MOVEMENT PATTERNS AND POPULATION STRUCTURE OF HARLEQUIN DUCKS WINTERING IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

September 2003

APPROVAL

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Degree: Doctor of Philosophy

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ABSTRACT

I investigated winter movement patterns and population structure of Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia, Canada. Because of winter pairing, delayed maturation, and long-term pair bonds, movement patterns at wintering areas, particularly those of young birds that have not yet paired, are important to population structure. I used nasal- and radio-marking to determine movement distances, and multi-stratum models in capture-mark-recapture analysis to estimate movement rates among locations.

I provide evidence that Harlequin Duck broods accompany their mothers from breeding streams to coastal wintering areas. Behavioural observations of family-like groups at the coast, and genetic analysis of blood samples from putative family members, suggested that observed groups were true families. Family migration in combination with philopatry, in the absence of dispersal, would lead to juvenile recruitment into the wintering populations of their relatives, and potentially to genetic and demographically isolated populations.

Winter movement distances and rates did not differ by sex, likely due to extreme philopatry of paired males, slightly reduced philopatry of unpaired males, and intermediate philopatry of previously paired females. However, they did differ by age, with young birds in their first and second winters dispersing greater distances and at higher rates than older individuals. Isolation by distance and stepping stone gene flow models generated estimates for the among population component of genetic variance of less than 1% for the Strait of Georgia. Thus, due to dispersal of young individuals, which counteracts the isolating effects of philopatry and family migration, groups of Harlequin Ducks are unlikely to be genetically distinct at this scale. However, estimates from the stepping stone model for an increased number of colonies did suggest that, due to their linear coastal distribution, genetic differences could develop at the scale of their entire west coast of North America wintering range. Low movement rates between the northern and southern Strait of Georgia suggested that groups of wintering birds may be demographically distinct at this scale, and dispersal by both sexes indicated that recolonization or rescue of extinct or reduced groups is likely.

This work is dedicated to the wild lives whose planet we share,
to the wild places they inhabit, and to their conservation.

ACKNOWLEDGEMENTS

This study would not have been possible without the contributions and support of a great many people. First I thank my supervisor, Fred Cooke, for giving me the opportunity for this study, for his interest, enthusiasm and support throughout all of its stages, and for procuring the funding that made it possible. I am especially grateful for his ability in helping me clarify my thoughts and objectives, and helping me to see a problem and the route to its solution in a more direct way. I have become a better scientist as a result. It was a great pleasure to work with a supervisor as supportive as Fred.

I also thank my other committee members, Sean Boyd, Felix Breden, and Dan Esler for their enthusiasm, interest, and time, and for their helpful and thought-provoking comments and discussions. I am grateful for their careful and critical reviews that greatly improved all aspects of this thesis. I am also grateful to Sean for donating radio transmitters and for instruction in attachment technique, to Felix for his advice with genetic analyses and population structure, and to Dan for taking such an interest in my work and joining my committee when he became part of the Centre for Wildlife Ecology. Working with all of the members of my committee has been a most enjoyable and rewarding experience.

I am deeply grateful to Carl Schwarz and Barry Smith for their invaluable help with multi-stratum mark-recapture analyses. I could not have learned all that I did without their help. I especially thank Carl for helping me to understand design matrices and for our many discussions. I am especially grateful to Barry for teaching me his goodness of fit technique and generously providing me with his program, and for devoting so much time to my questions. Both gave generously of their time and expertise, and were always available when I needed help.

I am grateful to Kim Scribner who accepted blood samples from juvenile Harlequin Ducks for analysis in his lab. I thank him also for discussion and advice regarding the results.

I thank my fellow graduate students for their friendship and discussion; I especially thank Matt Evans, Lesley Evans-Ogden, Carina Gjerdrum, Sam Iverson, Michael Rodway, Pippa Shepherd, and Laura Tranquilla. I also thank Alton Harestad for encouragement and advice.

The field work for this study required the capturing, marking, and resighting of many Harlequin Ducks. A large number of researchers and volunteers contributed time and energy to this project, and although I could not possibly list them all, I am grateful to every one of them. I especially thank Brian Arquilla, John Ashley, Cordula Baumbach, Rachel Botting, Sean Boyd, Lynn Campbell, Pete Clarkson, Fred Cooke, Frank Elkins, Mary Jane Elkins, Dave Genter, Ian Goudie, Janet Hardin, Stuart Jackson, Greg Robertson, Michael Rodway, Cyndi Smith, Richard Swanston, and Ken Wright. In particular, Pete Clarkson, Stuart Jackson, Michael Rodway, and

Ken Wright devoted a tremendous amount of time and energy to capturing and sighting Harlequin Ducks in the northern Strait of Georgia - this study would not have been possible without the efforts of these dedicated individuals. I thank Ian Goudie for initiating the banding project in 1993. I am grateful to Mary Jane Elkins and Frank Elkins for their generous hospitality on Hornby Island. I thank the Canadian Wildlife Service for providing equipment necessary for boat surveys, and I am grateful to Moira Lemon for making the use of this field equipment so easy for me. Special thanks go to Connie Smith for data management and for taking care of logistics such as banding permits and equipment. I also thank Sylvia Foran, Judy Higham, Marlene Nguyen, and Barb Sherman for administration.

I am grateful to Alan Afton, Jim Anderson, Todd Arnold, Brian Arquilla, Sean Boyd, Felix Breden, Fred Cooke, Dan Esler, Julian Fischer, Ian Goudie, Glen Mittelhauser, Arne Mooers, Michael Rodway, John Smallwood, Jean-Pierre Savard, Cyndi Smith, Peter Vickery, and several anonymous reviewers for critical reviews that greatly improved this thesis.

I thank the organizations that contributed funding to make this study possible. Funding was provided by the National Science and Engineering Research Council (NSERC) of Canada, Centre for Wildlife Ecology, Simon Fraser University, British Columbia Waterfowl Society, Institute of Waterfowl and Wetlands Research (IWWR), and the Canadian Wildlife Service.

I am grateful to my family for their encouragement and friendship. Their support throughout this program has been invaluable. I thank my father, Jacob Regehr, for his unwavering support of my choices and my dreams. I thank my sister, Vera Charles, my niece, Tiffany Haussermann, and my nephew, Dylan Haussermann, for their warmth and laughter. I thank my brother, Martin Regehr, and my sister-in-law, Vivian Lan Lai, for their devoted friendship. I also thank my brother, Martin, for his generous help with programming which simplified the manipulation of huge data files. I am grateful also to my mother, the late Gudrun Regehr, for sharing her passion for nature and for life. I thank Arleigh Rodway, Don Rodway, Colleen Moore, and Dan Rodway for their kindness, friendship, and generous hospitality.

Most of all I thank Michael Rodway for sharing all of this with me. I am grateful to have been able to share with him all of the pleasures, excitement, and frustrations of field work, data analysis, and writing. I thank him for the weeks spent in a zodiak during mid-winter, in the often stormy, wet, and cold northern Strait of Georgia. Without his boating expertise, our mid-winter surveys could not have been accomplished. I am grateful for our endless discussions, for his critical reviews of my work, for his ceaseless sense of adventure, for the warmth of beach campfires on remote islands, and for his laughter, friendship, support, and inspiration.

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CHAPTER 1

GENERAL INTRODUCTION

RESEARCH QUESTION

The arrangement of individuals in time and space has important evolutionary and conservation implications and is critical in population management (Simberloff 1988). Movements of individuals from their place of birth to their place of reproduction determine the relatedness of potential mates and the genetic and demographic relationships of subpopulations (Shields 1982, Slatkin 1985, Rockwell and Barrowclough 1987, Hanski 1991). This, in turn, has implications for many aspects of a species' biology, including social structure, degrees of genetic and phenotypic differentiation found throughout the species' range, and ability to persist through time (Andrewartha and Birch 1954, Mayr 1970, Wilson 1975, Lande 1988, Simberloff 1988, Hanski 1991). Movement patterns have important implications for conservation because the distribution of genetic variance within and among populations determines the uniqueness of sub-populations (Dizon et al. 1992, Moritz 1994), because migration rates among populations influence probabilities of rescuing or recolonizing sub-populations that are declining or have gone extinct (MacArthur and Wilson 1967, Levins 1970, Hanski 1991), and because conservation of the natural distribution of genetic variance is important for the conservation of evolutionary potential (Mayr 1970, Frankel and Soulé 1981).

The geographic configuration of populations in relation to the dispersal tendencies and abilities of individuals influences the degree of genetic differentiation among populations and the degree of their demographic connection (Wright 1943, Kimura and Weiss 1964, Hoopes and Harrison 1998). Complete geographic isolation of populations will lead to genetic differentiation due to random genetic drift, mutation, and selection favouring adaptation to local conditions, but these differentiating forces are typically counteracted by dispersal of individuals among populations that tend to homogenize gene frequencies (Mayr 1970, Slatkin 1987). Genetic population structure can also refer to separation in time rather than space (e.g., odd and even-year cohorts of Pacific pink salmon, *Oncorhynchus gorbuscha*, Hart 1980), however, separation in space is the more common consideration. I define a genetic population as a group of conspecifics in a geographic location that are genetically similar relative to those in other geographic locations. Population structure from a demographic, or metapopulation, perspective refers to the degree of demographic connection among populations. Specifically, metapopulation theory is a theoretical framework for the demography and persistence of a group of distinct populations (Levins 1970, Hanski 1991, Hoopes and Harrison 1998). For example, the extinction probability of a population is affected by immigration from other populations that are demographically independent (the probabilities of extinction are uncorrelated), which is in turn determined by the degree of separation of populations relative to the dispersal patterns of individuals. I define a demographic population as a group of conspecifics in a geographic location that are isolated enough from other groups of individuals to have relatively independent population dynamics. Because of the wide range of research questions surrounding populations, definition of the term "population" clearly depends on context. Moreover, the scale of the geographic space containing a population can vary widely and population boundaries are typically fixed arbitrarily by the investigator (Krebs 1994). Throughout this thesis, "population" is loosely defined as a group of conspecifics that share a geographic location and potentially differ from other groups of conspecifics with respect to genetic or demographic characteristics.

The relationship between spatial distribution and genetic and demographic population structure is more complex for species that have separate breeding and wintering distributions than for non-migratory species, and for those that pair at wintering areas rather than at breeding areas (Syroechkovsky et al. 1994, Cooke et al. 1995, Esler 2000, Scribner et al. 2001). Many waterfowl winter and breed at geographically distinct areas and pair during winter (Bellrose 1980, Rohwer and Anderson 1988). For many species of waterfowl, demographic population structure therefore needs to be defined for breeding and wintering areas separately (Esler 2000), and movements at wintering areas are of particular importance to genetic population structure (Robertson and Cooke 1999). If individuals pair at wintering areas, then move paired to breeding areas, and if no further mixing occurs at breeding areas, then the geographic location of breeding areas would be unimportant to genetic population structure, whereas the distribution and movement of unpaired individuals at wintering areas would be critical. Because some species of waterfowl pair at breeding areas (e.g., Oxyurini; Johnsgard and Carbonell 1996) or on migration (e.g., Aythya; Weller 1965), and because genetic mixing may occur at breeding areas through processes such as extra-pair fertilization and intraspecific nest parasitism (Afton 1985, Lank et al. 1989, McKinney and Evarts 1997), assumptions of winter pairing and lack of genetic mixing at breeding areas may be inappropriate for some species or may represent a simplification of a more complex situation for others.

