

Migration patterns of Western High Arctic (Grey-belly) Brant *Branta bernicla*

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Abstract

This study describes the seasonal migration patterns of Western High Arctic Brant (WHA, or Grey-belly Brent Geese), *Branta bernicla*, an admixed population that breeds in the Canadian High Arctic and winters along the Pacific coast of North America. Adult WHA Brant were captured in family groups on Melville Island (75°23'N, 110°50'W) in 2002 and 2005 and marked with satellite platform transmitting terminal (PTT) transmitters or very high frequency (VHF) transmitters. During autumn migration, all PTT-tagged Brant followed a coastal route around Alaska and staged for variable lengths of time at the following sites on the north and west coasts of Alaska: Kasegaluk Lagoon (69°56'N, 162°40'W), Ikpek Lagoon (65°55'N, 167°03'W), and Izembek Lagoon (55°19'N, 162°50'W). Izembek Lagoon was the most important staging area in terms of length of stay (two months on average) and the majority (67–93%) of PTT and VHF detections occurred in Moffet Bay (55°24'N, 162°34'W). After departing Izembek Lagoon, the PTT-tagged geese followed a *c.* 2,900 km trans-oceanic route to overwinter in the southern part of the Salish Sea (*i.e.* from north Puget Sound, Washington to south Strait of Georgia, British Columbia; centred at *c.* 48°45'N, 122°40'W). Most (*c.* 45%) PTT detections in the southern Salish Sea occurred in Samish Bay (48°36'N, 122°30'W) followed by Padilla Bay (48°30'N, 122°31'W; *c.* 26%). Brant migrated north from the Salish Sea along the coast to southeast Alaska and then followed either an interior route across the Yukon or a coastal route around Alaska. The “interior” birds staged for *c.* four days at Liverpool Bay (69°20'N, 133°55'W) in the Northwest Territories before flying on to Melville Island. They also departed the Salish Sea two weeks later than the coastal migrants and arrived at Melville Island two weeks earlier. This study and previous research suggest that WHA Brant use similar migration routes each year and

are faithful to their breeding, staging, and wintering grounds. Because WHA Brant constitute one of the smallest breeding stocks in the world (8,000–11,000 individuals), concentrate in only a few areas, and are likely highly site-faithful, they are susceptible to a range of threats such as excessive harvesting, habitat loss and/or degradation, and petroleum spills.

Key words: *Branta bernicla*, Grey-belly Brant, Melville Island, Izembek Lagoon, Salish Sea, satellite telemetry.

Western High Arctic Brant (WHA, or Grey-belly Brent Geese) *Branta bernicla* are a morphologically and genetically distinct population of North American Brant (Boyd & Maltby 1980; Reed *et al.* 1989b; Shields 1990; S. Talbot *et al.*, unpubl. data), believed to be formed by the admixture between Pacific Black Brant *Branta bernicla nigricans* and Light-bellied Brant *Branta bernicla brota* (S. Talbot *et al.*, unpubl. data). They constitute one of the smallest Arctic goose breeding populations in the world (8,000–11,000 individuals; Reed *et al.* 1998). WHA Brant have different migration patterns and use different breeding areas than the more numerous Pacific Black Brant (Reed *et al.* 1989a & b). In particular, WHA Brant breed on only a few islands in the Canadian Western High Arctic (Boyd & Maltby 1980; Handley 1950; Reed *et al.* 1998) while Black Brant nest over large regions of Alaska, Russia, and the Canadian Western Low Arctic (Sedinger *et al.* 1993; Reed *et al.* 1998). In winter, WHA Brant occur in a very restricted area of the south Salish Sea, from Padilla Bay, Washington, to Boundary Bay, British Columbia (referred to as Puget Sound in previous publications; Boyd & Maltby 1979; Reed *et al.* 1989a). In contrast, the winter range of Black Brant extends over 6,000 km from Alaska to Mexico (Reed

et al. 1989b; Reed *et al.* 1998). Along with the rest of the Pacific Flyway Population of Brant, WHA Brant stage for an extended period at Izembek Lagoon (hereafter referred to as Izembek) in late autumn (Reed *et al.* 1989a). Recent studies show that an unknown number of WHA Brant may also overwinter at Izembek and adjacent embayments along the lower Alaska Peninsula (Ward *et al.* 2005; Ward *et al.* 2009).

Nevertheless, little is known about the migration patterns of WHA Brant, including specific affiliations between breeding and wintering grounds, autumn/spring migration routes, and important staging areas. This lack of knowledge has important management implications given that habitat loss and/or intensive harvest levels could have a significant impact on this relatively small breeding population (Reed *et al.* 1989a; Boyd & Maltby 1979). Indeed, restricted hunting regulations in the 1980s and 1990s were likely responsible for a reversal in declining WHA Brant numbers (Reed *et al.* 1998).

As part of a companion study designed to confirm the genetic affinity of WHA Brant within the three subspecies of worldwide Brant geese (S. Talbot *et al.*, unpubl. data), this study uses telemetry to describe the migration and wintering patterns of WHA

Brant captured and marked on Melville Island in 2002 and 2005. Our specific objectives were to: 1) assess affiliations between breeding and wintering grounds; 2) identify routes and important staging areas used during autumn and spring migrations; 3) evaluate the timing and habitat use patterns at staging sites and wintering areas; and 4) assess evidence for route- and site-fidelity across years.

Methods

Helicopter-assisted drives were used to catch Brant on Melville Island (Fig. 1) in late summer 2002 (31 July–10 August) and 2005

(6–10 August) during adult remigial moult. Family groups were targeted for capture. Adults and goslings were measured, weighed, and marked with a standard metal leg-ring on one leg and an engraved, plastic tarsal ring on the other leg. Gender was determined by cloacal examination.

In 2002, adult Brant were marked with either a 30 g very high frequency transmitter (VHF; model A1330 from Advanced Telemetry Systems, Isanti Minnesota USA; $n = 42$, 36 females and six males) or a satellite platform transmitting terminal transmitter (PTT; model 100, Microwave Telemetry Inc., Columbia, Maryland, USA; 30 g units

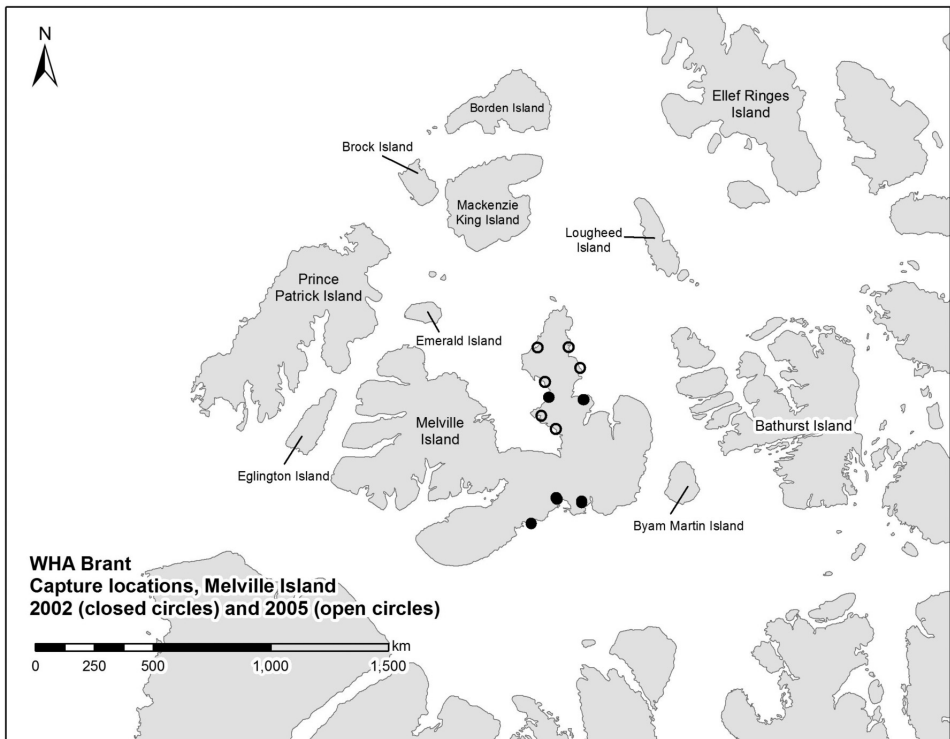


Figure 1. Capture locations for WHA Brant in 2002 (solid circles) and 2005 (open circles) on Melville Island, Nunavut, in the Canadian High Arctic.

for $n = 5$ females, 45 g units for $n = 5$ males). All transmitters were mounted between the scapulars using a backpack attachment protocol following Dwyer (1972), except that “knicker elastic” was used as the harness material.

