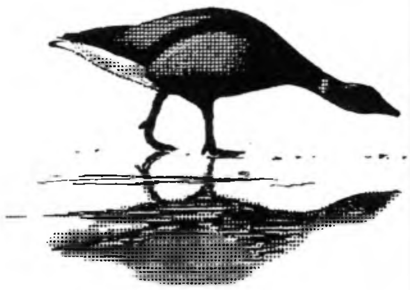
The fall migration of Pacific Flyway Brent *Branta bernicla* in relation to climatic conditions



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Fall migrations of Brent from Izembek Lagoon, Alaska, to wintering areas in Baja California, Mexico were studied for 30 years from 1959 to 1988. Surface and upper air weather patterns were analyzed for departure, approximate mid-route and arrival locations. Radar was used to determine the average departure direction and altitude of 30 migrating flocks within 130 km of Izembek Lagoon. Based on radar observations, upper air wind directions at the 850 millibar level were used to estimate the most favourable migration route to wintering areas in Mexico.

Estimated migration routes averaged 5301 km v *a direct route distance of 4408 km. Estimated time in route averaged 54.3 hours and average ground speed was 99 kph based on probable routes over the 30 year period. During 1974, 1983 and 1984, observers in Alaska and Mexico documented Brent departures and arrivals, estimating times* en route *to be 60, 60 and 95 hours, respectively. The configuration of the departure weather system, and the direction and velocity of winds, are important factors causing variability in observed flight duration. The rapid fall migration of Pacific populations of Brent is energetically costly with males and females, respectively, losing an estimated 33% and 31% of their total body weights. Physiological demands of migration from Izembek Lagoon to Mexico may exceed the amounts of body reserves accumulated during the fall staging period.*

The Pacific Flyway Brent *Branta bernicla* population breeds in coastal habitats of the Canadian and Soviet arctic and sub-arctic and arctic areas of Alaska. All geographic components of the population combine during the fall staging period on the Izembek National Wildlife Refuge (Jones 1970) prior to their long distance, short duration and energetically costly fall migration to wintering areas (Bellrose 1981). Analysis of such spectacular events in the annual cycle of this marine goose is difficult, however, biological and climatological data may help understand migratory phenology and the characteristics of weather systems selected for fall, *en masse* migrations.

Annual data on fall migration, productivity and population composition of Brent have been obtained on the Izembek refuge since 1959. This paper presents analyses of migratory phenology and behaviour as it relates to climatological conditions. The pattern of the fall departure system and wind speed and direction at Pacific coast reporting stations were used to estimate the probable route and duration of the flight of Brent across the northeastern Pacific Ocean to wintering areas in Mexico.

This and other studies of waterfowl migration suggest that correlations exist between migratory phenology and the intensity and other characteristics of fall storm systems (Richardson 1972, Blokpoel *et al.* 1975, Hawkings 1982). When physiologically prepared, wind speed and direction may be the primary factors triggering fall migration in Brent and other species (Blokpoel & Gauthier 1975, Evans 1979).

Study site and subjects

Izembek Lagoon supports nearly the entire Pacific Flyway population of Brent for up to one month during the spring, and three months during fall migration. Recent midwinter population estimates of birds in wintering areas from British Columbia to

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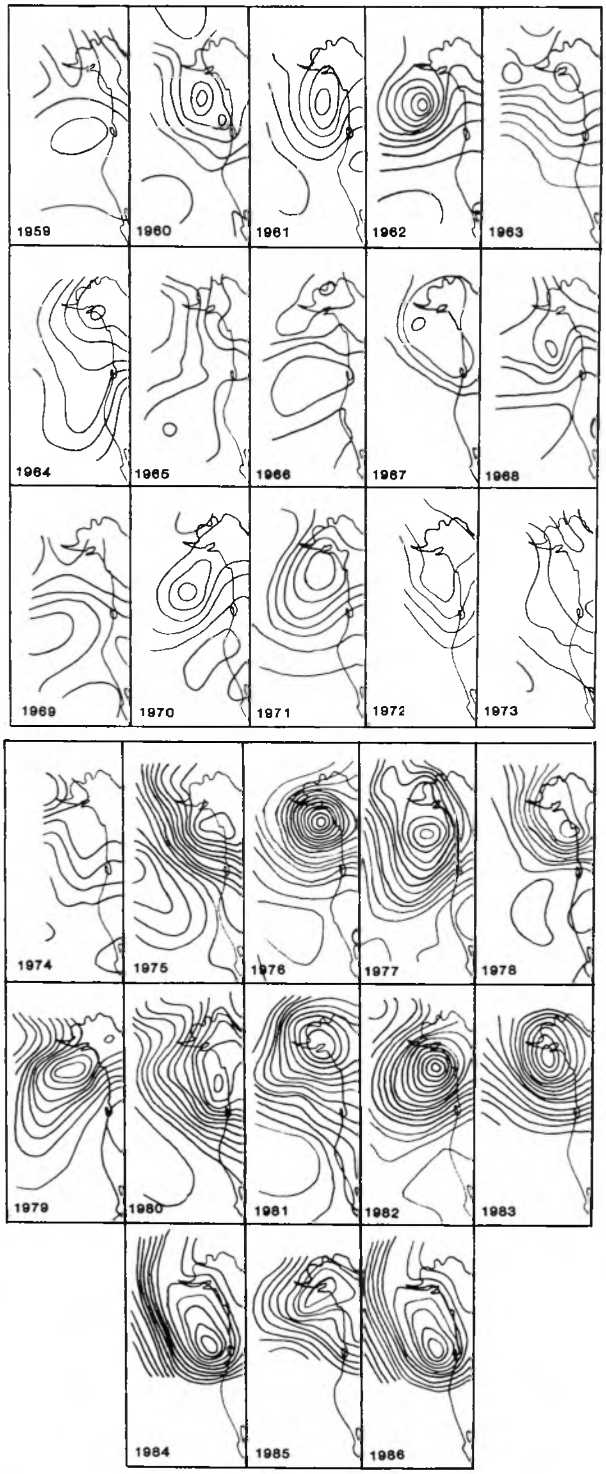

Figure 1. Low pressure weather systems in the Pacific Northwest at the 850 mb level on dates of peak Brent departures from Izembek Lagoon, 1959-88.

mainland Mexico approach the numbers that have been observed on Izembek Lagoon during the fall staging period in recent years (USFWS 1988).

