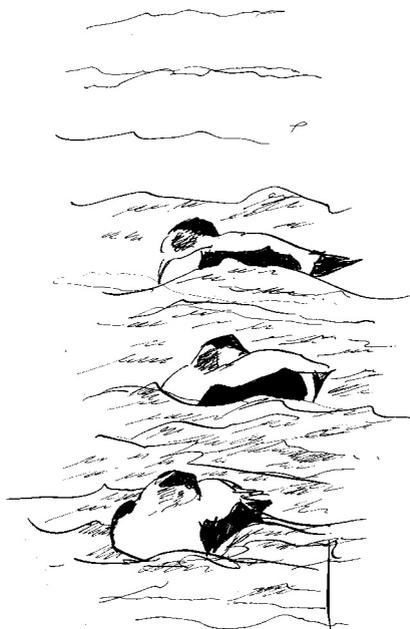


# Year-round movements of Northern Common Eiders *Somateria mollissima borealis* breeding in Arctic Canada and West Greenland followed by satellite telemetry

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We implanted satellite transmitters to track Northern Common Eiders *Somateria mollissima borealis* from breeding grounds in West Greenland and eastern Arctic Canada, and from their wintering grounds in SW Greenland. We compared distances moved, timing, duration, and patterns of movement between migration flyways and between spring and autumn migration. Common Eiders used two wintering areas linked by three routes. Eiders tracked from a NW Greenland breeding colony ( $n = 10$ ) migrated south along the coast to winter exclusively in west and southwest Greenland. Breeders from Arctic Canada wintered in two distinct areas with a tendency to segregate by sex. Some eastern Canadian Arctic Eiders from a colony near Southampton Island, migrated through Hudson Strait along the Labrador and Newfoundland coasts, to winter in Atlantic Canada. However, 60% ( $n = 25$ ) originating from this colony crossed the Davis Strait to winter in SW Greenland, returning in spring to breed in Canada, linking the two north-south flyways. Seven of 8 Eiders implanted in SW Greenland in winter crossed the Davis Strait into Arctic Canada in spring to breed. Apparently more females than males from the Canadian colony (14/18 females and 1/6 males) followed the shorter east-west flyway in fall. Spring migration was initiated later in the Canadian Arctic. Tracked movements ranged from sedentary birds that nested within 45 km of their wintering area in SW Greenland, to migration routes that exceeded 2000 km. Spring migration speeds averaged c. 60 km d<sup>-1</sup>, less than half that during moult migration (142 km d<sup>-1</sup>) and autumn migration (190 km d<sup>-1</sup>). This suggests that Eiders must stop to feed whilst travelling to breed, are constrained by sea ice conditions, or both. Climatic and sea ice conditions differ between the eastern Arctic Canada and west Greenland which influence wintering sites, timing and routes of spring migration.



Key words: annual migration patterns, migration rate, sea ice

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## INTRODUCTION

Many birds exploit different habitats for reproduction, moulting and wintering, often to avoid seasonal environmental extremes, the template for the evolution of migration in birds. Present migration patterns are generally thought to be the result of prevailing environmental conditions shaped by changes in the distribution of the species since the last glaciation (Alerstam & Hedenström 1998, Alerstam *et al.* 2003). The routes and timing of migration are thought to maximise fitness of birds (Drent *et al.* 2003) and differences detected in spring and autumn migration strategies may indicate that factors, which constrain birds during migration, also vary seasonally.

The Northern Common Eider *Somateria mollissima borealis* breeds in the eastern Canadian Arctic and western Greenland, much of which is ice-bound in winter (Fig. 1), forcing them to migrate to open water areas further south where they can reliably forage in winter. Ocean currents of the region have a profound influence on sea ice and climate. For example, the cold south-flowing current along Baffin and Labrador coasts perpetuate a prolonged season with coastal ice cover. Along the southwest Greenland coast (62–67°N), large areas of open water persist all year round (the Southwest Greenland Open Water Region, SGOWR) due to relatively warm contributions from the North Atlantic current to the north flowing West Greenland current. The SGOWR supports c. 460 000 Common Eiders and 300 000 king Eiders in winter (Mosbech and Johnson 1999, Merkel *et al.* 2002, Boertmann *et al.* 2004); almost all of which are thought to breed in the eastern Canadian Arctic (Gilliland *et al.*, unpubl.). The substantial harvest of Eiders in the SGOWR in winter has given concern about its sustainability (Piniarneq 2004, Merkel 2004, Gilliland *et al.* unpubl.). We therefore need to better understand Common Eider population structure and migration pathways throughout the eastern Canadian Arctic and west Greenland.

Our objectives were to contrast migration patterns and examine possible links between the breeding and wintering areas of Northern

Common Eiders in Canada and Greenland. Satellite transmitters provide periodic locations of individual tagged birds to show how migratory decisions may be influenced by seasonal conditions. To provide reliable information, transmitters must be small and deployed in a way that minimises their effects on bird behaviour. Surgical implantation of transmitters into the abdominal cavity of sea ducks have proven effective (e.g. Spectacled Eiders *Somateria fischeri*, Petersen *et al.* 1995, 1999). Here, we use this technique to compare timing, duration, distances moved and patterns of movement of Northern Common Eiders during both fall and spring migrations, and discuss the management implications of our findings.