In 2005, adult males were marked with implantable transmitters, receiving either a 24 g VHF transmitter (model AI-2 from Holohil Systems Ltd., Carp, Ontario, Canada; $n = 13$) or a 40 g satellite platform transmitting terminal transmitter (PTT, model 100 from Microwave Telemetry Inc., Columbia, Maryland, USA; $n = 20$). All transmitters had external antennae and were implanted into the coelomic cavity by an experienced veterinarian following procedures in Korschgen *et al.* (1996).

Because plumage characteristics of WHA Brant can overlap with other Brant stocks (Boyd & Maltby 1979), we recorded both

the degree of completeness of the “white necklace” on the back of the bird’s neck and the bird’s breast colour using a Munsell Soil Colour Chart (Hue 10YR, from Munsell Colour Co., Baltimore, Maryland, USA). All candidate geese selected for radio-marking had broken necklaces on the back of the neck and almost all ($> 93\%$) had breast colour values > 4 , plumage characteristics consistent with WHA Brant (Boyd & Maltby 1979).

The 2002 PTTs were programmed to transmit for six hours every 30–32 h (resulting in a battery lifespan of about seven months for 30 g units attached to females and about ten months for 45 g units attached to males), and have a duty cycle that ensured relatively frequent location data along the migration route from Melville Island to the winter grounds (Table 1). The 2005 PTTs (45 g) were programmed to

Table 1. Duty cycles of PTTs deployed on Melville Island in 2002 and 2005.

	Cycle start date	Cycle end date	# Hours on	# Hours off	PTT lifespan (months)
2002					
30 g transmitters	1-Aug-02	14-Feb-03	6	32	6.5
45 g transmitters	1-Aug-02	28-May-03	6	30	10
2005					
45 g transmitters	8-Aug-05	31-Aug-05	6	216	
	31-Aug-05	31-Oct-05	6	32	
	31-Oct-05	6-Dec-05	6	228	
	6-Dec-05	11-Jan-06	6	32	
	11-Jan-06	8-Jul-06	6	74	11.2

transmit for six hours but on a variable duty cycle (see Table 1) to provide location data over the entire annual cycle (*i.e.* from Melville to winter grounds and back to Melville) with relatively frequent signalling during autumn migration (especially at Izembek). PTT data were retrieved using the Argos Data Collection and Location System (CLS Inc., Largo, Maryland, USA). Data included latitude, longitude, location accuracy, temperature, battery voltage, and activity code.

Migration routes were mapped using the most accurate location class for each 6 h transmission period and these data were used to estimate mean timing (dates) of movements. All class 3 & 2 locations were used but class 1 & 0 locations were filtered if they suggested impossible ground speeds and/or implausible locations. Further, decisions on the migration route taken between two consecutive points several days apart were based on plausible ground speeds.

To calculate the proportion of signals detected within specific embayments within Izembek and in the Salish Sea, only one location per individual per transmission period and only the highest quality location data (*i.e.* classes 3 or 2) were used, thereby maximising data independence and data accuracy.

VHF radio-tracking surveys were conducted using standard ground telemetry protocols supplemented with aerial surveys. Radio-tracking at Izembek was conducted with scanner receivers and directional 3- or 4-element Yagi antennae from shoreline bluffs (15–40 m elevation) and a tracking station on Baldy Mountain (340 m elevation)

following Reed *et al.* (1989b). Monitoring occurred from this ground station almost daily between 5 September and 7 December in 2002. Radio-tracking was intermittent during the rest of December (two aerial surveys) and was concluded with a final ground survey on 18 January 2003 and an aerial survey on 6 March 2003. In 2005, monitoring at Izembek started on 13 September 2005 and was intermittent until 24 September when it occurred almost daily until 19 November 2005. Thereafter, tracking was intermittent (6 aerial surveys) until a final aerial telemetry flight during winter on 15 February 2006. In spring, aerial tracking flights occurred on five occasions between 15 and 31 May 2006 to determine presence or absence of VHF-tagged Brant. Relative use of specific embayments within Izembek was estimated by calculating the proportion of VHF-days in each embayment.

In the Salish Sea, five ground telemetry surveys were conducted in December and January 2002/03 but, because no transmitters were detected, the telemetry surveys were discontinued. In 2005/06, 40 ground and five aerial surveys were conducted but they were inconsistent over space and time (*i.e.* not all embayments were covered during each survey and they were spaced unevenly over the winter period). Therefore, data were not suitable to determine chronology of arrival/departure and habitat use patterns for VHF-tagged Brant but they were adequate to assess presence/absence at the site.

The VHF transmitters contained mortality switches that increased the pulse rate when transmitters, and presumably

birds, were motionless (dead) for > 12 h. Mortality events for PTT-tagged geese could be determined using activity code and movement data (2002) or temperature sensor data (2005). For the latter, a bird was determined deceased if temperature decreased significantly from a body core temperature of 39°C.

All results presented below are with means of ± 1 standard deviation (s.d.) unless otherwise indicated. Maps were generated with ArcGIS 9 (ESRI® 2006, Redlands, California, USA).

Results

Capture and fate of the birds

One hundred and fourteen (90 adults, 24 goslings) and 200 (132 adults, 68 goslings) Brant were captured on Melville Island in 2002 and 2005, respectively. Forty-two adult WHA Brant (36 females, six males) were marked with backpack VHF transmitters and ten adult geese (five females, five males) were marked with backpack PTT transmitters in 2002. In 2005, 13 adult WHA males were marked with implantable VHF transmitters and 20 males with implantable PTT transmitters. The average breast colour value of birds receiving transmitters was 4.5 ± 0.7 in 2002 and 4.8 ± 0.7 in 2005.

Mortality, transmitter loss, and/or premature transmitter failure rates were high (almost 100%) for the radio-tagged Brant in 2002. Of the 42 geese marked with backpack VHF transmitters, 18 were never detected and two others were suspected of arriving but had uncertain signals (≤ 3 days). Of the confirmed arrivals to Izembek, five lost their transmitters (recovered with

broken straps) while six others either lost their transmitters or probably died of avian predation (unbroken straps and transmitters found at Bald Eagle *Haliaeetus leucocephalus* perch sites). Eleven VHF-tagged geese were detected departing Izembek but none were located thereafter in winter though one bird was shot in the Salish Sea.

Of the ten geese marked with backpack PTTs in 2002, two transmitters stopped signalling (*i.e.* lost their transmitters or died of unknown causes) on Melville Island, three others failed during autumn migration between Melville Island and Kasegaluk Lagoon, two stopped signalling during autumn migration between Kasegaluk Lagoon and Izembek, and the remaining three geese subsequently staged at Izembek. Two of these last three geese departed Izembek on 13 December: one stopped signalling on 15 December *c.* 200 km southeast of Izembek while the other migrated across the Pacific Ocean but stopped signalling on 16 December as it approached Vancouver Island (< 200 km from the Salish Sea). The last staging bird departed Izembek on 16 December and reached the Salish Sea by 26 December but was depredated by a Bald Eagle around 6 January 2003 (Washington Dept. Fish & Wildlife, unpubl. data).

In 2005, mortality, transmitter loss, and/or premature transmitter failure rates were relatively low (36%). Of the 13 geese marked with implantable VHF transmitters in 2005, the transmitter of one goose failed on Melville Island (observed but radio not functioning in August 2005) while two others were never detected. Ten VHF-tagged geese were detected at Izembek in

autumn and one overwintered there. Of the nine birds that departed Izembek, eight were detected in the Salish Sea, of which two were shot in January 2006 by sport hunters and a third died of unknown causes in February 2006 (Washington Dept. Fish & Wildlife, unpubl. data). Three birds departed the Salish Sea in spring and one of these birds stopped at Izembek in May 2006.

Of the 20 geese marked with implantable PTTs in 2005, one transmitter stopped signalling near Izembek during late autumn staging (16 November 2005), three birds died of unknown causes at or near

Izembek (one during autumn migration, on 5 October; another in mid-winter, on 15 February 2006, presumably having attempted to overwinter, and the last during spring migration, on 19 May 2006), and two other birds were shot in the Salish Sea during winter (22 and 23 January; Washington State Dept. Fish & Wildlife, unpubl. data).