Izembek Lagoon and its vast beds of eelgrass *Zostera marina* is of international importance to migratory birds. Eelgrass beds cover approximately 53% of the 33,600 ha lagoon, making it one of the largest stands in the world. This area provides the last opportunity for Pacific Black Brent to build nutrient reserves necessary for migration prior to their flight to wintering areas.

Most Brent fly an estimated 5301 km (3287 miles) from Izembek Lagoon to the west coast of Mexico. Some sporadic landfalls occur in coastal areas of southern British Columbia, Washington, Oregon, and northern California, but the vast majority apparently fly directly to coastal lagoons of Baja California and the west coast of the Mexican mainland, where they winter. The entire flight to Mexico is thought to last approximately 54 hours. The exodus of most Brent from Izembek Lagoon characteristically occurs *en masse* during early evening hours after the passage of a strong low pressure system, and hence with tailwinds from a northerly wind flow. The term exodus is used to distinguish this massive departure from the undetected departure of small groups of birds earlier or later which probably occurs each year.

Methods

Migratory phenology, production and population composition were analyzed annually using data collected by ground-based observers using spotting scopes. Flocking behaviour, flock configuration and flight altitude were behavioural responses of Brent to seasonal phenology and were observable indicators of migratory restlessness. Climatological data collected throughout the fall staging period by the National Weather Service in Cold Bay, ten miles southeast of Izembek Lagoon, included graphic analysis of weather systems potentially suitable for migration. These data, in conjunction with observed behavioural responses of Brent to seasonal phenology, were used to indicate when departure monitoring should begin. Prior to 1974, this monitoring was conducted by either shore or boat based observers. After 1974, aerial reconnaissance was performed after migration to document departures.

Radar observations of departing Brent flocks were conducted by Izembek refuge personnel at the US Air Force facility at Grant Point on Izembek Lagoon in 1974, 1978, 1979, and 1984. These data provided appraisals of time of departure, initial flight direction, ground speeds and altitudes of departing flocks within line-of-sight of the facility. Brent movements were viewed on a Random Access Planned Position Indicator (RAPPI) which provides circular polarization with 0.8 km resolution. It was the impression of radar technicians that such units would detect only larger, dense flocks of Brent.

Brent depart Izembek Lagoon during nocturnal hours, with the first flocks usually leaving shortly after dusk. Rarely have diurnal departures been reported. Aerial assessments with small aircraft were the most efficient means of determining the magnitude of departure. Confirming aerial surveys were not performed routinely prior to 1974 (R.D. Jones Jr pers. comm.), hence the weather systems shown for these early years may be for up to one day after the actual date of departure (Fig. 1).

Migration watches were conducted in the centre of the Gulf of Alaska from 1958 to 1981. Ocean Weather Station "Papa" (Station "P"), a Canadian meteorological vessel, from which incidental bird counts were collected, was located at 50°N, 145°W, approximately 1306 km southeast of Izembek Lagoon (M.T. Myres pers. comm.). Vessels spent alternating six-week periods at this station. This location is approximately one-third of the way along the direct route to primary wintering areas in Mexico (Fig. 2). Station "P" is believed to be on or near the probable fall migration route that Brent would follow as determined by weather system circulation patterns and direction and velocity of winds. However, Brent have not been reported in large numbers at Station "P" or in coastal areas between Izembek Lagoon and wintering bays in Mexico during fall migration.

Bahia de San Quintin, at approximately 30°N, 116°W, was used as the destination of Brent in Mexico for the purpose of this analysis because it is an initial concentration area, its accessibility to observers and its importance to a large number of winter-

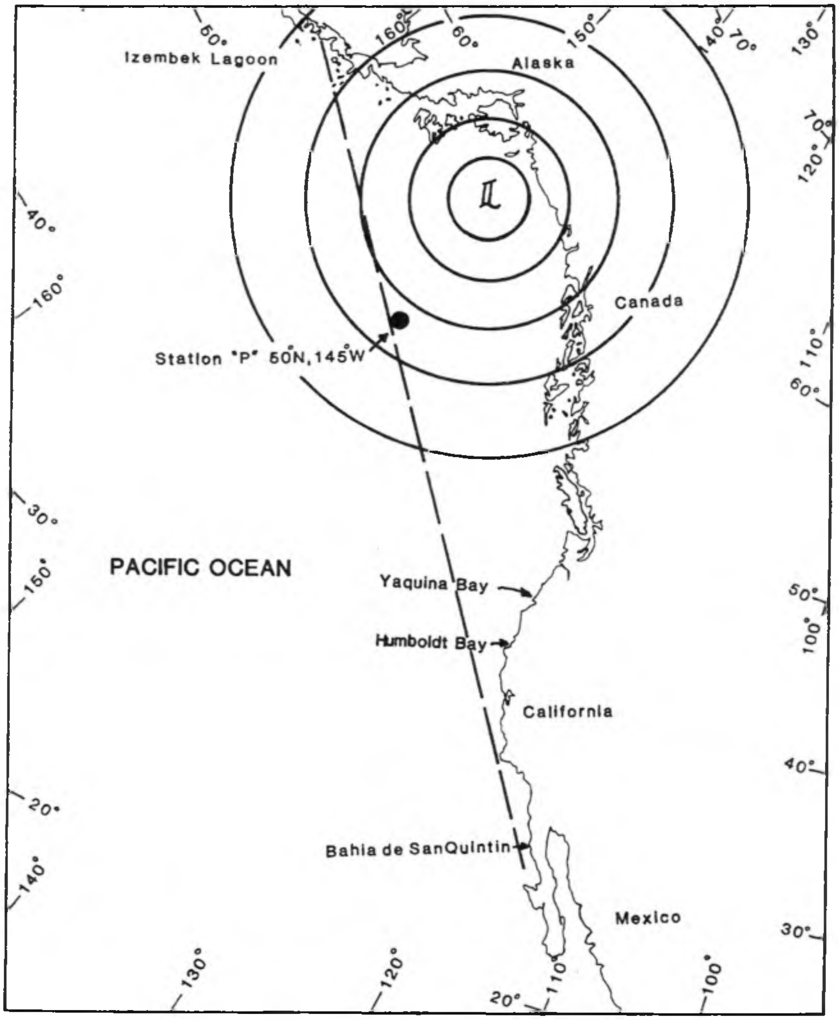

Figure 2. The 28-year average anticyclonic low pressure system (L) position in relation to a direct fall migration route of Brent on a gnomonic, great circle projection.

ing Brent. Monitoring of the fall arrival of geese was performed at this location in 1974, 1983, and 1984.

