MIGRATION PATTERNS AND PHILOPATRY

OF THE BLACK BRANT

(*Branta bernicla nigricans*)

IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA.

by

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Abstract

Philopatry is defined as the tendency of individuals to exhibit long term fidelity in the use of a particular area. Two major theories have been proposed to explain its adaptive significance: 1) the genetic theory, where individuals benefit from limited gene flow by the maintenance of successful alleles and allele combinations within the population, and 2) the environment familiarity theory, where individuals benefit from knowledge of local physical and social conditions. Geese pair in winter and early spring so the relevant units for studying the genetic implications of philopatry are the wintering and the spring staging populations.

There were no large scale movements of Black Brant (*Branta bernicla nigricans*) through Boundary Bay, British Columbia, after the arrival of birds from the breeding grounds in early November to the arrival of the first spring migrants from southerly wintering grounds in mid-February 1995 and 1996. The first departures occurred in early March and the rate of departure during spring migration was the same in both years. These results indicate that there was a resident population of Black Brant wintering in Boundary Bay. This site was not used as a fall migration stopover, however, it was used during the northbound spring migration.

Winter philopatry of Black Brant, estimated at 50% annually in Boundary Bay between 1992-93 and 1995-96, was low compared to the levels exhibited by other goose species. Spring staging philopatry was higher at Qualicum, British Columbia, than at Boundary Bay. Individuals that were seen in the study area for the first time had low philopatry (31% and 45.1% in Boundary Bay and Qualicum, respectively) indicating that there was significant emigration in the year following their first sighting. Estimates of philopatry for birds seen in more than one spring were high for Boundary Bay and Qualicum (82.1% and 87%). The differences in philopatry between these two sites were likely due to hunting mortality and/or disturbance that occured in Boundary Bay.

These results indicate that high levels of gene flow are likely to occur both in wintering and spring staging populations, and thus do not support the genetic hypothesis for the evolution of philopatry. Philopatry, in this case, is more likely explained by environmental aspects.

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Chapter 1

General Introduction

1.1   Introduction

Philopatry, defined as the tendency of individuals to exhibit long-term fidelity in the use of a specific area (Greenwood 1980), has been observed in many species (Mayr 1963). Philopatry has significant implications for the genetic structure of populations and their population dynamics. Philopatry increases the isolation of local populations and thus promotes adaptation to specific conditions encountered by these local populations. It also makes them more vulnerable to extinction because of this increased isolation (Levins 1970, Gadgil 1971).

Theories pertaining to the evolution of philopatry in birds and mammals can be broadly divided in two major groups. The first relates to the genetic consequences of philopatry. According to the genetic hypothesis, philopatry would have evolved as a way to promote optimal levels of inbreeding in order to conserve successful alleles within a population and also allow local adaptation (Shields 1982). Individuals bearing certain alleles and allele combinations that are particularly well adapted to a set of environmental conditions would benefit from increased fitness if they lived in that environment. Some dispersal may be expected because deleterious alleles are more likely to be expressed under high levels of inbreeding. Individuals which mate with close relatives may have offspring that suffer from inbreeding depression (Greenwood et al. 1978). Also, if gene flow is restricted and the population is small, genetic drift could result, with the subsequent loss of genetic variation.

The second theory applies to the environmental (somatic) consequences of philopatry. Many hypotheses fall within the environmental or somatic theory. These models predict that philopatric individuals would benefit by having knowledge of local social and physical conditions, and, as a result, would have a higher lifetime reproductive success than individuals which disperse. Such familiarity may enable individuals to be more effective in their search for

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food and in escaping predators (Bengtsson 1978). Individuals with prior familiarity of an area would have knowledge of the location of food patches, distribution and local behavior of predators, escape routes, and location of conspecifics.

Philopatry could also be the default behaviour. In year round resident species or populations, philopatry should be the norm . Indeed, Weatherhead and Forbes (1994) found that most studies that reported high levels of natal philopatry in Passerines involved sedentary resident populations and that migratory populations tended to show weak site-fidelity to their natal areas. The question in migratory species should then be why they would return to specific areas instead of settling in the first piece of suitable habitat encountered.

Obviously, even if philopatry has evolved for environmental reasons, high levels of philopatry could lead to genetic differentiation of local interbreeding populations. In such cases, it would be hard to separate the causes without relying on other sources of data. The use of an experimental design could provide valuable information. For example, one could increase or decrease the quality of a certain area and see how philopatry rates are correlated with that. A comparison of different locations can also yield useful information when inferences on the quality of the habitats can be made.

Most studies have focused on breeding ground philopatry in birds (Greenwood and Harvey 1982, Rohwer and Anderson 1988). However, in migratory species, other areas used at different stages of their life cycle could also be of importance to their population genetics and dynamics. Robertson and Cooke (1997) emphasized the importance of winter site philopatry in waterfowl because of their particular mating system and life history traits (outlined below). In this study, I concentrate on philopatry to wintering and spring staging areas of a goose species, the Black Brant (*Branta bernicla nigricans*).

1.2   Mating System

Most North American waterfowl species are migratory. Studies aimed at explaining the

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evolutionary consequences of philopatry in waterfowl have mostly concentrated on natal philopatry, that is philopatry to the nesting grounds (e.g. Rowher and Anderson 1988). However, unlike most other species of birds, waterfowl, in general, do not form pair bonds on the breeding grounds. Instead, pairs are usually formed in winter or in early spring (Robertson and Cooke 1997). The relevant unit (the deme) when examining the genetic consequences of philopatry is the area where gene exchange occurs which, in the case of geese, is the wintering and spring staging population.

Geese and swans differ from other waterfowl in that they form life-long pair bonds and that family units often stay intact for up to 10 months (Prevett and MacInnes 1980, Warren et al. 1993). This means that the same individuals have the potential to bring back their progeny to the same wintering site year after year. Once pairs are formed, gene exchange will be greatly reduced, but for the parents genetic contribution to stay within the deme, they need to be philopatric and bring their progeny back to their original mating area.

The timing of pair formation in geese is not well known, but it appears that most pair bonds are formed in late winter and early spring (Owen et al. 1988). Since geese are migratory, philopatry to wintering and spring staging areas is likely not the only determinant of gene flow. In non-terminal areas, i.e. in wintering areas that are not at the southern limit of a species' distribution, there is the potential that migrants might be present in the area when pair formation occurs. If mating was random, then the possibility for gene flow would be increased in such situations even if philopatry was high. Thus, a proper understanding of the migration patterns of geese in a particular area are needed in order to be able to make inferences on the potential genetic consequences of philopatry. Even if pair formation occurs away from the breeding grounds, some gene flow between inter-breeding populations could occur in those areas through extra pair copulation, egg dumping and fostering (Syroechkovsky et al. 1994).

1.2.1 Genetic Theory

Philopatry will likely increase the level of inbreeding in any population. From a genetic standpoint, inbreeding can be costly because it increases homozygosity and thus reduces variation among offspring and increases the risk of producing an offspring that will be homozygous for deleterious or lethal recessive alleles. On the other hand, individuals which mate with totally unrelated partners may also have offspring with reduced fitness due to the break-up of co-adapted gene complexes. The optimal discrepancy theory merges two somewhat competing theories: (1) the optimal outbreeding theory which assumes that inbreeding is costly and that an individual will gain in fitness by mating with genetically distant individuals (Bateson 1983), and (2) the optimal inbreeding theory where individuals increase their fitness by maximizing inbreeding (Shields 1982). In the optimal discrepancy theory, there exists a level of inbreeding that maximizes fitness and too much or two little inbreeding will result in reduced fitness for the individual's offspring. Inbreeding within local populations may be adaptive in that it keeps co-adapted gene complexes together (Shield 1982). On a population scale, it can also lead to local adaptation if the selection pressures differ from one local area to the next.

1.2.2 Local Knowledge

Philopatric individuals may have higher survival rates and increased fitness than dispersers because of the relatively low risks and energy use associated with living in familiar surroundings. Knowledge of local conditions on the wintering grounds may enable philopatric individuals to be more effective in their search for food and in escaping predators, which would lead to increased over winter survival. This assumes that there is some inter-seasonal consistency and predictability in the habitat (e.g. Johnson and Gaines 1990). Animals living in highly variable environments will be expected to show high dispersal rates compared to those living in stable environments. Coastal environments tend to be more stable because of the thermal effects of the water mass that generally prevents extreme winter conditions such as freezing. Dabbling

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ducks wintering in coastal habitats showed a lowered tendency to disperse than their counterparts

wintering in inland habitats (Hestbeck 1993, Diefenbach et al. 1988).

However, survival is not the only life history trait that individuals could maximize on the

wintering grounds. In geese, reproductive success of pairs was shown to be correlated with body

condition on the wintering and spring staging grounds (Ebbinge and Spaans 1995). Therefore,

philopatric individuals could benefit from feeding more successfully, which could result in better

breeding success. Finally, if philopatric individuals have local knowledge of location of

conspecifics, they may be more likely to find a suitable mate.

1.2.3 Social Aspects

Familiarity with conspecifics may reduce the levels of aggression and stress, and thus the

costs of social interactions. Geese have long term pair bonds and extended parental care, thus

philopatry may enable individuals to reunite at common wintering grounds if they become

separated. Fidelity to traditional roosting sites by family groups of Canada Geese (*Branta*

canadensis) likely served to reunite family members when they became temporarily separated

(Raveling 1969). Geese form long-term, monogamous pair bonds, and they do not pair until their

second winter (Owen et al. 1988). Complementarity and experience of partners is an important

determinant of successful breeding in Arctic-nesting geese (Cooke et al. 1981, Raveling 1981,

Choudhury et al. 1996). Familiarity with potential mates could reduce the amount of time needed

to gain experience between the mates and thereby increase breeding success in the first years of

breeding as well as the number of potential breeding years.

In gregarious animals such as geese, flock fidelity could be more important in population

dynamics and genetic structure than fidelity to a specific geographic area. Short-stopping, the

habit of geese to winter in more northerly locations when conditions are favorable, has been

documented in Canada geese (Hestbeck et al. 1991). If flock composition remains the same,

genetic isolation could still be maintained. Movements of flocks of Barnacle geese (*Branta*

leucopsis) wintering on Islay involved the same birds every time (Percival 1991), thus the integrity of the flock was social rather than geographic. However, other species of geese showed high levels of interchange between flocks (e.g. Snow geese (*Anser caerulescens*); Schroer and Chabreck 1974).

Philopatry could become maladaptive for various reasons. If the environment becomes sub-optimal, dispersers are likely to have increased fitness over philopatric individuals because they are more likely to find better conditions elsewhere (Cooch et al. 1993). If interbreeding populations (demes) are small, the possibility of a significant sex bias arising by random chance is possible and individuals from the sex that is in excess would be faced with increased competition for mates. Available mates might also be of lower quality in such areas if there is pressure for early pairing of high quality mates. Incompatibility between mates could result due to lack of choice. A limit may be set on philopatry through density dependent factors when the carrying capacity of a given area is reached (Ebbinge 1992)

Geese show high levels of philopatry to their wintering sites (e.g. Canada goose: 78% (Raveling 1979), 56 - 89% (Hestbeck et al. 1991); Barnacle goose: 74 - 80% (Percival 1991); Snow goose: 88% (Prevett and MacInnes 1980)). The presence of a variety of races in many goose species suggests that there is genetic isolation among different populations (Owen 1980, Van Wagner and Baker 1986). Novak et al. (1989) showed that, based on electrophoretic data, Atlantic Brant (*B. b. hrota*) were genetically segregated to some level on their wintering grounds in the eastern United States. Their study also showed that there was no direct link between wintering and breeding populations, indicating that birds from a given wintering population were likely to disperse to many breeding locations. However, this genetic sub-structure cannot be used to infer the process by which philopatry has evolved. If philopatry has evolved for purely somatic reasons, some level of genetic sub-structure could arise as a consequence. Assortative mating, which has been described in Atlantic Brant (Abraham et al. 1983), could also lead to some genetic sub-structuring of local populations.

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1.3 Migration and Winter Distribution

The Pacific Flyway population of Brant is composed of 2 genetically distinct populations: the Grey-bellied Brant and the Black Brant (Shields 1990). Grey-bellied Brant are segregated on their breeding grounds on Melville and Prince Patrick Island in the Northwest Territories, Canada (Boyd et al. 1988), on their fall staging grounds in Izembek Lagoon, Alaska (Reed et al. 1989a), and on their wintering grounds in Padilla Bay, Washington (Reed et al. 1989b). They are morphologically similar to Atlantic Brant but share the geographic range of the Black Brant. Although genetically different from the other two subspecies of North American brant, the Black Brant and the Atlantic Brant, the Grey-bellied Brant has not yet received the subspecies status and does not have a specific scientific name. The size of the population of Grey-bellied Brant is relatively small compared to that of the Black Brant. I focus on data from Black Brant in this study. In this thesis, if there is no distinction made between Black and Grey-bellied Brant, then Brant is used alone as the vernacular name. Otherwise, specific vernacular names are used.

Black Brant breed over a large expanse of Arctic and sub-Arctic coastal areas on Wrangel Island, Russia, Alaska and the Northwest Territories (Bellrose 1980). During fall migration, birds from the entire Pacific Flyway population of Black Brant make a stopover at Izembek Lagoon, Alaska, where they spend a month replenishing their body reserves before the last leg of the fall migration to the wintering areas (Reed et al. 1989a). The bulk of the population undertakes a non-stop oversea migration from Izembek Lagoon to the main wintering sites located in Baja California and the mainland of Mexico (Dau 1992). Other important wintering areas for Brant include Izembek Lagoon, Alaska (David H. Ward, *pers. comm.*) and Padilla Bay, Washington. Most Brant wintering in Padilla Bay are of the Grey-bellied Brant population (Reed et al. 1989b) but some Black Brant also winter in that area. Smaller aggregations of Black Brant are found wintering along the coast of British Columbia, Washington, Oregon and California (Fig. 1). Grey-bellied Brant were occasionally seen in

Boundary Bay, B.C., in small numbers but none were seen wearing readable plastic legbands (E.T. Reed, *pers. obs.*).

Black Brant usually leave Izembek Lagoon for their wintering locations in the fall in late October or early November (Dau 1992). After spending the winter months south, they start making their way north again following a stepping-stone migration pattern, where they have at least one stopover before reaching Izembek Lagoon again (Einarsen 1965). Black Brant are usually present in British Columbia from early November to early May, when all the migrants have moved north (Campbell et al. 1990).

The Strait of Georgia, British Columbia, is an important stop-over area for Black Brant during spring migration (Campbell et al. 1990). This and other areas along the Pacific Coast of North America have seen dramatic fluctuations in the number of wintering Black Brant. The most striking example of this is the major shift in winter distribution from California south to Mexico in the late 1950's (Bellrose 1980). In British Columbia, data are scarce and anecdotal prior to 1950 but it appears that there used to be large numbers of Brant wintering in the vicinity of Boundary Bay and on Vancouver Island at the turn of the 20th century (Fannin 1891). According to Christmas Bird Count data (Campbell et al. 1990), the number of Brant wintering in Boundary Bay steadily declined between 1936 and 1950, and they had all but disappeared by 1965. Numbers of Brant wintering in Boundary Bay started to increase in the late 1980's and the population is still expanding (Appendix 1, Fig. 7). It seems that between 1992-93 and 1995-96 the numbers have approximated those recorded during the 1940's (Appendix 1, Fig. 7)

Brant hunting was limited to the first ten days of March in 1977 (Munro 1979) in order to concentrate the harvest on spring migrants. Shore hunting at Beach Grove in Boundary Bay, BC, was prohibited and the bag limit further reduced to two Brant per day in 1993. All these measures were aimed at re-establishing a resident wintering population in Boundary Bay.

1.4   Study Area

- Most of my research was conducted in the Strait of Georgia in southwest British Columbia (Fig. 1). In winter (November to February), my efforts were mostly concentrated in Boundary Bay and Roberts Bank, on the Fraser River Delta, but some work was done in Birch Bay, Padilla Bay and Dungeness Bay, northern Washington State, USA, from 1993 to 1996. During the spring period (mid-February to May) from 1989 to 1995, the Parksville-Qualicum area, located on the east coast of Vancouver Island, British Columbia, was surveyed in addition to the other sites by R. Ian Goudie of the Canadian Wildlife Service.

Boundary Bay is a large (5162 ha.) and shallow intertidal area, covered at 55% by two species of eelgrass (*Zostera marina* and *Z. japonica*) (Ward et al. 1992). A feature of Boundary Bay is an area containing a fresh water output and a gravel and sand spit, locally known as the Beach Grove area. Brant use this sand spit throughout the winter and spring to haul out, preen and ingest grit. The Roberts Bank area is also important for Brant, as more than half of its surface area is covered by eelgrass (516 ha of eelgrass) (Ward et al. 1992).

Black Brant use Boundary Bay, Roberts Bank, Padilla Bay, and Dungeness Bay as their wintering and spring staging grounds from early November to early May, and Birch Bay, Point Roberts and the Parksville-Qualicum area mostly from mid-February to early May as spring staging sites (E.T. Reed. *pers. obs.*).

1.5   Goals of the Study

The goals of my thesis were threefold. One, was to determine the migration patterns of Black Brant in Boundary Bay. An understanding of this would provide the status (resident or transient) of the birds using Boundary Bay in fall, winter, and spring and determine the proportion of transients present in the study area when pair formation occurs. Two, to determine the level of philopatry of Black Brant during the winter in Boundary Bay and in the spring in Boundary Bay and Parksville-Qualicum which would allow me to make some inferences on the

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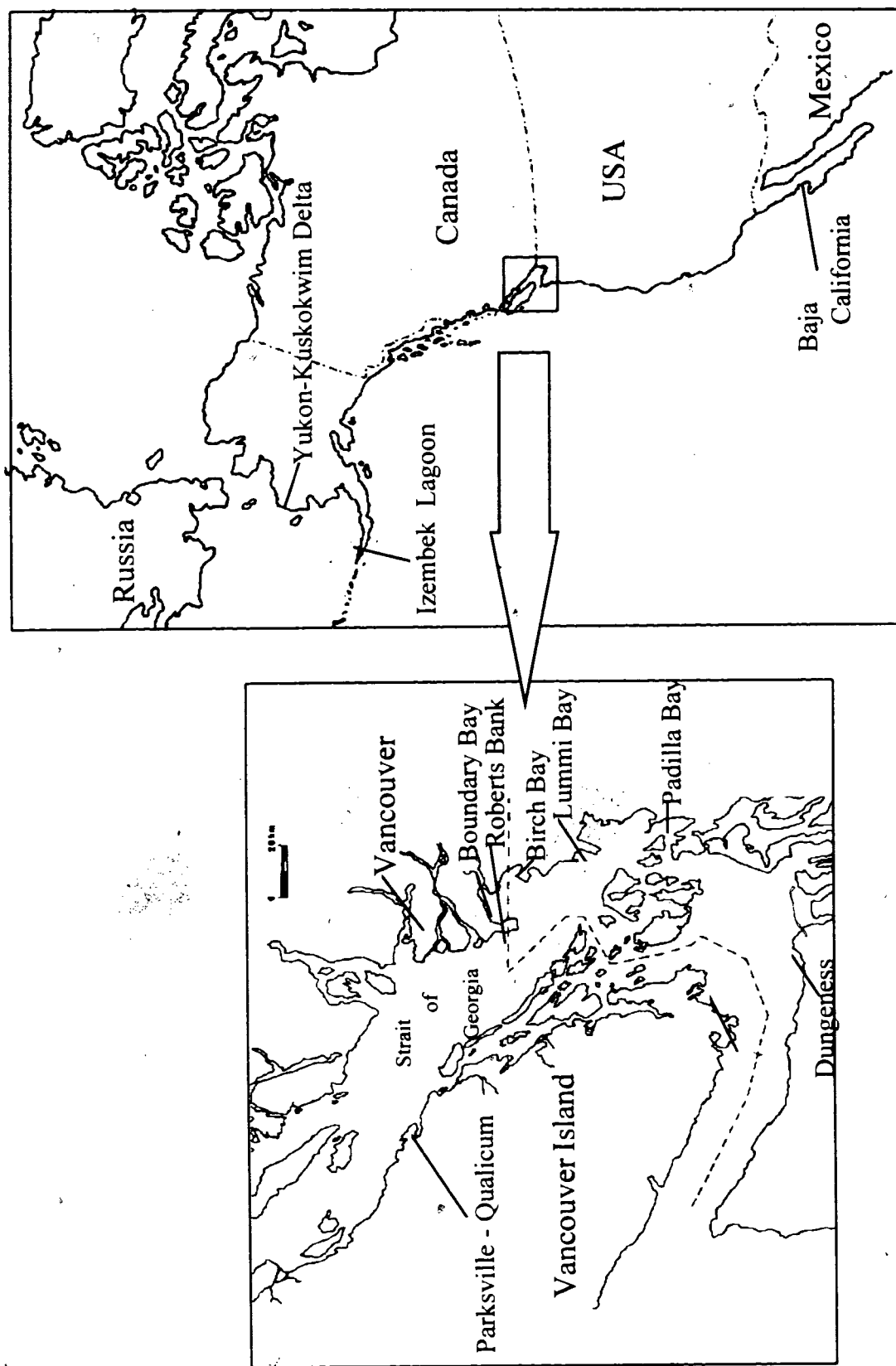
Figure 1. Locations of major wintering and spring staging areas within the study area in northern Washington and British Columbia, in relation to the Pacific coast of North America.

adaptive significance of philopatry in the Black Brant in particular and in geese in general. Finally, I wanted to study the impact of management decisions on the past and present population dynamics of Black Brant wintering and spring staging in Boundary Bay, British Columbia.