Autumn migration

During the southward migration from Melville Island, all 2002 and 2005 PTT-tagged Brant followed a coastal route around Alaska (Fig. 2, Fig. 3). The geese

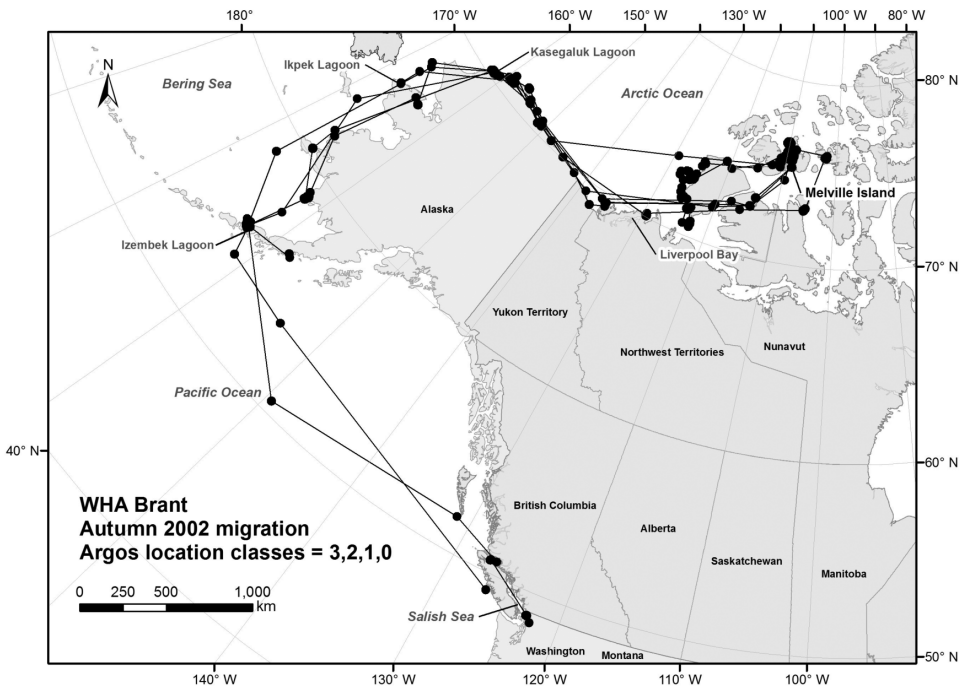


Figure 2. Autumn migration route followed by PTT-tagged WHA Brant in 2002. Notes: 1) The locations for each PTT-tagged Brant are accurate but the lines connecting consecutive locations may not describe the actual route followed, especially when large distances are involved. 2) All high quality PTT location classes (3 and 2) were used but class 1 and 0 locations were filtered if they suggested impossible ground speeds and/or implausible locations (see text); this resulted in gaps between some transmission periods.

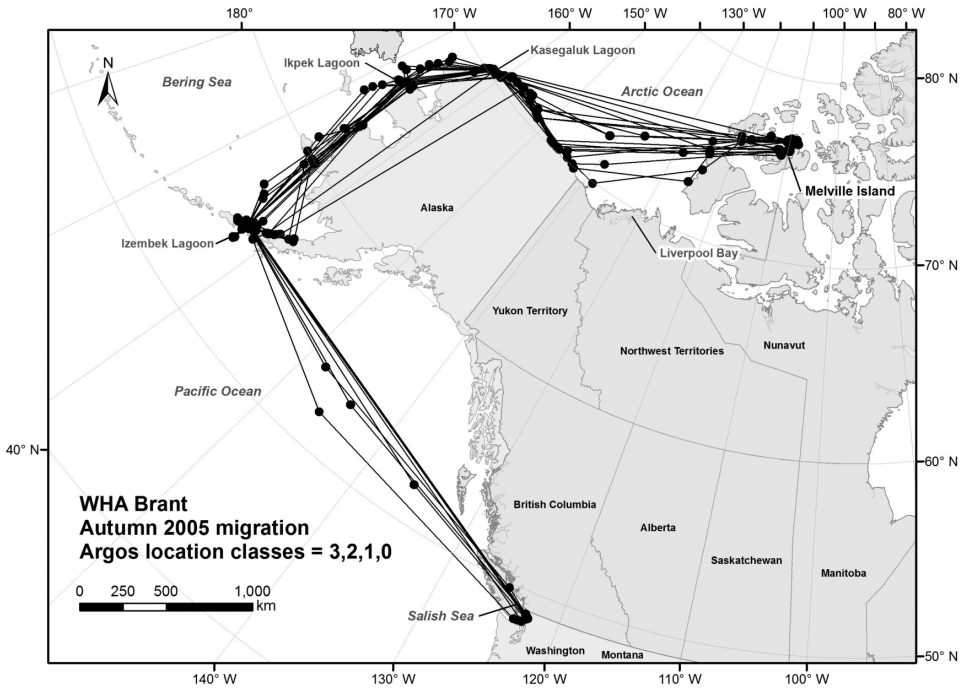


Figure 3. Autumn migration route followed by PTT-tagged WHA Brant in 2005. See Notes in Figure 2.

stopped for short periods along Alaska's north and west coasts and staged for variable lengths of time at Kasegaluk, Ikpek, and Izembek lagoons.

All PTT-tagged Brant with signalling transmitters were detected in Kasegaluk Lagoon in both years, and most were concentrated near Icy Cape. The PTT-tagged geese reached Kasegaluk Lagoon an average of 4–12 d after departing Melville Island and remained there for an average of 8–15 d (Table 2). Mean arrival dates at Kasegaluk in 2002 and 2005 were 15 and 8 September and mean departure dates were 29 and 16 September, respectively.

The next staging area was Ikpek Lagoon on the north coast of the Seward Peninsula.

Only one PTT-tagged goose in 2002 and at least 18 of 20 (90%) in 2005 stopped at this lagoon and remained there for an average of 4–7 d (Table 2). Mean arrival dates at Ikpek in 2002 and 2005 were 13 October and 18 September and mean departure dates were 19 October and 21 September, respectively.

The most important staging area in terms of length of stay was Izembek. All three of the 2002 PTT-tagged birds that were still signalling and all 20 of the 2005 PTT-tagged birds staged at this lagoon. The geese reached Izembek *c.* 38 d and *c.* 20 d after departing Melville Island in 2002 and 2005, respectively, and they remained there for an average of 62–65 d (Table 2). Mean arrival dates at Izembek in 2002 and 2005 were 10

Table 2. Arrival and departure dates at autumn staging, overwintering, and spring staging areas for WHA Brant marked with PTT transmitters on Melville Island in 2002 and 2005.

Location	Year	<i>n</i>	Mean arrival (range)	<i>n</i>	Mean departure (range)	Mean duration (d) (range)
Autumn						
Melville Island	2002	N/A	N/A	8	3 Sep. (29 Aug.–6 Sep.)	N/A
Melville Island	2005	N/A	N/A	20	4 Sep. (28 Aug.–13 Sep.)	N/A
Kasegaluk	2002	4	15 Sep. (12–20 Sep.)	4	29 Sep. (23 Sep.–3 Oct.)	15 (9–23)
Kasegaluk	2005	20	8 Sep. (2–18 Sep.)	20	16 Sep. (6–27 Sep.)	8 (1–18)
Ikpek Lagoon	2002	1	13 Oct.	1	19 Oct.	7
Ikpek Lagoon	2005	18	18 Sep. (9–26 Sep.)	18	21 Sep. (17–27 Sep.)	4 (1–12)
Izembek Lagoon	2002	3	10 Oct. (7–17 Oct.)	3	13 Dec. (12–15 Dec.)	65 (57–70)
Izembek Lagoon	2005	20	23 Sep. (7 Sep.–7 Oct.)	18	23 Nov. (14 Nov.–11 Dec.)	62 (47–81)
Winter						
Salish Sea	2002/03	1	26 Dec.	N/A	N/A	N/A
Salish Sea	2005/06	17	2 Dec. (26 Nov.–15 Dec.)	11	27 May (7 May–9 Jun.)	175 (152–190)
Spring						
Izembek Lagoon	2006	2	13 May (7–19 May)	1	28 May	15
Liverpool Bay	2006	6	3 Jun. (29 May–7 Jun.)	6	7 Jun. (5–9 Jun.)	4 (1–8)
Melville Island	2006	8	14 Jun. (9 Jun.–8 Jul.)	N/A	N/A	N/A

October and 23 September and mean departure dates were 13 December and 23 November, respectively.

Average dates of arrival to and departure from Izembek were similar between VHF- and PTT-tagged Brant within years (arrival: 5 October *vs.* 10 October in 2002, and 22 September *vs.* 23 September in 2005; departure: 5 December *vs.* 13 December in 2002 and 22 November *vs.* 23 November in 2005; Tables 2 & 3). Mean duration of staging at Izembek was *c.* 62 d and differed little (≤ 3 days) between VHF- and PTT-tagged birds within and between years (Tables 2 & 3).

During autumn staging at Izembek, the large majority of VHF and PTT detections occurred in the northern part of the lagoon, especially Moffet Bay: *c.* 73% (2002) and *c.* 91% (2005) of VHF detections and *c.* 67% (2002) and *c.* 71% (2005) of PTT detections (Figs. 4, 5 & 6). If the area immediately adjacent to Moffet Bay is included (Round Island to Strawberry Point) these proportions increase to: *c.* 91% (2002) and *c.* 99% (2005) of all VHF detections and *c.* 100% (2002) and *c.* 100% (2005) of all PTT detections.