As a basis for estimating their migration pattern, it was necessary to make several assumptions concerning the physical attributes of Brent flight and their response to weather conditions. It was assumed that:

(1) Brent migrate at a speed of about 80 kph (50 mph). Flight at up to 99 kph (62 mph) has been observed (Einarsen 1965).

(2) Migration speed was directly additive to the prevailing wind speed.

(3) The approximate altitudes attained by the migrating Brent at an average of 75 km (47 miles) from their departure point, as determined by radar observations, were maintained throughout the duration of their flight.

(4) Based on the radar observations of departure altitude, analyses of circulation patterns at the 850 millibar (mb) level (approximately 1400 m above sea level at standard pressure) best characterize the conditions faced by Brent throughout their migration.

(5) The majority of the birds departing Izembek Lagoon normally accomplish their fall migration non-stop and *en masse*.

Surface, 850 mb and 700 mb weather charts are prepared at 6-hour intervals, so specific charts valid at 21.00 h on the estimated exodus date (06.00 h GMT of the **next** day) were used because most birds are believed to depart Izembek Lagoon shortly after dusk between 19.00 and 22.00 h. The 850 mb chart depicts the conditions at approximately 1400 m (4600 feet above sea level ASL); the 700 mb level represents conditions at about 3000 m (10,000 feet ASL). Acetate overlays depicting surface and 850 mb circulation patterns between Izembek Lagoon and Baja California for the date of the departure were prepared. In addition, 850 mb and 700 mb charts at 15.00 h of the day following the exodus (00.00 h GMT of the **second** day after) were obtained to provide an appraisal of weather conditions faced by Brent midway *en route*, at approximately 45°N, 130°W, approximately 450 km west of the Oregon coast.

Results

The size of the Pacific Flyway Brent population fluctuated considerably during the study. The average winter population over the 30 year period was 143,699 ± 21,862 (1SD) birds, ranging from a low of 68,527 in 1959 to a high of 194,197 in 1980. Annual variation in population size had no observable effect on the timing or characteristics of the exodus from Izembek Lagoon. Mean mid-winter population sizes for years of early, mid and late departures were 139,584 ± 26,206; 147,334 ± 20,470; and 140,473 ± 15,777, respectively. No significant difference was found between any of these groupings ($U = 57$ early *v* mid, $U = 25$ late *v* mid, $U = 20$ early *v* late, $P<0.05$, Mann-Whitney U-test).

Brent begin arriving at Izembek Lagoon in mid to late August (range 15 August 1981 to 30 August 1986). Early migrants probably represent failed or non-breeders which complete the moulting period earlier than successful breeders. Jones (1966) reported non-breeding Brent arriving at Izembek earlier than reproducing adults and juveniles as indicated by productivity counts prior to 20 September with as few as 10% juveniles *v* an average for later counts of 22% juveniles. Productivity counts in subsequent years have confirmed the later arrival of breeding adults and juveniles and that the peak influx of Brent at Izembek Lagoon occurs during the last two weeks of September (Izembek National Wildlife Refuge unpubl. data). The entire PF Brent population congregates in the area during this fall staging period (Jones 1963) and geese from various breeding areas were believed to mix throughout Izembek Lagoon (Jones 1973). However, recent radio telemetry data suggests that, at least in some years, preference for certain segments of the lagoon is exhibited by Brent breeding in the Canadian arctic and possibly other areas as well (Reed *et al.* 1989). Movement patterns within the lagoon during the fall staging period are dictated by tidal cycles and the distribution of preferred feeding, sanding, and roosting areas.

Behavioural changes suggesting migratory restlessness ("Zugunruhe") occur in the latter part of the staging period most commonly in late October. Moderate to large flocks of Brent can be observed at this time in circling flights over Izembek Lagoon occasionally at altitudes above 450 m (1500 feet). These flights may provide the birds with a forecast of current or upcoming weather systems. This investigative behaviour occurs on, or within one or two days of, the day of the fall exodus and is a good indicator of impending departure.

Fall migration and cyclonic weather systems

The average date for the massive fall migration of Brent from Izembek Lagoon is 4 November (modal date 8 November). The range of departure dates is from 21 October (1963) to 22 November (1972) (Table 1, Fig. 1). Most flocks appear to depart over a two to three hour period during early evening but vocalizations of departing Brent have been heard as late as midnight and, on rare occasions, smaller daylight departures have been observed. Extensive aerial monitoring of Izembek Lagoon in recent years suggests that two or more dates of departure commonly occur rather than a single date as in earlier years.

Radar observations of 30 flocks, identified as Brent due to flock density and configuration, revealed an average east-southeasterly departure course at 131° True (114° Magnetic) heading from the Grant Point radar facility on Izembek Lagoon at an average altitude of 1149 ± 453 m (3768 ± 1487 feet). These flocks were tracked for

Table 1. Dates of Brent migration from Izembek Lagoon, Alaska, and related weather system characteristics.

	Peak Migration	Izembek Lagoon Surface Millibars	Izembek Lagoon 850 mb Level (m)	Surface Millibars	Low Centre Distance from Izembek Lagoon (km)	Low Centre Direction from Izembek Lagoon (°t)
1959	7 Nov	1022	1530	1002	1472	040
1960	9 Nov	999	1455	998	-	-
1961	23 Oct	1012	1455	994	1238	055
1962	25 Oct	992	1450	970	1653	045
1963	21 Oct	999	1208	959	1534	075
1964	27 Oct	1002	1329	976	1298	040
1965	14 Nov	1022	1510	990	2597	070
1966	1 Nov	1002	1389	994	1181	035
1967	8 Nov	992	1329	984	1653	095
1968	8 Nov	999	1399	975	1181	060
1969	8 Nov	1009	1369	985	1653	050
1970	11 Nov	1005	1409	976	1014	070
1971	7 Nov	1009	1449	974	1181	090
1972	22 Nov	999	1369	986	1014	040
1973	15 Nov	1019	1457	990	2949	095
1974	5 Nov	1002	1228	981	1062	070
1975	9 Nov	999	1389	984	709	060
1976	29 Oct	1005	1238	961	1416	095
1977	9 Nov	1005	1268	984	944	105
1978	31 Oct	995	1268	979	709	035
1979	12 Nov	1016	1419	988	1416	095
1980	6 Nov	1002	1419	974	2006	085
1981	28 Oct	1005	1238	976	1181	060
1982	23 Oct	1009	1389	970	1888	090
1983	22 Oct	999	1238	968	944	055
1984	2 Nov	988	1248	972	2125	095
1985	1 Nov	1009	1389	997	845	057
1986	26 Oct	999	1400	986	1523	097
1987	3 Nov	1007	1359	995	1726	162
1988	30 Oct	1002	1329	992	1623	160
Average	4 Nov±8.2	1004±8	1365±87	983±11	1438±513	076