The manner in which juveniles are incorporated into waterfowl populations has implications for genetic and demographic population structure. At two extremes, substantial population mixing can be achieved through the migration of juveniles from breeding areas into widely separated wintering populations, whereas populations have potential for isolation if juveniles arrive at wintering areas in family groups with one or both parents. When juveniles migrate in family groups, potential for genetic isolation of populations is increased because individuals are more likely to winter among relatives and therefore to choose more closely related individuals for mates than if they were to winter in a random group of birds. Similarly, potential for demographic isolation is increased because recruitment to local wintering populations comes from specific groups of birds. Family migration is common among swans and geese (Anserini), and juveniles generally accompany both parents throughout the first year of life (Prevett and MacInnes 1980). In contrast, males of migratory seasonally monogamous ducks (Anatini, Aythyini, Mergini) usually abandon their mates during incubation, and females are thought to leave juveniles typically near fledging (Afton and Paulus 1992). Juveniles of seasonally monogamous ducks therefore migrate from breeding to wintering areas on their own and are less likely to winter in the vicinity of their parents or close relatives.

Although focus has been placed primarily on dispersal and philopatry to breeding areas for waterfowl (Anderson et al. 1992), information on distribution and movement patterns at wintering areas is critical to an understanding of the population structure of many waterfowl species (Robertson and Cooke 1999). Philopatry to wintering sites contributes to population isolation whereas dispersal connects populations genetically and demographically. Thus, even if juveniles migrate to wintering areas in family groups, their dispersal prior to pairing will connect populations demographically, and homogenize populations genetically. Species most likely to have genetically and demographically isolated populations therefore are those that have life history characteristics of family migration in combination with philopatry to wintering areas. However, relatively little is known about winter movement patterns for most waterfowl. Philopatry to wintering areas is well documented for geese and swans but is less well documented for migratory ducks (Anderson et al. 1992). Species of migratory ducks that winter at interior wetlands or smaller bodies of water exhibit flexibility in wintering sites among years because interior wetlands are more variable and unstable than are coastal waters or larger bodies of fresh water (Baldassarre et al. 1988, Diefenbach et al. 1988, Nichols et al. 1983, Hestbeck 1993). Unstable habitats are therefore less conducive to philopatry than stable habitats. Several species of sea ducks (Mergini), that winter at coastal sites, have been documented to exhibit winter site fidelity (Alison 1974, Spurr and Milne 1976, Limpert 1980, Savard 1985, Breault and Savard 1999, Robertson et al. 1999).

I investigated movement patterns and population structure in the Harlequin Duck (*Histrionicus histrionicus*), a sea duck with dispersed and separate breeding and wintering distributions, at a wintering area in western North America. Harlequin Ducks breed at inland streams and molt and winter at coastal areas. The species is of conservation concern due to an apparent imbalance between recruitment and mortality (Rodway et al. 2003). In addition, low reproductive rates mean that population stability is highly sensitive to adult mortality (Goudie et al. 1994), and increasing human disturbance and development at their coastal wintering sites also are a conservation concern. Harlequin Ducks show delayed maturation, pair during winter, maintain long-term pair bonds, have a male-biased sex ratio, and show strong philopatry to coastal molting and wintering sites (Robertson and Goudie 1999). Because pairing occurs during winter, the mechanism by which juveniles arrive at coastal locations, in combination with the movement patterns of individuals at wintering areas, particularly those of unpaired individuals, are most important to genetic population structure. Reported strong philopatry to wintering areas (Breault and Savard 1999, Robertson et al. 1999, 2000) indicated a potential for isolation of populations; thus it was important to determine the scale at which wintering populations could be considered distinct, both genetically and demographically.

This study was conducted in the Strait of Georgia, British Columbia, Canada, an important wintering area for Harlequin Ducks (Robertson and Goudie 1999). Harlequin Ducks typically spend their daylight hours during winter near shore and therefore are relatively easy to observe. Over 2,500 Harlequin Ducks were marked with leg bands from 1994 to 2000 at several locations in the Strait of Georgia; thus this location and its marked population presented an ideal opportunity for the study of winter movement patterns. Objectives of this study were to determine how juvenile Harlequin Ducks are incorporated into wintering populations, to quantify movement rates and distances of individuals differing in sex and age at wintering areas, and to evaluate genetic and demographic population structure.

THESIS OUTLINE

This thesis has been developed in a "paper" format, that is, each chapter has been written to stand on its own.

In chapter 2, I present evidence that Harlequin Duck broods accompany their mothers from breeding streams to coastal molting or wintering areas. I report observations of family-like groups, consisting of an adult female with one or more juveniles, at wintering areas. I then discuss evidence that these family-like groups are indeed true families, and not just unrelated birds associating together, by describing the behaviour of individuals that were captured and marked as family groups and by genetic analysis of blood samples taken from putative family members. Evidence from wintering areas corroborated well with observations of radio-marked families at breeding streams (Smith 2000). This chapter is based largely on the publication Regehr et al. (2001) but differs from this publication in that data from breeding streams have been removed (this data was presented in the Smith (2000)), and that data from genetic analyses, that had not been conducted at the time of publication, have been added.

In chapter 3 I evaluate, for Harlequin Ducks, two common markers used on waterfowl: coloured leg bands and nasal discs. I compare marker visibility and life span, and determine effects of nasal discs on behavior and pairing. In studies using marked individuals it is important to evaluate effects of marks on behaviour because of potential biases to results. Information on marker life span and visibility is also critical to many studies, particularly demographic studies, in which marker wear or loss can bias estimates and differences in marker visibility can violate assumptions.

In chapter 4, I examine survival and movement of juvenile Harlequin Ducks in their first winter. I used radio-marking on a sample of juveniles captured at the coast and report movement distances and survival. I also used capture-mark-recapture analyses to generate sex and age-specific local survival estimates.

In chapter 5, I estimate movement distances and rates of Harlequin Ducks wintering in the Strait of Georgia and evaluate genetic and demographic population structure. I tested hypotheses that movement rates and distances differ by sex and age. Because the movement of unpaired individuals is most relevant to genetic population structure, and because Harlequin Ducks have a male-biased sex ratio and maintain long-term pair bonds, it is important to partition movement distances and rates by sex and age. I also tested the hypothesis that movement rates were related to distance between locations. Whether migrants are incorporated into recipient populations with equal probability from all possible subpopulations, or whether they move with highest probability to adjacent areas is an important assumption for gene flow models. I used resightings of nasal-marked individuals to determine movement distances, and multi-stratum models in capture-mark-recapture analyses to estimate movement rates among locations. I also tested the hypothesis that, given evidence for winter philopatry and family migration, wintering populations of Harlequin Ducks are physically isolated to an extent that may imply genetic or demographic isolation. I used results from movement analyses in conjunction with gene flow models to estimate the among population component of genetic variance and compared this to what has been estimated for other avian species.

In chapter 6, I summarize my findings from all chapters and draw general conclusions.

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CHAPTER 2

POST-FLEDGING BROODS OF MIGRATORY HARLEQUIN DUCKS ACCOMPANY FEMALES TO WINTERING AREAS

This chapter is based largely on the publication:
Regehr, H.M., C. M. Smith, B. Arquilla, and F. Cooke. 2001. Post-fledging broods of migratory Harlequin Ducks accompany females to wintering areas. Condor 103: 408-412.

ABSTRACT

This study provides evidence that Harlequin Duck (*Histrionicus histrionicus*) broods accompany their mothers from breeding streams to coastal molting or wintering areas. Family-like groups were observed at wintering areas in August and September. Observations of marked individuals indicated that family groups tended to separate quickly, although some family members continued to associate for at least six months. Blood samples taken from individuals captured together in family groups indicated that all juveniles had at least one allele at all of six biparentally inherited microsatellite loci in common with the adult female they were captured with and therefore could have been her genetic offspring. About half of other individuals sampled from the population at random did not have at least one allele at all six loci in common with each female captured with juveniles. Observations that all adult females captured in family groups were resighted with at least some of the juveniles captured with them, and that adult females interacted with the juveniles captured with them and defended them from other adults, provided additional evidence that most individuals captured in family-like groups were true families. This study contributes to our understanding of Harlequin Duck post-fledging ecology and identifies Harlequin Ducks as unusual among migratory ducks in that females bring their offspring to wintering areas, a pattern similar to geese and swans. This may be facilitated by an unusual strategy of wing molt, in which Harlequin Ducks molt after migrating to wintering areas. Due to winter pairing and strong philopatry in Harlequin Ducks, migration of families may contribute to genetic differentiation among populations.

INTRODUCTION

The age at which juveniles separate from their parents can be predicted from theories of parent-offspring conflict (Carlisle 1982). Parents should abandon their young when prospects for future fitness through abandonment are greater than fitness gained from attending the present brood. Among waterfowl there are two broad patterns of brood abandonment. In swans and geese (Anserini), which have long-term pair bonds, juveniles generally accompany both parents throughout the first year of life, staying with them during both migratory journeys between breeding and wintering grounds (Prevett and MacInnes 1980). In contrast, in seasonally monogamous ducks (Anatini, Aythyini, Mergini), males of migratory species abandon their mates, usually before young hatch, while females accompany their young for a variable period but typically are thought to leave them prior to fledging (Afton and Paulus 1992, Eadie et al. 1995, Mallory and Metz 1999).

Timing of brood abandonment is presumably an optimization of costs and benefits, which may vary with brood size and age, female condition, and other life history variables. Parental care enhances brood survival, particularly early in the lives of the offspring, through brooding, protection from predators, aiding in competitive interactions, finding suitable habitats, guiding offspring during migration, and helping them locate staging and wintering grounds. Conversely, caring for young may be costly for females because it may reduce their foraging time and they may suffer increased mortality risk while defending the young (Afton and Paulus 1992).

We examined the timing of brood abandonment by Harlequin Ducks (*Histrionicus histrionicus*). They have long-term pair bonds in common with Anserini, and uniparental care in common with the ducks. Some previous studies have suggested that females may abandon their broods prior to fledging (Wallen 1987, Cassirer and Groves 1991, Diamond and Finnegan 1993, Reichel et al. 1997), while others have suggested that they are still with their broods at fledging (Bengtson 1966, Kuchel 1977). There are anecdotal accounts of family groups at great distances from suitable breeding streams (Cooke et al. 2000). Research at a wintering area of the Pacific population allowed us to investigate the arrival and subsequent behaviour of family groups, to capture, mark, and observe some family groups, and to take blood samples of family group members for genetic analysis.