As was previously noted, two of the 2002 PTT-tagged geese (both females) signalled while over the Pacific Ocean but only one made it all the way to the Salish Sea (Fig. 2). This last bird took *c.* 60 h to fly from Izembek to Port McNeil on the northeast coast of Vancouver Island, where it staged for about five days before moving to the southern part of the Salish Sea, after which it was depredated. The other goose took *c.* 62 h to fly from Izembek to the southwest coast of Vancouver Island, after which its transmitter stopped signalling. The average ground speed over the mid-portion of the Pacific Ocean for these two geese was estimated at *c.* 50 km h⁻¹.

In 2005, 17 PTT-tagged geese migrated from Izembek to the Salish Sea. Thirteen of these geese did not signal anywhere between Izembek and the Salish Sea and this may be due to the fact that they migrated during the period of extended duty cycles (9 d between transmissions from 31 October to 6 December 2005; see Table 1). However, four birds transmitted while over the Pacific Ocean (Fig. 3) and three of these had sufficient high quality location data to

Table 3. Autumn arrival and departure dates at Izembek Lagoon for WHA Brant marked with VHF transmitters on Melville Island in 2002 and 2005.

Location	Year	<i>n</i>	Mean arrival (range)	<i>n</i>	Mean departure (range)	Mean duration (d) (range)
Izembek Lagoon	2002	21	5 Oct. (19 Sep.–28 Oct.)	11	5 Dec. (12 Nov.–30 Dec.)	62 (26–88)
Izembek Lagoon	2005	10	22 Sep. (20–28 Sep.)	9	22 Nov. (19–23 Nov.)	62 (55–64)

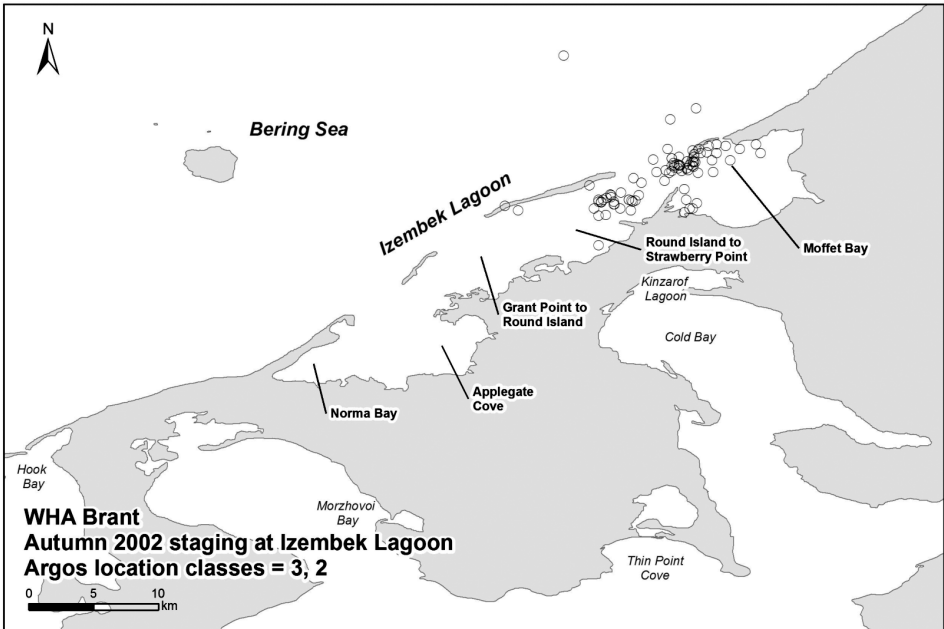


Figure 4. Map showing PTT-tagged WHA Brant detections at Izembek Lagoon, Alaska, during autumn staging in 2002.

estimate that they took *c.* 68 h to fly from Izembek to the Salish Sea. Allowing for some deviation from a perfect great circle distance of *c.* 2,900 km, this duration computes to an average ground speed of 50–55 km h⁻¹.

The first PTT-tagged bird reached the Salish Sea on 26 November and the average arrival date for all 17 geese was 2 December (Table 2). Altogether, the 2005 southward migration from Melville Island to the Salish Sea took on average 90 ± 8.0 d (range = 80–108 days; *n* = 17).

Over-wintering

In 2002/03, one VHF-tagged Brant was detected in Izembek Lagoon on 18 January 2003 and again on 6 March 2003. In

2005/06, two tagged Brant (one VHF and one PTT) are presumed to have overwintered at Izembek. Both birds remained in Moffet Bay until freeze-up in early December and then moved to Hook Bay, a relatively ice-free embayment 35 km west of Izembek. The VHF bird was detected on 26 January 2006 in Hook Bay and on 24 May 2006 in Izembek near Strawberry Point. The PTT bird died on 15 February 2006 in Hook Bay during a severe freezing event.

In winter 2005/06, *c.* 45% of high quality PTT detections in the south Salish Sea occurred in Samish Bay, followed by Padilla Bay (*c.* 26%), and the remainder (*c.* 29%) occurred from Bellingham Bay, Washington, to Boundary Bay, British Columbia (Fig. 7,

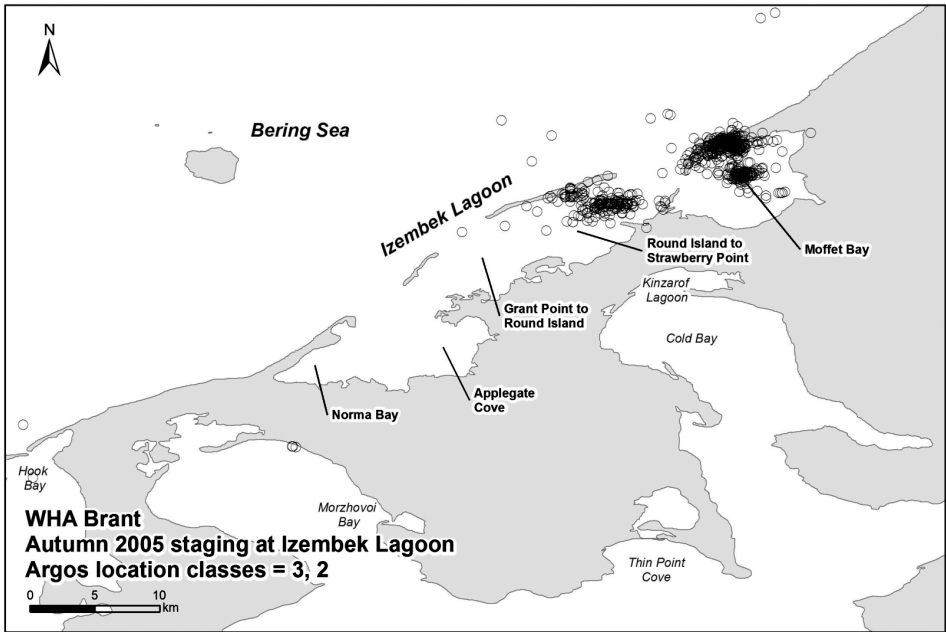


Figure 5. Map showing PTT-tagged WHA Brant detections at Izembek Lagoon, Alaska, during autumn staging in 2005.

Fig. 8). The geese moved very little over the winter period: two restricted their movements almost entirely to Samish Bay (*c.* 50 km²), two used Lummi Bay only (*c.* 25 km²), and eight geese restricted their movements to Samish Bay and adjacent Padilla Bay (*c.* 150 km²). This consistency in habitat use patterns is also reflected in the fact that there were no apparent differences in the detection densities across the winter months or between daytime versus nighttime hours.

Spring migration

No spring migration data were available in 2003 and the sample size of VHF-tagged birds in 2006 ($n = 2$) was too small to draw any conclusions. For these reasons, this

section focuses on the 2005 PTT-tagged Brant.

In spring 2006, 11 of the 2005 PTT-tagged Brant departed from the Salish Sea (mean departure date was 27 May 2006) and nine returned to their Arctic breeding grounds (mean arrival date was 14 June) (Table 2). Of the two birds that did not return to the breeding grounds, one died near Izembek on 19 May 2006 and another stopped signalling near Juneau, Alaska, on 19 June 2006. Regardless of the route chosen, the spring migration lasted an average of 19.8 ± 13.3 d which was roughly 4.5 times faster than the autumn migration.