an average distance of 75.4 km (46.8 miles).

The Brent population characteristically departs with northerly tailwinds of moderate velocity following the passage of a low pressure system. The average centre of the system with which the birds depart is east-northeast of Izembek Lagoon (069° True) and 1400 km (900 miles) away (Table 1, Fig. 2). Barometric pressure relating to migration weather systems averaged 983 mb (24.5 in. Hg) at the centre of the low and 1004 mb (29.3 in. Hg) at Cold Bay.

Weather conditions at the surface level probably affect departure timing for Brent, hence these charts were reviewed for any distinctive or diagnostic trends in barometric pressure, temperature, and wind speed and direction (Tables 2, 3 and 4). The departure of the Brent, based on the 21 October-22 November extremes, was divided into three 11-day periods to compare early, mid and late exoduses to meteorological data (Table 4). Surface barometric pressures were nearly identical for each departure period.

High wind speeds from directions favouring migration may be the most important proximate factor used by Brent as a departure cue. Departure winds were nearly always northwesterly. Surface wind direction for 11 early ($\bar{x}$ 311 ± 35°) *v* 15 mid and four late departures combined ($\bar{x}$ 322 ± 59°T) was not significantly different (F-test df 10,18, F = 6.47, P>0.01); however, the 230° range (280°-150°T) in wind direction suggested more variability for mid and late departures *v* the 135° (225°-360°T) range observed during early departures. Wind speeds at the 850 mb level for early, middle and late departures were not significantly different; however, surface wind speeds did decrease significantly with later departures (t-test df 12, P<0.05) (Fig. 3). The 850 mb level at Cold Bay occurred at a lower elevation, by approximately 55 m, for early *v* middle and 118 m for early *v* late departures. These data, although not significantly different, indicate that later migrating Brent depart during less intense weather systems with slower wind speeds and with less likelihood of direct tailwinds.

Temperatures at the surface during early departures were significantly higher than

Table 2. Air temperature (°C) at the surface and 850 mb levels along the Brent fall migration route.

	DEPARTURE		*EN ROUTE*		ARRIVAL	
	Surface	850 mb	Surface	850 mb	Surface	850 mb
1959	0	-7	13	5	22	20
1960	1	-7	10	3	12	13
1961	3	-5	13	3	20	17
1962	2	-7	5	10	20	22
1963	2	-10	11	-2	23	15
1964	1	-12	13	7	24	20
1965	1	-7	16	5	19	15
1966	-2	-10	13	10	27	15
1967	1	-5	13	5	20	15
1968	-1	-12	17	10	24	18
1969	0	-7	23	10	18	12
1970	-4	-10	18	2	17	15
1971	-	-10	13	0	16	15
1972	-3	-5	13	0	17	12
1973	2	-6	11	2	16	10
1974	-1	-5	10	5	16	10
1975	-3	-10	7	2	16	20
1976	-3	-12	-	5	21	17
1977	-1	-10	14	0	23	17
1978	1	-10	16	7	21	17
1979	-1	0	16	10	25	17
1980	3	-9	16	2	18	20
1981	-1	-10	15	5	19	13
1982	-1	-8	19	2	30	22
1983	-1	-12	7	0	-	20
1984	-1	-5	10	2	16	15
1985	4	-15	16	10	25	16
1986	7	-5	14	5	19	17
1987	0	-9	14	5	19	-
1988	2	-6	13	5	19	-
Average	0±3	-8±3	13±4	4±4	20±4	16±3

Departure conditions measured at Cold Bay 15 km south of Izembek Lagoon.
En route conditions measured near migration mid-point, 44°N; 133°W.

those recorded during middle (t = 3.33, df 22; $P<0.01$) and late (t = 3.66, df 12; $P<0.01$ departure periods. Monthly temperatures in October averages 5.2°C warmer than that for November however, less variability exists over the 21 October to 22 November range in departures. There was measurable precipitation on departure days for 24 of the 30 years of observation. Snow or freezing rain occurred during 23 of these departures (ten early dates, 12 middle dates, and one late date). These data also suggest that late departing Brent not only encounter less favourable migratory conditions with respect to wind speed and direction but also lower temperatures. However, late migrants less frequently encounter snow or freezing rain.

Conditions during trans-oceanic passage

For all departures from 1959-88, the accompanying weather data at Izembek Lagoon, at the estimated mid-route location and at Bahia de San Quintin, were tabulated (Tables 2 and 3).

Air temperatures increase at surface and 850 mb levels along the migration route in relation to decreasing latitude. However, it is not known whether temperatures encountered at departure or along the route effect migration altitude.

Observations of Brent from Station "P"

Counts of birds from ships at Station "P" are available for 23 years (1959-81) during which there are also Brent departure data from Izembek Lagoon. Observations were made for a few minutes each day at 08.00, 12.00 and 16.00 h with sightings of migrating waterfowl rare events (Myres 1970). During 12 years, foul weather or other factors prevented the making of observations on the day following the Izembek departure when Brent, theoretically, would have been passing Station "P". During ten of the remaining 11 years, probable Brent sightings were made near the Izembek departure date. Observations were of one or more flocks of up to 20 birds (Table 5) (M.T. Myres pers. comm.). The frequency

Table 3. Wind direction (°T) and speed (km/h) at the 850 mb level along the Brent fall migration route from Izembek Lagoon to Bahia de San Quintin.