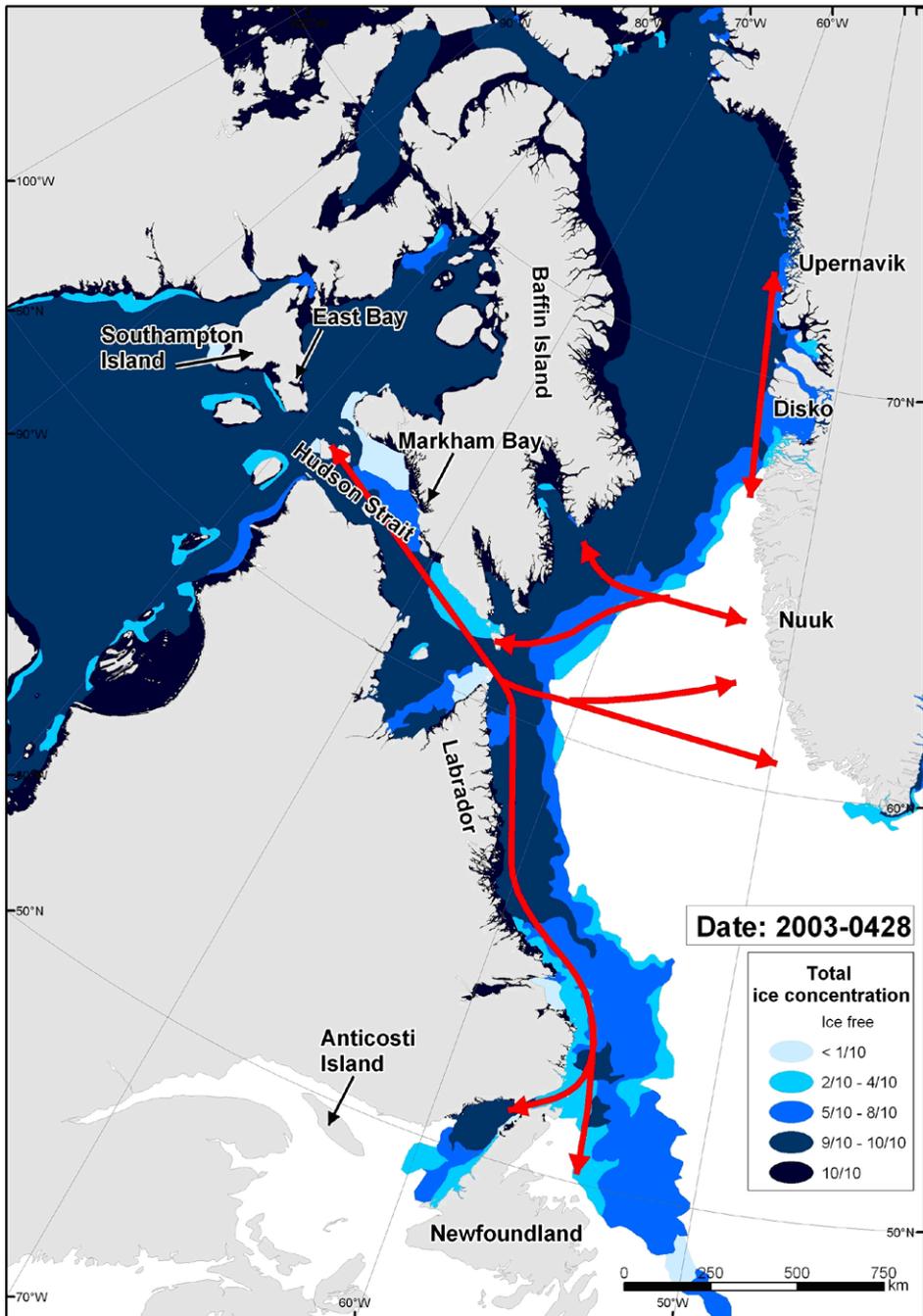
## METHODS

### Satellite transmitters

We implanted satellite transmitters (Platform Transmitter Terminals, PTTs) in Eiders to follow them during migration. Transmitters were 50 g pressure-proof implantable Model PTT-100 (Microwave Telemetry Inc). Most PTTs had expected battery life of 700 transmission hours ( $n = 76$ ), other PTTs were fitted with pressure transducers ( $n = 11$ ), which reduced expected battery life to 400–500 transmission hours. PTTs were programmed with a variety of duty cycles. Some PTTs had slow duty cycles (i.e. 4 hours of continuous transmission and 60 hours off) so that they actively transmitted for more than a year. Other PTTs were programmed with fast duty cycles (e.g. 4 hours transmission and 10 hours off) providing detailed, often daily, information on locations for a few months. In this study, we included only birds, which provided enough locations to track and classify autumn and/or spring migration routes between breeding and wintering areas.

### Field methods

We implanted 26 Common Eiders breeding at a large colony in East Bay, Southampton Island, Arctic Canada (10 between 22 and 25 June 2001 and 16 between 28 June and 8 July 2003), and 21



**Figure 1.** Map with marking localities (East Bay, Upernavik, Disko Island, Nuuk Fjord), spring ice conditions (28 April 2003) and main flyways for the Arctic eastern Canadian – West Greenland Common Eider population. (Ice data from the National Ice Center: <http://www.natice.noaa.gov/products/arctic/index.htm>)

at breeding colonies in Upernavik, West Greenland (15–23 June 2002). We also implanted transmitters into 33 Eiders between 23 February and 6 March in 2000 and 2001 at Nuuk fjord along the central coast of Southwest Greenland and into 7 Eiders at moulting sites on the west coast of Disko Island (7–14 September 2003). In total, we marked 87 Eiders in four areas (Fig. 1).

Birds were caught in large mist nets or in nest traps at breeding sites at both East Bay and Upernavik (Mosbech *et al.* 2001, Gilchrist 2003). At moulting (Disko Island) and wintering sites (Nuuk Fjord) Eiders were captured in mist nets raised between floating platforms (Mosbech *et al.* 2001) or in modified fishing nets (Mosbech *et al.* 2004). After capture, Eiders were immediately freed from the net and transported in a holding box of plywood or cardboard with absorbent padding prior to surgery.

At the capture sites, the surgical implantation procedure was performed using the abdominal implant technique developed by Korschgen *et al.* (1996a); 5 of the transmitters were deployed following a procedure for subcutaneous implantation, also described by Korschgen *et al.* (1996b) and modified as described in Merkel *et al.* 2006.

We estimated body condition as total carcass lipids (TCL, g) from the equation:

$$\text{TCL} = -100.13 - 39.38 \text{ Sex} + 0.32$$

$$\text{Body Mass} + 2.72 \text{ Wing Chord} - 8.92 \text{ Head}$$

The equation explained 61% of the variation in total carcass lipids of Common Eiders during the non-breeding season in Nuuk, Southwest Greenland (Jamieson *et al.* 2006) and is assumed to be a reasonable body condition estimator in other seasons as well.

### Data collection

Location data were received from the Argos Location Service Plus system in DIAG format. Locations are classified according to accuracy by Argos; Location Class (LC) 3, 2, and 1 locations have an estimated accuracy (within one SD) of <150 m, 150–350 m, and 350–1000 m, respectively, whereas the accuracy of non-standard loca-

tions (LC 0, A, and B) are >1000 m or unknown (Argos User's Manual <http://www.cls.fr/manuel>). However, most of the LC 0 and A locations are within 9 km of the true location (Britten *et al.* 1999).

To analyse migration routes, all PTT locations were included except obvious outliers (i.e. defined as a single low quality location (Z, 0, B, A) >100 km out of expected range). Based on this dataset, migration distances were calculated along routes defined by the best location per duty cycle using the ArcView GIS extension "Animal Movements" (Hooze *et al.* 1999, 2004) and the map projection WGS84 UTM 20N. However, for duty cycles less than 24 hours the best location per day was selected based on Argos Location Class. In the event of a tie, the location with the most messages received during the satellite overpass was selected for that day using the PC-SAS ARGOS filter ('bestpick'; Douglas 2003). Routes defined by direct distance between consecutive bestpick-locations sometimes made an unrealistic shortcut over land departing from the anticipated coastal route; presumably due to a time-lapse of several days between locations. Therefore, an alternative distance estimation was calculated by measuring the length of the smoothed coastal track using ArcView (ESRI Inc.). Unless otherwise stated, the direct distance between locations is used because it is unbiased from interpretation. Migration tracks with more than a week between consecutive bestpick locations were omitted from analysis of timing and duration (four routes).

