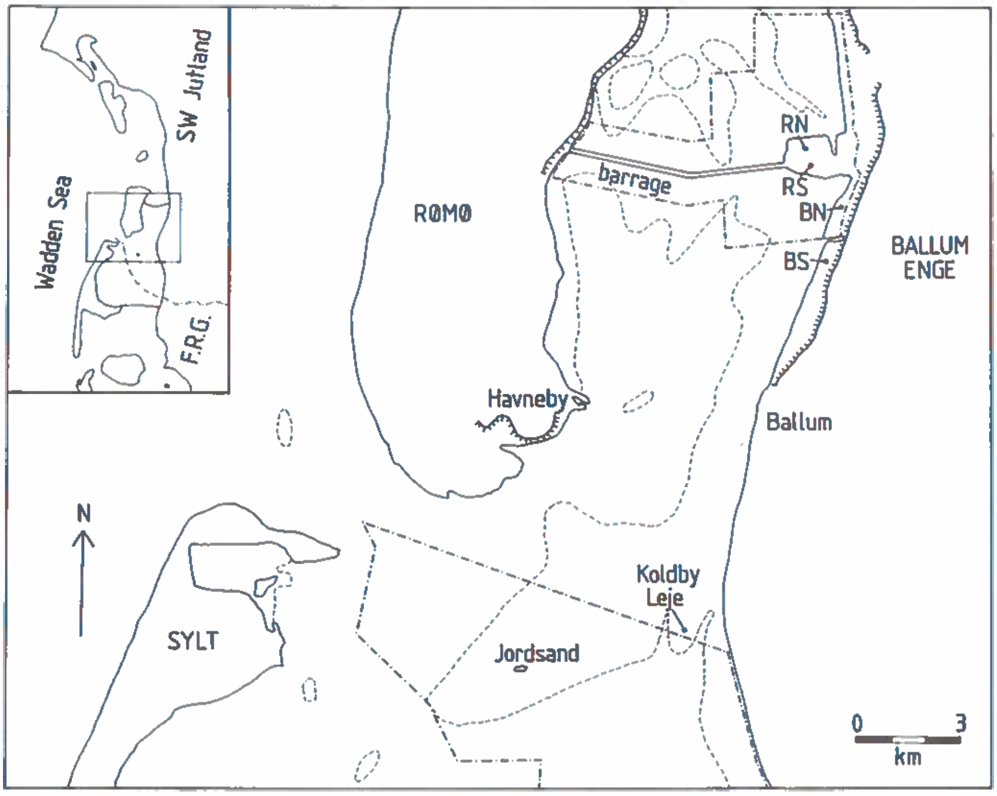


Fig. 1. Study area in the southern part of the Danish Wadden Sea. Study plots at Koldby Leje and the Rømø barrage are shown. RN: Rømø barrage north, RS: Rømø barrage south, BN: Ballum foreshore north, BS: Ballum foreshore south. Low water lines are indicated by punctuated lines, and reserve boundaries (non-shooting areas) by punctuated, dotted lines.

ranging from the dike to the edge of the old foreshore. Beyond this zone shooting is banned (Fig. 1).

Methods

Observations

The Rømø barrage and Koldby Leje were visited during the period 1 September to 20 December, 1985 and 1986, on average at intervals of six days. At each visit the number of wildfowl was counted, the distribution of flocks mapped, and their general activity (feeding, roosting) recorded. In addition, all types of human activity were noted and mapped. On the Rømø barrage, observations were carried out from the top of the barrage. At Koldby Leje, observations were made from land, and in 1986 also from a 4 m high observation tower placed in the middle of the *Zostera* bed. When observations were made from the tower, the observer entered approximately 2 hrs after high tide and left 2 hrs before the next high tide, so that disturbance was kept at a minimum. On some occasions, the observer remained in the tower during the high tide in order to continue observations during the next low water period.

Activity studies

Time expenditure of flocks of geese or ducks was recorded in relation to tidal rhythm and to time of season. At Koldby Leje, observations were carried out both during day and night, but at the Rømø barrage only during day-time.

At Koldby Leje the birds were under observation from time of arrival from the high water roost to departure from the *Zostera* bed. Every 15 minutes, the number of birds of each species engaged in various activities was recorded by 'instantaneous' scanning of the flock (after ALTMANN 1974). Recorded activities were feeding, roosting, walking, swimming, flying, aggression, and alertness. Four feeding techniques were distinguished:

1) swimming, including feeding by picking from surface, submerging head or neck, and upending;
2) paddling, only recorded in Brent Geese trampling in the sediment submerged under 5-10 cm of water. The geese took whole plants including roots and rhizomes, and left characteristic craters of roughly 20 cm diameter and 5-10 cm deep (also described by FOG (1967) and JACOBS et al. (1981));
3) grubbing, observed in geese and Wigeon, the birds taking turions and rhizomes;
4) pecking, taking leaves from the mud surface or leaves floating in shallow water.

During day-time, observations were carried out with a telescope (20-45 x). Every half hour the position of flocks was mapped and the water line drawn on a sketch map (1:10,000). In 1986, three transect lines with the observation tower in the centre were laid out over part of the *Zostera* bed, yielding 30 quadrats each of 50 m x 50 m. Corners were marked with stakes 20 cm above ground. During observations from the tower, the number of birds of each species within the quadrats was recorded at intervals of 30 minutes. Temporal and spatial overlap of two species was expressed by percentage similarity, O (HURLBERT 1978):

$$O = 1 - 1/2 \mid P_{ij} - P_{ik} \mid$$

where P_{ij} is the relative occurrence of the j'th species in square i, and P_{ik} is the relative occurrence of the k'th species in square i.

Night-time activity budgets of Wigeon and Brent Geese were recorded during three low water periods in 1986: 8-9, 9-10, and 21-22 October. Observations were carried out from the observation tower with a light-intensifying vision scope (around 8 x). The first two nights were one week prior to full moon and with overcast sky, the last night was four nights after full moon and with clear sky. During the first two observations, lights from the surrounding towns Havneby, List, and Skærbæk provided sufficient light to operate the night vision scope with success. However, during all three nights, the resolution only allowed the observer to distinguish between feeding, roosting, and flight activities.

At the Rømø barrage, observations followed the same procedure as at Koldby Leje. Ducks feeding in the salt marsh were often invisible whilst in the vegetation, but were assumed to be feeding when out of sight. Records were kept of birds flying to and from the salt marsh.

Three feeding parameters were timed by means of a stop-watch:

1) feeding bout length, i.e. the time of uninterrupted feeding with the head below the level of the shoulder;

2) pecking rate, measured as the time it took a feeding bird to make a total of 10 pecks in the vegetation. It was, however, not possible to measure pecks on the mudflats because the *Zostera* feeding birds often took turions which were chewed and swallowed in bits of varying size;
3) walking speed, measured as the time it took a feeding bird to make a total of 10 steps.

To achieve another indication of duck utilisation of the salt marshes apart from the mapping, droppings were counted within permanent plots. On the southside of the Rømø barrage 40 plots were laid out at 20 m distance; on Ballum Foreshore 20 plots. Each plot was circular with a radius of 2 m (12.6 m^2) and marked with a peg 10 cm above ground. Plots were emptied at around 10 day intervals throughout autumn. However, this method proved to be successful in 1985 only, because of too frequent flooding of the marshes in 1986.

Food and estimation of daily food consumption

Food selection of Brent Geese and Wigeon foraging on the mudflats was examined by means of microscopical identification of epidermal fragments in the droppings (for method see Owen 1975). Samples of 25 fresh droppings were collected at low tide, and only in situations when the birds had fed in the same area for most of the low-water period.

Daily food consumption by Brent Geese and Wigeon feeding on the mudflats was estimated by the 'marker substance' method (Drent et al. 1978). Retention rates were measured using ash content and lignin as food components not digested by gut passage. The change in concentration of the marker substance in droppings compared to food plants thus equals the retention rate. Hourly defaecation was measured in the field by keeping the abdomen of a goose under continuous observation for as long as possible, and recording the number of droppings produced in the particular period, which was timed by means of a stop-watch. Periods and numbers of droppings were summed for many individuals to achieve hourly blocks of dropping production (Bédard & Gauthier 1986). Defaecation periods were only timed from 1 hr before low tide to 3 hrs after, to ensure that defaecation rates were in equilibrium with food intake. Daily production of droppings was calculated from multiplication of average hourly defaecation and average time spent on the feeding grounds during the 24 hrs. Fresh droppings and food plants were collected for chemical analyses, and droppings for weighing. Samples of Brent Goose droppings were taken two days in October 1985, and Wigeon droppings one day in October 1986. Chemical analyses were carried out by the Central Laboratory of the National Institute of Animal Science, at Foulum. Ash content of plants and droppings was determined after removal of the silica fraction. Energetic value of the net food intake was calculated from energy content of pellets of food and droppings, measured on a Gallenkamp bomb calorimeter. All analyses were carried out in duplicate.

Standing crop and leaf cover of *Zostera*

In 1985, an exclosure experiment was set up at Koldby Leje to measure standing crop of *Zostera* throughout autumn, and to quantify wildfowl grazing impact on the vegetation.

A transect line, situated and marked as for the 1986 transect, was laid out in a part of the *Zostera* bed which visually appeared homogeneous. Four 3 m x 3 m exclosures were constructed using pegs reaching 40 cm above ground and also wires at two heights which connected the corners diagonally. The exclosures were visited weekly to clean them of material, especially algae, hanging upon the wires. At monthly intervals, samples were taken outside and inside exclosures. Outside the exclosures 15 samples were taken at 50 m distance along the transect line, and inside each exclosure two samples were taken at random. A sample consisted of a circular core of 227.6 cm^2. A plastic tube with sharpened edges was pressed 10 cm into the sediment, the sample was then dug out, transferred to a sieve, and the sediment superficially washed off. In the laboratory, samples were first sorted into live and dead material and also above- and below-ground biomass, then dried for 24 hrs at 80°C, cooled in an excicator, and weighed. To express biomass in ash-free dry weight, plant material was combusted for 3 hrs at 550°C. Thus, average ash content of dry weight of above-ground material and below-ground material was 14.3% and 27.1%, respectively.

To relate above-ground biomass to leaf cover, the percentage leaf cover was estimated to nearest 5% in all sample plots. In 1986, the leaf coverage was roughly estimated for the entire *Zostera* bed every three weeks from mid-September to mid-December. The map was based on permanent stations along the transect lines as well as stations at right angles to the transects. In the range from 0-90% leaf coverage, a linear correlation was found between cover and above-ground ash-free biomass: $y = 0.4x + 1.9$, where y is standing crop in g ash-free dry weight per m^2, and x is percentage leaf cover ($n = 61$, $r = 0.926$, $P < 0.001$). As expected, above 90% coverage, the relationship was no longer linear. For the present purpose an average value of the samples with 95% and 100% cover was used, viz. 80.2 g ash-free dwt/m^2 ($n = 5$).

Standing seed crop

To estimate the removal rate of *Atriplex* and *Suaeda* seeds by ducks in the salt marshes along the Rømø barrage, exclosure experiments were conducted in 1985 and 1986. In 1985, the experiments were carried out in both the southern and the northern marsh.

In each marsh area two exclosures, each 2 m × 2 m, were erected in visually homogeneous vegetation in early September. An exclosure consisted of either poles connected with wires at four heights, or sheep fence. Sample plots, i.e. areas visited by the ducks, were placed on transects 50-100 m from the exclosures. Along the transects, 40-60 plants were taken at random and individually marked with a small piece of white plastic tape just above ground. In each exclosure 20 plants were marked. The number of seeds per plant was counted repeatedly at 10-14 days intervals from September until all seeds had been removed from the plants, either due to duck foraging or natural seed fall. To follow seed ripening, plants were randomly picked on each sampling date in 1986. One hundred *Atriplex* and the same number of *Suaeda* seeds were picked and dried for 24 hrs at 80°C.

In early October 1986, the total seed crop per ha was estimated for the northern and the southern marsh along the Rømø barrage and for two sections of Ballum Foreshore. At 20 m intervals along the transects the number of seed-bearing dicotyledons was counted in 0.25 m^2 squares. The number of seeds per plant was counted for at least 100 plants of each species.

Results and discussion

Tidal flat feeding

Wildfowl numbers

Brent Geese and Wigeon were the most numerous waterfowl species in the tidal mudflats at Koldby Leje. In autumn 1985 the peak numbers were 4,500 and 8,000, respectively, and in autumn 1986, 6,000 and 6,500, respectively. Wigeon arrived in the middle of September (Fig. 2), peak numbers being reached from late September to early October. Thereafter, numbers dropped quickly; in 1985 a flock of 500-1,000 stayed until the end of November, whereas in 1986, no Wigeon remained after mid-October. In 1985 the Brent Geese arrived late September, and peak numbers were reached in October. In 1986, however, numbers already began to decline after the beginning of October. In 1985 the proportion of juveniles in the flocks observed throughout autumn was 35%, whilst in 1986 there were less than 1% juveniles. This difference in age structure, apparently affected neither time of arrival nor peak numbers observed. In 1985 the Brent Geese stayed until late November, whereas in 1986 they remained until mid-December.

Teal and Pintail were present in lower numbers; maxima recorded were 1,000 and 600, respectively. Both had a phenology similar to Wigeon, but numbers varied much between days.

The estimated number of bird-days spent on the mudflats in the two autumns is presented in Table 1. The number of Brent Goose-days was almost similar in the two years, whereas there was a 45% reduction in Wigeon-days in 1986 compared to 1985.

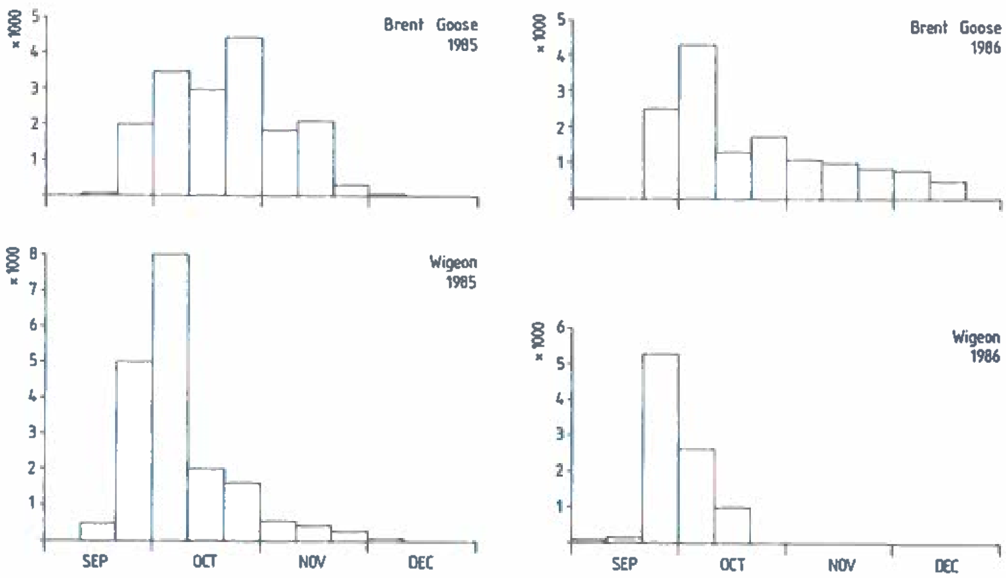


Fig. 2. Autumn occurrence of Brent Geese and Wigeon at Koldby Leje in 1985 and 1986, expressed as average numbers in 10-day periods.

Table 1. Number of bird-days spent by the most numerous wildfowl species on Koldby Leje, autumn 1985 and 1986.

	1985	1986
Brent Goose	176,200	143,400
Wigeon	176,500	96,700
Teal	19,500	23,000
Pintail	9,400	8,150

Feeding rhythm

During low water periods at day-time Brent Geese and Wigeon arrived from the high-water roost to the feeding grounds 3-4 hrs before low tide, and left 3-4 hrs after. For both species foraging was the predominant activity during low water (Fig. 3a, b). Just upon arrival and prior to departure the birds were unable to reach the flooded vegetation, and were thus roosting. As soon as they could reach the vegetation, feeding was very intense and virtually without breaks. The average active feeding period in Brent Geese and Wigeon was 6 hrs 32 minutes and 6 hrs 26 minutes, respectively.

Feeding methods changed in response to water level (Fig. 4). Brent Geese were initially swimming, and grazing *Zostera* leaves by submerging the head or neck, or by upending. When able to reach the bottom, they typically paddled in the mud for some time, but during most of the low water period they grazed by walking on the mudflats. Most of the feeding consisted of pecking leaves, and only 5-10% of the birds were grubbing. With the rising water the reverse sequence of feeding methods was observed.

Wigeon first fed by swimming, mostly submerging the head or neck, but switched to grazing by walking as soon as they could reach the bottom. The Wigeon were mainly grazing the leaves of *Zostera;* between 20-35% of the birds were judged to be grubbing, although this was sometimes difficult to ascertain.

During the three night-time observations, Brent Geese were present on all three occasions, whereas Wigeon were present only on the first two. Although the light conditions of the first two nights (overcast, dark) differed from the conditions of the third (bright, four days after full moon), activity patterns did not change in Brent Goose.

The period spent by the Brent Goose on the feeding ground did not differ from the day-time period (Fig. 3). The geese were feeding actively until low tide when feeding activity dropped, after which many birds roosted in the gullies or on the edge of the tidal flat. When the water rose the geese resumed feeding, probably triggered by the incoming water.

Wigeon started to feed approximately half an hour later than during day-time, but were feeding actively throughout the low-water period.

The nightly active feeding period of Brent Geese and Wigeon was on average 4 hrs 52 minutes and 6 hrs 16 minutes, respectively.

Combined over 24 hrs, Brent Geese and Wigeon were feeding actively for 11 hrs 24 minutes and 12 hrs 42 minutes, respectively.

Nocturnal feeding is well documented for Wigeon (OWEN 1973, CAMPREDON 1981), but virtually undocumented for Brent Geese. MAHEO (1976) did not record night-foraging Brent Geese in the *Zostera* beds in Golfe du Morbihan on the French Atlantic coast, and other authors do not mention the phenomenon (e.g., RANWELL & DOWNING 1959, CHARMAN 1979).

Overlap in distribution

The overlap of Brent Geese, Wigeon and Teal feeding in 50 m × 50 m squares was examined with regard to spatial and tem-

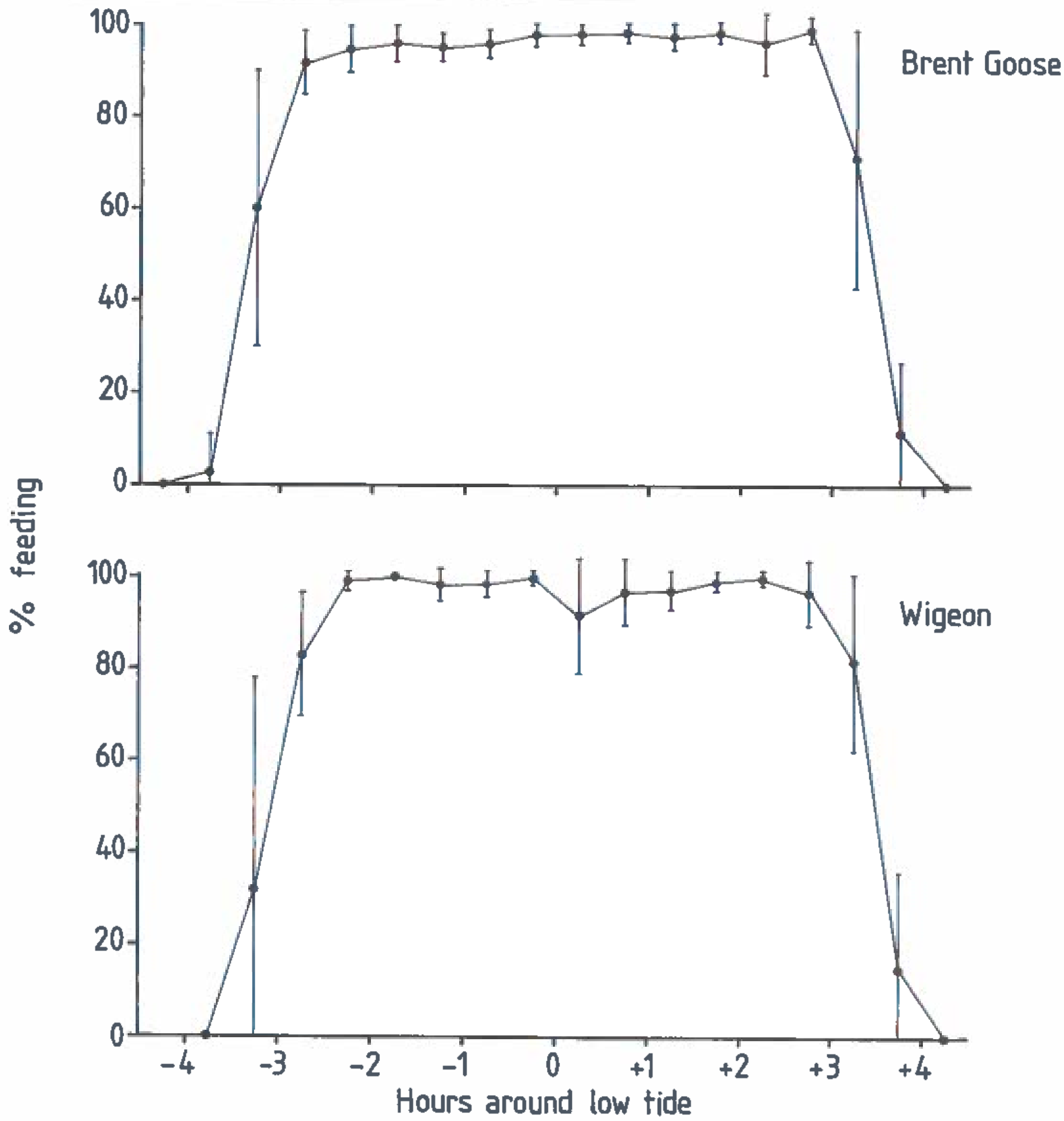


Fig. 3a. Feeding activity of Brent Geese and Wigeon during daytime at Koldby Leje (7 observation periods). Bars show one standard deviation. During high water, the wildfowl roost on Jordsand Flak.

poral distribution. Temporal overlap expresses simultaneous occurrence, i.e. the degree to which particular species occur in the squares at the same time.

The southern squares were in a depression, where a depth of about 5 cm water was retained during low tide, whereas the northern squares ran dry during low water. Between the two substrates there was no difference in occurrence of the three wildfowl species, and the overall spatial overlap was high between all three species (Table 2), indicating that the birds make use of the same substrate.

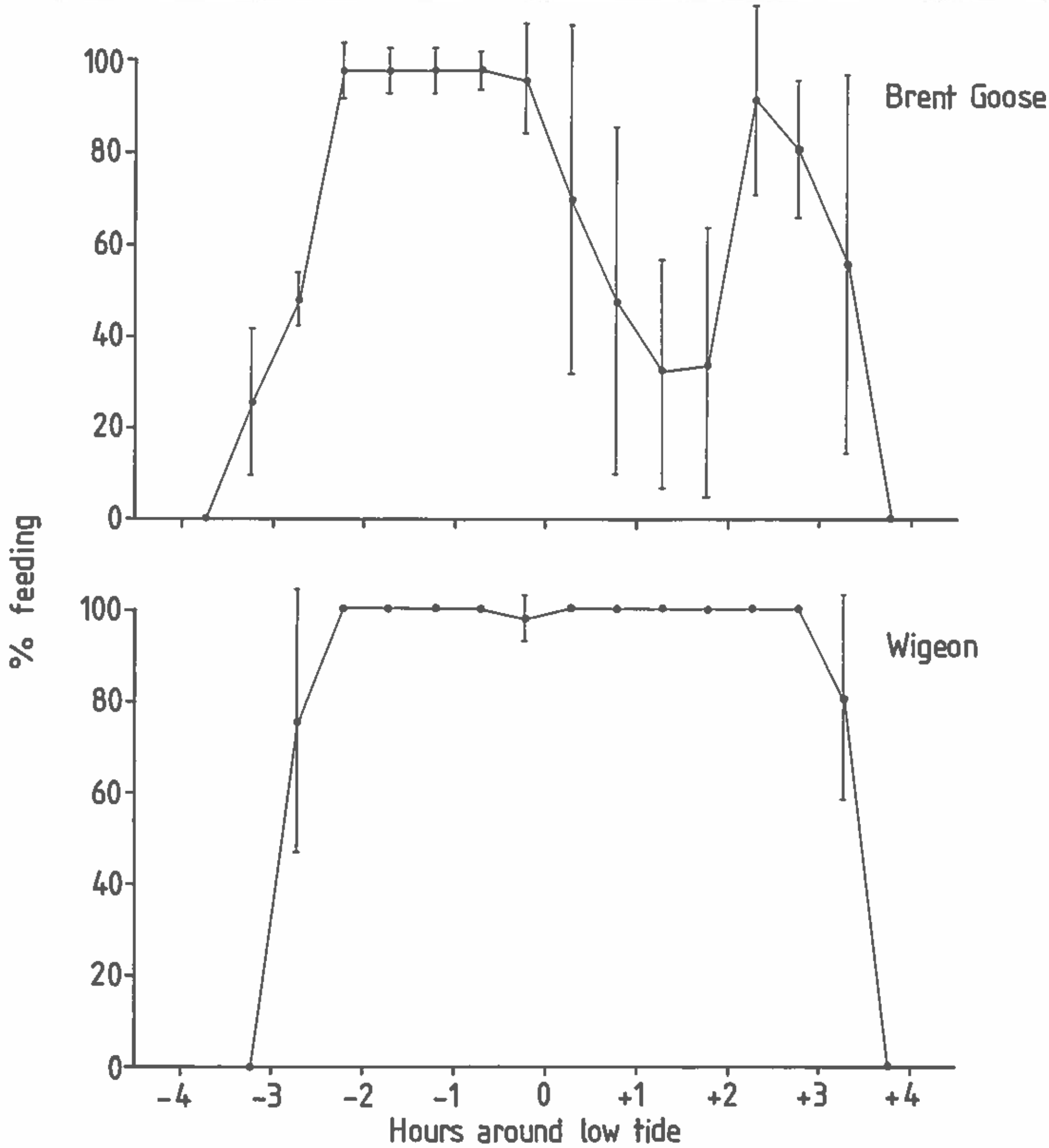


Fig. 3b. Feeding activity of Brent Geese and Wigeon at night at Koldby Leje in relation to tidal cycle (average of 3 observation periods).

Temporal overlap of Brent Geese and Wigeon was relatively high, in that the two species often were feeding in mixed flocks, walking over the mudflats at the same speed. Teal, on the other hand, had little temporal overlap with the two other species. The three species often occurred together in flocks, but Teal walked faster over the substrate, leaving the two other species behind.

Food and food consumption

Microscopic examination of droppings

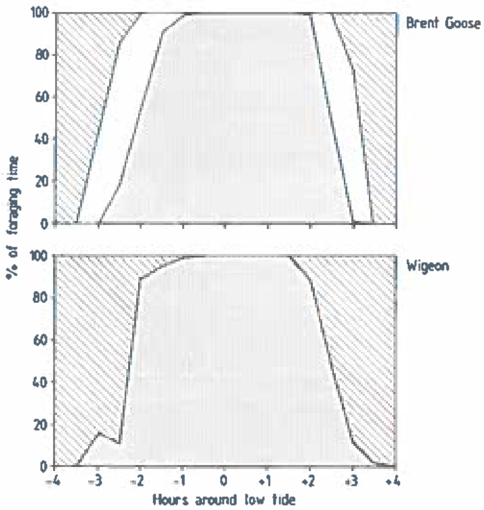


Fig. 4. Feeding techniques by Brent Geese and Wigeon at Koldby Leje in relation to tidal cycle. Hatched: feeding by swimming; open: paddling; shaded: feeding by walking. Average of two observation days in early October.

revealed that Brent Geese and Wigeon fed exclusively on *Zostera,* and that above-ground parts predominated in the diet. In three samples from October-November, leaves made up between 85 and 91% of the Brent Goose diet, and roots and rhizomes the remainder. Only in a sample from early

Table 2. Overlap in spatial and temporal distribution of Brent Geese, Wigeon and Teal in quadrats in Zostera vegetation at Koldby Leje.

	Spatial overlap	
	Wigeon	Brent
Brent	0.781	-
Teal	0.797	0.745

	Temporal overlap	
	Wigeon	Brent
Brent	0.563	-
Teal	0.142	0.106

December was the proportion of leaves lower, viz. 58%. In two samples of Wigeon droppings from October, leaves made up 98 and 92% of the diet, respectively.

Food selection by Teal was not thoroughly investigated. Direct observations indicated that Teal were filtering the top layer of the muddy substrate, probably feeding on seeds of *Zostera* and also invertebrates. In a sample of Teal droppings, broken shells of *Hydrobia* snails were frequent.

An estimate of daily food and energy intake for Brent Geese and Wigeon is shown in Table 3. Computations have been conducted under the assumption that the diet consisted exclusively of *Zostera noltii* leaves. Retention rates, achieved using ash and lignin, did not differ significantly, values shown in the table being averages based upon the two tracer substances. The calculated daily net energy intake of 986 kJ for Brent Geese is somewhat higher than the estimate for Brent Geese in winter, viz. 840 kJ (Drent et al. 1978). The difference may reflect that the geese put on weight in autumn (Fog 1967), thereby demanding more energy.

The estimated net energy intake of 592 kJ for Wigeon is somewhat lower than the daily existence energy (DEE) predicted for a 0.7 kg non-passerine by Drent et al. (1978), viz. 2.6x Basal Metabolic Rate (BMR) (736 kJ) (formula for BMR from Aschoff & Pohl 1970, Wigeon weight from Bauer & Glutz von Blotzheim 1968). It should be noted, however, that the 'marker substance' method as applied here is crude, because it only took above-ground material into account, and so the results must be regarded only as rough estimates.

Table 3. Estimates of daily food and energy intake by Brent Goose and Wigeon feeding on Zostera noltii leaves. All weights are in g ash-free dry weight.

	Brent Goose	Wigeon
Time on feeding ground (min)	684	762
Droppings per hour	17.0[a]	16.8[b]
Dropping weight (g)	0.452[c]	0.164[d]
Daily defaecation (g)	87.6	35.0
Retention rate	0.35	0.46
Daily food intake (g)	134.8	64.8
Energy content of food (kJ/g)	19.4	19.4
Energy content of droppings (kJ/g)	18.6	19.0
Daily net energy intake (kJ/)	986	592

Notes: a: n = 6 block hours; b: n = 3 block hours; c: n = 187; d: n = 99.

Zostera stock and wildfowl grazing impact

In late August 1985, the above-ground standing crop in the central part of the *Zostera* bed amounted to about 60 g ash-free dry weight (dwt) per m² (Fig. 5). From late August to early December the biomass gradually decreased, however, with a significant difference between grazed and ungrazed plots. In early December, the above-ground biomass in the exclosures was reduced by 59%, whereas in the grazed plots the reduction rate was 89%. This 30% difference represents the proportion consumed by wildfowl. Other avenues of biomass losses were: leaves dying off; leaves breaking off; and leaf consumption by invertebrates. In early December 1985, the geese abandoned the mudflats at a stage when the standing crop had been reduced to 6.6 g ash-free dwt/m², or about 10% leaf cover.

In late August 1985, below-ground biomass was on average 36 g ash-free dwt/m². During the autumn season there was an average increase of 26% in biomass in the ungrazed plots, whilst a 29% decrease in the grazed plots (Fig. 5). However, neither the increase, nor the decrease was significant at the 5% level (one-way analysis of variance). By the end of October and in early December there was, on the other hand, a significant difference in biomass in ungrazed plots (student t-test, $t = 3.807$, $P < 0.01$, and $t = 3.424$, $P < 0.01$, respectively). In December the biomass in the grazed plots was 48% lower than in the ungrazed plots. Thus, it is indicated that the wildfowl, and predominantly the grubbing Brent Geese, affected the below-ground biomass of *Zostera* as well.

Based upon both the mapping of the *Zostera* bed and the linear correlation between leaf cover and above-ground biomass established in 1985, the total above-ground standing crop of the bed was estimated at 38.8 tons ash-free dwt in early September 1986, equivalent to an average of 28.1 g ash-free dwt/m² for the whole *Zostera* bed (138 ha) (cf. Fig. 8). In mid-October, the standing crop had decreased to 25.6 tons, and in mid-December to 1.2 tons, this being 3.1% of the early September stock.

To achieve an estimate of total annual production, the value of the maximum standing stock was doubled (PETERSEN 1913). This factor is known to underestimate the production of *Zostera marina* (SAND-JENSEN 1975, JACOBS 1979, WIUM-ANDERSEN & BORUM 1984), but probably

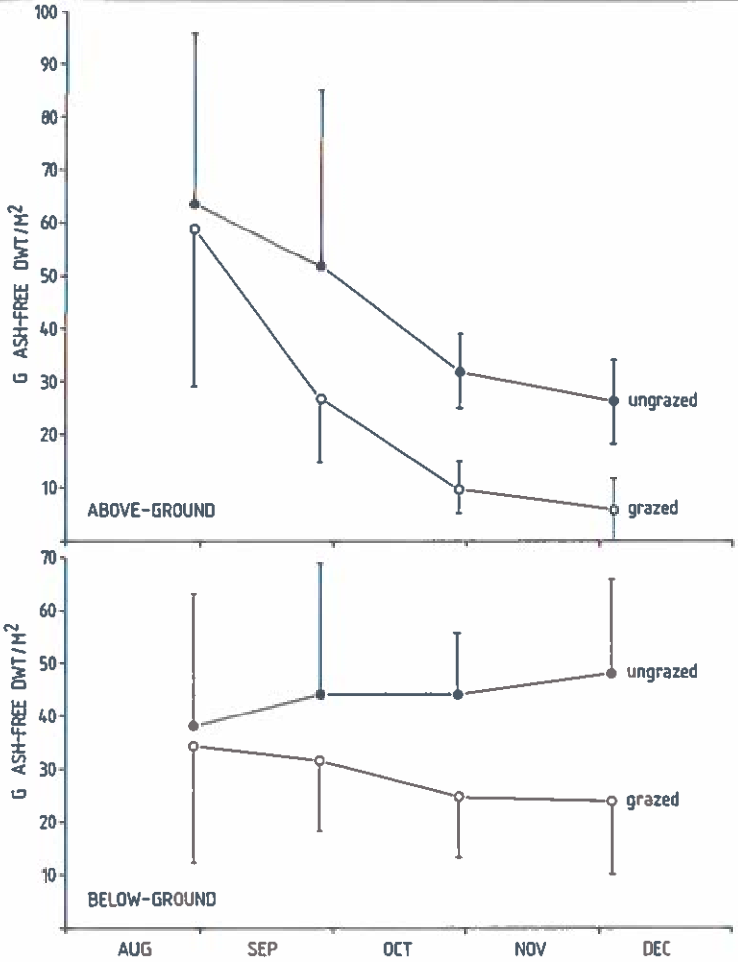


Fig. 5. Development in above-ground and below-ground standing crop of Zostera in grazed and ungrazed plots at Koldby Leje during autumn 1985. Bars represent 95% confidence limits.

gives a reasonably good estimate for *Z. noltii* (JACOBS et al. 1981). For the Dutch Wadden Sea JACOBS et al. (1983) found that the maximum standing crop of *Z. noltii* was reached in August-September. Therefore, it seems feasible to use the early September value of 38.8 tons as the maximum standing crop. Total above-ground production for the *Zostera* bed thus amounted to 77.6 tons ash-free dwt. From the estimate of the total number of Brent Goose-days and Wigeon-days spent in the area (Table 1) and their daily food consumption (Table 3), it is calculated that these wildfowl consumed a total of 35.2 tons and 25.6 tons in 1985 and 1986, respectively, of which the Brent Geese consumed 68% and 75% of the biomass, respectively. Between 1985 and 1986, there were no apparent differences in either leaf cover or *Zostera* distribution in the beginning of the autumn season, so the maximum standing crop was assumed to be similar for the two years. Thus, the consumption by wildfowl was equivalent to 45% and 33% of the total production in 1985 and 1986, respectively, or 91% and 66% of the maximum standing crop. The average grazing pressure was estimated at

25.5 and 18.6 g ash-free dwt/m², but was higher in the central parts of the *Zostera* bed.

Other studies have also evidenced that wildfowl grazing impact on *Zostera* can be considerable, although the values presented in literature are lower than the values from the present study.

For a *Z. noltii* bed in the Dutch Wadden Sea, JACOBS et al. (1981) found that wildfowl in autumn grazed the area down to a homogeneous stand with less than 10% leaf cover, and consumed 26% of the annual production, or 50% of the maximum standing crop.

For an estuary in southern England TUBBS & TUBBS (1983) found that grazing wildfowl, especially Brent Geese, likewise had a considerable effect on leaf cover of *Zostera* spp.

In none of the above cited studies was the consumption of below-ground biomass quantified. In the present study it was indicated that the wildfowl had an impact on this part of the biomass as well.

Impact of Zostera stock on feeding performance

Feeding efficiency as determined from feeding bout length and walking speed of Brent Goose and Wigeon at different levels of *Zostera* leaf cover, was compared (Table 4). Observations were carried out on birds feeding in areas where leaf cover had been assessed shortly before. For both species, it was found that efficiency was heavily hampered at low leaf cover. Thus, the birds had to walk faster over the substrate and the feeding bout length was reduced, indicating an increase in the distance between profitable patches of *Zostera* therefore resulting in the birds spending more time searching.

Brent Geese changed feeding method in response to the decreasing food supply, whereas Wigeon had no alternative feeding technique to which they could switch. On six days in 1986, where observations were performed over the entire low water period and leaf cover had been checked in advance, Brent Goose flocks spending the whole low water period in an area of even cover were observed. When areas of for example 10% and 90% leaf coverage were accessible, the geese selected the latter, but were sometimes forced to choose the former, due to presence of hunters in the more optimal parts of the *Zostera* bed (see next chapter).