	DEPARTURE		*EN ROUTE*		ARRIVAL	
	Dir.	Speed	Dir.	Speed	Dir.	Speed
1959	010	16	225	16	210	8
1960	305	48	260	48	135	8
1961	225	16	180	32	-	0
1962	315	32	230	32	-	0
1963	360	24	240	32	135	16
1964	315	56	250	32	135	24
1965	315	48	270	32	340	16
1966	290	32	270	32	200	16
1967	350	40	240	32	350	16
1968	315	48	200	16	340	8
1969	-	0	270	16	-	0
1970	345	48	215	32	350	3
1971	315	56	290	48	180	3
1972	290	32	270	32	360	32
1973	270	40	270	16	315	32
1974	150	88	200	64	200	24
1975	280	64	290	64	350	16
1976	315	64	240	40	270	16
1977	315	24	290	40	140	16
1978	315	32	250	48	315	8
1979	295	40	270	48	090	16
1980	350	48	280	64	300	16
1981	290	72	260	40	325	32
1982	350	64	240	64	040	16
1983	300	48	270	48	-	-
1984	080	16	330	56	360	8
1985	010	48	270	56	360	24
1986	320	24	210	64	210	8
1987	330	20	210	15	-	-
1988	315	20	200	25	-	-
Average	317±45	40±20	251±34	39±16	255±101	14±9

Departure conditions measured at Cold Bay 15 km south of Izembek Lagoon. *En route* conditions measured near migration mid-point, 44°N; 133°W.

Table 4. Average weather conditions for early, middle, and late Brent migratory departures from Izembek Lagoon.

		SURFACE				850 mb		
Departure Period	*n*	Pressure (millibars)	Temp (°C)	Dir. (°T)	Wind Speed (km/h)	Ht. MSL (m)	Dir.(°T)	Wind Speed (km/h)
EARLY (21-31 Oct)	11	1002±6	1±3	325±33	28±8	1322±90	311±35	41±20
MIDDLE (1-11 Nov)	16	1005±12	0±2	330±42	25±15	1376±78	320±63	40±21
LATE (12-22 Nov)	4	1009±10	0±2	291±25	20±10	1439±60	321±28	40±7

of Brent observations and the low numbers seen suggest that Station "P" is either off the primary flight route or that geese passed during non-observation periods or at altitudes out of view.

Flight altitude of migrating Brent after departure is unknown. Radar observations and pilot reports suggests that migration altitude of some waterfowl and shorebirds increases along the flight route (F.C. Bellrose pers. comm.). Lack (1960) suggested that migrating birds are unlikely to expend unnecessary energy to climb to altitudes higher than that required for safe terrain clearance. However, terrain clearance is not a consideration in trans-oceanic migrations (Bellrose 1970). Dall (1874) reported "enormous flocks" of Brent flying south and frequently landing on the water 160 km off the California coast in late October. This observation suggests that migration altitude of Brent decreases as the flight

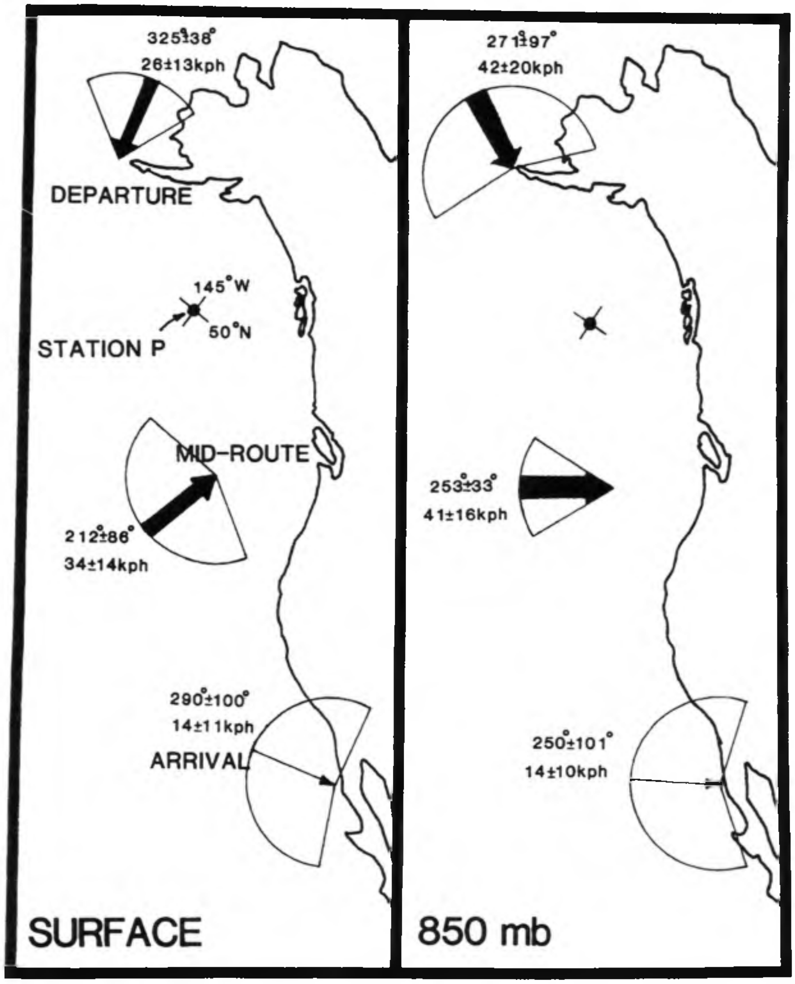

Figure 3. Average wind direction (°T) and speed at the surface and 850 mb levels at Izembek Lagoon (departure), 45°N; 130°W (mid-route) and Bahia de San Quintin (arrival).

progresses; however, no other similar observations have been reported.

Brent have been observed at flight speeds of up to 99 kph (62 mph) (Einarsen 1965). However, lacking data on actual migration speed of Brent, I assumed air speed to be additive to an estimated no wind flight speed of 80 kph (50 mph) and therefore estimated time *en route* should be considered minimum. Bruderer (1972) suggests that flight speed increases with altitude; hence potential biases in migration time calculation for Brent would be reduced if observed altitudes at departure are maintained or increased.