METHODS

Researchers and volunteers conducted observations at wintering areas from 1997 to 2000 at Hornby Island, the Cape Lazo area of eastern Vancouver Island (between Comox and Campbell River), and White Rock, British Columbia, Canada, and at Birch Bay and Point Roberts, Washington, USA. We surveyed White Rock once per week in 1997, two to three times per week in 1998 and 1999, and opportunistically in 2000. We surveyed Birch Bay and Point Roberts once every two weeks in 1999, Hornby Island from 8 to 13 September 1999 and from 10 to 15 September 2000, and the Cape Lazo area from 14 to 18 September 1999 and from 29 August to 8 September 2000. Many birds were identifiable by unique tarsal bands or nasal disks from previous banding operations. Juveniles were separable from adults by finely vermiculated plumage on the breast, belly, and vent, mottled yellow and gray legs and feet, dusky faces, and occasionally, notched tail feathers.

We defined a "family" as an association between one adult female and one or more juveniles in which the adult female had full old primaries, indicating recent arrival, and assumed a leading or vigilant role. To avoid duplicate recording of families, we report separate families only if they were seen concurrently, were separated in time by at least 10 days (this is the average time to the loss of primaries, F. Cooke unpubl. data), or if females were identified.

We recorded composition of all Harlequin Duck groups to determine the frequency of family groups and the social choices of juveniles in all locations in 1999 and at Hornby Island and Cape Lazo in 2000. We defined a group as one or more individuals separated from others by at least 10 m. Surveys conducted at the same location on different days may have included juveniles sampled on previous days. We did not attempt to correct for duplicate sightings, but conducted only one survey in any location on any day.

We captured three family groups, one at Cape Lazo in 1999, and one each at Cape Lazo and Hornby Island in 2000 (families had four, four, and two juveniles, respectively) using mist nets and decoys. We marked all individuals with a USFWS tarsal band, a colored plastic tarsal band with a uniquely engraved two digit code, and with nasal discs with unique combinations of shapes and colours. Tarsal bands could be read when birds hauled out on rocks and nasal disks were visible on both loafing and swimming birds. In 2000, each individual captured as part of a family group was also marked with an external radio transmitter attached mid-dorsally with subdermal wire anchors, and approximately 0.1 mL of blood was taken by tarsal venipuncture and was stored in approximately 1 mL of nonrefrigerated buffered lysis solution. We conducted 10-min to 2-hr behavioral observations on the two families marked at Cape Lazo on four and five occasions in 1999 and 2000, respectively. We observed both juveniles from the family at Hornby Island on three occasions one and two days following capture; both died shortly thereafter. During observations we recorded the relative locations and social interactions of family members.

Blood samples taken from individuals in the two family groups captured in 2000 were analyzed at the Department of Fisheries and Wildlife, Michigan State University. Six pairs of primers were used to amplify biparentally inherited microsatellite loci by polimerase chain reaction (PCR). Three of these primer pairs were described previously (Buchholz et al 1998), the other three were developed from a spectacled-eider genomic library (K. Scribner, unpubl. data). Amplifications were carried out in 25μl reaction volumes at 10mM Tris pH 8.5, 50mM KCl, 10μg/ml BSA, 0.025% Tween 20, 200μM dNTPs, 1pmol each primer, 100ng genomic DNA and 0.5U Ampli*Taq* DNA polymerase. The three primer pairs flanking CA-repeats (Hhi2, Hhi5 and Bca10) and the three primer pairs flanking GA-repeats (Sfi4, Sfi9, and Sfi10) were amplified at 1.5mM and 2.5mM $MgCl_2$, respectively. The forward primer of each pair was labelled with a fluorescent dye, either HEX or Fluorescein. Cycling was performed using an oil overlay in a Stratagene Robocycler. Samples were heated to 94°C for two minutes followed by 30 cycles of 94°C for 1 minute, annealing for 1 minute, and 1 minute at 72°C. The annealing temperatures for these microsatellite loci in harlequin ducks are as follows: Hhi2, 54°C; Hhi5, 50°C; Bca10, 54°C; Sfi4 60°C; Sfi9, 50°C; and Sfi10, 56°C. PCR products were resolved on 6% denaturing polyacrylamide gels and detected using a Hitachi FMBIO II.

We tested the hypothesis that adult females and juveniles captured together in family groups had genetic parent-offsping relationships. The null hypothesis was that other individuals selected at random from the population were as likely to be related to the adult female as were the juveniles that had been captured with her. To test this hypothesis, we compared alleles from six biparentally inherited microsatellite loci between juveniles and the adult females they were captured with, and between these adult females and other individuals sampled from the population. A juvenile could have been the genetic offspring of the adult female it was captured with if it had at least one allele in common with the female at all six loci. Otherwise, it could not have been her offspring. *G* tests were used to compare the proportion of juveniles that could have been the true offspring of the adult female they were captured with, with the proportion of individuals sampled from the population that also could have been the true offspring of the female. Genetic data for individuals sampled from the population to which comparisons of family members were made was provided by K. Scribner, Department of Fisheries and Wildlife, Michigan State University (unpubl. data) from data collected for genetic analyses at the population level. Individuals included in the sample from the population had been captured in the Strait of Georgia, British Columbia, prior to this study. Due to low variability of alleles (see Results) it was not feasible to examine genetic relationships other than that of mother-offspring. Similarly, analysis with program Kinship (Goodnight Software 2003), which evaluates probability of relatedness of pairs of individuals given allele frequencies of other individuals in the population, was abandoned due to unacceptably high type II error rates (0.5 and 0.9 Type II error rates for Type I error rates of 0.05 and 0.001, respectively) resulting from low variability of alleles.

RESULTS

Behaviour

We observed 25 different Harlequin Duck families at wintering areas from 22 August to 26 September from 1997 to 2000. Females were seen with one (n = 5), two (n = 8), three (n = 3), four (n = 4), five (n = 1), six (n = 3), and seven (n = 1) juveniles. Four previously banded females were seen in family groups at White Rock, and all were with juveniles when they were first observed at the site that season. We also observed one family-like association that was clearly not a family group: one female with four juveniles was a banded yearling that had been in the area throughout the year.

Most families separated shortly after arrival at wintering areas, but some individuals associated for many months. Previously banded females seen with juveniles were without them 9 to 46 days after the initial family sighting. All adult females captured in family groups were resighted with at least some of the juveniles captured with them. Only two juveniles from the family captured in 1999 remained with the adult female one day after capture, one remained after two days, and none remained after a month. The adult female from the family captured at Cape Lazo in 2000 was 2 km from the juveniles one day after capture, but all family members were together again after 13 days, and all were within 1 km of each other after 42 days. After 73 days, the adult female and two juveniles were together, the third juvenile was 2 km away, and the fourth had died. Death of the fourth juvenile was confirmed by pinpointing its transmitter to a small area (several m^2) of dense shoreline vegetation. Five and a half months after capture this adult female was together with two juveniles, and six months after capture she was seen together with one juvenile.

Observations of marked families suggested that adult females did not act aggressively toward the juveniles captured with them in a family group, but interacted with them and defended them from other adults. During 2 hr of observation of the family captured in 1999, the adult female defended her remaining two juveniles on four occasions. She struck another nearby adult female with her bill once, chased an adult female once, and twice was observed to guard one of her young from a nearby female by moving between them in a blocking motion. One of these blocking movements followed the chase of the nearby female. This sequence of events was immediately followed by the movement of the entire family group away from all other birds.

We observed behavioural interactions between the adult female captured at Cape Lazo in 1999 and her two remaining juveniles on four occasions. On three occasions the adult female nodded her head towards one of her young and the juvenile appeared to respond with a similar head nod or a series of sharp head jerks. One of these interactions occurred just before the female defended the juvenile from another female. We also observed the adult female making quick darting movements away from and towards the juveniles just before initiating the flight offshore for the night, which occurred as a tight group of three. Two days later, we observed the adult female and one remaining young diving together for 30 min apart from other birds. They dove and surfaced synchronously. On no occasion during any observation session for any family was an aggressive action by the adult female directed towards one of the juveniles captured with her.

We observed juveniles in a variety of group compositions. Of 161 juvenile sightings, juveniles were solitary (21 times), in the company of other juveniles only (24 times), in the company of non-vigilant or newly molted females only (23 times), in the company of adult males only (21 times), with a mix of adult males and females (44 times), and in family groups (28 times).

Genetics

All juveniles captured as part of the two family groups captured in 2000 had at least one allele in common with the adult female they were captured with at all six biparentally inherited microsatellite loci, and therefore could have been the offspring of the female. However, variability at most of the six loci was low, thus a high percentage of individuals sampled from the population also had at least one allele in common at each of the six loci with the two females captured with juveniles in 2000 (Table 2.1). For one of the adult females (female K47), the proportion of the juveniles captured with her in a family group that had at least one allele in common with her at all six loci (100%, $n = 4$) was greater than this proportion for other individuals sampled from the population (49%, $n = 57$; $G_1 = 5.415$, $P = 0.020$), thus we were able to reject the null hypothesis that other individuals from the population were as likely to be related to this adult female as were the juveniles captured with her. For the second adult female (female KAX), the proportion of the juveniles captured with her that had at least one allele in common with her at all loci (100%, $n = 2$) was not significantly greater than this proportion from individuals sampled from the rest of the population (56%, $n = 59$; $G_1 = 2.27$, $P = 0.132$), thus we were unable to reject the null hypothesis.

DISCUSSION

This study provides evidence that Harlequin Duck broods accompany females from breeding to wintering areas. Observations indicated that family-like groupings appeared at wintering areas, then generally separated rapidly; hence most juveniles were not seen in family groups but in a wide range of social associations. Thus, although some juveniles may arrive at the coast alone or in sibling groups without their mothers, the presence of juveniles on the coast without females is not proof that they arrived alone (cf. Robertson and Goudie 1999). Our results suggest that most family groups separate soon after arrival at the coast. However, some members of family groups may associate for several months. Several observations of family-like groups behaving in ways described in this study have been repeatedly seen since this study ended (W.S. Boyd, pers. comm.).

There are several lines of evidence supporting the hypothesis that most individuals captured in families groups were true families and not just groups of birds associating together. Although sample size was small and allelic variation was low, analysis of blood samples provided support for mother-offspring relationships between adult females and the juveniles captured with her in family groups. None of the six juveniles captured in two family groups could not have been the genetic offspring of the adult female they were captured with, whereas approximately half of other birds sampled from the population could not have been the offspring of each adult female. Furthermore, family-like groups that were captured and marked continued to associate afterwards, and defensive and interactive behaviour observed for family groups was consistent with what would be expected for a true family. Clearly some family-like groups seen at wintering areas were unrelated, because we observed one group that could not have been a true family, and because adoption and brood amalgamation have been observed at breeding areas (Bengston 1966, Rodway et al. 1998, Smith 2000).

Results from this study also concur with observations of family departure from breeding areas. Smith (2000) found that all members of radio-marked families departed from breeding streams synchronously after the young fledged when both the female and her brood survived at the time of fledging, suggesting that they had initiated their migration together. Moreover, some radio-marked family members were later sighted at the coast near each other, suggesting that they had arrived together, then separated (Smith 2000, Regehr et al. 2001).

