Overlap in diet and distribution of two goose species suggests potential for competition at a common moulting area in West Greenland

Katrine Raundrup, Nette Levermann & Michael Poulsen

(Med et dansk resumé: Overlap i fødevalg og rumlig fordeling i et fælles fældeområde i Vestgrønland indikerer potentiale for interspecifik konkurrence mellem to gåsearter)

Abstract Inter-specific competition can occur where two or more species overlap in diet and/or spatial distribution. Such interactions might be most prevalent where a species invades areas previously occupied by another species. In West Greenland, the number of native Greenland White-fronted Geese has decreased over the last 15-20 years, while the Canada Goose, a species new to the area, has increased. This study explores the overlap in diet and space use of these species in Mudderbugten and Kvandalen, together with factors that could influence the degree of competition between the two species. Data on activity budgets and spatial distribution were obtained from observations of behaviour, and diet selection was determined through analyses of plant epidermal fragments in faecal samples that were subsequently genotyped to goose species. No differences in diet or spatial distribution of the two species were found, and behavioural observations indicated only slight modifications in attentive behaviour and increased distance to the lakeshore in sympatry. This would seem to imply that the area has sufficient space and forage to support both species. If so, the local decline in Greenland White-fronted Goose may reflect population fluctuations for reasons other than the increased presence of the Canada Goose.

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Introduction

Arctic geese, such as the Greenland White-fronted Goose (*Anser albifrons flavirostris*) and the Canada Goose (*Branta canadensis*), migrate between their wintering and breeding areas (Boertmann 1994). At their arctic summer areas, most of their time is spent foraging (Madsen & Mortensen 1987, Prop & Vulink 1992); especially during moulting, when they need abundant high-quality food (Madsen & Mortensen op.cit., Fox et al. 1998b). Nitrogen is often limited, so selection for food with high protein content (Jefferies et al. 1994, Fox et al. 1998a, Cadieux et al. 2005) could potentially lead to inter-specific competition for food (Kristiansen & Jarrett 2002).

During the past 15-20 years, the Canada Goose has increased in numbers and range in West Greenland (Fox et al. 1996, Fox & Glahder 2010), during which time the population of the endemic White-fronted Goose has been showing contrasting trends in different parts of the breeding range (Egevang & Boertmann 2001, Kristiansen & Jarrett 2002, Fox & Glahder 2010). In Isunngua, Kangerlussuaq, White-fronted Goose takes lower-quality forage and has a broader food spectrum and a lower food intake in sympatry with Canada Goose, compared to allopatry (Kristiansen & Jarrett 2002), suggesting an adverse effect due to competition (Kristiansen 1997). In Mudderbugten and Kvandalen (Aqajarua and Sullorsuaq), Disko, West Greenland, an area considered of international importance for the population of Greenland White-fronted Goose, the number of Canada Goose has increased from one in 1979 (Frimer & Nielsen 1990) to 373 in 2001 (Egevang & Boertmann 2001). If the two species of geese rely on the same food and spatial resources, an increase in numbers of Canada Goose could incur an increased competition. We explore this by comparing diet, foraging behaviour, and distribution of the species in allopatry and sympatry.

Fig. 1. Map of Greenland with indication of the study area Mudderbugten/Kvandalen, and of Isunngua at Kangerlussuaq.
Kort over Grønland med angivelse af studieområdet Mudderbugten/Kvandalen samt af Isunngua nær Kangerlussuaq.

Methods

Study area
The study took place in Mudderbugten and Kvandalen, West Greenland (69°45'N; 52°00'W, Fig. 1), during 9-28 July 2004. Goose observations and activity data were gathered from an observation post c. 6.5 km from the coast and 1-1.5 km from the study lakes (a distance expected to not affect the geese); the observation post was situated 30 m above lakeshore level. Observations were assigned to 'allopatry' if only one species was present, and 'sympatry' if both species were present. Observations mainly covered moulting non-breeding geese. In cases were breeding birds (families) occurred, data (behaviour, distance to lake shore) were not included for the goslings. The lakes were under continuous observation, except under low-light conditions (22:20-8:30 local time (GMT-2)) or when geese were not visible due to *Salix glauca* cover.

Activity budget and foraging behaviour
Behavioural observations by binoculars and spotting scopes were done using 5-minute scan-sampling (Martin & Bateson 1993). Recorded were: goose species, distance to other geese, distance to lakeshore, and behaviour (foraging, resting, preening, sleeping, standing, walking, running, swimming, agonistic, and head up (vigilant); cf. Kristiansen & Jarrett 2002). Distances (between geese

and from geese to open water) were measured in goose lengths (GL) (cf. Kristiansen & Jarrett op.cit.), and differences in distance were analysed using a Kolmogorov-Smirnov two-sample test (Quinn & Keough 2002).