Several authors have found that migration speeds do not increase proportionally with wind speed (Bellrose 1967, Tucker & Schmidt-Koenig 1971, Schnell & Hellack 1979). Bellrose & Crompton (1981) showed that Canada Geese *Brenta canadensis* flying with a following wind, decrease their air speed as wind speeds increase. However, Bruderer (1972) reported that ground speed, although not directly influenced by wind speed, is increased by up to a 2/3 component of the wind vector along the route of flight. Blokpoel (1974) concluded that the air speed of migrating Snow Geese *Anser caerulescens* varied little, if at all, with different wind speeds or direction; however, his data did include mean air speeds from 49 to 62 kph. Speirs *et al.* (1971) found similar migration speeds

Table 5. Sightings of Brent during fall migration.

	Izembek peak departures	Station "P" (occurrence)	Yaquina Bay Oregon (first sighting)	Humboldt Bay California (first sighting)	Bahia de San Quintin, Mexico (peak arrival)
1966	1 Nov	31 Oct			
1967	8 Nov	10 Nov			
1968	8 Nov	9 Nov			
1969	8 Nov	14 Nov			
1970	11 Nov	None			
1971	7 Nov	1 Nov			
1972	22 Nov	22 Nov			
1973	15 Nov	16 Nov			
1974	5 Nov	14 Nov	12 Nov		8 Nov
1975	9 Nov		3 Nov	29 Oct-4 Nov	
1976	29 Oct		29 Oct	22-28 Oct	
1977	9 Nov	6 Nov	22 Oct	22-28 Oct	
1978	31 Oct	1 Nov	17 Nov		
1979	12 Nov	14 Nov	23 Oct	15-21 Oct	15 Nov
1980	6 Nov	None	3 Nov	5-11 Nov	
1981	28 Oct		24 Oct	5-11 Nov	
1982	23 Oct		24 Oct	22-28 Oct	
1983	22 Oct		24 Oct	22-28 Oct	24 Oct
1984	2 Nov		27 Oct	5-11 Nov	6 Nov
1985	1 Nov		26 Oct	5-11 Nov	
1986	26 Oct		4 Nov	20 Oct-4 Nov	
1987	3 Nov		4 Nov	29 Oct-4 Nov	
1988	30 Oct		29 Oct		

Blanks indicate no observations available.

averaging 57 kph (34 mph) for unidentified flocks of Canada and Snow Geese in southern Ontario.

Brent normally initiate their fall exodus from Izembek Lagoon largely *en masse*, usually during a single evening; however, in recent years a pattern of multiple departures has emerged. In 1984 the fall exodus was split with about half the population departing on 2 November and most of the remaining birds leaving on 9 November. In 1985, a split departure again occurred with up to 100,000 Brent leaving on 1 November with a much smaller flight occurring sometime after 5 November. In 1986, roughly equal numbers of Brent, representing nearly all the fall staging population, departed on 26 October and 9 November. In 1987 and 1988 small but noticeable departures occurred in the third week of October preceding the departure of most of the population on 3 November and 30 October, respectively. It is probable that a very few birds may leave in advance of the mass exodus each year.

Small departures of Brent would be undetectable by shore observations or during aerial surveys. Such movements likely occur, despite the fact that it has not been indicated by departure of radio-equipped Brent. Early, small departures do seem to be indicated by *en route* observations during migration. At Station "P", sightings of Brent indicate some flocks probably left Izembek Lagoon a night or two before the initial exoduses in 1966 and 1972. Likewise, in 1967 and 1979 some Brent appear to have departed either a night later than the main exodus, or they had taken 40-44 hours instead of 16-20 hours to reach the Station "P" location.

It is possible that, in some years, Brent depart over a two or three night period around the main exodus, rather than on one night only. Even though only a small number of flocks were seen at Station "P", it is significant that the frequency of observations was high and that most sightings fall within a day or two of the recorded exodus from Izembek Lagoon which supports the accuracy of departure documentation.

The relationship of departure timing from Izembek Lagoon to discrete population segments from various breeding locations is unclear. Insufficient numbers of radio-equipped birds, and variable reception of individual units, have resulted in few precise departure records. However, available data suggest that Brent from different breeding locations probably depart Izembek Lagoon together. Based on telemetry and banding data, there is a mixing of the Brent population segments when they arrive at wintering locations; however, different breeding components may exhibit fidelity for certain areas. This characteristic may be indicated by the large numbers of Light-bellied Brent *B. b. hrota* from the Canadian high arctic which utilize the Puget Sound area of Washington and British Columbia.

Brent have wintered historically at Izembek Lagoon in low numbers. Twelve years of ground counts through 1980 suggest that an average of 65 Brent overwintered (range 0 to 488). Many areas identified as important to wintering Brent in later years could not have been included in these counts. Subjective opinion of pilots familiar with Brent and the Izembek area suggest that the winter population may have been 'up to a few hundred birds' (T. Belleau pers. comm.). From 1981 to 1988, an average of 4400 Brent have overwintered, with a peak count of 9860 in 1982. Abnormally mild winter in the 1980s are probably important in providing available habitat for the increased numbers of overwintering geese. It is unknown what effect an increased tendency to overwinter may have on the timing or magnitude of fall departures. A relationship between these phenomena is perhaps suggested by the multiple departures observed during recent years which occurred along with increasing numbers of overwintering Brent. It is not known whether wintering Brent tend to be from discrete breeding locations or if physiological condition prevents them from migrating.

Landfalls on the US coast

Occasionally, small fall influxes of Brent occur in British Columbia, Washington, Oregon (i.e. 1976, 1982, 1983) or California (1983), at a time when the bulk of the migration is assumed to be passing offshore at the appropriate latitude (Table 6). Most often these influxes do not coordinate well with the migration timing based on the main departure of Brent from Izembek Lagoon, and hence may represent movements of birds that left before or

Table 6. Estimated flight distances and ground speeds of Brent during fall migration.