The arrival of entire families at wintering areas has implications for population genetic structure, demographics, and conservation. If juveniles arrive at the molting or wintering area of their mothers, then they may find themselves in the same wintering locations as their siblings from multiple breeding seasons, given high site fidelity of females to molting and wintering sites

(Breault and Savard 1999, Robertson et al. 1999). Due to winter pairing in Harlequin Ducks, this could lead to local wintering populations becoming more genetically similar over time, which could lead to genetically differentiated populations, something that is thought to be rare in migratory ducks (Anderson et al. 1992). Additionally, if all recruitment to local wintering populations comes from specific groups of birds, recovery from local population reductions could be slow.

In breeding areas, death of the mother, adoption, brood amalgamation, and brood mixing, could all result in juvenile migration from breeding to wintering areas alone or with a female that is not its biological parent (Regehr et al. 2001). Such juveniles are unlikely to migrate to their mother's molting or wintering location because coastal wintering habitat is extensive and individuals breeding in proximity can migrate to widely separated wintering sites (Robertson and Goudie 1999). Juveniles departing alone or with an adoptive parent would therefore not be related to the individuals that they wintered and subsequently paired with, and their introduction into local populations would have a homogenizing effect on population structure similar to winter dispersal. Presently there is no genetic evidence for fine scale differentiation in Harlequin Ducks (Brown 1998, Lanctot et al. 1999), but at a broader scale there is (K. Scribner unpubl., in Robertson and Goudie 1999). Research on winter movements of individuals and on frequencies of true versus adoptive families is required to determine the degree to which family migration could lead to population differentiation and to demographically closed populations.

Harlequin Ducks (at least on the Pacific coast) are unlike most species of ducks in that they often molt and winter in the same location (Breault and Savard 1999, Robertson et al. 1999), and this difference may allow Harlequin Duck juveniles to migrate with their mothers. Molting sites for females are not specific habitats close to breeding areas as they are in some duck species (Hohman et al. 1992), where an extended family bond could represent a fitness cost to both the flightless mother and her young. In Harlequin Ducks, both females and offspring could benefit from family migration because offspring would reach a wintering location that has been successful for the female in previous years, and females would improve their own fitness if the survival of their offspring were enhanced. Why Harlequin Ducks molt at wintering areas, whereas other ducks generally molt without their young close to breeding areas is unclear, but is likely related to survival and food availability, two important factors in selection of molting sites by waterfowl (Hohman et al. 1992). Coastal areas likely offer more abundant and dependable food resources and lower predation risk than breeding streams.

To our knowledge the evidence from this study conducted at wintering areas, in conjunction with that provided by Smith (2000) for breeding areas, is the first suggesting that female migratory ducks bring their offspring to wintering areas, a pattern that is well known in geese and swans. Such evidence is extremely difficult to obtain by traditional methods of study. Although there are several studies that provide convincing evidence of brood abandonment prior to fledging (Joyner 1977, Pöysä et al. 1997), it may be difficult to detect cases where families stay together. For example, permanent abandonment may be confused with temporary absences (Ball et al. 1975) or mortality of the female. Thus in many species the precise time of brood abandonment is not known, and often it is simply assumed to occur at fledging. With the development of satellite technology, it should be possible to investigate this question more thoroughly and in a wider range of species.

ACKNOWLEDGEMENTS

We are grateful to Michael Rodway, Ken Wright, Rachel Botting, and Pete Clarkson for assistance with capture of family groups in wintering areas and for donating behavioral data. We thank Sean Boyd for providing transmitters and instruction for attachment, Felix Breden for providing lysis buffer, and Kim Scribner for accepted blood samples for analysis in his lab and for providing advice on the interpretation of results. Many thanks to Alan Afton, Sean Boyd, Felix Breden, Dan Esler, Arne Mooers, and Jean-Pierre Savard, whose critical reviews substantially improved the manuscript. Funding was provided by NSERC of Canada, Centre for Wildlife Ecology, and Simon Fraser University, British Columbia Waterfowl Society, Institute of Waterfowl and Wetlands Research (IWWR), and the Canadian Wildlife Service.

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Table 2.1. Percentage of Harlequin Ducks captured in coastal British Columbia (not including members captured as part of each family group) that had at least one allele in common with a female captured with juveniles in a family group, for each of the six biparentally inherited microsatellite loci and for all six loci together. Number of alleles is given in parentheses below each locus in column headings. Sample sizes are given in parentheses in the table next to percentages. Females K47 and KAX were captured with 4 and 2 juveniles, respectively.

	Loci (number of alleles)						
Female id	sfi4 (2)	sfi9 (3)	sfi10 (5)	bca10 (3)	hhi2 (5)	hhi5 (3)	All six loci
K47	95 (57)	91 (56)	89 (57)	100 (57)	65 (57)	100 (57)	49 (57)
KAX	100 (59)	97 (58)	90 (59)	95 (59)	75 (59)	83 (59)	56 (59)

CHAPTER 3

EVALUATION OF NASAL DISCS AND COLORED LEG BANDS AS MARKERS FOR HARLEQUIN DUCKS

This chapter is published as:
Regehr, H.M., and M.S. Rodway. 2003. Evaluation of nasal discs and colored leg bands as markers for Harlequin Ducks. Journal of Field Ornithology 74: 129-135.

ABSTRACT

We evaluated nasal discs and colored leg bands for Harlequin Ducks (*Histrionicus histrionicus*) wintering in the Strait of Georgia, British Columbia, by comparing marker visibility and life span, and determining effects of nasal discs on behavior and pairing. Proportions resighted and frequency of sightings were higher for individuals marked with nasal discs than for those marked only with leg bands. Nasal disc loss followed a logistic function that predicted 50% loss by 396 d. Due to wear of leg bands, number of sightings per individual decreased with leg band age following a cubic function. We detected no effects of nasal discs on time spent in various behaviors, timing of pairing, or female pairing success. However, males with nasal discs had lower pairing success and females with nasal discs were less likely to reunite with previous mates. We speculate that the effect of nasal discs on male pairing success may be due to a male-biased sex ratio and sexual selection on male appearance. Leg band wear should be considered for demographic models because its effects can violate assumptions and bias sighting and survival estimates.

INTRODUCTION

Behavioral and demographic studies of birds often rely on markers that allow identification of individuals. Markers vary in life span, visibility, and effect on individuals, and thus in their usefulness for different research objectives. However, marker induced changes in behavior or survival, or biases resulting from marker loss, are frequently not considered or accounted for (Calvo and Furness 1992). Markers can affect survival (Byers 1987, Schmutz and

Morse 2000), pairing and breeding behavior (Frankel and Baskett 1963, Kinkel 1989, Metz and Weatherhead 1991), and time spent in different behaviors (Brua 1998, Pelayo and Clark 2000). Marker life span may violate assumptions and bias estimates from mark-recapture analyses (Arnason and Mills 1981, Nichols and Hines 1993).

Colored tarsus markers (leg bands) and nasal markers (discs or saddles) are two common marking techniques for waterfowl (Bartonek and Dane 1964, Sugden and Poston 1968). Nasal markers allow identification during most behaviors, whereas leg bands can only be seen when the legs are exposed. Nasal markers are thus an attractive choice, especially when birds spend most of their time in the water or when they mix in flocks. Nasal markers may have the disadvantage of a short life span (Sherwood 1966), however, leg bands also decline in usefulness over time due to loss or wear (Mills 1972, Spendelow et al. 1994). Some studies using nasal markers have reported changes in behavior (McKinney and Derrickson 1979, Evrard 1996, Pelayo and Clark 2000), reduced pairing success (Koob 1981), delayed timing of breeding (Howerter et al. 1997), and injury or increased mortality from entanglement in netting and submerged vegetation (Erskine in Bartonek and Dane 1964, Sherwood 1966, Evrard 1986) and from icing (Greenwood and Bair 1974, Byers 1987), whereas others have reported no such effects (Bartonek and Dane 1964, Sugden and Poston 1968, Raveling 1969, Savard 1988).

We evaluated nasal discs and colored leg bands as markers for Harlequin Ducks (*Histrionicus histrionicus*) at coastal wintering areas in British Columbia. To our knowledge no information has been published evaluating markers for Harlequin Ducks, and few studies have evaluated markers for diving ducks at wintering areas. Our objectives were to compare marker visibility and life span, to determine if nasal discs affect behavior and pairing success, and, considering the life-span of leg bands, to test the assumption of mark-recapture analysis that all marked individuals have equal probability of being sighted (Cormack 1964).

METHODS

Study area and capture

As part of a larger study, over 2500 Harlequin Ducks were captured during their wing molt by corralling them into a drive trap erected along the shoreline (Clarkson and Goudie 1994) in July through September, 1994 – 2000. Primary capture locations were White Rock, Hornby Island, Quadra Island, and the east coast of Vancouver Island between Comox and Campbell River, in the Strait of Georgia, British Columbia, Canada.

Marking methods

All captured individuals were marked with a metal (aluminum before 1999; stainless steel in 1999-2001) United States Fish and Wildlife Service band on the left tarsus, and a laminated plastic 2-digit alphanumerically encoded color band with code cut out to expose the inner color layer (manufactured by Protouch Engraving, Saskatoon, Sask) on the right tarsus. Overlapping ends were glued with acetone. Worn leg bands were replaced on recaptured birds. Individuals were aged as adult (after-third yr) or sub-adult (third-yr and younger) by absence or presence of the Bursa of Fabricius (Kortright 1942, Mather and Esler 1999).

In 1997 – 2000 we marked 457 individuals with nasal discs in addition to colored leg bands. Most (96%) were marked in 1998 and 1999. Discs of four shapes (circle, diamond, rectangle, triangle) and eight colors (aqua, black, blue, green, orange, red, white, yellow) were cut, 9 mm maximum diameter, from Darvic plastic (a PVC plastic resistant to UV light manufactured by A.C. Hughes Ltd., Middlesex, England). We attached disks using a 36 kg monofilament fishing line connector and marked each individual with a unique combination of two nasal discs attached on either side of the nares, as described by Bartonek and Dane (1964).

Resighting of marked individuals

Marked individuals were identified by spotting scope opportunistically throughout the fall, winter, and spring, 1997-2001. In addition, a large band-reading effort involving many researchers and volunteers was conducted each yr at Hornby Island during March and April when large numbers of Harlequin Ducks congregate at Pacific herring (*Clupea pallasi*) spawning sites.

Marker visibility

We compared the visibility of colored leg bands and nasal discs during winter, when birds spend much of their time feeding (Goudie and Ankney 1986, Fischer and Griffin 2000) and their legs are infrequently exposed, and during the herring-spawning period in spring at Hornby Island, when birds frequently haul out. For each period we compared the probability that an individual was sighted, equal to the number of marked individuals that were seen at least once during that period out of the total number known to be alive (i.e., seen in that period or at a later date), and for those that were seen at least once, the number of sightings per individual. We included only sightings from 1998 to 2001 when both markers were in use, thereby equalizing observer effort for the two marker types.

Nasal disc loss

We recorded nasal disc loss when individuals previously marked with nasal discs were identified without them by their leg bands. Loss of both markers was unlikely because no individuals with nasal discs were seen with an illegible or missing leg band. We estimated date of loss as the midpoint between observations with and without discs. To calculate loss rate, we regressed number of individuals retaining discs on number of days after disc attachment. Individuals that were not resighted or whose nasal disc status could not be assessed at the end of the study were excluded.