Habitat use and vegetation analyses

A reference collection of plant species present at the lakes was made, comprising dried specimens (for species determination) and epidermis peals preserved in 96% alcohol (for reference slides) (cf. Patterson et al. 1989). Eight transects (length 15-50 m depending on the extent of *Salix glauca* cover) were sampled perpendicular to the shore to estimate species composition, using Raunkiær circles (1/10 m^2, radius: 17.8 cm) at 5 m intervals (Böcher & Bentzon 1958). A paired t-test was applied to test for differences in plant composition between the study lakes, after arcsin$\sqrt{x}$ transformation. Information on local distribution of feeding geese was obtained on 28-29 July from the same transects by counting goose droppings in 2 m^2 quadrates (cf. Patterson et al. 1989). Log(x+1) transformed dropping densities were analysed using ANOVA, with independent variables being locality (the two lakes) and distance to shore. Twenty-four droppings were collected for analysis of diet; half of each sample was sun-dried and stored in paper bags for plant identification, while the remaining half was preserved in 96% alcohol for genetic analyses.

Diet selection was analysed by identifying 100 random epidermal fragments per dropping and calculating the frequency of individual plants (Owen 1975). Selection was assessed using Jacobs' index: $D = (d-f)/(d+f-2df)$, where d = the proportion of plant species in the diet (droppings) and f = the proportion of plant species in the vegetation ($D = -1$: complete avoidance, $D = +1$: complete preference; Jacobs 1974). Niche-breadths were calculated using Levins' standardised equation: $B_A = (1/\Sigma p_i^2 - 1)/(n-1)$, where p_i = the frequency of each type of forage in the diet, and n = the number of forage types ($B_A = 0$: narrow niche-breadth, $B_A = 1$: broad niche-breadth; Krebs 1999). Multinomial logistic regression was used to test for diet differences, with the response variable being the distribution of plant groups in droppings, and independent factors being plant group, goose species, and the plant group*goose species interaction term (Crawley 1993).

Genetic analyses

Faecal samples were genotyped to origin (goose species) by extracting DNA using the UltraClean™ Fecal DNA Kit (MO BIO Laboratories, Carlsbad, CA) from ca 0.25 g of 96% ethanol-stored faecal samples after alcohol evaporation. Cytochrom b was amplified using published primers [Cytb1 (L14990) and Cytb2 (H15298) (Kocher et al. 1989) or Cytb3 (L15104) (Sorenson et al. 1999) and Cytb4 (H15021) (Kocher et al. 1989)]. PCR using 2xGotaq® Green MasterMix (Promega Corp., Madison, WI) were run on for 3 min. at 93°C, 30-40 cycles of 1 min. at 93°C, 1 min. at 44.0-50.0°C, and 4 min. at 72°C, and 10 min. at 72°C. Products were cleaned with a DNA Clean and Concentrater™-5 kit (Zymo Research, Orange, CA). Sequencing reactions (2µl Big Dye, 2µl buffer, 0.4µl primer, 4.6µl ddH_2O and 1µl clean PCR product per sample) were run for 3 min. at 95°C, 35 cycles of 20s at 95°C, 30s at 45°C, 4 min. at 60°C, and 7 min at 72°C. Reactions were cleaned using CleanSeq Reaction Clean-Up (Agencourt Bioscience Corporation, Beverly, MA), and sequenced at the UW-Madison Biotechnology Center (http://www.biotech.wisc.edu). Sequences were aligned in Sequencher 4.6 (Gene Codes Corporation, Ann Arbor, MI) and base pair sites between new sequences and sequences from GenBank were compared at the 26 sites where divergences exist (8.5% of the region; Paxinos et al. 2002).