At high leaf cover the geese spent less than 10% of the entire low water feeding period paddling (Fig. 6). As the cover be-

Table 4. Feeding parameters of Brent Goose and Wigeon at approximately 80% and 10-20% leaf cover of Zostera at Koldby Leje. Means, their standard deviations, and sample sizes are presented together with Student-t values and significance levels in two-tailed Student t-test.

	80%			10-20%				
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	t	P
Wigeon								
Feeding bout length (sec)	34.1	22.74	41	9.4	10.42	19	5.77	<0.001
Walking speed (sec for 10 steps)	38.4	37.63	32	10.7	5.08	20	4.10	<0.001
Brent Goose								
Feeding bout length (sec)	36.0	30.14	19	9.7	6.62	32	3.75	<0.01
Walking speed (sec for 10 steps)	59.4	37.80	19	22.4	8.40	18	4.17	<0.001

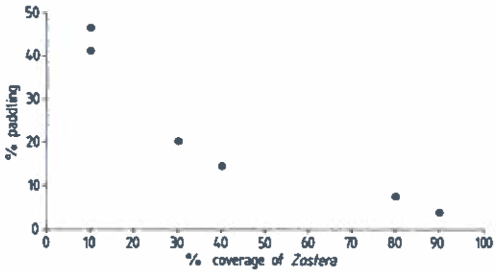


Fig. 6. Proportion of the low-water feeding period spent paddling for roots and rhizomes of Zostera by Brent Geese in relation to leaf cover.

came more sparse, the geese were paddling to a greater extent, and at 10% cover they spent almost half of the feeding period paddling for roots and rhizomes.

Due to a higher intake of below-ground parts, it was not possible to estimate food and energy intake in geese feeding at low *Zostera* cover. However, defaecation rates indicated that profitability in terms of energy intake was reduced. Thus, hourly defaecation rate at 10-20% leaf cover was estimated at 11.5 droppings/hr (3 hourly blocks), versus 17.0 at 70-90% cover (6 hourly blocks) ($Z = 5.83$, $P < 0.05$; for statistical method see BÉDARD & GAUTHIER 1986).

CHARMAN (1979) studied the energetics and performance of *Zostera noltii* feeding Brent Geese in southern England. An apparent threshold cover for *Zostera* leaf exploitation was determined as being around 15%, below which food consumption decreased markedly, and time spent feeding and also dispersion increased. In the course of the winter, the geese shifted from mudflats to salt marshes and agricultural crops, and it was demonstrated that this shift was related to the depletion of the *Zostera* resources. The data from the present study are in agreement with those results of CHARMAN (1979), and it is here added that the Brent Geese can also switch feeding technique during instances of decreasing resources.

The overlap in diet and the feeding congregation of Brent Geese and Wigeon gives rise, potentially, to interspecific competition. As the food stock at Koldby Leje was gradually depleted over the autumn, the competition probably became profound and especially critical to Wigeon which did not switch to the below-ground parts of *Zostera*. No interference was observed between the two species, and it is hypothesised that the interspecific competition is exploitative, limiting the number of birds that can utilise the food supplies.

In Golfe du Morbihan (1961-79) it was found that with the increase in the number of wintering Brent Geese, which reflected the general population increase, the number of Wigeon-days spent in the gulf decreased (CAMPREDON 1982), and this was suggested to be the result of interspecific competition for the *Zostera* resources.

However, it remains to be tested experimentally whether interspecific competition does affect bird numbers, though there are good reasons to believe that it does take place.

Effect of shooting on wildfowl distribution

Shooting in the mudflats at Koldby Leje was highly specialised. The hunters arrived around 3 hrs before low tide, and walked out on the still flooded mudflats. They placed themselves on the small hillocks and laid out duck decoys in the shallows nearby. As the water fell, the hunters lay down on the mudflat. Shooting was most intense from 3 hrs to 1 hr before low tide. Sometimes, the hunters left the mudflats around low water.

Hunting was concentrated to the period

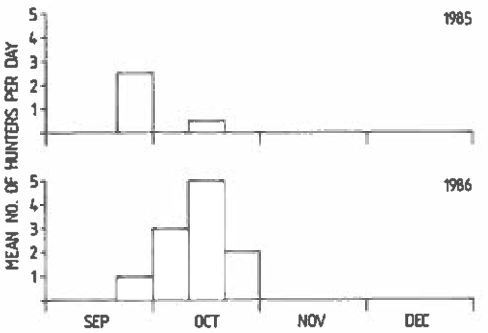


Fig. 7. Mean number of hunters present at Koldby Leje during low-water periods in autumns 1985 and 1986.

from mid-September to late October (Fig. 7), this being highly related to presence of dabbling ducks. There was, however, a big difference in the average number of hunters present between 1985 and 1986, and the estimated number of hunter-days over the seasons was 30 and 121, respectively. The peak number of hunters recorded was nine. The hunters usually placed themselves in the northern part of the *Zostera* bed. Only a few times were hunters sitting in the southern part, inside the Jordsand refuge with a complete shooting ban.

The ducks and geese reacted strongly to the presence of hunters and shooting, which was documented by a natural experiment. In Fig. 8 the size of the *Zostera* bed is depicted during the periods from mid-September to early October, and from mid- to late October 1986, respectively, and in parallel the distribution of wildfowl is shown with and without hunters present on the mudflats. Additionally, the distribution of wildfowl at night is shown. Flocks of wildfowl mapped in the field have been distributed in a 200m x 200m grid placed over the field maps. Data for Wigeon and Brent Geese have been pooled because there was neither a significant difference in the distribution pattern, nor in the reaction to hunting.

Several points emerge from Fig. 8:

1) From mid-September to late October the *Zostera* bed clearly diminished in size and biomass. Only within a 100 m radius around the observation tower was a 75-100% leaf cover of *Zostera* retained during late October.
2) When there were no hunters present, wildfowl distribution was mainly overlapping that of *Zostera,* and the birds were feeding in the zones with greatest leaf cover. However, the observation tower affected wildfowl in a radius of 150-200 m. In the second half of October the wildfowl concentrated in the northeastern part of the bed.
3) The nightly distribution of wildfowl was almost completely similar to that of day-time distribution, when the birds were undisturbed.
4) When hunters were present, the wildfowl flocks were displaced from the northern to the southern part of the *Zostera* bed, or to the western and eastern edges of the bed. From mid-September to early October, the flocks were able to withdraw to areas with good leaf cover of *Zostera.* However, during that period, hunters were present most days and the increased grazing pressure in the southern parts of the *Zostera* bed led to a fast depletion of the standing stock. During the second half of October, there was less than 25% leaf cover in those areas, to where the wildfowl were displaced due to hunting. In late October, the presence of a single hunter in the northern part was sufficient to displace the birds.

The wildfowl responded quickly to cessation of shooting. Twice it was observed that the hunters left the mudflats around low tide, and within the next hour all ducks and geese switched from the southern and eastern parts of the *Zostera* bed to the northern part with good leaf cover.

In the course of the season, shooting be-

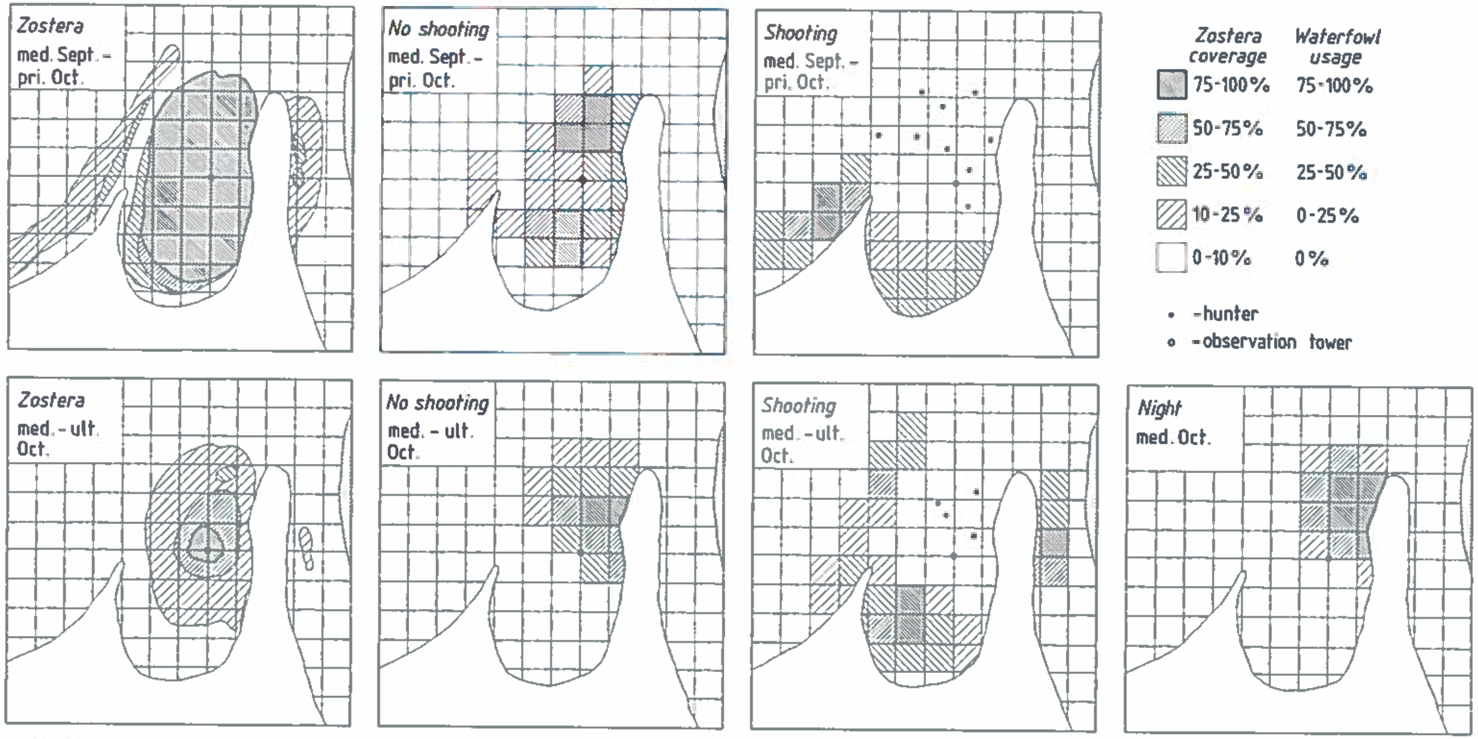


Fig. 8. Zostera resources and distribution of wildfowl (Brent Geese and Wigeon pooled) with and without hunting activity at Koldby Leje, during two stages in autumn 1986. Grid size is 200 m × 200 m. Waterfowl usage is expressed as percentage of the quadrat with the highest numbers. Each situation represents 2-3 complete low-water periods with mapping every ½ hr. The pooled numbers of hunters are shown.

came an increasingly disturbing activity, which was reflected in the flight distances of the Brent Goose flocks. The flight distance of a flock was estimated using a walking person as a standard stimulus triggering escape flight. The distance from the observer to the flock was controlled by pacing out. In late September the flight distance of a flock of 200-500 Brent Geese was on average 211 m (n = 10, S.D. = 32.4), whereas in late October it had increased to 367 m (n = 8, S.D. = 51.6), which is significantly higher (t = 7.46, P <0.001). Flight distances of Wigeon flocks were not quantified, but were comparable to those of Brent Geese.

Salt marsh feeding

Wildfowl numbers

The most numerous wildfowl around the Rømø barrage in autumn were Wigeon and Teal. In 1985 peak numbers were 10,000 and 3,500, respectively, in 1986 15,000 and 2,500, respectively. Up to 700 Pintail, 2,500 Mallard *Anas platyrhynchos,* 900 Brent Geese, and 500 Barnacle Geese *Branta leucopsis* were also present, but more irregularly. Brent Geese occurred only in autumn 1985, and it was almost exclusively family flocks, which visited the salt marshes.

Wigeon and Teal arrived from late Au-

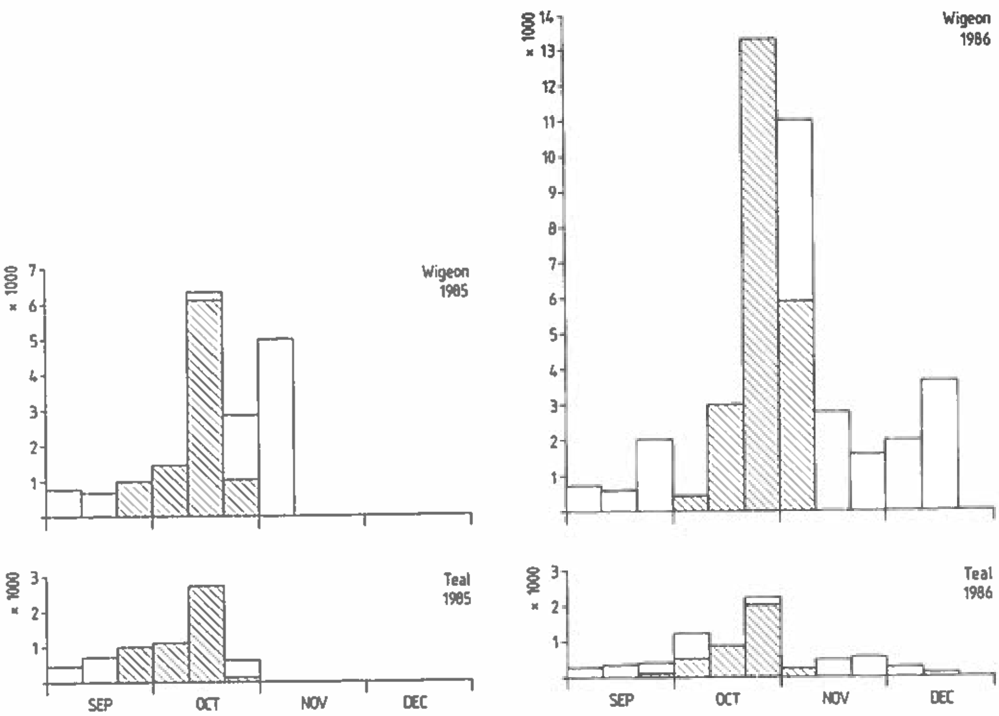


Fig. 9. Autumn occurrence of Wigeon and Teal at the Rømø barrage in 1985 and 1986, expressed as average numbers in 10-day periods. Hatched columns indicate the number of birds feeding in the salt marshes during diurnal high tides, open columns the number resting during high tide.

gust to early September (Fig. 9). For both species, peak numbers were reached in the second half of October, 2-3 weeks later than at Koldby Leje. In 1986, many ducks remained until mid-December.

In the beginning of the autumn staging period, the ducks used the barrage area as a high water roost, and fed during low water on adjacent mudflats north of the barrage. From the end of September, the ducks started salt marsh feeding. In 1985, this proceeded until late October, whereas in 1986 it continued until early November (Fig. 9). In 1985, the ducks left the area shortly after the salt marsh feeding period, whereas many stayed longer in 1986. In November, following the salt marsh feeding period, the remaining ducks roosted throughout day-time, irrespective of the tidal cycle. Evening flights of ducks into the hinterland were observed and heard on several occasions in November, though the exact feeding grounds were not identified. An indication of the Wigeon flight range comes from a bag analysis (LAURSEN 1985), which showed that Wigeon were shot up to 10 km inland from the Ballum Foreshore, i.e. into Ballum Enge. Flocks of Wigeon were also heard at night on Ballum Foreshore.

Table 5. Estimated number of bird-days spent by ducks feeding on seeds of salt marsh vegetation along the Romo barrage, autumn 1985 and 1986. Brackets indicate that the numbers are under-estimates.

	1985	1986
Wigeon	101,000	227,000
Teal	51,000	38,000
Pintail	4,000	7,000
Mallard	(9,000)	(9,000)

The number of feeding-days spent by ducks on the salt marsh vegetation is shown in Table 5. There was a doubling in number of Wigeon-days from 1985 to 1986, while Teal and Pintail feeding-days for the 2 years did not differ significantly. The higher amount of Wigeon-days was the result of a higher feeding intensity in the northern marsh, while feeding intensity in the

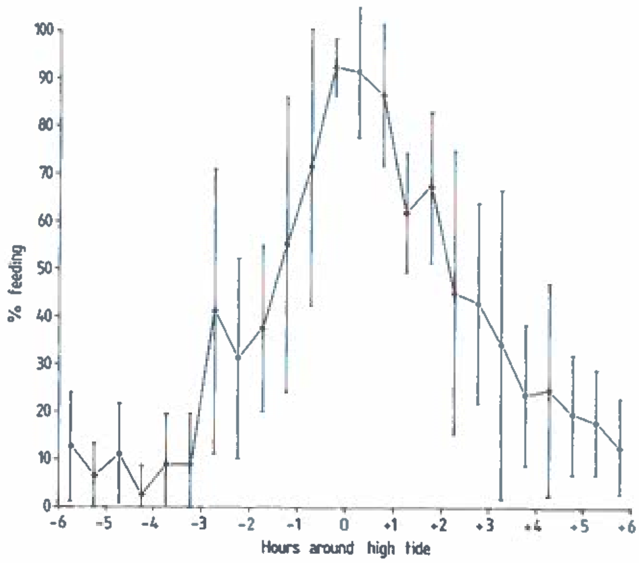


Fig. 10. Diurnal feeding activity of Wigeon at the Romo barrage during October, in relation to the tidal cycle (average of several observation periods). Bars show one standard deviation.

southern marsh did not change noticeably. This impression is based on the mapping of the flocks during day-time. The number of Mallard-days could not be ascertained because the Mallards occurred scattered in small flocks in the ditches.

Feeding rhythm

During day-time in mid-October duck feeding in the salt marshes was most intense around high water (Fig. 10). During low water, only about 10-20% of the ducks fed, while the rest were roosting on the mudflats beyond the marshes. The feeding rhythms of Wigeon, Teal and Pintail on salt marsh were identical. Whilst feeding in the marshes the ducks concentrated in dense flocks; in October up to 8,000 ducks in a flock were observed walking over the sward. During their stay in the marshes, the ducks fed intensively. Thus, on average 97.7% were feeding while in the marsh.

Nightly feeding activity could not be quantified, but it definitely occurred. In October, Wigeon and Teal were heard in the marsh areas several nights.

Seed stock and impact of duck feeding

From early September to mid-October 1986, the weight of *Atriplex* and *Suaeda* seeds more than tripled, and the maximum average weight was reached in the second half of October. Subsequently, seed weights declined (Fig. 11).

The highest standing seed stock was found on the marsh north of the Rømø barrage, followed by the marsh to the south, and the southern Ballum Foreshore (Table 6). Seed crops of grasses and other dicotyledons were negligible, and the *Salicornia* zones were, according to mappings, little used by the ducks.

The results of the exclosure experiments in 1985 and 1986 are shown in Figs. 12 and 13, respectively. In the marsh south of the

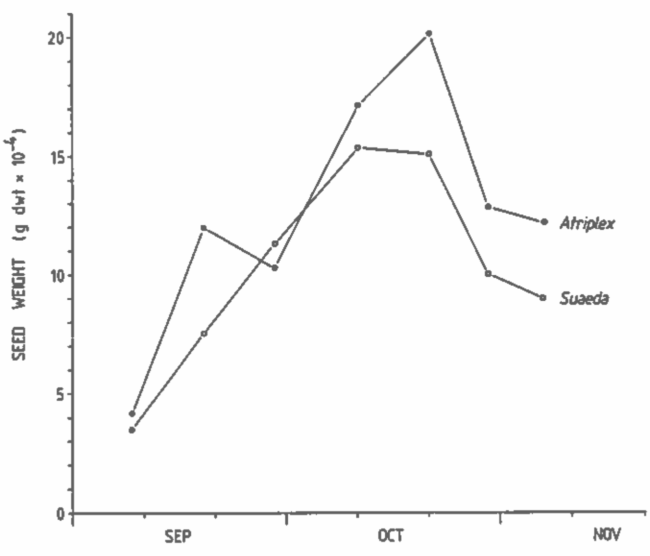


Fig. 11. Development in average seed weight of Atriplex litoralis and Suaeda maritima in autumn 1986.

Table 6. Standing seed biomass of Suaeda maritima and Atriplex litoralis on four salt marsh sections along the Romo barrage and Ballum Foreshore, 1-10 October 1986. Mean seed weight of Suaeda and Atriplex was 0.0015 g dwt and 0.0017 g dwt, respectively, and mean number of seeds per plant 77.2 and 121.7, respectively (no significant differences between areas).

	Romo barrage North		Romo barrage South	
	Suaeda	*Atriplex*	*Suaeda*	*Atriplex*
Plants/m²	928.5	4.6	38.1	204.8
Seeds/m²	71680	560	2941	24924
Seed weight (g dwt)/m²	107.5	1.0	4.4	42.4
Seed biomass (kg dwt)/ha	1090		470	
	Ballum North		Ballum South	
	Suaeda	*Atriplex*	*Suaeda*	*Atriplex*
Plants/m²	0.7	13.7	362.2	7.3
Seeds/m²	54	1667	27962	888
Seed weight (g dwt)/m²	0.08	2.8	41.9	1.5
Seed biomass (kg dwt)/ha	29		434	

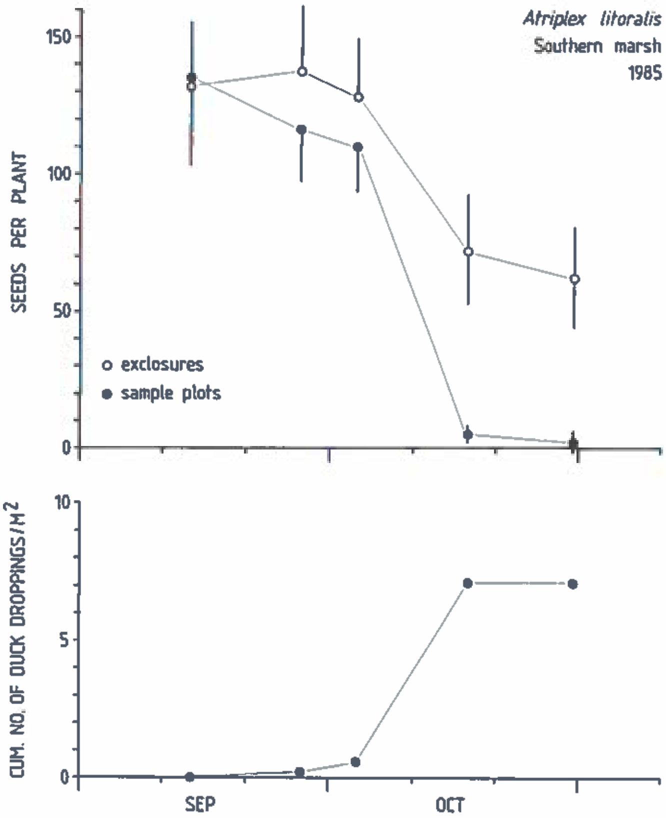


Fig. 12. Development in seed numbers per Atriplex plant (individually marked) within exclosures and duck visited plots in the southern marsh along the Romo barrage during autumn 1985. Bars show 95% confidence limits. Below is shown the cumulative number of duck droppings counted within permanent plots in the same marsh.

Rømø barrage, for *Atriplex* seeds outside the exclosures, the reduction (representing the natural seed fall and seeds swept away during flooding) was 52% from early September to late October in both years. In other words, ducks consumed about half the standing seed stock accessible. In 1985, the *Atriplex* seed stock was depleted by the ducks in mid-October, while in 1986 this did not happen until early November. The dropping counts in 1985 showed that the substantial decline in seed stock was correlated to duck utilisation (Fig. 12). Flooding of the marshes and associated wave action was another major contributor to seed removal. After a period of flooding, a rim of seeds could be found along the barrage and the Ballum dykes. In the northern marsh dominated by *Suaeda,* the same pattern of seed removal was observed. From early September to early November 1986 the number of seeds per plant in the sample plots was reduced by 92%, and in the exclosures by 58%. Thus, the ducks consumed about 40% of the seed stock available, and the rest either fell off or was swept away during flooding. It is unknown to what extent the ducks fed on the seeds that had fallen off, but observations indicate that most ducks were picking seeds from the plants.

On the southern Ballum Foreshore seeds were counted on *Suaeda* plants on 2 October and 6 November 1986. Over that period, the average number of seeds per plant declined from 82.3 to 41.5, equivalent to a 50% reduction. This is comparable to the exclosure plots in the marsh north of the Rømø barrage, indicating that there had been no significant duck grazing.

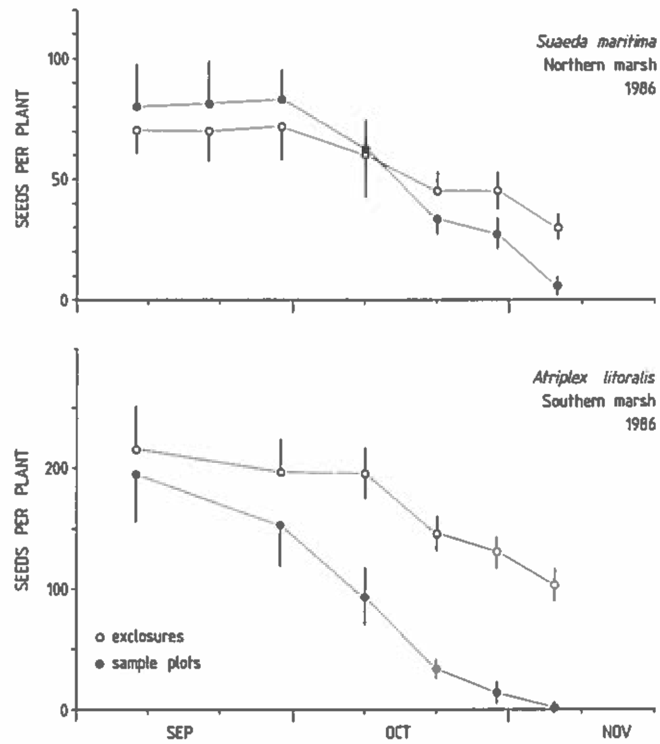


Fig. 13. Development in seed numbers for Suaeda and Atriplex plants within exclosures and duck visited plots in the marshes north and south of the Rømø barrage during autumn 1986. Bars show 95% confidence limits.

Impact of seed stock on foraging

The decreasing seed stock had a significant effect on duck foraging. This was demonstrated by the foraging parameters, walking speed and pecking rate, deployed by Wigeon feeding on *Atriplex* (Fig. 14). Unfortunately, it was not possible to relate the feeding parameters directly to seed density. However, as the curves in Fig. 13 show, date gives an approximate indication of density.

Walking speed was highly affected by the decreasing seed stock. In the start of the salt marsh feeding period the Wigeon lay down in the vegetation, stripping the seeds off the plants in the immediate surroundings. Later on in the season the ducks had to move continuously while feeding. At first, the ducks could compensate for decreasing seed density by walking faster, and pecking speed was not affected. However, by 6 November pecking speed had also decreased. This was the last date on which the ducks were seen feeding in the marshes.

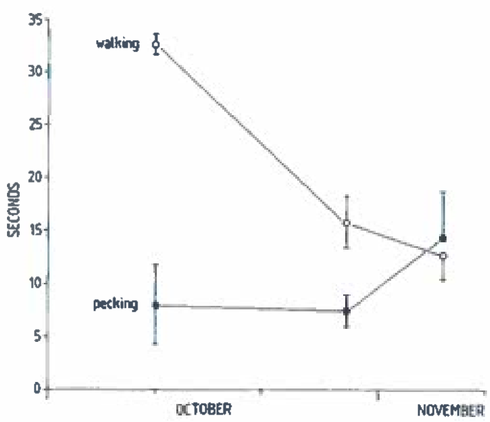


Fig. 14. Feeding parameters of Wigeon feeding on Atriplex seeds in the marsh south of the Rømø barrage, autumn 1986. Walking speed expressed as the time it took to make 10 steps, pecking speed as the time it took to make 10 pecks. Bars show 95% confidence limits.

Effect of shooting

The hunting practice and its effect on wildfowl utilisation of the Ballum Foreshore is dealt with in detail by LAURSEN, FRIKKE & BØGEBJERG (unpublished). They indicate that despite the fact that shooting closes 1 1/2 hrs after sunset (in November-December 1 hr after sunset), the ducks do not visit the marshes at night to any significant extent. Only in the outer marsh zones were duck droppings found at fair densities, but even then only infrequently over the autumn, and never at densities comparable to those found in the marshes along the Rømø barrage. Flocks of ducks were also only heard infrequently at night. These findings are supported by the seed counts in the Ballum marshes, which gave no indication of duck exploitation.

Apparently, despite the night-time being peaceful, the ducks did not feel safe enough to fly into the marshes when there was shooting during the preceding dusk. This has also been demonstrated by JAKOBSEN (1986), who made counts of dabbling ducks at night in the Skallingen salt marshes in the northern part of the Danish Wadden Sea. On nights when shooting had not occurred during the previous dusk, the number of ducks in the marshes was six times higher than compared to nights when there had been shooting during the previous evening.

Conclusions

The Danish Wadden Sea is situated in the migratory tract of the northwest European population of Wigeon numbering around 750,000 birds (RÜGER et al. 1986) and of the Siberian population of Dark-bellied Brent Goose numbering 150,000-200,000 birds (IWRB GOOSE RESEARCH GROUP unpubl.). The number of wildfowl, that can be counted at any one time in autumn, does not give a realistic picture of the total numbers passing through and making use of the food resources during autumn. Indeed, the turnover rate of birds is probably high. For the Northfriesian Wadden Sea just south of the Danish part, PROKOSCH (1984) found that the maximum staging period of Brent Geese was four weeks. Thus, over the autumn season probably double, or more, of the peak numbers present at a given time stay for a shorter or a longer period.

Within the study area, a temporal sequence of habitat shifts by wildfowl could be ascertained (Fig. 15). Wigeon first frequented the tidal mudflats, then the salt marshes, and finally the hinterland pastures. Brent Geese stayed on the mudflats throughout autumn 1986, but in 1985 part of the staging population shifted to the salt marshes. In Fig. 15, the arrows indicate that an unknown proportion of the staging population is exchanged over the season.

The wildfowl exerted heavy grazing pressure on the food supplies, both on the mudflats and on the salt marshes. By the time the birds abandoned Koldby Leje and the Rømø barrage marshes, the food resources had been exhausted to an extent where feeding efficiency was hampered, and foraging probably no longer profitable (for Brent Goose, see also CHARMAN 1979). The depletion of food supplies, in part, presents a meaningful explanation as to why wildfowl shift between habitats, and ultimately leave the area.

However, shooting actively modified movement patterns. On the mudflats hunting was a disturbing activity, displacing the ducks and geese to areas where food supplies were quickly depleted, such that feeding efficiency of the birds quickly decreased. Even if the birds were allowed to feed undisturbed at night, this was probably not sufficient to fulfil their energy demands. Wigeon, especially, were affected because they were dependent on above-ground parts of *Zostera,* whereas Brent Geese could cope better because they were able to switch to below-ground parts. However, in 1986, both the major part of the protected Brent Geese and the hunted Wigeon left the mudflats before the resources were exhausted, and this is interpreted to be a result of shooting disturbance. To the 'luck' of the Brent Geese, shooting ceased when the ducks emigrated. The remaining geese could thus stay undisturbed and utilise the rest of the *Zostera* supplies.

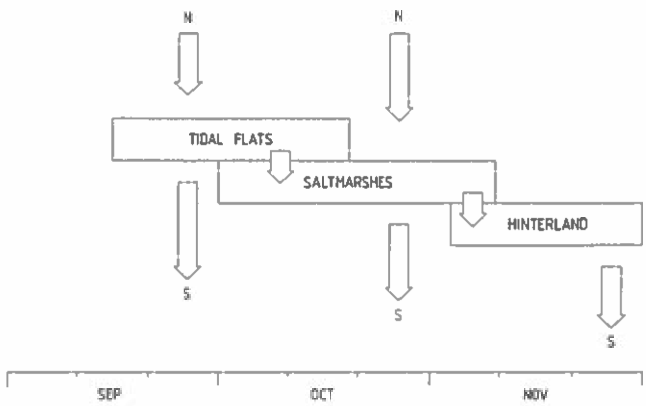


Fig. 15. A generalised outline of the movements between habitats for Wigeon over the autumn season in the Danish Wadden Sea. Arrows indicate that an unknown number moves in and out of the area.

As the *Zostera* stock decreased, exploitative competition between Wigeon and Brent Goose was another agent forcing particularly the Wigeon to leave. Shooting disturbance made the interspecific competition critical at an earlier stage in autumn than would be expected without shooting.

The Wigeon-grazing of seed in the salt marshes coincided with seed ripening. However, this time period also coincided with the time when shooting disturbance on the mudflats became critical, with the result that the ducks migrated from there. Thus, it cannot be said conclusively whether the ducks actually timed their flight to seed ripening, or whether shooting modified their movements. A combination of the two factors is feasible. Shooting in the Ballum Foreshore prevented the ducks from using those marshes in the day-time, and night-time feeding was not prevalent either. When food resources along the protected Rømø barrage were depleted, the majority of the ducks were thus forced to leave the area. The remaining ducks only fed at night and in other areas. Thus, shooting affected the activity of the ducks and also prevented them from using potential resources. In consequence, the ducks had to leave the area prematurely.

Dansk resumé

Fødeøkologi hos planteædende andefugle i Vadehavet om efteråret, og fødemængdens og jagtens effekt på flokkenes træk.

Den sydlige del af det danske Vadehav (Fig. 1) er en vigtig efterårsrasteplads for store flokke af svømmeænder og knortegæs. I september-oktober forekommer op til 6.000 knortegæs og 8.000 pibeænder på vadefladerne ved Koldby Leje, Jordsand Flak (Fig. 2), hvor de afgræsser en stor banke af ålegræs; senere i oktober-november opholder op til 15.000 pibeænder og 3.500 krikænder sig ved Rømødæmningen (Fig. 9), hvor de tager frø af marskplanterne.

Formålet med dette arbejde har været at beskrive forekomsten af andefugle og undersøge deres økologi under opholdet i Vadehavet. Det centrale spørgsmål var: hvad betinger antallet af fugle i området, og hvad forårsager træk-bevægelserne mellem delområderne? I hvor høj grad udnytter fuglene føderessourcerne, og har jagten, der drives på vadeflader og forlande, en forstyrrende effekt, så fuglene må trække bort, inden føden er brugt op?

Ved Koldby Leje kan andefuglene kun nå ålegræsset fra ca. 3 timer før til 3 timer efter lavvande. Ved lavvande i dagtimerne fouragerer fuglene næsten uden ophold (Fig. 3a). Ved hjælp af en lysforstærkende kikkert blev det påvist, at fourageringen også pågår om natten (Fig. 3b); pibeænderne fouragerer med samme intensitet som om dagen, mens knortegæssene afbryder fourageringen midt i lavvandsperioden. På det 138 ha store ålegræsbed, der primært består af dværgålegræs *(Zostera noltii)*, står der i september ca. 39 tons overjordisk biomasse (tørvægt). I løbet af efteråret falder den overjordiske biomasse drastisk (Fig. 5), så der i december kun står omkring 1 ton tilbage (3%). Andefuglene konsumerer mellem 26 og 35 tons i løbet af efteråret, svarende til 66-91% af den maksimale biomasse, eller 33-45% af årets produktion. Den øvrige reduktion skyldes naturligt henfald og planter, som knækkes af bølgeslag. Også den underjordiske biomasse af ålegræsset tages af fuglene og specielt af knortegæssene som »tramper« rødder og jordstængler frem af sedimentet. Ved sæsonens slutning var der 48% mere biomasse i ugræssede end i græssede felter (Fig. 5). Den faldende fødemængde reducerer andefuglenes effektivitet under fødesøgning (Tabel 1). På grund af den faldende fødemængde stiger fødekonkurrencen mellem knortegæssene og pibeænderne. Knortegæssene klarer sig tilsyneladende bedst, idet de gradvist skifter over til at tage rødder og jordstængler af ålegræsset, mens pibeænderne, der udelukkende tager bladene, nødsages til at forlade området.

I 1985 blev der kun drevet jagt på vaderne i få dage; i 1986 steg jagtintensiteten imidlertid kraftigt (Fig. 7). Den øgede jagt forringede fuglenes muligheder for at søge føde (Fig. 8). På dage uden jagt fordelte andefuglene sig jævnt over ålegræsbeddet. På dage med jægere fortrængtes fuglene til den sydlige zone, der er en del af Jordsand reservat med jagtforbud. Her blev ålegræsset nedgræsset i løbet af kort tid, og i midten af oktober var der kun ålegræs tilbage i jagtzonen. På dage uden jægere fouragerede fuglene, men på dage med jægere fortrængtes de igen til den fredede zone, hvor ålegræsset allerede var nedgræsset. Om natten fouragerede fuglene i jagtzonen. I 1986 forlod ænderne Koldby Leje tidligere end i 1985, hvilket kunne have været forårsaget af, at fuglene ikke kunne få dækket deres fødebehov pga. den jagtlige forstyrrelse på ålegræsbeddet i dagtimerne. Også antallet af knortegæs, der er jagtfredede, blev reduceret. Jagten ophørte imidlertid, da ænderne fortrak, og knortegæssene kunne således gå uforstyrrede på det resterende ålegræsbed resten af efteråret 1986.

På Rømødæmningens forland fouragerer ænderne især i timerne omkring højvande (Fig. 10). Deres forekomst på forlandet i oktober er sammenfaldende med frømodningen hos fødeplanterne Strandgåsefod *(Suaeda maritima)* og Strandmælde *(Atriplex litoralis)* (Fig. 11). I begyndelsen af oktober 1986 var der en frøsætning på op til 1 tons tørvægt pr. ha. Optælling af frø på hhv. planter, der blev afgræsset af ænderne, og på planter, der var indhegnede, viste at ænderne i løbet af oktober konsumerede omkring halvdelen af frøsætningen. Resten blev tabt naturligt eller skyllet bort ved oversvømmelse af forlandet. I 1985 var næsten alle frø forsvundet i midten af oktober, i 1986 først i begyndelsen af november (Fig. 12 og 13). På samme tid ophørte ænderne med at gå på forlandet. Hovedparten trak bort, mens den resterende del dagrastede på vaden ud for forlandet. De fouragerede udelukkende om natten, enten i landet bag digerne eller på Ballum Forland. På grund af jagt kunne ænderne ikke fouragere frit på Ballum Forland om dagen, og på trods af stor frøsætning viste optællinger af ande-ekskrementer, at forlandet kun blev benyttet ekstensivt om natten.