	DEPARTURE TO MID-ROUTE			*EN ROUTE* TO ARRIVAL			DEPARTURE TO ARRIVAL		
	Distance (km)	Time (hrs)	Speed (kph)	Distance (km)	Time (hrs)	Speed (kph)	Distance (km)	Time (hrs)	Speed (kph)
1959	2579	26.9	96	2650	34.0	78	5229	60.9	86
1960	2677	20.9	128	2650	31.6	84	5327	52.5	102
1961	2782	29.0	96	2650	55.2	48	5432	84.2	65
1962	3312	29.6	112	2650	33.1	80	5962	62.7	95
1963	2760	26.5	104	2650	34.0	78	5410	60.5	89
1964	2485	18.3	136	2650	32.3	82	5135	50.6	102
1965	2579	20.2	128	2650	30.1	88	5229	50.3	104
1966	2530	22.6	112	2650	33.1	80	5180	55.7	93
1967	2714	22.6	120	2650	30.1	88	5364	52.7	102
1968	2714	21.2	128	2650	33.1	80	5364	53.5	100
1969	2576	32.2	80	2650	32.3	82	5226	64.5	81
1970	3037	23.7	128	2650	32.3	82	5687	56.0	102
1971	2669	19.6	136	2650	28.5	93	5319	48.1	111
1972	2587	23.1	112	2650	26.5	100	5237	49.6	106
1973	2957	24.6	120	2650	29.4	90	5607	54.0	104
1974	2565	20.0	128	2650	40.2	66	5215	60.2	87
1975	2403	16.7	144	2650	25.5	104	5053	42.2	120
1976	2464	17.1	144	2650	32.3	82	5114	49.4	104
1977	2710	26.1	104	2650	30.8	86	5360	56.9	94
1978	2659	20.8	128	2650	30.1	88	5309	50.9	104
1979	2710	22.6	120	2650	30.8	86	5360	53.4	100
1980	2834	21.5	128	2650	27.0	98	5484	48.5	113
1981	2650	17.4	152	2650	28.5	93	5300	45.9	116
1982	3128	21.7	144	2650	31.6	84	5778	53.3	108
1983	2502	19.6	128	2650	30.8	86	5152	50.4	102
1984	2346	22.6	104	2650	23.7	112	4996	46.3	108
1985	2253	17.6	128	2650	26.8	99	4903	44.4	110
1986	2378	22.9	104	2650	34.0	78	5028	56.9	88
1987	2344	23.4	100	2650	33.1	80	4994	56.5	88
1988	2625	26.3	100	2650	31.9	83	5275	58.2	91
Average	2651	22.6	119.7	2650	31.8	85.3	5301	54.3	99.2
(SD)	(235)	(3.8)	(17.2)	(0)	(5.5)	(11.6)	(235)	(7.9)	(11.5)

Estimated migration speed at 80 km/hr plus wind aid. Migration route follows winds at the mb level. *En route* to arrival distance constant due to little wind effect.

after the main departure or individuals incapable of sustaining a non-stop migration.

Arrival in Mexico

Approximately 80% of the Pacific Brent population winters in Mexico and, of these, up to 15% winter at Bahia de San Quintin (30°N, 116°W), the most northerly concentration area being in Baja California. Observations of Brent arriving at Bahia de San Quintin were made in 1974, 1983 and 1984, providing the best available appraisals of *en route* migration time. Although this location was used as the destination, some wintering Brent disperse to areas up to 1280 km (800 miles) south along the Mexican coast. The 1974 (Kramer *et al.* 1979) and 1983 fall migrations were completed in 60 hours, near the assumed average duration of approximately 54 hours. In 1984, however, observers documented a flight duration of a minimum of 95 hours (B. Eldridge pers. comm.). The low pressure system affecting the 1984 migration was large and centred farther south than normal. Circulation patterns of this system may have directed birds along a longer than usual migration route.

The probable Brent migration route from Izembek Lagoon to Bahia de San Quintin averages 5301 ± 235 km (3287 ± 146 miles) (Table 6). However, the shortest distance on a gnomonic, great circle projection is 4408 km (2775 miles). Estimated ground speed to the mid-route location averaged 120 ± 17 kph (74 ± 11 mph), while that along the remainder of the migration route is assumed to be equal to the estimated migratory flight speed of 80 kph (50 mph) due to winds of reduced speed and variable direction. Average ground speed for the entire flight, estimated at 99 ± 12 kph (61 ± 7 mph), would result in an average flight duration of 54 ± 8 hours, approximating that observed in 1974 and 1983 (Table 6).

Discussion

The Pacific Flyway population of Brent congregates in the Izembek Lagoon area during the fall staging period prior to dramatic *en masse* departures to wintering areas. The purpose of this study was to attempt to identify relationship between migratory phenology and fall weather conditions relating to this event. Most Brent utilize the Izembek area for a five week period, centred around October, building body fat for a non-stop flight of over 5000 km to the west coast of Mexico. Migratory phenology varies; however, climatological conditions characterizing the period prior to and during the fall departure are similar every year. Wind speed and direction and lower temperatures near the surface appear to be important departures cues.

The entire Pacific population, of approximately 150,000 Brent, is found in the Izembek area every fall. First arrivals occur in late August, with peak influxes in mid to late September, allowing for a 30 to 50 day staging period prior to migratory departures for wintering areas. Some Brent stage on Izembek Lagoon for up to three months during which time they recover from the physiological stresses of breeding and moulting. Eelgrass, their primary food, is abundant in Izembek Lagoon and comprises 53% (17,868 ha) of its 33,688 ha surface area (McRoy 1966). Although rapid reductions in standing stock, measured by leaf mass, occur in early August due to increasing water temperature, the abundance of available eelgrass in relation to numbers of geese suggests that food is not a limiting factor at Izembek Lagoon during the fall. McRoy (1966) estimated fall eelgrass consumption by Brent to be approximately 13% of the standing stock. Food availability, in addition, does not appear to affect timing or magnitude of the fall exodus.

Body weight of fall staging Brent at Izembek Lagoon increases by an estimated 10.0 and 7.8 g per day in males and females, respectively (D.V. Derksen unpubl. data). Male and female Brent lose approximately 650 and 550 g or 33% and 31% of their average body weights respectively, during the estimated 54-hour fall migration from Izembek Lagoon to Mexico. This suggests that a minimum of 65 and 70.5 days, respectively, are necessary if the birds are to gain sufficient weight to compensate for that lost due to the energetic demands of migration. Hypothetically, Brent arriving at Izembek Lagoon on 1 September would be ready to initiate their fall migration on 4-9 November. As most migrants arrive by mid-September, directly from breeding areas, but depart as early as late October, it appears that the time available to build necessary fat reserves may be limited. Some recovery of body reserves may occur on breeding areas; however, flights from these areas to Izembek Lagoon are of short duration offering little opportunity for fattening. Much of the weight gain by fall staging Brent is accounted for in abdominal and subcutaneous fat which has been found, in other birds, to be available for rapid utilization during migration (Berthold 1975).