Results

Activity budget and foraging behaviour

Behavioural observations were made for a total of 110 hours: 58 hours of allopatric situations (32 hours on White-fronted Goose and 26 hours on Canada Goose) and 52 hours of sympatric situations. In allopatry, White-fronted Goose and Canada Goose spent 25% and 20% of their time foraging, respectively, which was marginally non-significantly different ($D = 0.083$, $P = 0.051$) (Fig. 2a). In sympatry, White-fronted Goose fed for 28% of time, significantly more than Canada Goose (14%, $D = 0.172$, $P < 0.05$). Canada Goose spent less time foraging in sympatry than in allopatry ($D = 0.117$, $P < 0.05$), in contrast to the White-fronted Goose ($D = 0.038$, $P > 0.85$). The White-fronted Goose spent less time resting, whereas Canada Goose spent 13% and 25% of the time resting in sympatry and allopatry, respectively. Canada Geese increased their time swimming from 19% in allopatry to 31% in sympatry, while White-fronted Geese did not show any such change (28% in allopatry and 26% in sympatry). Finally, Canada Goose showed a higher degree of alert behaviour (head up) in sympatry, whereas it was reduced in White-fronted Goose (Fig. 2a). In allopatric situa-

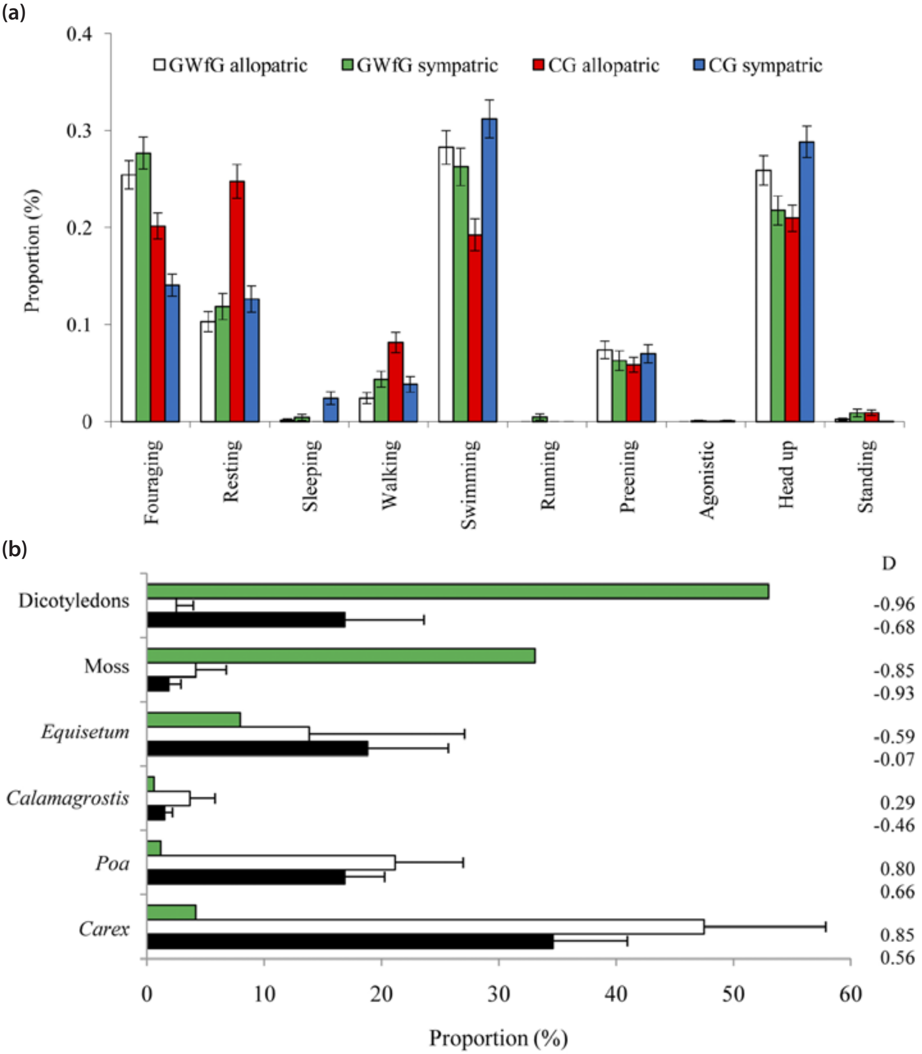

Fig. 2. (a) Activity budget with proportions (±SE) of the observed behaviours for Greenland White-fronted Goose (GWfG) in allopatry (☐) and sympatry (🟩), and Canada Goose (CG) in allopatry (🟥) and sympatry (🟦). **(b)** The frequency of plant species in the goose droppings of GWfG (☐) and CG (■) (mean+SE) and in the vegetation (🟩). Jacobs' preference index, *D*, indicates the degree of selectivity from -1 (complete avoidance) to +1 (complete preference).