Det konkluderes, at antallet af andefugle i det sydlige Vadehav er reguleret af fødemængden, og at trækket mellem delområder og i sidste ende sydpå til overvintringsområderne forårsages af de svindende ressourcer. Jagten bevirker, at fuglene ikke kan udnytte ressourcerne maksimalt, men må trække bort tidligere end nødvendigt.

Резюме на русском языке:

Экология питания травоядных утиных на датских морских отмелях осенью, и эффект наличного количества пищи и охоты на перелеты стай.

Южная часть датских морских отмелей (Фиг. I) служит важным местом осеннего привала для больших стай водоплавающих уток и казарок. В сентябре-октябре до 6.000 казарок и 8.000 свиязей встречаются на пространствах отмелей у Кольби Лейе и мели Иордзанд Флак (Фиг. 2), где они стравливают обширную банку с водяной травой, а позднее в октябре и ноябре до I5.000 свиязей и 3.500 чирков-свистунков обитают у плотины к острову Рёмё (Фиг. 9), где они щиплют зерна растений на топи.

Целью настоящего труда было описать местонахождения утиных и исследовать их экологию во время пребывания на морских отмелях. Центральным вопросом было: от чего зависит численность птиц в этом районе, и что вызывает их перелеты из одного подрайона в другой? До какой степени используют птицы ресурсы пищи, и оказывает-ли ведущаяся на мелководных пространствах и берегах охота какой-нибудь нарушающий покой эффект, заставляющий птиц улетать, не успев потребить всю пищу?

У Кольби Лейе утиные могут достать водяную траву только от прибл. 3 часов до отлива до прибл. 3 часов после него. Во время отлива днем птицы фуражируют почти непрерывно (Фиг. 3а). При помощи светоэффективного бинокля было выяснено, что фуражирование также происходит ночью (Фиг. 3b); свиязи фуражируют так-же интенсивно, как днем, между тем как казарки прерывают фуражирование в середине периода отлива. На обросшем водяной травой пространстве в I38 га, главным образом покрытом мелкой травой Zostera noltii, в сентябре имеется прибл. 39 тонн надземной биомассы (по сухому весу). В течение осени количество надземной биомассы резко понижается (Фиг. 5), так что в декабре остается только около I тонны (3%). В течение осени утиные потребляют от 26 до 35 тонн, что соответствует 66 - 91% максимального количества биомассы или 33 - 45% годовой продукции. Остальное понижение количества объясняется естественным распадом и поломкой растений волнами. Подземная биомасса из травы также потребляется птицами, в особенности казарками, "вытаптывающими" из отстоя корни и подземные части стебельков. В конце сезона на нестравленных птицами участках было на 48% больше биомассы, чем на стравленных (Фиг. 5). Уменьшающееся количество пищи понижает эффективность поисков её утиными (Табл. I), и соревнование между казарками и свиязями обостряется. Как кажется, казарки лучше приспособляются к этому, постепенно переходя на питание корнями и подземными частями стебельков водяной травы, между тем как свиязи, питающиеся только листиками, принуждаются оставить данный район.

В I985 г. на мелководных пространствах было только немного дней охоты; зато интенсивность охоты в I986 г. сильно повысилась (Фиг. 7). Более интенсивная охота ухудшает возможности поиска пищи птицами (Фиг. 8). В дни без охоты, утиные равномерно распределялись по всему участку с водяной травой, а в дни с охотниками птицы вытеснялись в южный участок, составляющий часть Иордзандского заповедника, где охота запрещена. Здесь водяная трава была стравлена в течение краткого времени, и в середине октября осталась водяная трава только в зоне охоты. В дни без охотников птицы фуражировали, но при появлении охотников снова вытеснялись в зону заповедника, где водяной травы уже не было. Ночью птицы фуражировали в зоне охоты. В I986 году птицы покинули Кольби Лейе раньше, чем в I985-м, что могло объясняться невозможностью удовлетворения их потребности в пище вследствие нарушения их покоя на участке с водяной травой охотой во время дневного света. Понизилась также численность казарок, на которых охота запрещена. Однако, охота кончилась одновременно с отлетом уток, так что казарки до конца осени I986 г. могли спокойно использовать оставшийся участок с водяной травой.

На прибрежном участке перед плотиной к острову Рёмё утиные в особенности фуражируют в часы около прилива (Фиг. I0). Их появление в этом участке в октябре совпадает с созреванием семян служащих им для пищи растений, прибрежной гусиной лапки (Suaeda maritima) и прибрежной крапивы (Atriplex litoralis) (Фиг. II). В начале октября I986 г. количество этих семян составляло до I тонны сухого веса на га. Подсчет семян на растениях, стравленных утиными, и на огороженных растениях показал, что утиные в течение октября потребили около половины всех семян. Остальное количество либо отпало естественным образом, либо пропало при наводнениях прибрежного участка. В I985 г. почти все семена исчезли в середине октября, а в I986-м только в начале ноября (Фиг. I2 и I3). Одновременно с этим утиные перестали ходить по прибрежному участку. Наибольшая часть их улетела, а остальные днем отдыхали на отмели перед прибрежным участком. Они фуражировали только ночью, либо на участках за плотинами, либо на прибрежном участке Баллум. Днем они вследствие охоты не могли спокойно фуражировать на участке Баллум, и, несмотря на изобилие созревших в этом участке семян, подсчеты испражнений уток показали, что этот участок экстенсивно использовался только ночью.

Из этого следует, что численность утиных на южной части датских морских отмелей регулируется количеством наличной пищи, и что перелеты между подрайонами и, в конце сезона, на места зимовки дальше к югу, вызываются истощением ресурсов. Эффект охоты состоит в том, что птицы не могут максимально использовать ресурсы, и принуждаются улетать раньше, чем это необходимо.

References

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. - Behaviour **49:** 227-267.

ARCTANDER, P., FJELDSÅ, J. & JENSEN, A. 1984. Sejlads med luftpudebåde, jagt og andre forstyrrelser af fugle og sæler ved Saltholm. - Report, Zoological Museum, Copenhagen: 103 pp.

ASCHOFF, J. & POHL, H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. - J. Orn. III: 38-47.

BAUER, K.M. & GLUTZ VON BLOTZHEIM, U.N. 1968. Handbuch der Vögel Mitteleuropas. 2. - Akad. Verlagsgesellschaft, Frankfurt: 534 pp.

BÉDARD, J. & GAUTHIER, G. 1986. Assessment of faecal output in geese. - J. Appl. Ecol. **23:** 77-90.

CAMPREDON, P. 1981. Hivernage du Canard siffleur *Anas penelope* en Camargue (France). - Alauda **49:** 161-193.

CAMPREDON, P. 1982. Démographie et ecologie du Canard Siffleur *Anas penelope* L. pendant son hivernage en France. - PhD thesis, Acad. de Montpellier, Univ. du Languedoc.

CHARMAN, K. 1979. Feeding ecology and energetics of the Dark-bellied Brent Goose *(Branta bernicla bernicla)* in Essex-Kent. - In: Jefferies, R.L. & Davy, A.J. (eds.). Ecological Processes in Coastal Environments. Blackwell Sci. Publ., Oxford: 451-465.

DRENT, R.H., EBBINGE, B. & WEIJAND, B. 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. - Verh. orn. Ges. Bayern **23:** 239-264.

DRENT, R.H. & SWIERSTRA, P. 1977. Goose flocks and food finding: field experiments with Barnacle Geese in winter. - Wildfowl **28:** 15-20.

EERDEN, M.R. VAN 1984. Waterfowl movements in relation to food stocks. In: Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds.). Coastal waders and wildfowl in winter. - Cambridge Univ. Press. Cambridge: 84-100.

FOG, M. 1967. An investigation on the Brent Goose *(Branta bernicla)* in Denmark. - Dan. Rev. Game Biol. **5**(1): 40 pp.

HURLBERT, S.H. 1978. The measurement of niche overlap and some relatives. - Ecology **59:** 67-77.

JACOBS, R.P.W.M. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. - Aquatic Botany **7:** 151-172.

JACOBS, R.P.W.M., HARTOG, C. den, BRASTER, B.F. & CARRIERE, F.C. 1981. Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). - Aquatic Botany **10:** 241-259.

JACOBS, R.P.W.M., NOTEN, T.M.P.A. & CLAASSEN, E. 1983. Population and growth characteristics of the seagrass *Zostera noltii* Hornem. in the Dutch Wadden Sea. - Proc. Int. Symp. Aquat. Macrophytes, Nijmegen: 95-100.

JAKOBSEN, B. 1986. Jagtudøvelsen på Skallingen 1982-85 og betydningen for fuglelivet. - Report, National Agency for the Protection of Nature, Monuments and Sites, Ministry of Environment, Copenhagen: 30 pp.

JOENSEN, A.H. & MADSEN, J. 1985. Waterfowl and raptors wintering in wetlands of Western Greece, 1983-85. - Natura Jutlandica **21:** 169-200.

LAURSEN, K. 1985. Waterfowl and Wader shooting in the Danish Wadden Sea and Southern Jutland. - Danske Vildtundersøgelser **39:** 60 pp. (In Danish with an English summary).

LAURSEN, K. & FRIKKE, J. in prep. Surveys of waterfowl, waders and gulls in the Danish Wadden Sea 1980-1983. - To be published in Dan. Rev. Game Biol.

LORENZEN, B. and MADSEN, J. 1985. The goose populations at the Tipper peninsula, Western Jutland, Denmark. II: Grazing ecology in relation to the carrying capacity of the area. - Dansk Orn. Foren. Tidsskr. **79:** 113-132. (In Danish with an English summary).

MADSEN, J. 1986. Status of the staging goose populations and their haunts in Denmark, 1980-1983. - National Agency for the Protection of Nature, Monuments and Sites, Ministry of Environment, Copenhagen: 114 pp. (In Danish with an English summary).

MAHEO, R. 1976. The Brent Geese of France, with special reference to the Golfe du Morbihan. - Wildfowl **27:** 55-62.

MELTOFTE, H. 1982. Shooting disturbance of waterfowl. - Dansk Orn. Foren. Tidsskr. **76:** 21-35. (In Danish with an English summary).

NIENHUIS, P.H. & IERLAND, E.T. VAN 1978. Consumption of eelgrass, *Zostera marina*, by birds and invertebrates during the growing season in Lake Grevelingen (S.W. Netherlands). - Neth. J. Sea Res. **12:** 180-194.

OWEN, M. 1973. The winter feeding ecology of Wigeon at Bridgwater Bay, Somerset. - Ibis **115:** 227-243.

OWEN, M. 1975. An assessment of faecal analysis technique in waterfowl feeding studies. - J. Wildl. Mgmt. **39:** 271-279.

OWENS, N.W. 1977. Responses of wintering Brent Geese to human disturbance. - Wildfowl **28:** 5-14.

PETERSEN, C.G.J. 1913. Om Bændeltangens *(Zostera marina)* Aarsproduktion i de danske Farvande. - Mindeskr. Japetus Steenstrups Føds., **9:** 1-20. G.E.C. Gad, Copenhagen.

PROKOSCH, P. 1984. Population, annual cycle and traditional relationships to feeding areas of the Dark-bellied Brent Goose *(Branta b. bernicla L. 1758)* in the Northfrisian Waddensea. - Ecol. Birds **6:** 1-99. (In German with an English summary).

RANWELL, D.S. & DOWNING, B.M. 1959. Brent Goose *(Branta bernicla L.)* winter feeding pattern and *Zostera* resources at Scolt Head Island, Norfolk. - Anim. Behav. **7:** 42-56.

RÜGER, A., PRENTICE, C. & OWEN, M. 1986. Results of the IWRB International Waterfowl Census 1967-1983. - IWRB Special Publ. No. **6**, Slimbridge: 118 pp.

SAND-JENSEN, K. 1975. Biomass, net production and growth dynamics in an eelgrass *(Zostera marina L.)* population in Vellerup Vig, Denmark. - Ophelia **14:** 185-201.

TUBBS, C.R. & TUBBS, J.M. 1983. The distribution of *Zostera* and its exploitation by wildfowl in the Solent, southern England. - Aquatic Botany **15:** 223-239.

WIUM-ANDERSEN, S. & BORUM, J. 1984. Biomass variation and autotrophic production of an epiphyte-macrophyte community in a coastal Danish area: I. Eelgrass *(Zostera marina L.)* biomass and net production. - Ophelia **23:** 33-46.

5

DANISH REVIEW OF GAME BIOLOGY Vol. 13. No. 7

Spring Feeding Ecology of Brent Geese *Branta bernicla*:

Annual Variation in Salt Marsh Food Supplies and Effects of Grazing on Growth of Vegetation

by
Jesper Madsen

Med et dansk resumé:
Fødeøkologi hos knortegæs
Branta bernicla om foråret:
årsvariation i saltmarskens fødemængde
og gåsegræsningens effekter
på vegetationens vækst.

Резюме на русском языке:
Пищевая экология черной казарки Branta bernicla весной: Годовые изменения количества пищи на солончаковых приморских лугах и эффект пастьбы гусей на рост растительности.

ISSN 0374-7344

COMMUNICATION NO. 224 FROM VILDTBIOLOGISK STATION
Vildtbiologisk Station, Kalø, 8410 Rønde, Denmark
1989

Abstract

Madsen, J. 1989: Spring feeding ecology of Brent Geese *Branta bernicla:* annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. – Dan. Rev. Game Biol. 13 (7).

In the spring seasons 1986-1988 grazing by Brent Geese on salt marsh vegetation was studied in two localities in the Danish Wadden Sea: the island Langli and the foreshore Indvindingen. On Langli, goose grazing pressure in a *Puccinellia* community varied between 31 (1987) and 65 goose droppings per m^2 (1988) cumulated over the spring season, equivalent to a consumption of 47 to 97 g dwt per m^2. Estimates of net above-ground primary production (NAPP) of grazed *Puccinellia* (from mid March to early June) varied between 54 (1987) and 114 (1988) g dwt per m^2. Weekly addition of fresh goose droppings (in the same number per area as found in the grazed sward) to exclosed *Puccinellia* plots increased NAPP compared to control plots (87 vs. 28 g dwt per m^2). In the grazed sward protein content remained high (30%) throughout spring, whereas in control plots it decreased (to 25%). Simulated grazing of *Puccinellia* did not change NAPP significantly compared to control plots.

It is concluded that Brent Geese depleted the *Puccinellia* food supplies, which had bearing on goose numbers. Food supplies varied between seasons as a result of difference in weather conditions. The geese stimulated vegetation growth by defaecation.

Contents

Introduction

In spring the major part of the world population of Dark-bellied Brent Goose *Branta bernicla bernicla* is concentrated in the Wadden Sea (EBBINGE et al. 1981, PROKOSCH 1984, MADSEN et al. in press), building up bodily nutrient reserves, which are vital for later reproduction on the high-arctic Siberian breeding grounds (EBBINGE et al. 1982, THOMAS 1983). During the staging period, the geese feed on natural and semi-natural salt marshes. When they leave in late May they fly almost non-stop to the breeding grounds. Thus, the acquisition of nutrient reserves is dependent on the amount and quality of the spring forage.

From the 1960s to the 1980s, the population has increased from approximately 40,000 to 150,000-200,000 geese (IWRB GOOSE RESEARCH GROUP, unpubl.). It has been hypothesised, and indirectly indicated by counts, that the habitat capacity (defined as the number of geese an area can support without detrimental effects on the vegetation) of some of the Dutch spring staging areas has been reached (EBBINGE 1979, EBBINGE & BOUDEWIJN 1984). Intensive Dutch studies of exploitation of salt marsh vegetation by the Brent Geese flocks (DRENT & VAN EERDEN 1980, PROP & LOONEN in press) have also shown that the geese heavily graze *Plantago maritima*, one

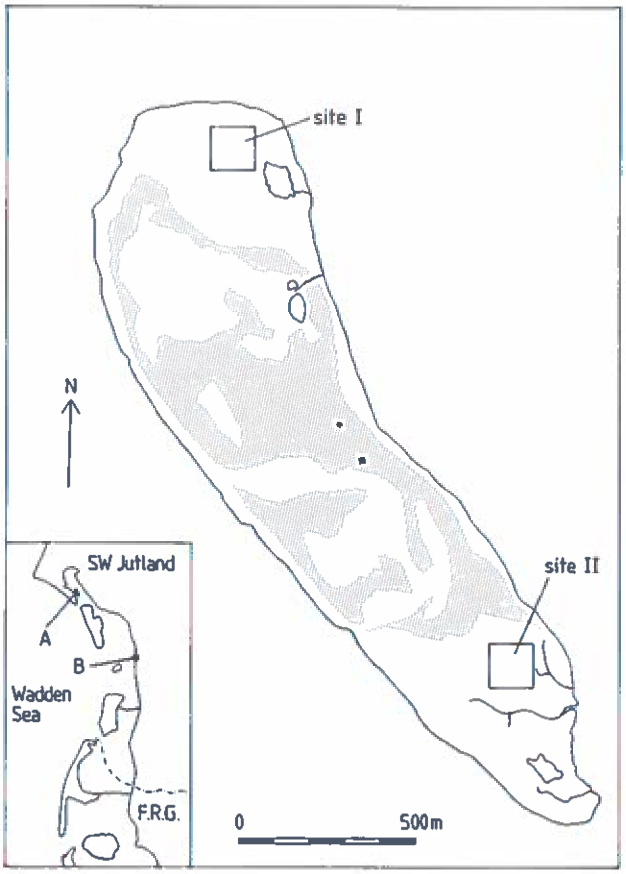


Fig. 1. Langli study area. Shaded areas represent dunes. In site I (northern salt marsh) dropping counts and exclosure experiments were conducted, whereas in site II (southern salt marsh) only dropping counts were performed. Positions of Langli (A) and Indvindingen (B) are indicated on inserted map.

of their primary food plants, so leading to depletion of local food supplies.

It is too early to evaluate possible density dependent impacts of food limitation in spring on reproductive output of the population. One question is whether or not the situation found in the Dutch Wadden Sea is general for the rest of the spring staging range.

The objective of this work has been (1) to assess annual variation in spring standing crop and productivity of salt marsh vegetation in the Danish Wadden Sea and exploitation rates by Brent Geese, and (2) to analyse some mechanisms by which the foraging goose flock affects the growth of vegetation, viz. fertilising effect of faeces and removal of biomass by grazing.

Acknowledgements

The National Forest and Nature Agency of the Ministry of Environment is thanked for granting access to Langli. The staff of Langli field station, Kim Fischer, Steen Kjeldsen, Jesper Kyed Larsen, Finn Olufsen and Lars Maltha Rasmussen, are thanked for assisting with tedious counts of goose droppings. Jouke Prop, Arne Jensen, Bent Lorenzen and Poul Hald-Mortensen are kindly thanked for comments on the manuscript. Janice G. Mather did the English technical language revision.

Study area

The study was carried out in spring over the years 1986-1988 on the island of Langli (105 ha) in the northern part of the Danish Wadden Sea (Fig. 1). The soil is sandy with a thin layer of clay in low-lying areas. The northern and southern ends of the island are salt marshes, approximately 50 ha in total. The lower parts are dominated by *Puccinellia maritima*, with *Plantago maritima* and *Artemisa maritima*, and the higher areas by *Festuca rubra* with *Juncus gerardi*. The island is a nature reserve and since 1981 there has been no agricultural practice. Prior to 1981, the island was used for cattle grazing in summer for decades.

In spring 1986, a supplementary study was carried out on Indvindingen, a 130 ha foreshore created by land reclamation, further south in the Danish Wadden Sea (Fig. 1). Here, the salt marsh is dominated by *Puccinellia maritima* with *Plantago maritima*, and is subjected to grazing by cattle from June to October.

Weather conditions

Weather conditions in spring 1986-1988 differed greatly. Meteorological data were available from Sædden Strand meteorological station, situated six km east of Langli. The date for which the temperature sum t-200 (the daily mean, positive temperatures (°C) summed from 1 January) was reached, was used as an indicator of start of

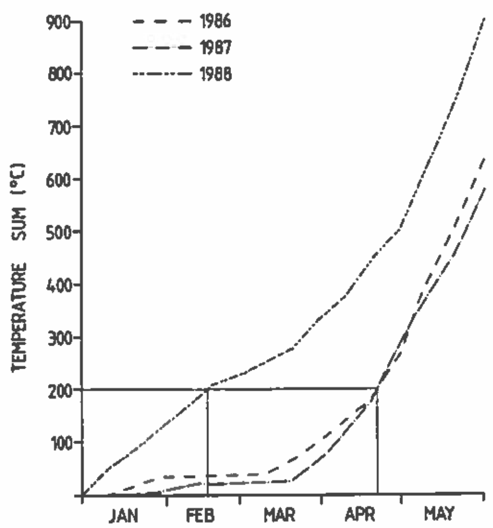


Fig. 2. Development of daily mean, positive temperature sums (°C) from 1 January to 31 May, 1986-1988. Dates for which t-200 was reached are indicated (temperatures registered at Sædden Strand meteorological station six km east of Langli).

the growing season. Fig. 2 shows that in 1986 and 1987 t-200 was reached on 23 April, and in 1988 on 18 February.

The monthly precipitation is presented in Tab. 1. It was about normal in April and May 1986, May 1987 and 1988, whereas precipitation in April 1987 and 1988 was far below normal. In all three years, and especially in 1988, precipitation in March was above normal.

Tab. 1. Monthly precipitation in mm, March to May 1986-1988, compared to normal (average for the period 1931-1960). Average values for Ribe county (based on monthly reports from the National Meteorological Institute).

	Normal	1986	1987	1988
March	37	63	49	115
April	41	40	23	23
May	42	50	51	45

Methods

Counts of birds, including geese, are routinely made by the staff at Langli field station. In March to May 1986-88, counts were performed on average every second day.

To elucidate food selection, fresh goose droppings were collected from the northern Langli salt marsh in mid April, early May and late May during both 1986 and 1987. Each sample consisted of 20-30 droppings. From a microscopical examination of epidermal plant fragments in the droppings, the frequency of component plant species in the diet was estimated by use of a point quadrat analysis (OWEN 1975).

The timing and intensity of goose grazing in the *Puccinellia* zone in the northern and southern salt marshes (sites I and II, Fig. 1) was measured by counting goose droppings in 10 permanent circles (12.6 m^2) situated at intervals of 20 m along a transect in each marsh. In both areas the transect was placed in a homogeneous sward, approximately 100 m from the coast. Plots were marked with 10 cm high pegs. Once a week in the spring seasons of 1986-88, droppings were counted and then squeezed, or if dry, removed. In 1987, an additional transect was placed in the *Festuca* zone in the northern marsh.

In spring 1987, an experiment was set up in the *Puccinellia* zone in the northern Langli salt marsh (site I, Fig. 1) to estimate net above-ground primary production (NAPP) in a) grazed, b) ungrazed, and c) ungrazed vegetation with fresh goose droppings added.

NAPP of vegetation ungrazed by geese (i.e. b and c) was estimated by use of exclosures. On 24 March, before the geese started visiting the salt marsh, four 3 m^2 exclosures were established at approximately 30 m intervals along a line in a visually homogeneous *Puccinellia* sward. Exclosures were constructed of stakes (height 40 cm above-ground) connected with strings at two heights. Geese grazed freely immediately outside the exclosures. Two exclosures were used as control plots; in the other two, fresh droppings (produced on the same day) were added once a week in the same number per area as they were counted in the permanent counting plots visited by the geese.

Standing crop was estimated on four occasions between 24 March and 6 June. On 24 March, six turfs, each of 0.06 m^2, were collected at random in the *Puccinellia* zone; on the other three dates 5-6 turfs were randomly collected outside the exclosures, and 2-3 turfs inside each exclosure. In the laboratory, the vegetation was clipped at the soil surface, washed, separated into live and dead material, and into component species. Samples were dried at 80°C for 24 hours, cooled in an exicator, and then weighed.

NAPP of vegetation ungrazed by geese (b and c) was estimated by adding all increments in biomass over the spring season, excluding the standing crop at the first sample date, which was regarded as production of the previous growing season.

NAPP of vegetation grazed by geese (a) was estimated by the amount of vegetation consumed by the geese:

$$NAPP = C + x_f - x_i,$$

where C is the forage consumed, x_i the biomass present at the start of the season, and x_f the biomass remaining after the departure of the geese (CARGILL & JEFFERIES 1984). C was calculated from the cumulated amount of droppings in the permanent counting plots and the retention rates of the food plants after gut passage. Retention rates were measured using ash content (after removal of silica fraction) and lignin as food components not digested (DRENT et al. 1978). Fresh droppings and samples of live vegetation were collected in mid April and early May.

To achieve an estimate of annual differences in NAPP, dropping counts were repeated in 1988 together with vegetation sampling in the grazed zone before and after the geese had visited the island (16 March and 31 May, respectively).

Live biomass from the vegetation samples were submitted to triplicate analysis of total nitrogen content (Kjeldahl technique) at the Central Laboratory, Animal Science Institute, Foulum, Denmark. Crude protein content was calculated by multiplying per cent nitrogen content by a factor of 6.25.

In 1986, an experiment similar to that performed at Langli in 1987 was set up in the *Puccinellia* zone at Indvindingen. However, due to displacement of the geese by a Goshawk *Accipiter gentilis* (MADSEN 1988), the salt marsh remained ungrazed during April and May and the experiment had to be abandoned. To achieve an estimate of the effect of pure mechanical removal of biomass on NAPP, NAPP of vegetation in two exclosures (3×3 m^2), ungrazed by geese, was compared to NAPP of vegetation in six plots of 0.059 m^2 each, where simulated grazing was performed by clipping. From 24 March to 6 June, samples of standing crop were randomly collected in the exclosures seven times, and the six plots were clipped six times. On each occasion, vegetation was clipped to a height of 1 cm above ground surface. On 6 June, the turfs in the plots were collected. NAPP in the clipped plots was estimated by summation of the biomass clipped and the standing crop on 6 June, subtracting an estimate of biomass at the beginning of the season. Average standing crop in the control plots in March was used as estimate of biomass at the start.

Results

Goose numbers

The first Dark-bellied Brent Geese arrived at Langli from early to mid March, and numbers peaked around the end of April (Fig. 3). In 1988 the geese arrived about 10 days earlier than in 1986 and 1987.

As it appears from Fig. 3, the number of geese on the island was not constant over the staging period. Part of the flock sometimes flew to adjacent feeding grounds (Skallingen and northern Fanø, MADSEN et al. in press). From mid May the geese began their migration from the island, and by the turn of the month there were only a few individuals remaining.

In 1986-1988, the peak number of Brent Geese recorded was 1,650 (1986), and the

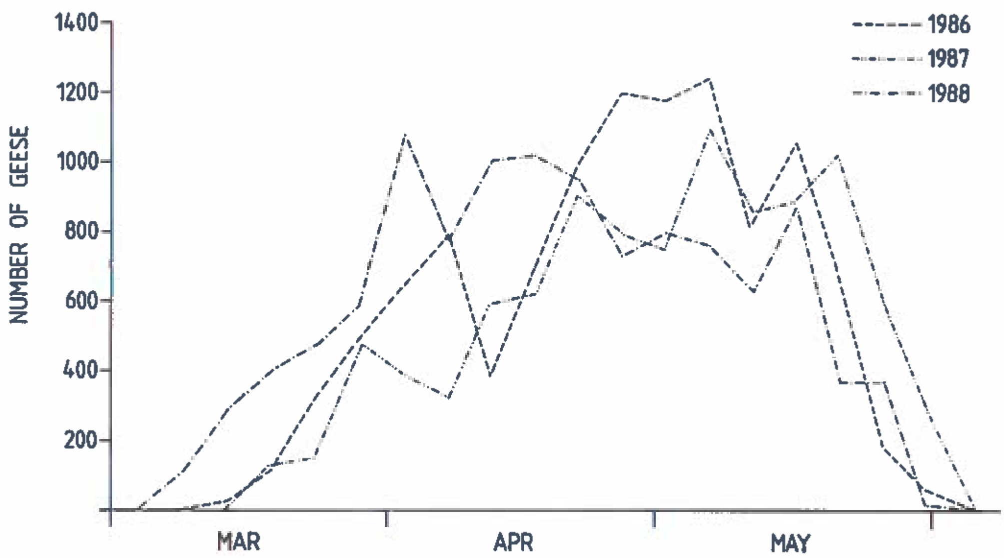


Fig. 3. Number of Dark-bellied Brent Geese on Langli, spring 1986-1988, expressed as mean number in international 5-day periods.

total number of goose-days spent on Langli varied between 39,100 (1987) and 56,000 (1988) (Tab. 2). The variation in number of goose-days was not only related to differences in the peak number of geese, but also to the irregularity in numbers staging at the island. In general, there were fewer geese on the island in 1987 compared to 1986 and 1988.

Selection of feeding zones and food

Throughout their stay on Langli the Brent Geese foraged in the *Puccinellia* marsh zone (Fig. 4). In 1987, there was a positive correlation between the weekly dropping deposition in the *Puccinellia* and *Festuca* marsh zones ($r=0.923$, $n=11$, $P<0.01$), indicating that there was no difference in timing of use of the two zones. Grazing pressure, as determined from cumulated dropping density, was highest in the *Puccinellia* zone, viz. 31 droppings per m² vs. 17 in the *Festuca* zone.

Puccinellia was the staple part of the goose diet from arrival to departure, the frequency varying between 49 and 72% with an average of 65%, and without any apparent seasonal trend. *Festuca* was the second-most frequent component species constituting on average 28% of the diet. *Plantago maritima* made up on average 6% of the diet and did not display any trend.

Tab. 2. Brent Goose numbers in spring 1986-1988 and grazing pressure in Puccinellia *marsh zones on Langli, expressed as the cumulated number of droppings counted in permanent plots.*

Year	Goose-days	Peak number	Cumulative no. of goose droppings per m²	
			N marsh	S marsh
1986	54,200	1,650	57	50
1987	39,100	1,266	31	30
1988	56,000	1,385	65	46

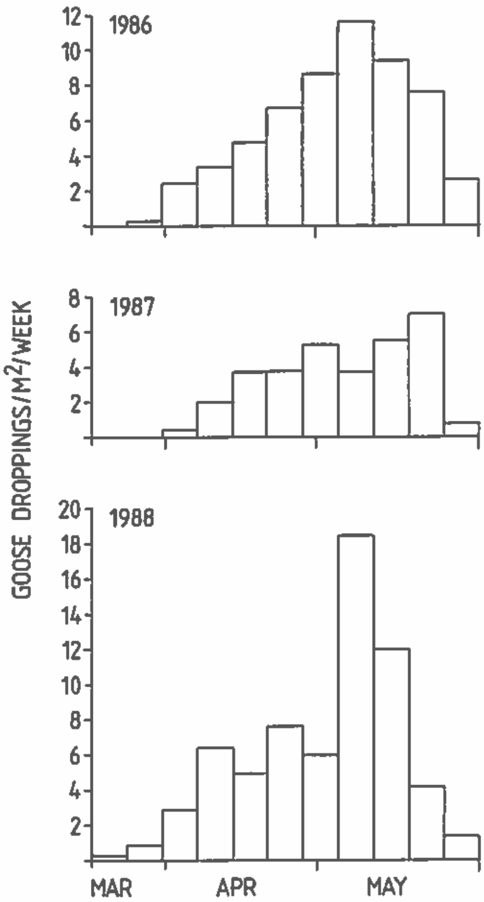


Fig. 4. Grazing pressure exerted by Brent geese in the Puccinellia *zone of the northern salt marsh on Langli, spring 1986-1988, expressed as dropping densities.*

Grazing pressure and NAPP in grazed vegetation

In 1986 and 1987, there was a significant positive correlation between the intensity in use of the *Puccinellia* zone in the northern Langli marsh and the number of goose-days on the island (Fig. 5). In 1988 there was no such relationship; in March and April the dropping deposition was lower than expected, but in May it was higher. The reason for this remains obscure, but in 1988 there was (unlike the previous two years) an occupied Red Fox *Vulpes vulpes* den close to the marsh, and foxes may have caused disturbance (carcasses of geese taken by foxes were actually found).

Between seasons, the cumulated dropping density varied from 31 (1987) to 65 (1988) per m^2 (Tab. 2). In all three years the highest densities were found in the northern marsh, but the seasonal variation was similar for both marshes.

The retention rate of ingested vegetation increased from April to May (Tab. 3). To calculate the total consumption of vegetation over the spring season, the retention rate found in early April has been used for the period from early March to 20 April, and the retention rate found in mid May for the rest of the staging period. On the basis of data in Tab. 2 and 3, the grazing pressure, expressed as amount of vegetation consumed, can be calculated to vary between 47 (1987) and 97 (1988) g dwt per m^2.

NAPP in grazed vegetation, estimated as the integral of consumption, showed a high degree of variation between seasons, being highest in 1988 and lowest in 1987 (Tab. 4). Based on this estimate, the geese consumed between 85 and 87% of the NAPP of *Puccinellia.*

Effect of droppings on vegetation

The experiment in the *Puccinellia* zone in the northern Langli marsh in 1987 revealed

Tab. 3. Estimates of amount of Puccinellia *leaves ingested per Brent Goose dropping in early April and mid May.*

	early April	mid May
Weight of dropping (g dwt)	1.01 (n = 102)	1.05 (n = 82)
Retention rate (%)	25	32
Vegetation ingested per dropping (g dwt)	1.35	1.54

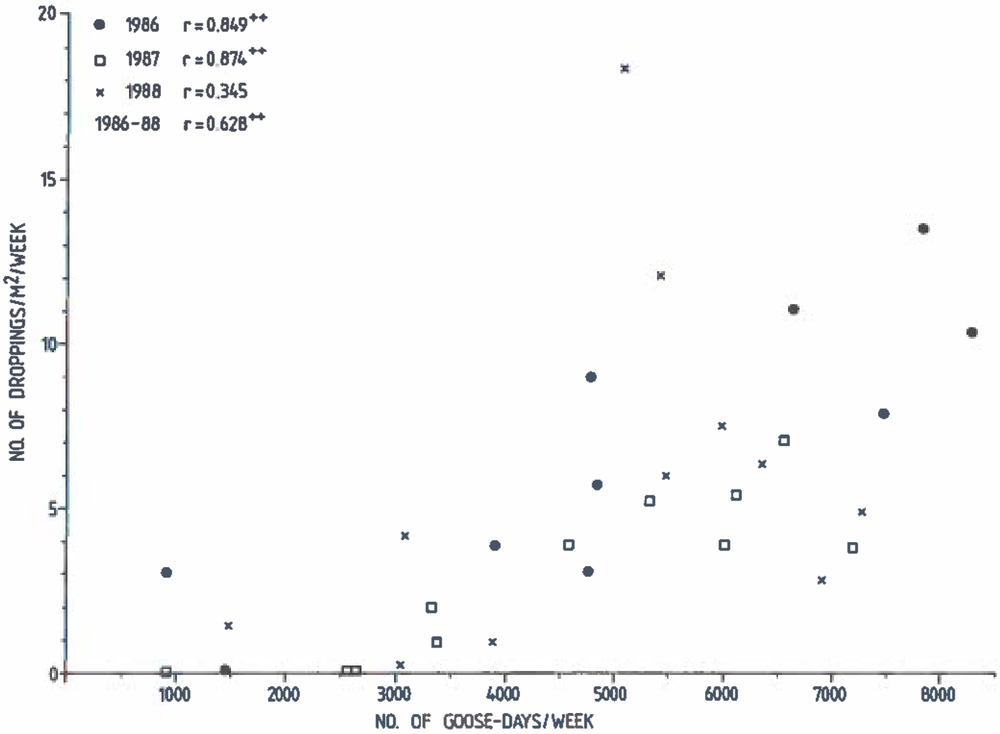


Fig. 5. Correlations between dropping deposition in the Puccinellia *zone in the northern salt marsh on Langli and the number of goose-days per week on the island, 1986-1988. + + indicates a 1% significance level; no signature indicates non-significance.*

that fresh goose droppings had a significant stimulating effect on NAPP (Fig. 6A). In late May, there was nearly three times more live standing crop in exclosures with droppings added compared to control exclosures (Student t-test, $t=4.26$, $P<0.01$). In the grazed sward the standing crop remained below 8 g dwt per m² throughout spring.

In March, there was 0.16 g dwt dead biomass per m² in the sward. In the grazed sward and in control exclosures, the dead biomass varied between 0.44 and 0.83 g dwt per m² in April and May (no significant de-

Tab. 4. Estimates of net above-ground primary production (NAPP) of Puccinellia *in the northern Langli salt marsh 1986-1988, on basis of goose consumption of vegetation, biomass before arrival (x_i) and biomass after departure (x_f) of the geese. For 1986, biomass values have been calculated as a mean of 1987 and 1988. Standard deviation of the mean is given in brackets.*

Year	Live biomass (g/m²)		Dead biomass		x_f–x_i	Consumption	NAPP
	x_i	x_f	x_i	x_f	(live + dead)	(g/m²)	(g/m²)
1986	-	-	-	-	(12.57)	85.9	(98.5)
1987	3.38	10.36	0.16	0.74	7.56	46.6	54.2
	(3.13)	(6.80)	(0.11)	(0.54)			
1988	9.08	26.12	0.09	0.63	17.58	96.6	114.3
	(3.12)	(9.12)	(0.04)	(0.28)			

velopment); in exclosures with droppings added the dead biomass increased from 0.66 g dwt per m² in April to 3.70 g in late May ($t=3.24$, $P<0.05$).

NAPP calculated as the positive increment in biomass from late March to late May was 27.7 g dwt per m² in control exclosures, and 87.2 g dwt per m² in exclosures with droppings added (3.2 × control).

Protein levels in grazed *Puccinellia* were constant throughout spring (Fig. 6B). In ungrazed vegetation, the protein content peaked in mid April and then decreased. The rate of decrease was highest in the vegetation where droppings had been added.