Chapter 2

Migration Patterns of the Black Brant in Boundary Bay, British Columbia

2.1   Introduction

Black Brant winter along the west coast of North America and, in small numbers, in Japan (Einarsen 1965). The wintering range in North America spreads from Alaska to Baja California and the mainland coast of Mexico, their main wintering site (Bellrose 1980). A small proportion of the population winters in Boundary Bay, British Columbia (Campbell et al. 1990).

Estimates from winter survey counts have shown that the size of the Pacific Flyway population of Brant, which includes 2 genetically distinct populations, the Black and Grey-bellied Brant (Shields 1990), has been declining steadily since 1965 (Derksen and Ward 1993). A decline has also been observed in the number and size of nesting colonies of Black Brant on the Yukon-Kuskokwim Delta, Alaska (Sedinger et al. 1993). Also, the fluctuations in numbers of Black Brant wintering in particular areas of the Pacific coast have sometimes been dramatic. Numbers of Brant detected by the mid-winter survey in California declined by more than fifty percent in the late 1950's, while those in Mexico increased substantially (Bellrose 1980).

In British Columbia, data are scarce and anecdotal prior to 1950 but it appears that there used to be large numbers of Brant wintering in the vicinity of Boundary Bay and on Vancouver Island at the turn of the 20th century (Fannin 1891). According to Christmas Bird Count data (Campbell et al. 1990; Appendix 1, Fig. 7), the numbers of Brant wintering in Boundary Bay steadily declined between 1936 and 1950, and they had all but disappeared by 1965. The Strait of Georgia, which includes Boundary Bay, B.C., is an important stopover site for Pacific Flyway Black Brant during spring migration (Campbell et al. 1990).

It is unclear whether the trend in the reduction of Brant wintering in Boundary Bay represents a decline in this segment of the population or a change of fall migration and wintering

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behaviour. In California, increased human activity, especially hunting and pleasure boating, were

believed to be responsible for the shift in distribution to Mexico (Denson 1964). In BC, it is

believed that overhunting during the winter is responsible for the observed decline (Leach 1979).

In Boundary Bay, management considerations have pertained to the protection of the

wintering population so Brant hunting was restricted to the period of 1-10 March starting in

1977-78 (Munro 1979) in order to concentrate the harvest on spring migrants. Since the

introduction of these hunting regulations the number of Black Brant wintering in the area has

been recovering (Appendix 1, Fig. 7). However, it is of utmost importance to understand the

migration patterns of Black Brant wintering and staging on the US and Canada coasts in order to

influence sustainable management of local units throughout the Pacific Flyway.

Consequently, the goals of our study were to determine the periods when migrants were

present in Boundary Bay and whether or not the birds seen during the winter constitute a distinct

resident wintering population. We also wanted to assess the timing and intensity of the migration

events in the area from survey data and by using mark-resight techniques applied within a season.

2.2   Methods

2.2.1   Study Area

This study was conducted in the Boundary Bay and Roberts Bank area, in south-western

British Columbia. Boundary Bay is large and shallow, and 55% of its extensive intertidal area

(5162 ha.) is covered by eelgrass (Ward et al. 1992). A feature of Boundary Bay is an area

containing a fresh water outlet and a gravel-sand spit, locally known as the Beach Grove area.

Brant use this spit throughout the winter and spring to haul out, preen and ingest grit. All the

legband sightings used in this paper were collected at Beach Grove, as well as most of the Brant

counts. The Roberts Bank area is also an important area for Brant, as more than half of its

surface area is covered by eelgrass (516 ha) (Ward et al. 1992). Use of this area was not

consistent throughout the winter, and there were no spits on which Brant could haul out.

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Therefore, only Brant censuses were conducted in this area. Brant were usually present in the study area from approximately 1 November until the first week of May.

2.2.2 Sighting Methods

Black Brant have been banded using individually coded plastic legbands at five major breeding or moulting locations in Alaska, Russia and the Northwest Territories since 1987. During our study, approximately 8% of the Black Brant seen in Boundary Bay wore such markers. Efforts to record marked birds in winter and spring have been made in Boundary Bay for the period of 1992-93 to 1995-96. However, the 1992-93 and 1993-94 data sets contained relatively few observations so we restricted our analyses to the 1994-95 and 1995-96 season (referred as the 1995 and 1996 season respectively in the text). Observations were conducted from shore using spotting scopes on most days when Brant were present in the Bay (early November to early May). Information on age, pair, and family status of marked birds, as well as age ratios was collected. The maximum number of Brant present at Beach Grove, Boundary Bay, and at Roberts Bank was estimated during each visit.

2.2.3 Data Sets

Mark-resight methods, applied within a season, can provide useful information on the rate of immigration and emigration from the area. When the interval between sighting occasions is small, such as is the case in this study, mortality is usually not a major factor and most of the apparent changes in *local survival* can be attributed to emigration from the area. Thus, the use of individually marked birds from our legband sighting data set, combined with total counts of marked and unmarked birds, allowed us to test when birds arrived and departed from the study area and test whether there were two or more separate segments of the population using Boundary Bay. For both years, the entire season (early November to early May) was divided into 7-day periods, within which all sightings were pooled. We pooled the data in the shortest interval

possible to increase the precision of our model estimates. Several period lengths were tested and the interval of 7 days was the shortest for which we had sufficient data to do the modeling. The results were also similar to those derived from longer time intervals (e.g. 10 days). The more sighting occasions we have, the less the estimates of *local survival* could be biased by heterogeneity in sighting rates (see Appendix 2). However, having more sighting periods also results in a higher probability of rejecting the assumptions of the basic Cormack-Jolly-Seber (CJS) model (Appendix 2).

Black Brant were present in the area for a maximum of 180 days, so we had 26 sighting periods over the time that they were present in the study area. Because we wanted to study the fall migration separately from the spring migration we divided the year in two and modeled the fall and winter (hereafter referred as the winter period) separately from the spring period. Separating the year in this way was also consistent with our observation of different patterns of use in the winter and the spring period (see Fig. 2). It also permitted us to avoid the problem of fall migrants showing up again during spring migration. Because mark-resight studies usually do not permit the estimation of temporary emigration, individuals seen in fall and in spring would be considered as having been present in the study area throughout that interval, whether or not they actually wintered in the area. These would induce higher estimates of *local survival* rates and lower estimates of resight rates for the winter, and induce heterogeneity in sighting rates (migrants have lower sighting rates than residents in the winter because they are not present in the area). The winter period included 10 sighting periods from 22 November to 7 February, which permitted us to model both the fall migration and most of the winter period together. The spring period spanned 14 sighting periods, from 17 January to 25 April. We overlapped the spring period with that of the winter in order to have a stable period prior to the onset of spring migration. This allowed us to get the maximum precision on the start of spring migration. The first four weeks of November as well as the last week of April were dropped from the mark-resight analyses because of the lack of sightings in one or both years.

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2.2.4 Model Notation

Model notation followed Lebreton et al. (1992). All models were parameterized with survival and sighting probabilities defined as:

Φ_i = *local survival*, i.e. the probability that a bird alive and present in the study area during period i survives and is present in the area during period $i + 1$,

p_i = sighting rate, i.e. the probability that a bird present in the study area during period i is sighted.

We used as a base model the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965). In this model, survival (Φ) and sighting (p) probabilities are time specific and the model is denoted as (Φ_t, pt). The notation Φ_{a2} was used to define a two class effect on survival with the following meaning: the survival following the first observation in the study area is allowed to differ from subsequent survivals. The survival between the first period an individual was seen in the study area and the following period refers to survival for the first class, while subsequent survivals refer to the second class. Effects could be combined in an additive way, that is without interaction: for example, (Φa2+t) indicated that survival was allowed to vary over time in both classes but with a constant difference (on a logit scale) between the two classes. With an interaction term the survivals were allowed to vary independently within each class, and this was denoted as (Φa2*t). The estimates could also be constrained to be a linear function of time, with (Φa1lin*a2lin) or without (Φa1lin+a2lin) an interaction term. Finally, when no subscripts were used, we constrained the estimates to be constant over time. Sighting probabilities (p) followed the same notation.

2.2.5 Model Selection

The model selection procedures followed Lebreton et al. (1992). As a first step, we tested the fit of the full time-dependent CJS model (Φt, pt) on each year separately using the goodness-of-fit (GOF) tests provided by program RELEASE (Burnham et al. 1987). RELEASE uses 2 tests (TEST2 and TEST3) to assess deviations from predictions based on the assumptions of the starting model. TEST2 deals only with animals known to have been alive at period i and $i+1$. It tests for the assumption of equal sightability. TEST3 examines whether all marked animals alive at period i have the same probability of being alive at period $i+1$. Both tests are composed of 2 sub-tests: TEST2.CT, TEST2.CM, TEST3.SR, and TEST3.SM. We paid particular attention to the TEST3.SR component of RELEASE, which compares, for each sighting occasion, the fates (seen again or not seen again) of animals entering the experiment (newly marked or newly sighted) on a given occasion with those seen previously. This test is useful in detecting true age effects, handling effects on survival (Brownie and Robson 1983), transients in the population (Pradel 1992) or heterogeneity in capture (or sighting) rates (Loery et al. 1987). If TEST3.SR was rejected, we then looked for systematic structural deviations in the chi-square table for each cohort. Random variation in observed frequencies relative to expected values may be due to extra binomial variation in the data, whereas a systematic trend in the pattern observed suggests a potentially biologically important factor. For example, the presence of transients in the population will result in lower probability (on average) of seeing again a bird that entered the population on a given occasion (because transients, by definition, will emigrate permanently) than that of a bird that was seen prior to this occasion (those remaining are residents). This is structurally analogous to an age (or class) difference in survival rates. It is possible to do a GOF test on a model that takes this into account, denoted ($\Phi a2*t$, pt), by adding the 3.SM, 2.CT and 2.CM tests together (Lebreton et al. 1992).

Once a suitable general model had been determined by means of GOF tests, we proceeded to test the significance of the factors in the model and their interactions by sequential

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model fitting using program SURGE (Cooch et al. 1996). A relative deviance is given, for each model, in the SURGE output. The difference in deviance between nested models follows asymptotically a χ^2 distribution with the difference in number of estimable parameters as number of degree of freedom. This allows the computation of likelihood ratio tests (LRT's). The Akaike Information Criterion (AIC) was used to compare unnested models.

Biologists are usually more concerned about making type I errors (the null hypothesis is wrongly rejected) than type II errors (a false null hypothesis is accepted) so they usually set a low α level for their test statistic (usually .05). However, when model testing, we are seeking non-significance to accept a less parameterized model, therefore we felt that avoiding type II errors was more important. To decrease our type II error rate, we used an α level of 0.15 for identification of the general model and all subsequent testing, as suggested in Lebreton et al. (1992).

Two major problems arise when analyzing mark-resighting data in the fashion presented in this paper. One of the basic assumptions of the CJS model is that sightings are instantaneous, and that the interval between sightings is long. It was not possible to gather enough data in short periods (e.g. 1 or 2 days) and we had to pool the data over 7-day periods. The effect of pooling data is not well understood but it is clear that individuals that are seen at the beginning of one time interval (time x) have a longer amount of time to go before the next time interval (time x+1), and therefore have a greater chance to die or emigrate and, if they live, of being seen before that next interval (time x+1), than those seen only at the end of the interval (time x). This will likely induce heterogeneity in survival or in sighting rates. We wanted to have short intervals between sighting periods in order to be able to document emigration. We think that violating this assumption will likely induce heterogeneity in our analysis. The effects of heterogeneity in sighting rates on model selection and *local survival* rate estimate are shown in Appendix 2.

The second problem deals with the fact that the birds probably do not enter the population at the same time. This will be a problem especially in spring because the migration

spans a long period and it is not synchronous in the population. Again, individuals arriving later in the study area may not have the same probability of staying in the area compared to birds that have been present for a longer time. We cannot determine when an individual has entered the study area because of the low sighting rates, so individuals seen for the first time at a given time period may have been in the area for varying amounts of time. Again, this is likely to induce heterogeneity in survival rates.

2.3 Results

2.3.1 Counts 1995

The first Brant in the study area were recorded on 1 November 1994, and numbers slowly increased thereafter until early December, when numbers started to stabilize (Fig. 2a). There was some significant day to day variation in the number of Brant recorded in the study area throughout the year, however, no major influx could be noted from December to early February (Fig. 2a). The maximum number of Brant observed in the study area during the winter period was 363 birds. A slight increase (450 birds) was noted on 14 February, probably indicative of the arrival of the first northbound spring migrants. Large numbers moved through the area during spring migration, and migration peaked during the last half of March (Fig. 2a).

2.3.2 Counts 1996

Fall arrival was later in 1996 than in 1995. The first Brant were recorded in the area on 11 November 1995, a week and a half later than the previous year (Fig. 2b). Numbers remained low for a week, but by 21 November arrival was apparently completed with more than 450 Brant in the study area. Again there was day to day variation in the use of the study area, but the maximum number of Brant observed during the winter period wâs higher than the year before

A)

B)
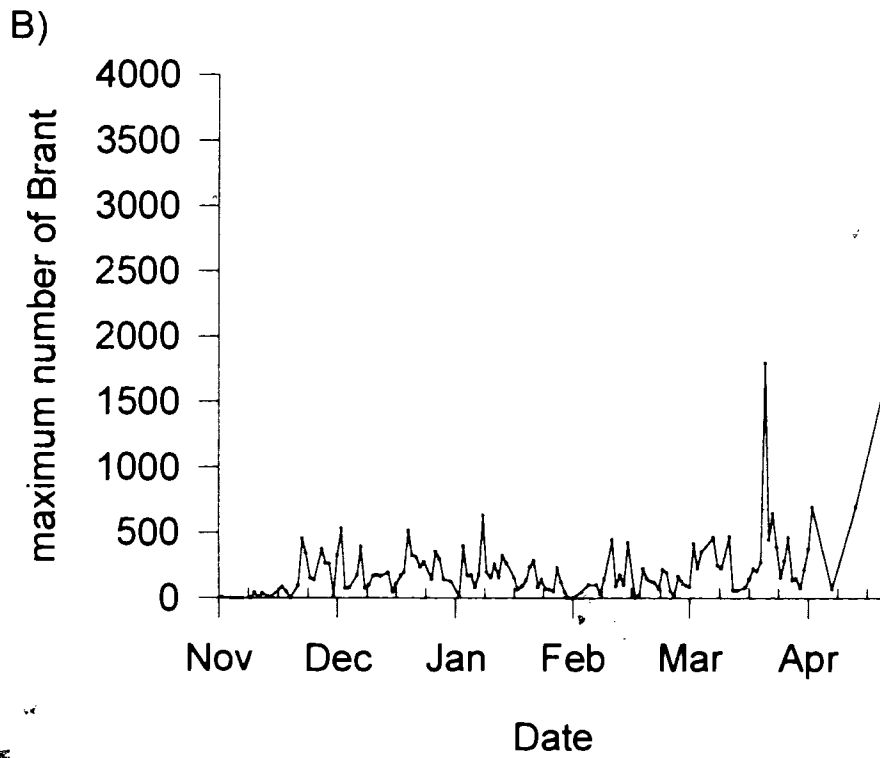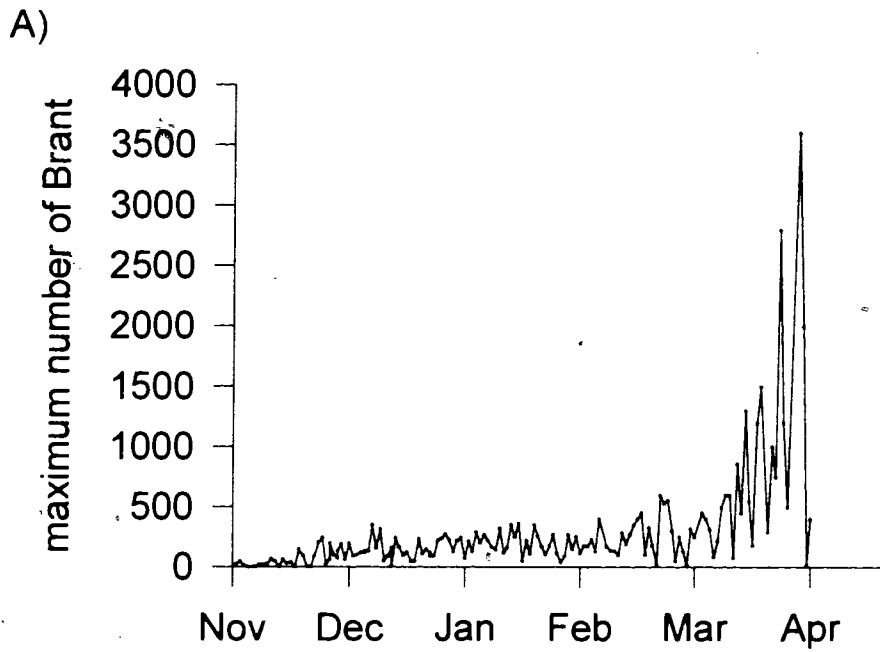
Figure 2. Maximum daily number of brant present in Boundary Bay and Roberts Bank, British Columbia during a) the 1994-95 season, and b) the 1995-96 season.