(a) *Aktivitetsbudget for observeret adfærd hos Blisgæs i allopatri (☐) og sympatri (🟩), samt Canadagæs i allopatri (🟥) og sympatri (🟦).* ***(b)*** *Frekvensen af plantearter i gåseafføring for Blisgæs (☐) og Canadagæs (■) (gennemsnit +SE) samt i vegetationen (🟩). Jacobs præference index, D, angiver graden af selektivitet og rangerer fra -1 (fuldstændig undgåelse) til +1 (fuldstændig præference).*

tions, White-fronted Goose kept the same distance to the shore as Canada Goose, but this changed in sympatry, where White-fronted Geese were further away from the shore (Table 1). For both species, individuals were further from each other in allopatry than in sympatry.

Genetic analyses

Sequences generated in this study did not differ from published sequences, so they were not submitted to GenBank. Comparisons to published sequences (Paxinos et al. 2002) identified 17 samples from Canada Goose and seven from White-fronted

Table 1. Distances in goose lengths (GL) to the lakeshore and to other geese for Greenland White-fronted Goose (GWfG) and Canada Gooose (CG) in allopatric (AS) and sympatric situations (SS) in Mudderbugten and Kvandalen. Test coefficients (D) and P-values from the Kolmogorov-Smirnov two-sample tests are listed.
Afstande i gåselængder (min., max. og gennemsnit (mean)) til søbred og til andre gæs for Blisgås (GWfG) og Canadagås (CG) i allopatriske og sympatriske situationer i Mudderbugten og Kvandalen. AS: allopatri, SS: sympatri. Testkoefficienter (D) og P-værdier fra Kolomogorov-Smirnov two-sample test er angivet.

		n	Min	Max	Mean±SE	Test coefficient	P-value
Distance to shore							
AS	GWfG	486	0	25	2.2±0.15	D=0.099	P=0.08
	CG	227	0	30	2.1±0.23		
SS	GWfG	447	0	40	4.0±0.32	D=0.146	P<0.05
	CG	447	0	30	2.3±0.15		
AS→SS	GWfG					D=0.131	P<0.05
AS→SS	CG					D=0.114	P<0.05
Distance between individuals							
AS	GWfG	446	1	300	15.4±1.52	D=0.336	P<0.05
	CG	221	1	500	38.6±4.45		
SS	GWfG	418	1	200	9.0±0.70	D=0.195	P<0.05
	CG	408	1	500	12.0±1.61		
AS→SS	GWfG					D=0.090	P=0.054
AS→SS	CG					D=0.410	P<0.05

Goose. From a binomial distribution of the samples with a White-fronted Goose frequency of 0.32 in the study area (112 GWfG, 238 CG), $P = 2\sum p(x) = 0.96$ was obtained, supporting that droppings represented a random sample of the area.

Habitat use and vegetation analyses

Twenty-four different plant taxa were found along the eight transects: 13 species of dicots (*Hippuris vulgaris*, *Ranunculus hyperboreus*, *Salix arctica*, *Lychnis alpina*, *Sagina nivalis*, *Empetrum nigrum*, *Vaccinium uliginosum*, *Stellaria* sp., *Betula nana*, *Polygonum viviparum*, *Ledum palustre*, *Draba* sp. and *Pedicularis* sp.), four monocot genera (*Poa* sp., *Carex stans*, *Calamagrostis hyperborea* and *Juncus arcticus*), two pteridophytes (*Equisetum arvense* and an unidentified fern), mosses, and four unidentified species. Unidentified plants (<5%) were not included in the analyses. There was no significant difference in plant distribution between the two lakeshores ($t = -0.757$; $df = 7$; $P = 0.47$), so the combined data set was used in the following analyses. Goose dropping densities were neither significantly different along transects ($\bar{x} = 3.0$ (±0.82) pr 2 m^2, $F_{1,49} = 0.176$; $P = 0.68$) nor between lakes ($F_{1,49} = 0.136$; $P = 0.71$).

The proportion of epidermis remains in 22 of the 24 collected droppings (one sample from each goose species was excluded due to absence of plant remains) was used for dietary selection and niche breadth analyses. Species of dicots were indistinguishable in the faecal samples; thus, they were grouped. Jacobs' index of preference D showed that the geese selected for *C. stans* and *Poa* spp. (48% and 21% of the diet of White-fronted Goose; 35% and 17% in Canada Goose; Fig. 1b). White-fronted Goose further selected for *C. hyperborea*, even if constituting only 4% of the diet. *E. arvense* also constituted a portion of the diet (Fig. 2b), but the geese generally did not select this species. Although 17% of the diet of Canada Goose was dicots, these as well as mosses were generally avoided. Diets were not significantly different between species ($F_{5,120} = 1.330$; $P = 0.256$), and dietary niche breadths were overlapping [GWfG: $B_A = 0.228$ (±0.054); CG: $B_A = 0.227$ (±0.035)].