Travel times to the breeding grounds varied considerably depending on the route taken: three birds (two with complete

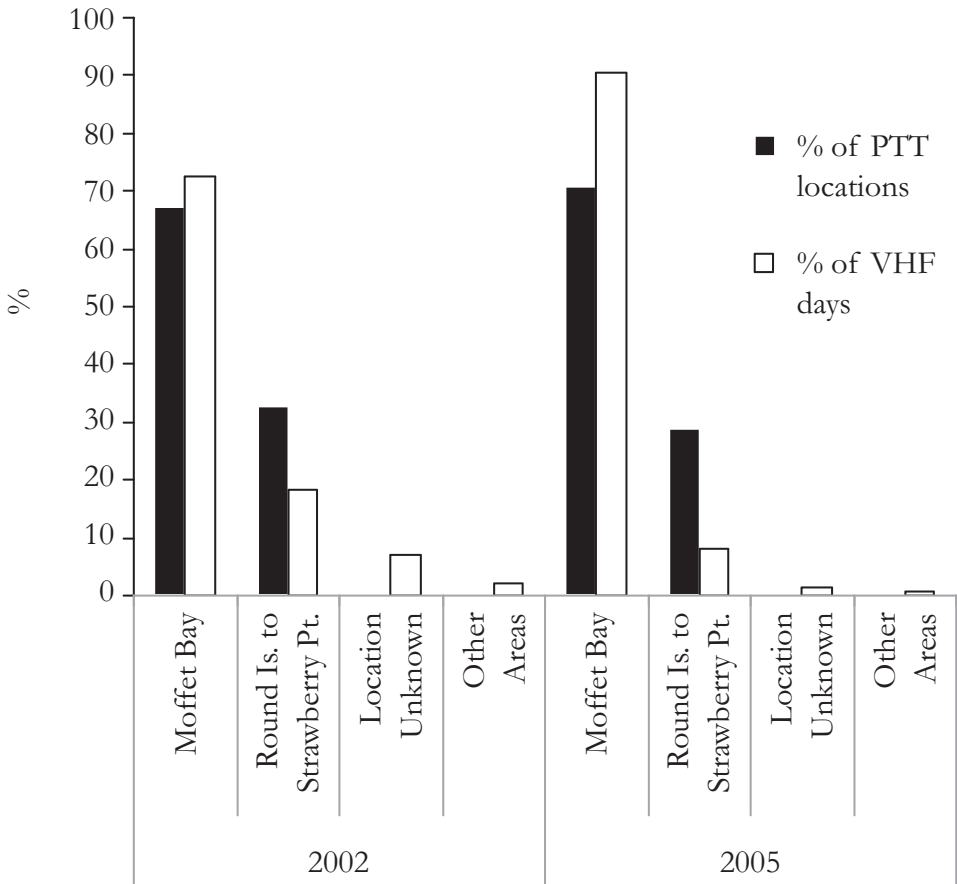


Figure 6. Proportional distribution of PTT- and VHF-tagged WHA Brant detections during autumn staging in 2002 and 2005 at Izembek Lagoon, Alaska (PTT class 3 & 2 detections only, $n = 602$; VHF days = 147).

location information) used a coastal route around Alaska and seven birds (six with complete location information) followed an interior route across the Yukon (Fig. 9). These last six Brant took 12.8 ± 1.9 d to migrate from the Salish Sea to Melville Island, while the two birds using the coastal route took 40.8 ± 7.0 days. The interior migrants departed the wintering grounds approximately two weeks later than the

coastal birds and arrived on the breeding grounds about two weeks earlier; mean departure from the Salish Sea for the interior birds was 31 May compared to 16 May for the coastal birds and mean arrival to Melville Island was 11 June and 25 June, respectively.

Based on PTT location, timing and an average ground speed of 50 km h^{-1} , five of the 11 PTT-tagged geese likely flew non-

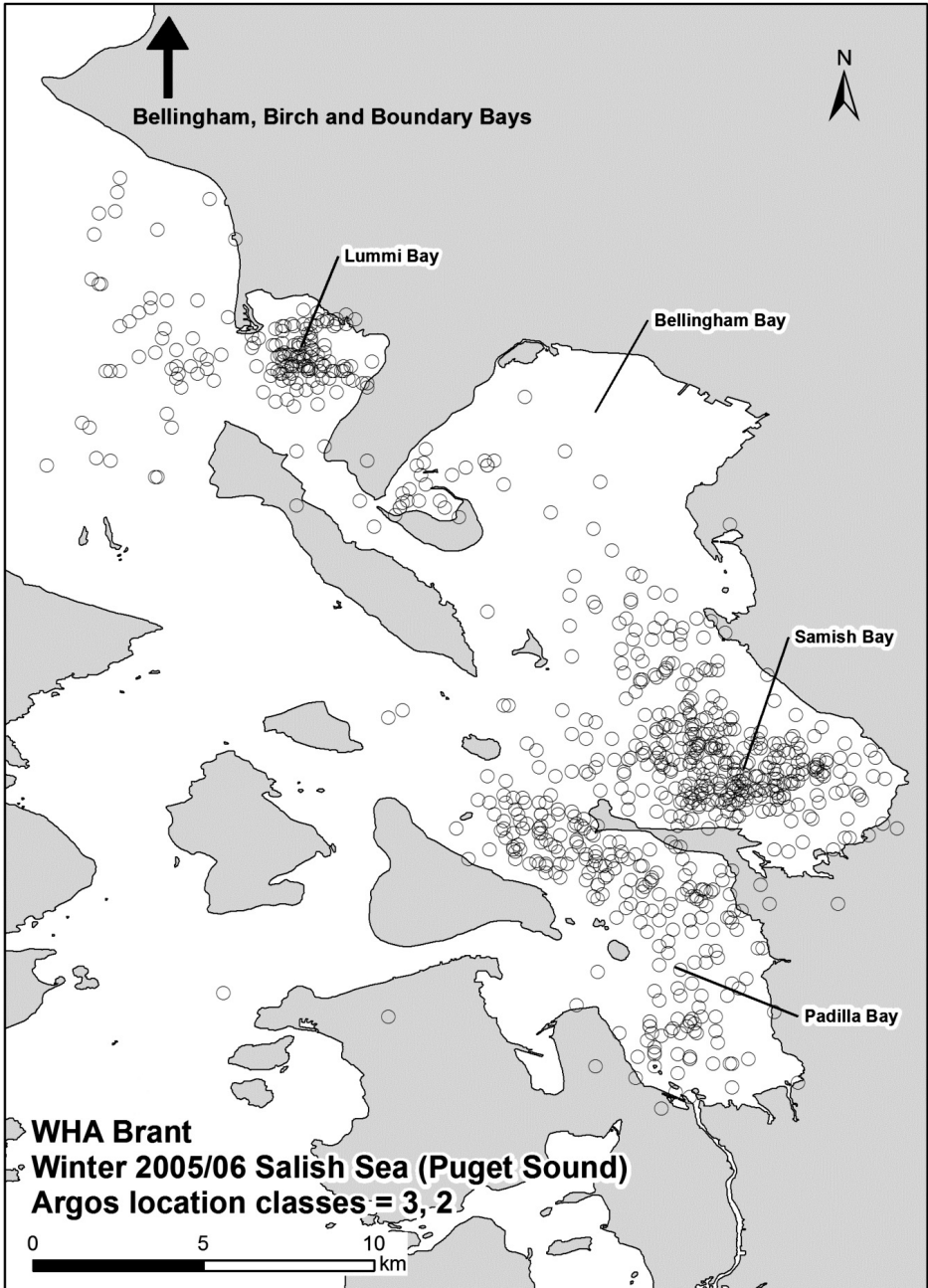


Figure 7. Map showing PTT-tagged WHA Brant detections in the Salish Sea (north Puget Sound, Washington) during winter 2005/06.

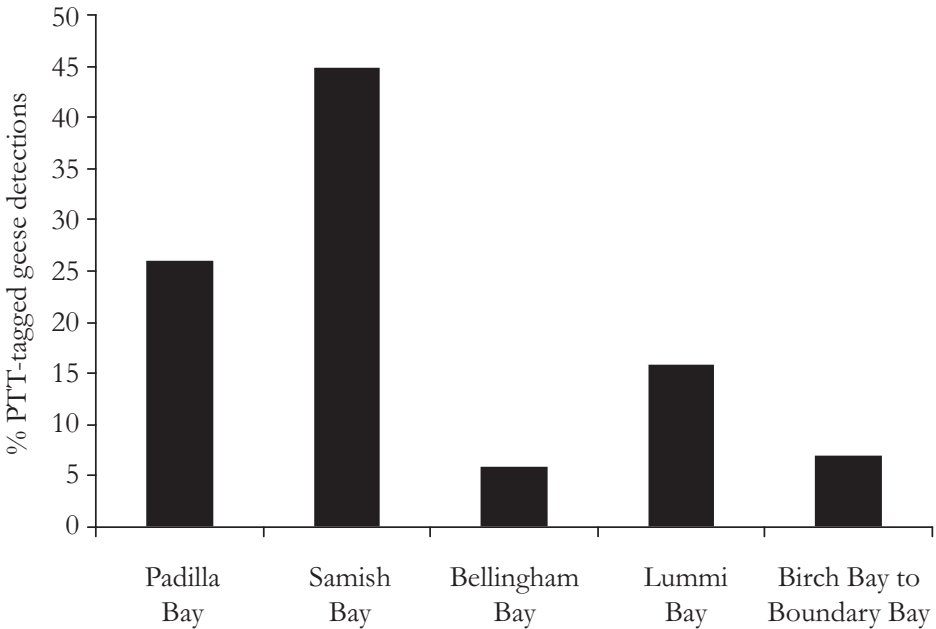


Figure 8. Proportional distribution of PTT-tagged WHA Brant detections in the Salish Sea (north Puget Sound, Washington) during winter 2005/06 (PTT class 3 & 2 detections only, $n = 819$).

stop from the Salish Sea to either Izembek (coastal migrants) or to Liverpool Bay (interior migrants), while the other six individuals stopped along the coast for varying lengths of time (mean duration = 6 days, range = 3–8 days). Five birds staged in southeast Alaska near Juneau (55°19'N, 162°50'W).