Low temperatures, northerly winds and snow or freezing precipitation characterize the passage of large low pressure systems which trigger the annual fall exodus of Brent from Izembek Lagoon. Snow squalls of short duration but high intensity are most common following the passage of such systems. A general tendency has been observed for other species of waterfowl to avoid migration in cloudy conditions or precipitation (Hochbaum 1955, Miskimen 1955). However, lower air temperatures or decreased food availability increase nocturnal restlessness (Berthold 1975, Richardson 1978). Decreasing temperatures and northerly winds result in considerably lower chill temperatures during departures which may be important in triggering the fall exodus of Brent from Izembek Lagoon.

Although food does not appear to limit the duration of the fall staging period, it is possible that the quantity or quality at preferred feeding locations may be reduced. Therefore, food availability should not be eliminated as a potential factor affecting migration timing.

Brent depart from Izembek Lagoon to the southeast with northwesterly tailwinds at the surface and 850 mb altitudes which increases their ground speed during migration. Radar observations of altitude of departing Brent range from 488 to 2196 ($\bar{x}$ 1149 m) m above sea level. Altitudes of departing flocks, within 72 km of Izembek Lagoon, averaged 1068 ± 451 m (n = 16) v 1220 ± 458 (n = 12) for flocks at ranges up to 131 km; this suggests that some Brent may be climbing to higher altitudes where stronger favourable wind speeds are more likely to occur. Brent generally select uniform conditions for departure each year with respect to barometric pressure and wind direction, and no clear differences in these parameters were found between years of early, middle or late departures. Wind speeds did decline significantly during later departures providing less ground speed advantage to migrating geese. Northwesterly wind speeds averaged slower, and temperatures lower, during late fall and winter storms than during October and early November. Blokpoel & Gauthier (1975a) found that later migrating Snow Geese encountered less favourable wind conditions than did earlier migrants. Hawkings (1982) observed that "by carefully timing trans-Gulf departures from the Alaska Peninsula in autumn, many birds can take advantage of tailwinds on the west side of the same systems which provided tailwinds along the coast in spring". Myres & Cannings (1971), Myres (1972), and Guzman & Myres (1983) have analyzed spring migrations of Canada Geese and Sooty Shearwaters *Puffinus griseus* in coastal British Columbia and found correlation with the passage of low pressure systems across the Gulf of Alaska.

Annual migration routes were plotted on charts of the 850 mb circulation pattern which best portray conditions at the average migration altitude at departure. Routes probably followed most favourable winds as it is assumed that wind direction and velocity largely dictate flight direction while under the influence of the departure weather system. Mid-way in the migration, Brent usually leave the effects of the departure weather system. It is probable that little annual variation in migration route or ground speed occurs from this mid-way point south to coastal Mexico as wind speed and direction tend to be light and variable. Approximate ground speeds were calculated assuming 850 mb wind speed, and estimated migration speed, were directly additive. Several studies of migrating waterfowl and other species suggest that migration speed is correlated inversely with velocity of tailwind which would provide an overall energetic saving (Bellrose 1967, Tucker & Schmidt-Koenig 1971, Bruderer & Steidinger 1972, Tucker 1974, Schnell & Hellack 1979, Bellrose & Crompton 1981, Wege & Raveling 1984). Blokpoel (1974) found that in Lesser Snow Geese, wind speed resulted in little, if any, change in air speed. Meinertzhagen (1954) reviewed bird flight in numerous species and suggest that waterfowl and other groups migratory flight exceeds normal speed but the effects of wind were not discussed.

Blokpoel *et al.* (1975) surmised that Snow Geese migrating along the Atlantic coast probably levelled off at an altitude with favourable wind conditions, but Bellrose

(1981 pers. comm.) suggested that migration altitudes of Snow Geese in the Mississippi River Valley increase throughout the migration, being highest near the point of arrival. Richardson (1971, 1972) found that spring and fall migrants making nocturnal flights climbed rapidly early in the night, flew level for several hours, and then began to descend after midnight. Some Brent may follow this pattern as indicated by the small numbers of birds observed at sea level at Station "P" (Myres pers. comm.).

The importance of weather conditions at destinations has been correlated positively with departures (Nisbet & Drury 1968, Richardson 1978). Richardson (1978) and Blurton Jones & Gillmor (1955) further pointed out the highly adaptive significance of departures from northern latitudes when there is cold weather and snowfall or freezing conditions. It seems unlikely that the Brent migration is keyed to precise weather conditions at mid-route or beyond, due to the large distances involved. Conversely, climatic conditions encountered at Izembek Lagoon do appear to be critical in initiating migratory restlessness and subsequent departure. Brent departing Izembek Lagoon capitalize on climatic conditions thus receiving the advantage of following winds.

Many observers interested in the biology of Brent contributed essential effort and information during the study. Izembek National Wildlife Refuge managers R.D. Jones Jr (1959-1975) and J.E. Sarvis (1976-1987) had the interest and foresight to initiate and continue the analysis of migration from Izembek Lagoon. They and their staffs contributed most of the data presented. The US Air Force provided assistance by permitting important radar evaluations of the Izembek Lagoon Brent departure from their Grant Point facility. The National Weather Service offices in Cold Bay, Alaska, and Asheville, North Carolina, generously made weather records available. Dr M.T. Myres of the University of Calgary provided published and unpublished information from Weather Station 'Papa'. Numerous individuals including from the U.S. Fish and Wildlife Service, D.V. Derksen, W. Eldridge, B. Henry, R. Lowe, G. Mensik, E. Nelson, P. Springer and U. Wilson; G. Fellers (National Park Services), R.C. Parker (Washington Department of Game), R.P. Henderson (Point Reyes Bird Observatory), L. Johnson (Alaska Department of Fish and Game) and R. Bayer (Newport, Oregon). J. Hawkings, A. Reed and D. Smith (Canadian Wildlife Service) generously provided unpublished information and constructive comments. F.C. Bellrose, D.V. Derksen, J. Hawkings, R.D. Jones Jr, M.T. Myres and A. Reed, P. Springer contributed helpful reviews and suggestions on earlier drafts of the manuscript.

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