### Analysis of movements

Migration routes were defined as starting (and ending) with the first (and last) directional movements in excess of 100 km from specific breeding, moulting or wintering areas in the general migration periods: (1) Moulting migration (August–September), (2) Autumn migration (August–December) (classified as either autumn migration following local moult or autumn migration following moulting migration), and (3) Spring migration (April–June). No birds initiated spring migrations before April.

We defined moult migration as a directional movement in excess of 100 km from the breeding area to an area where the birds staged for more than 3 weeks (i.e. whilst flightless) sometime in August and September. Birds moulting closer than 100 km to the breeding area were defined as 'local moulters'.

A full migration route (autumn, spring or moult) was defined as the distance between 'start' and 'end' locations, and typically consisted of short periods of movement interspersed with periodic stopovers. To analyse the course of each bird, travel was sequenced into 'major movements' which were empirically defined as a sequence of directional movements in excess of 100 km and without potential stopovers that exceeded 3 days. Therefore, a major movement ended if distance to the next location (bestpick) was less than 100 km or if the time to next location was more than 3 days. In practice, there was little ambiguity because the total length of major movements virtually equated to the entire migration distance in most cases.

The 'start day' for a movement was defined as the median day between the last location before movement and the first location on the movement, (as there were often several days between PTT locations). The 'end day' of a movement was defined as the median of the last day in the movement and the first day after the movement. Durations of movements were calculated as time from last location before movement to first location after movement.

### Statistical analysis

We applied analysis of variance (one or two-way ANOVA including interaction; Zar 1999) to test for differences in the means of the dependant variables (distances, timing, speed, duration) between independent variables (migration season, and main flyway). The ANOVA included the independent variables as factors together with their interaction. The interaction effect was removed from the ANOVA if not significant at the 5% level according to type III Sum of Squares test, and the analysis was rerun. Fishers PLSD test was used as

a *post-hoc* test. Data on mean speed revealed a lack of normality when tested by Shapiro Wilk W-test, but following logarithmic transformation, rates of migration became normally distributed (Shapiro-Wilk  $W = 0.98$ ).

Averages are given as mean  $\pm$  SD. For small sample sizes medians and ranges are given.

## RESULTS

### Tracking rates

We classified 66 individual migration routes among 45 Eiders tracked between their breeding and wintering areas, with full migration routes identified for 38 autumn and 16 spring migrations. Among the latter one Eider was sedentary and for two Eiders departure dates could not be determined with adequate accuracy leaving full details of 13 spring migrations (Table 1). In addition, migration start day (Table 2) and most of the migration routes could be identified for another 3 autumn migrations and 9 spring migrations, although we could not confirm that all of these Eiders reached their final migration destination. The 45 Eiders tracked were followed on average 270 days  $\pm$  97 days, and 14 were tracked for more than 330 days, and 10 gave information on timing and duration of both spring and autumn migrations (Table 3).

There were no indications that the migration of implanted birds was significantly affected by implantation, but all females tracked from the Upernavik and East Bay breeding colonies abandoned their nests and apparently skipped breeding for the season, although some remained near their respective colonies and in Upernavik two were observed accompanying ducklings at sea. At East Bay, two females were observed incubating normally two years after the implantation in 2003. It is presumed that the 16 spring migrants we followed to breeding areas initiated breeding normally.

**Table 1.** Spring migration details for 15 Eiders from different marking locations tracked in different flyways from winter area to breeding area. CA: Canadian Arctic flyway; CA-WG: Canada – West Greenland flyway; WG: West Greenland flyway.

PTT ID	Main flyway	Marking location	Sex	Overall spring migration					Major movements during spring migration			
				Distance km	Smoothed route km	Departure date	Duration days	Speed km d <sup>-1</sup>	Number	Distance longest km	Speed longest km d <sup>-1</sup>	Distance last km
E40464	CA	East Bay	m	2228	3100	25-05-2004	23	96	2	1887	129	341
E40472	CA	East Bay	m	2654	2800	21-04-2004	43	62	3	1435	513	805
E40476	CA	East Bay	m	2399	2800	14-05-2004	42	58				
E30058	CA-WG	East Bay	f	1684	1730	29-05-2004	20	85	2	895	157	537
B30062	CA-WG	Nuuk	f	796	820	23-05-2000	7	122	1	796	122	796
B6934	CA-WG	Nuuk	f	1637	1800	-						
B6837	CA-WG	Nuuk	m	999	1000	-						
C23168	CA-WG	Nuuk	f	1075	1150	30-04-2001	28	39	2	818	109	208
C30056	CA-WG	Nuuk	f	1606	1425	21-05-2001	28	57	2	969	306	969
E41194	CA-WG	Disko	m	1815	1720	16-05-2004	38	48	4	708	139	316
E41188	WG	Disko	m	1137	1190	27-04-2004	21	55	3	541	180	541
D23172	WG	Upernavik	f	944	1100	27-04-2003	22	44	3	435	79	435
D23326	WG	Upernavik	f	480	500	18-04-2003	26	18	2	281	53	281
D30056	WG	Upernavik	f	501	530	10-04-2003	32	16	2	311	59	311
D30059	WG	Upernavik	f	1146	1265	26-04-2003	28	41	4	365	72	225

- Too few locations received to identify date of departure with adequate accuracy.

**Table 2.** Start of migration in different flyways for each marking location. Given are means  $\pm$  SD, range in parentheses, and sample size.

Flyway	Marking location	Autumn (without moult migration)	Moult migration	Autumn (post-moult)	Spring
CA	East Bay	19 Oct $\pm$ 3 (16-21 Oct) <i>n</i> = 2	2 Aug $\pm$ 11 (16 Jul - 24 Aug) <i>n</i> = 8	18 Oct $\pm$ 16 (1 Oct - 20 Nov) <i>n</i> = 8	11 May $\pm$ 13 (21 Apr - 25 May) <i>n</i> = 6
CA-WG	East Bay	27 Oct $\pm$ 4 (19 Oct - 3 Nov) <i>n</i> = 8	6 Aug $\pm$ 13 (10 Jul - 15 Aug) <i>n</i> = 7	23 Oct $\pm$ 17 (1 Oct - 9 Nov) <i>n</i> = 7	15 May $\pm$ 10 (2 May - 29 May) <i>n</i> = 5
CA-WG	Disko			21 Dec <i>n</i> = 1	16 May <i>n</i> = 1
CA-WG	Nuuk	7 Oct $\pm$ 14 (27 Sep - 17 Oct) <i>n</i> = 2			6 May $\pm$ 15 (18 Apr - 23 May) <i>n</i> = 5
WG	Disko		<i>n</i> = 1	3 Nov <i>n</i> = 1	27 Apr <i>n</i> = 1

**Table 3.** Migration travel days for 10 Eiders which were tracked through all migration seasons.

PTT ID	Main flyway	Marking location	Sex	Migration Season (travel days)			
				Moult	Autumn after moult	Spring	Total (travel days)
e40464	CA	East Bay	m	1	50	23	75
e40476			m	9	6	42	56
e40472			m	1	71	43	114
e30058	CA-WG	East Bay	f	0 <sup>a</sup>	5	20	25
c23168		Nuuk	f	0 <sup>a</sup>	3	28	30
c30056			f	0 <sup>a</sup>	7	28	35
d23172	WG	Upernavik	f	0 <sup>a</sup>	47	22	69
d23326			f	0 <sup>a</sup>	16	26	42
d30056			f	0 <sup>a</sup>	79	32	110
d30059			f	0 <sup>a</sup>	26	28	54