Leg band wear

To estimate rate of leg band wear and test the assumption that sighting probability does not vary among marked individuals, we regressed number of sightings (>0) per individual on age (number of partial or full yr since attachment) of their colored leg bands. We used data from the annual spring band-reading effort at Hornby Island, excluding individuals marked with nasal discs. We expected the number of sightings per individual to be highly variable and affected by many factors, such as bird behavior and location, as well as leg band age. However, we assumed that the effect of leg band age was independent, and that declines in numbers of sightings with leg band age could be attributed to leg band wear. New leg bands put on first-captured birds of various ages, and replacement leg bands put on some recaptured birds during each fall maintained new leg bands in the sample and ensured that neither bird age nor yearly fluctuations in observer effort were correlated with leg band age. However, because few yr of data contributed to the oldest leg band ages, we examined the last two yr separately to confirm that trends in leg band wear rates also held within yr and were not biased by annual differences in observer effort.

We also compared proportions of colored leg bands that were worn and replaced on recaptured birds among leg band ages. These proportions did not equal the rate of leg band loss to the study because leg bands were frequently replaced before they were illegible. We considered recaptured individuals a representative sample of the marked population.

Effect of nasal discs on time budgets

We conducted 834 continuous, 30 min behavioral observation sessions on random individuals (Altman 1974), 450 on males and 384 on females from February to April in 1998 and 1999. Eighty-eight of these sessions were on individuals marked with nasal discs. Sampling from large numbers of birds throughout daylight hours and over a 3 mo period minimized the chance of repeatedly sampling the same individuals. We were unable to assess the effect of leg bands on behavior because during many behaviors it was not possible to distinguish leg-banded from unmarked individuals. We conducted observations using a 15-60 × spotting scope from a hidden or distant location to ensure that we did not affect behavior. We tested the null hypotheses that time spent in feeding, maintenance, and courtship behavior did not differ between unmarked individuals and those marked with nasal discs.

Effect of nasal discs on pairing behavior

Harlequin Ducks pair during winter and form long-term pair bonds (Robertson and Goudie 1999). We compared pairing success, timing of pairing, and the proportion reuniting with a previous mate between birds marked with nasal discs and birds marked only with leg bands. We included only adults in these analyses because pairing probability differs with age (Robertson et al. 1998). Birds were considered paired if they remained in close proximity, behaved synchronously, and exhibited defense behaviors such as mate guarding (Gowans et al. 1997). Our observations indicated that individuals behave contrary to their paired status for short periods of time but that 30 min was usually adequate to confidently assess paired status. We thus considered paired status confirmed if birds appeared paired or unpaired for most of a 30 min behavioral observation or if we had at least two consistent records from opportunistic sightings. We determined proportions of birds that successfully paired in a particular yr only from observations and sightings made in spring (March, April, or May) to avoid bias caused by the fact that paired status could be confirmed throughout the winter but unpaired status could only be confirmed in the spring. We estimated pair date as the date of the first paired record. To ensure that pair dates were accurate within 30 d, we accepted all pair dates prior to 31 October, because pairing rarely occurs before end of September, but required that individuals were seen unpaired no more than 30 d prior to a pair date after 31 October. Only pairs in which both partners were marked and known to be alive were considered to calculate proportions reuniting.

Statistical analyses

To compare proportions we used Fisher's Exact Test when more than 20% of cells had expected counts less than five, otherwise we used Chi-squared tests. In our analysis of marker visibility we used ANCOVA, including the effect of leg band age, to test for a nasal disc effect on numbers of sightings. We estimated rates of nasal disc loss and leg band wear using the Curve Estimation function in SPSS 8.0 (1997) to test for curvilinear relationships, and compared model fit based on R^2 values and biological realism. To analyze the effect of nasal discs on time spent in feeding, maintenance, and courtship behavior we compared arcsine transformed (Sokal and Rohlf

1995) proportions of time spent in each behavior between individuals with and without nasal discs. Paired status, as well as location, date, sex, and the interaction of location and date, which were known to be important explanatory variables in time budget analyses (MSR unpubl. data), were included in General Linear Models (SPSS 8.0 1997). We used ANOVA to compare pair dates. We examined residuals from parametric tests to ensure that assumptions of normality and homoscedasticity were met. Type I error rate at was set at 0.05, except in the analysis of time budgets where the risk of making a type II error (accepting the null hypothesis of no marker effect if it is false) was of greater concern to us than of making a type I error; thus we set the type I error rate to 0.1. Adjusted means ± SE are reported.

RESULTS

Marker visibility

During winter, the proportion of marked individuals seen at least once was over three times greater for those marked with nasal discs (53.2%, $n = 356$) than for those marked only with leg bands (15.8%, $n = 441$; $\chi^2_1 = 427.3$, $P < 0.001$), and those identified were seen over twice as often if they had nasal discs (3.2 ± 0.1 times / winter) than if they did not (1.5 ± 0.1 times / winter; $F_{1,780} = 83.8$, $P < 0.001$). During spring the proportion of marked individuals that were seen at least once was also greater for those marked with nasal discs (63.2%, $n = 423$) than for those without nasal discs (56.4%, $n = 1576$; $\chi^2_1 = 10.4$, $P = 0.001$), and those with nasal discs were seen more frequently (7.0 ± 0.2 times / spring) than those without (4.1 ± 0.1 times / spring; $F_{1,1938} = 131.7$, $P < 0.001$).

Nasal disc loss

Of 212 individuals whose nasal disc fates were known 900 d after attachment, 196 individuals had lost their discs and 16 retained them. The rate of disc loss was best described by a logistic equation: number remaining = $1/(1/250 + (0.0007 * (1.0052^{d})))$ ($R^2 = 0.99$, $F_{2,195} = 15185.0$, $P < 0.001$; Fig. 3.1). This function predicted that half of all discs were lost by 396 d after attachment and that 6% remained after 900 d. Because nasal disc loss assessment depended on identification by leg bands, and because sighting probability was lower for leg banded than nasal marked birds, the true nasal disc loss rate was likely higher.

Leg band wear

The relationship between number of sightings per individual marked only with colored leg bands and leg band age was best described by a cubic relationship (number of sightings = 6.23

+ (-1.35 * leg band age) + (0.28 * leg band age^2) + (-0.02 * leg band age^3)) ($R^2 = 0.04$, $F_{4,2994} = 40.9$, $P < 0.001$; Fig. 3.2), predicting that a 6-yr-old leg band would be seen about 0.5 times as often, and an 8-yr-old leg band about 0.1 times as often, as a 1-yr-old leg band. This significant cubic relationship also held when data from 2000 ($R^2 = 0.04$, $F_{4,497} = 7.6$, $P < 0.001$) and 2001 ($R^2 = 0.04$, $F_{4,391} = 4.8$, $P = 0.003$) were analyzed separately. The proportion of colored leg bands replaced on recaptured individuals increased rapidly over six yr. We replaced 11% ($n = 185$), 36% ($n = 92$), 66% ($n = 61$), 79% ($n = 38$), 93% ($n = 15$), and 100% ($n = 1$), of leg bands aged one, two, three, four, five, and six yr, respectively.

Effect of nasal discs on time budgets

There were no significant differences in the percentage of time spent by individuals with and without nasal discs in feeding (49.2 ± 3.1 vs. 45.3 ± 1.2; $F_{1,825} = 1.83$, $P = 0.18$), maintenance (17.9 ± 2.1 vs. 17.5 ± 0.8; $F_{1,825} < 0.01$, $P = 0.99$), or courtship behaviors (1.4 ± 0.6 vs. 2.2 ± 0.2; $F_{1,825} = 1.35$, $P = 0.25$). Power analysis revealed that differences in effect size of 5, 3, and <1% could have been detected with a power of 0.8 for feeding, maintenance, and courtship behaviors, respectively.

Effect of nasal discs on pairing behavior

Pairing success was lower for adult males with (28.1%, $n = 64$) than without (89.0%, $n = 309$; $\chi^2_1 = 116.6$, $P < 0.001$) nasal discs. We found no difference in the proportion of males reuniting with previous mates between males with (100%, $n = 5$) and without (96.6%, $n = 117$) nasal discs (Fisher's Exact Test, $P = 0.84$), although sample size of paired males with nasal discs was small. There was no difference in pairing success for adult females with (100%, $n = 113$) and without (99.6%, $n = 254$) nasal discs (Fisher's Exact Test, $P = 0.69$), although fewer females with (81.3%, $n = 16$) than without (98.2%, $n = 111$) nasal discs reunited with previous mates (Fisher's Exact Test, $P = 0.014$). The lower proportion of nasal marked females reuniting was not due to nasal marking of their mates because all paired males with nasal disks reunited with previous mates. We did not detect any differences in pair dates for birds with and without nasal discs for either males (23 Oct ± 4.6 vs. 18 Nov ± 8.1; $F_{1,63} = 1.43$, $P = 0.24$) or females (11 Nov ± 6.2 vs. 30 Oct ± 5.9; $F_{1,95} = 1.89$, $P = 0.172$).

DISCUSSION

Nasal discs and colored alpha numerically coded leg bands used as markers for Harlequin Ducks differed in visibility and life span. More individuals were identified and those identified were sighted more frequently when marked with nasal discs than when marked with leg bands only, especially during winter when birds rarely haul out. However, the life span of nasal discs was much shorter than that of leg bands. Half of all nasal discs were lost within 13 mo, while only 11% of 1-yr-old leg bands on recaptured individuals were replaced due to wear, and some of these would still have been legible when replaced and were not yet lost to the study.

Information on marker life span is critical to many studies, particularly demographic studies in which marker wear or loss can bias survival, movement, and sighting estimates. Relatively long life spans of colored leg bands in this study implicate these as suitable markers for demographic studies. However, our results indicate that leg band wear reduces sighting probabilities, thereby violating an important assumption in mark-recapture analysis. Severe leg band wear is equivalent to marker loss and is confounded with mortality and emigration. Known rates of marker wear and loss can be used to reduce biases and improve precision of the estimates (Arnason and Mills 1981, Nichols and Hines 1993).

Retention rates of nasal markers vary widely among published studies (Bartonek and Dane 1964, Sugden and Poston 1968, Greenwood 1977, Lokemoen and Sharp 1985), ranging from 20% retention in the first yr for Canada geese (*Branta canadensis*; Sherwood 1966), to 86% retention in over one yr for Blue-winged Teal (*Anas discors*) and Mallards (*A. platyrhynchos*) (Evrard 1996). Retention rates likely vary due to differences in materials and attachment methods, and to differences in behavior among species. Rapid loss rates in Canada Geese have been explained by the abrasive action of sand, gravel, and mud on the nylon monofilament connector during feeding (Sherwood 1966). Similarly, Harlequin Ducks dive and probe for benthic invertebrates beneath small rocks and cobbles, often highly abrasive from barnacle growth (Robertson and Goudie 1999), which likely causes poor nasal disc retention. Use of stainless steel pins (Doty and Greenwood 1974, Lokemoen and Sharp 1985) could improve disc retention if loss is primarily caused by weakening of the monofilament connector (Greenwood 1977). However, wear of the plastic shapes was observed for some individuals, and exposure to sunlight would eventually cause colors to fade.