(maximum 634 birds). Numbers stayed relatively low during February, and there was no indication of an early spring migration.

Although these counts can give us a reasonable measure of the timing and intensity of migratory events in the study area, it was not a sensitive method and was probably inadequate to detect small but important movements in the area. Methods involving individually marked birds provide estimates that are potentially more powerful.

2.3.3   Immigration

Ratio of New Bands

To evaluate the proportion of immigrants in the population, we calculated the ratio of marked birds that were seen in the study area for the first time of the year versus the total number of marked individuals seen during that same time period (Fig. 3). Both years show a similar pattern throughout the season: i) a high proportion of marked birds never observed in the study area from the moment of the first arrivals to the first week of December, indicative of the arrival of the birds from their last fall staging grounds, ii) a period of low percentage of newly sighted marked birds in each period, spanning from the second week of December to late February - early March, indicating that immigration during that period was limited, and iii) a period with high percentage of new birds, likely due to the arrival of northbound spring migrants in the area. The arrival of the spring transients in the Boundary Bay area occurred a week later in 1996 than in 1995, when the ratio of new birds did not go up until the period of 28 February to 6 March, 1996.

2.3.4   Emigration

Winter Period: Identification of the General Model

The basic assumptions of the CJS model were met, so that it could be used as a general model for the 1995 winter period (TEST2 + TEST3 with sufficient data: $\chi^2_{11} = 9.06$, P=0.62).

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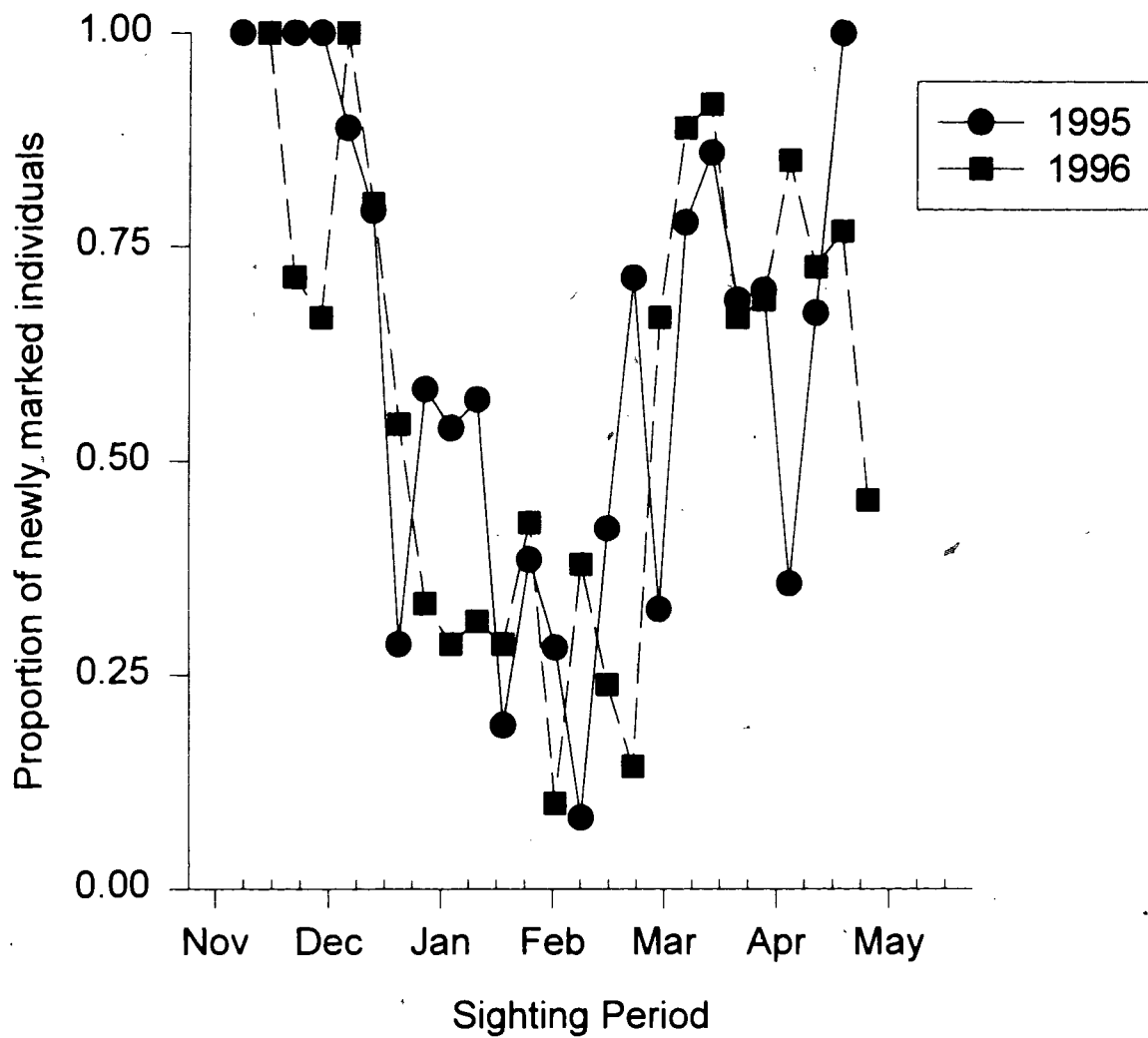
Figure 3. Relative frequency of newly sighted banded brant in the population at each time period throughout the 1995 and 1996 season. This proportion gives an indication of the amount of immigration that occurs in the population at each sighting period. Sighting are pooled over 7 day periods.

The overall results of program RELEASE also seemed to indicate that the CJS model was a good starting model for the 1996 winter period (TEST2 + TEST3 with sufficient data: $\chi^2_{11} = 9.06$, P=0.62), however TEST 3.SR was rejected ($\chi^2_5 = 12.40$, P=0.03). A model where class-structure was taken into account fitted the data satisfactorily (model $[\Phi_{a2*t}, p_t]$: $\chi^2_6 = 2.02$, P=0.92) and was used as a general starting model. Due to the major structural difference between those two starting models, we decided to model each year separately.

Winter 1995

Local survival rates varied linearly with time for the winter period of 1995 (model (2) vs. (1): $\chi^2_7 = 4.57$, P=0.71) (Table 1). Furthermore, the slope of the linear model was not significant so the weekly *local survival* rate was constant throughout the winter (model (3) vs. (2): $\chi^2_1 = 0.11$, P=0.74). There was significant time variation in sighting rates (model (4) vs. model (3): $\chi^2_9 = 35.15$, P<0.01) and the model could not be reduced any further. Therefore, a model in which *local survival* was constant over time, while sighting rates varied (model $[\Phi, p_t]$, Fig. 4a), explained the data in the most parsimonious way. The *local survival* rate between weekly intervals derived from this model was estimated at 0.965 ± 0.023 and thus indicated that there was little, if any, emigration from Boundary Bay between 22 November and 7 February 1995.

Winter 1996

The *local survival* estimates of the two classes varied with time in an additive way, that is without interaction (model (2) vs. (1): $\chi^2_7 = 8.08$, P=0.43) (Table 2). There was also overall time variation in both classes (model (3) vs. (2): $\chi^2_6 = 4.03$, P=0.01 for a linear model; model (4) vs. (2): $\chi^2_9 = 17.20$, P=0.05 for the constant survival model). A model in which the first class *local survival* estimate was constant over time and the second class estimate varied with time (model $[\Phi_{a1, a2*t}, p_t]$) did not result in a better fit when the AIC was used for comparison (model (6): AIC = 445.28 vs. model (2): AIC = 440.20). A model in which the first class

Table 1. Model selection for the intra-seasonnal resighting data on the Black Brant for the winter period of 1995. Sighting occasions are pooled over periods of 7 days. np = number of parameters, DEV = model deviance, AIC = Akaike's information criterion.

Model	np	DEV	AIC	Comparison
(1) Φ_t, p_t	19	395.47	433.47	
(2) Φ_{lin}, p_t	12	400.04	424.04	
				linearity on Φ
				(2) vs. (1): $\chi^2_7 = 4.57$, P=0.71
(3) Φ, p_t	11	^{r} 400.15	422.15	
				time variation on Φ
				(3) vs. (2): $\chi^2_1 = 0.11$, P=0.74
(4) Φ, p	2	435.30	439.30	
				time variation on p
				(4) vs. (3): $\chi^2_9 = 35.15$, P<0.01

Table 2. Model selection for the intraseasonnal resighting data on the Black Brant for the winter period of 1996. Sighting occasions are pooled over periods of 7 days, from 22 November to 6 February. np = number of parameters, DEV = model deviance, AIC = Akaike's information criterion.

Model	np	DEV	AIC	Comparison
(1) Φ_{a2*t}, p_t	28	392.12	448.12	
(2) Φ_{a2+t}, p_t	20	400.20	440.20	**additivity on Φ** **(2) vs. (1): χ^2_8= 8.08, P=0.43**
(3) $\Phi_{a2lin+t}$, p_t	14	416.74	444.74	linearity on Φ (no interaction) (3) vs. (2): χ^2_6= 16.54, P=0.01
(4) Φ_{a2}, p_t	12	417.40	441.40	overall time variation on Φ (4) vs. (2): χ^2_8= 17.20, P=0.03
(5) $\Phi_{a1*t,a2}$, p_t	21	399.10	441.10	**As good as model (2)** **Diff. AIC<1**
(6) $\Phi_{a1,a2*t}$, p_t	21	403.28	445.28	
(7) Φ_{a2+t}, p	12	431.80	455.80	time variation on p (7) vs. (2): χ^2_8= 31.60, P<0.001
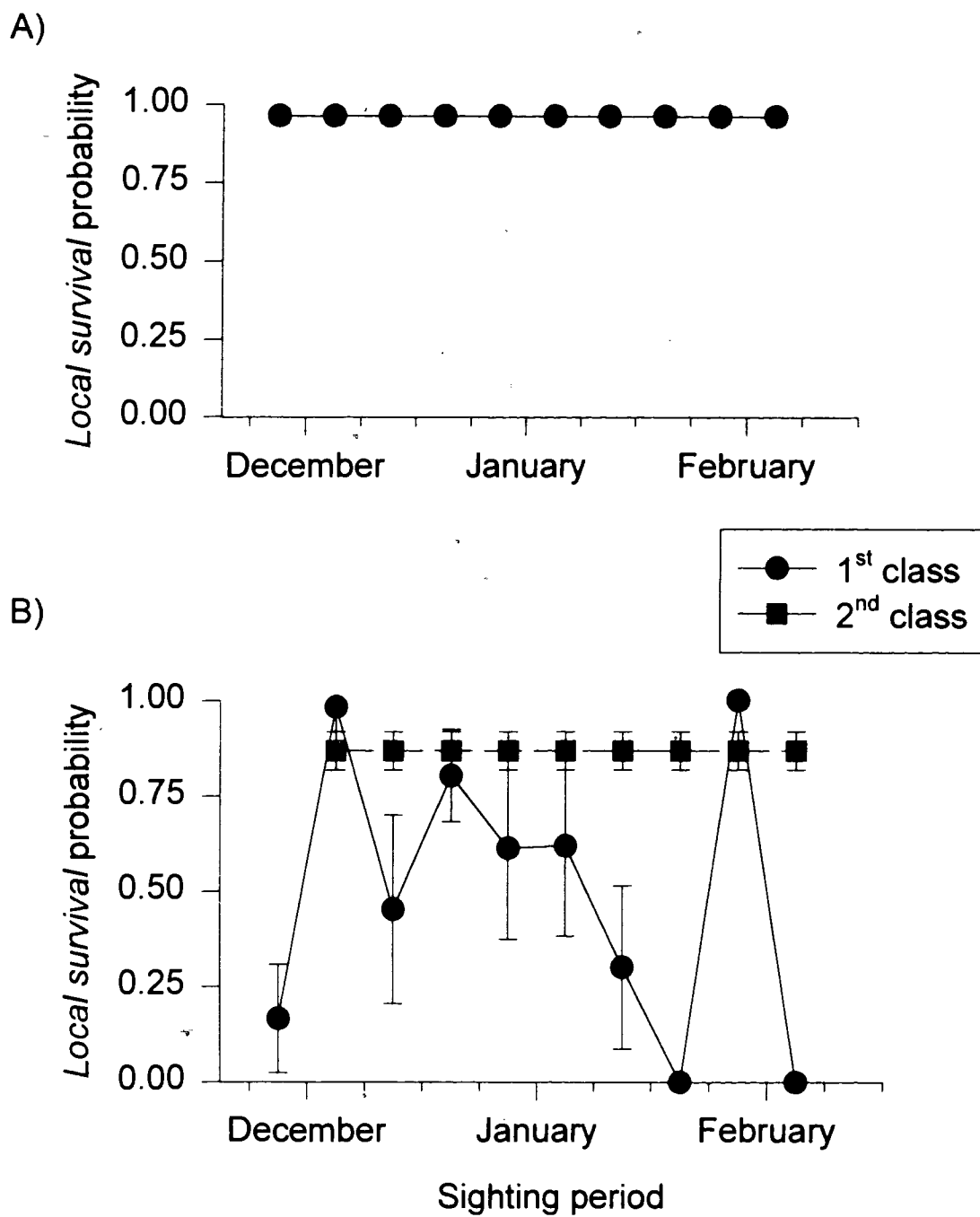
Figure 4. *Local survival* estimates for a) the 1994-95 (from model [Φ, p_t])and b) the 1995-96 winter (from model [$\Phi_{a1}*t$, a2, p_t])(22 November to 7 February) period in Boundary Bay, British Columbia. The first class refers to *local survival* probabilities following the first sighting of an individual in the study area and the second class estimate refers to *local survival* probabilities for individuals seen in more than one 7 day period.

local survival estimates were allowed to vary over time, while the second class estimates were constant (model [$\Phi_{a1}*t, a2, p_t$]) had a slightly higher AIC than the additive survival model (441.10 vs. 440.20). However, the difference in AIC between these two models was so low (<1) that they were considered identical in fit. The sighting rates could not be constrained in any way. Model [$\Phi_{a1}*t, a2, p_t$] represents more closely the situation that we observed in the 1995 winter, where resident wintering birds (noted as the second class in an class model) had a constant *local survival* rate from 22 November to 7 February, so we chose to use it for further analysis. *Local survival* for winter residents (second class), estimated at 0.868 ± 0.050 (Fig. 4b), during the 1996 winter did not differ significantly from the estimates for residents in the 1995 winter (P<0.05). The estimates of *local survival* derived for the first class in the 1996 winter data set is consistent with varying degrees of heterogeneity in the area and, as the simulations have shown, the second class *local survival* estimate should not be biased (Appendix 2). Thus, estimates of *local survival* for the winter of 1996 again indicated that there was practically no emigration from Boundary Bay between 22 November and 8 February.

Spring - Identification of the General Model

The results of GOF tests using program RELEASE suggested that the assumptions of the CJS model were not met for the spring period data set in 1995 (TEST2 + TEST3 with sufficient data χ^2_{16}= 27.22, P=0.04). Most of the variation could be explained by the TEST3.SR component of RELEASE (χ^2_5= 15.31, P=0.01), and all the cells forming this test were skewed in the same direction, indicating that birds that had just entered the population at a certain time period had less chance of being seen again than those that had been seen previously. Adding a class-effect on *local survival* resulted in a better fit (model [$\Phi_{a2}*t, p_t$]: χ^2_{11}= 11.91, P=0.37) and an acceptable starting model.

In the 1996 spring period, we did not have sufficient data to calculate either TEST3.SM or TEST2.CM. However, TEST3.SR was rejected (χ^2_4= 9.18, P=0.06) and again all the cells

were skewed in the same direction as for the 1995 data set. TEST2.CT was not significant ($\chi^2_3=$ 0.95, P=0.81), so we decided to use a two class model as a starting model (model [Φ_{a2*t}, p_t]). Since the general model derived for both years was the same, we could directly compare both years as groups.

Further Modeling

There was no annual variation in *local survival* (model (2) vs. (1): $\chi^2_{23}=$ 24.00, P=0.40) but there was on sighting rates (model (3) vs. (1): $\chi^2_{12}=$ 29.88, P<0.01; model (4) vs. (2): $\chi^2_{14}=$ 75.69, P<0.001) (Table 3). Thus we could pool the data from both years to model *local survival* and analyze them separately for sighting rates. The first three sighting periods in the spring (17 January to 7 February) corresponded to the last three periods of the winter period. Since the models derived from the winter data indicated that *local survival* for these three sighting periods was constant, we tried to fit a model where the first three survival estimates would be constant and the next 10 would be time dependent with a two-class effect. This model (model [Φ_{3cons}, $10a2*t$, p_t*year]) had a better fit than model [Φ_{a2*t}, p_t*year] on the basis of the AIC comparison.

We knew that new birds were entering the population between the second and the third week of February because of the increase in population size (Fig. 2) and the ratio of newly sighted banded individuals in the area (Fig. 3), but we did not know when the birds started to leave the area. A model in which the first five survival rates were constrained to be constant and the eight others were class and time dependent (model [Φ_{5cons}, $8a2*t$, p_t*year]) had a lower AIC than the precedent model (Table 3), thus suggesting that the birds did not start to emigrate from the study area before the first week of March. We could also constrain the last 8 survival estimates to be constant over time, but different for both classes (model (7) vs. (6): $\chi^2_{14}=$

Table 3. Model selectioh for the intraseasonnal resighting data on the Black Brant for the spring period of 1995 and 1996. Sighting occasions are pooled over periods of 7 days, from 17 January to 25 April. np = number of parameters, DEV = model deviance, AIC = Akaike's information criterion.