<sup>a</sup>0 indicates local moult <100 km from breeding colony

### Autumn migration

Our findings confirm that Northern Common Eiders predominantly use two wintering areas: eastern Atlantic Canada and the southwest coast of Greenland. Three migration flyways between breeding and wintering areas were confirmed including, (1) Eiders breeding in eastern Arctic Canada that migrate to winter in maritime Canada (termed East Canada flyway (CA); Online appendix, Fig. A1), (2) Eiders breeding in west Greenland that migrate to winter in south West Greenland (termed the West Greenland flyway (WG); Online appendix, Fig. A2), and (3) Eiders that breed in eastern Arctic Canada that migrate east to winter in south West Greenland (termed the East Canada – West Greenland flyway (CA-WG); Online appendix, Fig. A3).

From the *Upernavik colony*, west Greenland, all birds (10 females) migrated south along the west coast of Greenland and wintered along the coast from the Disko Bay south to Nuuk fjord (latitudes 69.0–64.2°N).

From the *Canadian East Bay colony* near Southampton Island, Nunavut, we tracked 25 Common Eiders on autumn migration (18 females and 7 males; two years combined). Ten (40%, 4 females and 6 males) wintered along CA coasts from

Labrador (58.6°N) to the southern tip of Newfoundland (47.8°N), with four wintering along the Gulf of St. Lawrence and at Anticosti Island. Fifteen Eiders (60%, 14 females and 1 male) followed CA-WG, migrating through Hudson Strait west across Baffin Bay to winter in southwest Greenland, between 64.5° to 60.0°N. Sexes were unequally distributed among flyways as 14 out of 18 females (2001 and 2003 combined) and only 1 out of 7 males (males tracked in 2003 only) followed the CA-WG flyway (both years combined:  $\chi^2 P = 0.004$ ,  $n = 25$ , only data from 2003:  $\chi^2 P = 0.003$   $n = 16$ ). Most males were caught in flight while they closely accompanied a female to the nesting colony during the laying period (see Methods). For two of these pairs, we implanted both the male and female and tracked their fall migration respectively. In one pair both the male and female followed the CA-WG flyway to winter in Greenland (e6935 and e41177), whereas the female of the second pair followed the CA-WG flyway (e40470) while the male followed the CA flyway (e40469).

Eiders from the *Disko Island moulting area* generally wintered along the West Greenland Coast from Disko Bay (69°N) south to Sisimiut (66°N). Three marked in the *Nuuk wintering area* migrated

to Canada in spring and were tracked in the subsequent fall migration; two returned to the *Nuuk wintering area* while the third arrived along the Greenland coast 100 km south of Nuuk Fjord, then proceeded further south to winter in South Greenland (61°N).

In fall, most Eiders headed south in the second half of October (Table 2). The start day of the autumn migration (excluding apparent moult migrants) differed between marking locations (one-way ANOVA,  $F = 5.67$ ,  $P = 0.01$ ) (Table 2). And the autumn migration for hens that wintered in maritime Canada started significantly earlier (CA flyway; 19 October  $\pm 3$  d ( $n = 2$ ; 16 Oct – 21 Oct) than for hens migrating from Canada to west Greenland (CA–WG flyway; 27 October  $\pm 4$  d ( $n = 8$ ) (19 Oct – 3 Nov  $t$ -test  $P = 0.04$ ).

In East Bay and Upernavik, the monthly mean temperature falls below zero from September to October, when the risk of temporary icing in sheltered areas on clear calm nights increases. The East Bay monthly means for September and October 2003 respectively are 3.1°C (1.1°C) and –4.0°C (–7.3°C) (average for 1971–2000 in brackets; Coral Harbour weather station, Environment Canada). The Upernavik monthly means are 3.2°C (0.8°C) and –1.8°C (–4.0°C) for September and October 2002, respectively (average for 1961–1990 in brackets; Upernavik weather station, Danish Meteorological Institute).

### Moult migration

Eiders moult their flight feathers post-breeding, either locally near the breeding colony prior to autumn migration to winter quarters or by a moult migration to a moulting area followed by autumn migration to ultimate wintering areas. Among Upernavik colony Eiders, nine out of ten (all hens) moulted within 100 km of the colony, as did two (females) of the three birds (two females and one male) breeding on the south coast of Baffin Island in Canada, which were marked and tracked from the *Nuuk wintering area*.

All 7 males and approximately half of the females in each flyway (2 out of 4 females in the CA flyway and 6 out of 14 females in the CA–WG

flyway) migrated from East Bay to distant moulting sites; the remaining 10 females moulted <100 km from their colony. Males at East Bay initiated moult migration earlier than females (25 July  $\pm 9$  d and 12 August  $\pm 6$  d respectively,  $t$ -test  $P = 0.0005$ ). Locally moulting females had, at the time of implantation, had both better body condition (estimated Total Carcass Lipid (TCL), see Methods) and greater body mass than moult migrant females (body condition: 311  $\pm 61$  g TCL and 212  $\pm 54$  g TCL respectively,  $t$ -test  $P = 0.004$ ,  $df = 14$ ; body mass 2042  $\pm 237$  g and 1741  $\pm 176$  g respectively,  $t$ -test  $P = 0.009$ ,  $df = 16$ ).

### Population delineation in winter

East Bay Eiders that migrated to West Greenland wintered further south along the Greenland coast (60–64.5°N) than Eiders originating from Upernavik (64.2–69°N), and from the Disko moulting area (66–69°N). Birds implanted in the *Nuuk wintering area* were tracked to breeding areas extending from the Hudson Strait to northern Baffin Bay. Interestingly, East Bay females that migrated to Greenland were significantly smaller in structural size (total head) than Eider females marked at Upernavik (WG flyway) and Eider females marked at Nuuk (CA–WG flyway) ( $F = 14.82$ ,  $P < 0.0001$ ), while the two latter groups did not differ in structural size. East Bay males were smaller than males marked at Nuuk ( $F = 4.15$ ,  $P = 0.028$ ).

### Spring migration

Eight Eiders (2 males and 6 females) were tracked in spring from the *Nuuk wintering area*. One female moved just 45 km south of the wintering area in spring where it likely nested. The remaining 7 (88%) migrated to Canada from west Greenland wintering areas, one female to Coburg Island, by Ellesmere Island at 76°N, the others to south-western Baffin Island. There, a male and a female remained in Cumberland Sound, Baffin Island, where the female likely nested, with other females potentially nesting in Markham Bay, Baffin Island and on the south coast of Meta Incognita Peninsula, Baffin Island.