High nasal disc visibility and short life span have both positive and negative aspects. High visibility make nasal discs attractive markers for winter studies when identification using leg bands is difficult, and for behavioral studies in which marked individuals must be identifiable during all behaviors. In contrast, the short life span of nasal discs make them less suitable for studies that require monitoring known individuals for extended periods of time. Rapid loss of a highly visible marker may, however, be an attractive quality for ethical and aesthetic reasons, particularly for species such as Harlequin Ducks, whose near-shore shore habitat and colorful plumage make them popular for wildlife viewing. Short retention times also ensure that any negative impacts on marked individuals, such as icing, entanglement, or decreased pairing success are minimized.

We did not detect a marker effect on the proportions of time spent in the behaviors measured in this study, possibly partly because our nasal markers were small relative to bill size. Proportion of time spent in maintenance did not increase and we observed no increase in bill scratching, which is frequently noted for nasal marked waterfowl (McKinney and Derrickson 1979, Koob 1981, Evrard 1996, Pelayo and Clark 2000). However, pairing success of males was reduced from 89 to 28% due to nasal marking, and fewer marked than unmarked females re-united with previous mates. Koob (1981) also observed that male Ruddy Ducks (*Oxyura jamaicensis*) with nasal saddles had low pairing success and rapidly lost their mates following marking. In contrast to our study, however, Ruddy Ducks with nasal markers decreased time spent in courtship and dramatically increased time spent in maintenance, the latter resulting almost entirely from maintenance behavior directed specifically at the nasal saddle (Koob 1981). Because nasal discs did not affect time budgets in our study, it seems likely that the effects of nasal discs on pairing success and repairing were not attributable to indirect effects, as was observed for Ruddy Ducks, but more likely reflect direct effects of nasal discs on appearance.

Colorful plumage of male Harlequin and other migratory ducks has been sexually selected and likely functions in female mate choice, male-male competition, or species recognition (Andersson 1994). Greater female choosiness due to a male-biased sex-ratio (Robertson and Goudie 1999) may explain why pairing success of male but not female Harlequin Ducks was reduced by nasal marking. Interestingly, even though female pairing success was unaffected by nasal markers, females with nasal discs were less likely to reunite with previous mates. Thus nasal discs may have reduced their attractiveness to experienced males, resulting in mate change, or affected individual recognition.

The impact that nasal discs had on pairing behavior suggests that nasal discs should not be used to study pairing success of males or repairing in either sex. However, because some aspects of courtship and pairing behavior may be relatively unaffected (e.g., timing of pairing, pairing success of females), and because pairing occurs during winter when birds rarely haul out, some such studies may benefit from nasal markers.

ACKNOWLEDGEMENTS

This study was possible only with the efforts of many individuals too numerous to list entirely. We give special thanks for the capture and marking of Harlequin Ducks and for data collection to Brian Arquilla, John Ashley, Sean Boyd, Pete Clarkson, Fred Cooke, Frank Elkins, Mary Jane Elkins, Dave Genter, Ian Goudie, Janet Hardin, Stewart Jackson, Greg Robertson, Cyndi Smith, Richard Swanston, and Ken Wright, and to Ian Goudie for initiating the banding project in 1993. We are grateful to Connie Smith for data management, to Barb Sherman for financial administration, and to Mary Jane Elkins and Frank Elkins for their hospitality on Hornby Island. We thank Alan Afton, Jim Anderson, Felix Breden, Sean Boyd, Dan Esler, Julian Fischer, Ian Goudie, and an anonymous reviewer for critical reviews of the manuscript. Funding was provided by the National Science and Engineering Research Council (NSERC) of Canada, Centre for Wildlife Ecology, Simon Fraser University, British Columbia Waterfowl Society, Institute of Waterfowl and Wetlands Research (IWWR), and the Canadian Wildlife Service.

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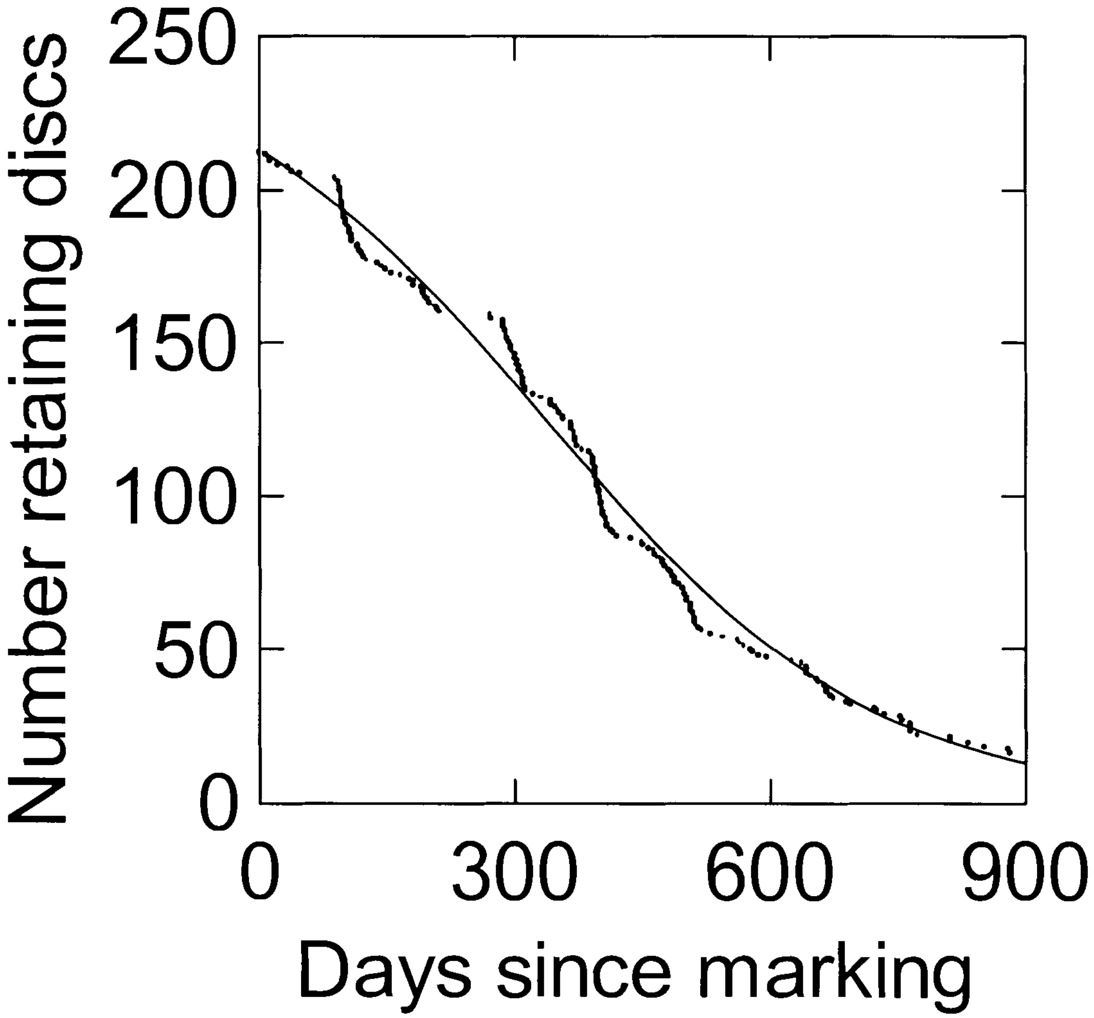

Figure 3.1. Number of Harlequin Ducks retaining nasal discs for up to 900 d after attachment in the Strait of Georgia, British Columbia, 1997-2001.

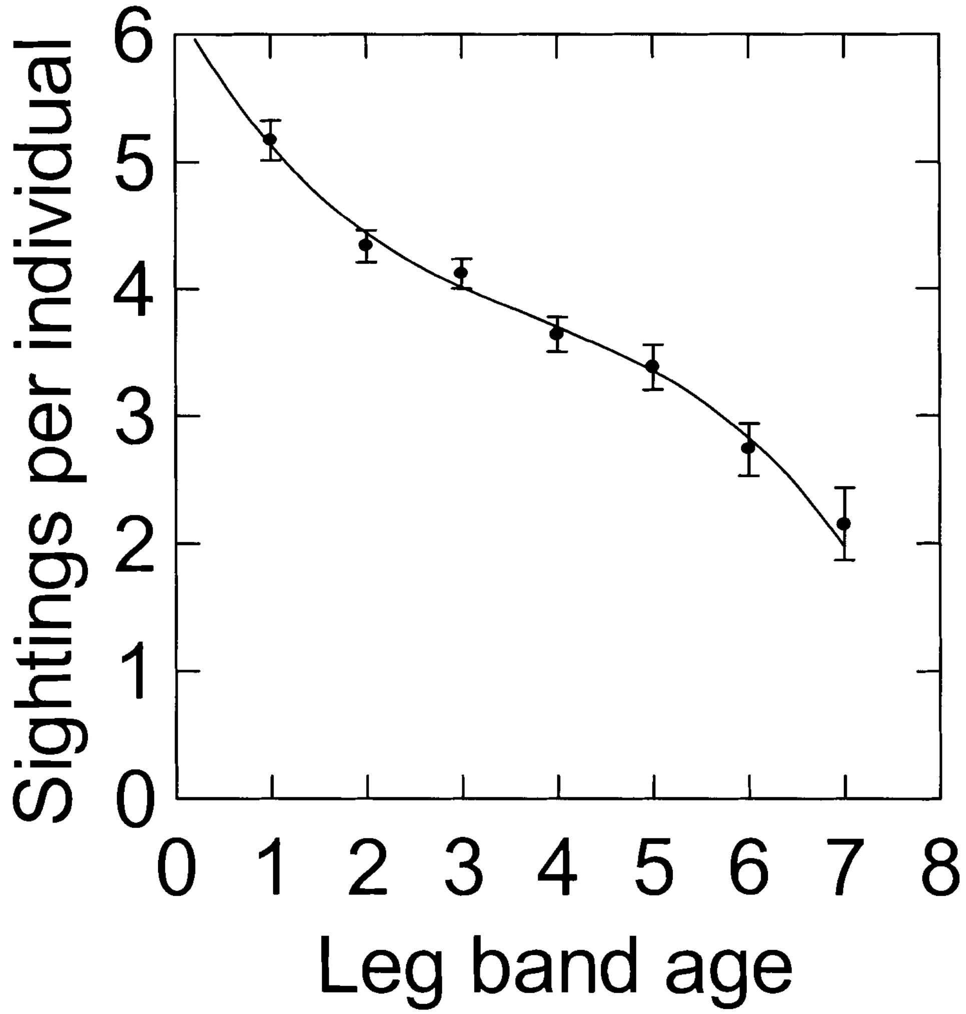

Figure 3.2. Relationship between leg band age and the mean (± SE) number of sightings per individual of Harlequin Ducks known to be alive and marked only with colored leg bands at Hornby Island, British Columbia, during the herring spawning period in March and April, 1997-2001. Sample size is given for each mean.