Effect of simulated grazing

The results of the clipping experiment on Indvindingen in 1986 are summarised in Tab. 5. The estimate of NAPP is based on data from seven sampling dates. Although there was a tendency for higher biomass and NAPP in control plots compared to clipped plots in June, the difference in standing crop was not significant ($t=1.847$, $P>0.05$). The NAPP estimates from Indvindingen are about double that for the grazed marsh on Langli (compare Tab. 4).

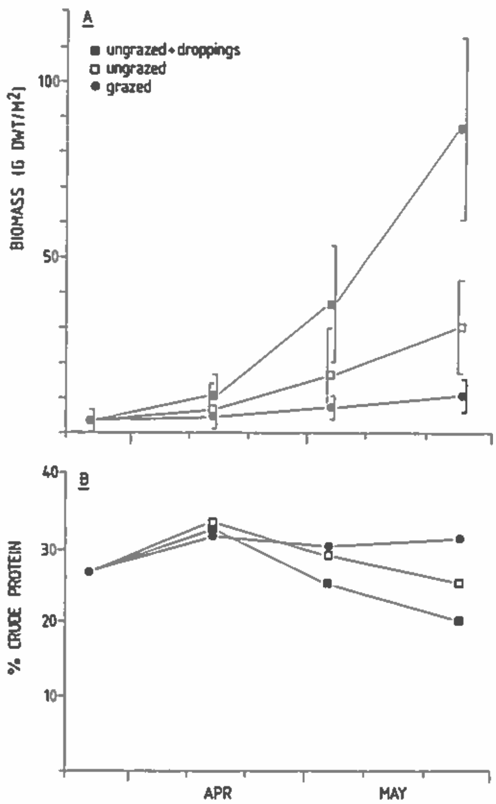


Fig. 6. Development in live standing crop (A) and protein content (B) of Puccinellia *in the northern salt marsh on Langli, spring 1987, shown for grazed sward, control exclosures, and exclosures with fresh goose droppings added, respectively. Bars indicate standard deviation.*

Tab. 5. Effects of simulated grazing by clipping on biomass and net above-ground primary production (NAPP) of Puccinellia, *Indvindingen 1986. Standard deviation of the mean is given in brackets.*

	24 March		6 June		March-June
	Biomass (g/m²)		Biomass (g/m²)		NAPP (g/m²)
	live	dead	live	dead	
Control plots	7.58 (2.62)	0.53 (0.17)	221.76 (47.03)	9.56 (2.58)	223.4
Clipped plots [1]	-	-	188.20 (18.41)	3.83 (1.66)	184.6

Note 1: including material clipped off during the period.

Discussion

The results of this study show that Brent Geese removed a substantial proportion of the spring net above-ground primary production of the *Puccinellia* sward on Langli. Furthermore, the results indicate that there was a large seasonal variation in food supplies caused by differences in spring weather conditions. Thus in the early spring of 1988, geese arrived earlier, and the number of goose-days, the grazing pressure and NAPP were higher than in 1986 and 1987. The data suggest that variation in available food supplies was responsible for seasonal variation in grazing intensity and number of geese on Langli.

According to EBBINGE (1979), Brent Geese start putting on weight from early to mid April and maintain a weight increase rate of approximately 10 g per day until departure at the end of May. In mid April 1987, growth of *Puccinellia* on Langli had hardly started, and so food may have been in short supply. This suggests that in late spring seasons such as in 1987 the amount of food in the natural habitat can be critical for acquisition of adequate nutrient reserves for the subsequent nesting season.

In the present study, goose droppings significantly enhanced NAPP of *Puccinellia* (by 215%), and the effect was so immediate that the geese benefitted from the increased growth within the same spring season.

Stimulation of vegetation productivity by grazing herbivores has been reported from other studies (MCNAUGHTON 1976, CARGILL & JEFFERIES 1984), and in some recent studies the underlying mechanisms have been analysed.

Two studies have demonstrated a fertilising effect of goose droppings on vegetation growth. BALKENKOL et al. (1984) reported that addition of goose droppings to meadow vegetation in early spring enhanced standing crop at harvest in summer. The most comprehensive study has been done by BAZELY & JEFFERIES (1985) who demonstrated that growth of salt marsh vegetation in sub-arctic Canada was highly stimulated by droppings from grazing Snow Geese *Anser caerulescens*. In a previous study, CARGILL & JEFFERIES (1984) had found that in swards of *Carex subspathacea* and *Puccinellia phryganodes* goose grazing resulted in a 35-77% increase in NAPP compared to ungrazed vegetation. BAZELY & JEFFERIES (1985) found that much of the nitrogen in goose faeces was soluble (mainly ammonia), and within a few days following defaecation the soluble nitrogen content of the droppings declined considerably. Transport of nitrogen to the sediment was not quantified but was believed to be considerable. The authors suggested that the geese were agents for acceleration of transfer of mobile nitrogen, leading to higher productivity of the food plants.

The salt marsh under study in Canada was nitrogen-deficient, which accounted for the pronounced effect of droppings on NAPP. The same situation probably applies to the *Puccinellia* zone on Langli. JENSEN et al. (1987) found that addition of 150 kg N per ha to *Puccinellia maritima* communities in Danish salt marshes resulted in a 42-67% increase in yield compared to control plots.

Estimates of NAPP in exclosures with addition of goose droppings, and of NAPP in grazed *Puccinellia* sward should be expected to be alike, provided defaecation was the only mechanism increasing NAPP. The former estimate was, however, higher than the latter (87 vs. 54 g dwt per m^2). The difference may have arisen from methodological bias or variation, but the lower productivity in the grazed sward may also be interpreted as a negative effect of heavy grazing. The clipping experiment performed on Indvindingen revealed a tendency, although not significant, for decreased standing crop and NAPP in clipped plots compared to control plots. In other studies it has been shown that increased cutting frequency decreases yield (CHESTNUTT et al. 1977, DETLING et al. 1979), and the same may apply to the *Puccinellia* marsh which is grazed by the geese at frequent intervals and kept extremely short (vegetation height less than 0.5 cm).

Turnover of plant material has not been taken into account in the calculation of NAPP. Decay of *Puccinellia* can be considerable as a direct effect of goose trampling of vegetation and grazing of leaves (J. PROP pers. comm.). Considering this, the NAPP of the grazed sward in particular is probably under-estimated, and the consumption rates over-estimated. However, this does not affect the general conclusion that the geese depleted the food supplies. Removal of biomass by grazing may, on the other hand, have a positive effect on NAPP. For example, KOTANEN & JEFFERIES (1987) found that shoots of *Carex subspathacea* grazed by Snow Geese produced more leaves than ungrazed shoots.

From various studies it is well-known that geese flocks grazing on the spring growth of vegetation can keep the forage plants in a state with high nitrogen content and low content of structural cell wall components (HARWOOD 1977, PRINS et al. 1980, YDENBERG & PRINS 1981, CARGILL & JEFFERIES 1984, MADSEN & MORTENSEN 1987). The results of the present study are consistent with these reports.

Dansk resumé

Fødeøkologi hos knortegæs *Branta bernicla* om foråret: årsvariation i saltmarskens fødemængde og gåsegræsningens effekter på vegetationens vækst.

I forårssæsonerne 1986-1988 blev knortegæssenes græsning på saltmarsken i Vadehavet studeret på øen Langli, suppleret med undersøgelser på forlandet Indvindingen (Fig. 1). Fra midten af marts til slutningen af maj opholder der sig op til 1.650 Mørkbugede Knortegæs *B. b. bernicla* på Langli (Tab. 2, Fig. 2). Antallet af gåsedage tilbragt på øen i løbet af foråret var højst i 1988 og lavest i 1987 (Tab. 2).

Udtrykt ved den samlede tæthed af gåseekskrementer igennem en forårssæson i udvalgte felter i et plantesamfund domineret af annelgræs *Puccinellia maritima*, varierede gæssenes græsningstryk mellem 31 (1987) og 65 gåseekskrementer pr. m² (1988) (Tab. 2).

Det er omregnet til, at gæssene konsumerede 47-97 g tørvægt pr. m² (Tab. 3 og 4). Gæssene holdt vegetationen kortgræsset gennem hele foråret. Nettoprimærproduktionen i det gåsegræssede annelgræssamfund blev fra midten af marts til begyndelsen af juni beregnet til at variere mellem 54 (1987) og 114 (1988) g tørvægt pr. m² (Tab. 4).

Indhegnede felter, hvor gæssene ikke kunne græsse, blev i foråret 1987 ugentligt tilført friske gåseekskrementer med samme tæthed som fundet i felter inden for afgræssede områder. I forhold til indhegninger, der ikke fik tilført ekskrementer, blev nettoprimærproduktionen af annelgræs næsten tredoblet i felter med tilførsel af ekskrementer (Fig. 6A). Proteinindholdet forblev højt gennem hele foråret i annelgræs, der blev afgræsset af gæssene, mens det faldt i ugræsset annelgræs (Fig. 6B).

Simuleret afgræsning ved gentagen afklipning af friske skud af annelgræs, ændrede ikke nettoprimærproduktionen i forhold til ikke-afklippet annelgræs (Tab. 5).

Bæreevnen af saltmarsken på Langli var i alle tre forår næsten nået, og antallet af gæs blev sandsynligvis reguleret af fødemængden. Årsvariationen i vegetationens produktion syntes

forårsaget af vejrforholdene, som var meget forskellige i forårene 1986-1988 (Tab. 1, Fig. 2). Gæssene kan få problemer med at nå at opbygge tilstrækkelige fedt- og proteindepoter på kroppen i sene og tørre forår, som i 1987. Depoterne er af afgørende betydning for, om gæssene kan gennemføre ynglesæsonen på de nordsibiriske ynglepladser med succes.

Резюме на русском языке:

Пищевая экология черной казарки *Branta bernicla* весной: Годовые изменения количества пищи на солончаковых приморских лугах и эффект пастьбы гусей на рост растительности.

В весенних сезонах 1986-1988 г. изучалась пастьба черных казарок на приморских лугах ниже уровня моря у датских морских отмелей на острове Лангли, с дополнительными исследованиями на приморской полосе Индвиндингей (Фиг. 1). С середины марта по конец мая на Лангли находятся до 1650 темнобрюхих черных казарок *B. b. Bernicla* (Табл. 2, Фиг. 2). Число гусе/дней, проведенных на острове в течение весны, было высшим в 1988 г. и низшим в 1987 г. (Табл. 2).

Выражено общей плотностью гусиных испражнений в течение весеннего сезона в избранных участках растительности, в которой предобладает трава *Puccinellia maritima*, интенсивность пастьбы гусей колебалась между 31 (в 1987 г.) и 65 гусиных испражнений (в 1988 г.)(Табл. 2). В пересчете из этого следует, что гуси поедали 47-97 г сухого веса за $м^2$ (Табл. 3 и 4). В течение всей весны гуси содержат траву короткой. Первичная продукция нетто в участке пастьбы гусей на траве *Puccinellia* по расчету с середины марта до начала июня колеблется между 54 (в 1987 г.) и 114 г сухого веса за $м^2$ (Табл. 4).

В огороженные участки, на которых гуси не могли пастись, весной 1987 г. еженедельно вводились свежие гусиные испражнения той-же плотностью, которая была определена на участках пастьбы. По сравнению с огороженными участками, в которые гусиные испражнения не вводились, продукция нетто травы *Puccinellia* на участках с введенными испражнениями повышалась почти втрое (Фиг. 6А). Содержание протеина в течение всей весны оставалось высоким в траве, на которой паслись гуси, а понижалось в траве, на которой они не паслись (Фиг. 6В).

Пастьба, симулированная неоднократным срезыванием свежих побегов травы *Puccinellia*, не изменяла продукцию нетто по сравнению с несрезанной травой (Табл. 5).

Предел способности питания на солончаковых лугах острова Лангли во все три весны был почти достигнут, и численность гусей вероятно регулировалась количеством пищи. Казалось, что годовые изменения продукции растительности были вызваны погодой, которая в веснах 1986-1988 г. была очень неодинаковой (Табл. 1, Фиг. 2). У гусей могут возникнуть проблемы, так как они должны успеть создать на теле достаточные запасы протеина такой поздней и сухой весной, как в 1987 г. Эти запасы имеют рашающее значение для способности гусей успешно провести сезон их размножения в северно-сибирских районах гнездования.

References

BALKENKOL, B., BERGMANN, H.-H., HOLLÄNDER, R. & STOCK, M. 1984. On the impact of wild goose faeces on meadow vegetation. Ecol. Birds **6**: 223-247 (In German, English summ.).

BAZELY, D.R. & JEFFERIES, R.L. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. J. Appl. Ecol. **22**: 693-703.

CARGILL, S.M. & JEFFERIES, R.L. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. J. Appl. Ecol. **21**: 669-686.

CHESTNUTT, D.M.B., MURDOCH, J.C., HARRINGTON, F.J. & BINNIE, R.C. 1977. The effect of cutting frequency and applied nitrogen on production and digestibility of perennial ryegrass. J. Br. Grassld. Soc. **32**: 177-183.

DETLING, J.K., DYER, M.I. & WINN, D.T. 1979. Net photosynthesis, root respiration and regrowth of *Boutelova gracilis* following simulated grazing. Oecologica **41**: 127-134.

DRENT, R.H., EBBINGE, B. & WEIJAND, B. 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. orn. Ges. Bayern **23**: 239-264.

DRENT, R.H. & EERDEN, M.R. VAN 1980. Goose flocks and food exploitation: how to have your cake and eat it. Int. Ornithol. Congr. **17**: 800-806.

EBBINGE, B. 1979. The significance of the Dutch part of the Wadden Sea for *Branta bernicla bernicla*. Pp. 77-87 in: Smart, M. (ed.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. IWRB, Slimbridge.

EBBINGE, B. & BOUDEWIJN, T. 1984. Richtlijnen voor het beheer van rotganzen in het Nederlandse waddengebied. RIN-rapport 84/4, Rijksinst. voor Natuurbeheer, Leersum. 76 pp.

EBBINGE, B., FOG, M. & PROKOSCH, P. 1981. Brent Goose *(Branta bernicla* L.*)*. Pp. 28-37 in: Smit, C.J. & Wolff, W.J. (eds.) Birds of the Wadden Sea. Balkema, Rotterdam.

EBBINGE, B., ST JOSEPH, A., PROKOSCH, P. & SPAANS, B. 1982. The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. Aquila **89**: 249-258.

HARWOOD, J. 1977. Summer feeding ecology of Lesser Snow Geese. J. Wildl. Manage. **41**: 48-55.

JENSEN, A., BLICHER-MATHIESEN, G. & SKOVHUS, K. 1987. The effect of nitrogen, phosphorus and potassium fertilizers on yield and yield quality in natural salt marsh vegetation. Marginaljorder og miljøinteresser. Miljømin. projektundersøgelser 1986, Teknikerrapport nr. **30** (In Danish with English summ.).

KOTANEN, P. & JEFFERIES, R.L. 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. J. Ecol. **75**: 961-975.

MADSEN, J. 1988. Goshawk *Accipiter gentilis* harassing and killing Brent Geese *Branta bernicla*. Dansk orn. Foren. Tidsskr. (In Danish, English summ.).

MADSEN, J., FRIKKE, J. & LAURSEN, K. in press. Occurrence and habitat selection of the Dark-bellied Brent Goose *(Branta bernicla bernicla)* in Denmark. Danske Vildtundersøgelser (In Danish with English summ.).

MADSEN, J. & MORTENSEN, C.E. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. Ibis **129**: 25-44.

MCNAUGHTON, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science **191**: 92-94.

OWEN, M. 1975. An assessment of faecal analysis technique in waterfowl feeding studies. J. Wildl. Manage. **39**: 271-279.

PRINS, H.H.T., YDENBERG, R.C. & DRENT, R.H. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neërlandica **29**: 585-596.

PROKOSCH, P. 1984. Population, annual cycle and traditional relationships to feeding areas of the Dark-bellied Brent Goose (*Branta b. bernicla* L. 1758) in the Northfrisian Waddensea. Ecol. Birds **6**: 1-99. (In German, English summ.).

PROP, J. & LOONEN, M. in press. Goose flocks and food exploitation: the importance of being first. Proc. Int. Ornithol. Congr. 18.

THOMAS, V.G. 1983. Spring migration: the prelude to goose reproduction and a review of its implications. Pp. 73-81 in: Boyd, H. (ed.) First Western Hemisphere waterfowl and waterbird symp. Can. Wildl. Serv., Ottawa.

YDENBERG, R.C. & PRINS, H.H.T. 1981. Spring grazing and the manipulation of food quality by Barnacle Geese. J. Appl. Ecol. **18:** 443-453.

6

The significance of Jameson Land, East Greenland, as a moulting and breeding area for geese: results of censuses 1982-1984

JESPER MADSEN, DAVID BOERTMANN and CHRISTIAN EBBE MORTENSEN

(Med et dansk resumé: Betydningen af Jameson Land, Østgrønland, som fældnings- og yngleområde for gæs: resultater af optællinger 1982-1984)

INTRODUCTION

In connection with a planned oil exploration in Jameson Land, East Greenland (71°N, Fig. 1), a study of the goose populations has been carried out since 1982 as part of an environmental baseline study (Madsen 1984). The goose studies have been carried out by the Zoological Museum, University of Copenhagen, as consultants for the Greenland Fisheries and Environment Research Institute under the Ministry for Greenland. The aim has been 1) to evaluate the importance of the area as a breeding and moulting ground, 2) to investigate the ecology and behaviour of the geese, and 3) to evaluate the possible effect of disturbance from drilling operations and associated activities on the goose populations.

From earlier reports parts of Jameson Land are known to be breeding and moulting areas for Barnacle Geese *Branta leucopsis* and Pink-footed Geese *Anser brachyrhynchus* (Marris & Ogilvie 1962, Hall 1963, Hall & Waddingham 1966, Marris & Webbe 1969, Ferns & Green 1975, Meltofte 1976). The Barnacle Geese are part of the East Greenland population breeding between 78°N (north of Germania Land) (Meltofte 1975) and 70°N (Scoresby Sund) (Bay 1894) and wintering in Scotland and western Ireland. At present (1983) the population numbers c. 25,000 birds (Ogilvie 1983a). The Pink-feet belong to the population breeding in Iceland and in East Greenland between 76°30'N (Hochstetter Forland) (Meltofte et al. 1981) and 66°20'N (Tugtilik-Nigertussoq) (Ray 1973). The population counts c. 90,000 birds (1982) (Ogilvie 1983b). A part of the East Greenland summer population is made up by non-breeders undertaking a moult migration from Iceland in the second half of June (Taylor 1953, Christensen 1967).

This paper summarizes the results of three years censuses (1982-84) of the goose populations in Jameson Land, including three aerial surveys of the area. Data on major phenological events such as timing of moult and breed-

Dansk Orn. Foren. Tidsskr. (1984) 78: 121-131

ing are presented, and observations from other parts of the breeding ranges of the two goose species briefly reviewed. Detailed results from the 1982 and 1983 field seasons have been published (Madsen & Boertmann 1982, Madsen et al. 1984). The results from the ecological work and the impact study will be published elsewhere.

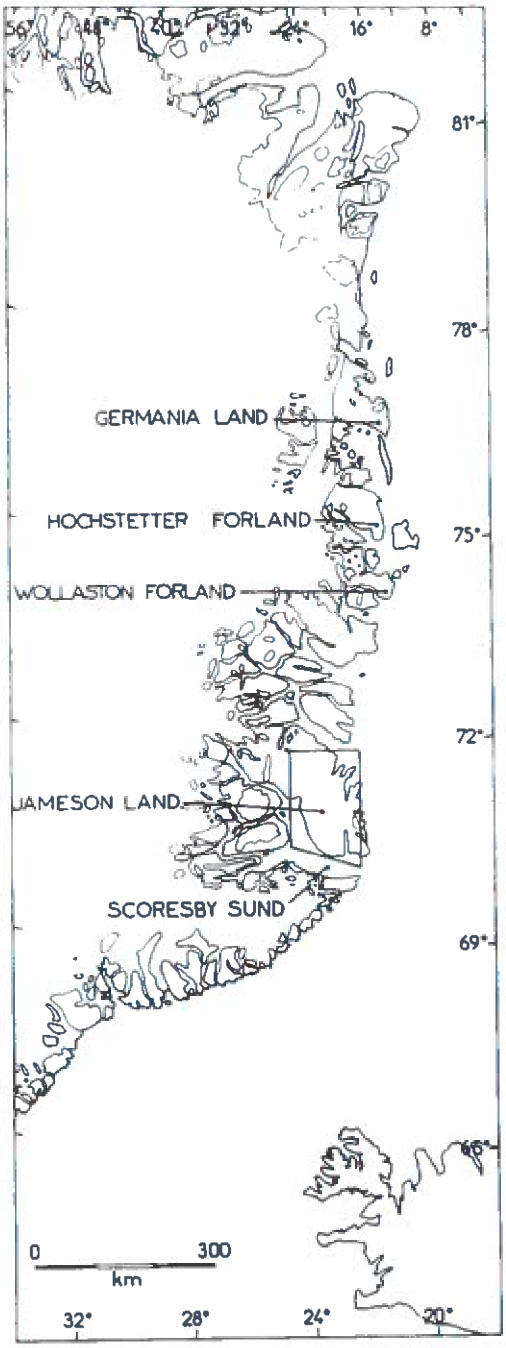


Fig. 1. Map of Northeast Greenland and Iceland with the study area framed.
Kort over Nordøstgrønland og Island med undersøgelsesområdet indrammet.

STUDY AREA

Most of Jameson Land (Fig. 2) is a lowland tundra, gradually rising from SW to a northern and eastern plateau reaching 700-1000 m a.s.l. The plateau is cut by rivers forming several valleys, e.g. Ørsted Dal and Schuckert Dal. The western part, Heden, is flat tundra characterized by many rivers, lakes and ponds. The vegetation on the lowland tundra is mainly dwarf scrub heath. The primary goose habitats

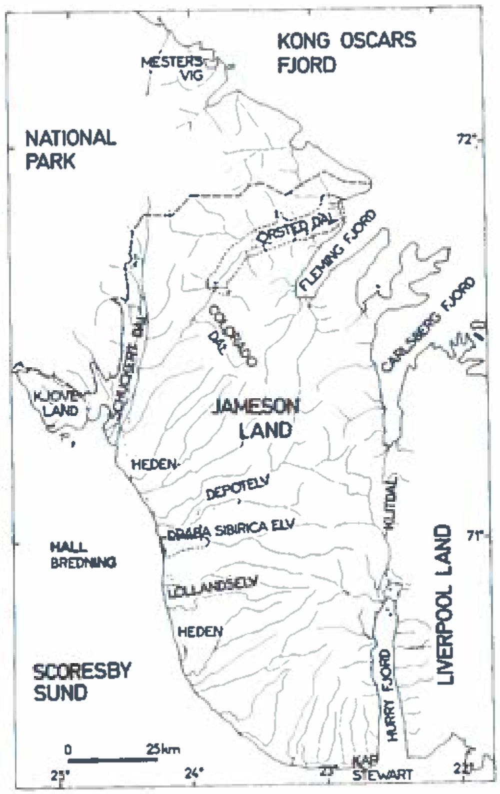


Fig. 2. Map of Jameson Land. Reference areas are framed with dashed lines. The border of the Northeast Greenland national park is indicated by heavy dashed line.
Kort over Jameson Land. Referenceområder er indrammet med stiplede linier. Grænsen for den nordøstgrønlandske nationalpark er angivet.

are graminoid marshes and wet grasslands adjacent to lakes and streams, and salt marshes along certain coast lines (for further details see Bay & Holt 1984).

METHODS

The field work was carried out 29 June to 3 August 1982, 29 June to 26 August 1983 and 15 June to 1 August 1984. Two types of censuses were performed:

1) Ground counts in reference areas. Population size and productivity was assessed in two reference areas each year: on Heden around Draba Sibirica Elv and in Ørsted Dal (Fig. 2). In 1983 and 1984 Ørsted Dal was visited by an English/Irish goose study group (D. Cabot & S. Newton pers. comm.) which performed the counts following the 1982 outlines given by Madsen & Boertmann (1982).
2) Aerial surveys. In order to get an overall impression of the distribution and numbers of geese, aerial surveys were carried out in 1982 (a reconnaissance flight 29-30 June), 1983 (full surveys 15-18 July and 22-25 August) and 1984 (full survey 20-21 July). Except from the 1982 survey, the same routes were flown in 1983 and 1984, covering all main water systems (lakes, rivers and coast lines). Mid-July was chosen, as experiences in 1982 showed that non-breeding geese were moulting at that time and concentrated along rivers, lakes and coasts, and because all nests had hatched and the families frequented the same habitats as the non-breeders (routes and further details are given by Madsen et al. 1984). In 1982 and 1983 the surveys were conducted with a one-engined Cessna 206, in 1984 with a two-engined Partinavia Observer with optimal outlook. Flight speed was generally 65-75 knots in July, while a faster speed was used in August 1983 (80-100 knots) when the geese had regained flight. Flight level was c. 400 feet above ground. The surveys were performed by two observers, and most goose flocks were checked with 10× binoculars and records kept on tape recorders.

The timing and duration of the flight feather moult of non-breeders and breeders was recorded by observation of flocks. In 1984 a census of the breeding geese in a 23 km² inland area around Draba Sibirica Elv was conducted and the fate of the nests and timing of hatching recorded.

Tab. 1. Population composition of geese in the reference area in Ørsted Dal, mid-July 1982-84.
Bestandssammensætning af gæs i referenceområdet i Ørsted Dal i midten af juli 1982-84.

	1982	1983	1984
Anser brachyrhynchus			
Non-breeders *Ikke-ynglende*	970	387	313
Parents *Forældrefugle*	0	62	12
Pulli *Pulli*	0	79	21
Branta leucopsis			
Non-breeders *Ikke-ynglende*	1184	1246	1017
Parents *Forældrefugle*	48	114	98
Pulli *Pulli*	49	116	87

RESULTS

The breeding populations

The counts in the reference areas (Tabs 1 and 2) and the aerial surveys (Fig. 3) showed that the breeding populations are small and scattered. The breeding Barnacle Geese are mainly distributed in the northern valleys where they breed on steep cliffs in colonies of 10-30 pairs, and the distribution pattern is determined by available nest sites (a full account on the breeding in Ørsted Dal will be given by Cabot and Newton elsewhere). In addition, de Korte (1973, 1974) and Meltofte (1976) mention

Tab. 2. Population composition of geese in the reference area around Draba Sibirica Elv, mid-July 1982-84.
Bestandssammensætning af gæs i referenceområdet omkring Draba Sibiria Elv i midten af juli 1982-84.

	1982	1983	1984
Anser brachyrhynchus			
Non-breeders *Ikke-ynglende*	1202	1167	752[a]
Parents *Forældrefugle*	14	30	32
Pulli *Pulli*	19	48	60
Branta leucopsis			
Non-breeders *Ikke-ynglende*	136	155	132
Parents *Forældrefugle*	4	0	2
Pulli *Pulli*	5	0	1

Note: a) an additional 350 had abandoned the area due to helicopter disturbance few days prior to the census.

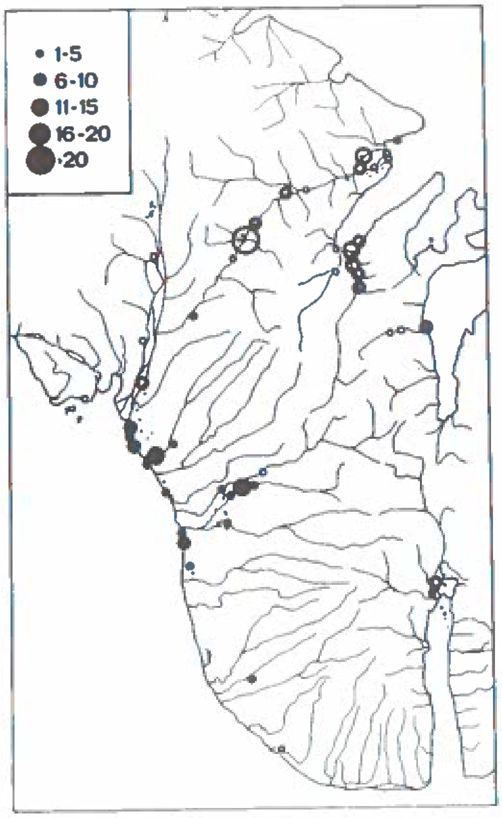


Fig. 3. Distribution of goose families recorded by aerial survey in mid-July 1984. Circles are Barnacle Geese, filled circles Pinkfeet.
Fordelingen af gåsefamilier ved flytælling i midten af juli 1984. Cirkler angiver Bramgæs, udfyldte cirkler Kortnæbbede Gæs.

small colonies around Kap Stewart and on Fame Øer in Hurry Fjord.

As evidenced by the post-hatching distribution of families (Fig. 3), most Pinkfeet breed on Heden. However, some Pinkfoot families are surely overlooked by the aerial surveys, because the geese sometimes walk far inland; the map thus only gives a relative distribution. In Ørsted Dal 53 nesting pairs were found in 1984 (Cabot & Newton pers. comm.), but only five families were counted later in July. Breeding pairs have also been found in the Hurry Fjord region and around Kap Stewart (de Korte 1973, 1974, Meltofte 1976, Madsen et al. 1984). Pinkfeet mostly nest along rivers with steep banks or on small islands or lake borders. The pairs generally nest in small colonies of 2-5 nests with 10-20 m between neighbours.

In the 23 km^2 census plot around Draba Sibirica Elv 15 pairs nested in 1984. Only six nests hatched (40%); the rest were predated, in most instances probably by Arctic Foxes *Alopex lagopus*, which were numerous in the area (two dens). On one occasion egg robbing by an Arctic Skua *Stercorarius parasiticus*, on another by a Long-tailed Skua *S. longicaudus*, was observed. In both cases the predation was caused by the observer flushing the goose from an uncovered nest.

By the aerial survey in 1984, where the goose families were more easily recognized due to the improved outlook, a total of 75 families of Pinkfeet and 140 families of Barnacle Geese was observed. A simultaneous ground count in Ørsted Dal (Cabot & Newton pers. comm.) showed that the aerial survey gave a reasonably good estimate of the number of Barnacle Goose families (aerial count: 64 families, ground count: 49 families; the discrepancy is probably explained by non-breeding pairs or failed breeders associated with the families counted as breeders by the aerial survey). From the reference area around Draba Sibirica Elv it was indicated that the aerial survey underestimated the number of Pinkfoot families, approximately by 50%.

Therefore, an estimate of the size of the breeding populations can only be tentative. The population of successfully breeding Barnacle Geese is estimated at 150-200 pairs, of Pink-footed Geese at 150-250 pairs, in 1984. A success rate for nests of 40% indicates that twice that number of Pinkfoot pairs may attempt to breed. From observations in Ørsted Dal (Cabot & Newton pers. comm.), the predation rate for Barnacle Geese seems to be of the same magnitude as for Pinkfeet (though the

Tab. 3. Brood sizes in different areas and years. Sample sizes are given in brackets.
Kuldstørrelser i forskellige områder og år. Antal kuld er angivet i parentes.

	1982	1983	1984
Anser brachyrhynchus			
Heden	2.7 (7)	2.7 (25)	3.7 (18)
Ørsted Dal	-	2.6 (31)	3.5 (6)
Mesters Vig	-	-	3.0 (4)
Branta leucopsis			
Heden	-	2.3 (3)	2.2 (9)
Ørsted Dal	2.0 (25)	2.0 (57)	2.1 (42)
Mesters Vig	-	-	2.3 (25)

Tab. 4. The number of adult geese counted during three complete aerial surveys in 1983 and 1984.
Antallet af adulte gæs talt ved tre fuldstændige flytællinger i 1983 og 1984.

Locality *Lokalitet*	July 15-18, 1983		August 22-25, 1983		July 20-21, 1984	
	Branta leucopsis	*Anser brachyrhynchus*	*Branta leucopsis*	*Anser brachyrhynchus*	*Branta leucopsis*	*Anser brachyrhynchus*
Ørsted Dal	1263	382	298	667	1115	255
Coloradodal	362	530	152	183	741	261
Schuckert Dal	334	68	24	453	273	0
Kjoveland	291	288	20	175	450	480
Fleming Fjord	392	160	96	404	262	100
Carlsberg Fjord	12	0	17	46	161	60
Klitdal	474	0	86	116	387	46
Hurry Fjord	22	74	0	393	20	2
Heden North[a]	990	670	132	1291	398	1415
Heden Central[b]	1511	2385	401	855	773	1480
Heden South[c]	493	1004	110	917	429	831
Total	6144	5561	1336	5500	5009	4930

Notes: a) from Schuckert Dal to Depotelv (excl.), b) from Depotelv to Lollandselv (excl.), c) from Lollandselv to Kap Stewart.

predation pressure is not so much on nests as on goslings). The breeding population of Barnacle Geese is thus estimated at 300-400 pairs, the Pinkfoot population at 300-500 pairs. These estimates are rough, and numbers may vary between years (Tabs 1 and 2). 1984 seems to have been a good breeding season.

The majority of the Barnacle Goose nests hatch from around 28 June to 5 July (range in Ørsted Dal in 1984 was 27 June to 11 July (Cabot & Newton pers. comm.)), with the Pinkfeet 3-7 days later. Average brood size of Barnacle Geese was 2.0-2.3 pulli/brood (Tab. 3). Pinkfeet had bigger broods, on average varying between 2.6 and 3.7 pulli/brood (mid-July), with bigger broods in 1984 compared to the previous two years.

Parents of Barnacle Geese moult from around 20 July and regain flight in mid-August (1983). Parents of Pinfeet moult approximately 5 days later and regain flight by 20-25 August.

The non-breeding population

The major part of the goose population in Jameson Land is comprised by non-breeders summering in the area and moulting remiges (Tabs 1 and 2). By the two complete aerial surveys in July 1983 and 1984 the total adult population was estimated at 11,700 and 9,950 individuals, respectively (Tab. 4), with an even numerical distribution between the two species and with a high dominance of non-breeders. When ground counts and aerial counts in the reference areas are compared, a good accordance between the results is apparent (Madsen et al. 1984). The estimated 175 and 200 successfully breeding pairs of Barnacle and Pinkfooted Geese, respectively, comprise only 6-8% of the population in both species.

Inside the reference areas, the non-breeding population of Barnacle Geese was stable through the three census years (Tabs 1 and 2). The Pinkfoot population in Ørsted Dal declined (Tab. 1), probably due to human disturbance mainly from ground activities (including round-ups of geese for ringing in 1984). In the reference area around Draba Sibirica Elv the Pinkfoot population was similar in numbers in 1982 and 1983 (Tab. 2). In 1984 helicopter operations in the area few days prior to the census probably displaced part of the population.

In mid-July the non-breeding, moulting geese were concentrated along rivers, lakes and coast lines (Fig. 4). The Pinkfeet were mainly distributed along the coast of Hall Bredning, along rivers and on lakes on Heden, in Kjoveland and in Ørsted Dal and Coloradodal. The Barnacle Geese were similarly distributed, but were also observed in the Fleming Fjord region and in Klitdal and Schuckert Dal. Except from the northern valleys, Jameson Land almost exclusively serves as a moulting area for the Barnacle Geese.

In 1983 the mean flock size of moulting Pinkfeet was 42.6 (range 1-240) individuals, and of Barnacle Geese 32.1 (range 1-350) individuals.

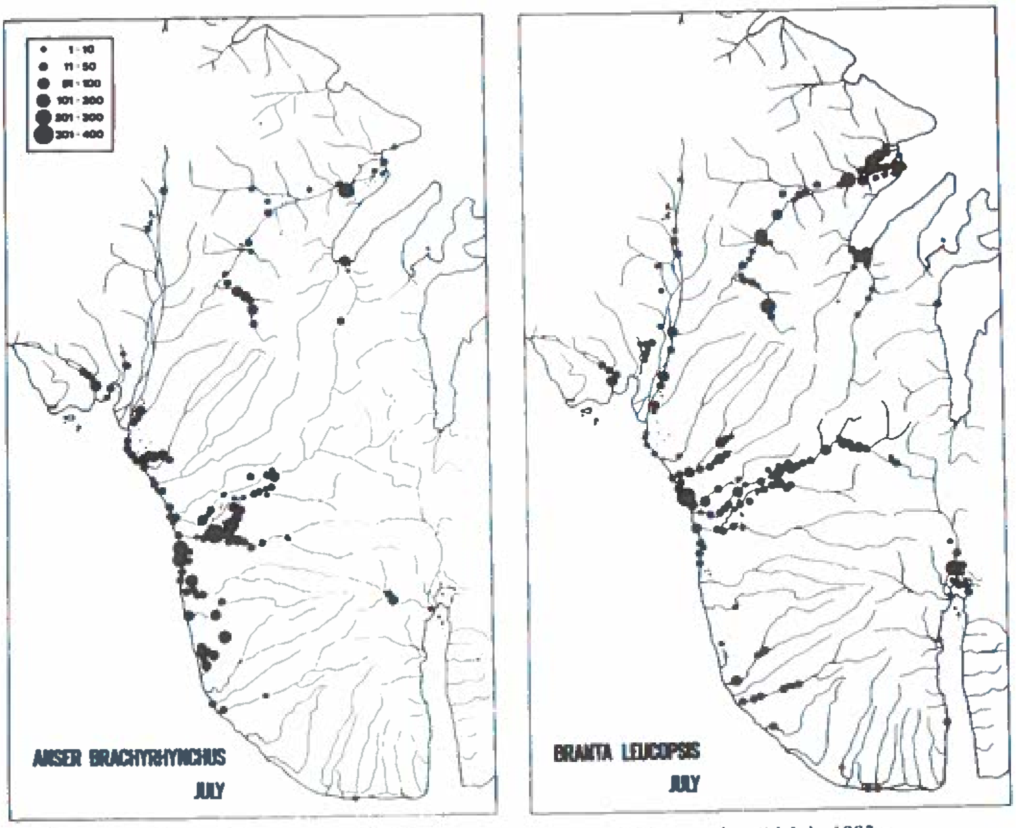


Fig. 4. Distribution of Pinkfeet and Barnacle Geese recorded by aerial survey in mid-July 1983.
Fordelingen af Bramgæs og Kortnæbbede Gæs ved flytælling i midten af juli 1983.