Two of the three Brant following the coastal route stopped at Izembek. One bird staged there from 7–28 May before flying on to Melville Island, and the majority of its detections were in the area from Round Island to Strawberry Point (whereas its autumn detections were split equally between Moffet Bay and Round Island to Strawberry Point). The other goose reached

Izembek on 19 May but it died within a few days.

Six of the seven Brant that migrated north using the interior route across the Yukon stopped at Liverpool Bay for approximately four days (Table 2, Fig. 9) before continuing on to Melville Island. All detections in Liverpool Bay were near Campbell Island (69°35'N, 130°44'W).

Altogether, nine males with transmitting PTTs returned to the High Arctic during the June–July breeding period. Of these nine geese, four returned to within five km of their 2005 capture sites, three settled on average 45 km away from their capture sites, and two birds settled about 200 km from their capture sites.

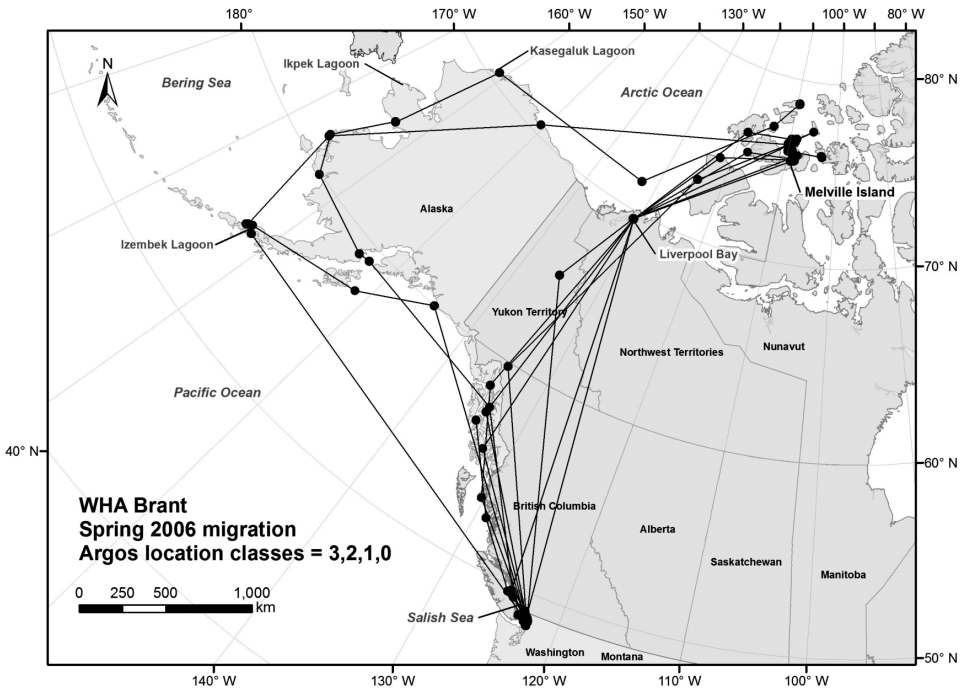


Figure 9. Spring migration route followed by PTT-tagged WHA Brant in 2006. See Notes in Figure 2. Also, the rationale for connecting the last location in southeast AK to Liverpool Bay for some individuals is because these geese would have had to fly the 4,000–4,500 km coastal route around Alaska in < 50 h, which equates to an average ground speed of 80–90 km h⁻¹. This speed would, in turn, require a series of 30–40 km h⁻¹ tail-winds from all directions and along the entire route, which is highly unlikely.

Discussion

This is the first study to document the migration and habitat use patterns of WHA Brant over their entire range and annual cycle. Our results confirm the findings of previous research and have led to several new discoveries, such as: 1) the importance of Kasegaluk Lagoon for WHA Brant as the first major autumn staging area after departure from Melville Island and the use of Ikpeke Lagoon in autumn and Liverpool Bay in spring, 2) the critical use

of Izembek as the last autumn staging area prior to a (likely) non-stop, trans-oceanic migration to the Salish Sea, 3) the importance of Izembek and other embayments on the Alaska Peninsula as a key wintering and spring staging area, 4) the northward shift of wintering geese in the Salish Sea, 5) the dichotomy of spring migration routes (coastal or overland paths), and finally, 6) evidence that WHA Brant are likely site- and route-faithful across years. These results are discussed in more detail below.

Transmitter attachment

The backpack attachment technique we used in 2002 was problematic. Relatively large numbers of the radio-tagged geese in 2002 did not migrate successfully from Melville to Izembek or from Izembek to the Salish Sea and, many of those that did, lost or shed their transmitters, or suffered unusually high predation rates. Further, they migrated later and used more stopover sites compared to the 2005 transmitter-implanted geese. These patterns suggest that our use of “knicker elastic” compromised movements and survival in 2002, even though this technique has been used successfully to track the spring migration patterns for other Brant populations (Clausen *et al.* 2003).

Nevertheless, although the resulting sample size was small, the 2002 backpack PTT-tagged geese exhibited a similar autumn migration pattern as the 2005 implantable PTT-tagged geese. They followed the same coastal route from Melville Island around Alaska and across the Pacific Ocean to the Salish Sea, they staged at Izembek for the same extended period in autumn, and they exhibited similar habitat use patterns within Izembek (this latter finding is also consistent with that of Reed *et al.* 1989a,b). These similar movement and habitat use patterns suggest that WHA Brant are likely site- and route-faithful across years as has been reported for other populations of Brant (Reed *et al.* 1998; Lindberg *et al.* 2007; Sedinger *et al.* 2008).

Autumn migration

Results indicate a strong affiliation between breeding grounds on Melville Island and three autumn staging areas in Alaska:

Kasegaluk, Ikpek, and Izembek lagoons. WHA Brant used these areas presumably because they provide foods for replenishing and building reserves to fuel migration and for augmenting growth in hatching-year birds (Ward *et al.* 2005). The length of stay at these areas likely corresponds to the distribution and abundance of preferred foods and climatic conditions encountered (Ward & Stehn 1989; Johnson 1993; Reed *et al.* 1998). Salt-tolerant plants, such as Hoppner’s Sedge *Carex subspathacea* and Common Salt-marsh Grass *Puccinellia maritima*, are key foods for Brant post-hatch. These plants are abundant along the northwest coast of Alaska (Jorgenson *et al.* 1996) and likely represent the first source of nitrogen-rich foods for WHA Brant since leaving the High Arctic (O’Brian *et al.* 1998; Ward *et al.* 2005). Late summer blooms of algae (*Ulva* and *Enteromorpha*) are also likely important foods at Kasegaluk Lagoon (Johnson 1993). This lagoon is recognised as a critical staging area for a large (> 40%) portion of the Black Brant population (Johnson 1993) and, based on the findings in this study, it also appears to be an important autumn staging area for WHA Brant. The significance of the north coast of the Seward Peninsula as a staging area is less well known for Arctic-nesting Brant, but is likely related to the extensive salt-tolerant plants found there (Jorgenson *et al.* 2009). Marine plants, such as eelgrass *Zostera* sp. and sea lettuce *Ulva* sp., occur on the Seward Peninsula but in low abundance and limited availability (primarily subtidal; D. Ward pers. obs.). Eelgrass becomes the dominant food for Brant in southwest Alaska and is most abundant at Izembek and other

embayments along the lower Alaska Peninsula (Ward *et al.* 1997).