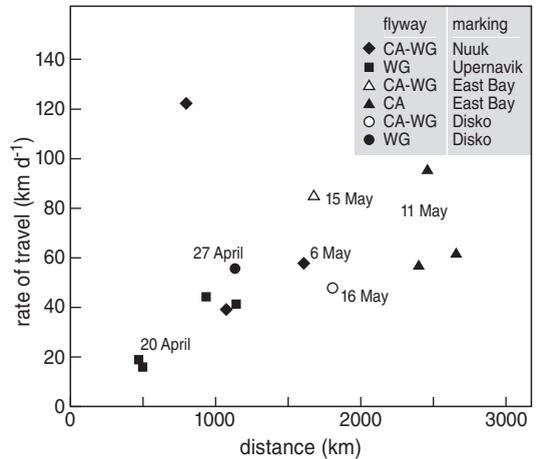
Six *East Bay* Eiders implanted in 2003 (5 males and 1 female) were tracked during *spring* migration in the CA-flyway until at least the end of May 2004. Of these, three were followed throughout their spring migration in the CA flyway (smoothed route along coast: 2800–3100 km,  $36 \pm 3$  days one way, range: 2–4 major movements). Three of the six birds were tracked back to the same general breeding region (Southampton Island, Foxe Channel and Basin), with one male arriving at Southampton Island (East Bay) 14 June (6 June – 23 June) about 3 weeks before median start of incubation on 5 July 2004 (Gilchrist pers. comm.) while the female from Anticosti Island (e40459) gave last locations 29 May at the Labrador coast.

Four Upernavik birds were tracked during spring migration, and all returned north to the same breeding area. They migrated north along the West Greenland coast from pre-migration staging areas (Nuuk, Maniitsoq, and southwest Disko Bay). The median arrival date was 11 May (7–20 May), nearly a month prior to the median start of incubation based on data from the colony the year before (median incubation start June 8,  $n = 39$ ; Nyegaard et al., unpubl.).

Birds tracked from the *moult locality at Disko Island* during autumn and winter only, could not be assigned to flyway because their breeding provenance was unknown. However, one of the Disko Island male birds was tracked in spring to northern Upernavik before crossing Melville Bay to Avernersuaq (75°N, Northwest Greenland). A second male Eider was tracked to southern Baffin Island and into Hudson Strait where it remained (21 June – 31 July), and apparently bred on an island off the coast of Ungava Peninsula.

The start of spring migration differed between flyways (Fig 2, Tables 1 and 2; one-way ANOVA,  $F = 4.98$ ,  $P = 0.018$ ). Birds following the WG flyway started 20 and 19 days earlier than birds following the CA–WG flyway (*post-hoc* test,  $P = 0.008$ ) and CA flyway respectively (*post-hoc* test,  $P = 0.016$ ) (Table 2).

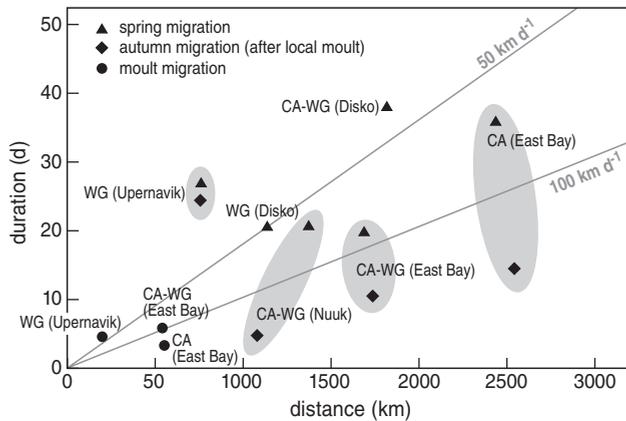
Upernavik Eiders initiated spring migration c. 3 weeks before East Bay Eiders – regardless of whether the latter wintered in Canada or Green-



**Figure 2.** Spring migration rate of travel of 13 individual Eiders in relation to migration distance. Flyways are colour coded and marking locations coded with different marker styles. Average day of departure is given for the 6 combinations of flyway and marking location including data from all Eiders where a day of departure could be identified ( $n = 22$ , not only the 13 Eiders where the full spring migration was recorded). See details in Table 1 and 2.

land. Eiders migrating from Greenland to the Hudson Strait also initiate migration earlier than Eiders heading for the more westerly East Bay, which experiences later ice break-up.

Contrary to our expectations among the four Eiders that were tracked on their spring migration back to Upernavik, Eiders with the longest spring migration distances initiated migration last, Fig. 2 (linear regression,  $F = 5.9$ ,  $P = 0.13$ ,  $R^2 = 0.75$ ). The same picture was seen among the Eiders migrating towards the East Bay colony where the three Eiders (2 males and 1 female) wintering farthest away, at Anticosti Island, Canada (about 3000 km from the East Bay colony if the migration track is smoothed around the coast), initiated spring migration in 2004 significantly later than three Eiders wintering along coasts of Newfoundland and Labrador (ANOVA,  $F = 11.2$ ,  $P = 0.029$ ). The median migration start date for Eiders starting from Anticosti Island was 24 May (range 14–25 May), whereas the median start date for three



**Figure 3.** Average migration distance and duration for combinations of flyways and marking locations for spring, moult and autumn (after local moult only) migrations. Data points representing averages for spring and autumn migrations for the same flyway and marking location have been circled. Help lines have been inserted indicating where the combination of distance and duration correspond to a rate of travel of 50 km d<sup>-1</sup> and 100 km d<sup>-1</sup>.

Eiders starting from Newfoundland (two Eiders) and Labrador (one Eider) was 30 April (range, 21 April – 9 May).

Collectively, these results suggest that the timing of spring migration is adapted by tradition to spring ice conditions in the breeding area rather than conditions at their wintering area (see Fig. 1). However, the closer to the breeding area that birds winter, the more they can take local weather into account when timing their migration. The more severe ice condition at East Bay is reflected in the air temperature. The East Bay monthly means for April and May 2004 respectively are -18.3°C (-16.7°C) and -6.3°C (-6.8°C) (average for 1971–2000 in brackets; Coral Harbour weather station, Environment Canada). The Upernavik monthly means are -11.8°C (-13.3°C) and -2.3°C (-3.8°C) for April and May 2003, respectively (average for 1961–1990 in brackets; Upernavik weather station, Danish Meteorological Institute).

### Migration rate and duration

The mean migration duration differed significantly between seasons, but not between flyways (Fig. 3; two-way ANOVA on log-transformed duration data,  $F = 12.5$ ,  $P < 0.0001$ , and  $F = 2.7$ ,  $P =$

0.08, respectively). Moult migrations were of shorter duration than entire flyway migrations ( $4.4 \text{ d} \pm 3.9 \text{ d}$ ,  $n = 16$ , *post-hoc* test,  $P < 0.002$ ). Among all flyways combined, spring migration ( $27.3 \text{ d} \pm 9.8 \text{ d}$ ,  $n = 13$ ) lasted longer than the autumn migration following local moult ( $16.1 \text{ d} \pm 18.7 \text{ d}$ ,  $n = 21$ , *post-hoc* test,  $P = 0.007$ ). The average duration of the spring migrations in each flyway ranged from 24 days (CA–WG) to 36 days (CA) and the individual variation in migration duration were much less than in the autumn flights (Table 3).