Model	np	DEV	AIC	Comparison
(1) $\Phi_{a2*t*yr}$, P_{t*yr}	74	1651.88	1799.88	
(2) Φ_{a2*t}, P_{t*yr}	51	1675.88	1777.88	
				year effect on Φ
				(2) vs. (1): χ^2_{23}= 24.00, P=0.40
(3) $\Phi_{a2*t*yr}$, P_t	62	1681.76	1805.76	
				year effect on p
				(3) vs. (1): χ^2_{12}= 29.88, P<0.01
(4) Φ_{a2*t}, P_t	37	1751.57	1825.37	
				year effect on p
				(4) vs. (2): χ^2_{14}= 75.69, P<0.001
(5) $\Phi_{3cons, 10a2*t}$, P_{t*yr}	47	1680.67	1774.67	
(6) $\Phi_{5cons, 8a2*t}$, P_{t*yr}	43	1682.58	1768.58	
(7) $\Phi_{5cons, 8a2+t}$, P_{t*yr}	35	**1686.24**	**1756.24**	
				additivity on Φ (last 8 estimates)
				(6) vs. (5): χ^2_{14}= **10.13, P=0.75**
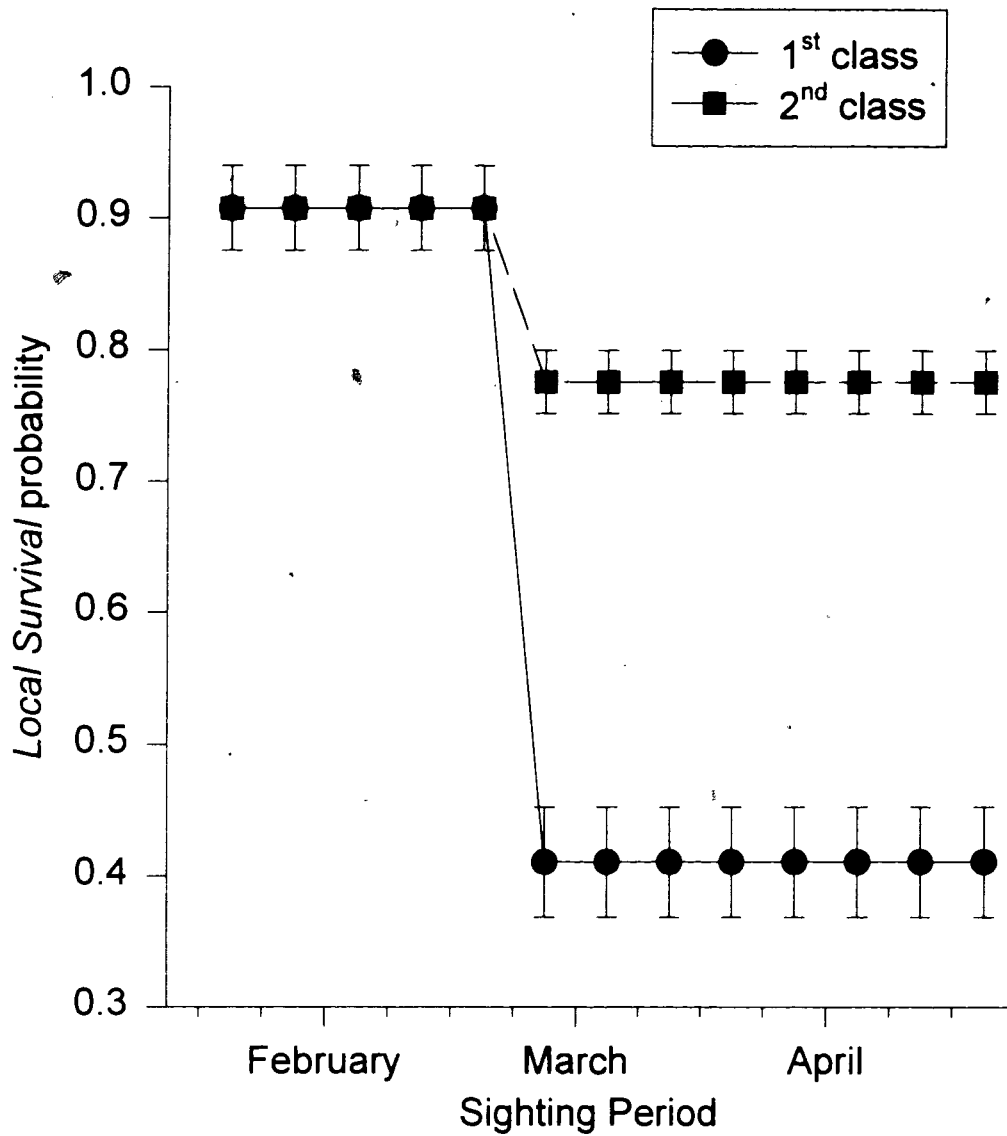
Figure 5. *Local survival* estimates for the 1995 and 1996 spring period (17 January to 25 April) in Boundary Bay, British Columbia. The first class refers to *local survival* probabilities following the first sighting of an individual in the study area and the second class estimate refers to *local survival* probabilities for individuals seen in more than one 7 day period. Estimates were derived from model [$\Phi 5_{cons}$, $8a2+t$, $Pt*Yr$]. The spring period overlapped with the winter period in order to get maximum model precision at the beginning of the period.

10.13, P=0.75). This model fit the data significantly better than a model where both classes are constant from the first occasion (model [Φ_{a2}, p_t*year]). This is further proof that the birds did not start emigrating from the study area until the beginning of the first week of March (Fig. 5). The model also showed that the rate of emigration was constant in Boundary Bay during spring migration (Fig. 5), at least until 25 April when our model ended.

2.4   Discussion

Dau (1992) suggested that Black Brant undertook a direct oversea migration from their last staging area in Izembek lagoon, Alaska, to their wintering grounds in Baja California in the fall. However, his data could not explain the fall migration pattern of Black Brant making landfall in British Columbia or on the US coast. The patterns of fall appearance of Black Brant that we have documented in Boundary Bay, British Columbia, seems to support Dau's (1992) hypothesis. There was no detectable influx of birds in Boundary Bay in fall as would be predicted if it were a stopover area for Brant migrating to wintering areas located further south. Also, our models did not show decreased *local survival* rates, which would have indicated higher emigration rates, prior to the onset of spring migration. Even though we did not have emigration rates of Brant prior to 22 November (about 3 weeks after the arrival of the first birds), it is unlikely that we would have missed fall migration given that the number of Brant present at that time was low (Fig. 2). However, we did not have sufficient data to prove that Brant wintering in Boundary Bay arrived directly via an oversea flight from Izembek lagoon. Numbers of Black Brant in Padilla Bay, Washington (approx. 60 Km. south of Boundary Bay), reached a peak in November and later decreased (Reed et al. 1989b), suggestive of a build-up of birds that subsequently dispersed to other wintering areas.

Although there was a distinct resident group of Black Brant wintering in the Boundary Bay area during our study, the pattern of use of the Bay was different between the two seasons. In the 1994-95 winter, the juvenile ratio was low (5.3% juv. from Nov. to Feb.) and the

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population was stable, with few, if any, transients showing up before spring. In 1995-96, recruitment was higher (21.0% juv.) and there was significantly more heterogeneity in sighting rates during that winter than during the previous winter. This increase in heterogeneity was likely due to higher rates of movement between nearby sites, and hence differing levels of site attendance during the 1995-96 season than during the 1994-95 season. Family units in most species of geese stay intact throughout the fall and winter period and, often, for the early stages of the spring migration (Boyd 1953; Prevett and MacInnes 1980; Warren et al. 1993). However, Black Brant show weak family cohesiveness in winter, therefore increasing the likelihood of juveniles getting separated from their parents (Reed 1993). In general, family groups of geese are dominant over pairs without goslings and single birds respectively, and adults over juveniles (Lamprecht 1986; Black and Owen 1989), so in years in which the production of young is high, increased competition on the wintering grounds could result. This in turn could result in an increased rate of dispersal of subordinate individuals and explain the movement pattern observed during the 1996 winter. Lone juveniles may be more likely to be displaced than adults because they are at the bottom of the social hierarchy (Lamprecht 1986; Black and Owen 1989). Also, when separated from their families, juveniles may be more likely to move in order to find their parents and reunite with the family group. Therefore it is possible that the increased number of juveniles in the population during the 1996 season accounted for the increased heterogeneity in Boundary Bay during that winter period.

Although limited to two years, our data suggest that the onset of spring migration may have been determined by physiological constraints, as well as by weather conditions. The arrival of Brant on their wintering grounds was 10 days later in 1996 than in 1995. Northbound migrants did not appear in significant numbers in Boundary Bay until the third week of February in 1995 and a week later in 1996, which might indicate that birds were not ready to undertake migration at the same time as in 1995. However, we do not know if this difference represents natural variation in migration phenology or if 1996 was truly a late year. Many studies have shown that

Arctic nesting geese carried significant amounts of body reserves during spring migration, and that the amount of endogenous fat reserves upon arrival on the breeding grounds was positively correlated with breeding success (Ankney and MacInnes 1978; Ankney 1984; Ebbinge and Spaans 1995). The importance of accumulating some body reserves prior to spring migration might impose constraints on how much time a bird has to spend on the wintering grounds. The importance of body reserves in shaping the migration patterns of the Black Brant is further demonstrated by the fact that they undertake a direct, non-stop migration from Izembek lagoon to their wintering areas in fall (Dau 1992), at a time when they only need to carry enough reserves to complete the migration. The spring migration is characterized by a stepping-stone process in which geese make at least one stop between their wintering areas and Izembek lagoon (Einarsen 1965; Bellrose 1980). In Boundary Bay, 12.4% of the marked individuals sighted (15.4% winter residents and 84.6% spring transients) during the 1995 season were subsequently seen in other coastal locations of British Columbia during the spring period (R.I. Goudie, *unpubl. data*). The probability of seeing a bird at 2 different sites is the product of the sighting rates from both sites. During the 195 spring season, sighting rates were estimated at 0.70 ± 0.08 in Boundary Bay and 0.70 ± 0.05 in Qualicum, hence the probability of observing interchange between those two sites was 0.49. Thus, the level of interchange between sites during the 1995 spring migration was approximately twice as important as had been observed. This might reflect the need for Brant to fatten up and also avoid depleting their reserves during spring migration so that they can arrive on the breeding grounds with sufficient energy reserves to produce and lay a clutch of eggs. A comparative study of body condition of early migrants in early, normal and late years would lead to a better understanding of the factors controlling spring migration phenology.

Although the arrival of spring migrants was delayed by one week in 1996, the timing of departure from Boundary Bay, British Columbia, did not differ between the two seasons. Spring migrants could be broadly separated in two categories: those that staged in Boundary Bay for a short period of time (1st class in our model), and those that staged for an extended period of time

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(2nd class). When probabilities of survival are constant over a period, such as is the case in our study, we can approximate mean residence time as $-1/\ln(\Phi)$ (Brownie et al. 1985). In our case, some birds stayed for an estimated 1.1 period (8 days) while others stayed for 3.9 periods (27 days) on average. Thus, it seems that some birds used Boundary Bay as their primary staging site while others only stopped briefly. We do not know if those birds that have a low residency time staged in other areas for extended periods of time of if they simply adopt a different migration strategy. The timing of the first departures of migrants from our study area coincides with the opening of the Brant hunt in both years. Although we could not distinguish between the effects of hunting disturbance and mortality, and volunteer emigration, it is possible that spring hunting had an effect on the timing of migration in our area. Interannual *local survival* rates were shown to differ between Boundary Bay and Qualicum Beach (a non-hunted area) and this difference was mainly attributed to hunting mortality and/or emigration (Chap. 3). Black Brant spring migration is characterized by an age bias in the early parts of the migration, and the first birds to arrive are mostly paired breeders (Palmer 1976). If hunting pressure influenced the migration patterns of Brant, then the spring hunt in Boundary Bay could have adverse effects on nutrient acquisition for early migrants in years when migration is delayed, especially if opportunities to acquire nutrients elsewhere up the coast are limited. This, in turn, could lead to reduced breeding success for that segment of the population that is thought to be the most productive, if opportunities to compensate are not found before reaching the breeding grounds. Spring hunting could also have adverse effects on breeding success when one individual from a pair is killed because the other individual may not have enough time to re-pair before the breeding season. On a local scale, the existing harvest regulations seem to fulfill their mandate of protecting the population wintering in Boundary Bay, British Columbia, as mostly migrants were harvested (Appendix 3; Appendix 4) and the winter resident population is currently expanding (Appendix 1, Fig. 7). However, spring migrant arrival should be closely monitored if spring hunting is used as a management tool for this or other local wintering populations.

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Chapter 3

Philopatry of Black Brant (*Branta bernicla nigricans*)
wintering and spring staging
in the Strait of Georgia, British Columbia

3.1   Introduction

Philopatry, the tendency of individuals to exhibit long-term fidelity in the use of a certain

area, is a behaviour that has been observed in many species of birds and mammals (Greenwood

1980). The costs and benefits of philopatry may be categorized as being either genetic or somatic

(Shields 1987). Genetic considerations pertain to the conservation of successful genomes within

the population. Animals would return to specific areas to breed or mate in order to limit gene

flow and, through inbreeding, preserve gene complexes coadapted by common selective

pressures (Shields 1982). Thus, philopatry allows local adaptation and should result in genetic

sub-structuring of the population if the amount of exchange between demes is small. Somatic

aspects include increased survival and reproductive success. Through philopatry, animals may

benefit from knowledge of local physical and social conditions. Such familiarity may enable

individuals to be more effective in their search for food and in escaping predators (Bengtsson

1978). Familiarity with conspecifics may also reduce the levels of aggression and stress and thus

the costs of social interactions. Philopatric individuals may have higher survival rates and an

increased fitness than those that disperse because of the relatively low risks and energy use

associated with living in familiar surroundings.

High levels of natal and breeding philopatry have been documented in many bird species,

and a high proportion of these studies showed a male-bias in philopatry rate that could be

explained by the mating system of those species. Most bird species have a resource-defense

mating system where males usually compete for breeding territories that attract females

(Greenwood 1980). Philopatry to breeding locations has been widely studied in waterfowl, but comparatively little attention has been given to winter philopatry. Geese are unique because most pair bonds are formed in winter and early spring (Owen et al. 1988), they exhibit life long monogamy, and they return to the wintering areas accompanied by their young-of-the-year (Prevett and MacInnes 1980; Reed 1993). They also acquire much of the nutrient reserves needed for spring migration and egg laying on the wintering and spring staging areas (Ankney 1984). Geese in general are highly philopatric to their wintering sites (Hestbeck et al. 1991; Percival 1991), often returning year after year to the same roost and feeding areas (Raveling 1979). Therefore, the genetic considerations for the evolution of philopatry in waterfowl apply to the wintering and spring staging populations, which are the effective demes.

Black Brant come from several distinct breeding colonies distributed over much of the Arctic and subarctic coastal areas of Alaska, the Northwest Territories, the Yukon, and northeastern Russia (Einarsen 1965; Palmer 1976; Bellrose 1980). They mainly winter along the Pacific coast of North America, from Alaska to Baja California and the mainland of Mexico. The genetically distinct grey-bellied form of Pacific Brant (Shields 1990) is largely segregated from populations of Black Brant on its high Arctic breeding grounds, on its main staging area near Izembek, Alaska (Reed et al. 1989a), and on its wintering grounds in Padilla Bay, Washington (Reed et al. 1989b). However, Atlantic Brant from different nesting populations widely overlap on their wintering range at both regional and local scales (K. Abraham, pers. comm.). Other species of Arctic nesting geese also exhibit this wintering overlap (Cooke et al. 1975). Vangilder and Smith (1985) suggested that, although Atlantic Brant from different breeding areas mix on the wintering grounds, birds from certain breeding areas may be represented disproportionately in some winter locations. Wintering populations of Atlantic Brant showed some genetic differences and thus did not represent a totally panmictic population (Novak et al. 1989). These genotypic differences between wintering populations, however, did not suggest a strict correspondence between breeding and wintering locations. That study concluded that there was

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some restriction in gene flow between the wintering populations on the migration route and/or on the wintering grounds or some degree of non-random migration between nesting and wintering populations.

In this paper, I used data from a resighting study of individually marked Black Brant in southwestern British Columbia to estimate probabilities of surviving and returning (*local survival*) to wintering and spring staging areas. Estimates of *local survival* can be corrected to provide an index of philopatry when estimates of true survival are known. I modeled survival rates and sighting rates, and used the estimates derived from the most parsimonious model to draw comparisons in site fidelity between seasons and, for the spring season, between locations. I also compared the origin of birds in the different populations to see if differences in philopatry could be explained by differential winter and spring staging distribution of breeding units, and I assessed the impact of hunting on philopatry. Finally, I combined these results to evaluate if genetic isolation of wintering and spring staging populations of Black Brant was possible or if somatic factors were more likely to influence their distribution.

3.2   Methods

Data on Black Brant wintering and staging in the Strait of Georgia have been collected annually on Vancouver Island (Parksville-Qualicum area) from 1989 to 1995 (R.I. Goudie, *unpubl. data*) and in Boundary Bay, B.C. from 1993 to 1996 (Fig. 1). During this study, approximately 8% of all Black Brant observed were marked with individually coded plastic leg bands by researchers on five major breeding or molting locations in Alaska, Russia and the Northwest Territories, Canada. Birds at each location are marked with a different band color, enabling identification of the origin of birds seen on the wintering and staging grounds. Observations were conducted from shore using spotting scopes on most days when Black Brant were present in the area. Black Brant were usually present in Parksville-Qualicum from early March to mid-May and in Boundary Bay from early November to mid-May. Information on age,

pair and family status of marked birds was also collected. Because Brant show little sexual dimorphism in winter, I had to use information from the original banding records to assign sexes for the marked individuals seen in the study area. On each visit, the maximum number of Brant present at Beach Grove, Boundary Bay, was estimated. Counts were also conducted in Parksville-Qualicum, but not with the same intensity. All band reading in Boundary Bay was done at Beach Grove while the Parksville-Qualicum data set contained band readings from three separate locations: Parksville, French Creek and Qualicum beach.

3.2.1 Study Populations

Local survival is defined as the probability that a bird seen in the study area in a given year will survive and return to that area the next year. It is a function of mortality and emigration. Previous work has shown that the period in which the birds were present at Boundary Bay could be divided in two seasons, winter and spring (Chap. 2). There was no detectable migratory movement through the area in fall and the birds that arrived in fall stayed for the winter, so there was no need to study the fall separately from the winter. Spring migrants did not appear in the study area before the second week of February. Therefore, I defined winter resident birds as those seen prior to 8 February, and spring migrants as those seen on or after 8 February in any given year. The Parksville-Qualicum area was used by Brant only during the spring migration. The years used to describe the winter period will be those corresponding to the spring of that year. For example, the winter of 1993 will refer to the period spanning from November 1992 to February 1993.

3.2.2 Model Notation

Model notation followed Lebreton et al. (1992). All models were parameterized with survival and sighting probabilities defined as:

ϕ_i = *local survival*, i.e. the probability that a bird alive and present in the study area during year i survives (true survival rate) and is present (philopatry rate) in the area during year $i + 1$,

P_i = probability that a bird present in the study area during year i is sighted.

I used as a base model the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). In this model, survival (ϕ) and sighting (P) probabilities are time specific and the model is denoted as (ϕ_t, P_t). Whenever parameter estimates were allowed to vary between males and females, the subscript ($_{sex}$) was used. The notation ϕ_{a2} refers to a two class effect on survival with the following meaning: survival following the first observation in the study area is allowed to differ from subsequent survivals. Survival between the first year an individual was seen in the study area and the following year refers to survival for the first class, while subsequent survival estimates refer to the second class. Effects could be combined in an additive way, that is without interaction: for example, (ϕ_{a1+a2}) indicated that survival was allowed to vary over time in both classes but with a constant difference (on a logit scale) between them. With an interaction term the survivals were allowed to vary independently within each class, denoted as (ϕ_{a2*t}). Estimates could also be constrained to be a linear function of time, with ($\phi_{a1lin*a2lin}$) or without ($\phi_{a1lin+a2lin}$) an interaction term. Finally, when no subscripts were used, I constrained the estimates to be constant over time. In the comparison between sites, ($\phi_{a2*t*loc}$) was used to describe a situation where survival was allowed to vary between classes, time and location. Sighting probabilities (p) followed the same notation.