This study confirms earlier research by Reed *et al.* (1989b) indicating that Izembek is a key autumn staging area for WHA Brant to build body reserves to fuel their trans-oceanic flight to the Salish Sea. This is reflected in the longer length of stay of PTT-tagged birds at Izembek (*c.* 62–65 d) compared to Kasegaluk Lagoon (*c.* 8–15 d) and Ikpek Lagoon (*c.* 4–7 d). The duration of the autumn staging period at Izembek of 62 d for both PTT- and VHF-tagged geese in 2005 is about 15 d longer than that found by Reed *et al.* (1989b) for WHA Brant at Izembek in 1987 using backpack VHF technology. The lengthier stay at Izembek appears to be caused more by an earlier arrival (22–23 September 2005 *vs.* 3 October 1987) than by a later departure (22–23 November 2005 *vs.* 19 November 1987), which is consistent with patterns of climate warming in the Arctic (Melville) and temperate (Izembek) regions; changes in the onset of Arctic springs are greater than changes in the delays in the start of temperate winters (Stafford *et al.* 2000, IPCC 2007).

The development of migratory routes is thought to be influenced by the direction of favourable tail-winds associated with the onset of low-pressure systems (Able 1972; Gauthreaux 1980; Piersma & van de Sant 1992; Rappole & Ramos 1994; Williams & Webb 1996; Dau 1992; Purcell & Brodin 2007). Empirical evidence further supports the association between favourable winds and migration timing for arctic-nesting geese (*e.g.* Gudmundsson 2008). The 2002 and 2005 PTT data indicate an over water

migration from Izembek to the Salish Sea and this is consistent with the notion of a trans-oceanic route used by Black Brant from Izembek to Mexico (Dau 1992). The *c.* 50 km h⁻¹ ground speed estimated for both the 2002 and 2005 geese is well within the flight capability of Brant (Dau 1992, Clausen *et al.* 2003), suggesting that the WHA Brant could have flown non-stop from Izembek to the Salish Sea.

By back-extrapolating flight durations from their known at-sea locations, we estimated that two geese departed Izembek between 02:00h–06:00 h Coordinated Universal Time (UTC) on 11 December 2005 and another individual departed only about 10 h later, indicating that there may have been an exodus of Brant from Izembek on that day. The average daily wind speed and direction at nearby Cold Bay on 11 December were 20 km h⁻¹ and 310°, respectively, suggesting that these birds were likely using a tail-wind to aid their trans-oceanic voyage, at least initially.

Over-wintering

Historically, few (< 5,000) Brant overwintered in Alaska but in recent years numbers have grown to over 40,000 individuals (the large majority being Black Brant), probably in response to climate warming (Ward *et al.* 2009). If the two geese that overwintered in 2005/06 are truly representative of all WHA Brant then Izembek may be supporting 5–10% of the current breeding stock.

The core wintering area for Melville WHA Brant is clearly the southern Salish Sea. Comparatively few WHA Brant used Boundary Bay in the 1970s as indicated by

only one individual observed there during surveys of colour-marked birds tagged from the High Arctic in 1973/75 (Boyd & Maltby 1979). In 1987/88, Padilla Bay supported a large wintering flock of *c.* 15,000 Brant made up almost exclusively of WHA Brant and very few (< 1%) of the geese overwintering from Birch Bay to Boundary Bay were WHA Brant (Reed *et al.* 1989a). However, recent observations of increasing numbers of WHA Brant overwintering in Canada (Reed *et al.* 1998; International Brant Monitoring Project 2012) and results from this PTT study indicate that their distribution has shifted northward since the late 1980s. Approximately 7% of all winter 2005/2006 PTT detections occurred from Birch Bay (just north of Lummi Bay) to Boundary Bay, British Columbia. The reason for this northward redistribution is unknown.

Spring Migration

Most (78%) PTT-tagged WHA Brant returning to Melville Island in spring flew across the interior of the Yukon, a route identified decades earlier by Cottam *et al.* (1944). These Brant departed the Salish Sea wintering grounds later than the coastal migrants and arrived at the breeding grounds earlier. The interior route may be riskier than the coastal route in terms of freezing weather events and/or lack of key foods, but the risks may be offset by the fact that early nesters hatch relatively more eggs and their young grow faster and larger and survive longer than individuals that arrive and nest later (Sedinger & Raveling 1986; Sedinger & Flint 1991; Lepage *et al.* 1998; Prop *et al.* 2003; Bêty *et al.* 2003, 2004). Possibly even more important is that the

interior route decreases overall flight distance by > 3,000 km and this equates to a significant reduction in the amount of reserves needed to migrate successfully.

In contrast to the above, there are several possible reasons why some Brant may choose a coastal route. They may be non-breeders and therefore have no intention to reach the breeding grounds at some optimal time. Brant require a certain level of body reserves, especially lipids, to breed successfully (Ebbinge & Spaans 1995), and they can decide whether or not to breed based on the size of their reserves prior to embarking (Spaans *et al.* 1998). Flight costs rise with increasing body mass due to increased wing loading (Green *et al.* 2002; Purcell and Brodin 2007) so it is possible that non-breeders or birds in poor condition may forego the direct migration route to increase refuelling opportunities and reduce energetic costs. Furthermore, Brant in poor condition have little to gain by attempting a direct migration since their fuel requirements for breeding successfully could never be met. There are other potential advantages to opt for a coastal migration such as avoiding additional energetic costs of crossing mountainous regions (Alerstam *et al.* 1990; Gudmundsson *et al.* 1995; Clausen *et al.* 2003; Green & Alerstam 2000) and taking advantage of visual navigation references (especially for learning juveniles; Purcell & Brodin, 2007), shelter availability, and fresh water sources (Green *et al.* 2002).

Stock segregation

The morphological and genetic separation of WHA Brant and Black Brant populations

is likely driven, in part at least, by temporal and spatial differences during the breeding and non-breeding seasons. WHA Brant breed further north than Black Brant, migrate later in autumn and spring, and segregate spatially during periods of overlap. Segregation may be linked to plumage, size, and behavioural differences (Reed *et al.* 1989a,b; S. Boyd pers. obs.), but physiological differences may also play a role. For example, salinity levels are generally relatively low in areas preferred by WHA Brant at Izembek (26–27 PSU; Hogrefe *et al.* 2011) and in the Salish Sea (26–29 PSU; Newton *et al.* 2002; Bulthuis 2013), suggesting that they may have a lower salinity tolerance than Black Brant.

Further to the above, three adult males assumed to be Eastern High Arctic (EHA) Brant, were marked with implantable PTTs on Bathurst Island in August 2005 (S. Boyd & K. Colhoun, unpubl. data). Bathurst Island and Melville Island are only *c.* 50 km apart, yet these three Bathurst birds migrated via Iceland to Ireland where they spent the winter. The divergent migration patterns of the Melville-tagged geese that overwintered in the eastern North Pacific and the Bathurst-tagged geese that overwintered in Ireland suggest a geographic dividing line between the two islands with the large majority of WHA Brant breeding from Melville to the west and most EHA Brant breeding from Bathurst to the east. This is consistent with earlier findings where only *c.* 1% of (suspected) WHA Brant marked with metal bands on Melville Island in the 1970s were found in Europe (Boyd and Maltby, 1979) and only *c.* 1% of (suspected) WHA Brant colour-marked on Melville and Prince Patrick

islands in 1987 were sighted in Ireland the following winter (Boyd *et al.* 1988).

Recommendations

Despite the above findings, there remain important knowledge gaps inhibiting the management and conservation of WHA Brant. We know that they breed across several Arctic islands other than Melville, including Prince Patrick and Eglington, and potentially Borden, Brock, Byam Martin, Eight Bears, Emerald, Fitzwilliam Owen, and Mackenzie King (Boyd & Maltby 1979; Boyd *et al.* 1988; see Fig. 1), but nothing is known about their proportional distribution patterns, including nesting and moulting ‘hotspots’. One way to fill this information gap would be to capture a large number of WHA Brant in winter, mark them with implantable PTTs, and track them over at least one annual cycle. The results would better define the breeding and moulting range of WHA Brant and provide critical information for designing future aerial surveys in the Arctic. Also, the mid-winter (January) survey of Brant to estimate the size of the WHA Brant population should be expanded northward given that 30% of all PTT detections in the Salish Sea were between Lummi Bay and Boundary Bay.

The WHA Brant population is relatively small, unique and concentrates in only a few restricted areas at different periods of the annual cycle. For these reasons, the stock is susceptible to a range of threats such as excessive harvesting, habitat loss and/or degradation, and petroleum spills. These factors, and the increasing numbers of overwintering WHA Brant in Alaska, need to be considered in the management of the population.