Average migration speed (km d<sup>-1</sup>) differed significantly between both migration seasons and main flyways (Fig. 3; two-way ANOVA on log-transformed speed data,  $F = 4.63$ ,  $P = 0.005$ , and  $F = 10.72$ ,  $P = 0.0001$ , respectively), while the interaction was not significant. For the flyways combined the mean speed of the spring migration ( $57.0 \pm 29.5 \text{ km d}^{-1}$ ,  $n = 13$ ) was significantly slower than that of both the moult migration ( $141.5 \pm 66.5 \text{ km d}^{-1}$ ,  $n = 16$ ; *post-hoc* test,  $P = 0.0031$ ) and the autumn migration following local moult ( $190.3 \pm 146.7 \text{ km d}^{-1}$ ,  $n = 21$ , *post-hoc* test,  $P = 0.0020$ ). For all seasons combined the mean migration speed in the shorter WG flyway

( $77.3 \pm 91.6$  km d<sup>-1</sup>,  $n = 17$ ) were less than the mean migration speed in the CA ( $116.1 \pm 73.7$  km d<sup>-1</sup>,  $n = 21$ , *post-hoc* test,  $P = 0.097$ ) and CA–WG flyway ( $181.2 \pm 133.3$  km d<sup>-1</sup>,  $n = 30$ , *post-hoc* test,  $P < 0.0001$ ).

The number of major movements during migration were strongly influenced by season (Kruskal-Wallis,  $H = 14.9$ ,  $P = 0.002$ ,  $df = 3$ ), but not flyway. Almost all moult migrations occurred quickly in one step ( $1.1 \pm 0.3$ ,  $n = 15$ ), while autumn migration (following local moult) occurred in 2–3 movements (overall mean number of movements  $1.8 \pm 1.0$ ,  $n = 21$ , and 1.5, 1.5 and 2.2 for CA, CA–WG and WG flyway, respectively). In contrast, autumn migration in the CA flyway following the moult migration and moult occurred in more movements ( $3.1 \pm 1.1$ ,  $n = 7$ ). Apart from the latter, the autumn migrations were split up in shorter steps than during spring (spring overall mean  $2.5 \pm 0.9$ ,  $n = 12$ , and 2.5 (2), 2.2 (5) and 2.8 (5) major movements for CA, CA–WG and WG flyway, respectively).

The distance travelled on the longest major movement for each migration season was analysed separately for females and males. For females the longest major movements during autumn ( $991 \pm 601$  km,  $n = 21$ ) were significantly longer than those in spring ( $609 \pm 287$  km,  $n = 8$ ), and all three flyways differed (two-way ANOVA,  $F = 4.5$ ,  $P = 0.045$  and  $F = 38.5$ ,  $P < 0.0001$  respectively, *post-hoc* test  $P = 0.003$  and  $P < 0.0001$ , respectively).

## DISCUSSION

### General migration patterns

This study revealed variability in length of migration routes between breeding and wintering areas for the Northern Common Eider, ranging from a sedentary bird at Nuuk Fjord to migrations exceeding 3000 km along the eastern Canadian Atlantic coast. Clear differences were found between three major migration flyways: the Canadian Flyway, the West Greenland Flyway and the Canada – West Greenland Flyway crossing the Davis Strait. The

latter clearly links Canadian breeding areas with the southwest Greenland winter area and provides evidence that much of the Greenlandic wintering population (460 000 Common Eiders, Merkel *et al.* 2002) originates from Arctic Canada.

### Winter distribution in relation to breeding population

There appeared to be some segregation of Eiders on Greenlandic wintering areas that reflected the origin of their breeding locations, supported by satellite tracking data of migration routes and data from ringing recoveries of Eiders ringed in Upernavik during 1933–1972 and at East Bay in the 1990s (Lyngs 2003). Both sources confirmed that Eiders breeding in Upernavik winter in the north of the SGOWR north of Nuuk (64°N) (Online appendix, Fig. A2). In contrast, East Bay breeding Eiders from Southampton Island, Canada that migrated to west Greenland typically wintered in the south of SGOWR, south of Nuuk (Online appendix, Fig. A3).

This winter segregation corresponded to differences in structural size of the tracked birds. It has been proposed that Eiders often pair on the wintering area (Spurr & Milne 1976, Goudie *et al.* 2000), and the structural differences found between females from Upernavik and East Bay colonies support a reproductive segregation. Eiders migrating from the East Bay colony to Greenland were structurally larger than those wintering in Atlantic Canada. Collectively, these results suggest that northern Eiders may be philopatric to specific wintering areas (Robertson & Cooke 1999), are segregated on wintering areas based upon the breeding population of origin, and therefore the northern Eider population may consist of several subpopulations.

The prevalence for East Bay males to follow the Canadian flyway does not fit with winter pairing. However, no clear skewed sex ratio has been reported from the wintering areas, so this may be an artefact resulting from more males from the Canadian flyway courting females during laying at the East Bay colony at the time of capture.

### Autumn and moult migrations

Following moult migration, autumn migration was slow and characterised by several major movements. In the Canadian flyway, Eiders that moulted away from the breeding colony slowly headed south along Baffin and Labrador coasts. In contrast, Eiders that moulted near the East Bay colony performed a rapid autumn migration with few major movements post-moult. Brood-caring females must moult locally or postpone moult. Females in poor body condition are more likely to abandon their young to safeguard their own survival (Bustnes *et al.* 2002). This may explain why tracked females staying near the colony were in better body condition than females performing moult migration. Most likely tracked females that moulted locally joined family flocks and migrated with juveniles. Rapid migration to safer areas and better feeding conditions may benefit inexperienced juveniles, and fits with observations of juvenile and female Common Eiders arriving at wintering areas in autumn before adult males in Atlantic Canada (Goudie *et al.* 2000).

Female Eiders tracked from Upernavik conformed to previous suggestions that most Common Eiders breeding in west Greenland undergo wing moult locally near breeding areas (Salomonsen 1968). By contrast, all males and half of the females undertook moult migrations from East Bay, where there is a higher risk of early sea-ice formation. The moult migrations were rapid, with males typically departing earlier than females (Salomonsen 1968). One of the two moulting Eiders from Disko went to breeding areas in Arctic Canada, confirming a long-distance moult migration from Canada, as suggested by Abraham & Finney (1986) and Frimer (1993).