When the aerial survey in August 1983 was performed, the non-breeding geese had regained flight. The number of Pinkfeet was almost identical to the July number (Tab. 4), whilst the number of Barnacle Geese had declined from 6,140 to 1,340 individuals. The geese had abandoned the moulting grounds completely, and those remaining had dispersed to marshes not used during moult or to inland tundra areas (Fig. 5), especially on western Jameson Land, but also in Ørsted Dal, Fleming Fjord and the Hurry Fjord region. The mean flock size of Pinkfeet had declined significantly to 20.7 (range 2-75) individuals (χ^2=43.5, df=5, P(0.001), and the flock size of Barnacle Geese to 17.1 (range 1-150) individuals (χ^2=12.0, df=4, P(0.05).

Arrival of non-breeders and timing of moult

In 1984 the field season on Heden started prior to the arrival of the non-breeding geese. The populations of non-breeders of both species arrived on the moulting grounds between 23 June and 7 July (Fig. 6). The geese arrived in small flocks, and skeins at high altitudes were not seen at all. Mean flock size of Pinkfeet observed flying around in the area was 5.0 individuals (n=81, range 1-16), of Barnacle Geese 4.0 individuals (n=26, range 1-17). Flight activity peaked 21 June to 1 July for both species (Fig. 6).

The first Pinkfoot with shed remiges was seen on 30 June, but on the major moulting place in the area it was estimated that most geese were not in full moult until 6 July, about one week after peak arrival (Fig. 6). One flock of Barnacle Geese was in full moult on 30 June, 3-4 days after the arrival, whereas another flock was starting moult one week later.

The general impression from all three years is that there is high synchronisation of moult within flocks, but up to one week's variation between flocks. Generally, non-breeding Pink-

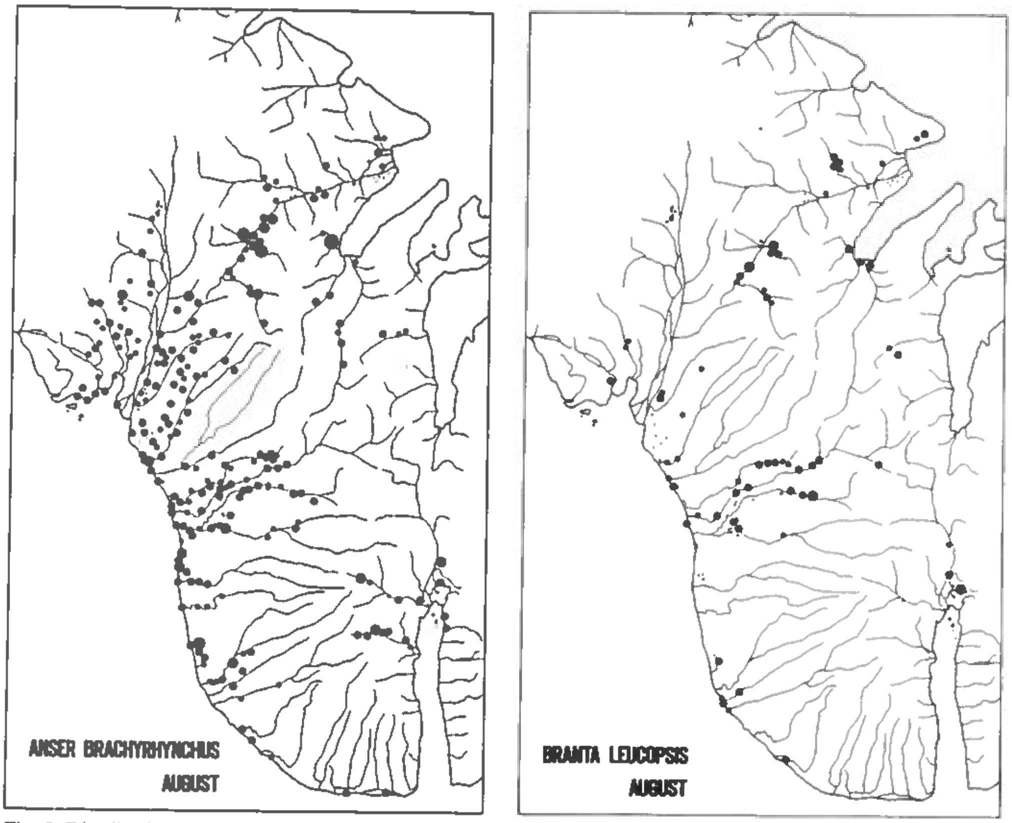


Fig. 5. Distribution of Pinkfeet and Barnacle Geese recorded by aerial survey by the end of August 1983. Scale as in Fig. 4.
Fordelingen af Bramgæs og Kortnæbbede Gæs ved flytælling i slutningen af august 1983. Skala som i Fig. 4.

feet initiate moult 5-10 July (range 29 June to 15 July) and regain flight 1-5 August (range 27 July to 10 August). The Barnacle Geese initiate moult 3-7 July (range 24 June to 8 July) and regain flight 26 July to 1 August (range 25 July to 3 August). In a flock of Barnacle Geese kept under observation throughout the flightless period, the geese regained flight in 23-25 days, which is in accordance with observations from Svalbard (Owen & Ogilvie 1979).

DISCUSSION

The surveys have revealed that Jameson Land is of prime importance as a moulting place as well as a breeding area for geese in East Greenland. In July the area houses 20-25% of the entire East Greenland population of Barnacle Geese. From data on population dynamics obtained on the wintering grounds on Islay in Scotland (Ogilvie 1983a) and on Inishkea in Ireland (Cabot & West 1983) it can roughly be calculated that about 1500 pairs in the population breed successfully each year. Jameson Land contributes with at least 150 pairs (10%) of the successfully breeding segment of the population.

Moulting concentrations of Barnacle Geese of the same size as recorded in Jameson Land are not known from other parts of the breeding range. In Hudson Land Hjort (1976) estimated the population (mostly non-breeders) at 1500 Barnacle Geese (1973), and from Germania Land and Hochstetter Forland flocks of 100-150 and 300, respectively, have been recorded (Meltofte 1975, Meltofte et al. 1981). The high numbers of moulting Barnacle Geese in Jameson Land in the southern part of the breeding range, and the fact that an immigration of non-breeding birds takes place in the second half of June, indicates that non-breeders undertake a moult migration in southerly directions. The exact origin of the non-breeders is unknown, and from literature there are no reports

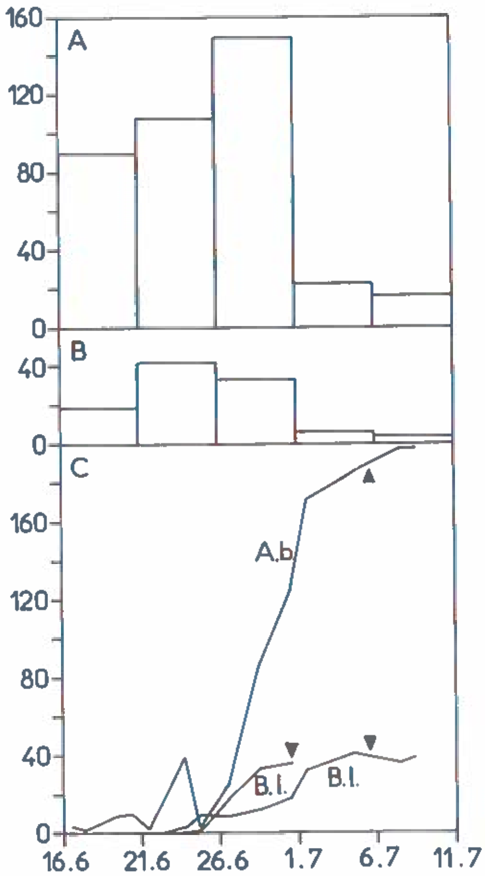


Fig. 6. Arrival of non-breeding geese on the moulting grounds on Heden, 1984. A: number of flying Pinkfeet observed in 5-day periods; B: do. Barnacle Geese; C: the build-up of moulting flocks of Pinkfeet (A.b.) and Barnacle Geese (B.I., two localities). Triangles indicate when most geese had shed remiges. *Ankomsten af ikke-ynglende gæs på fældningspladser på Heden i 1984. A: antal flyvende Kortnæbbede Gæs set i 5-dages perioder; B: do. Bramgæs; C: opbygningen af fældningsflokke af Kortnæbbede Gæs (A.b.) og Bramgæs (B.I.). Trekanter angiver hvornår de fleste gæs havde fældet svingfjerene.*

of south-migrating Barnacle Geese in June. Meltofte (1977) noticed that the numbers of non-breeders declined in June near colonies in Germania Land and suggested that they moved towards west. The immigrants to Jameson Land may come from colonies in the southern half of the breeding range, and the migration cannot be regarded as »genuine moult migration« (D III type, Salomonsen 1968), but rather as a smaller assembly of geese in a »local« moulting center (D II type, Salomonsen 1968). However, moult migration in a southerly direction is exceptional among goose populations, which usually undertake a northward moult migration (Salomonsen 1968, Owen 1980). The only hitherto known exceptions from this rule are small segments of German Greylag Geese *Anser anser* moving west (Ogilvie 1978) and East Siberian Brants *Branta bernicla* moving southeast to Alaska (Palmer 1976).

The number of moulting Pinkfeet in Jameson Land is likewise the highest recorded in Northeast Greenland. Other known concentrations are: 1000 in Germania Land (Meltofte 1975), 3000 on Hochstetter Forland (Meltofte et al. 1981), 1700 in Hudson Land (Hjort 1976), 1400 in the region between Hudson Land and Kong Oscars Fjord (Goodhart & Wright 1958) and 130 on Wollaston Forland (Rosenberg et al. 1970). With the proviso that the information stems from different years, the total number of moulting Pinkfeet accounted for in East Greenland, incl. Jameson Land, sums up to c. 12,000 geese. From data on population dynamics (Ogilvie 1978, 1983b) the non-breeding segment of the population is calculated to be c. 50,000 geese. In Iceland only 2-3000 non-breeding moulting geese have been observed (Gardarsson & Sigurdsson 1972), and the moult migration to East Greenland probably involves 40,000-50,000 geese. Thus only 25-30% of the moulting population is actually accounted for in East Greenland. However, immense areas in East Greenland are still unexplored by ornithologists.

Since 1961 goose counts have been carried out six times in mid-July in Ørsted Dal (Tab. 5). For the Barnacle Geese there is a good correlation between the number in the valley and in the entire population. In the period 1961-78 the total population increased from 14,000 to 34,000 geese, and since then the population has declined to 25,000 in 1983 (Ogilvie 1983a). The same trend is found in Ørsted Dal. For the Pinkfeet the development in the valley is not correlated to population development. Since 1961 the total population has increased from 59,000 to 90,000 individuals in 1982 (Ogilvie 1978, 1983b), while the population in Ørsted Dal has been fluctuating without significant trends. The Pinkfeet are extremely sensitive to human disturbance on the breeding and moulting grounds (Meltofte 1975, Meltofte et al. 1981, Madsen 1984), and the mere passage by

Flock of moulting Pink-footed Geese on a pond on Heden, Jameson Land, ult. July 1984. Staunings Alper are seen in the background. Photo: C. R. Olesen.
Flok af fældende Kortnæbbede Gæs på dam på Heden, Jameson Land, ult. juli 1984. I baggrunden ses Staunings Alper.

humans through the valley can make the geese abandon the area.

Several papers have concurrently reported on the northward moult migration in June (Conradsen 1957, Rosenberg et al. 1970, Meltofte 1975, 1976, 1977, Hansen 1981, Meltofte et al. 1981). Mean date of the first skein of geese seen is 20 June (n=7), of the last 6 July (n=6) (range 14 June to 12 July), and generally the migration culminates in the last days of June. Mean flock size varies between 16 and 27 individuals (range 2-100). In 1984 no migrating skeins were observed in the inland of Jameson Land, and the moulting population was gradually built up by small flocks of geese. This indicates that the migrating flocks have split up prior to dispersal to the moulting grounds, e.g. on staging areas along the coasts.

The time of arrival of the breeding populations of both species in spring is documented by several authors. Mean date of first sighting is 20 May for the Pink-footed Goose (range 9-29 May, n=14), and likewise 20 May for the Barnacle Goose (range 16-27 May, n=16) (Bay 1894, Pedersen 1926, 1930, Løppenthin 1932, Petersen 1941, Conradsen 1957, Rosenberg et al. 1970, de Korte 1973, 1974, de Korte & Bosman 1975, Meltofte 1975, 1976, 1977, Hansen

Tab. 5. Goose counts in Ørsted Dal, 1961-84.
Gåsetællinger i Ørsted Dal 1961-84.

	1961[a]	1963[b]	1974[c]	1982[d]	1983[e]	1984[e]
Anser brachyrhynchus						
Adults	300	225	394	970	449	325
Pulli	0	25	83	0	79	21
Branta leucopsis						
Adults	450	564	1518	1232	1360	1115
Pulli	23	172	170	49	116	87

Sources *Kilder*: a) Marris & Ogilvie (1962), b) Hall & Waddingham (1966), c) Ferns & Green (1975), d) present study, e) Cabot & Newton pers. comm. (present study).

1981, Meltofte et al. 1981), and the reports generally state that most geese arrive between 20 May and 5 June.

The hatching dates recorded in this study are in agreement with dates from other parts of the breeding ranges (Pinkfeet: Hardy 1979, Meltofte et al. 1981; Barnacle Geese: Madsen 1925, Rosenberg et al. 1970, Meltofte 1975, 1977). From the dates it is calculated that egg laying in both species is initiated in the first 10 days of June, which is in accordance with the observation by Meltofte et al. (1981) that Pinkfeet on Hochstetter Forland started egg laying from the end of May to 10 June (1976). Compared to the breeding schedule of Pinkfeet nesting in Iceland, the egg laying is approximately 10 days delayed (Scott et al. 1953, Inglis 1977).

The 40% success of nests found in Jameson Land in 1984 is similar to the success of Pinkfoot nests on Hochstetter Forland in 1976 (42%) (Meltofte et al. 1981). In Thjorsarver in Iceland Gardarsson (1976) found a hatching success of 58%, and Inglis (1977) a nest success of 59%, and also compared to other goose populations the success in East Greenland is low (see Tab. 6 in Ogilvie 1978). Predation by Arctic Foxes seem to be the main cause of the low success.

Following moult, the major part of the non-breeding Barnacle Geese left Jameson Land, while the Pinkfeet remained although they went to other habitat types (Madsen et al. 1984). Possibly the Barnacle Geese went to areas in the inner Scoresby Sund fiord.

For both species the emigration from East Greenland takes place from approximately 25 August to 15 September (Meltofte 1976, Madsen et al. 1984), but southward movements apparently start somewhat earlier (c. 10-20 August) in the northern ranges (Meltofte 1975, Meltofte et al. 1981). Parts of the populations probably congregate in the Scoresby Sund fiord region prior to emigration. Meltofte (1976) thus reported of hundreds of geese of both species migrating into the fiord system during late August and early September.

ACKNOWLEDGMENTS

J. Fjeldså, H. Meltofte, N.O. Preuss and H. Petersen are thanked for much advice throughout the studies. The staff at Mesters Vig airport are thanked for their kind hospitality. D. Cabot and S. Newton are thanked for good coorporation and communication of unpublished data.

DANSK RESUMÉ

Betydningen af Jameson Land, Østgrønland, som fældnings- og yngleområde for gæs: resultater af optællinger 1982-1984

I forbindelse med en planlagt olieeftersøgning i Jameson Land har Zoologisk Museum siden 1982 foretaget undersøgelser af Bramgæs og Kortnæbbede Gæs i området (Fig. 1 og 2). Et af formålene har været at vurdere områdets betydning for gæs og kortlægge bestandenes udbredelse.

Ved optællinger fra landjorden i to referenceområder (Fig. 2) samt ved flytællinger har det vist sig, at området især er fældningsområde. I juli huser området ca. 10-12.000 gæs, hvoraf anslået 92-94% er ikke-ynglende fugle (Tab. 1, 2 og 4). Antallet af ynglepar er anslået til 300-400 par Bramgæs og 300-500 par Kortnæbbede Gæs, men antallet af succesrige par er betydeligt lavere p.g.a. predation, især fra Polarræve.

Ikke-ynglende Kortnæbbede Gæs ankommer fra Island i slutningen af juni for at gennemgå svingfjersfældningen (Fig. 6). Samtidig ankommer Bramgæs fra det østgrønlandske område. I en 3-4 ugers periode er fuglene ude af stand til at flyve (Bramgæssene ca. 5.-28. juli, de Kortnæbbede Gæs ca. 7. juli til 1. august), hvor de koncentreres omkring elve, på søer og ved kysterne (Fig. 4). Efter endt fældning forlader de fleste Bramgæs området (Tab. 4, Fig. 5), hvorimod de Kortnæbbede Gæs forbliver indtil borttrækket til Island i begyndelsen af september.

Jameson Land er det største, kendte fældningsområde for Bramgæs i Østgrønland og et af de vigtigste yngleområder. I juli opholder 20-25% af den samlede østgrønlandske bestand (ca. 25.000) sig i området, og ca. 10% af ynglebestanden befinder sig her. Ligeledes er området det største, kendte fældningsområde for Kortnæbbet Gås i Østgrønland.

REFERENCES

Bay, E. 1894: Hvirveldyr. – Meddr Grønland 19(1): 1-51.

Bay, C. & S. Holt 1984: Botaniske undersøgelser i Jameson Land, 1983. – Report, Grønlands Fiskeri- og Miljøundersøgelser, Grønlands Botaniske Undersøgelser.

Cabot, D. & B. West 1983: Studies on the Population of Barnacle Geese *Branta leucopsis* Wintering on the Inishkea Islands, Co. Mayo. 1. Population Dynamics 1961-1983. – Irish Birds 2: 318-336.

Christensen, N.H. 1967: Moult migration of Pinkfooted Goose (*Anser fabalis brachyrhynchus* Baillon) from Iceland to Greenland. – Dansk Orn. Foren. Tidsskr. 61: 56-66.

Conradsen, F.R. 1957: Ornithologiske iagttagelser ved Daneborg, N.Ø. Grønland. – Dansk Orn. Foren. Tidsskr. 51: 12-18.

Ferns, P.N. & G.H. Green 1975: Observations of Pink-footed and Barnacle Geese in the Kong Oscar Fjord region of north-east Greenland, 1974. – Wildfowl 26: 131-138.

Gardarsson, A. 1976: Population and production of the Pink-footed Goose *(Anser brachyrhynchus)* in Thjórsárver, 1971-1974. – University of Iceland, Reykjavik (Icelandic with English summary).

Gardarsson, A. & J.B. Sigurdsson 1972: Rannsoknir a heidagaes *(Anser brachyrhynchus)* 1971, Adrar attruganir i Pjorsarverum 1971. – Icelandic National Energy Authority, Reykjavik.

Goodhart, J. & T. Wright 1958: North-east Greenland Expedition 1956. – Wildfowl Trust Ann. Rep. 9: 180-192.

Hall, A.B. 1963: Goose observations from Scoresby Land, 1962. – Wildfowl Trust Ann. Rep. 14: 94-97.

Hall, A.B. & R.N. Waddingham 1966: The breeding birds of Ørsted Dal, East Greenland, 1963. – Dansk Orn. Foren. Tidsskr. 60: 186-197.

Hansen, J.M. 1981: Hurry Fjord ekspeditionen 1979. Avifaunistical survey. – Report, Nat. Hist. Mus., Århus.

Hardy, D.E. 1979: Observations on geese of the Kong Oscars Fjord region of North-east Greenland, 1971. – Dansk Orn. Foren. Tidsskr. 73: 185-189.

Hjort, C. 1976: Notes on the bird fauna of Hudson Land and Hold With Hope, Northeast Greenland, 1973. – Dansk Orn. Foren. Tidsskr. 70: 35-44.

Inglis, I.R. 1977: The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. – Anim. Behav. 25: 747-764.

Korte, J. de 1973: Nederlandse Groenland Expeditie 1973. – Report, Inst. Taxonom. Zool., Amsterdam.

Korte, J. de 1974: Nederlandse Groenland Expeditie 1974. – Report, Inst. Taxonom. Zool., Amsterdam.

Korte, J. de & C. Bosman 1975: Nederlandse Groenland Expeditie 1975. – Report, Inst. Taxonom. Zool., Amsterdam.

Løppenthin, B. 1932: Die Vögel Nordostgrönlands zwischen 73°00' und 75°30'N.Br. – Meddr Grønland 91(6).

Madsen, C. 1925: Ornithologiske iagttagelser fra Østgrønland. I. Bramgaasen *Anser leucopsis.* – Dansk Orn. Foren. Tidsskr. 19: 33-37.

Madsen, J. 1984: Study on the possible impact of oil exploration on goose populations in Jameson Land, East Greenland: a progress report. – Norsk Polarinst. Skr. 181.

Madsen, J. & D. Boertmann 1982: Gåseundersøgelser i Jameson Land 1982. – Report, Grønlands Fiskeriundersøgelser. Zool. Mus., Copenhagen.

Madsen, J., D. Boertmann & C.E. Mortensen 1984: Gåseundersøgelser i Jameson Land 1983. – Report, Grønlands Fiskeri- og Miljøundersøgelser. Zool. Mus., Copenhagen.

Marris, R. & M.A. Ogilvie 1962: Ringing of Barnacle Geese in Greenland in 1961. – Wildfowl Trust Ann. Rep. 13: 53-64.

Marris, R. & A.H.F. Webbe 1969: Observations of birds in East Greenland, 1966. – Dansk Orn. Foren. Tidsskr. 63: 161-170.

Meltofte, H. 1975: Ornithological Observations in Northeast Greenland between 76°00' and 78°00'N. Lat. 1969-71. – Meddr Grønland 191(9).

Meltofte, H. 1976: Ornithological observations from the Scoresby Sund Area, East Greenland, 1974. – Dansk Orn. Foren. Tidsskr. 70: 107-122 (Danish with English summary).

Meltofte, H. 1977: Ornithological observations in Germania Land, Northeast Greenland, 1975. – Dansk Orn. Foren. Tidsskr. 71: 81-94 (Danish with English summary).

Meltofte, H., M. Elander & C. Hjort 1981: Ornithological observations in Northeast Greenland between 74°30' and 76°00'N. lat., 1976. – Meddr Grønland, Biosci. 3.

Ogilvie, M.A. 1978: Wild Geese. – Poyser, Berkhamsted.

Ogilvie, M.A. 1983a: The numbers of Greenland Barnacle Geese in Britain and Ireland. – Wildfowl 34: 77-88.

Ogilvie, M.A. 1983b: Numbers of geese in Britain and Ireland, 1982-1983. – Wildfowl 34: 172.

Owen, M. 1980: Wild Geese of the World. – Batsford, London.

Owen, M. & M.A. Ogilvie 1979: Wing molt and weights of Barnacle Geese in Spitsbergen. – Condor 81: 42-52.

Palmer, R.S. 1976: Handbook of North American Birds, Vol 2. – Yale Univ. Pr., New Haven.

Pedersen, A. 1926: Beiträge zur Kenntnis der Säugetier – und Vogelfauna der Ostküste Grönlands. – Meddr Grønland 68(3): 149-249.

Pedersen, A. 1930: Fortgesetzte Beiträge zur Kenntnis der Säugetier- und Vogelfauna der Ostküste Grönlands. – Meddr Grønland 77(5): 341-507.

Petersen, J. 1941: Dagbogsoptegnelser om Fuglenes Forekomst ved Scoresbysund Station fra Efteraaret 1934 til Sommeren 1935. – Dansk Orn. Foren. Tidsskr. 35: 123-125.

Ray, H.P.C. 1973: Some notes on the birds observed in the Kungmiut and Tugtilik Areas of East Greenland during the summer of 1967. – Dansk Orn. Foren. Tidsskr. 67: 43-52.

Rosenberg, N.T., N.H. Christensen & B. Gensbøl 1970: Bird observations in Northeast Greenland. – Meddr Grønland 191(1).

Salomonsen, F. 1968: The moult migration. – Wildfowl 19: 5-24.

Scott, P., J. Fischer & F. Gudmundsson 1953: The Severn Wildfowl Trust Expedition to Central Iceland, 1951. – Wildfowl Trust Ann. Rep. 5: 79-115.

Taylor, J. 1953: A possible moult-migration of Pink-footed Geese. – Ibis 95: 638-642.

MS received 31 August 1984

Authors' address:
Zoological Museum, Universitetsparken 15,
DK-2100 Copenhagen Ø

7

Forekomst og habitatvalg hos Mørkbuget Knortegås *(Branta bernicla bernicla)* i Danmark, og specielt Vadehavet

Occurrence of and habitat utilisation by the Dark-bellied Brent Goose (Branta bernicla bernicla) in Denmark, with special reference to the Danish Wadden Sea

Af Jesper Madsen, John Frikke og Karsten Laursen

DANSKE VILDTUNDERSØGELSER
HÆFTE 45

DANMARKS MILJØUNDERSØGELSER
AFDELING FOR FLORA- OG FAUNAØKOLOGI

Indhold

Indledning

Den mørkbugede knortegås *(Branta bernicla bernicla)* yngler langs den nordsibiriske Ishavskyst og trækker til Vesteuropa for at overvintre. Danmark ligger på den trækvej, bestanden benytter efterår og forår. Under efterårstrækket udgør de danske kyster gæssenes første rasteområde, hvor de forbliver i længere tid, inden trækket går videre til overvintringspladserne i Holland, England og Frankrig. Om foråret raster næsten hele bestanden i det hollandske, tyske og danske Vadehav inden trækket nordpå til ynglepladserne (St Joseph 1979a, Madsen 1987).

Forårsperioden er specielt betydningsfuld i gæssenes årscyklus, idet de forøger deres vægt kraftigt forud for den forestående ynglesæson. En række undersøgelser tyder på, at en tilstrækkelig opbygning af fedt- og næringsreserver om foråret er en forudsætning for, at gæssene kan gennemføre ynglesæsonen med succes (Ankney & MacInnes 1978, Ebbinge et al. 1982, Thomas 1983). Reserverne skal ikke blot bruges som brændstof under trækket, men også til ægdannelse og til at tære på i den første tid på ynglepladsen. Når gæssene ankommer til de højarktiske ynglepladser, er størstedelen af tundraen snedækket, og hunnen må gennemføre det meste af rugeperioden uden at tage føde til sig.

Bestanden af mørkbuget knortegås er steget fra ca. 40.000 fugle i begyndelsen af 1970'erne til 150.000-200.000 i 1980'erne (IWRB GOOSE RESEARCH GROUP unpubl.). Efter en god ynglesæson i 1988 steg bestanden til det hidtil højeste niveau, nemlig 235.000.

Analyser af omsætningsforholdene i bestanden tyder på, at fredningen af bestanden - specielt fredningen i Danmark fra 1972 bidrog væsentligt til stigningen (Prokosch 1984, Ebbinge 1985). Bestanden har nu muligvis nået et niveau, hvor antallet af ynglende fugle begrænses, og det kan forventes, at bestanden snart når »loftet« for sin udvikling (Ebbinge 1985). Hvilke faktorer i gæssenes årscyklus, der er afgørende for begrænsningen af bestanden, er endnu ikke klarlagt. Der mangler således bl.a. elementære undersøgelser af gæssenes økologi på de nordsibiriske ynglepladser.

Observationer fra flere hollandske og tyske forårsrastepladser (Ebbinge 1979 og upubl., Prokosch upubl.) samt fra Langli i det danske Vadehav (Madsen 1989) tyder på, at nogle af de saltmarskområder, som gæssene afgræsser, udnyttes maksimalt af knortegæssene.

En hollandsk undersøgelse viser desuden, at der er en væsentlig fødekonkurrence blandt de enkelte fugle i gåseflokken. Det kan resultere i, at visse individer ikke får mulighed for at opbygge tilstrækkelige næringsreserver til at gennemføre yngleperioden med held (Teunissen et al. 1985, Prop & Loonen 1989). Da forårsperioden ser ud til at have en afgørende betydning for gæssenes ynglesucces, kan saltmarskens bæreevne som fourageringsplads måske vise sig at være en af de afgørende, begrænsende faktorer for bestandens videre udvikling.

Formålet med dette hæfte er:

1) At give en status over den mørkbugede knortegås' forekomst og udnyttelse af forskellige habitattyper i Danmark i 1980'erne og derigennem opfølge en tidligere status for perioden 1966-1971 (Fog 1972).
2) At analysere forekomsten af mørkbugede knortegæs i Vadehavet i forhold til områdets bæreevne som fourageringsplads om foråret.

En sammenlignelig status for forekomsten og habitatvalget hos den lysbugede knortegås *(Branta bernicla hrota)* for 1980-1983 er givet af Madsen (1984).

En del oplysninger om gæssenes forekomst og habitatvalg er indsamlet i forbindelse med landsdækkende optællinger af gæs, som Dansk Ornitologisk Forenings gåsegruppe (nu den danske gåsearbejdsgruppe) har foretaget. I arbejdsgruppen indgår Dansk Ornitologisk Forening, Miljøministeriets Vildtforvaltning, Miljøministeriets Skov- og Naturstyrelse og Zoologisk Museum, København. Tællingerne i Vadehavet og de egentlige feltundersøgelser er led i Vildtbiologisk Stations undersøgelser af fuglelivet i området.

En tak skal rettes til de omkring 100 frivillige deltagere i gåsetællingerne. Uden deres entusiastiske indsats havde det ikke været muligt at give denne oversigt. Skov- og Naturstyrelsen takkes for data vedr. gæssenes græsning på Langli.

Materiale og metoder

Materialet til denne artikel er indsamlet i forbindelse med flere undersøgelser:

I perioden 1980-1983 udførte Dansk Ornitologisk Forenings gåsegruppe landsdækkende, midt-månedlige optællinger af rastende gæs i Danmark. I alt 104 lokaliteter blev dækket. De vigtigste lokaliteter for mørkbuget knortegæs er vist i Fig. 1. Ved hver optælling blev gæssenes fordeling på biotoptype registreret, og det blev noteret, om gæssene benyttede biotopen til fouragering eller hvile. På basis heraf er antallet af gåsedage på forskellige biotoptyper pr. måned og pr. sæson beregnet. Gåsedage udtrykker gæssenes udnyttelse af et område. Er der en dag talt 200 gæs og 10 dage efter 400 gæs, beregnes antallet af gåsedage i den mellemliggende periode til 300 gæs × 10

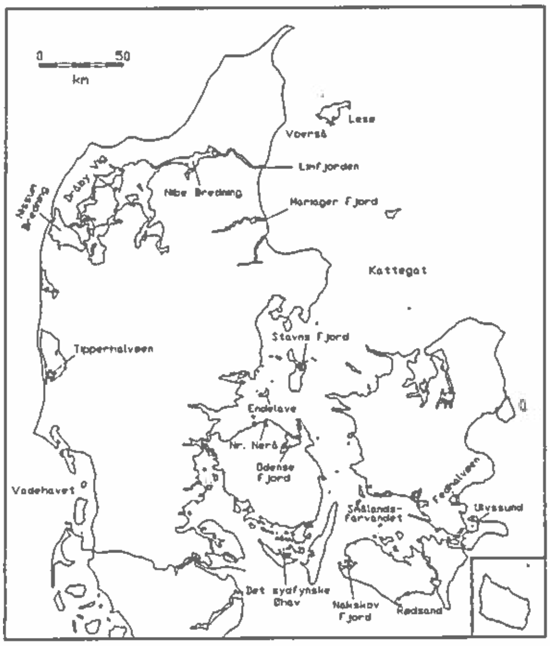


Fig. 1. De vigtigste rastepladser for mørkbuget knortegås i Danmark.
Fig. 1. Map of the most important haunts for the Dark-bellied Brent Goose in Denmark.

dage = 3.000. Arbejdet og metoden er beskrevet af Madsen (1986).

Siden efteråret 1979 har Vildtbiologisk Station gennemført månedlige optællinger af vandfugle fra fly i Vadehavet. Ved flytællingerne er Vadehavet opdelt i 65 delområder, som overflyves i løbet af en højvandsperiode. Metode og delresultater er beskrevet af Laursen & Frikke (i trykken).

Siden 1986 har den danske gåsearbejdsgruppe gennemført opgørelse af den samlede bestand af knortegæs i Danmark i januar og maj som led i International Waterfowl and Wetlands Research Bureau's (IWRB) årlige overvågning af knortegåsebestandens størrelse. Da knortegæssene i visse områder er svære at registrere fra landjorden, foretages tællingerne ved en kombination af fly- og landtællinger. Flytællingerne foretages af Vildtbiologisk Station.

For at belyse knortegæssenes græsningstryk på saltmarsken i Vadehavet blev der i forårene 1986-1988 optalt gåseekskrementer i forskellige marskområder (Fig. 2). I dagtimerne taber gæssene en fæces med 3,5 minutters mellemrum (Madsen upubl.), og tætheden af gåseekskrementer giver et godt udtryk for gæssenes udnyttelse af marskvegetationen.

I de pågældende områder blev der udvalgt en ensartet og sammenhæn-

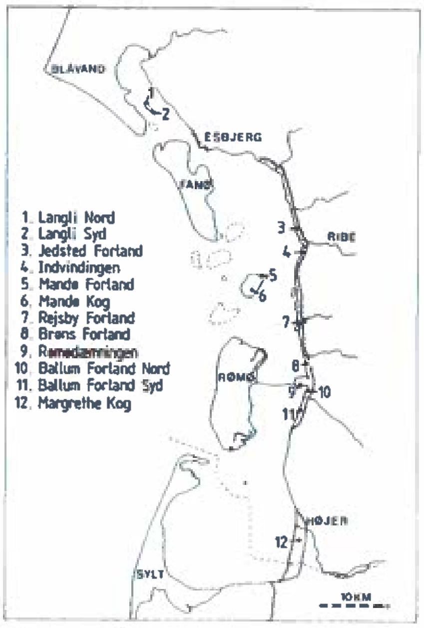


Fig. 2. Marsk- og kogsområder i Vadehavet, hvor der er optalt gåseekskrementer i forårene 1986-1988 (se Tabel 2).

Fig. 2. Salt marshes and polders in the Danish Wadden Sea, where goose dropping counts were performed in spring 1986-1988 (see Table 2).

gende zone, der var domineret af annelgræs *(Puccinellia maritima)*, som er gæssenes foretrukne fødeplante om foråret (Madsen 1989). Områderne blev valgt ud fra et forudgående kendskab til, hvor gæssene koncentreres. I hvert af saltmarksområderne blev der udlagt 10-40 felter på linie med en indbyrdes afstand på 20 m. Hvert felt blev afmærket med en lille træstok. Fra midten af marts til slutningen af maj blev der med 7-10 dages mellemrum optalt gåseekskrementer i en radius på 2 m omkring stokkene (svarende til et areal på 12,6 m²). Gåseekskrementerne blev enten fjernet eller »trådt ud«. For hvert felt er den sammenlagte tæthed af ekskrementer beregnet for forårsperioden.

Der blev foretaget optællinger af ekskrementer på i alt 10 saltmarskstrækninger samt i Margrethe Kog og Mandø Kog. På Langli blev der optalt ekskrementer i to saltmarskzoner i forårene 1986-1988 som led i en mere detaljeret undersøgelse af gæssenes græsning (Madsen 1989).

Temperatursummen, der er beregnet som summen af alle positive (+°C), daglige gennemsnitlige temperaturer fra 1. januar og fremefter, angiver vegetationens vækststart. Den dato, hvor temperatursummen er 200°C, er derfor beregnet for at se, om der er en sammenhæng mellem gæssenes antal i Vadehavet om foråret og marskvegetationens vækstbetingelser. Temperaturoplysninger til disse beregninger er hentet fra Sædden Strand meteorologiske station nord for Esbjerg.

Resultater

Tidsmæssig forekomst

De første mørkbugede knortegæs ankommer fra ynglepladserne til de danske rastepladser i midten af september (Fig. 3), hvilket også andre undersøgelser har vist (Fog 1967, Meltofte 1973, Møller 1978). Trækket kulminerer i oktober, og i december er de fleste knortegæs trukket bort igen. I milde vintre kan mørkbugede knortegæs overvintre i landet, men i kolde vintre fortrækker alle gæssene.

Trækket fra overvintringsområdet til de danske forårsrastepladser indledes i midten af marts, og antallet af rastende gæs kulminerer i maj. Trækket videre mod ynglepladserne sker i løbet af de sidste 14 dage af maj (Møller 1978, Madsen 1985a).

Antal og fordeling

I årene 1980-1983, da der blev foretaget månedlige, landsdækkende tællinger, var det maksimale antal mørkbugede knortegæs om efteråret 11.200-40.300, og gennemsnittet var 21.100.

Det tilsvarende forårsmaksimum varierede mellem 14.300 og 23.300 gæs med et gennemsnit på 16.000. I forårene 1986-1989 er der talt henholdsvis 19.400, 14.700, 12.700 og 23.800.

I januar 1980-1983 og 1986-1989 har bestanden varieret mellem 0 og 5.400 - afhængigt af temperaturen.

Ved landsdækkende optællinger af vandfugle fra fly i oktober/november 1987 og 1988 er der talt hhv. ca. 9.000 og 7.000 mørkbugede knortegæs (Laursen et al. 1988, 1989). Efterårstallene de to sidste år har således været betydeligt lavere end i perioden 1980-1983. Hovedårsagen til tilbagegangen på landsbasis er et lavere antal end tidligere i Vadehavet (se side 13).

Der er stor regional forskel i såvel antal som tidsmæssig fordeling af de mørkbugede knortegæs (se Fig. 3 og 4). I det følgende redegøres for forekomsten i de regioner, hvor der traditionelt forekommer knortegæs (se Fig. 1). Hvor der indgår flere lokaliteter i regionen, er det højeste, månedlige, gennemsnitlige antal for perioden 1980-1983 angivet i parentes (efter Madsen 1986).