Discussion

The absolute number of the two species of geese in Mudderbugten and Kvandalen has increased over the past 15-20 years; however, with a decrease of White-fronted Goose in some areas. The colonisation by, and increase of, Canada Goose in the area may have increased the level of sympatric occurrence of the species, cf. that occurrence at both lakes was not exclusively allopatric or sympatric during this study. Increased sympatry could imply increased competition if foraging ecology and space use of the species overlap.

Comparing the composition of plant species in

Photo: Carsten Egevang.

På trods af Canadagåsens indtog som ynglefugl i de områder i Grønland, hvor Blisgåsen yngler, synes der ikke at være større konkurrence mellem dem.

the vegetation and the plant remains in the genotyped goose faeces indicated a preference for *Poa* and *Carex*, corresponding to food preferences in Isunngua, although at different proportions [Isunngua: *Poa*: 46-57% and *Carex* 10-35% (Kristiansen & Jarrett 2002); this study: *Poa*: 17-21% and *Carex* 35-48%]. These differences likely reflect vegetation composition differences between the areas [Isunngua: 10-15% *Poa* and 1-10% *Carex* (Kristiansen & Jarrett op.cit.); this study: 1% *Poa* and 4% *Carex*]. In both studies, dicots and mosses were generally avoided, even though there was a tendency for moss selection by sympatric White-fronted Goose in Isunngua (Kristiansen & Jarrett op.cit.), and a higher proportion of dicots in Canada Goose diet in the present study. The narrow and overlapping niche breadths, averaging 0.23 for both species, are similar to results obtained in Isunngua (0.18-0.21; Kristiansen & Jarrett 2002), and support the potential for diet competition between the two species.

Increasing number of geese implies the potential for competition for suitable foraging space, which may affect behaviours and possibly have a negative impact when high food intake is needed (Madsen & Mortensen 1987, Fox et al. 1998b). White-fronted Goose showed only minor behavioural changes in the presence of Canada Goose, which could partly be due to a higher rate of alertness (Fig. 2a). Both species spent less time foraging (14-28%) in Mudderbugten and Kvandalen compared to observations from Isunngua (24-31%; Kristiansen & Jarrett 2002). Canada Geese seemed to be most affected, since they reduced time spent on foraging and resting, clumped together more often, stayed closer to the shore, and appeared more mobile and vigilant than White-fronted Goose (Fig. 2a; Table 1). The increased distance of White-fronted Goose to the shore in sympatry could be disadvantageous in the presence of predators, such as the arctic fox (*Alopex lagopus*). In Isunngua, White-fronted Goose forage closer to the shore in sympatric situations (Kristiansen & Jarrett 2002), but this is disadvantageous because forage is of lower quality. A similar shift in this study was likely precluded by *Salix glauca* cover at the lakeshore (KR & NL, personal observations).

Although based on limited sampling, our findings suggest that the impact of Canada Goose on White-fronted Goose in Mudderbugten and Kvandalen is minor at present goose densities, in contrast to findings in Isunngua (Kristiansen & Jarrett 2002). The explanation for this difference may be topographical: Isunngua is located in a mountainous terrain, where geese feed in discrete units (lakes and associated wetlands) separated by extensive unsuitable habitat. The geese are consequently "trapped" during the flightless period and must suffer the consequences of sharing the space. Geese in that terrain are expected to be more affected than individuals in a broad open valley system, like that of Mudderbugten and Kvandalen. However, if the number of Canada Geese continues to rise, competition is likely to increase, considering the narrow and overlapping dietary niches.

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Resumé

Overlap i fødevalg og rumlig fordeling i et fælles fældeområde i Vestgrønland indikerer potentiale for interspecifik konkurrence mellem to gåsearter

Interspecifik konkurrence kan forekomme i områder, hvor to eller flere arter har overlap i fødevalg og/eller rumlig fordeling. Interspecifikke interaktioner forventes at være tydelige i områder, hvor arter koloniserer hidtil ubesatte områder, og kan potentielt resultere i ugunstige effekter for såvel den koloniserende som den eller de oprindelige arter. Arktiske gæs, som Grønlandsk Blisgås (*Anser albifrons flavirostris*) og Canadagås (*Branta canadensis*), har brug for store mængder føde af høj kvalitet, især i sommerområderne (Madsen & Mortensen 1987, Fox et al. 1998b). Da kvælstof ofte er begrænsende, er der selektion for føde med højt indhold af protein, og dette kan føre til interspecifik konkurrence (Kristiansen & Jarrett 2002).