### Migration patterns in relation to energy reserves

Female Eiders are considered largely capital breeders, losing c. 45% of body mass from pre-laying to hatching (Goudie *et al.* 2000), so it is necessary that they acquire sufficient body reserves prior to laying. Breeding Eiders generally arrive at the East Bay colony with significant fat reserves necessary for breeding (Bottitta *et al.* 2003) but only after

accruing reserves towards the end of their spring migration and in proximity to breeding areas (Jamieson 2003). This study shows that there is time for intensive feeding during spring migration, given the average rate of travel of only 60 km d<sup>-1</sup>, equivalent to c.1 hour of flying per day and less than 30% of the speed of post moult autumn migration. Early arrival at the breeding areas relative to the mean start of incubation (c. 4 weeks and c.3 weeks respectively for Upernavik and East Bay colonies) confirms the importance of local feeding at these areas.

Hedenström and Alerstam (1998) calculated the theoretical limits for overall rate of travel (km d<sup>-1</sup>) during migration based on power consumption and limits for fuel deposition. For flapping flight (as in the case of the Eider) they found a declining maximum rate of travel with increasing mass. For large birds migration rates will be ranging from 70–100 km d<sup>-1</sup> for typical energy deposition rates to 150–200 km d<sup>-1</sup> for maximum energy deposition rates. Our mean rate of spring travel (60 km d<sup>-1</sup>) is well within these theoretical limits, while the rate for some birds during autumn approaches the maximum energy deposition rate. In comparison, the overall speed of Brent Goose *Branta bernicla* migration from the Wadden Sea to the summering grounds in Taimyr (5000 km) averaged 118 km d<sup>-1</sup> (Green *et al.* 2002) falling to 62 km d<sup>-1</sup> including the pre-migratory fattening period in the Wadden Sea

The duration of spring migration varied little between birds from different flyways compared to considerable differences in the duration of autumn travel (Table 3 and Fig. 3). This suggests that stopping to feed en route during spring may be a general migration strategy, while different strategies are adopted in autumn when the fastest migrating individuals most likely undertake pre-migration fattening like the Brent geese mentioned above. Our findings support recent findings that the lipid content of Eiders collected during spring migration was higher among hens arriving at the breeding grounds at Cape Dorset, Hudson Strait, than among hens in west Greenland before they started their migration despite the high energy expendi-

ture involved in flying there. Two thirds of west Greenland Eiders collected in late winter and spring had lipid reserves greater than 166 g (enough to cross 600 km of the Davis Strait (estimated at c. 22 g lipid per 100 km based on body mass, wing span and wing area for an Eider weighing 2 kg Rayner 1990, Guillemette 1994, Jamieson 2003). Females collected at Cape Dorset in 2000, 2001 and 2002 carried 87, 22, and 103 g more lipid, respectively, than the female Eiders collected at wintering grounds in West Greenland (Jamieson 2003).

Fuelling en route saves the energetic costs of transporting fat reserves during migration from the wintering area. However, this strategy requires a reliable and accessible spring food resource. Eiders typically feed on sessile long-lived benthic organisms such as blue mussels *Mytilus edulis*. Their abundance and location are typically predictable unless prey depletion occurs, or they become inaccessible (e.g. due to sea ice). Being present in the non-breeding environment of the Eider ('survival habitat' sensu Alerstam & Högstedt 1982) food will probably not be limited and the timing and speed of migration is apparently adjusted to regional sea ice conditions. Hence, the slow spring migration speed enables exploitation of high quality foraging areas along the route, which negates the added costs of an extended migration route. It is, however, remarkable that the most northerly wintering Eiders closest to the breeding area start spring migration before those wintering further south in the same flyway which are heading for the same colony. These more southerly wintering birds have less 'cues' for assessing the ice conditions at the breeding areas, but can afford to be more cautious about moving north.

In conclusion, we have found subpopulations of Eiders each with its own migration pattern, differing in migration length, timing and partitioning of the autumn migration in moult and post-moult migration. The differences seem to be adaptations to different ice cover regimes in the different breeding and moulting areas. However, knowledge of differences in food availability and the neces-

sary foraging effort in different areas is needed to further understand the factors shaping each of the migration patterns.

It appears that while each Eider has some flexibility in migration route and timing to adapt to climatic variation, the main explanation for the prevalence of a particular migration strategy is to be found in the fitness of the subpopulation associated with a given strategy (see Miller *et al.* 2005 for a similar case involving Pintails *Anas acuta*) The use of PTTs gathering data over more than one year will help unravel how much flexibility in migration each individual bird has to adapt to between-year variation in weather conditions.

### Conservation implications

Our findings confirm the clear and dramatic contribution of the Canadian breeding population to the Greenlandic wintering population. They also demonstrate population delineation on the wintering grounds based upon the origin of breeding populations. Results from ringing recoveries, satellite tracking and morphometric differences confirm the simultaneous presence of different subpopulations. Because regional hunting intensity varies (Piniarneq 1993–2003), sub-components of the wintering population may be at greater risk if they are philopatric to wintering areas subject to intense hunting activity. However, we also found that birds from one colony can winter in two widely separated areas, which may help some segments of the colony survive extremes in regional environmental conditions and local catastrophic events. A segment of the colony would be expected to escape regional detrimental conditions during winter such as heavy ice conditions, industrial activity, or human exploitation/disturbance. Finally, patterns of spring and autumn migration suggest important habitat requirements during migration and moult. Marine coastal areas that support abundant, reliable and accessible benthic prey are apparently critical during spring migration to enable Eiders to accumulate necessary energy reserves for reproduction en route to breeding areas. Similarly, these feeding areas are important for Eiders moulting in autumn, where a flight-

less period constrains their ability to move between feeding areas. In these areas foraging efficiency could be impeded by human disturbance.