Østersøen incl. Det sydfynske Øhav. Østersølokaliteterne omfatter Smålandsfarvandet (>200), Nakskov Fjord (150), Hyllekrog/Rødsand syd for Lolland (>200), Ulvssund (550), Ulvshale og Nyord på Møn (200). Disse lokaliteter er, sammen med Lunkebugten på Sydfyn (700), rastepladser for knortegæssene under trækket i september-oktober. På dage i oktober kan flere tusinde knortegæs opholde sig nord og syd for Lolland, men gæssene opholder sig tilsyneladende kun kort tid på lokaliteterne, og der sker en stor udskiftning af fugle.

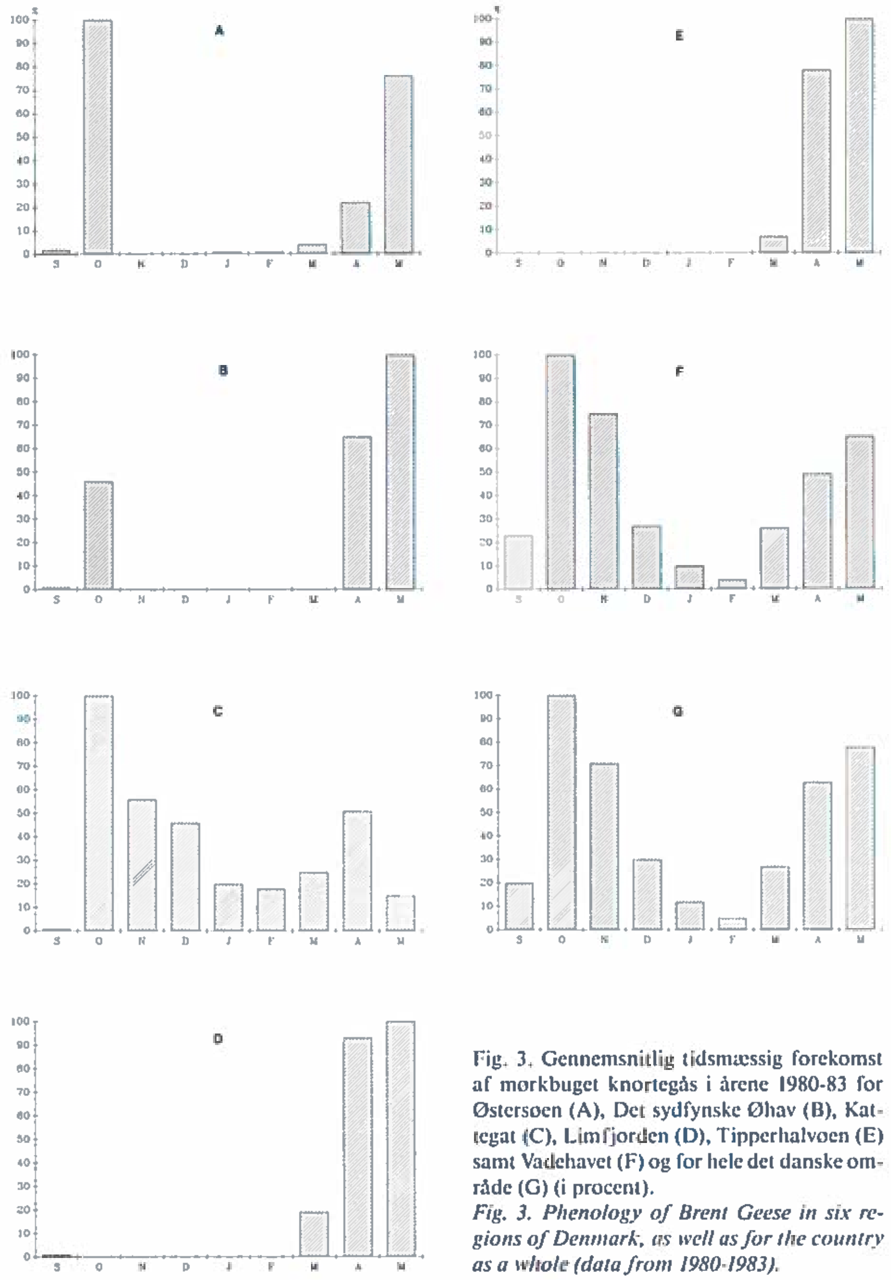


Fig. 3. Gennemsnitlig tidsmæssig forekomst af mørkbuget knortegås i årene 1980-83 for Østersøen (A), Det sydfynske Øhav (B), Kattegat (C), Limfjorden (D), Tipperhalvøen (E) samt Vadehavet (F) og for hele det danske område (G) (i procent).

Fig. 3. Phenology of Brent Geese in six regions of Denmark, as well as for the country as a whole (data from 1980-1983).

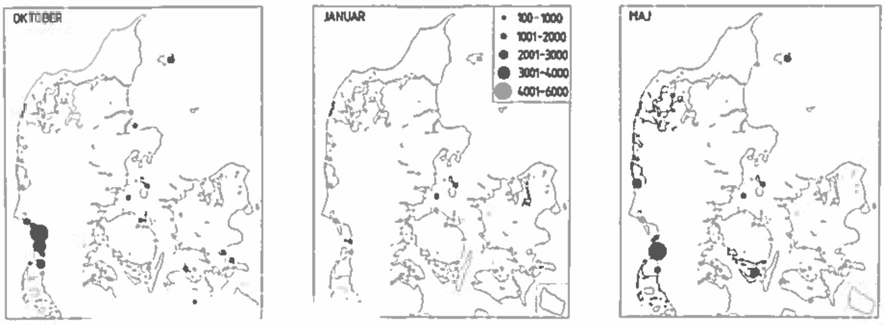


Fig. 4. Gennemsnitlig fordeling af mørkbuget knortegås i oktober, januar og maj for årene 1980-83.
Fig. 4. The average distribution of Brent Geese in October, January and May during 1980-83.

I april-maj raster der 1.500-2.000 knortegæs i Det sydfynske Øhav (i 1989 4.000), koncentreret omkring de ubeboede holme Store Egholm, Bredholm, Storeholm og Hjortø.

Holmene i Nakskov Fjord og Hyllekrog samt Ulvssund er forårsrastepladser for 2-300 knortegæs (i 1989 2.100).

Kattegat. Lokaliteterne i Kattegat omfatter Læsø (1.960), Voerså-Stensnæs (90) og kysten fra Mariager Fjord til Store Sjørup Strand i Ålborg Bugt (300), Stavns Fjord på Samsø (380), Endelave (340), Odense Fjord (460) og Nørre Nærå Strand på Nordfyn (190).

Kattegatøerne og de nordfynske lokaliteter er de nordligste overvintringspladser for den mørkbugede knortegås (Fig. 4). I milde vintre kan der stå op til 2.000 gæs. Odense Fjord og Nørre Nærå Strand er vinterrastepladser; på de øvrige lokaliteter forekommer knortegæssene på alle tider fra september til maj.

Tipperhalvøen. Tipperne, Værnengene, Nymindestrømmen og Havrvig Grund i den sydlige del af Ringkøbing Fjord (2.540) udgør en samlet rasteplads, som næsten udelukkende benyttes om foråret (Fig. 3). Forekomsten og den historiske udvikling i knortegåsebestanden på Tipperhalvøen er beskrevet af Madsen (1985a).

Limfjorden. Dråby Vig på Mors (385) er en fast forårsrasteplads. Småflokke af mørkbugede knortegæs kan ses blandt de lysbugede knortegæs, som raster på det sydvestlige Mors (Madsen 1984).

I Nissum Bredning og Nibe Bredning kan småflokke (op til 50) forekomme om efteråret.

Vadehavet. Samlet udgør Vadehavet det vigtigste danske rasteområde for de mørkbugede knortegæs. For årene 1980-1983 tilbragte knortegæssene gennemsnitligt 2,2 mio. gåsedage her i landet igennem en sæson; deraf de 75% i Vadehavet.

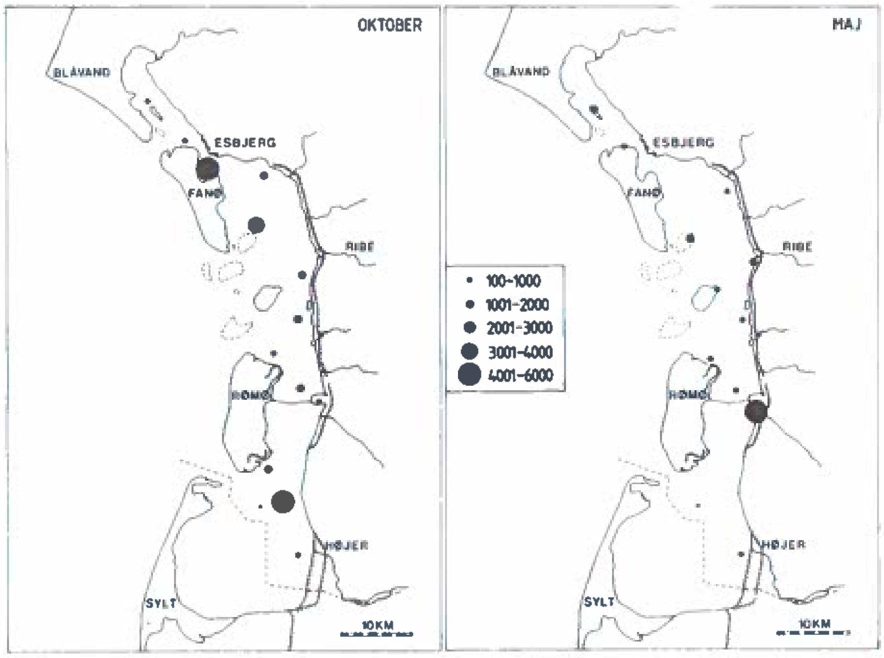


Fig. 5. Gennemsnitlig forekomst og fordeling af mørkbuget knortegås i det danske Vadehav i oktober (a) og maj (b) for årene 1980-88.

Fig. 5. The average distribution of Brent Geese in the Danish Wadden Sea October (a) and May (b) (data from 1980-1988).

Om efteråret forekommer de største flokke af knortegæs ved Søjord (2.100) og Albuebugten-Keld Sand (3.500) på østkysten af Fanø, ved Mandø Låningsvej (1.300), nord for Rømø (1.300) og ved Koldby Leje ved Jordsand Flak (1.100) (Fig. 5a,b).

Om foråret er knortegæssene fordelt anderledes. Det kan forbindes med deres habitatvalg (se side 14). De største flokke forekommer ved Ballum Forland og Rømødæmningen (6.300), Langli (1.200), Indvindingen syd for Kammerslusen (800) og i opgrøden på Keld Sand (800).

Ud fra flytællinger, der er foretaget om efteråret og foråret siden 1980, er det muligt at sammenligne udviklingen i antallet af rastende knortegæs i Vadehavet med den totale bestands størrelse og ungeproduktion i den forudgående ynglesæson. En sådan analyse vil kunne vise de første tegn på, hvorvidt antallet af gæs i Vadehavet er begrænset.

I årene 1980-1988 har totalbestanden varieret mellem 130.000 og 235.000 (se Fig. 8); andelen af unge fugle i bestanden har været mellem 0 og 50%. Det maksimalt optalte antal i Vadehavet om efteråret svingede mellem 3.700 og 34.900 – om foråret

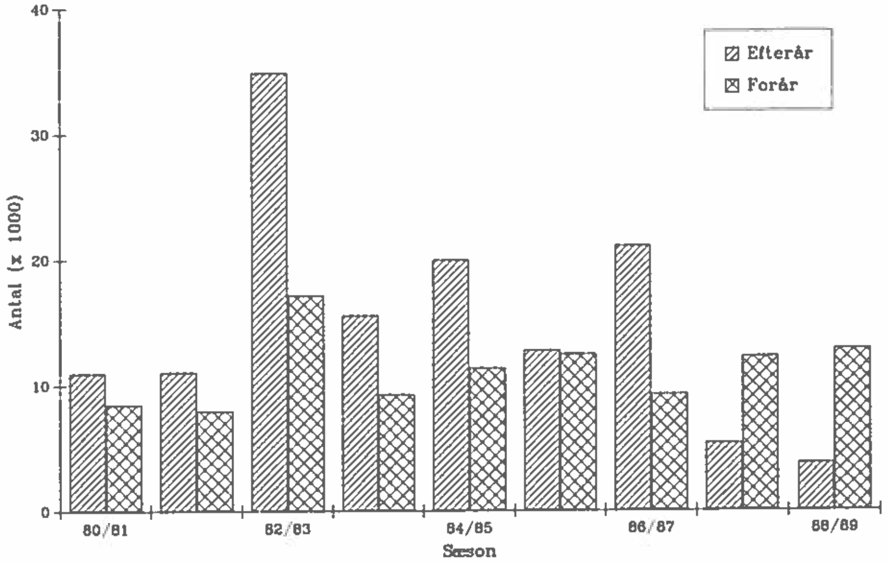


Fig. 6. De højest registrerede antal mørkbugede knortegæs efterår og forår i det danske Vadehav 1980-1988.

Fig. 6. Maximum number of Brent Geese observed in the Danish Wadden Sea autumn (black columns) and spring (hatched columns), 1980-1988.

mellem 8.000 og 17.200 (Fig. 6).

Data fra før 1980 er i sammenligningen udeladt, idet bygningen af det fremskudte dige ved Højer betød en væsentlig miljøforandring, som også berørte forekomsten af knortegæs (se s. 20-21). Siden 1980 har der ikke været påført området væsentlige, menneskeskabte forandringer, der kan tænkes at påvirke knortegæssene.

Udsagn på baggrund af kun ni sæsoners materiale må naturligvis blive forsigtige. En undersøgelse af sammenhæng mellem de fire ovennævnte forhold vha. korrelationsanalyse, der tester den indbyrdes indflydelse af de observerede størrelser (se Tabel 1) viser, at der generelt set er en positiv indbyrdes sammenhæng mellem den samlede bestands størrelse, andelen af unge gæs og forårsbestandens størrelse i Vadehavet.

Efterårsbestandens størrelse hænger imidlertid mindre tydeligt sammen med de tre andre forhold. Skønt der er en positiv gensidig sammenhæng mellem efterårs- og forårsbestandens størrelse, så afspejler Fig. 6, at efterårsbestanden har varieret betydeligt mere end forårsbestanden, der har holdt sig på et niveau omkring 10.000 gæs.

På øen Langli blev der i forårene 1986-1988 fundet en betydelig variation fra år til år såvel i gæssenes af-

Tabel 1. Indbyrdes sammenhæng mellem den samlede knortegåsebestands størrelse, ungeproduktion og antallet i Vadehavet efterår og efterfølgende forår i 1980'erne (n=9), udtrykt ved korrelationskoefficienten r. *: P<0,01. Parentesen omkring r-værdien for korrelationen mellem den samlede bestand og % juvenile angiver, at de to variable ikke er indbyrdes uafhængige.
Table 1. Relationship between the size of the total Brent Goose population, the proportion of juveniles, and the autumn and spring numbers in the Danish Wadden Sea in the 1980's (n=9), expressed by the correlation coefficient r. The r value for the correlation between the total population and % juveniles is in bracket, indicating that the two variables are not independent.

	Samlet bestand	% ungfugle	Vadehav efterår	Vadehav forår
Samlet bestand	-	(0,740)	0,054	0,646
% juvenile		-	0,285	0,825*
Vadehav efterår	-	-	-	0,452

græsningstryk som i deres antal (Tabel 2 i Madsen 1989). Det var sandsynligvis forårsaget af forskelle i græssernes vækstbetingelser pga. vejrforholdene. Men for Vadehavet som helhed ses en sådan sammenhæng ikke. En analyse af sammenhængen mellem antallet af gæs i Vadehavet om foråret 1981-1989 og den dato, hvor temperatursummen når 200°C, viser ingen sammenhæng ($r=0,102$, $P>0,05$). Det betyder sandsynligvis, at den variation, der observeredes i gæssenes antal på Langli, udlignes over de andre lokaliteter i Vadehavet; gæssene omfordeles inden for Vadehavet.

Habitatvalg

Gæssenes overordnede fordeling på habitattyper i løbet af sæsonen, baseret på registreringerne i årene 1980-1983, er vist i Fig. 7.

Om efteråret søger knortegæssene næsten udelukkende føde på fladvand og vade. Gæssenes føde består af ålegræs og andre marine undervandsplanter samt grønalger, som hentes ved svømmefouragering eller afgræsning af vade ved lavvande.

I november og i vintermånederne bevæger en del af gæssene sig ind på strandengene for at søge føde, men frem til og med marts sker fourageringen stadig overvejende på fladvand og vade.

I forårsmånederne sker der et gradvist skift til fouragering på strandenge og vedvarende, ferske græsarealer. Udnyttelsen af de vedvarende græsarealer forekommer næsten udelukkende på Tipperhalvøen i Ringkøbing Fjord.

I Vadehavet fordeler knortegæssene sig forskelligt efterår og forår. Om efteråret søger de føde ude på vadefladerne, mens de om foråret næsten udelukkende går inde på saltmarsken.

Denne habitatfordeling er stort set forekommet uændret frem til 1989, men et par ændringer, hvor gæssene har skiftet fra de traditionelle, mere

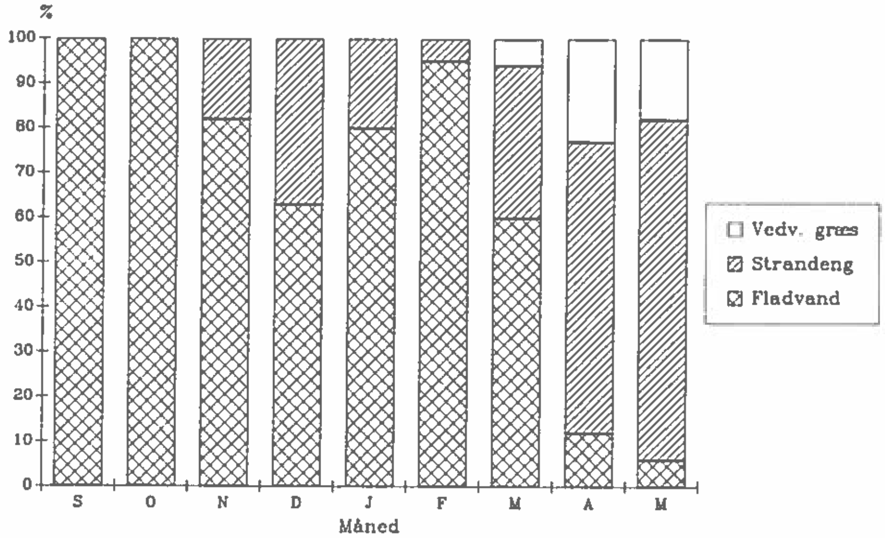


Fig. 7. Habitatfordeling af mørkbugede knortegæs. Antallet af gåsedage, der er tilbragt med fouragering på 1) vedvarende græs, 2) strandeng og 3) fladvand/vade er angivet i procent pr. måned.
Fig. 7. Brent Goose habitat distribution during a season, expressed by the proportion of goose-days spent foraging in a given habitat (data from 1980-1983). Double-hatched: shallow-water and mudflat, hatched: salt marsh, open: rough pasture.

eller mindre naturlige biotoptyper til dyrkede arealer, bør fremhæves.

Siden efteråret 1984 er flokke på op til 1.000 knortegæs registreret på vintersædsmarker på Fedhalvøen i Præstø Fjord. Græsningen har i to efterår været så intens, at gæssene er forsøgt bortskræmt for at beskytte afgrøderne.

Siden foråret 1985 har en flok knortegæs søgt føde inden for digerne på Mandø. I foråret 1987 og 1988 gik der 5-600 gæs på græsarealer, der benyttes til kreatur- og fåregræsning i juni-oktober. Gæssene er forsøgt bortskræmt for at forhindre dem i at tage den vegetation, som var tiltænkt kreaturerne.

Græsningsintensitet i Vadehavet

Tællingerne af gåseekskrementer i saltmarskområderne og i kogene i forårene 1986-1988 er – sammen med angivelse af arealernes størrelser og landbrugsmæssige udnyttelse – samlet i Tabel 2.

De gennemsnitlige, sammenlagte tætheder for forårssæsonen varierede fra 0 til 65 gåseekskrementer pr. m^2 for forsøgsfelterne. De største sammenlagte tætheder for en sæson blev fundet i saltmarsken på Langli, efterfulgt af Mandø Kog, det sydlige Ballum Forland og Indvindingen (1987).

I 1986 blev gæssene på Indvindingen skræmt bort af en duehøg *(Acci-*

Tabel 2. Knortegæssenes udnyttelse af 10 marsk- og to kogsområder, udtrykt ved ekskrementtætheder i løbet af foråret, sammenholdt med områdernes areal, bredde og landbrugsmæssige udnyttelse. N angiver antallet af optællingsfelter. Udnyttelsesgraden er udtrykt som 1: ingen, 2: ekstensiv (< 1 kreatur/3 får pr. ha), 3: intensiv (1-1,5 kreaturer/3-6 får pr. ha) og 4: meget intensiv (> 1,5 kreatur/6 får pr. ha); k: kreatur, f: får. Data vedr. areal og udnyttelse er fra Frikke (1987 og upubl.).

Table 2. Brent Goose usage of 10 salt marshes and two polders (nos. 6 and 12) in the Danish Wadden Sea during the spring staging period, expressed by cumulative dropping densities in Puccinellia maritima dominated marsh zones, and related to size, width and agricultural usage of the areas. N gives the number of sample plots (12.6 m^2 each). The degree of usage is expressed as 1: no usage, 2: extensive (< 1 cattle/3 sheep per ha), 3: intensive (1-1.5 cattle/3-6 sheep per ha), and 4: very intensive (> 1.5 cattle/6 sheep per ha); k: cattle, f: sheep.

		Sammenlagte antal gåseekskrementer pr. m^2			Arealdata		
Lokalitet	År	Gennemsnit	Maksimum	N	Areal (ha)	Bredde (km)	Udnyttelse
1. Langli Nordmarsk	1986	57,3	76,7	10	20	0,3	1
	1987	31,4	38,1	10			
	1988	64,6	81,1	10			
2. Langli Sydmarsk	1986	50,1	71,1	10	30	0,5	1
	1987	29,5	44,0	10			
	1988	45,6	53,2	10			
3. Jedsted Forland	1986	0,2	1,1	30	210	0,8	4 k/f
4. Indvindingen	1986	7,4	11,9	22	130	0,7	2 k
	1987	14,6	17,0	20			
5. Mandø Forland	1987	2,2	5,2	10	250	0,6	2 f
6. Mandø Kog Syd	1987	30,0	37,8	14	300	0,8	3 k/f
7. Rejsby Forland	1986	0,0	0,0	13	180	0,6	4 k/f
8. Brøns Forland	1986	2,8	5,8	24	340	1,0	2 k/f
9. Rømødæmningen	1986	10,3	22,8	36	120	0,7	3 f
10. Ballum Forland Nord	1986	6,6	14,2	30	90	0,8	3 f
11. Ballum Forland Syd	1986	20,7	26,2	12	250	0,9	3 f/k
12. Margrethe Kog	1986	2,2	5,7	40	40	0,5	2 f

piter gentilis), der slog mindst fire knortegæs (Madsen 1988a), og tætheden af ekskrementer var derfor lavere på dette forland, end det kunne forventes ud fra antallet af gæs i de forudgående sæsoner.

Annelgræszonen i Margrethe Kog udnyttedes kun lidt af knortegæssene. På Brøns, Rejsby, Jedsted og Mandø forlande foretog knortegæssene ligeledes kun ringe eller ingen afgræsning.

Et groft udtryk for græsningsintensiteten kan opnås ved at beregne antallet af gåsedage pr. ha saltmarsk i løbet af et forår. I forårene 1986-1988 var knortegæssene i gennemsnit 995 gåsedage pr. ha på Langli. På Ballum Forland og Rømødæmningen blev der tilbragt 450 gåsedage pr. ha, på Indvindingen 210 og på Mandø Forland 95. Disse værdier svarer således godt overens med de resultater, der er opnået ved tællingerne af gåseekskrementer.

Diskussion

Den mørkbugede race af knortegåsen benytter primært de danske rastepladser under efterårs- og forårstrækket. I oktober står der i Danmark på et givent tidspunkt 12% af den samlede knortegåsebestand (dog passerer den overvejende del af bestanden gennem landet på vej mod overvintringsområderne), i januar 2% og i april-maj 11% (i beregningen er der ikke taget højde for vinterdødelighed i bestanden).

I maj 1966-1971 taltes i gennemsnit omkring 4.000 mørkbugede knortegæs i Danmark (Fog 1972). I perioden frem til 1980'erne er den rastende forårsbestand firedoblet, mens den samlede bestand er femdoblet (Fig. 8). Stigningstakten har således været næsten den samme i den danske delpopulation og den samlede population. Dette kan udlægges sådan, at der i dette tidsrum ikke har været specielle forhold, der har begrænset bestanden på de danske rastepladser.

Under opholdet i Danmark udnytter knortegæssene naturlige habitater (fladvand/vade) og delvist naturlige habitater (strandenge og vedvarende græsarealer). Kun lokalt er der forekommet flokke, som fouragerer på opdyrkede arealer. Det observerede skifte fra fladvand/vade til strandeng i løbet af sæsonen ses også i Holland (Ebbinge & Boudewijn 1984) og England (Ranwell & Downing 1959, Charman & Macey 1978), mens knortegæssene i Frankrig næsten udelukkende fouragerer på vader (Maheo 1976). I Holland og England skifter gæssene først til strandenge, men siden også til græsarealer bag digerne og, specielt i England, til vintersædsmarker (St Joseph 1979b, White-Robinson 1982). Fouragering bag digerne startede i Sydengland i midten af 1970'erne og er taget til i takt med bestandens stigning.

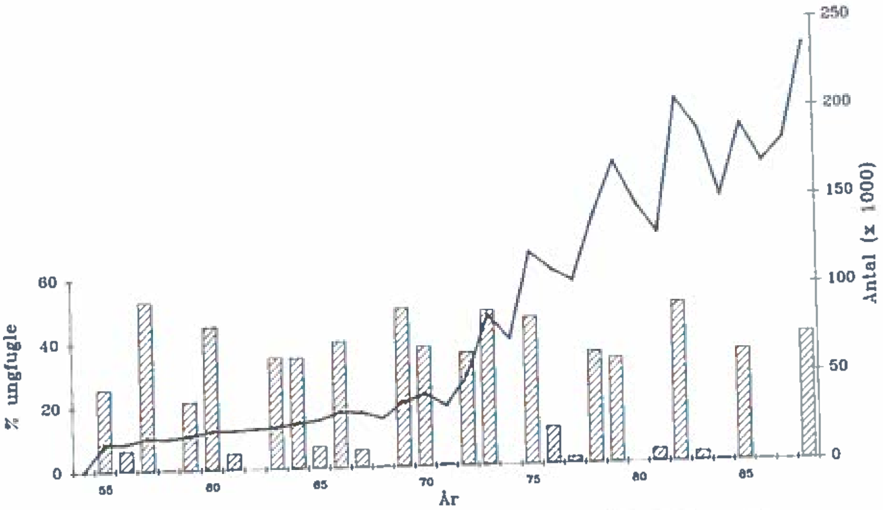


Fig. 8. Den samlede bestand af mørkbuget knortegås 1955-1988 (kurve) og andelen af ungfugle i % (søjler) (IWRB GOOSE RESEARCH GROUP upubl.). Andelen af ungfugle varierer meget fra år til år, hvilket giver sig udslag i variation i bestandens størrelse.
Fig. 8. Development of the Dark-bellied Brent Goose population, 1955-1988 together with the proportion of juveniles in the population.

Habitatskiftet ser ud til at være forårsaget af, at føderessourcerne på vaderne mindskes pga. naturlig hendøen og gæssenes græsning. I et af de største ålegræsbede i Vadehavet, Koldby Leje ved Jordsand Flak, konsumerede knortegæs og pibeænder *(Anas penelope)* næsten al tilgængelig ålegræs i løbet af efteråret, dvs. hvad der var af ålegræs efter naturlig hendøen (Madsen 1988b). Lignende resultater er fundet i det hollandske Vadehav (Jacobs et al. 1981) og i et par engelske vadeområder (Charman 1979, Tubbs & Tubbs 1983).

For det danske Vadehavs vedkommende foreligger der kun målinger af ålegræssets udbredelse og biomasse i Koldby Leje. Da ålegræsbedenes udstrækning og størrelse i det øvrige Vadehav ikke kendes og derfor er baseret på formodninger, kan vi ikke generelt konkludere, at antallet af knortegæs er begrænset af fødemængden, og vi kan ikke entydigt forklare årsagerne til svingningerne i efterårsbestandens størrelse.

I efterårene 1987 og 1988 blev der iagttaget usædvanlig få knortegæs i Vadehavet, og observationer fra det nordlige Vadehav tyder på, at ålegræsset var forsvundet fra store flader, som plejer at være vegetationsdækket (K. Fischer pers. medd.). Det efterlader det indtryk, at der er en sammenhæng mellem antallet af gæs og fødemængde, men der mangler dokumentation for dens eksistens.

Fra undersøgelsen i Koldby Leje er

det endvidere klart, at vadejagten efter ænder kan forstyrre de jagtfredede knortegæs, og at den kan medvirke til at fordrive gæssene fra et område. I ét af to undersøgelsesår var jagtintensiteten så høj, at ænderne og de fleste knortegæs forlod området lang tid før føderessourcerne var ædt op (Madsen 1988b).

Størrelsen af forårsbestanden i Vadehavet har ikke udvist de samme store svingninger som efterårsbestanden. Ifølge de optællinger, som IWRB foretager af den samlede bestand i januar og maj, er der ubetydelig forskel i de vurderinger af bestandene, der er opnået ved de to tællinger (IWRB GOOSE RESEARCH GROUP upubl.). Den mindre variation, der ses i Vadehavet om foråret, kan derfor ikke alene tilskrives vinterdødelighed.

Resultatet af undersøgelsen på Langli viste, at saltmarskens bæreevne for knortegæs i et forår med gode vejrforhold er lige ved at være nået med en græsningsintensitet, der svarer til, at gæssene producerer gennemsnitligt 65 ekskrementer pr. m^2 igennem foråret, svarende til ca. 1.000 gåsedage pr. ha (Madsen 1989). Denne værdi er i overensstemmelse med de resultater, der er fundet på de mest intensivt afgræssede hollandske rastepladser. Det har også fået hollandske forskere til at mene, at bæreevnen dér er nået (Ebbinge & Boudewijn 1984).

De øvrige forårsrastepladser i Vadehavet synes imidlertid ikke at være »fyldt op« med gæs. På Ballum Forland, der er den største rasteplads i Vadehavet, er græsningsintensiteten kun halvt så stor som på Langli, og på de resterende rastepladser er den endnu lavere. Jedsted Forland er formentlig ikke en velegnet forårsrasteplads pga. mange kreaturhegn, som indskrænker gæssenes brug af området, idet de ikke bevæger sig tæt på hegnene (Madsen 1985b). Rejsby Forland er formentlig heller ikke velegnet, idet annelgræszonen er smal og ligger tæt på diget, som synes at have en skræmmende effekt på gæssene. Det samme gør sig sandsynligvis gældende for annelgræszonen i Margrethe Kog.

Derimod er der øjensynligt ingen hindringer for, at gæssene kunne udnytte Indvindingen, Brøns og Mandø Forland i samme omfang som Ballum eller Langli. Et særdeles velegnet forland ud for Gammel Hviding benyttes af uforklarlige grunde – overhovedet ikke af knortegæssene. Det er bemærkelsesværdigt, at de mest intensivt gåsegræssede saltmarksområder findes på Langli, hvor der ikke har været kreatur- og fåregræsning siden 1981.

Der er ingen umiddelbart indlysende sammenhæng mellem gæssenes græsningsintensitet og den landbrugsmæssige udnyttelse af saltmarsken. Den høje intensitet på Langli skyldes måske et samspil med andre faktorer, f.eks. niveauet af forstyrrelser. På Langli, der er naturreservat, er der minimal menneskeskabt uro, hvorimod der på forlandene er nogen færdsel i forbindelse med tilsyn af får, kreaturer, diger m.v. samt mennesker, der færdes til fods. Observationer af den menneskelige færden på forlandene tyder imidlertid ikke på, at den kan være af afgørende betydning (Laursen 1982).

Der er store forskelle på saltmarsken i det danske og slesvig-holstenske Vadehav, hvor de største forårskoncentrationer af knortegæs findes (Prokosch 1984). De tyske marskområder er generelt bredere, og afgræsningen med især får er mere intensiv. Vegetationen er holdt lav som på en golfbane og domineret af planter, som tåler græsning, især annelgræs (Prokosch & Kempf 1987). Den kortere og afgræssede vegetation er en fordel for græssende knortegæs, fordi de lettere kan færdes i den og fordi andelen af dødt materiale er mindre end i en mindre intensivt græsset vegetation (Boudewijn 1984, Lorenzen & Madsen 1985).

Indtrækket af knortegæs til kogen på Mandø er sandsynligvis ikke opstået pga. direkte fødemangel på forlandene, men snarere som følge af, at kulturgræsserne spirer tidligere på foråret og derfor er mere attraktive end strandengsgræsserne tidligt på sæsonen (Lorenzen & Madsen 1985). Det skulle forventes, at gæssene ville vende tilbage til forlandet senere på foråret, når græsserne begynder at spire dér. Det gør de da også i nogen grad, men græsningen i kogen fortsætter frem til midten af maj. I Holland optræder der flokke af knortegæs, som udelukkende søger føde på kulturgræsarealer om foråret (Ebbinge & Boudewijn 1984). Det tyder på, at gæssene ikke er absolut afhængige af strandengsvegetationen til opbygning af næringsreserverne.

Der er ikke foretaget egentlige målinger af, hvor stor en andel af græsproduktionen gæssene æder i kogen på Mandø. Det er sandsynligt, at græsningseffekten er målelig i de mest intensivt afgræssede parceller på det tidspunkt, hvor kreaturerne sættes ud. Men da gæssene kun afgræsser et begrænset areal i kogen intensivt, vurderes belastningen at være ubetydelig for kogen som helhed. Et forhold, der kan kompensere for effekten af afgræsningen, er, at gæssenes ekskrementer gøder vegetationen, så græsproduktionen forøges (Madsen 1989).

Bygningen af det fremskudte dige ud for Højer og Rodenäs medførte, at den rastende forårsbestand på omkring 7.000 mørkbugede knortegæs stort set ophørte med at benytte den danske del af området (Laursen et al. 1984). Gæssene flyttede bl.a. til Ballum Forland, hvor bestanden mere end fordobledes i forhold til perioden før digebyggeriet. På den tyske side forblev en del af flokken i området, mens en del gæs skiftede til sydligere forlande (P. Prokosch upubl. rapport).

På Mandø Forland steg forårsbestanden kraftigt i årene efter digebyggeriet (N. Rattenborg pers. medd.), og det samme gjorde sig gældende på Langli (L. Maltha Rasmussen pers. medd.). Disse observationer tyder på, at der har været »ledig kapacitet«

i saltmarskområderne i Vadehavet. Når gæssene først kom til de danske områder efter bygningen af diget, kan det antyde, at de har været sekundære habitater af ringere kvalitet.

Ud over undersøgelserne fra Vadehavet foreligger en opgørelse over knortegæssenes græsningsintensitet og effekt på vegetationen på Tipperne (Lorenzen & Madsen 1985). Konklusionen var, at gæssenes græsningstryk om foråret var så lavt, at områdets bæreevne ikke var nået.

Samlet tyder observationerne og analyserne på, at kun på Langli i Vadehavet er bæreevnen om foråret lige ved at være nået. Den forholdsvis konstante forårsbestand i Danmark tyder imidlertid på, at en eller flere faktorer alligevel kan være begrænsende for bestanden. Forlandene er muligvis ikke velegnede rastepladser pga. for ringe bredde og manglende afgræsning med får og kreaturer.

En undersøgelse, der sammenligner saltmarskens tilstand i hele bestandens udbredelsesområde om foråret, vil muligvis kunne afdække de faktorer, der begrænser bestanden, men som ikke bliver iøjnefaldende ved blot at se på situationen i Danmark.

En årlig monitering af udvalgte ålegræsbedes udbredelse og vurderinger af biomasse i Vadehavet vil givetvis bidrage væsentligt til at styrke vurderingen af, hvad der influerer på antallet af knortegæs og andre planteædende vandfugles antal i Vadehavet om efteråret.

English summary

Occurrence of and habitat utilisation by the Dark-bellied Brent Goose *(Branta bernicla bernicla)* in Denmark, with special reference to the Danish Wadden Sea

This paper reviews the status of Dark-bellied Brent Geese staging and wintering in Denmark in the 1980's. The data have been compiled from counts made by the Danish Goose Working Group and the Game Biology Station.

The first Brent Geese arrive in the middle of September. Numbers peak in October with an average of 21,100 (1980-1983) and again in April-May with an average of 16,000 (Fig. 3), representing 10-12% of the world population (Fig. 8). In mild winters 2,000-5,000 Brent Geese remain in Denmark but in cold winters the geese move on to their main wintering quarters in France, England and the Netherlands.

The Wadden Sea is the most important Danish staging area (Fig. 3), followed by the Tipper Peninsula in western Jutland, Læsø in the Kattegat, and the south Funen Archipelago. The islands in the Kattegat are the northern-most wintering grounds of the population (locality names, see Fig. 1).

In the years 1966-1971, spring numbers

in Denmark reached approximately 4,000 geese (Fog 1972). Hence, since then the number of staging geese has increased by a factor of four. During the same period the world population has increased by a factor of five.

In the 1980's, the number of Dark-bellied Brents in the Danish Wadden Sea in autumn has fluctuated between 3,700 and 34,900 (Fig. 6). In the autumns of 1987 and 1988 the numbers were low, which may relate to a reported decline in *Zostera* food supplies.

Spring numbers have been more stable, fluctuating between 8,000 and 17,200 which suggests that something is acting to limit their numbers (Fig. 6). Generally, there are positive pair-wise correlations between the size of the total population, the proportion of juveniles in the population, Wadden Sea autumn numbers and Wadden Sea spring numbers (Table 1).