3.2.3   Model Selection

The model selection procedures followed Lebreton et al. (1992). As a first step, I tested the fit of the full time-dependent CJS model (ϕ_t, p_t) using the goodness-of-fit (GOF) tests provided by program RELEASE (Burnham et al. 1987) on males and females separately. Release uses two tests (TEST2 and TEST3) to assess deviations from predictions based on the

assumptions of the starting model. I paid particular attention to the TEST3.SR component of RELEASE, which compares, for each sighting occasion, the fates (seen again or not seen again) of animals entering the experiment (newly marked or newly sighted) on a given occasion with those seen previously. This test is useful in detecting true age effects, handling effects on survival (Brownie and Robson 1983), transients in the population (Pradel 1992) or heterogeneity in capture (or sighting) rates (Loery et al. 1987). If TEST3.SR was rejected, I looked for systematic structural deviations in the chi-square table for each cohort. Random variation in observed frequencies relative to expected values may be due to extra binomial variation in the data, whereas a systematic trend in the pattern observed suggests a potentially biologically important factor. For example, the presence of transients in the population will result in lower probability (on average) of seeing again a bird that entered the population on a given period (because transients, by definition, will emigrate permanently) than that of a bird that was seen prior to this occasion (those remaining are residents). This is structurally analogous to an age difference in survival rates. To avoid confusion, I used the term class instead of age because classes do not refer to true age. It is possible to do a GOF test on a model that takes this into account, denoted (ϕ_{a2*t}, p_t) (Lebreton et al. 1992). Random deviations from expectations under a given model (e.g. CJS) may reflect extra-binomial variation. In such cases, when no biological explanation exists (such that the variation can be explained by changing the model structure), I used a variance inflation factor. This correction factor was calculated as:

$$c = (TEST\,2 + TEST\,3) / df ,$$

where TEST2 and TEST3 are the sum of the χ^2 values given by program RELEASE,

df = number of estimable parameters in the model.

When using the variation inflation factor, the LRT (see below) is transformed into an F-test as:

$$F = \frac{\chi^2_{LRT} / df_{LRT}}{c}$$

and the AIC becomes:

$$AIC = \frac{DEV}{c} + 2 \times np$$

where DEV is the deviance of the model given by SURGE

and np = number of parameters in the model.

If the model fits the data, $c = 1$. Excess variation in the data will result in a higher value of c, but even then the structural part of the model can be correct. As a rule of thumb, values of $c > 3$ indicate that the model structure is inadequate (Lebreton et al. 1992).

Once a suitable general model had been determined by means of GOF tests, I proceeded to test the significance of the factors in the model and their interactions by sequential model fitting using program SURGE (Cooch et al. 1996). A relative deviance is given, for each model, in the SURGE output. The difference in deviance between nested models follows asymptotically a χ^2 distribution with the difference in number of estimable parameters as number of degrees of freedom. This allows the computation of likelihood ratio tests (LRTs) (Lebreton et al. 1992). The Akaike Information Criterion (AIC) was used to compare unnested models.

Because we are seeking non-significance when model testing, we have to be concerned about making a type II error (a false null hypothesis is accepted). Because of this, I used, as suggested in Lebreton et al. (1992), an α level of 0.15 for identification of the general model and all subsequent testing. Raising the α level increases the risk of making a type I error (rejecting the null hypothesis when in fact its true), thus incorrectly assigning significance to a model effect, but I believe that the risk of doing so is not as serious as incorrectly accepting a less

parameterized model. This would lead to oversimplification of the model and loss of potentially important parameters.

Capture-recapture analysis makes a series of basic assumptions (Pollock et al. 1990) that are testable to some degree with GOF statistics. In my study, I believe that the assumption most likely to pose a problem is that of independence of fates and identity of rates among individuals. The fact that the sighting effort spanned a long period meant that there was possibility for multiple sightings of some birds within a year. Also, sampling was done at fixed sites within the study area. The site fidelity of a bird, within a year, could then influence its probability of being sighted in that year. Such variation would likely induce heterogeneity in capture rates (not all the birds would have the same probability of being seen) or in interannual site fidelity. Heterogeneity in capture rates can negatively bias the survival estimates derived from the model (Loery et al. 1987). In a model with class structure, only the estimates for the first class are affected.

3.3   Results

3.3.1   Boundary Bay: Winter 1993 to 1996

Identification of the General Model

A total of 240 individually marked birds were observed during this period. The number of marked individuals recorded each year was 7 in 1993, 108 in 1994, 83 in 1995 and 118 in 1996. The assumptions of the CJS model were met for winter residents (1993 - 1996), according to the GOF test computed with program RELEASE. Although I had insufficient data to calculate TEST2 and TEST3.SM, the data were sufficient to calculate TEST3.SR. The overall TEST3.SR was non-significant (males: χ^2_1=0.47, P=0.49; females: χ^2_2=1.48, P=0.48), indicating that heterogeneity in sighting rates was not a problem, so the CJS model was accepted as a starting point.

Further Models

There were no differences in *local survival* and in sighting rates between males and females (model (2) vs. (1), P=0.66 and model (4) vs. (3), P=0.30) (Table 4). The omnibus test for overall variation between sexes also showed no significant differences between males and females (model (4) vs. (1), P= 0.37) so the sexes were pooled for further analysis. There was no significant annual variation in either *local survival* rates (model (5) vs. (4), P=0.55) or in sighting rates (model (6) vs. (4), P=0.26). Because these two models were unnested (model [ϕ_t, P] and [ϕ, P_t]), I used the AIC to identify which was the most parsimonious. Model (5) [ϕ, P_t] had the lowest AIC (302.89) and was thus considered as the most parsimonious, although the difference between the AIC values of the two models was small. I could not further reduce the model, as sighting rates varied significantly with time (model (7) vs. (5), P=0.07). The constant *local survival* rate was estimated at 0.42 $\pm$ 0.04 while the sighting rates were estimated at 0.87 $\pm$ 0.52, 0.68 $\pm$ 0.09, and 1.00 $\pm$ 0.00 for the 1994, '95 and '96 season respectively.

3.3.2 Boundary Bay: Spring 1993 to 1996

Identification of the General Model

A total of 1040 individually marked birds were observed in Boundary Bay during the spring period (birds seen from 8 February to May, 1993 - 1996). The results of the GOF test indicated rejection of the basic CJS model for males (TEST2 + TEST3: χ^2_4 = 23.90, P<0.001) and for the females (χ^2_4 = 7.47, P=0.11). However, virtually all of the lack of fit was due to the 3.SR component (TEST3.SR: χ^2_2 = 23.56, P<0.001 for males and χ^2_2 = 6.78, P=0.03 for females), suggesting a class effect on *local survival*. This effect could be due to heterogeneity in sighting rates or the presence of transients in the population. Although I had sparse data and could not fully assess the validity of this test, the GOF test on model [ϕ_{a2*t}, P_t] showed that it was an acceptable model to start with for both sexes (χ^2_2 = 0.34, P=0.84 for males and χ^2_2 = 0.69, P=0.71 for females).

Table 4. Model selection for the interannual resighting data of individually marked Black Brant for the winter period of 1992-93 to 1995-96 in Boundary Bay, B.C.. The data is restricted to birds seen from 1 November to 8 February of each year (np = number of parameters, DEV = deviance, AIC = Akaike's information criterion).

Model	np	DEV	AIC	comparison
(1) ϕ_{sex*t}, P_{sex*t}	10	289.15	309.15	
(2) ϕ_t, P_{sex*t}	8	289.98	305.98	
				sex variation on ϕ
				(2) vs. (1): $\chi^2_2 = 0.82$, P = .6637
				(4) vs. (3): $\chi^2_3 = 3.67$, P = .2994
(3) ϕ_{sex*t}, P_t	8	290.86	306.86	
				sex variation on P
				(3) vs. (1): $\chi^2_2 = 1.71$, P = .4253
				(4) vs. (2): $\chi^2_3 = 4.55$, P = .2079
(4) ϕ_t, P_t	5	294.53	304.53	
				overall time variation on sex
				(4) vs. (1): $\chi^2_5 = 5.38$, P = .3713
(5) ϕ, P_t	**4**	**294.89**	**302.89**	
				time variation on ϕ
				(5) vs. (4): $\chi^2_1 = 0.36$, P = .5485
				(6) vs. (7): $\chi^2_2 = 4.30$, P = .1165
(6) ϕ_t, P	4	295.81	303.81	
				time variation on P
				(6) vs. (4): $\chi^2_1 = 1.28$, P = .2579
				(5) vs. (7): $\chi^2_2 = 5.22$, P = .0735
(7) ϕ, P	2	300.11	304.11	
				overall time variation
				(7) vs. (4): $\chi^2_3 = 5.58$, P = .1339

Further Models

There were no sex differences in *local survival* rates (model (2) vs. (1): $\chi^2_4 = 2.56$, P=0.63, model (4) vs. model (3): $\chi^2_5 = 3.04$, P=0.69) (Table 5) or in sighting rates (model (3) vs. (1): $\chi^2_2 = 0.37$, P=0.83, model (4) vs. model (2): $\chi^2_3 = 0.85$, P=0.84). The overall test of a sex effect on survival and sighting rates was also non-significant (model (4) vs. (1):$\chi^2_7 = 3.41$, P=0.84) so the data from both sexes could be pooled. A model where the *local survival* rates for both classes was constrained to be constant over time, while the sighting rates were allowed to vary (model [ϕ_{a2}, p_t]), fitted significantly better than the initial time-dependent model (model (5) vs. (4): $\chi^2_2 = 1.71$, P=0.43)(Table 5). The time variation on sighting rates was significant (model (6) vs. (4): $\chi^2_1 = 5.18$, P=0.02) so the model could not be reduced any further. The estimates of *local survival* and sighting rates derived from model [ϕ_{a2}, p_t] are given in Table 6.

3.3.3 Parksville-Qualicum: Spring 1989 to 1995

Identification of the General Model

The data collected from the Parksville-Qualicum area showed some important structural problems. All tests in program RELEASE were significant (TEST 3: $\chi^2_{12} = 188.21$, P<0.001; TEST 2: $\chi^2_8 = 25.76$, P<0.001), indicating that the basic assumptions of the CJS model were not met. This result could not be attributed solely to extra binomial variation because systematic deviations in some of the component tests were apparent (e.g., all cells in TEST3.SR were skewed in the same direction; of the birds seen in the study area at year *i*, those that had been seen in previous years were more likely to be seen in year *i*+1 than those that were seen for the first time at year *i*). This pattern suggested that some biological factor was responsible for some of the variance in the model. To minimize excess variation, especially with sighting rates, I used only data from birds seen at Qualicum Beach. This site had the most sightings for the study period, and those sightings were distributed more evenly between years than those from the other sites. The results of RELEASE on the Qualicum data still showed a departure from the CJS

Table 5. Model selection for the interannual resighting data on individually marked Black Brant for the spring period of 1992-93 to 1995-96 in Boundary Bay, B.C.. The data is restricted to birds seen after 8 February of each year (np = number of parameters, DEV = deviance, AIC = Akaike's information criterion).

Model	np	DEV	AIC	comparison
(1) $\phi_{sex*a2*t}$, P_{sex*t}	14	774.43	802.43	
(2) ϕ_{a2*t}, P_{sex*t}	10	776.99	796.99	
				sex variation on ϕ
				(2) vs. (1):χ^2_4=2.56, P =.6339
				(3) vs. (4):χ^2_5=3.04, P =.6938
(3) $\phi_{sex*a2*t}$, P_t	12	774.80	798.80	
				sex variation on P
				(3) vs. (1):χ^2_2=0.37, P =.8311
				(2) vs. (4):χ^2_3=0.85, P =.8375
(4) ϕ_{a2*t}, P_t	7	777.84	791.84	
				overall sex effect
				(4) vs. (1):χ^2_7=3.41, P =.8447
(5) ϕ_{a2}, P_t	**5**	**779.55**	**789.55**	
				time variation on ϕ
				(5) vs. (4):χ^2_2=1.71, P=.4253
(6) ϕ_{a2*t}, P	6	783.02	795.02	
				time variation on P
				(6) vs. (4):χ^2_1=5.18, P =.0228

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model's assumptions (TEST 2 + TEST 3 $=\chi^2_{17} = 58.94$, P<0.001 for males, and $\chi^2_{15} = 69.19$, P<0.001 for females). However, most of this variation was explained by the TEST 3 component of RELEASE. All cells in TEST 3.SR varied significantly from predicted values for both sexes (TEST 3.SR: $\chi^2_5 = 38.94$, P<0.001 for males and $\chi^2_5 = 42.00$, P<0.001 for females) and were all skewed in the same direction. This suggested that either transients were present in the study area, or heterogeneity in sighting rates was significant. TEST 3.SM was also rejected ($\chi^2_5 = 10.36$, P=0.07 for males and $\chi^2_5 = 20.91$, P<0.001 for females).

The value of the variance inflation factor for the CJS model ($c = 3.47$ for males and 4.61 for females) indicated a significant departure from the assumptions of the CJS model. A class structured model seemed to fail to fit the data (model $[\phi_{a2*t}, p_t]$: GOF $\chi^2_{12} = 20.00$, P=0.0671 for males and $\chi^2_{10} = 27.19$, P<0.01 for females). However, the variance inflation factor for this model (males: $c = 1.67$, females: $c = 2.72$, total: $c = 2.14$) indicated that the latter model fitted the structure of the data satisfactorily.

Further Models

As for Boundary Bay, the sex effect on *local survival* and sighting rates was not significant (model (2) vs. (1): $F_{(32,10)} = 0.41$, P>0.75; model (3) vs. model (1): $F_{(32,5)} = 0.45$, P>0.75)(Table 7). The overall sex effect on *local survival* and sighting rates was also non significant (model (4) vs. (1): $F_{(32,16)} = 0.38$, P>0.75) so I modeled males and females as one group. The interaction term (time x class) was not significant for *local survival* (model $[\phi_{a1+a2}, p_t]$ vs. model $[\phi_{a2*t}, p_t]$: $F_{(32,3)} = 0.56$, P>0.75)(Table 7). Furthermore, time variation in *local survival* rates could be constrained linearly (model (6) vs. model (4): $F_{(32,4)} = 0.44$, P>0.75). The estimated slopes for both classes did not differ significantly from zero so I constrained the survival estimates for the two classes to be constant over time (model (7) vs. model (6): $F_{(32,1)} = 0.06$, P>0.75). Finally, a model where *local survival* rates for both classes and the sighting rates were constant (model $[\phi_{a2}, p]$) failed to explain the data in a more parsimonious

Table 6. Summary of estimates of annual survival (ϕ) and capture (P) probabilities for the spring migration data on the Black Brant in Boundary Bay and Qualicum, B.C.. The estimates are derived from model [ϕ_{a2}, P_t].

	Boundary Bay	Qualicum
Estimates of survival		
1st class	0.28 ± 0.04	0.40 ± 0.02
2nd class	0.70 ± 0.09	0.73 ± 0.03
Recapture estimates		
P_2	0.45 ± 0.09	0.71 ± 0.09
P_3	0.70 ± 0.08	0.68 ± 0.06
P_4	0.53 ± 0.03	0.45 ± 0.05
P_5	-	0.49 ± 0.04
P_6	-	0.57 ± 0.04
P_7	-	0.70 ± 0.05

Table 7. Model selection for the interannual resighting data of individually marked Black Brant for the spring period of 1989 to 1995 in Qualicum, B.C. (np = number of parameters, DEV = deviance, AIC = Akaike's information criterion).

Model	np	DEV	AIC	comparison
(1) $\phi_{sex*a2*t}$, P_{sex*t}	32	2443.77	1205.95	
(2) ϕ_{a2*t}, P_{sex*t}	22	2452.63	1190.09	
				sex effect on ϕ
				(2) vs. (1): $F_{(32,10)} = 0.41$, $p>0.75$
				(3) vs. (4): $F_{(32,11)} = 0.36$, $p>0.75$
(3) $\phi_{sex*a2*t}$, P_t	27	2448.58	1198.20	
				sex effect on P
				(3) vs. (1): $F_{(32,5)} = 0.45$, $p>0.75$
				(2) vs. (4): $F_{(32,6)} = 0.34$, $p>0.75$
(4) ϕ_{a2*t}, P_t	16	2456.95	1180.11	
				overall sex effect
				(4) vs. (1): $F_{(32,16)} = 0.38$, $p>0.75$
additivity on ϕ				
(5) ϕ_{a1+a2}, P_t	13	2460.55	1175.79	
				additivity on ϕ
				(5) vs. (4): $F_{(32,3)} = 0.56$, $p>0.75$
linear model				
(6) $\phi_{a1lin + a2lin}$, P_t	9	2464.34	1169.56	
				linearity on ϕ
				(6) vs. (4): $F_{(32,4)} = 0.44$, $p>0.75$
(7) ϕ_{a2}, P_t	**8**	**2464.46**	**1167.62**	
				time variation on ϕ
				(7) vs. (6): $F_{(32,1)} = 0.06$, $p>0.75$
(8) ϕ_{a2}, P	3	2488.79	1168.99	
				time variation on P
				(8) vs. (7): $F_{(32,5)} = 2.27$, $p<0.10$

way (model (8) vs. model (7): $F_{(32,5)} = 2.27$, P<0.10). The *local survival* estimates were 0.40 ± 0.02 and 0.73 ± 0.03 for the first and second class respectively (Table 6). The estimated sighting rates varied from 0.45 ± 0.05 to 0.71 ± 0.09 (Table 6).

3.3.4 Differences Between Sites: Spring Migration

Data were collected during the spring migration at both Qualicum Beach and Boundary Bay in 1993, 1994, and 1995. I had only 3 sighting occasions so I could not do any goodness of fit testing on the starting model. Because both the Qualicum and the Boundary Bay spring data sets showed class structure in the survival rates, I used, as a starting model, model [$\phi_{a2}*t*loc$, p_t*loc]. The effect of the location on sighting rates was not significant (Table 8)(L.R.T. $\chi^2_1 = 1.61$, P=0.20), indicating that the sighting rate was equal at both locations within years. The effect of the location on *local survival* rate, however, was strongly significant (L.R.T. $\chi^2_3 = 25.93$, P<0.001), suggesting that true survival and/or philopatry levels differed from one site to the other. Model [$\phi_{a2}*t*loc$, p_t] was the most parsimonious model I could derive from the data.

Estimates derived from this model showed a sighting rate of 0.55 ± 0.05 for both locations. *Local survival* estimates were consistently higher for the Qualicum area than for Boundary Bay. The first class *local survival* estimates for Qualicum were 0.50 ± 0.04 for the period between 1993 and 1994 and 0.53 ± 0.07 between 1994-1995. The same *local survival* estimates for Boundary Bay gave values of 0.25 ± 0.05 between 1993 and 1994 and 0.35 ± 0.06 from 1994 to 1995. The value for the *local survival* rate of the second class was 0.96 ± 0.09 for Qualicum Beach and 0.88 ± 0.18 for Boundary Bay. Although the values of the point estimates were not very useful because I already had estimates derived from larger data sets for these two sites, they were useful in showing that birds using Qualicum during spring migration showed a significantly higher degree of *local survival* than birds migrating through Boundary Bay.

Table 8. Between sites comparison for the spring period between 1993 and 1995. Boundary Bay and Qualicum, B.C., are compared.

Model	np	DEV	AIC	comparison
(1) $\phi_{a2*t*loc}$, P_{t*loc}	8	1437.90	1453.90	
(2) $\phi_{a2*t*loc}$, P_t	7	1439.51	1453.51	
				location variation on P
				(2) vs. (1): $\chi^2_1 = 1.61$, P = .2045
(3) ϕ_{a2*t}, P_t	4	1465.44	1473.44	
				location variation on ϕ
				(3) vs. (2): $\chi^2_3 = 25.93$, P = .0000

3.3.5 Philopatry Levels

Winter Residents

Annual survival of Black Brant, based on resighting data, was estimated as being
constant at 0.84 over the period of 1983 to 1993 (Ward et al. 1997). This value is comparable to
survival estimates derived from band recovery models for the Atlantic Brant (*Branta bernicla
hrota*) (Kirby et al. 1986). Assuming that 0.84 was the true survival rate for the Black Brant
during this study, and that the birds in the samples were subject to the same mortality risks as any
other population, the estimates of *local survival* can be corrected to provide an index of
philopatry. This was done by dividing the estimate of *local survival* derived from the models by
the true survival rate (0.84) from the literature, expressed as a percentage. In this way, I separated
mortality and emigration rates in the estimate. The philopatry level derived for the winter was:
0.42/0.84x100 = 50.0%, meaning that half of the birds emigrated permanently from the study
area each year. Due to the relatively short duration of my study, some temporary emigration
could appear as permanent emigration, so this represents a minimum estimate of philopatry.