I Vestgrønland er antallet af Blisgæs faldet i løbet af de seneste 15-20 år samtidig med, at antallet af Canadagæs, en ny art i området, er steget. Hvorvidt dette skyldes øget konkurrence mellem de to arter er uvist. I denne undersøgelse målte vi overlappet i fødevalg samt den rumlige fordeling af de to gåsearter i Mudderbugten og Kvandalen på Disko i Vestgrønland, da disse faktorer kan være styrende for graden af konkurrence mellem dem.

Adfærdsobservationer tillod udarbejdelsen af aktivitetsbudgetter samt undersøgelse af gæssenes rumlige fordeling i området. Ti forskellige adfærdstyper blev registreret: fødesøgning, hvile, fjerpudsning, søvn, ståen, gang, løb, svømning, agonistisk interaktion og årvågenhed. Yderligere blev afstanden mellem gæs og mellem gæs og åbent vand (nærmeste sø) estimeret, udtrykt i gåselængder (jf. Kristiansen & Jarrett 2002). Alt i alt fandt vi ingen statistisk signifikante forskelle i de to gåsearters rumlige fordeling i området under allopatriske forhold. Der var dog et mindre omfang af adfærdsændringer og ændring i afstand til søbreden i sympatriske situationer. Blisgæs udviste færre adfærdsændringer ved tilstedeværelsen af Canadagæs end omvendt (Figur 1a). Samlet set brugte begge arter dog mindre tid på at fouragere (14-28%) i Mudderbugten og Kvandalen sammenlignet med observationer fra Isunngua længere mod syd i Vestgrønland (24-31%; Kristiansen & Jarrett 2002). Canadagæs syntes at være mest berørte, da de brugte mindre tid på fouragering og hvile, blev hyppigere observeret tættere på hinanden, var tættere på søbreden, og syntes mere mobile og årvågne end Blisgæs (Figur 2a, tabel 1).

Fødevalg blev bestemt ved hjælp af undersøgelser af plantemateriale i afføringsprøver, som efterfølgende blev henført til gåseart ved brug af sekventering af ekstraheret gåse-DNA fra afføringen. Plantesammensætningen i disse fæcesprøver viste en præference for *Poa* og *Carex*, svarende til præferencen i Isunngua, om end i et andet omfang, hvilket sandsynligvis afspejler forskelle i vegetationssammensætning mellem de områder. Der var overlappende nichebredder og en ikke-signifikant forskel i fødevalg mellem de to gåsearter. Disse resultater svarer til resultater opnået i Isunngua (Kristiansen & Jarrett 2002) og tyder på potentiale for fødekonkurrence mellem de to arter.

Undersøgelsen bygger på et relativt begrænset datamateriale, men indikerer dog, at Kvandalen og Mudderbugten har tilstrækkelig størrelse og fødegrundlag til begge arter med de nuværende bestandsstørrelser, idet vi ikke fandt evidens for interspecifik konkurrence mellem dem. Dette kontrasterer til situationen i Isunngua, og forskellen kan skyldes topografien: Isunngua ligger i et bjergrigt terræn, hvor gæs fouragerer i diskrete enheder (søer og tilknyttede vådområder), adskilt af omfattende områder af uegnede levesteder. I fældningsperioden er gæssene derfor "fanget" og lider under følgerne af at måtte dele den begrænsede plads. De kan altså forventes at være mere påvirkelige af konkurrence, end de vil være i et bredt, åbent dalsystem som det i Mudderbugten og Kvandalen. Den lokale nedgang i antallet af Blisgæs i Mudderbugten og Kvandalen er derfor sandsynligvis snarere et udtryk for fluktuationer i populationen end et resultat af den øgede tæthed af Canadagæs.

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Katrine Raundrup[1], Nette Levermann[2] & Michael Poulsen[3]
Department of Population Biology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

[1] *Present address*: Greenland Institute of Natural Resources, P.O. Box 570, 3900 Nuuk, Greenland

[2] *Present address*: Ministry of Hunting, Fishery and Agriculture, Government of Greenland, P.O. Box 269, 3900 Nuuk, Greenland

[3] Corresponding author (mpoulsen@bio.ku.dk). Present address: Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen, Denmark