In autumn the Brent Geese staging in Denmark feed almost exclusively on mudflats and in shallow waters (Fig. 7). In late autumn and in winter, flocks of Brent Geese move to salt marshes to feed but mudflats and shallow waters still remain the predominant feeding habitat until March. In spring the geese gradually switch to salt marshes and, at the Tipper Peninsula, to rough pastures. Only at one site, Mandø, in the Wadden Sea, do the geese feed on pastures inside the sea walls. At one autumn stopping place the geese have in recent years moved onto winter cereal fields. In the Wadden Sea a seasonal re-distribution of Brent Geese (Figs. 5a,b) reflects the shift from mudflats to salt marshes.

To achieve an estimate of goose grazing intensity in salt marshes in the Wadden Sea, repeated counts of goose droppings were performed in permanent plots at 12 sites in spring 1986-1988 (Fig. 2, Table 2). The highest grazing-intensity was found on the island of Langli, followed by Mandø Polder and Ballum Foreshore, which holds the largest concentration of Brent Geese in the Wadden Sea. Grazing pressure on Langli was 995 goose-days per ha for an average spring season; on Ballum Foreshore it was 450 goose-days per ha. Goose grazing was extensive or absent at the remaining salt marshes studied, despite the fact that at least some of the areas appeared suitable as goose feeding grounds.

Compared to the salt marshes in Schleswig-Holstein, the Danish sites are less subjected to intensive sheep and cattle grazing and are generally narrower, which may make them less suitable for Brent Geese. In conclusion, it seems that only on Langli has the carrying capacity of the habitat for Brent Geese been reached (see Madsen 1989). At other sites in the Danish Wadden Sea, there still seems to be room for more geese. However, these areas are probably not optimal for Brent Geese.

Litteratur

Ankney, C.D. & C.D. MacInnes 1978: Nutrient reserves and reproductive performance of female Lesser Snow Geese. - Auk 95: 459-471.

Boudewijn, T. 1984: The role of digestibility in the selection of spring feeding sites by Brent Geese. - Wildfowl 35: 97-105.

Charman, K. 1979: Feeding ecology and energetics of the Dark-bellied Brent Goose *(Branta bernicla bernicla)* in Essex. 451-465 i: Jefferies, R.L. & A.J. Davy (red.) Ecological processes in coastal environments. - Blackwell Sci. Publ., Oxford.

Charman, K. & A. Macey 1978: The winter grazing of saltmarsh vegetation by Dark-bellied Brent Geese. - Wildfowl 29: 153-162.

Ebbinge, B. 1979: The significance of the Dutch part of the Wadden Sea for *Branta bernicla bernicla*. 77-87 i: Smart, M. (red.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. - IWRB, Slimbridge.

Ebbinge, B. 1985: Factors determining the population size of arctic-breeding geese, wintering in Western Europe. - Ardea 73: 121-128.

Ebbinge, B. & T. Boudewijn 1984: Richtlijnen voor het beheer van rotganzen in het Nederlandse waddengebied. - RIN-rapport 84/4, Rijksinst. voor Natuurbeheer, Leersum. 76 s.

Ebbinge, B., A. St Joseph, P. Prokosch & B. Spaans 1982: The importance of spring staging areas for arctic-breeding geese, wintering in Western Europe. - Aquila 89: 249-258.

Fog, M. 1967: An investigation of the brent goose *(Branta bernicla)* in Denmark. - Dan. Rev. Game Biol. 5(1): 40 s.

Fog, M. 1972: Status for knortegåsen *(Branta bernicla)*. Rapport Vildtbiologisk Station, 105 s.

Frikke, J. 1987: Die Nutzung der Salzwiesen im dänischen Wattenmeer. 95-100 i: Kempf, N., J. Lamp & P. Prokosch (red.). Salzwiesen: Geformt von Küstenschutz, Landwirtschaft oder Natur? Tagungsbericht 1 der Umweltstiftung WWF-Deutschland. Husum.

Jacobs, R.P.W.M., C. Den Hartog, B.F. Braster, F.C. Carriere 1981: Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). - Aquatic Bot. 10: 241-259.

Laursen, K. 1982: Recreational activities and wildlife aspects in the Danish Wadden Sea. - Schriftenreihe des Bundesministers für Ernährung, Landwirtschaft und Forsten 275: 63-83.

Laursen, K., I. Gram & J. Frikke 1984: Trækkende vandfugle ved det fremskudte dige ved Højer, 1982. - Danske Vildtundersøgelser 37. 36 s.

Laursen, K., S. Pihl, M. Hansen & J. Frikke 1988: Landsdækkende optælling af vandfugle fra flyvemaskine, oktober/november 1987. Rapport fra Vildtbiologisk Station. 27 s.

Laursen, K., S. Pihl, M. Hansen & J. Frikke 1989: Landsdækkende optælling af vandfugle fra flyvemaskine, oktober/november 1988. Rapport fra Vildtbiologisk Station. 24 s.

Laursen, K. & J. Frikke, i trykken: Surveys of waterfowl, waders and gulls in the Danish Wadden Sea 1980-1983. - Dan. Rev. Game Biol.

Lorenzen, B. & J. Madsen 1985: Gåsebestandene på Tipperhalvøen. II: Græsningsøkologi i relation til områdets bæreevne. - Dansk Orn. Foren. Tidsskr. 79: 113-132.

Madsen, J. 1984: Status of the Svalbard population of Light-bellied Brent Geese *Branta bernicla hrota* wintering in Denmark 1980-1983. Nor. Polarinst. Skr. 181: 119-124.

Madsen, J. 1985a: Gåsebestandene på Tipperhalvøen. I: Forekomst og udvikling 1929-1983. Dansk Orn. Foren. Tidsskr. 79: 19-28.

Madsen, J. 1985b: Impact of disturbance on

field utilization of Pink-footed Geese in West Jutland, Denmark. – Biol. Conserv. 33: 53-63.
Madsen, J. 1986: Danske rastepladser for gæs. Miljøministeriet, Fredningsstyrelsen. 114 s.
Madsen, J. 1987: Status and management of goose populations in Europe, with special reference to populations resting and breeding in Denmark. – Dan. Rev. Game Biol. 12 (4). 76 s.
Madsen, J. 1988a: Duehøg *Accipiter gentilis* forstyrrer og dræber Knortegæs *Branta bernicla* ved specialiseret jagtteknik. Dansk Orn. Foren. Tidsskr. 82: 57-58.
Madsen, J. 1988b: Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. – Dan. Rev. Game Biol. 13(4). 32 s.
Madsen, J. 1989: Spring feeding ecology of Brent Geese *Branta bernicla bernicla*: annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. – Dan. Rev. Game Biol. 13 (7). 16 s.
Maheo, R. 1976: The Brent Geese of France, with special reference to the Golfe du Morbihan. Wildfowl 27: 55-62.
Meltofte, H. 1973: Trækket af gæs *Anserinae* ved Blåvandshuk 1963-1971. – Dansk Orn. Foren. Tidsskr. 67: 35-41.
Moller, A.P. 1978: Nordjyllands Fugle – deres yngleudbredelse og trækforhold. Scandinavian Sci. Press, Klampenborg. 372 s.
Prokosch, P. 1984: Population, Jahresrhythmus und traditionelle Nahrungsplatzbindungen der Dunkelbäuchigen Ringelgans *(Branta bernicla bernicla)* im Nordfriesischen Wattenmeer. Ökol. Vögel 6: 1-99.
Prokosch, P. & N. Kempf 1987: Die Nutzung der Salzwiesen im schleswig-holsteinischen Wattenmeer. 101-112 i: Kempf, N., J. Lamp & P. Prokosch (red.) Salzwiesen: Geformt von Küstenschutz, Landwirtschaft oder Natur? Tagungsbericht 1 der Umweltstiftung WWF-Deutschland. Husum.
Prop, J. & M. Loonen 1989: Goose flocks and food exploitation: the importance of being first. Acta XIX Congr. Int. Ornith.: 1878-1887.
Ranwell, D.S. & B.M. Downing 1959: Brent Goose *(Branta bernicla)* winter feeding pattern and *Zostera* resources at Scolt Head Island, Norfolk. – Anim. Behav. 7: 42-56.
St Joseph, A.K.M. 1979a: The seasonal distribution and movements of *Branta bernicla* in Western Europe. 45-59 i: Smart, M. (red.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge.
St Joseph, A.K.M. 1979b: The development of inland feeding by *Branta bernicla bernicla* in southeastern England. 132-145 i: Smart, M. (red.) Proc. First Techn. Meeting Western Palearc. Migr. Bird Management. – IWRB, Slimbridge.
Teunissen, W., B. Spaans & R. Drent 1985: Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. – Ardea 73: 109-119.
Thomas, V.G. 1983: Spring migration: the prelude to goose reproduction and a review of its implications. 73-81 i: Boyd, H. (red.) First Western Hemisphere waterfowl and waterbird symposium. – Can. Wildl. Serv., Ottawa.
Tubbs, C.R. & J.M. Tubbs 1983: The distribution of *Zostera* and its exploitation by wildfowl in the Solent, southern England.-Aquatic Botany 15: 223-239.
White-Robinson, R. 1982: Inland and saltmarsh feeding of wintering Brent Geese in Essex. Wildfowl 33: 113-118.

8

IBIS 129: 25–44

Habitat exploitation and interspecific competition of moulting geese in East Greenland

JESPER MADSEN* & CHRISTIAN EBBE MORTENSEN

Ornithological section of the Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

Accepted 27 September 1985

Jameson Land, East Greenland is a moulting area of *c.* 5000 non-breeding Pink-footed Geese and 5000 Barnacle Geese. Breeding populations of both species in the area are small and scattered. The moulting Pinkfeet originate from Iceland, and the Barnacle Geese from other parts of East Greenland. Both species arrive in the area at the end of June and moult their remiges in July.

Moulting flocks of the two species seldom mix. Pinkfoot flocks are common along coastlines, in wide rivers and on lakes with open views to all sides, while Barnacle Geese predominate in smaller rivers and on lakes with surrounding hills. During moult the geese, and especially the Pinkfeet, are extremely wary and depend on a safe area of water serving as a refuge with nearby food supplies (sedge-dominated marshes). Barnacle Geese graze in a zone 0–100 m from the refuge, Pinkfeet up to 200–250 m from the refuge. The moulting sites fill up with geese according to available marsh areas, and the grazing pressure on average amounts to 594 goose-days per ha during the moulting period. Food intake is estimated at 149 g and 138 g organic material per 24 h by Pinkfeet and Barnacle Geese, respectively. In 1984, which was sunny and warm, net above-ground primary production of a *Carex subspathacea* marsh (the prime feeding ground during moult) from the beginning of growth to the end of July was 13–15 g dw m^2, and it is estimated that the geese consumed 60–69% of the production. In 1983, which was cold, geese probably consumed the entire production. Goose grazing did not affect productivity, but nutrient levels were high in grazed compared with ungrazed shoots, and peaked in early July.

When separate, the diet of both species comprises sedges and grasses. Where the species co-exist the amount of mosses in the diet increases, especially in Barnacle Geese. With respect to nutrient and fibre contents, moss is a suboptimal food compared to sedges and grasses. When separate, the geese spend 41–46% of the 24 hr grazing. Where they co-exist, Barnacle Geese spend 62% of the time grazing, while Pinkfeet seem unaffected by the presence of Barnacle Geese.

It is argued that carrying capacity for moulting geese is reached. Geese compete for resources, the Barnacle Goose suffering from the presence of the other. The observed distribution pattern is suggested to result from (1) Pinkfeet being limited to certain sites due to extreme wariness, and (2) Barnacle Geese trying to avoid competition by utilizing sites which Pinkfeet are reluctant to use. The experience of older Barnacle Geese of stress when settling with Pinkfeet may be the segregation mechanism.

Moult coincides with the onset of growth and peak nutrient levels in the vegetation. It is suggested that the geese undertake moult migrations to Jameson Land both to avoid competition for resources with breeding geese and because they gain advantage from a growing, nutritious vegetation.

During the summer moult of remiges, non-breeding geese congregate at special moulting grounds (e.g., Paludan 1965, Salomonsen 1968). For 3–4 weeks they are unable to fly, and the moulting site must afford protection against predators as well as sufficient food supplied throughout the flightless period.

The ecology of non-breeding, moulting geese is, however, not well known. A recent study by Derksen *et al.* (1982) described the salient features of an Alaskan moulting ground of three goose species, and analysed how the area was exploited by the geese.

The aim of this paper is to describe the ecology of moulting Pink-footed Geese *Anser brachyrhynchus* and Barnacle Geese *Branta leucopsis* at a common moulting

* Present address: Game Biology Station, Kalo, DK-8410 Ronde, Denmark.

ground in Jameson Land, East Greenland. Evidence is presented that the carrying capacity of the area for moulting geese is reached and the two species compete for limited resources, affecting their distribution in the area.

The study, which was undertaken in 1982–84, is part of an environmental base line investigation in connection with planned oil exploration. Results of censuses of geese and a study of the possible effects of human activities on the moulting goose populations have been published by Madsen *et al.* (1984) and Madsen (1984), respectively.

Study area and goose population

Jameson Land, situated north of the Scoresby Sund Fjord (Fig. 1), is a lowland tundra which gradually slopes from SW and W towards a northern and eastern plateau (500–1000 m a.s.l.) cut by several valleys, e.g., Ørsted Dal. The western part, Heden, is a flat inland tundra intersected by many rivers and dotted with lakes. Fieldwork was carried out in an area around the river Draba Sibirica Elv at Heden as well as in Ørsted Dal.

The dominating vegetation type in the study area on Heden (0–200 m a.s.l.) is continuous dwarf scrub with 75–100% coverage (with *Cassiope tetragona*, *Vaccinium uliginosum*, *Empetrum hermaphroditum* and *Betula nana* predominating) and, near rivers, streams and lakes, graminoid marshes (mosses with protruding *Carex stans*, *C. subspathacea* and *C. saxatilis* and *Eriophorum scheuchzeri*). Along the west coast salt marshes (dominated by *Carex subspathacea* and *Puccinellia phryganodes*) are found. In Ørsted Dal graminoid marshes (mosses with *C. stans*, *C. saxatilis* and *Eriophorum triste*) are abundant on the valley floor together with fellfield (*Dryas octopetala* and *Salix arctica*) dry dwarf scrub (see Bay & Holt 1984 for details).

Jameson Land is situated on the limit between high and low arctic regions of East Greenland. The frost-free period ranges from around the middle of June to the beginning of August. Except for the valleys opening towards the Greenland Sea (e.g., Ørsted Dal) the summer climate is usually continental with much sun and low precipitation. This was prevalent in 1982 and 1984, while in 1983 the summer was rainy, cold and with only little sun.

Two species of geese, the Pink-footed Goose and Barnacle Goose, occur as summering and breeding species in Jameson Land. The Pinkfeet belong to the population breeding in Iceland and East Greenland and wintering in Scotland and England (*c.* 90 000, Ogilvie 1983a). The Barnacle Geese are part of the East Greenland breeding population wintering in Scotland and Ireland (*c.* 25 000, Ogilvie 1983b).

Aerial surveys and ground counts (Madsen *et al.* 1984) revealed that Jameson-Land is primarily a moulting area for geese. In July the populations consist of 5000–5500 Pinkfeet and 5000–6100 Barnacle Geese, of which approximately 93% are non-breeders or failed breeders. Non-breeding Pinkfeet arrive from Iceland at the end of June and, at the same time, Barnacle Geese arrive from the East Greenland breeding range. During a 3–4 week period (Pinkfeet *c.* 7 July to 1 August, Barnacle Geese *c.* 5 to 28 July) the geese moult their remiges and are flightless. The moulting flocks, and especially the Pinkfeet, are extremely wary and concentrate along rivers, coast lines and around lakes which serve as refuges from predators, mainly arctic foxes *Alopex lagopus*, which are abundant. Mean flock size of Pinkfeet during moult is 43 (range 1–240) and of Barnacle Geese 32 (range 1–350). Having regained the power of flight the geese abandon the moulting grounds; the Pinkfeet disperse to other sites in Jameson Land, while most Barnacle Geese leave Jameson Land and fly to other, unknown

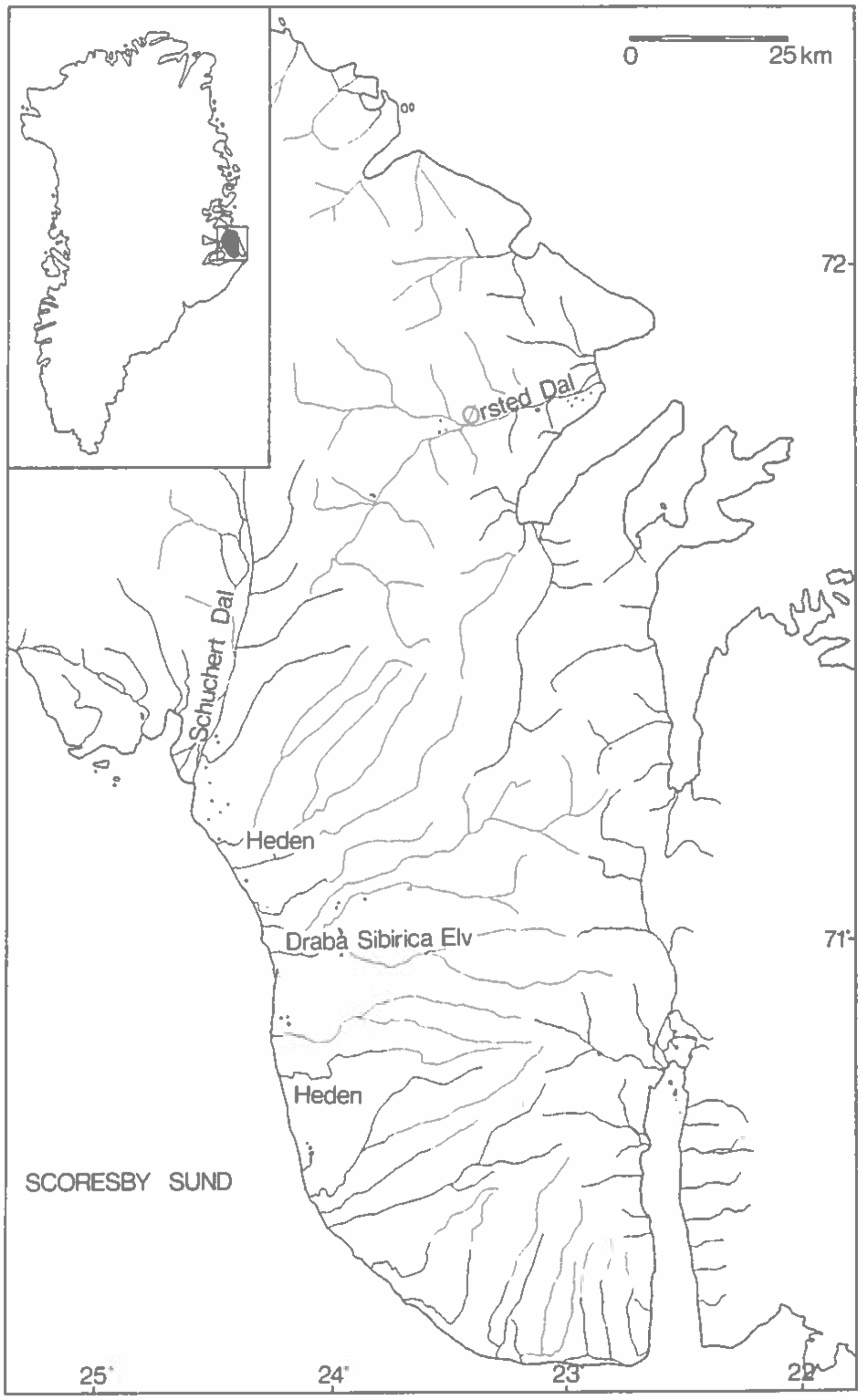


Figure 1. Map of Jameson Land, showing the major river systems and areas where field work was carried out.

sites outside the area. The geese emigrate from Greenland during the first half of September.

Methods

Habitat selection

In different areas visited by moulting geese dropping densities were used as a measure of habitat utilization. Droppings were counted in plots with a radius of 1·1 m (4 m^2), 20–40 m apart along transects in the terrain. Transects were laid out in different plant communities and always at right angles to the edge of the refuge. From the results the vegetation zones exploited by the geese during moult were delimited. The plant communities used were then identified using a vegetation map (1:25000) of Jameson Land, prepared on the basis of false coloured infra-red photography by the botanical base line studies (C. Bay & S. Holt unpubl.).

Width of lakes and rivers were measured from the maps. As the safety of a river as a refuge depends both on river width and depth, an index combining the two factors was developed. Rivers were classified according to the following crude scale:

(A) River *c.* 50 m wide and *c.* 1 m deep in most of the course;
(B) River *c.* 30 m wide and 0·5–1 m deep in most of the course;
(C) River *c.* 20 m wide and *c.* 0·5 m in most of the course;
(D) River *c.* 10 m wide and less than 0·5 m in most of the course;
(E) River *c.* 5 m wide and less than 0·5 m in most of the course.

During the aerial censuses the position of all observed flocks of geese was recorded, and in July 1984 river sections were classified according to the above index. Estimates were later checked from the ground.

Food selection

Geese have an inefficient digestion of their food plants which leaves the epidermis of the ingested vegetation intact in the droppings. As most plant species have specific epidermal characteristics, a dietary analysis is possible on the basis of microscopical identification of epidermal fragments in the droppings (Owen 1975).

In the field, fresh droppings were collected in sites where goose flocks had been grazing on the same day. At least 25 droppings were taken per sample. During the moulting period droppings were collected from sites where the two species occurred alone as well as from sites where they co-existed (the latter sampling only around isolated lakes from which the geese could escape during moult and where the food supplies were the same for both species). To separate the droppings of the two species a mixed, roosting flock was kept under observation for some time, ensuring that the droppings could be collected from the exact positions where individuals of the particular species had been roosting.

A sample was preserved in 70% alcohol and thoroughly mixed before examination. Subsamples (more than 10) were taken at random and spread on microscope slides. Food composition in sample was quantified by determination of 100 fragments, following a quadrat sampling procedure described by Owen (1975). By the aid of a reference collection of epidermis of potential food plants, all fragments (except mosses) were identified to species or genus level. Because mosses fragment much more than the epidermis of vascular plants during gut passage, the point quadrat sampling method will bias the diet composition in favour of mosses

(Derksen *et al.* 1982). To correct for this, only fragments of at least 20 epidermis cells were included in the counts.

To relate the frequency distribution of plant species in the droppings to plant community, plant species frequency in a *Carex subspathacea*-dominated sward grazed by moulting Pinkfeet was assessed by a pin-point method. A 200-m-long transect was laid out in the marsh perpendicular to the refuge. At 15-m intervals a secondary transect was laid out at right angles to the main transect. At 10-cm intervals along the secondary transect the presence or absence of species was recorded in up to 180 contact points.

Time budgets

Diurnal time budgets of non-breeding moulting flocks of geese were studied by observation of time allocation. This was done from portable hides placed near permanent moulting grounds, and using spotting scopes (× 20–45). Within an observation period the flock was scanned at 5- or 10-min intervals, and the number of individuals engaged in various activities recorded. Observation periods varied from a few hours to 48 hr, and were evenly distributed over the diurnal cycle.

Estimation of daily food intake

Daily food consumption was estimated by the 'marker substance' method developed for geese in the wintering quarters (Ebbinge *et al.* 1975, Drent *et al.* 1981). Digestibility was measured using ash content as a natural food component not digested by gut passage. The increase in the concentration of the marker in the droppings compared to the food plants thus equals the retention rate. Defaecation rate was measured in the field by keeping the abdomen of a goose under continuous observation for as long as possible (timed on a stop watch) and recording the number of droppings produced in the period. Periods and number of droppings were summed for many individuals to achieve an average defaecation rate. Fresh droppings were collected from two moulting sites on Heden together with potential food plants. Before analysis, plant species were lumped in the proportion found in the droppings from the site (faecal analysis). Ash content of both plants and droppings were determined and the silica fraction removed. All analyses were carried out in duplicate.

Productivity of vegetation

To estimate the potential food supplies available to the moulting geese, the net above-ground primary production (NAPP) of marsh vegetation was studied.

In 1983 an experiment was set up in a wet marsh dominated by *Carex subspathacea* protruding through a moss carpet and grazed by Pinkfeet during the moulting period. On 5 July, four exclosures of 1 m^2 each were erected at *c.* 10 m intervals on a line 10–20 m parallel to the lake serving as refuge. Exclosures were constructed of four stakes (40 cm above ground) connected with strings in various heights. Six circular turves, each of 0·11 m^2, were collected randomly outside the exclosures. Sampling was repeated inside and outside the exclosures on 4 August when the majority of the geese had regained flight and abandoned the area. Vegetation was clipped at soil level, washed, separated into live and dead material, and the live material sorted into species (mosses excluded). Samples were wind and sun dried in paper bags in the field, dried at 60° C in a vacuum oven for 24 hr, and weighed after return to the laboratory.

In 1984 another approach was used, as NAPP was estimated by simulation of goose-grazing in two sites by repeated clipping of all vegetation above the level of the moss carpet in permanent plots. Both sites were snow-covered until 15–20 June.

Site I

A *Carex subspathacea*-dominated marsh adjacent to a lake used by moulting geese. The marsh gradually sloped upwards towards a snow bed which supplied the marsh with melt water throughout the summer. Within a 10 × 10 m exclosure, constructed as in 1983, and 40 m from the lake, four permanent 0·11 m^2 plots were harvested at ten-day intervals from 21 June to 30 July. To elucidate whether clipping, and by analogy, grazing, had an effect on NAPP, the numbers and weight of shoot of *C. subspathacea* in clipped and unclipped plots were compared on 30 July.

Site II

A *Carex stans*-*Poa pratensis*-dominated marsh along a tributary to a river. The marsh sloped upwards towards a snow bed supplying the marsh with melt water. The ground was sandy and with low coverage of mosses. Within a 10 × 10 m exclosure 15 m from the river five 0·028 m^2 plots were harvested at 5–7-day intervals as at Site I. NAPP of a grazed marsh was estimated in two ways:

(1) By summation of the biomass clipped in the permanent plots (1984), or as the positive increment in the biomass in exclosures (1983). Green biomass present at the time of snow melt was assumed to be production of the previous year and not included in the estimate of NAPP.

(2) By the amount of vegetation consumed by the geese:

$$\text{NAPP} = C + x_f - x_i,$$

where C is the forage consumed, x_i the biomass present at the onset of grazing (pre-moult), and x_f the biomass remaining after the departure of the geese (Cargill & Jefferies 1984).

Chemical analyses of food plants

Paralled with the clipping of *C. subspathacea* on permanent plots in 1984, samples of green shoots were collected between the plots for comparison of nutrient and fibre contents in clipped and unclipped shoots. Analyses of total nitrogen, crude fibre, phosphorus and potassium were carried out by the Central Laboratory of the National Institute of Animal Science, Denmark.

Samples of green shoots of a variety of food plant species were collected for nutrient and fibre analyses. Plants were only collected from sites visited by moulting geese and at the end of July.

Results

Habitat selection

The dropping counts and direct observations revealed that during moult, both goose species feed exclusively in marshes dominated by sedges and grasses. Figure 2 shows the significance of the proximity to the water body serving as refuge. The Barnacle

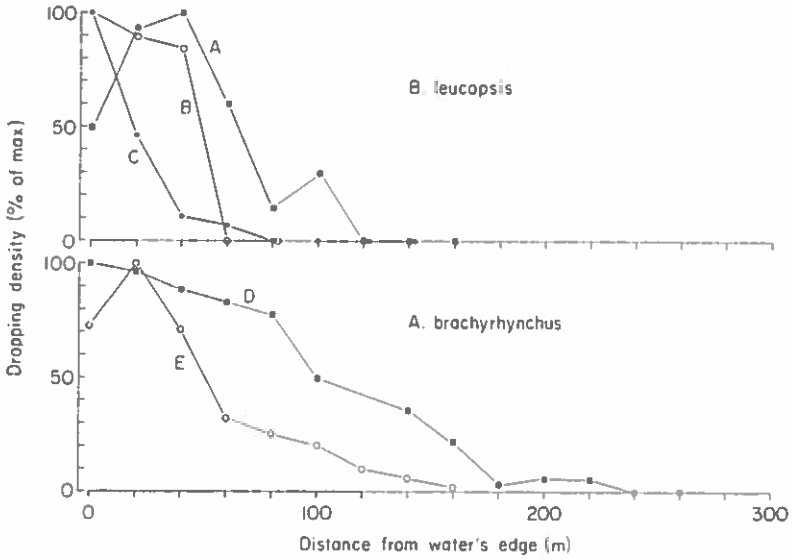


Figure 2. Utilization of sedge-dominated marshes during goose moult in relation to proximity to open water, expressed by dropping densities (each point represents at least 8 squares of 4 m^2 each). Densities are expressed as percentage of the maximum density, and results from five sites (A–E) are shown.

Geese only exploit a narrow zone around the water's edge (up to 100 m into the marshes), while the Pinkfeet utilize a broader zone (up to 200–250 m into the marshes). The interspecific difference in utilization probably results from a better sprinting ability of Pinkfeet than of Barnacle Geese, which is valuable in case of fox attack.

The crucial importance of keeping close to water is demonstrated by the record of remnants of goose carcasses—obvious remnants of fox kills—at almost every moulting site. Successful and unsuccessful attacks by foxes were observed on several occasions. Remarkably, the victims were always Pinkfeet, and it seems that they are more vulnerable to predation than Barnacle Geese due to their foraging strategy.

During moult there exists a significant segregation of sites used by the two goose species, and mixed flocks are seldom seen. In 1983, which was representative of all three census years, flocks of Pinkfeet were found at a total of 118 sites, and Barnacle Geese at 114 sites, with mixed flocks on only 18 of the sites. Since all potential moulting sites in Jameson Land seem to be occupied (see below) the frequency of mixing is far below that expected from a random distribution ($\chi^2 = 167$, d.f. = 1, $P < 0{\cdot}001$).

The two species segregate by overall habitat utilization. Pinkfeet are more frequent than Barnacle Geese along coastlines (Table 1), and the two species also diverge in selection of lakes and rivers. On Heden (Fig. 3), which has the highest concentrations of moulting geese, the segregation pattern is apparent. In most of the river systems Barnacle Geese are most widespread, while Pinkfeet inhabit other rivers and almost all lakes. In other parts of Jameson Land, especially in the eastern valleys, the lakes are occupied by Barnacle Geese. In both species the minimum acceptable width of a refuge lake is *c.* 20 m. Although not quantified in detail, the difference in lake occupancy between areas is probably explained by the open view to all sides from most lakes on Heden and the hilly surroundings of lakes in the eastern

Table 1. *Habitat distribution of flocks of moulting geese. The species diverge significantly in habitat occupancy*

	Anser brachyrhynchus	*Branta leucopsis*
Lake	28	20
River	50	85
Coastline	40	9
n	118	114

Note: $\chi^2 = 20{\cdot}1$, d.f. = 2, $P < 0{\cdot}01$.

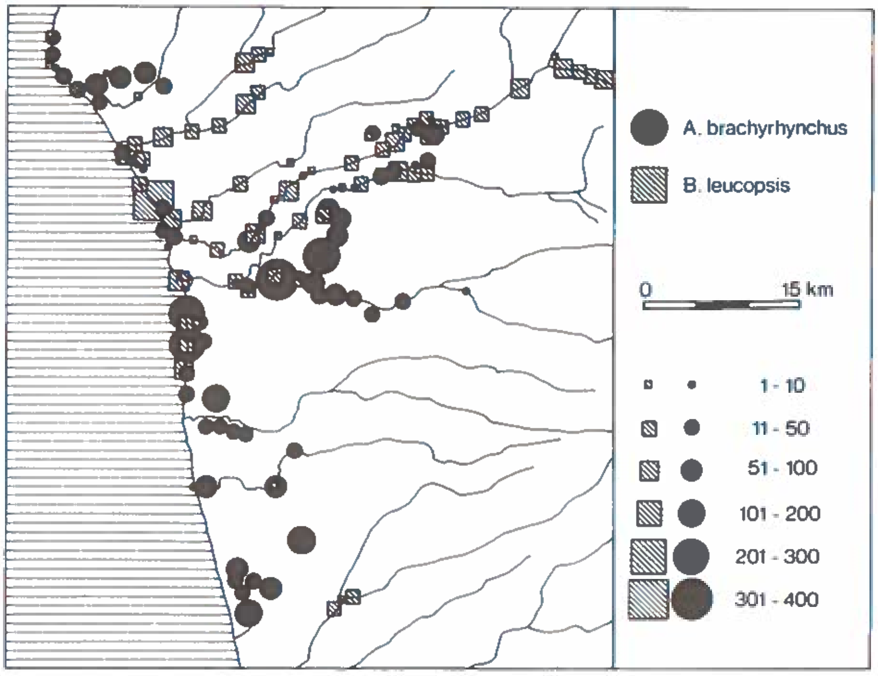


Figure 3. Distribution of moulting geese at Heden, western Jameson Land, as revealed by aerial count, July 1983.

valleys. The extremely wary Pinkfeet are probably reluctant to use the latter type, while the Barnacle Geese do.

The segregation on rivers seems to be a function of river size (Fig. 4). Thus, Pinkfeet are commonest on the larger rivers and do not utilize those less than 20 m wide, while Barnacle Geese are under-represented in the largest rivers but make use of rivers down to 10 m width.

Food selection

From their arrival in the middle of June to the start of moult at the beginning of July, both species fed in small parties on grassy slopes and on snow free marshes along

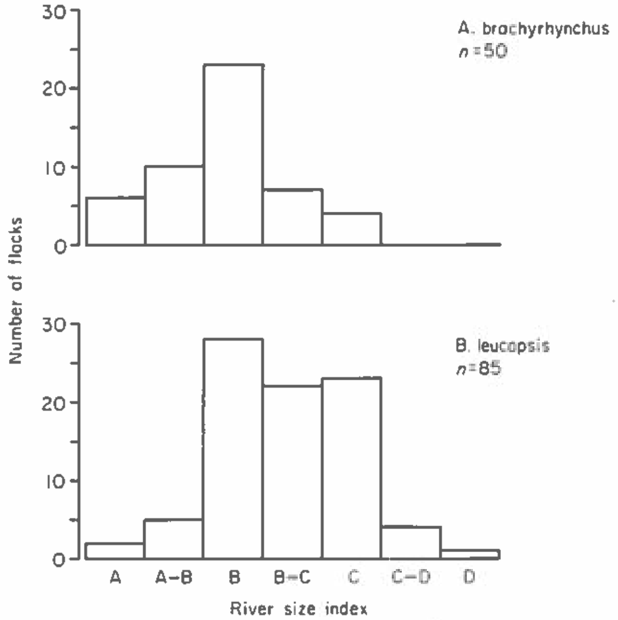


Figure 4. Distribution of moulting flocks of geese in relation to river size. For explanation of index see Methods. The distributions are significantly different ($\chi^2 = 21{\cdot}6$, d.f. = 6, $P < 0{\cdot}01$).

streams and rivers. Many geese were seen probing for the first leaves and for roots and rhizomes of grasses and sedges in wet moss carpets. In both species *Poa pratensis* dominated the diet (Table 2). However, root fragments, which were not quantified in the faecal analysis, probably made up more than 50% of the diet in both species.

During moult the diets of both species became dominated by the new growth of sedges and grasses (Table 2 and Fig. 5). Site-to-site differences in food composition reflect differences in composition of plant communities. The frequency distribution of the plant species in the droppings was quite similar to the presence of species in the marsh sward (Fig. 6), although there was a positive selection of sedges and negative selection of mosses. Although not represented in the dropping analyses, field observations showed that the geese picked off buds and flowering heads of *Saxifraga foliolosa* and *Polygonum viviparum* in the marsh areas. The geese totally avoided *Hippuris vulgaris* and other dicots and hardly grazed *Eriophorum scheuchzeri*, which was abundant in most moulting areas.

The chemical analyses of the food plants showed that the moulting geese selected plants with maximum nutrient and lowest fibre contents (Table 3). Mosses, which have low nutrient contents and high fibre contents, are clearly suboptimal food plants.

When separate the two goose species showed almost identical diets ($\chi^2 = 2{\cdot}8$, d.f. = 4, NS) (Fig. 5). Where co-existing with Pinkfeet, the food composition of the Barnacle Geese changed significantly, compared to where separate ($\chi^2 = 26{\cdot}3$ d.f. = 4 $P < 0{\cdot}001$), while the food composition of the Pinkfeet did not ($\chi^2 = 4{\cdot}2$ d.f. = 4, NS). The change in diet of the Barnacle Geese was caused by an increased intake of mosses ($t = 3{\cdot}86$, $P < 0{\cdot}05$). At the extreme, at one site in Ørsted Dal mosses made up 33% of the Barnacle Goose diet while 17% of the Pinkfoot diet.

In the post-moult period in August the geese fed widely dispersed on the tundra and on marshes not hitherto exploited in the season. Sedges and grasses still

Table 2. *Diet of non-breeding geese in different periods and areas (%)*

	Pre-moult		Moult						Post-moult	
	Heden		Ørsted Dal		Heden		Hall Br		Heden	
	A.b.	*B.l.*	*A.b.*	*B.l.*	*A.b.*	*B.l.*	*A.b.*	*B.l.*	*A.b.*	*B.l.*
n	1	1	3	4	2	1	2	2	3	2
Cyperaceae										
Carex subspathacea	—	—	—	—	81·6	52·1	67·4	44·1	—	—
Carex saxatilis	—	—	1·0	21·2	0·4	—	1·0	2·7	1·9	5·4
Carex stans	—	27·1	65·5	46·8	—	—	—	—	34·0	45·7
Eriophorum scheuchzeri	—	—	—	—	—	1·7	1·2	0·9	—	—
Poaceae										
Festuca sp.	3·6	—	2·6	0·9	0·8	—	2·2	10·8	—	1·1
Poa pratensis	83·6	61·0	16·5	18·1	11·6	41·9	11·0	—	17·9	14·1
Trisetum spicatum	—	—	0·6	—	—	1·7	0·3	4·5	—	1·1
Phippsia algida	—	—	1·2	—	—	—	—	—	—	—
Puccinellia phryganodes	—	—	—	—	—	—	9·2	5·4	—	—
Alopecurus alpinus	7·4	—	—	—	—	—	0·4	—	1·5	1·1
Arctagrostris latifolia	1·8	—	—	0·3	—	—	—	—	—	—
Poaceae sp.	—	3·4	—	—	—	—	—	—	2·9	4·2
Dicotyledones										
Saxifraga sp.	—	—	—	—	0·8	—	1·0	—	—	3·3
Polygonum viviparum	3·6	—	1·0	0·2	—	—	—	—	—	1·1
Stellaria sp.	—	—	—	—	—	—	0·3	—	—	—
Equisetum										
Equisetum sp.	—	6·8	—	0·4	—	—	1·6	12·6	39·6	19·6
Bryophyta										
Bryophyta sp.	—	1·7	11·6	12·1	4·8	2·6	4·4	18·9	2·2	3·3

Note: A.b. = Pink-footed Goose; *B.l.* = Barnacle Goose; *n* number of samples.

dominated the diet, but *Equisetum* spp., probably mostly *E. variegatum*, which emerged late along the falling rivers, also became an important food (Table 2). In August there was quite a rich fruiting of berries in the tundra scrubs on Heden, and the geese were seen picking off berries, also evidenced by blue and red colouring of the droppings and by finding seeds in most droppings.