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References

- Able, K.P. 1972. Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf region. *Wilson Bulletin* 84: 231–242.
- Alerstam, T., Gudmundsson, G.A., Jönsson, P.E., Karlsson, J. & Lindström, Å. 1990. Orientation, migration routes and flight behaviour of Knots, Turnstones and Brant Geese departing from Iceland in spring. *Arctic* 43: 201–214.
- Boyd, H. & Maltby, L.S. 1979. The brant of the western Queen Elizabeth Islands, N.W.T. In R.L. Jarvis and J.C. Bartonek (eds.), *Management and biology of Pacific Flyway geese, a symposium*, pp. 5–21. Oregon State University Book Stores, Corvallis, Oregon, USA.
- Boyd, H. & Maltby, L.S. 1980. Weights and primary growth of brent geese moulting in the Queen Elizabeth Islands, N.W.T., Canada. *Ornis Scandinavica* 11: 135–141.
- Boyd, H., Maltby, L.S. & Reed, A. 1988. Differences in the plumage patterns of Brant breeding in High Arctic Canada. Canadian Wildlife Service Progress Note 174, Ottawa, Ontario, Canada.
- Bulthuis, D.A. 2013. The ecology of Padilla Bay, Washington: an estuarine profile of a national estuarine research reserve. Padilla Bay National Estuarine Research Reserve – Shorelands and Environmental Assistance Program. Washington State Dept. of Ecology, Olympia, USA.
- Clausen, P., Green, M. & Alerstam, T. 2003. Energy limitations for spring migration and breeding: the case of brent geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland. *Oikos* 103: 426–445.
- Cottam, C., Lynch, J.J. & Nelson, A.J. 1944. Food habits and management of American sea brant. *Journal of Wildlife Management* 8: 36–56.
- Dau, C.P. 1992. Fall migration of Pacific Brant in relation to climatic conditions. *Wildfowl* 43: 80–95.
- Ebbinge, B.S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b.*

- bernicla* in the High Arctic. *Journal of Avian Biology* 26: 105–113.
- Green, M. & Alerstam, T. 2000. Flight speeds and climb rates of Brent Geese: Mass-dependent differences between spring and autumn migration. *Journal of Avian Biology* 31: 215–225.
- Green, M., Alerstam, T., Clausen P., Drent, R. & Ebbinge, B.S. 2002. Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration. *Ibis* 144: 106–121.
- Gudmundsson, G.A. 2008. The spring migration pattern of arctic birds in southwest Iceland, as recorded by radar. *Ibis* 135: 166–176.
- Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F. & Lilliendahl, K. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 261: 73–79.
- Handley, C.O. 1950. The brant of Prince Patrick Island, Northwest Territories. *Wilson Bulletin* 62: 128–132.
- Hogrefe, K., Ward, D.H., Donnelly, T.F. & Fairchild, L. 2011. Eelgrass and seaweed assessments at Izembek National Wildlife Refuge, 2007–2010. USGS Unpubl. Progress Report, US Geological Survey, Anchorage, USA.
- International Brant Monitoring Project. 2012. Observation logs: 2012–2013 Observations. <http://www.padillabay.gov/brant/observationlogs/log1213.asp>.
- Intergovernmental Panel on Climate Change (IPCC). 2007. Climate Change 2007: Synthesis report, contribution of working groups I, II, and III to the fourth assesment of the intergovernmental panel on climate change. Core writing team, Pachauri, R.K. & Reisinger, A. (eds.). IPCC, Geneva, Switzerland.
- Johnson, S.R. 1993. An important early-autumn staging area for Pacific Flyway Brant (*Branta bernicla*): Kasegaluk Lagoon, Chukchi Sea, Alaska. *Journal of Field Ornithology* 64: 539–548.
- Jorgenson, M.T., Roth, J.E., Pullman, E.R., Burgess, R.M., Reynolds, M., Stickney, A.A., Smith, M.D. & Zimmer, T.M. 1996. An ecological land survey for the Colville River Delta, Alaska. Final Report to Arco Alaska Inc. and Kuukpik Unit Owners. ABR Inc., Fairbanks, Alaska, USA.
- Jorgenson, M.T., Roth, J.E., Miller, P.F., Macander, M.J., Duffy, M.S., Wells, A.F., Frost, G.V. & Pullman, E.R. 2009. An ecological land survey and landcover map of the Arctic network. Alaska Biological Research, Inc. Technical Report to the National Park Service, Nome, Alaska, USA.
- Korschgen, C.E., Kenow, K.P. Gendron-Fitzpatrick, A. Green, W.L. & Dein, F.J. 1996. Implanting intra-abdominal radiotransmitters with external whip antennas in ducks. *Journal of Wildlife Management* 60: 132–137.
- Lepage, D., Gauthier, G. & Reed, A. 1998. Seasonal variation in growth of greater snow goose goslings: The role of food supply. *Oecologia* 114: 226–235.
- Lindberg, M.S., Ward, D.H. Tibbitts, T.L. & Roser, J. 2007. Winter movement dynamics of black brant. *Journal of Wildlife Management* 71: 534–540.
- Newton, J. A., Albertson, S.L. Van Voorhis, K., Maloy, C. & Siegel, E. 2002. Washington State Marine Water Quality, 1998 through 2000. Washington State Dept. of Ecology Environmental Assessment Program. Washington State Dept. of Ecology, Olympia, USA.
- O’Briain, M., Reed, A. & MacDonald, S. D. 1998. Breeding, moulting, and site fidelity of brant (*Branta bernicla*) on Bathurst and Seymour Islands in the Canadian High Arctic. *Arctic* 51: 350–360.
- Piersma, T. & van de Sant, S. 1992. Pattern and predictability of potential wind assistance for

- waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica* 2: 55–66.
- Prop, J., Black, J.M., & Shimmings, P. 2003. Travel schedules to the high arctic: Barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103: 403–414.
- Purcell, J. & Brodin, A. 2007. Factors influencing route choice by avian migrants: A dynamic programming model of Pacific brant migration. *Journal of Theoretical Biology* 249: 804–816.
- Rappole, J.H. & Ramos, M.A. 1994. Factors affecting migratory bird routes over the Gulf of Mexico. *Bird Conservation International* 4: 251–262.
- Reed, A., Davison, M.A. & Kraege, D.K. 1989a. Segregation of brant geese *Branta bernicla* wintering and staging in Puget Sound and the Strait of Georgia. *Wildfowl* 40: 22–31.
- Reed, A., Stehn, R. & Ward, D. 1989b. Autumn use of Izembek Lagoon, Alaska, by brant from different breeding areas. *The Journal of Wildlife Management* 53: 720–725.
- Reed A., Ward, D.H., Derksen, D.V. & Sedinger, J.S. 1998. Brant (*Branta bernicla*). In A. Poole & F. Gill (eds.), *The Birds of North America No. 337*, pp. 1–32. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C., USA.
- Sedinger, J.S. & Flint, P.L. 1991. Growth-rate is negatively correlated with hatch date in Black Brant. *Ecology* 72: 496–502.
- Sedinger, J.S., Lensink, C.J., Ward, D.H., Anthony, R.M., Wege, M.L. & Byrd, G.V. 1993. Current status and recent dynamics of the black brant *Branta bernicla* breeding population. *Wildfowl* 44: 49–59.
- Sedinger, J.S. & Raveling, D.G. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *Journal of Animal Ecology* 55: 1083–1102.
- Sedinger, J.S., Chelgren N.D., Lindberg, M.S. & Ward, D.H. 2008. Fidelity and breeding probability related to population density and individual quality in black brant geese (*Branta bernicla nigricans*). *Journal of Animal Ecology* 77: 702–712.
- Shields, G.F. 1990. Analysis of mitochondrial DNA of Pacific Black Brant (*Branta bernicla nigricans*). *Auk* 107: 620–623.
- Spaans, B., Blijleven, H.J., Popov, I.U., Rykhlikova, M.E. & Ebbinge, B.S. 1998. Dark-bellied Brent Geese *Branta bernicla bernicla* forego breeding when Arctic Foxes *Alopex lagopus* are present during nest initiation. *Ardea* 86: 11–20.
- Stafford, J.R., Wendler, G. & Curtis, J. 2000. Temperature and precipitation of Alaska: 50 year trend analysis. *Theoretical Applied Climatology* 67: 33–44.
- Ward, D.H., Markon, C.J. & Douglas, D.C. 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany* 58: 229–240.
- Ward, D.H., Dau, C.P., Tibbitts, T.L., Sedinger, J.S., Anderson, B.A. & Hines, J.E. 2009. Change in abundance of Pacific brant wintering in Alaska: evidence of a climate warming effect? *Arctic* 62: 301–311.
- Ward, D.H. & Stehn, R.A. 1989. Response of brant and other geese to aircraft disturbance at Izembek Lagoon, Alaska. U.S. Fish and Wildlife Service Final Report No. 14-12-0001-30332, Alaska Fish and Wildlife Resource Center, Anchorage, Alaska, USA.
- Ward, D.H., Reed, A., Sedinger, J.S., Black, J.M., Derksen, D.V. & Castelli, P.M. 2005. North American brant: effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11: 869–880.
- Williams, T.C. & Webb, T. 1996. Neotropical bird migration during the ice ages: Orientation and ecology. *Auk* 113: 105–118.