This estimate of winter ground philopatry is low compared to that of other Arctic nesting
geese. Also, a companion radio-telemetry study conducted in Boundary Bay during the 1995-96
winter showed considerable individual variation in site fidelity within a season in this area. Some
individuals were present in the Bay on most days while others were present only on rare
occasions (Appendix 5). Daily counts at Beach Grove, Boundary Bay also showed day to day
variation in the maximum number of Brant present (Fig. 2), suggesting that use of the Bay was
not consistent throughout the winter.

This lead me to believe that the *local survival* estimate was biased low for the Boundary
Bay winter residents and that heterogeneity in sighting or in *local survival* rates could be in part
responsible for this bias. When birds seen only once in any given year were compared to birds
seen more than once, the most parsimonious model indicated that *local survival* differed
significantly between these two groups but that sighting rates did not (Table 9). Thus, individuals

for which I had multiple sightings throughout a winter were more faithful to Boundary Bay in subsequent years than birds seen only once in a given year. In all, 56.25% of the birds were seen only once in Boundary Bay in any given winter during the study. There was no sex bias in those birds seen only once compared to the total wintering population ($\chi^2_1=0.68$, P=.41). Analyzing the data in this fashion prevented estimating the 1993 *local survival* rate because all the birds seen in the first year (1993) were only recorded once during that winter. The estimate of *local survival* for birds seen only once in a year was .39 $\pm$ .06 and, for individuals seen twice or more in a year, .58 $\pm$ .01. Therefore the philopatry level for winter residents seen twice or more within a year was estimated at 69.2%, which compared well with the levels observed in other goose populations.

Spring Migrants

Local survival differed significantly between Boundary Bay and Qualicum (model 2 vs. model 3, Table 8). I estimated the philopatry level for Boundary Bay spring transients as 31.0% between the time they were first seen in the area and the following year, and 82.1% for subsequent years. Philopatry for birds staging at Qualicum was estimated at 45.1% and 87.0% for the same intervals, significantly higher than those from Boundary Bay.

Even after correcting for some heterogeneity, the *local survival* estimates for the winter and the spring migration period in Boundary Bay were consistently lower than those derived for Qualicum. This difference in philopatry levels between Boundary Bay and Qualicum could be a consequence of several factors: quantity and quality of habitat could differ between sites, birds using Boundary Bay come form a different population than those using Qualicum, or there could be differential mortality between the two sites.

Table 9. Comparison between individually marked Brant seen once in any given year (low fidelity group) and Brant seen more than once in a year (high fidelity group).

Model	np	DEV	AIC	comparison
(1) ϕ_{gr}, P_{t*gr}	6	311.18	323.180	
(2) ϕ, P_{t*gr}	5	314.08	324.08	
				fidelity effect on ϕ
				(2) vs. (1): $\chi^2_1 = 2.91$, P = .0883
				(3) vs. (4): $\chi^2_1 = 6.82$, P = .0090
(3) ϕ_{gr}, P_t	**4**	**314.02**	**322.02**	
				fidelity effect on P
				(3) vs. (1): $\chi^2_2 = 2.84$, P = .2417
(4) ϕ, P_t	4	320.84	328.84	

3.3.6   Origin the Birds

To determine whether or not the composition of the study populations differed from one another, I compared the proportion of band colors, derived from five different breeding and molting areas, for birds observed from 1994 to 1996 in Boundary Bay in winter and in spring separately, and those observed in Qualicum in spring. Only comparisons within a year were possible because some banding operations were still active while others had not been for a number of years.

Each of the five banding locations was represented equally between the winter and the spring period in Boundary Bay for the three years studied (winter vs. spring: 1994: $\chi^2_4=4.27$, P=.37; 1995: $\chi^2_4=3.25$, P=.52; 1996: $\chi^2_4=4.22$, P=.38). The relative frequency of birds of different origin observed in spring migration did not differ significantly between Boundary Bay and the Parksville-Qualicum area (Boundary Bay vs. Parksville-Qualicum: 1994: $\chi^2_4=1.46$, P=.83; 1995: $\chi^2_4=1.55$, P=.82). The frequency of occurrence of birds from the five banding areas for the pooled data from Boundary Bay showed that birds from all marking areas (breeding and molting) mixed on the wintering grounds and during spring migration (Fig. 6). Thus, the origin of the birds using Boundary Bay can not explain the difference in *local survival* between this site and Qualicum.

3.4   Discussion

I used mark-resighting methods to estimate philopatry rates of wintering and spring staging Black Brant in southwestern British Columbia. I wanted to compare site fidelity between the resident wintering population and the spring transients in Boundary Bay as well as make comparisons between spring transients using Boundary Bay and Qualicum.
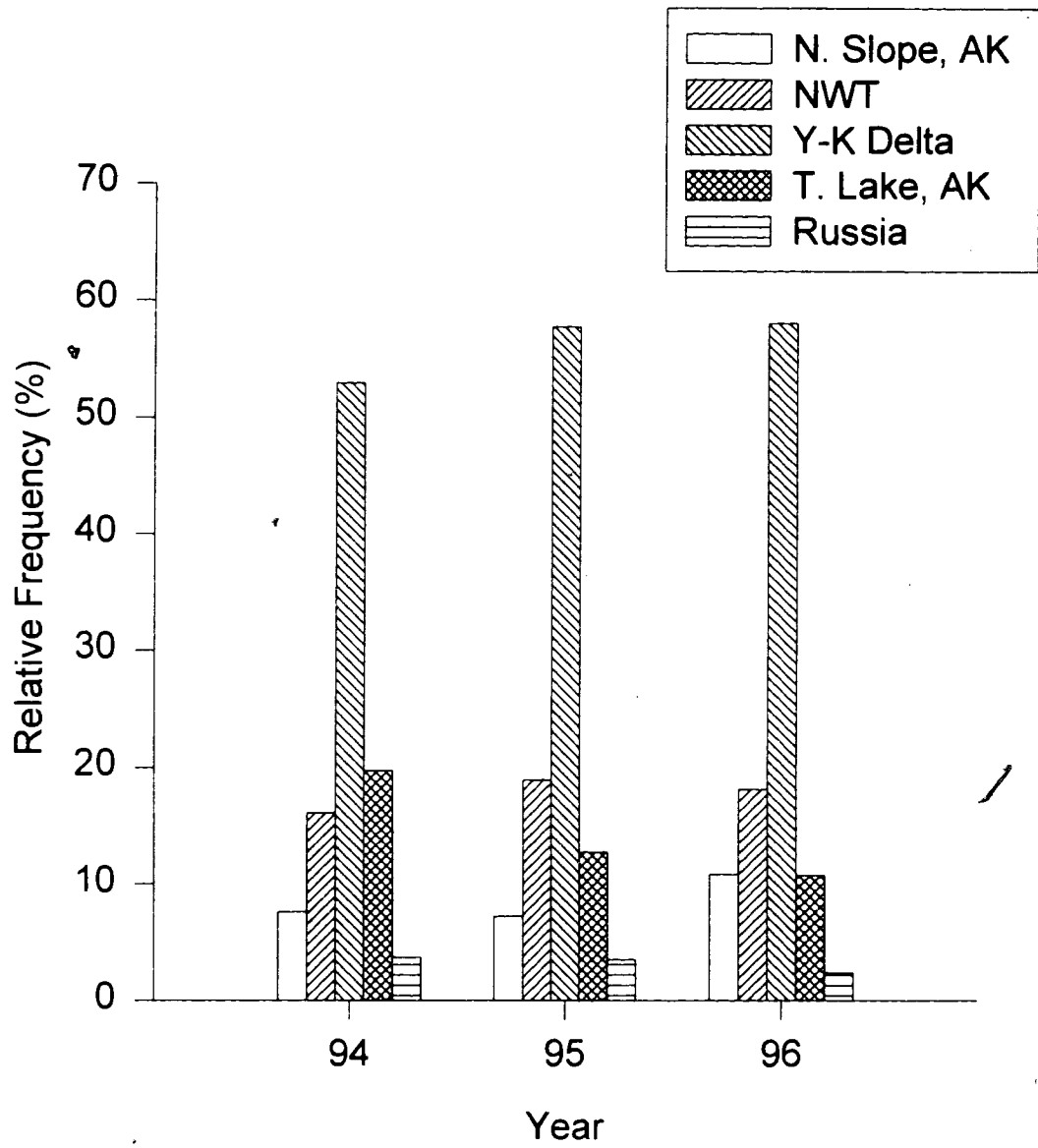
Figure 6. Origin of banded Brant observed in Boundary Bay between 1993-94 and 1995-96 period. The data from the winter and the spring are pooled.

3.4.1 Winter Philopatry

My results showed that Black Brant did not disperse randomly over the wintering range, but were philopatric, to a certain level, to specific areas. However, the estimates of philopatry for the winter residents (50%) were much lower than those derived from the second class estimate for spring migrants and were in fact closer to the estimates derived from the first class for both sites. They were also very low compared to that of other Arctic nesting geese (e.g. Canada goose: 78% (Raveling 1979), 56 - 88% (Hestbeck et al. 1991); Barnacle goose: 74 - 80% (Percival 1991); Snow goose: 88% (Prevett and MacInnes 1980)).

Evans (1980) showed that Bewick's Swans (*Cygnus columbianus bewickii*), wintering on the Severn Estuary in England, that returned in at least one subsequent winter had significantly longer previous attendance than those that did not return. My results corroborate those of Evans (1980), as the birds that had been seen only once in a year had lower probability of coming back to Boundary Bay. A large proportion of birds (>50%) showed little site fidelity to Boundary Bay within, and consequently between years. Both males and females were equally represented in this subset of the wintering population so it is unlikely that males in search of a mate were more mobile and more likely to disperse than females.

Pradel (1992) showed the presence of a large transient sub-population of Common Teal (*Anas crecca*) wintering in the Camargue, France. In his study, the sex-ratio of the transient component of the population fluctuated, and he hypothesized that unpaired birds were more likely to leave the area than paired individuals. Studies on waterfowl suggest that family units and paired birds are socially dominant for feeding (Lamprecht 1986; Black and Owen 1989) so that juveniles and unpaired birds might be forced to move. In fact, nonbreeders comprise 40-50% of the total population of Black Brant, a large proportion of which are adults (Sedinger et al. 1994). One thus would expect high movement rates as a consequence. It is also possible that some Brant with low philopatry may have occupied winter territories centered some distance from my observation site and that I documented their fidelity to peripheral, rather than core

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areas. Difficulty in reading bands in winter from locations other than Boundary Bay precluded conducting a multi state analysis which would have quantified the amount of movement between wintering locations (Nichols et al. 1993). However, some movement of radioed and legbanded birds between Boundary Bay and Padilla Bay, Lummi Bay and Birch Bay, Washington, was noted (Appendix 5; Appendix 6). Estimates of philopatry for the winter residents seen twice or more in a year are high (69.2%) and comparable to those found for other goose species (e.g. Raveling 1979; Hestbeck et al. 1991; Percival 1991; Prevett and MacInnes 1980). These results suggested that there was a stable resident population with a component of more mobile birds wintering in Boundary Bay.

3.4.2   Spring Philopatry

In both Boundary Bay and Qualicum, the models derived from the spring data set showed that there was class structure in survival rates. Again, classes refer to the time an individual was sighted for the first time in the area (1st class estimate is *local survival* between the year first seen and the next one while 2nd class estimate is *local survival* for subsequent years). Brant showed little first year philopatry for their spring stopover area (31.0 and 45.1% for the interval following the first sighting in Boundary Bay and Qualicum respectively) but those that returned in subsequent years showed a degree of philopatry higher than that of the winter residents (82.1 and 87.0% for Boundary Bay and Qualicum, respectively, vs. 71.4% for winter residents). Thus, there is a large proportion of transients in the spring population in any given year, but the birds that returned to Boundary Bay and Qualicum in later years developped a traditional attachment to their spring staging site and so were highly philopatric. Bean Geese (*Anser fabalis*) also showed high levels of site tenacity to a fall staging site in Sweden (Nilsson and Persson 1991) but comparisons with my study were not possible because they used return rates (which do not permit separate estimation of *local survival* and sighting rates) to estimate site fidelity. This result emphasizes the importance of spring staging areas on the life history of

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Brant. Ebbinge and Spaans (1995) showed that Dark-bellied Brent (*B. b. bernicla*) that had larger fat reserves during spring migration brought more juveniles back to the wintering areas the following year.

3.4.3 Comparison Between Sites

Local survival estimates for the spring period in Boundary Bay were consistently lower than those derived from the Qualicum data set. The difference in *local survival* between Boundary Bay and Qualicum spring transients could be attributed to a variety of factors. I can rule out the hypothesis that this difference is a consequence of the segregation of breeding units during migration because I found no significant differences in the origin of the banded birds present in winter and spring in Boundary Bay or those seen in Qualicum in spring. Birds from all five major breeding and molting locations were represented in the wintering and spring staging flocks. Habitat suitability could be responsible for the difference in *local survival*. However, the wintering population of Boundary Bay re-established itself in the past 5-7 years after being almost completely decimated 15 years ago (Campbell et al. 1990; Appendix 1, Fig. 7). Meanwhile, the wintering population of the Parksville-Qualicum area has not yet re-established after being decimated itself at about the same time. As well, recent expansion of the exotic eelgrass, *Z. japonica*, in Boundary Bay has greatly enhanced the food stock available for Brant (Baldwin and Lovvorn 1994). It does not compete with the native species, *Z. marina*, and Brant have shifted their diet to take advantage of this new food source (Baldwin and Lovvorn 1994). Thus habitat appears to have improved, or at least has not degraded, in Boundary Bay in recent years. The most likely explanation for the difference in *local survival* between these two sites in spring is the fact that there is a ten day hunting season on Brant in Boundary Bay in early March, whereas the Parksville-Qualicum area is closed to Brant hunting year round. Band returns show that both winter residents and spring transients are killed by hunters in Boundary Bay. There is some evidence that hunting is an additive mortality factor in goose populations (Francis et al.

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1992) and that survival estimates can be 5-10% lower in hunted than in non-hunted populations, which is the magnitude of the difference observed between *local* survival in Boundary Bay and Qualicum. Thus, the assumption of equal survival between populations may not hold. Also, disturbance due to hunting might be enough for some birds to emigrate permanently from the area, and again reduce the estimate of *local survival*. Therefore, hunting has the potential of influencing the dynamics of local populations as well as the genetic structure of those populations, if individuals subjected to hunting pressure permanently emigrate from the local population.

Unlike the Black Brant, Grey-bellied Brant show a high degree of segregation on their breeding, staging (Reed et al. 1989a) and wintering areas (Reed et al. 1989b). It is therefore not surprising that plumage characteristics (Boyd et al. 1988) and genetic structure (Shields 1990) of Grey-bellied Brant are different from Black Brant. The latter occupies a wide winter range and, as I have shown, mix extensively on both wintering and migration areas. Canada geese also show some plasticity in the choice of their wintering location depending on weather conditions in the northern parts of their winter range (Hestbeck et al. 1991) which likely induces high levels of gene mixing between the different sub-populations.

Black Brant are philopatric to some degree to their wintering and spring staging sites, however, large scale movements and the presence of transient birds make genetic arguments for the evolution of philopatry unlikely for this sub-species. Wintering and spring staging habitats show long term stability and predictability, therefore philopatry in the Black Brant likely evolved as a consequence of somatic (ecological) factors. However, I can not rule out the possibility that interbreeding populations cover a much larger area than my study area (e.g. Pacific Northwest population, Mexican population) and that those large aggregations of smaller wintering sub-units show different adaptations to the conditions encountered on the wintering areas. A large scale study would be needed to answer this question.

Chapter 4

Summary and Conclusions

4.1 Brant Abundance and Distribution

Brant were considered abundant in winter in the Lower Mainland of British Columbia, and particularly in Boundary Bay, between the turn of the 20th century (Fannin 1891) until the early 1930's (Cumming 1932). The number of Brant wintering in Boundary Bay remained high between 1940 and 1948, at which point there appeared to be a sharp decline (Appendix 1, Fig. 7). No comparisons with the early 1900's were possible due to lack of quantitative data. Brant were uncommon in winter during the early 1950's and, by 1965, wintering Brant had all but disappeared from Boundary Bay. It was not until the late 1980's that a recovery was detected, and the wintering population has now increased in numbers to levels comparable to those recorded during the 1940's (Appendix 1, Fig. 7).

The environmental changes that have occurred around the Lower mainland in the past century are mainly from anthropogenic sources but they have probably not affected the inter-tidal plant communities, on which Brant are highly dependent for food, to a large extent (Leach 1979). The negative effects that may have occurred have most likely been equalled by the positive effect of the introduction of Z. *japonica* in the last few decades (Baldwin and Lovvorn 1994). It is believed that the decline of Brant wintering in Boundary Bay was the result of over harvesting and human disturbances rather than the result of degradation of the habitat.

Black Brant wintering in Boundary Bay between 1992-93 and 1995-96 came from several breeding and moulting locations distributed over a large expanse of Arctic and sub-Arctic coastal areas of Russia, Alaska, and the Canadian Northwest Territories (Fig. 6). Although it was thought that Brant formerly wintering in Boundary Bay were part of the Canadian Arctic population (Leach 1979), it seems unlikely that it was the case. Support for this hypothesis came

from the banding and collaring of a number of Brant nesting on Prince Patrick, Melville, and Meglington Islands, Canada. Most band returns from this study came from the Puget Sound area in Northern Washington, thus the author concluded that birds using Boundary Bay, 60 Km. to the north, had to be part of the same population (Leach 1979). Subsequent studies have shown that Brant nesting on these islands were part of the Grey-bellied Brant population which are morphologically (Boyd et al. 1988) and genetically different (Shields 1990) from Black Brant. It was also shown that they were segregated on their wintering grounds in Puget Sound and that they were seldom reported in Boundary Bay (Reed et al. 1989b). Evidence from my study indicated that Grey-bellied Brant were sometimes seen in Boundary Bay during the winter, but always in small numbers (E.T. Reed, *pers. obs.*), and that they did not form the core of the local population. Also, hunter shot Brant seen on photographs from the early part of the century were all Black Brant (E.T. Reed, *pers. obs.*).

The main concentration of Grey-bellied Brant occurs in Padilla Bay, Washington, during the winter, but some Black Brant also occur in winter in that area (Reed et al. 1989b). Information from radio-marked Black Brant from Boundary Bay (Appendix 5) and sightings of marked individuals (Appendix 6) indicate that there is some exchange between Boundary Bay and Birch Bay, Lummi Bay and Padilla Bay in the winter or early spring. A similar pattern occurs with the Lesser Snow geese that spend part of the winter on the Fraser river Delta, BC, and part of the winter on the Skagit river Delta, just south of Padilla Bay, Washington (Boyd 1995). One Grey-bellied Brant banded in December 1995 in Boundary Bay was also recorded in Oak Harbour on the Olympic Peninsula in the spring of the same year. It is thus likely that Black Brant wintering in Boundary Bay have a relatively large home range that extends at least as far south as Padilla Bay, and maybe west to the Olympic peninsula, Washington. Also, one pair that wintered in Boundary bay in 1994-95 wintered in Dungeness, on the Olympic peninsula, Washington, in 1995-96 (E.T. Reed, *pers. obs.*), but band reading and radio tracking at

Dungeness during the 1994-95 and 1995-96 winters failed to detect any intraseasonal movements of individuals between this site and Boundary Bay.