Time budgets

Under the continuous daylight of the arctic summer the time budget was characterized by a regular pattern of alternation between feeding and resting. In both species feeding periods were evenly distributed over 24 hr (Fig. 7), and there was a high degree of synchrony in activities between individuals in a flock. The duration of a feeding bout in a marsh lasted from a few minutes to 1·5 hr, and the feeding was finished either spontaneously by walking back to the water's edge or because the flock was suddenly scared and ran back to the water. The average period when at least 50% of the members of a Pinkfoot flock grazed without interruption was 26·3 minutes ($n = 70$, s.d. = 17·9), and of Barnacle Geese 39·6 minutes ($n = 49$, s.d. = 25·3) ($t = 3{\cdot}15$, $P < 0{\cdot}005$). The shorter feeding bouts of Pinkfeet probably relate to their extreme wariness.

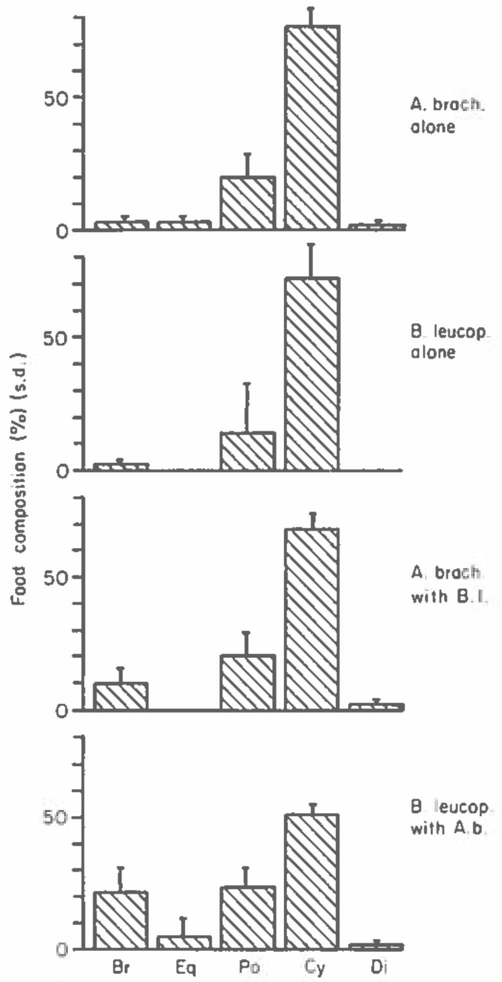


Figure 5. Food selection of Pinkfeet and Barnacle Geese during moult when they are separate and together. Br: Bryophyta, Eq: Equisetum, Po: Poaceae, Cy: Cyperaceae, Di: Dicotyledones. In each case samples have been taken from three sites.

In both species grazing was the most time-consuming activity, followed by resting (Table 4). When the two species were separate there was no significant difference in time budgets ($\chi^2 = 2{\cdot}14$, d.f. $= 4$, NS).

Mixed flocks of Pinkfeet and Barnacle Geese were observed on three occasions, each time with Pinkfeet as the most numerous species. In these situations Pinkfeet did not alter time budgets, whereas Barnacle geese grazed more at the expense of resting. On average they devoted 61·8% of the time to grazing ($n = 54$ h observations), which is significantly more than when separate ($\chi^2 = 17{\cdot}8$, d.f. $= 4$, $P < 0{\cdot}01$). As long as the Pinkfeet grazed in the marsh zone close to the refuge the Barnacle Geese usually followed, but stayed behind when the Pinkfeet went into more distant marsh areas. Thus, the Barnacle Geese were forced to graze in a zone already exploited by the Pinkfeet. The observations indicate that the Barnacle Geese suffer from a decreased intake rate when flocking with Pinkfeet. The opposite needs not to be the case, as the Pinkfeet exploit zones not available to Barnacle Geese.

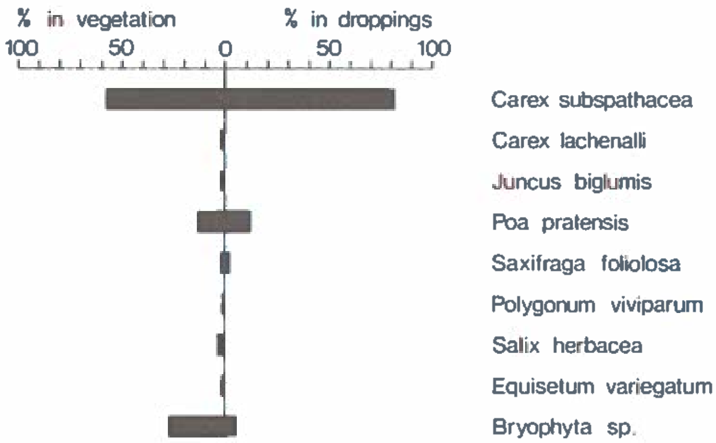


Figure 6. Food selection by Pinkfeet during moult on sedge-dominated marsh.

Table 3. *Selectivity of Pink-footed Geese on a* Carex subspathacea *sward, and some chemical components of food plants (% of dry weight)*

	Selection[a]	Total No.	Crude fibre	Prot./fibre[b]	Potassium	Phosphorus
Carex subspathacea (leaves)	1·5	4·3	16·1	1·7	1·8	0·4
Poa pratensis (leaves)	1·0	3·2	17·6	1·1	1·7	0·3
Saxifraga foliolosa (flowering heads)	> 2	3·9	9·5	2·6	1·7	0·5
Bryophyta sp. (leaves)	0·2	1·4	23·5	0·4	0·7	0·2

Notes: a: ratio between % in droppings/% in vegetation; b: ratio between 6·25 × % N/% Crude fibre.

Unfortunately, the situation with more Barnacle Geese than Pinkfeet was not observed.

One observation strongly indicates that the two species compete for food. In a river bend where flocks of both species moulted, a mixed flock of 16 Barnacle Geese and 40 Pinkfeet was observed for four h on 7 July 1984. The Barnacle Geese grazed along the river on emerging shoots of *Poa pratensis* while the Pinkfeet were upending for roots or rhizomes in the river (plant species not identified). Four times the Barnacle Geese approached the Pinkfeet to participate in the feeding in the river, but were refused access by direct attacks from the Pinkfeet. After 2·5 hr the Pinkfeet for unknown reasons became alert and swam up the river. Immediately after the Barnacle Geese took over the river feeding.

Daily food intake and grazing pressure

The estimates of daily food intake of the two species during moult is presented in Table 5. The 'marker substance' method proved to be particularly suited for the arctic situation. The geese fed on a very uniform food supply, and they spread their

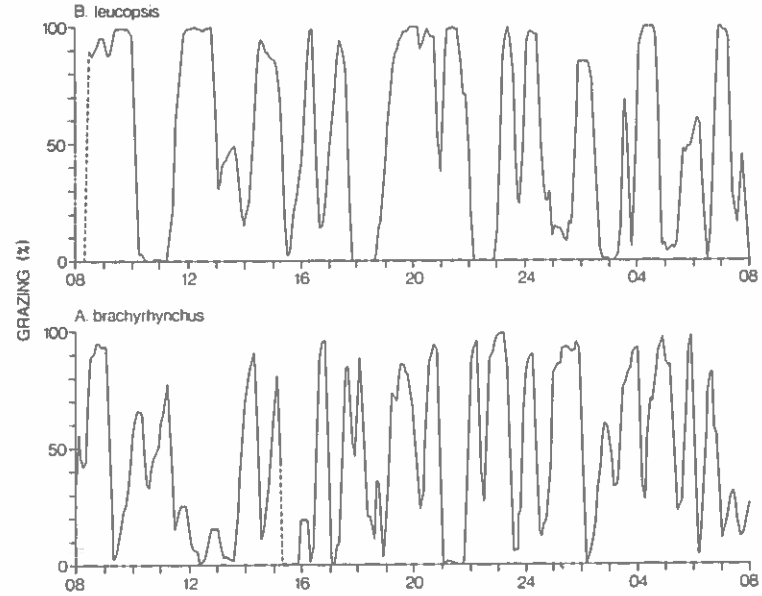


Figure 7. Diurnal pattern of grazing by geese during moult. Curves show moving averages of three observations. Time intervals are 10 minutes. Dashes lines show start of observations.

Table 4. *Average diurnal time budgets (%) of moulting, non-breeding flocks of geese*

	Grazing	Resting	Preening	Walking	Swimming	Alert	*n* (hours)
A. brachyrhynchus	40·9	38·1	7·8	3·2	9·2	0·8	103
B. leucopsis	46·0	36·5	9·4	3·5	5·7	0·4	69

Table 5. *Estimates of daily food intake of geese grazing on sedge-dominated marshes during moult. Sample size is shown in parentheses*

	Anser brachyrhynchus	*Branta leucopsis*
Daily defaecation (droppings/24 h)	139 (621 min.)	144 (903 min.)
Dry weight of dropping (g)	0·86 (84)	0·80 (86)
Organic content (g ash-free)	0·74	0·61
Retention rate	0·31	0·37
Daily food intake (g ash-free)	149	138

grazing activity over a 24 h cycle, thus defaecating at a relatively constant rate. Compared to the situation on the wintering grounds, throughput time is probably

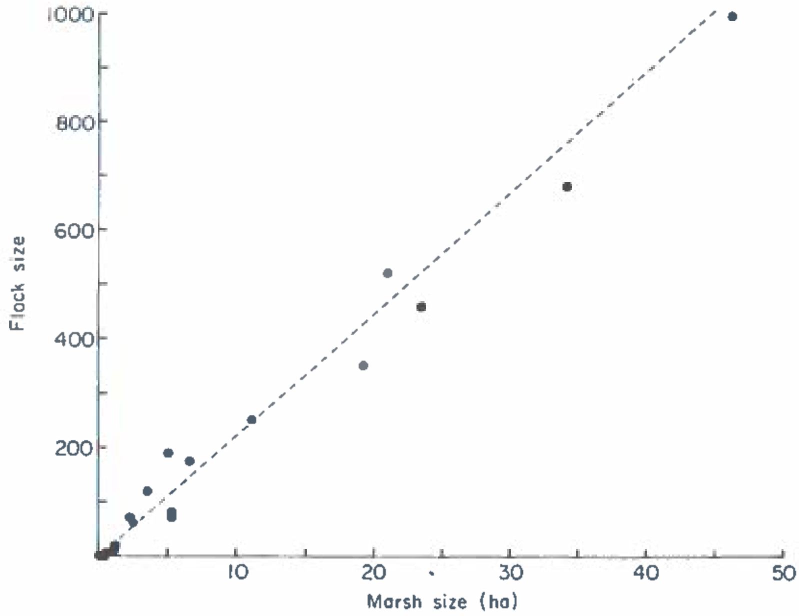


Figure 8. Relationship between size of moulting flocks of geese (both species included) and size of moulting area (sedge-dominated marshes), $Y = 19{\cdot}6X + 7{\cdot}2$, $r = 0{\cdot}992$, d.f. = 18, $P < 0{\cdot}001$.

slow, which may explain the high retention rates (compare with Ebbinge *et al.* 1975, Drent *et al.* 1981, Boudewijn 1984, Madsen 1985a).

As habitat selection of the moulting geese is so clearly confined to sedge marshes close to the refuge, the grazing intensity can be calculated. The exploitable feeding areas could, from the vegetation maps, be estimated to the nearest 0·1 ha. In Figure 8 the relationship between the available marsh area and the number of moulting geese is shown (no differentiation between species). Only areas where the moulting flocks were known to be stable (i.e., isolated lakes, some river systems and the coast, where the mobility of the geese was limited) have been used. The correlation indicates that the sites are occupied according to available food supplies, and the direct proportionality shows that the grazing pressure is similar at all sites. The results of the aerial observations indeed suggested that all potential sites in Jameson Land were occupied by geese; if geese were lacking from a lake, this coincided with lack of marshes, and alternatively lack of geese in large marsh coincided with lack of a refuge.

The geese arrive at the moulting ground about a week in advance of the moult and leave the areas immediately after regaining flying powers. Thus, it is estimated that the geese graze in the marsh areas for some 30 days. From the regression in Figure 8 we calculate an average grazing pressure of 594 goose-days/ha, equivalent to the availability of 17 m^2 to each goose per day. The mean food intake of a goose (average for both species) is 144 g organic matter/24 hr (152 g dwt). Thus, 9 g dwt of biomass are removed per m^2 by the geese in the course of the moult.

NAPP and nutrients of marsh vegetation

The 1983 sampling was started after the arrival of moulting Pinkfeet, and the marsh had been grazed already. From 5 July to 4 August the live above-ground biomass in

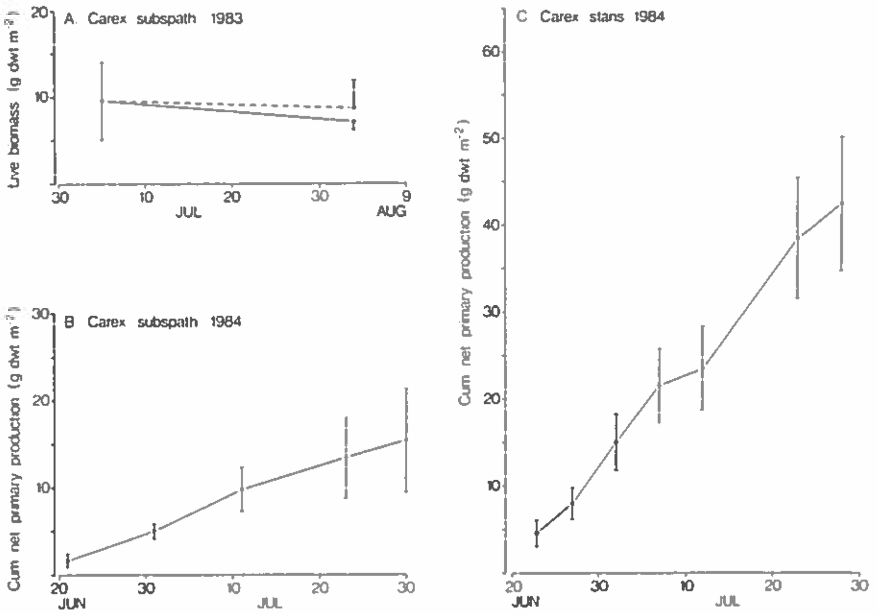


Figure 9. A: Development in live, above-ground biomass inside (——) and outside (– – –) exclosures of sward dominated by *Carex subspathacea*. B: Cumulative net above-ground production of a *Carex stans-Poa pratensis* sward. C: as B in a *Carex stans-Poa pratensis* sward. Bars show 95% confidence limits.

the exclosures dropped significantly ($F = 20{\cdot}2$, $v_1 = 2_1$, $v_2 = 15$, $P < 0{\cdot}01$) (Fig. 9A), while the dead biomass increased from 0·5 to 1·9 g dwt/m^2. On 4 August there was no significant difference between biomass outside and inside exclosures ($t = 0{\cdot}98$, d.f. = 10, NS), indicating that the marsh had not been grazed to any extent since 5 July. Over the period 5 July to 4 August, NAPP inside exclosures is estimated at less than 1 g dwt/m^2. This extremely low productivity was caused by the cold weather with mostly overcast sky. On 4 August vegetation height was below 0·5 cm (measured to the moss carpet).

The summer in 1983 was contrasted by the sunny and warm 1984 season with a continuous growth in the *C. subspathacea* marsh from snow melt to the end of July (Fig. 9B). The NAPP calculated on the basis of the clipping experiments was on average 13 g dwt/m^2.

Also in the *Carex stans-Poa pratensis* marsh growth continued throughout the moult period (Fig. 9C), though growth rates declined during the second half of July. The NAPP estimated from the clipping experiments was 38 dwt/m^2 with 87% *C. stans*.

The estimate of NAPP based on goose consumption is relatively crude, as data from 1983 and 1984 have to be combined, and can only be calculated for the *C. subspathacea* marsh. The biomass at the end of moult in 1983 was 7 g dwt/m^2. As the consumption of a goose has been calculated at 9 g dwt/m^2 during moult, NAPP can be calculated to be 11 g dwt/m^2. Unfortunately, no data exist concerning the biomass at the end of the 1984 moult. However, judging from vegetation heights in grazed swards ultimo July, there was estimated to be more standing crop in 1984 than in 1983. The calculated NAPP is thus probably an underestimate, and is instead believed to be *c.* 15 g dwt/m^2.

In the ungrazed plots of *C. subspathacea* sward, which were only clipped on 30

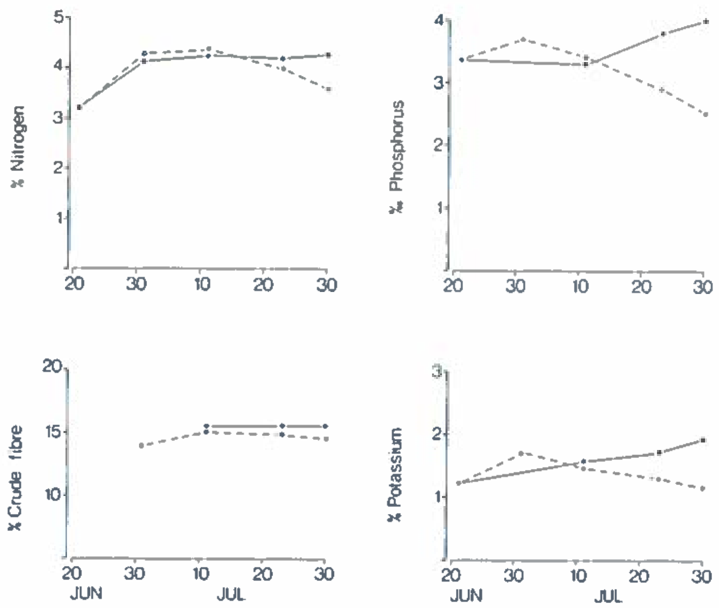


Figure 10. Trends in nutrient and fibre contents of *Carex subspathacea* without grazing (dashed lines) and with simulated grazing (solid lines). Values are percentage of per mille of dry weight. Analyses were carried out in duplicate.

July 1984, NAPP was estimated at 15 g dwt/m^2, not significantly different from the NAPP estimate of the clipped plots. Shoot density and average weight of 100 shoots of clipped and unclipped plots also did not diverge, indicating that clipping did not affect NAPP.

Nutrient contents, i.e., total nitrogen, phosphorus and potassium of *C. subspathacea* in 1984, showed similar trends over the period from snow melt to the end of July (Fig. 10). Due to lack of sufficient material for analysis, data from all collection dates cannot be shown. In the ungrazed vegetation, nutrient contents peaked in early July, while in the clipped vegetation contents remained high (nitrogen) or increased (phosphorus and potassium). The crude fibre contents did not show any trend during the course of July nor any difference between ungrazed and cut vegetation.

Discussion

Moult migration

Non-breeding geese of most populations undertake a moult migration which, with few exceptions, is northerly (Salomonsen 1968, Ogilvie 1978). Several hypotheses concerning the cause of the migration have been put forward, the most recent being avoidance of competition for food resources with breeding geese (Salomonsen 1968, Derksen *et al.* 1982), lessening of predation risk (Stirling & Dzubin 1967, Ebbinge & Ebbinge-Dallmeijer 1977), and optimal exploitation of spring growth (Owen & Ogilvie 1979).

As the breeding populations in Jameson Land are small (Madsen *et al.* 1984) the non-breeding geese arriving at the end of June fill up an almost empty niche. The timing of moult is closely correlated with the growth season. Around mid June most marsh areas are still snow-covered, and the arrival coincides with snow melt and the start of vegetation growth. Food quality peaks at the beginning of July, at which time the geese start to moult. This coincidence has also been shown between Black Brant *Branta bernicla nigricans* and the nutrient contents of vegetation in Alaska (Derksen *et al.* 1982).

The Pinkfeet originating from Iceland come from a situation of limited food resources. It has been suggested that the carrying capacity of the main breeding area, Thjórsárver, to breeding geese has been reached, and that the number of suitable moulting grounds is small (Gardarsson & Sigurdsson 1972). The moult migration to East Greenland is apparently of quite recent origin. In the 1920s acknowledged zoologists positioned in the Scoresby Sund region did not notice any north migrating geese in June (Pedersen 1926, 1930, Petersen 1941). The first reports of moult migrating Pinkfeet come from the 1950s (Taylor 1953, Conradsen 1957). The start of the moult migration coincides with a population increase, which may indicate that the migration developed because of a 'saturation' of the Icelandic moulting grounds. Exact population data prior to 1950 do not exist (Ogilvie 1978, pers. comm.), but the population probably did not exceed 20 000 individuals, while in the mid 1950s the population had increased to 40 000.

These findings are in support of both the hypothesis that the geese (at least the Pinkfeet) avoid competition with breeding geese by undertaking a moult migration, and that the geese make an optimal utilization of a nutritious and unused spring growth.

The predation hypothesis does not present a plausible explanation for the moult migration of the Pinkfeet. As already argued by Owen & Oglvie (1979), predators (foxes) are few in Thjórsáver, while they pose a constant threat to the moulting geese in East Greenland. However, the hypothesis that the Pinkfeet migrate from a situation of few suitable refuge areas to a situation of plenty relatively peaceful refuges cannot be ruled out.

Carrying capacity and grazing effects

Three circumstances point to the conclusion that the populations of moulting geese are close to the carrying capacity of Jameson Land:

(1) All suitable sites, i.e., coastlines and rivers and lakes with a certain minimum width, and with sufficient food supplies, are occupied by geese. The sites are filled up according to the size of the food resources with a constant grazing intensity of about 600 goose-days per ha and year.

(2) In the *Carex subspathacea* marsh, which is the most common moulting habitat in western Jameson Land, the geese remove a significant part of NAPP. In 1984, when growth conditions were probably optimal, NAPP was 13–15 g dwt/m^2, and the geese consumed on average 9 g dwt/m^2, viz. 60–69% of the production; in cold summers, such as 1983, the geese probably removed the entire production. In the *Carex stans-Poa pratensis* marsh the geese removed less, in 1984 *c.* 24% of the production. This marsh type has, however, a limited distribution in Jameson Land and is quite rare as feeding habitat during moult.

(3) By the end of the moult, which probably coincides with the end of the plant growing season, the marsh vegetation has been grazed below 0·5 cm height. In 1983 the geese abandoned the sites immediately after they regained flight and then utilized habitats which were not used earlier in the season.

The NAPP in the *Carex subspathacea* marsh is less than 1/5 compared to a *Carex subspathacea*-dominated salt marsh at Hudson Bay in subarctic Canada, grazed by Snow Geese *Anser c. caerulescens* (Cargill & Jefferies 1984). Presumably the difference is explained by the shorter and colder growing season in Jameson Land, although there may also be differences in nutrient input into the two areas.

The clipping experiments in the *Carex subspathacea* marsh in 1984 indicate that the geese did not affect productivity significantly. However, clipping and, by analogy, grazing, led to a maintenance of high nutrient contents throughout the moulting period, contrary to the ungrazed sward. It is suggested that repeated grazing keeps the plants in an early growth stage with maximal nutrient contents. Thus, the geese are able to optimize nutrient intake without diminishing the harvestable biomass.

Increase in nutrient content as a result of goose grazing has also been found on breeding grounds of Snow Geese (Harwood 1977, Cargill & Jefferies 1984) and spring staging areas of Barnacle Geese (Ydenberg & Prins 1981). In two studies it has, furthermore, been found that goose grazing may stimulate productivity. Cargill & Jefferies (1984) found an increase in productivity of *Carex subspathacea* by 35–80%, and Prins *et al.* (1980), in a study of Brent Geese grazing *Plantago maritima* in spring, showed that productivity was increased by repeated grazing.

Interspecific competition

It has been indicated that the species compete for limited resources. The Barnacle Goose, especially, seems to suffer from this, as its feeding efficiency is reduced by presence of Pinkfeet. In order to meet their energy requirements, the Barnacle Geese have to spend more time grazing, and they are forced to feed on mosses, which are less nutritious than sedges and grasses. One observation showed that by aggressive interference Pinkfeet may keep Barnacle Geese away from preferred food patches. Pinkfeet, on the other hand, seem not to be affected seriously by presence of Barnacle Geese, because they can exploit vegetation zones not available to Barnacle Geese.

Thus, it is advantageous for the Barnacle Geese to avoid sites preferred by Pinkfeet, and this is clearly reflected by the segretation of the two species. Compared to Barnacle Geese, Pinkfeet are extremely wary during the moult (Madsen 1984). As a result the Pinkfeet are limited to sites which offer a secure refuge, and—unlike Barnacle Geese—they dare not enter small rivers and 'closed' lakes.

Thus, the segregation involves (1) the Pinkfeet being restricted to open sites due to their wariness, and (2) the Barnacle Geese, in an attempt to avoid competition from Pinkfeet, selecting refuge areas which are too small or 'closed' to be accepted by Pinkfeet.

By what mechanisms this segregation happens is unknown. Despite intensive observations during the arrival phase in 1984, no encounters between flocks of the two species were seen. The moulting flocks established 'invisibly' by gradual arrival of groups of 2–5 birds (Madsen *et al.* 1984) to sites which were—by our experience from 1982 and 1983—traditional sites of the species. It is suggested that older Barnacle Geese who have visited the area in previous seasons have learned by experience which sites the Pinkfeet usually occupy and thus are likely to be unsuitable. Probably the older birds decide where to settle, presumably avoiding sites which they associate with stress. This mechanism will strongly reduce the chance that a site, jointly occupied by the two species during one year, will be occupied by Barnacle Geese during the following year. The explanation for the existence of mixing may be that the Pinkfeet arrive after the Barnacle Geese have started their moult, which traps the latter in a site.

Comparing aerial census data from 1983 and 1984, when complete surveys of Jameson Land were performed (Madsen *et al.* 1984) it is found that when separate in sites during the first year, Barnacle Geese re-occupied the same sites with a frequency of 0·86 the following year. When jointly occupied with Pinkfeet during the first year, the re-occupation frequency decreased to 0·55 ($n = 18$), and was especially low for sites where Barnacle Geese has been the minority species (0·33, $n = 12$). Although data are few, these results support the 'avoidance' hypothesis.

Few studies have focused on the carrying capacity and its consequences for breeding and moulting goose populations. In Spitsbergen, Prop *et al.* (1980, 1984) showed by a long term study that the depletion of food resources on the breeding grounds of Barnacle Geese limits the breeding output. Correspondingly, Gardarsson & Sigurdsson (1972) have indicated the same for breeding Pinkfeet in Thjórsárver in Iceland.

It has not been shown previously that competition for food resources occurs between goose species at the breeding or moulting grounds, and interspecific competition has only recently been demonstrated in the wintering quarters (Lok 1981, Madsen 1985b). Here one goose species avoids a more numerous species, analogous to the East Greenland situation. It has been suggested (Madsen 1985b) that avoidance due to exploitative competition is the explanation of the phenomenon, namely that the exploitative depression of the food supplies by one species makes it disadvantageous for the other species to flock with it. The same explanation may apply to the situation on the moulting grounds, although interference competition also seems to play a role.

In the light of the increase in most of the world's goose populations within this century, interspecific competition should be looked for in future studies. As shown in East Greenland, competition may affect local distribution of the involved species, and ultimately it may become a factor limiting population growth.

The studies were carried out by the Zoological Museum, Copenhagen as consultants to the Greenland Fisheries and Environment Research Institute. David Boertmann took part in the field studies in 1982 and 1983. Sune Holt and Christian Bay are thanked for help in the preparation of maps of goose habitats. Jon Fjeldså and Soren Toft kindly commented on the manuscript.

References

Bay, C. & Holt, S. 1984. Botaniske undersogelser i Jameson Land, 1983. Copenhagen: Greenland Fisheries and Environment Research Institute. (89 pp.).

Boudewijn, T. 1984. The role of digestibility in the selection of spring feeding sites by Brent Geese. Wildfowl 35: 97–105.

Cargill, S.M. & Jefferies, R.L. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. J. Appl. Ecol. 21: 669–686.

Conradsen, F.R. 1957. Ornithologiske Iagttagelser ved Daneborg, N.O. Gronland. Dansk Orn. Foren. Tidsskr. 51: 12–18.

Derksen, D.V., Eldridge, W.D. & Weller M.W. 1982. Habitat ecology of Pacific Black Brant and other geese moulting near Teshekpuk Lake, Alaska. Wildfowl 33: 39–57.

Drent, R., Ebbinge, B. & Weijland, B. Balancing the energy budget of arctic-breeding geese throughout the annual cycle: a progress report. Verh. orn. Ges. Bayern 23: 239–264.

Ebbinge, B., Canters, K. & Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl 26: 5–19.

Ebbinge, B. & Ebbinge-Dallmeijer, D. 1977. Barnacle Geese (*Branta leucopsis*) in the arctic summer—a reconnaissance trip to Svalbard. Norsk Polarinst. Arbok 1975: 119–138.

Gardarsson A. & Sigurdsson, J.B. 1972. Rannsoknir a heidagaes (*Anser brachyrhynchus*) 1971, Adrar attruganir i Thjorsarverum 1971. Reykjavik: Icelandic National Energy Authority.

Harwood, J. 1977. Summer feeding ecology of lesser snow geese. J. Wildl. Manage. 41: 48–55.

LOK, C.M. 1981. Beinvloden Brandganzen (*Branta leucopsis*) het voorkomen van andere ganzensoorten op de grasgorzen lang het Haringvliet? Watervogels 6: 78–87.

MADSEN, J. 1984. Study of the possible impact of oil exploration on goose populations in Jameson Land, East Greenland. A progress report. Norsk Polarinst. Skr. 181: 141–151.

MADSEN, J. 1985a. Relations between change in spring feeding habitat and daily energetics of Pink-footed Geese *Anser brachyrhynchus*. Ornis Scand. 16: 222–228.

MADSEN, J. 1985b. Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. Ornis Scand. 16: 140–144.

MADSEN, J., BOERTMANN, D. & MORTENSEN, C.E. 1984. The significance of Jameson Land, East Greenland, as a moulting and breeding area for geese: results of censuses 1982–1984. Dansk Orn. Foren. Tidsskr. 78: 121–131.

OGILVIE, M.A. 1978. Wild Geese. Berkhamsted: T. & A. Poyser.

OGILVIE, M.A. 1983a. Numbers of geese in Britain and Ireland, 1982–1983. Wildfowl 34: 172.

OGILVIE, M.A. 1983b. The numbers of Greenland Barnacle Geese in Britain and Ireland. Wildfowl 34: 77–88.

OWEN, M. 1975. An assessment of fecal analysis technique in waterfowl feeding studies. J. Wildl. Manage. 39: 271–279.

OWEN, M. & OGILVIE, M.A. 1979. Wing molt and weight of Barnacle Geese in Spitsbergen. Condor 81: 42–52.

PALUDAN, K. 1965. Grågåsens træk og fældningstræk. Danske Vildtundersøgelser 12 (54 pp.).

PEDERSEN, A. 1926. Beiträge zur Kenttnis der Säugetier—und Vogelfauna der Ostküste Grönlands. Meddr Grønland 68 (3): 149–249.

PEDERSEN, A. 1930. Fortgesetze Beiträge zur Kenttnis der Säugetier—und Vogelfauna der Ostküste Grönlands. Meddr Grønland 77 (5): 341–507.

PETERSEN, J. 1941. Dagbogsoptegnelser om Fuglenes Forekomst ved Scoresbysund Station fra Efteraaret 1934 til Sommeren 1935. Dansk Orn. Foren. Tidsskr. 35: 123–125.

PRINS, H.H.T., YDENBERG, R.C. & DRENT, R.H. 1980. The interaction of Brent Geese *Branta bernicla* and Sea Plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neerl. 29: 585–596.

PROP, J., EERDEN, M.R. VAN, DAAN, S., DRENT, R.H., TINBERGEN, J.M. & ST. JOSEPH, A.M. 1980. Ecology of the Barnacle Goose (*Branta leucopsis*) during the breeding season: preliminary results from expeditions to Spitsbergen in 1977 and 1978. Pp. 50–112 in Proceedings of the Norwegian-Netherlands Symposium on Svalbard (Arctic Centre, Groningen).

PROP, J., EERDEN, M.R. VAN & DRENT, R.H. 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk Polarinst. Skr. 181: 87–117.

SALOMONSEN, F. 1968. The moult migration. Wildfowl 19: 5–24.

STIRLING, T. & DZUBIN, A. 1967. Canada Goose molt migrations to the North-west Territories. Trans. N. Am. Wildl. Nat. Resour. Conf. 31: 355–373.

TAYLOR, J. 1953. A possible moult-migration of Pink-footed Geese. Ibis 95: 638–642.

YDENBERG, R.C. & PRINS, H.H.T. 1981. Spring grazing and the manipulation of food quality by Barnacle Geese. J. Appl. Ecol. 18: 443–453.

Danmarks Miljøundersøgelser

Danmarks Miljøundersøgelser er en forskningsinstitution i Miljøministeriet.

Opgaverne er at varetage og rådgive om dataindsamling og øge kendskabet til de processer og sammenhænge i naturen, der er af betydning for såvel anvendelsen som beskyttelsen af Danmarks natur- og miljøværdier.

Desuden skal Danmarks Miljøundersøgelser udvikle værktøjer og metoder, der kan sikre en sammenhængende og konsekvent politisk prioritering samt formidle resultaterne af forskningen og rådgive offentlige myndigheder og private virksomheder.

Den overordnede ledelse af Danmarks Miljøundersøgelser varetages af en bestyrelse, mens den daglige ledelse varetages af direktør og vicedirektør. Institutionen er i øvrigt organiseret med et økonomi- og personalesekretariat, et forsknings- og udviklingssekretariat og syv forskningsafdelinger.

Direktion:
Direktør Henrik Sandbech
Vicedirektør John Tychsen
Direktionssekretær Jytte Keldborg

Økonomi- og personalesekretariat:
Sekretariatschef Marianne Viltoft

Forsknings- og Udviklingssekretariat:
Vicedirektør John Tychsen

Adresse: Danmarks Miljøundersøgelser
Thoravej 8, 3. sal, 2400 København NV
Tlf. 31 19 77 44
Telefax: 38 33 26 44 og 31 19 76 92

Forskningsafdelinger:

Afd. for Forureningskilder og Luftforurening
Forskningschef: Christian Lohse
Frederiksborgvej 399, 4000 Roskilde
Tlf. 42 37 11 37. Telefax: 42 37 21 03

Afd. for Miljøkemi:
Forskningschef: Kons. Niels Henrik Spliid
Mørkhøj Bygade 26, 2860 Søborg
Tlf. 31 69 70 88. Telefax: 31 69 88 07

Afd. for Havmiljø og Mikrobiologi:
Forskningschef: Merete Reuss
Jægersborg Allé 1B, 2920 Charlottenlund
Tlf. 31 61 14 00. Telefax: 31 61 09 06

Afd. for Ferskvandsøkologi
Forskningschef: Torben Moth Iversen
Lysbrogade 52, 8600 Silkeborg
Tlf. 86 81 07 22. Telefax: 86 81 14 13

Afd. for Terrestrisk Økologi
Forskningschef: Hans Løkke
Vejlsøvej 11, bygn. J., 8600 Silkeborg
Tlf. 86 81 60 99. Telefax 86 81 49 90

Afd. for Flora- og Faunaøkologi
Forskningschef: Helmuth Strandgaard
Grenåvej 12, 8410 Rønde
Tlf. 86 37 25 00. Telefax: 86 37 24 35

Afd. for Systemanalyse
Forskningschef: John Holten-Andersen
Thoravej 8, 3. sal, 2400 København NV
Tlf. 31 19 77 44. Telefax: 38 33 26 44

Konsulent i Systemeksport: Hans Flyger
Frederiksborgvej 399, 4000 Roskilde
Tlf. 42 37 11 37. Telefax: 42 37 21 03

Datablad

Titel: Træk- og overvintringsstrategier hos gæs
Undertitel: Faktorer, der influerer på valg af rasteplads
Forfatter: Madsen, Jesper
Afdelingsnavn: Afd. for Flora- og Faunaøkologi, Kalø

Serietitel og nummer: Faglig rapport fra DMU, nr. 10
Udgiver ©: Miljøministeriet. Danmarks Miljøundersøgelser
Udgivelsesår: 1990

ISBN: 87-7772-010-5
ISSN: 0905-815X
Papirkvalitet: 90 g, mat
Tryk: offset
Oplag: 1000
Sideantal: 240
Pris: 160,- kr.

Trykkeri: Handy-Print A/S, Skive

Bedes citeret: Madsen, J. 1990. Træk- og overvintringsstrategier hos gæs: Faktorer, der influerer på valg af rasteplads. Faglig rapport fra DMU, nr. 10. Danmarks Miljøundersøgelser. 240 sider.

Kan rekvireres ved:
Danmarks Miljøundersøgelser
Afd. for Flora- og Faunaøkologi, Kalø
Grenåvej 12, 8410 Rønde
Tlf. 86 37 25 00