CHAPTER 4

SURVIVAL AND MOVEMENT OF POSTFLEDGING JUVENILE HARLEQUIN DUCKS

This chapter is provisionally accepted for publication in Wilson Bulletin.

ABSTRACT

Age specific survival and movement are important components of demography and population structure, and quantification of these rates is useful for management and conservation. However, information on the postfledging ecology of waterfowl species frequently is unavailable to managers. I studied postfledging survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia, using radio marking and capture-mark-recapture analysis of banded birds captured at coastal wintering areas. Survival of juvenile females was high, providing evidence that female winter survival may be similar among age groups. Radio-marked juvenile males were more likely to die than juvenile females, and juvenile males had lowest local survival rates of all sex-age classes. Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and at least 25% ($n = 9$) of radio-marked females moved more than 30 km from their capture location. These results were unexpected, based on previous evidence for female philopatry and theories of male-biased dispersal in waterfowl, and suggest that males and females both likely contribute to gene flow and demographic connection among populations.

INTRODUCTION

The immature stage has been shown to play an important role in population dynamics in some waterfowl species (Coulson 1984, Cooch and Cooke 1991). However, information on postfledging survival and movement patterns frequently are unavailable to managers. Although age ratios may provide a measure of production for hunted species (Bellrose 1980) and for species with visually identifiable first-year plumage (Smith et al. 2001, Iverson et al. 2003, Rodway et al. 2003a), age specific survival rates are needed to estimate recruitment into the breeding population (Cooch and Cooke 1991, Perrins 1991, Anderson et al. 2001). Survival rates of juveniles generally are difficult to estimate. Juveniles can be difficult to identify or capture, frequently resulting in small sample sizes. Also, survival rates often are confounded by juvenile dispersal from study areas, and dispersal can be difficult to assess without simultaneous sampling of neighboring populations (Clobert and Lebreton 1991). Thus, information on dispersal is needed to separate mortality from emigration (Lebreton et al. 1992), which is an important distinction for large scale management of populations. In addition, although much emphasis has been placed on philopatry of waterfowl to breeding areas (Anderson et al. 1992), little attention has been paid to winter philopatry and dispersal (Robertson and Cooke 1999). Because many waterfowl pair during winter, it is the movements of unpaired individuals among wintering areas that largely influence the degree of genetic structuring among populations for many species (Rockwell and Barrowclough 1987). Information on movement patterns during winter also are important to the understanding of demographic connection among wintering populations (Esler 2000).

I investigated survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) captured at wintering areas. Harlequin Ducks breed at inland streams, winter at coastal areas, show delayed maturation, pair during winter, and form long term pair bonds (Robertson and Goudie 1999). Previous analysis for a small wintering population indicated that local (or apparent) survival (the probability of surviving and returning to the study area; Lebreton et al. 1992) of juvenile and subadult males was lower than that of adults, but that local survival rates of females did not differ among age groups (Cooke et al. 2000). Assuming that differences in local survival rates of young males and females were due to differences in emigration rates and not death, these results supported theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992), and suggested that dispersal of males resulted in a considerable amount of gene flow among populations. My objectives were to use radio marking to estimate survival and movement of juveniles during their first winter and to allow separation of mortality from emigration, to use capture-mark-recapture (CMR) analysis to compare local survival among sex-age classes, to determine whether age specific mortality rates should be incorporated into estimates of recruitment, and to test predictions of male-biased dispersal. I chose the juvenile age class because survival and movement rates during the first year of life are likely to differ most from that of mature birds and because information on postfledging ecology is lacking almost entirely, not only for Harlequin Ducks, but also for other sea ducks and many waterfowl species.

METHODS

Researchers captured juvenile Harlequin Ducks at coastal wintering areas using two methods. We captured 15 juveniles among older birds in drive traps designed to capture flightless molting adults from mid-August through mid-September, 1995-1998. In addition we specifically searched for juveniles and captured 19 of them using mist nets and decoys during the first half of September in 1999 and 2000. We captured juveniles on Hornby Island (49° 32' N, 124° 40' W) and on the east coast of Vancouver Island between Comox (49° 42' N, 124° 52' W) and Campbell River (49° 58' N, 125° 12' W) in the northern Strait of Georgia (Fig. 4.1), and at White Rock (49° 02' N, 122° 51' W) in the Lower Mainland, British Columbia. We identified juveniles by the finely vermiculated plumage on their breast, belly, and vent, their mottled yellowish legs and feet, and their dusky faces, full primaries, and notched tail feathers (Regehr et al. 2001), and sexed them by cloacal examination. We marked all captured juveniles with a United States Fish and Wildlife Service band on the left tarsus, and a colored, laminated plastic band uniquely engraved with two alpha numeric digits on the right tarsus. During September 2000, we also marked 15 juveniles (nine females, six males) with external radio transmitters attached mid-dorsally with subdermal wire anchors. We captured radio-marked juveniles at Hornby Island, Comox, and Willow Point (Fig. 4.1). Nine radios weighed 9 g each and had 2-cm wide wire anchors; six weighed 3 g each with 1-cm wire anchors. We distributed radio types equally between the sexes. Radio transmitters weighed a maximum of 2% body mass for all juveniles and were assumed not to affect behavior.

Researchers reported sightings of individuals marked with colored bands from 1995 to 2001 during the fall (August to October), when postjuvenile birds molt, and during spring (March), when many Harlequin Ducks aggregate at Pacific herring (*Clupea pallasi*) spawning sites (Rodway et al. 2003b). At these times birds spend less time feeding than during winter and frequently haul out on shoreline rocks. Two to several observers typically searched for marked birds for a number of days approximately equivalent to one to six weeks during fall, and one to four weeks during spring. From September to December 2000, I located juveniles with radio transmitters from land, or with fixed-wing aircraft. I conducted three telemetry flights in October and November and covered the northern Strait of Georgia, from the North end of Quadra Island to Nanaimo (Fig. 4.1) at least once, and most areas at least twice. I determined distances individuals had moved from capture locations using a handheld GPS unit or from measurements taken from marine charts. I report records during winter (mid-October through February) separately from those during spring (March) because movement during spring can be associated with aggregation at herring spawning sites (Rodway et al. 2003b). I could not compare movement distances between radio-marked males and females due to small sample size of surviving males (see Results). However, I was able to compare philopatry between the sexes by comparing proportions of all marked juveniles (captured before 2000) seen at their capture location during their second winter at the coast.

I was able to monitor survival of most juveniles carrying transmitters from September through November, until batteries failed or transmitters were lost, after which juveniles were resighted opportunistically. I confirmed death of radio-marked juveniles by pinpointing their transmitters to small areas (several m^2) of dense shoreline vegetation (two cases), or by retrieving the carcass (one case).

I estimated local survival rates and tested hypotheses that they differed by sex and by age (juvenile and postjuvenile) using sightings of all juveniles marked with bands (21 females, 13 males) and the CMR program MARK (White and Burnham 1999). I developed a candidate model set that included the models containing effects necessary to test my hypotheses and that were based on a-priori biological and sampling information (Lebreton et al. 1992, Anderson and Burnham 1999). Because sightings were recorded biannually (fall and spring), I estimated survival rates for six-month periods, with the juvenile age class considered to last for one year (two six-month periods). Biannual sightings permitted estimation of season specific survival and sighting rates, the inclusion of which I expected would improve model fit. Juveniles remain at the coast during their first summer and likely gain experience over time, suggesting that survival may be lower during winter (fall to spring) than summer (spring to fall); postjuvenile females incur costs of breeding during summer suggesting that their survival is likely higher during winter than summer (Robertson and Goudie 1999, Cooke et al. 2000). I also expected sighting rates to differ between fall and spring due to seasonal differences in observer effort and bird behavior. Models in the candidate model set therefore included those with and without the effects of age, sex, and season on survival, and with and without the effect of season on sighting rates (Table 4.1). I assumed that sighting probabilities did not differ by sex or age. Models with time dependence had too many parameters for the data to be fit properly. Competing models were ranked using Akaike's Information Criterion (AIC), which is based on the concept of statistical parsimony and is calculated as the best compromise between minimizing the number of parameters while maximizing model fit (Lebreton et al. 1992, Anderson and Burnham 1999, Cooch and White 2001).

I evaluated model fit and overdispersion with bootstrap goodness-of-fit testing (Cooch and White 2001). In this method, encounter histories are simulated using model parameters, generating simulated data sets that exactly meet model assumptions that individuals behave independently and that their rates are identical within classes (Lebreton et al. 1992). Comparison of observed and simulated model deviances then allows evaluation of model fit and estimation of the variance inflation factor, c-hat, a measure of the magnitude of overdispersion. I adjusted model fit for overdispersion and used the Quasi Akaike's Information Criterion ($QAIC_c$) to indicate models substantially supported by the data. I determined relative model support by the ratio of $QAIC_c$ weights. Effects of band wear (Regehr and Rodway 2003) were unlikely to bias estimates of juvenile survival rates because bands wear little during their first year, however, band wear likely caused the survival rates of the postjuvenile age class to be underestimated slightly.

I used Fisher's exact test to compare proportions of juveniles dying and remaining in their capture location. I set type I error rate at 0.05.

RESULTS

Among radio-marked juveniles, a greater proportion of males died (50%, $n = 6$) than did females (0%, $n = 9$; Fisher's exact test, $P = 0.044$). All deaths occurred within 46 days after capture. Two of the males that died were unusually light at capture (males N and O, Table 4.2). The death of the third male 46 days after capture (male K, Table 4.2) most likely was due to predation; four days earlier he had been observed 2 km from his capture location, feeding alongside two juvenile females. Based on sightings during and after the study period, I determined that ≥ 8 of the 9 radio-marked females (89%) survived the winter.

I contrasted 10 models in CMR analysis to test hypotheses that local survival rates differed by sex and age, and to estimate sex and age specific local survival rates (Table 4.1). Bootstrap goodness-of-fit testing with 1000 simulations revealed adequate model fit: the probability of a deviance as large or greater than that of the most general model was 0.12, and the variance inflation factor, c-hat, was estimated at 1.24. Three models had similar $QAIC_c$s (differing by < 2), thus they were fairly similar in their abilities to describe the data in a parsimonious manner and I drew inferences from this subset of models (Lebreton et al. 1992, Anderson and Burnham 1999). The most saturated of the three models estimated separate six-month local survival rates for juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31-0.80), postjuvenile males (0.94 ● 0.09 SE; 95% CI = 0.44-1.00), juvenile females (0.84 ± 0.08 SE; 95% CI = 0.61-0.95), and postjuvenile females (0.89 ± 0.06 SE; 95% CI = 0.71-0.96). Based on these rates I built an additional model in which survival of juvenile males was set different from all other sex-age classes (four parameters). This model was well supported by the data ($QAIC_c = 111.84$, with 3.4 times the support of the highest ranking model in Table 4.1), indicating that local survival of juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31-0.81) was different from all other sex-age classes, and that I was unable to detect differences in local survival among juvenile females, postjuvenile females, and postjuvenile males (0.88 ± 0.04 SE; 95% CI = 0.77-0.94). Models were improved consistently by including the effect of season on sighting rates (fall: 0.31 ± 0.09 SE; 95% CI = 0.16-0.51; spring: 0.95 ± 0.05 SE; 95% CI = 0.72-0.99), but inclusion of season specific survival rates did not improve model fit.