4.2   Migration Patterns

There was no fall migration through Boundary Bay in 1994-95 or 1995-96 (Chap. 2). The birds that entered the area in November and December of these years were winter residents arriving from their last fall staging stopover area. The first fall arrivals occurred 11 days later in 1995-96 than in 1994-95 and there was no detectable movement of birds through the area until the arrival of the first spring migrants in mid-February 1995 and a week later in 1996. Thus Boundary Bay harboured, within a year, a fairly closed population during the winter.

My data supports the idea that Black Brant make at least one stop between their wintering grounds and Izembek Lagoon, Alaska, during the spring migration. I have evidence that some birds that wintered or staged in northern Washington later stopped in Boundary Bay during spring migration and that some birds seen in Boundary Bay were also seen in Parksville-Qualicum in the spring (R.I. Goudie, *unpubl. data*). The structure of the spring emigration model from Boundary Bay (Chap. 2) also suggests that some birds stay for a longer period of time in the study area during spring migration than others, and that this pattern is evident throughout the spring migration. It seems likely that birds have at least one spring staging site of importance along the Pacific coast of North America and any number of secondary sites where they only stop for brief periods of time before reaching Izembek Lagoon in Alaska.

The arrival of the first spring migrants in Boundary Bay in late February and early March coincided with the peak in mating activity (Black and Owen 1988) and pair formation (Owen et al. 1988) described for other species of geese. Spring migrants using Boundary Bay and Parksville-Qualicum likely wintered in areas located throughout the Pacific coast of North America, south of British Columbia. However, lack of data from other wintering areas precludes me from verifying that statement. To my knowledge, there is no evidence of segregation of

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winter flocks during spring migration in the Black Brant. The mixing of birds from various wintering locations during spring migration increases the opportunities for gene flow between those populations, unless mating is non-random. Assortative mating based on plumage characteristics has been observed in Atlantic Brant (Abraham et al. 1983) and in Lesser Snow Geese (Cooke et al. 1976). If mating is not a random process, then genetic integrity of interbreeding populations could arise even with low levels of philopatry. Also, the presence of migrants and residents in Boundary Bay at the time of pair formation does not necessarily mean that the genetic argument for the evolution of philopatry is rejected. If spring transients were highly philopatric and family integrity was maintained throughout spring migration (see Prevett and MacInnes 1980), then the genetic integrity of local interbreeding units would still be possible.

The timing and the location of the first contact between potential mates is more important that the actual pair formation event on the genetic structure of a population. This information is hard to obtain as usually the individual sighting rates, at least in large goose populations, are low and the efforts required to follow an entire population throughout the year (and its range) too high to provide useful information. Fragmentary data from Barnacle geese indicates that such contact between individuals that later form pairs sometimes occurs in late summer, on the moulting grounds (Owen et al. 1988). Thus the possibility that the interbreeding population is not the wintering or the spring staging populations exists.

4.3   Philopatry

Philopatry levels between 1992-93 and 1995-96 were low for winter residents in Boundary Bay, as an estimated 50% of the birds seen in any given winter, and that survived to the next, came back to winter in the area (Chap. 3). It is possible that I monitored philopatry in a peripheral area and that information from a core area would have given different results. However, I suspect that Boundary Bay was a core area for certain individuals since some radio-

marked birds were recorded in the vicinity of Boundary Bay on an almost daily basis while others were recorded sporadically (Appendix 5). Birds that showed high fidelity to Boundary Bay within a given winter were more likely to come back the following year. This tends to support the idea that birds using Boundary Bay in winter may also use several other locations to which they show different levels of fidelity. Thus, birds that had a better knowledge of the area were more likely to come back in the following winter.

The very low levels of philopatry following the first observation in the study area, both at Boundary Bay (31%) and at Qualicum (45%), would result in extensive gene flow if pairing actually occurred on the spring staging sites. Also, the fact that 12% of the marked Brant observed in Boundary Bay in 1995 were subsequently seen in other coastal locations of British Columbia indicates that there is some movement between spring staging sites, and that the possibilities for gene exchange are there. However, the high levels of philopatry exhibited by birds seen in two or more years shows that a traditional attachment to the site is formed.

Cooke et al. (1975) did not find any genetic differences among wintering populations of Lesser Snow Geese and therefore concluded that there was extensive gene flow among these populations. However, wintering populations of Atlantic Brant were segregated to some degree and genetic integrity of state wide populations was partly achieved (Novak et al. 1989). Genetic integrity of wintering populations does not mean that philopatry has evolved as a mechanism to promote inbreeding. If philopatry evolved for somatic reasons and the levels of fidelity exhibited by individuals of a given population were high, then genetic integrity could arise as a consequence, rather than the cause, of philopatry.

The difference in annual *local survival* between Boundary Bay and Qualicum during the spring migration was mainly attributed to hunting mortality and permanent emigration following hunting disturbances, but could also be due to differences in habitat suitability. The shift in distribution of wintering Black Brant, that occurred in the 1950's, between California and Mexico

was also attributed to increased human activities in California Bays (Denson 1964). My study provides the first quantitative indication of how such a shift in population could occur.

4.4   Causes and Consequences of Philopatry

Although I could not test directly what were the causes and the consequences of philopatry in the Black Brant, some inferences can be drawn from my results. They tend to suggest that the genetic arguments for the evolution of philopatry are not likely to be valid for the Black Brant. The genetic argument for the evolution of philopatry states that when, for similar adaptations, some gene complexes are incompatible, selection would favour inbreeding and philopatry (Greenwood 1987). I do not have information on inbreeding levels, but the low levels of philopatry tend to refute this argument. The coincident arrival of the first spring transients and the peak in pair formation in geese (Owen et al. 1988), as well as the low philopatry levels of winter residents and spring transients using an area for the first time, suggests that gene flow is extensive between Black Brant populations. On the other hand, the increased philopatry rates of birds that showed high intra annual fidelity to Boundary Bay in the winter, and the traditional attachment to spring staging sites, both tend to support the idea that prior knowledge of an area is an important determinant of philopatry. This information tends to support the somatic arguments for the evolution of philopatry in the Black Brant. However, to assess the importance of somatic factors, we would need to know what impact dispersal (or philopatry) has on survival or reproductive success of Black Brant. Also, knowledge of the age and the breeding status of the birds that are philopatric might provide some clear indication as to what influences an individual's decision to disperse or not.

The high levels of dispersal that I have documented have important consequences for the genetic structure and the dynamics of the Black Brant population. The wintering range of the Black Brant in North America covers a wide range of environmental conditions. One could expect birds wintering in Baja California or mainland Mexico to face different selective regimes

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than birds wintering in British Columbia or Alaska. For example, physiological adaptations to long distance migration could be expected in birds wintering in Baja and Mexico, whereas adaptations to cold environments, such as larger body size or higher metabolic rate, could be expected for birds wintering in the northern portions of the range. Therefore, latitudinal clines in specific morphological or physiological components could be expected. Latitudinal clines are a product of local evolutionary forces and gene flow between local populations. By counteracting the effects that selection might have on a local scale, by diluting the genes selected for with those from other areas under the influence of a different selective regime, gene flow can act as a buffer on natural selection (Rockwell and Barrowclough 1987). In the specific case of the Black Brant, local adaptation or latitudinal clines are not likely to occur because of the high levels of gene flow resulting from the mixing of birds from different wintering and breeding locations throughout the year. It is possible, however, that Black Brant are philopatric to a larger area than my study area, and that genetic integrity is partly achieved on a large scale.

The population dynamics of the Black Brant, given the high levels of dispersal from the wintering and spring staging grounds, is likely to be affected by global, rather than local, scale effects. The rate of increase of the population wintering in Boundary Bay could not be accounted for by recruitment of juveniles in the population alone (Chap. 3). The high levels of dispersal between years, coupled with the fact that the local population has expanded during my study, indicates that there is significant immigration of birds from other wintering locations in the area. Therefore, the dynamics of the wintering and spring staging populations is likely to be highly dependent on factors occurring outside of the study area.

4.5   Management Implications

The management of Brant in Boundary Bay, BC, has been a subject of controversy over the years. My study provides the first quantitative data on *local survival* of Brant using this area

and on the precise timing of migratory events. Many censuses had been previously conducted and the timing of the migratory events had been estimated from those with reasonable precision.

The focus of Brant management in Boundary Bay has been on protecting the wintering population since 1977, when the hunting season was restricted to the first ten days of March (Munro 1979). At that time, the number of Brant seen in Boundary Bay during the winter had reached historically low levels (Campbell et al. 1990; Appendix 1, Fig. 7). However, nothing was known of those birds seen during the winter and the existence of a distinct winter residents population in Boundary Bay remained controversial. My study showed that birds seen between the first fall arrivals (early November) until at least the second week of February were resident birds with few, if any, transients showing up in any given winter. The winter population is, at its actual level, too small to sustain hunting pressure on its own and, as long as this winter resident population remains small, the potential of holding a fall hunt instead of a spring hunt will be non-existent. Thus, the spring hunt remains the only viable option for this particular population if hunting is allowed to continue. However, if migration is late in certain years, the impact on winter residents could be high and have detrimental effects on the population dynamics. Therefore, the timing of spring migration in Boundary Bay should be closely monitored, and, in years when migration is late, a temporary closure at the beginning of the season might be appropriate. If possible, a ten day 'floating' season starting no earlier than 1 March might be implemented. The opening of such a season would occur when sufficient numbers of migrants are present in Boundary Bay. This would probably be a good compromise for both naturalist's and hunter's interests in the Lower Mainland of British Columbia.

There appears to be some movement of Brant between Boundary Bay and Padilla Bay, Washington, during the winter and in early spring. Brant hunting in the State of Washington is restricted to Samish County and was held in December during my study. One bird banded in December 1995 in Boundary Bay was shot in Padilla Bay a few days later. This means that some winter residents from Boundary Bay are subjected to two hunting seasons within a year, and

potentially to subsistence hunting by native people on the breeding grounds. The hunter kill in Padilla Bay is mostly composed Grey-bellied Brant in normal years (M. Davison, *pers. com.*). However, in the 1995-96 season, an estimated 8 000 Grey-bellied Brant were missing (M. Davison, *pers. com.*) in Padilla Bay. A similar pattern was also noted in 1996-97 (D.H. Ward, *pers. com.*). With a hunting pressure of the same intensity and the number of Grey-bellied Brant diluted, Black Brant are likely to have suffered from increased hunting mortality. To determine the impact that this has on birds using Boundary Bay, the amount of movement of birds between Boundary Bay and the Padilla Bay area during the winter should be monitored closely.

Black Brant do not disperse randomly on the wintering grounds, and although the philopatry levels are probably too low to lead to genetic integrity of the local populations, it is important for the dynamics of these populations. Because of increased isolation due to philopatry, the winter resident population of Boundary Bay is more prone to local extinction (Levins 1970; Gadgil 1971). Furthermore, interannual *local survival* rates were shown to differ between Boundary Bay and Qualicum Beach (a non-hunted area) and this difference may be attributed to hunting mortality and/or emigration (Chap. 3). Hunting pressure in Boundary Bay may be slowing the population recovery process by lowering the survival and/or increasing the dispersal of winter residents to other wintering areas. Factors occurring outside Boundary Bay will be as important in determining the dynamics of this population, given the high number of immigrants in each year.

Approximately 196-250 Brant were shot and retrieved in the Lower Mainland of British Columbia each year between 1994-95 and 1995-96 (Appendix 3) and, according to information from band returned by hunters, approximately 14% of the marked birds taken during the hunting season were winter residents (Appendix 4). If we assume that marked Black Brant are representative of the entire population in regards to behaviour, hunting mortality and return rates, then approximately 27-35 winter residents are harvested each year. This represents a low figure and should not cause a marked decline in the wintering population (at least 600 ind. in 1995-96,

Fig. 2). However, crippling rates are known to be high in Brant (Kirby et al. 1983), and the potential effects on survival and reproductive success must not be overlooked.

Brant wintering and spring staging in Boundary Bay are an amalgamation of birds from most major breeding and moulting areas (Fig. 6). The concerns for the local segment of the population thus have implications for the entire Pacific Flyway brant population. The migration patterns of brant documented here are likely to be representative of the whole Pacific coast of North America, allowing managers the possibility to establish regulations appropriate for both wintering and spring staging stocks when local concerns arise.

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Appendix 1. Past and Present Winter Population Trends

Unpublished reports and occasional surveys were used to develop a perspective on Brant abundance in Boundary Bay. I used data from surveys conducted by M.W. Holdom at Crescent Beach in Boundary Bay, between the 1939-40 and 1964-65 seasons. Data drawn from the Vancouver bird reports were used for the 1970-71 season and a series of Brant surveys conducted during the winter in Boundary Bay and Roberts Bank were used to cover the 1977-78 to 1979-80 seasons (Jury 1980). Data from winter reports (American Birds) was available, intermittently, between 1971-72 and 1989-90. Data are scant for that period and thus the estimates may not be accurate. Finally, data from the present study was used to estimate population size between 1992-93 and 1995-96.

I compared those population estimates with data available from the Audubon Society's Christmas Bird Count (CBC). I used CBC counts from Crescent Beach between 1937 and 1959 (*in* Canadian Field Naturalist) and from Ladner between 1965 and 1995 (*in* American Birds). These counts are conducted each year during the last two weeks of December.

Assuming that the migration and overwintering patterns were similar to those recorded in Boundary Bay in 1994-95 and 1995-96 (see chap. 2), I used all the counts made prior to 8 February to estimate population size of the wintering population. I did not try to estimate the size of the spring staging populations because of the high turnover rate of individuals at that time of year. It is doubtful that the historical data would have been complete enough to provide a useful index for that part of the year.

The maximum number and the mean number of Brant observed during the winter period were positively correlated ($r^2 = .91$, $P<.0001$). Therefore I used the maximum number of Brant observed during a winter as the population size (Fig. 7) index because I felt that it represented more closely true population size.

Appendix 1 continued...

CBC data was also positively correlated with the maximum number of Brant recorded by naturalists and researchers surveys (r^2 = .32, P<.003). Therefore, they seem to be a good indicator of the size of the wintering population (Fig. 7).
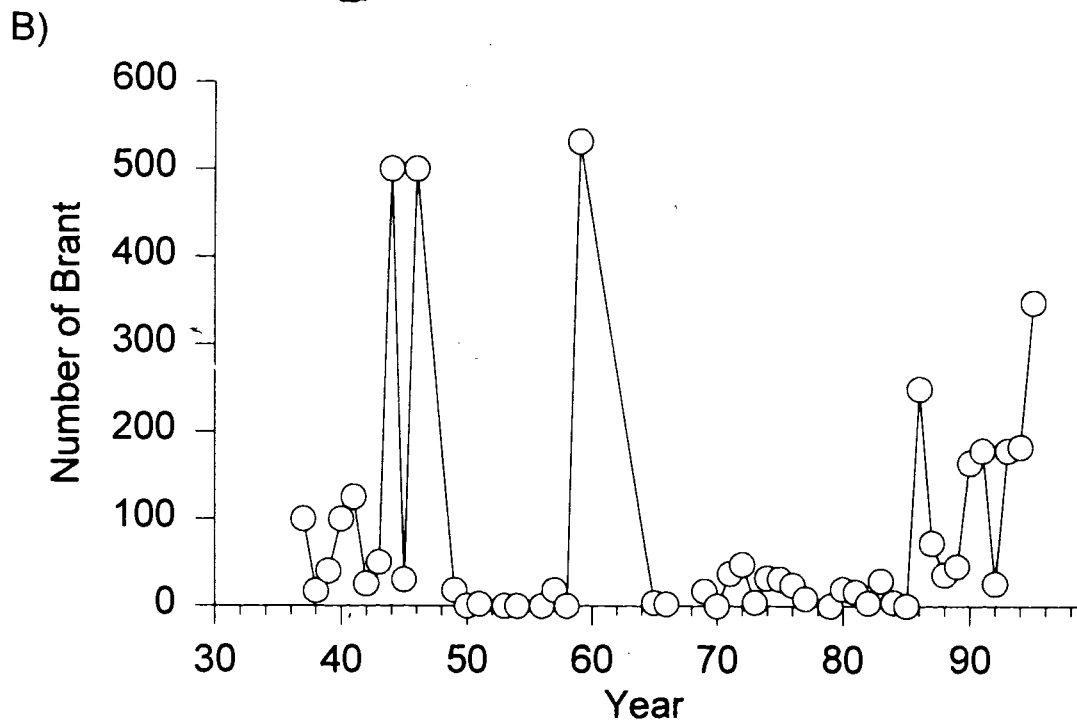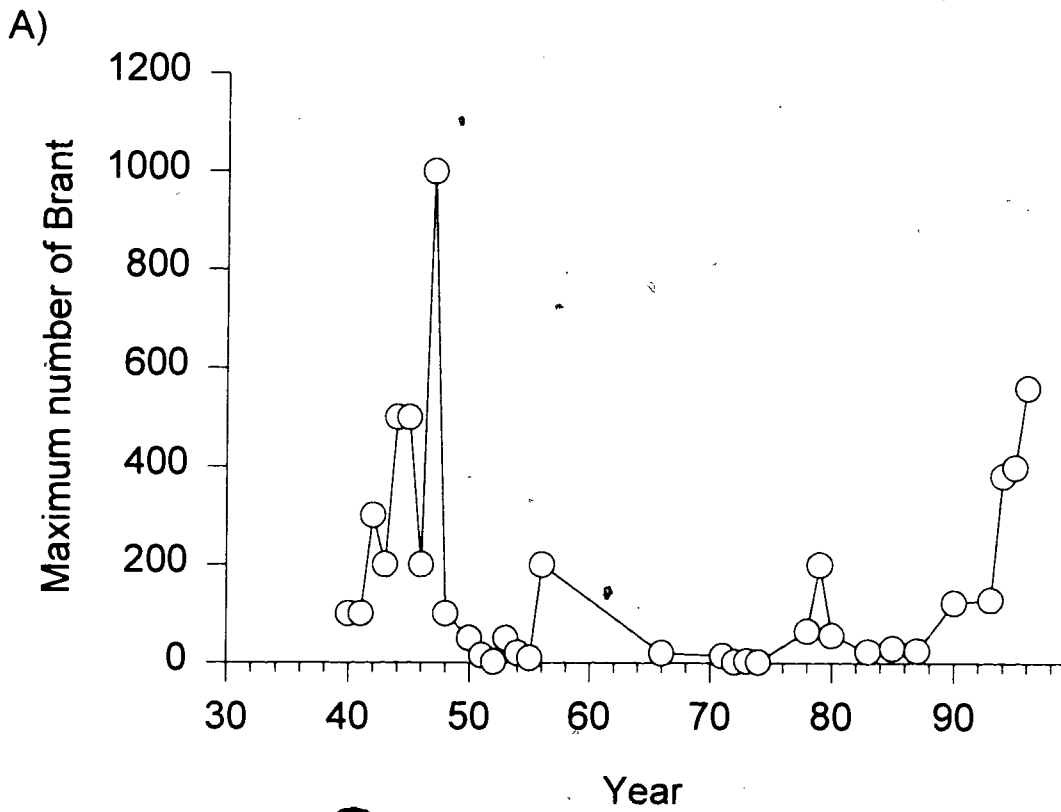
Figure 7. Population trends of Brant in Boundary Bay during the winter period (1 November to 7 February) A) based on the maximum daily number of Brant recorded during the winter by naturalists and researchers, and B) based on Christmas Bird Counts.