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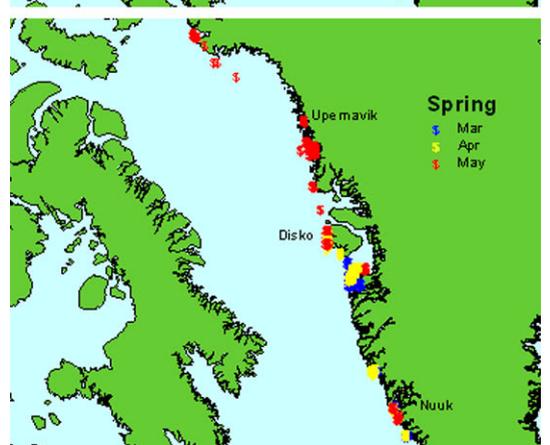
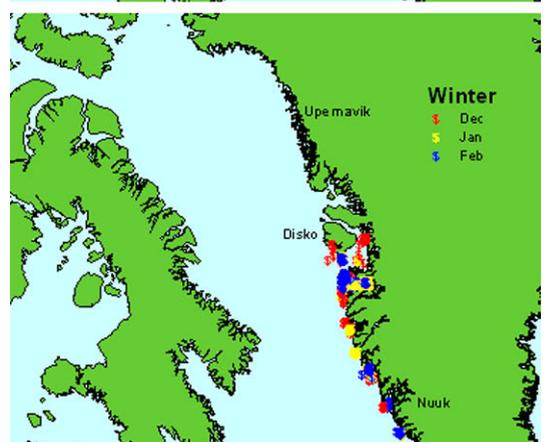
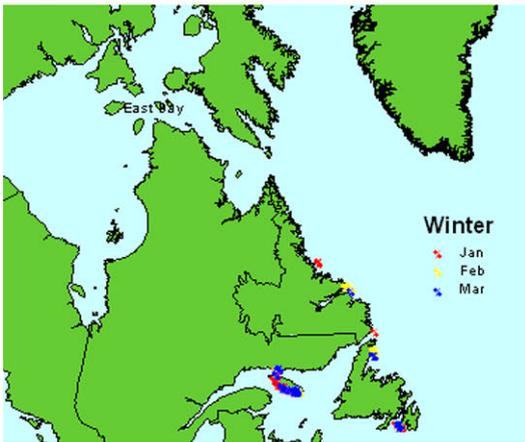
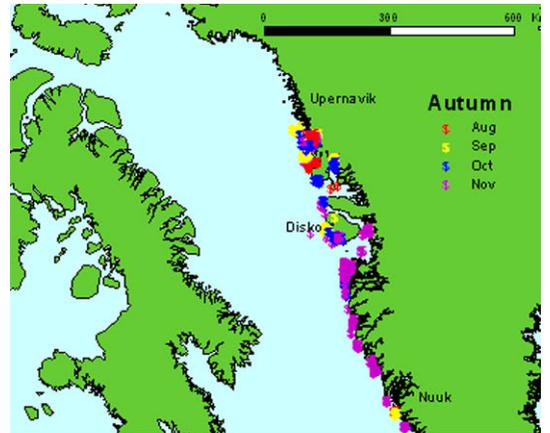
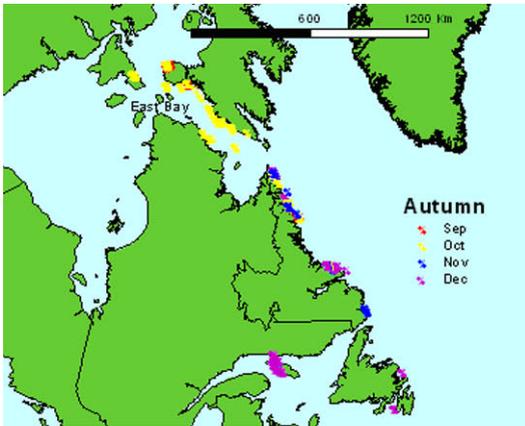
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## SAMENVATTING

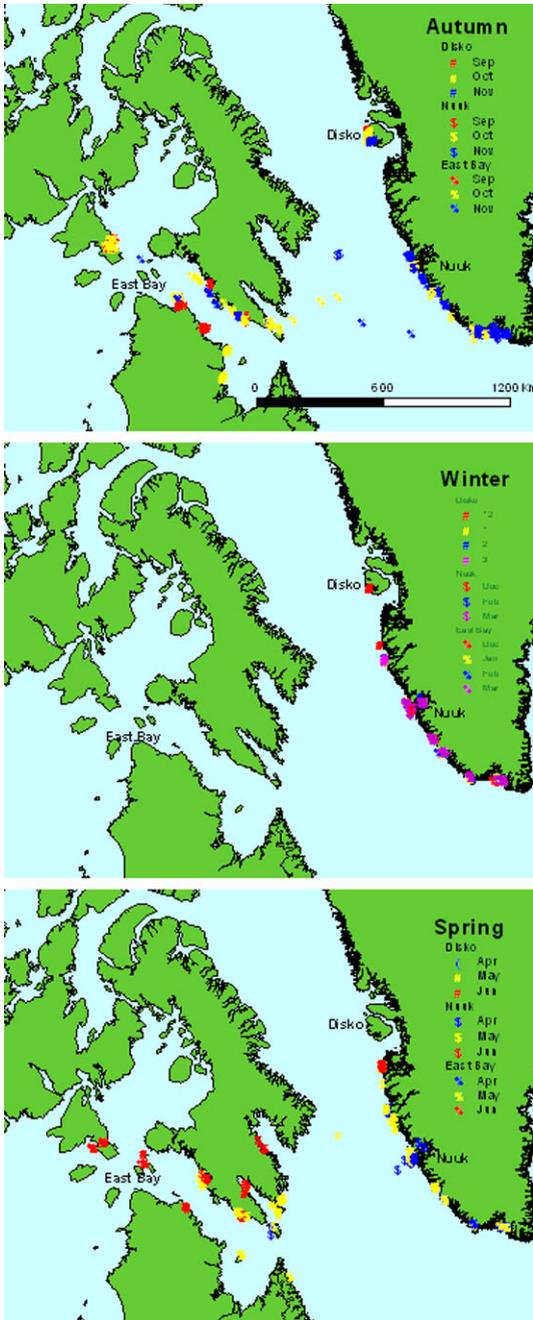
Dit onderzoek richtte zich op de trekbewegingen van Noordelijke Eiders *Somateria mollissima borealis* tussen broedgebieden in West-Groenland en Noordoost-Canada en overwinteringsgebieden in het zuidwesten van Groenland. De gegevens werden verzameld met behulp van geïmplanteerde satellietzenders. Eiders die in Noordwest-Groenland broedden ( $n = 10$ ), trokken langs de kust om in het westen en zuidwesten van Groenland te overwinteren. Broedvogels uit het noorden van Canada overwinterden in twee verschillende gebieden. Vogels uit een kolonie bij Southampton Eiland (noordoosten van Canada) trokken door Straat Hudson langs de kust van Labrador en Newfoundland om te overwinterden in de Atlantische Oceaan voor de kust van Canada. Een ander deel van de kolonie bij Southampton Eiland (60%,  $n = 25$ ) stak de Straat Davis over om in zuidwestelijk Groenland te overwinteren. Deze route werd vooral door vrouwtjes gevolgd (14 van de 18), veel minder door mannetjes (maar 1 van de 6). Zeven van de acht Eiders die in de winter in Zuidwest-Groenland waren gevangen, staken Straat Davis over om in Noord-Canada te broeden. Individuen uit Zuidwest-Groenland trokken niet en bleven binnen 45 km van de nestplek overwinteren, terwijl vogels van andere broedpopulaties afstanden van meer dan 2000 km aflegden. Tijdens de voorjaars trek werd gemiddeld 60 km per dag afgelegd, tijdens de ruitrek 142 km per dag, en tijdens de najaars trek 190 km per dag. Het lijkt er daarom op dat Eiders tijdens de voorjaars trek moeten voedsel zoeken, of dat ze tijdens de trek belemmerd worden door ijsomstandigheden. Omdat klimatologische en ijsomstandigheden verschillen tussen noordoostelijk Canada en West-Groenland, gedragen Eiders uit beide gebieden zich anders wat betreft overwintering en trek.

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Online appendix, Fig. A1. Canada flyway, seasonal distribution of the tracked birds.

Online appendix, Fig. A2. West Greenland flyway, seasonal distribution of the tracked birds.



Online appendix, Fig. A3. Canada – West Greenland fly-way, seasonal distribution of the tracked birds.



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