Appendix 2. The Effects of Heterogeneity in Capture (Sighting) Rates on Model Selection and on *Local Survival* Estimates

We created data sets that simulated the effects of heterogeneity of capture rates on model selection and *local survival* estimates. We varied the number of occasions (5, 8, and 11 sighting occasions) and the amount of heterogeneity in order to determine which variable was more sensitive to heterogeneity. At each sighting occasion, 100 individuals were released, half of which had a high resighting rate (p=0.65) and half a low resighting rate (p=0.05, 0.25, 0.45, 0.65). *Local survival* was held constant over time at 0.80. Only one value of low resighting rate was used in each data set, therefore, the bigger the difference between the high and the low resighting rate, the greater the heterogeneity in sighting rates was. Each data set thus consisted of 10 simulation runs for a given low p and a given number of occasions.

The capture histories were analyzed using program RELEASE to see if heterogeneity in sighting rates could be responsible for the rejection of the basic assumptions of the CJS model. We also documented which of the sub-tests in program RELEASE were affected by heterogeneity. We then used program SURGE to estimate *local survival* under model ϕ, p (which is what we simulated for) and a model with class (or age) structure ($\phi_{a2}*_t$, p), which would likely be used as a general starting model if CJS was rejected.

Assumptions of the CJS Model

The overall test on the assumptions of the CJS model were rejected for all number of occasions when heterogeneity was high (p_{low}=.05 and .25). As a rule, all the sub-tests given in the RELEASE output were affected significantly by high levels of heterogeneity (p_{low}=.05 and .25). When heterogeneity was still present, but at a lower intensity (p_{low}=.45), only the data sets with the higher number of occasions (8 and 11) were affected. The overall results of RELEASE indicated that the assumptions of CJS were not met for those two data sets. Of all the sub-tests of RELEASE, only test3.sr was not affected when the low sighting rate was 0.45, whatever the

number of occasions was. Finally, when the low sighting rate was equal to the high sighting rate (p=.65, no heterogeneity) the data met the assumptions of the CJS model.

Low P	# occ.	3.SR	3.SM	2.CT	2.CM	total
	5	$\chi^2_{30}=579.65$ p=.0000 (100)	$\chi^2_{27}=9.16$ p=.9995 (20)	$\chi^2_{20}=30.33$ p=.0647 (30)	$\chi^2_{10}=5.66$ p=.8430 (10)	$\chi^2_{87}=624.80$ p=.000 (100)
.05	8	$\chi^2_{60}=1596.78$ p=.0000 (100)	$\chi^2_{101}=147.69$ p=.0017 (40)	$\chi^2_{50}=216.03$ p=.0000 (100)	$\chi^2_{54}=122.72$ p=.0000 (60)	$\chi^2_{265}=2083.22$ p=.0000 (100)
	11	$\chi^2_{90}=2759.08$ p=.0000 (100)	$\chi^2_{190}=357.85$ p=.0000 (80)	$\chi^2_{80}=604.70$ p=.0000 (100)	$\chi^2_{150}=430.45$ p=.0000 (100)	$\chi^2_{510}=4152.08$ p=.0000 (100)
	5	$\chi^2_{30}=106.94$ p=.0000 (100)	$\chi^2_{40}=56.24$ p=.0457 (40)	$\chi^2_{20}=19.96$ p=.4604 (10)	$\chi^2_{10}=17.12$ p=.0718 (30)	$\chi^2_{100}=200.26$ p=.0000 (70)
.25	8	$\chi^2_{60}=319.71$ p=.0000 (100)	$\chi^2_{150}=255.22$ p=.0000 (80)	$\chi^2_{50}=199.87$ p=.0000 (100)	$\chi^2_{74}=102.99$ p=.0146 (30)	$\chi^2_{334}=877.79$ p=.0000 (100)
	11	$\chi^2_{90}=372.29$ p=.0000 (100)	$\chi^2_{308}=613.29$ p=.0000 (90)	$\chi^2_{80}=653.98$ p=.0000 (100)	$\chi^2_{205}=356.55$ p=.0000 (90)	$\chi^2_{683}=1996.11$ p=.0000 (100)
	5	$\chi^2_{30}=37.31$ p=.1638 (20)	$\chi^2_{40}=44.23$ p=.2976 (10)	$\chi^2_{20}=15.30$ p=.7590 (10)	$\chi^2_{10}=4.48$ p=.9231 (0)	$\chi^2_{100}=101.32$ p=.4443 (10)
.45	8	$\chi^2_{60}=56.77$ p=.5945 (20)	$\chi^2_{165}=198.83$ p=.0372 (20)	$\chi^2_{50}=121.69$ p=.0000 (60)	$\chi^2_{64}=72.94$ p=.2077 (20)	$\chi^2_{339}=450.23$ p=.0000 (50)
	11	$\chi^2_{90}=89.94$ p=.4820 (10)	$\chi^2_{293}=385.93$ p=.0002 (50)	$\chi^2_{80}=185.75$ p=.0000 (90)	$\chi^2_{137}=163.38$ p=.0616 (10)	$\chi^2_{600}=825.00$ p=.0000 (70)
	5	$\chi^2_{30}=27.89$ p=.5763 (10)	$\chi^2_{40}=34.12$ p=.7314 (0)	$\chi^2_{20}=16.98$ p=.6543 (20)	$\chi^2_{10}=10.36$ p=.4095 (10)	$\chi^2_{100}=89.35$ p=.7685 (0)
.65	8	$\chi^2_{60}=67.89$ p=.2263 (10)	$\chi^2_{124}=130.52$ p=.3266 (30)	$\chi^2_{50}=27.11$ p=.9966 (0)	$\chi^2_{40}=35.21$ p=.6855 (0)	$\chi^2_{274}=260.73$ p=.7081 (0)
	11	$\chi^2_{90}=76.15$ p=.8509 (10)	$\chi^2_{249}=228.67$ p=.8178 (0)	$\chi^2_{80}=76.31$ p=.5961 (20)	$\chi^2_{77}=76.20$ p=.5043 (0)	$\chi^2_{496}=457.33$ p=.8925 (10)

Survival Estimates

Local survival was underestimated when heterogeneity was present. The bigger the difference between high resighting (.65) and low resighting, the more the survival rate was underestimated. Also, the more sighting occasions there was, the closer the estimates of survival were from the real value of survival. Therefore, short-term studies with few sighting occasions are likely to suffer much more estimate bias if heterogeneity in capture rates is present than long term studies would.

# Occasions	Low Resighting	*Local Survival* Rate
	.05	.6233
5	.25	.7342
	.45	.7827
	.65	.7973
	.05	.6625
8	.25	.7572
	.45	.7899
	.65	.7982
	.05	.6965
11	.25	.7703
	.46	.7906
	.65	.8010

When a class-model was applied to the same data, the same pattern as for model (ϕ, p) was apparent for estimates of the first class. *Local survival* was underestimated, and the bigger the difference between the high and the low resighting rate, the more *local survival* was underestimated. Again, data sets which had more sighting occasions were not as biased as those with few sighting occasions. However, these first class estimates were biased much lower than

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those of the previous model. As Loery et al. (1987) showed, the estimates for the second class were not affected by heterogeneity.

# Occasions	Low Resighting Rate	*Local Survival* class1	*Local Survival* class2
	.05	.4774	.7907
5	.25	.6698	.7825
	.45	.7673	.8010
	.65	.8051	.7914
	.05	..4789	.8014
8	.25	.6755	.7989
	.45	.7792	.7998
	.65	.8048	.7989
	.05	.5140	.8007
11	.25	.7009	.8015
	.45	.7817	.7961
	.65	.8003	.8018

Appendix 3. Brant Harvest in the Lower Mainland of British Columbia in 1994-95 and 1995-96.

Brant hunting season was restricted to 1 to 10 March in both years. I surveyed the Brant hunt 7 out of the 10 possible days in both 1994-95 and 1995-96 in Boundary Bay and in Roberts Bank. A telephone survey, at the end of the hunting season, was also carried out in 1994-95. On each survey, I noted the number of boats and shore hunters present in Boundary Bay and Roberts Bank separately in order to estimate hunting pressure for the entire season. I checked 75 Brant collected by hunters in 1994-95 and 103 in 1995-96 and determined the age, sex and the presence of bands when possible. Also, when possible, I recorded the number of hunters present.

1994-95

Hunting pressure
B. Bay => 27 boats/7 days = 3.9 boats/day
       3.9 boats/day X 10 days = 39 boats for the season
       # hunters: 23 hunters/3 days = 7.7 hunters/day

R. Bank => 26 boats/7 days = 3.7 boats/day
       3.7 boats/day X 10 days = 37 boats for the season
       # hunters: 45 hunters/6 days = 7.5 hunters/day

Harvest
B. Bay => By boat:
       45 Brant/20 boats = 2.25 Brant/boat
       2.25 X 39 boats = 88 Brant
     By hunter:
       31 Brant/23 hunters = 1.35 Brant/hunter
       1.35 X 77 hunters = 104 Brant

R. Bank => By boat:
       47 Brant/19 boats = 2.47 Brant/boat
       2.47 X 37 boats = 91 Brant
     By hunter:
       45 Brant/37 hunters = 1.21 Brant/hunter
       1,21 X 75 hunters = 91 Brant

Brunswick point => 1 Brant shot
Semihamoo Bay => closed to hunting. 14 Brant were collected for contaminant study.

Estimated harvest: 180-196 Brant have been shot in B.C. this year. A phone survey gave me a total of 181 birds. Knowing that I didn't reach everybody, I think that 196 Brant is the best estimate. To that we have to add the 14 birds collected in Semihamoo.

Age composition of harvest
9 juveniles were shot out of 108 birds for a percentage of 8.33 %. During the winter, the percentage of juveniles was estimated at 5.3%.

Appendix 3 continued...

Band return

Four bands were returned by hunters, all from birds shot in Roberts Bank. Over the duration of the hunting season, 7.22% of the Brant observed hauled out at Beach Grove, Boundary Bay, were marked. When adjusted for age, 7.07% of the adults and 0.15% of the juveniles were banded.

Estimated number of banded birds in harvest

8.33% juveniles killed with total harvest of 196 birds => 16 juveniles killed
bands on juveniles expected: 0.15% X 16 = 0.02
Adults: 196 - 16 juv. = 180 adults killed
bands on adults expected: 7.07% X 180 = 12.76

Total # of bands expected: 12.76 + 0.02 = 13

Recovery rate: 4/13 x 100 = 31%

1995-96

Hunting pressure

Boundary Bay: 31 boats and 4 shore hunters / 5 days of survey
=> 6.2 boats/day and 0.8 shore hunters/day
=> 12 hunters/day => 120 hunter day

Roberts Bank: 39 boats / 7 days
=> 5.6 boats/day => 110 hunter day

Brunswick Point => no Brant shot
Semihamoo Bay => closed to hunting

Estimated harvest

The hunter survey and my calculations were consistent, and I determined that 250 Brant were harvested. The harvest was equally separated between Roberts Bank and Boundary Bay and 7 grey-bellied Brant were taken in Boundary Bay.

Sex and age composition of harvest

20.4% juveniles (n=103 birds checked) in the harvest
adult sex ratio: 1.16 males: 1 female (n=54 birds)
juvenile sex ratio: 1 male: 1.67 female (n=11 birds)
total sex ratio: 1 male: 1.03 female

Band return

11 bands were returned by hunters in 1995-96. Four of those birds were shot in Boundary Bay and 7 in Roberts Bank.

Appendix 3 continued...

Estimated number of banded birds in harvest
250 X 7.50% (estimate of percentage of banded birds in the population) = 19 bands

Recovery rate: 11 bands / 19 bands = 58% band return

Appendix 4. Marked Individuals Shot by Hunters in Boundary Bay (BB) and Roberts Bank (RB), BC, from 1994 to 1995.

Sightings within the year of death are shown. One individual, captured in Boundary Bay and subsequently shot in Padilla Bay (PB), Washington, in 1995-96, is also mentionned. BB = Boundary Bay, RB = Roberts Bank, PB = Padilla Bay.

Individual's code	Date Shot	Prior Sightings
BHZR	BB 05-03-94	
BRL5	BB 05-03-94	BB 17-12-93
		BB 12-01-94
		BB 26-01-94
		BB 05-02-94
		BB 17-02-94
WT29	BB 05-03-94	
WSGY	BB 10-03-94	
GK82	RB 10-03-94	
Y54L	BB 10-03-94	
Y56R	BB 10-03-94	
AG7Y	RB 06-03-95	BB 16-02-95
		BB 04-03-95
WKN2	RB 09-03-95	
WKE9	RB 09-03-95	
OAHK	RB 09-03-95	BB 26-11-94
		BB 13-12-94
		BB 19-01-95
		BB 27-01-95
Y008	PB ??-12-95?	BB 15-12-95
		BB 01-01-96
GSVK	RB 01-03-96	
BZHR	RB 06-03-96	
W6NS	RB 06-03-96	BB 17-12-95
		BB 19-02-96
BLE2	RB 07-03-96	
GG03	RB 08-03-96	
GG7A	RB 08-03-96	
AN86	BB 09-03-96	
GLGN	BB 09-03-96	
GV90	BB 09-03-96	
GVEN	RB 10-03-96	
W397	BB 10-03-96	

Appendix 5. Time and Locations of Radio-marked Brant (1995-96)

BB = Boundary Bay, offshore; BG = Beach Grove area, Boundary Bay; LB = Lummi Bay, Washington; PB = Padilla Bay, Washington. Stars indicate that the legband was seen and that the radio had failed.

Code	Y001	Y004	Y006	Y007	Y072	Y008	Y010	Y011	Y013	Y014	Y029
	BG 15-12-95	BG 15-12-95	BG 15-12-95	BG 15-12-95	BG 15-12-95	BG 18-12-95	BG 18-12-95	BG 18-12-95	BG 18-12-95	BG 18-12-95	BG 18-12-95
	BB 20-12-95	RB 16-12-95	BB 16-12-95	BB 16-12-95	BB 18-12-95	BB 20-12-95	BG 12-02-96		BB 16-02-96	BG 19-12-95	
	BG 16-01-96	RB 17-12-95		BG 17-12-95	BG 18-12-95	PB ??-12-95			BB 20-02-96	BG 20-12-95	
	*					SHOT					
		BB 17-12-95		BG 18-12-95	RB 16-01-96				PB 20-02-96		
		RB 19-12-95		BG 20-12-95	BB 16-01-96						
		BG 21-12-95		BG 21-12-95	RB 17-01-96						
		*									
				BG 06-01-96							
				BG 07-01-96							
				BG 10-01-96							
				BB 14-01-96							
				BB 16-01-96							
				BB 25-01-96							
				BB 29-01-96							
				BB 02-02-96							
				BB 12-02-96							
				BB 16-02-96							
				LB 20-02-96							

Appendix 6. Intra- and Inter-annual Interchange of Marked Individuals in Washington and British Columbia

BB = Boundary Bay, BC; BI = Birch Bay, WA; OP = Northeast Olympic Peninsula (Dungeness and east), WA; PB = Padilla Bay, WA; PR = Point Roberts, WA; RB = Roberts Bank, BC

Intra-annual

Band #	where	date	where	date	comments
ATZ9	OP	10-2-96	PR	12-4-96	
AASE	OP	20-3-96	BB	19-4-96 25-4-96	Migration
Y006	OP	16-3-96	BB	15-12-95 21-12-95	WINTER- SPRING
W25A	OP	16-11-95	OP	16-3-96	
WNR6	OP	16-11-95	OP	16-3-96	
W1H8	OP	10-02-96	OP	23-03-96	
WT91	OP	4-4-96	BB	25-4-96	Migration
WYZR	OP	14-4-96	BI	24-4-96	Migration
WGGA	OP	4-22-93	BB	19-12-93 19-1-94	WINTER SPRING
WGR4	OP	4-22-93	BB	19-12-93 20-12-93 30-12-93 19-1-94	PAIRED WITH GGA
GL5Y	PB	11-28-92 12-27-92	BB	26-3-93	
GLK7	PB	11-28-92 12-27-92	BB	26-3-93	
AGS0	PB	21-3-96	BB	3-2-95 4-2-95 11-1-96 2-1-96 25-1-96	BB-WASH
W869	PB	21-3-96	BB	21-11-95 24-11-95 2-1-96	BB-WASH

Appendix 6 continued...

<u>Inter-annual</u>

BAND #	WHERE	DATE	WHERE	DATE	COMMENT
Y4NV	RETSIL	7-4-94	BB	20-3-95	
		18-4-94		22-3-95	
				23-3-95	
				16-3-96	
				20-3-96	
Y6Y3	RETSIL	11-4-94	BB	26-1-95	BB-WASH.
		25-4-94		9-2-95	
RA1S	PB	17-11-92	BB	27-2-95	BB-WASH.
GA3T	MANCHESTER	7-4-94	BB	13-3-95	
OAHK	PB	17-11-92	BB	15-12-93	WINTER
				17-12-93	BB-WASH
				18-12-93	
				19-12-93	
				20-12-93	
				10-1-94	
				12-1-94	
				23-1-94	
				<u>25-2-94</u>	
				26-11-94	
				13-12-94	
				19-1-95	
				27-1-95	
			RB	9-395SHOT	
OAKR	PB	17-11-92	BB	<u>16-12-94</u>	WINTER
				24-12-95	BB-WASH
				6-1-96	
				12-1-96	
				8-2-96	
				31-3-96	
			PR	21-3-96	
WEZR	SOUTH COLBY	25-4-94	BB	12-1-96	
AG6T	PB	28-11-92	BB	3-2-95	WINTER
				14-2-95	BB-WASH
				21-3-95	

WGGA	OP	22-4-93	BB	13-12-94	WINTER
				14-12-94	SPRING BB-
				20-12-94	WASH
				29-12-94	
				31-12-94	ALSO IN
				2-2-95	WITHIN YR
				9-2-95	
				15-2-95	
				6-2-97	
WGR4	OP	22-4-93	BB	13-12-94	WINTER
				14-12-94	SPRING BB-
				29-12-94	WASH
				31-12-94	
				2-2-95	
				9-2-95	ALSO IN
				15-2-95	WITHIN YR
				6-2-97	
RGSK	DOSEWALL	20-4-94	BB	19-4-96	
				26-4-96	
WKSV	MANCHES	20-4-94	BB	19-1-95	
				2-2-95	
				14-2-95	
				17-3-95	
				2-4-95	
				4-4-95	
				17-4-95	
WLY0	JORSTEAD CREEK	24-3-95	BB	25-3-96	
GRG8	OP	22-4-93	BB	1-1-95	
GT9L	PB	17-11-92	BB	28-2-95	WINTER BB
				17-3-95	AND
				12-4-95	PADILLA
				13-4-95	
				20-12-95	
GTNT	DOSEWALL	20-4-94	BB	23-4-96	
			PR	12-4-96	
WTVV	OP	28-2-95	BB	24-2-97	
		10-3-95			