Of the three potentially surviving radio-marked males (Table 4.2), one may have left the study area (male L). I last detected his radio signal about 15 km south of his capture site, possibly over open water, 64 days after capture. Although I conducted a telemetry flight over the entire study area six days later, he was never found again. I could not locate the second male (male M) during winter but sighted him close to his capture location on Hornby Island during March, suggesting a lost or malfunctioning radio during winter. The third male (male J) was seen 10 km north of his Campbell River capture location four days after capture but was never sighted again thereafter. This male received a 3-g transmitter with a small subcutaneous anchor which he probably lost shortly after this sighting.

Of nine radio-marked females, I was able to determine the locations of eight during winter, and of seven during both winter and spring (Table 4.2, Fig. 4.1). I could not relocate one female (female A) because she lost her radio 7 km from her capture site soon after capture; she was confirmed alive during spring 2002. Female B was not resighted during spring, however, her wintering location at Quadra Island could not be revisited at that time. The mean maximum distances females were found from their capture locations were 14.0 km ± 6.3 SE (n = 8) and 13.2 km ± 5.7 SE (n = 7) during winter and spring, respectively.

I detected no significant difference between the sexes in the proportion of marked juveniles resighted at their capture location during their second winter (males: 29%, n = 7; females: 25%, n = 12; Fisher's exact test, P = 1.00).

DISCUSSION

Results of this study provide new information important to understanding the postfledging ecology and population dynamics of Harlequin Ducks. First, radio marking of juvenile females indicated that, contrary to previous evidence for philopatry (Robertson and Goudie 1999, Cooke et al. 2000), some juvenile females moved substantial distances during winter. Second, contrary to predictions from theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992), and assumptions of male-biased dispersal in young Harlequin Ducks (Cooke et al. 2000), proportions of banded male and female juveniles resighted at their capture locations during their second winter did not differ, suggesting equal dispersal rates. Third, radio marking in combination with CMR analysis indicated that first-winter survival of juvenile Harlequin Duck females was high, providing further evidence that female winter survival may be similar among age groups. Conclusions pertaining to female survival rates must, however, be treated with caution due to sample size limitations.

Results of this study also suggest that juvenile male Harlequin Ducks may be more likely to die than juvenile females, however, inferences regarding differences in survival between the sexes are weak due to small sample sizes of radio-marked birds. Although lower survival of juvenile males relative to the other sex-age classes also was supported by CMR analyses, the local survival rates estimated by CMR analysis reflect a combination of mortality and emigration, and large confidence intervals surrounding point estimates limit confidence in apparent differences. The reason for a higher death rate of male than female juveniles is not clear, but might be related to differences in vulnerability to predation resulting from differences in conspicuousness of plumage, or to differences in susceptibility to the effects of food shortage due to larger size and higher growth rate of males (Clutton-Brock 1986, Cooch et al. 1997). My results suggest that the assumption that low local survival of juvenile and subadult males reflects emigration and not mortality (Cooke et al. 2000) should be re-assessed.

Juvenile survival rates generally are lower than those of adults in waterfowl (Johnson et al. 1992), however most juvenile mortality occurs during the prefledging and migration periods (Nichols and Hines 1987, Francis et al. 1992, Johnson et al. 1992), and hunting mortality tends to be juvenile biased (Bellrose 1980). The high winter survival observed for juvenile Harlequin Duck females in this study therefore may at least partly reflect the fact that juveniles were captured after migrating to wintering areas and that hunting mortality is low for Harlequin Ducks on the west coast of North America (Robertson and Goudie 1999). Results of this study, in combination with that of Cooke and coworkers (2000), who primarily included subadult (second and third year) and adult (after third year) females in CMR analyses, suggest little difference in winter survival rates of female Harlequin Ducks with age, provided that juveniles have completed their first migration, and that these rates likely can be set equal for estimates of recruitment into the breeding population. However, the possibility remains that the similar adult and subadult female local survival rates observed by Cooke and coworkers (2000) were due to subadults having lower death rates balanced by higher emigration rates (Cooke et al. 2000). Also, conclusions pertaining to juvenile females remain tentative due to sample size limitations in this study. Clearly, size of the study area also may affect conclusions. Considering movement rates and distances observed in this study, reduced juvenile female local survival due to emigration would be more likely if the study area were small. Summer survival rates of juvenile and subadult females might be expected to be somewhat higher than those of adult females because at least some immature females do not breed and hence do not incur associated mortality (Robertson and Goudie 1999, Cooke et al. 2000).

Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and at least 25% of radio-marked females moved > 30 km from their capture location. These results were unexpected, based on previous evidence for juvenile female philopatry (Robertson and Goudie 1999, Cooke et al. 2000), and theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992). However, I was unable to compare movement distances between sexes. Dispersing juvenile male Harlequin Ducks may move greater distances than dispersing juvenile females, as has been observed for some other waterfowl species (Kirby 1976, Rienecker 1987, Baldassarre et al. 1988). One of three surviving radio-marked males may have left the study area, whereas no female did. Individuals that disperse greater distances are less likely to be resighted than those moving smaller distances. Thus, greater male dispersal distances, possibly in combination with higher death rates, could account for lower local survival of male than female juveniles.

Results of this study have implications for genetic and demographic population structure of Harlequin Ducks. Juvenile Harlequin Ducks are believed to leave inland breeding areas and arrive at coastal wintering areas in family groups accompanied by their mothers, at least when families are intact at the time of fledging (Regehr et al. 2001). In this study, juveniles of both sexes dispersed from their coastal capture locations, suggesting that both sexes likely contribute to gene flow among populations. Also, dispersal of females in addition to males increases the potential for demographic connection among populations because successful recolonization or rescue of extinct or reduced populations are dependent upon female movement (Avise 1995). Further study is required to test the idea that low local survival rates of juvenile males may be partly due to higher death rates, to resolve potential sex differences in juvenile dispersal distances, and to investigate what factors affect differences in dispersal strategies among individuals of the same sex. Exceptions to patterns of sex-bias in subsets of populations can aid in our overall understanding of the evolutionary forces shaping dispersal patterns.

ACKNOWLEDGEMENTS

I thank all those who participated in capturing, marking, and observation of juveniles. I especially thank B. Arquilla, R. Botting, P. V. Clarkson, M. S. Rodway, and K. G. Wright. I am grateful to W. S. Boyd for supplying transmitters and to W. S. Boyd and R. I. Goudie for advice with transmitter attachment, to C. J. Schwarz for advice on CMR analysis, to S. M. Sanders for providing a local anesthetic, to C. M. Smith for data management, and to B. F. Sherman for financial administration. I thank A. D. Afton, T. Arnold, W. S. Boyd, F. Breden, F. Cooke, D. Esler, A. O. Mooers, M. S. Rodway, J. A. Smallwood, P. Vickery, and an anonymous reviewer for critical reviews of the manuscript. Funding was provided by the National Science and Engineering Research Council of Canada, Centre for Wildlife Ecology, Simon Fraser Univ., British Columbia Waterfowl Society, Inst. of Waterfowl and Wetlands Research, and the Canadian Wildlife Service.

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Table 4.1. Candidate models ranked in order of increasing $QAIC_c$ indicate that survival rate differs by age (juvenile versus postjuvenile) and resighting rate differs by season (fall versus spring) for banded Harlequin Ducks, captured as juveniles, in the Strait of Georgia, British Columbia, 1995-2000. AIC_c values were adjusted for c-hat of 1.24.

Model description	Number of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
Survival rate differs by age, sighting rate differs by season	4	114.26	0.00	0.4552
Survival rate differs by sex, sighting rate differs by season	4	115.28	1.02	0.2728
Survival rate differs by age and sex, sighting rate differs by season	6	115.88	1.62	0.2020
Survival rate differs by age, sex, and season for the juvenile age class, sighting rate differs by season	8	119.21	4.95	0.0382
Survival rate differs by age, sex, and season for the juvenile age class and for postjuvenile females, sighting rate differs by season	9	120.17	5.91	0.0237
Survival rate differs by age, sex, and season for both age classes, sighting rate differs by season (general model)	10	122.32	8.06	0.0081
Survival and sighting rates are constant	2	138.56	24.30	0.0000
Survival rate differs by age, sighting rate is constant	3	139.65	25.39	0.0000
Survival rate differs by sex, sighting rate is constant	3	140.21	25.95	0.0000
Survival rate differs by sex and age, sighting rate is constant	5	142.07	27.81	0.0000

Table 4.2. Maximum movement distances from the capture sites of radio-marked juvenile female (f) and male (m) Harlequin Ducks during winter (mid-October through February) and during the herring spawning period in spring (March) in the northern Strait of Georgia, British Columbia, 2000-2001. At least 25% of females moved more than 30 km from their capture sites during winter and spring. Three of six radio-marked males died (marked with an asterisk). Locations are given in parentheses (see Fig. 1) for movement distances > 10 km.

				Winter location			Spring location	
Identity code	Sex	Mass at capture (g)	Capture location[a]	maximum movement distance (km)	months recorded[b]	number of records[c]	maximum movement distance (km)	number of records[c]
A	f	580	Comox	unknown[d]	–	–	unknown	–
B	f	570	Comox	48 (Quadra)	Oct. – Nov.	4	unknown[e]	–
C	f	515	Comox	3	Oct. – Feb.	9	4	4
D	f	500	Comox	7	Oct. – Jan.	7	3	1
E	f	485	Comox	3	Oct. - Feb.	8	1	1
F	f	610	Comox	2	Oct. – Feb.	7	35 (Hornby I.)	8
G	f	530	Hornby I.	36 (Comox)	Jan. – Feb.	3	11[f] (Bowser)	1
H	f	460	Hornby I.	1	Nov. – Jan.	3	4	4
I	f	535	Hornby I.	12 (Bowser)	Oct.	3	35 (Roberts Creek)	1
J	m	605	Willow Pt.	unknown[g]	–	–	unknown	–
K*	m	590	Comox	2	Oct.	1	–	–
L	m	565	Comox	15[h]	Nov.	1	unknown	–

Table 4.2. continued

				Winter location			Spring location	
Identity code	Sex	Mass at capture (g)	Capture location[a]	maximum movement distance (km)	months recorded[b]	number of records[c]	maximum movement distance (km)	number of records[c]
M	m	485	Hornby I.	unknown	–	–	2	6
N*	m	415	Hornby I.	–	–	–	–	–
O*	m	410	Hornby I.	–	–	–	–	–

[a] Juveniles were captured between September 3 and 14, 2000.

[b] Range of months during which records were obtained for winter location.

[c] Number of sightings and detections of radio frequency at winter or spring location, with maximum of one per day.

[d] Radio lost 7 km from capture location on tidal shelf; individual sighted during spring 2002.

[e] Winter location could not be surveyed during spring.

[f] Also seen once at Hornby Island, 2 km from capture location.

[g] Located four days following capture then suspect radio loss.

[h] Radio signal last indicated a location ~ 15 km south of capture site on 11 Nov.

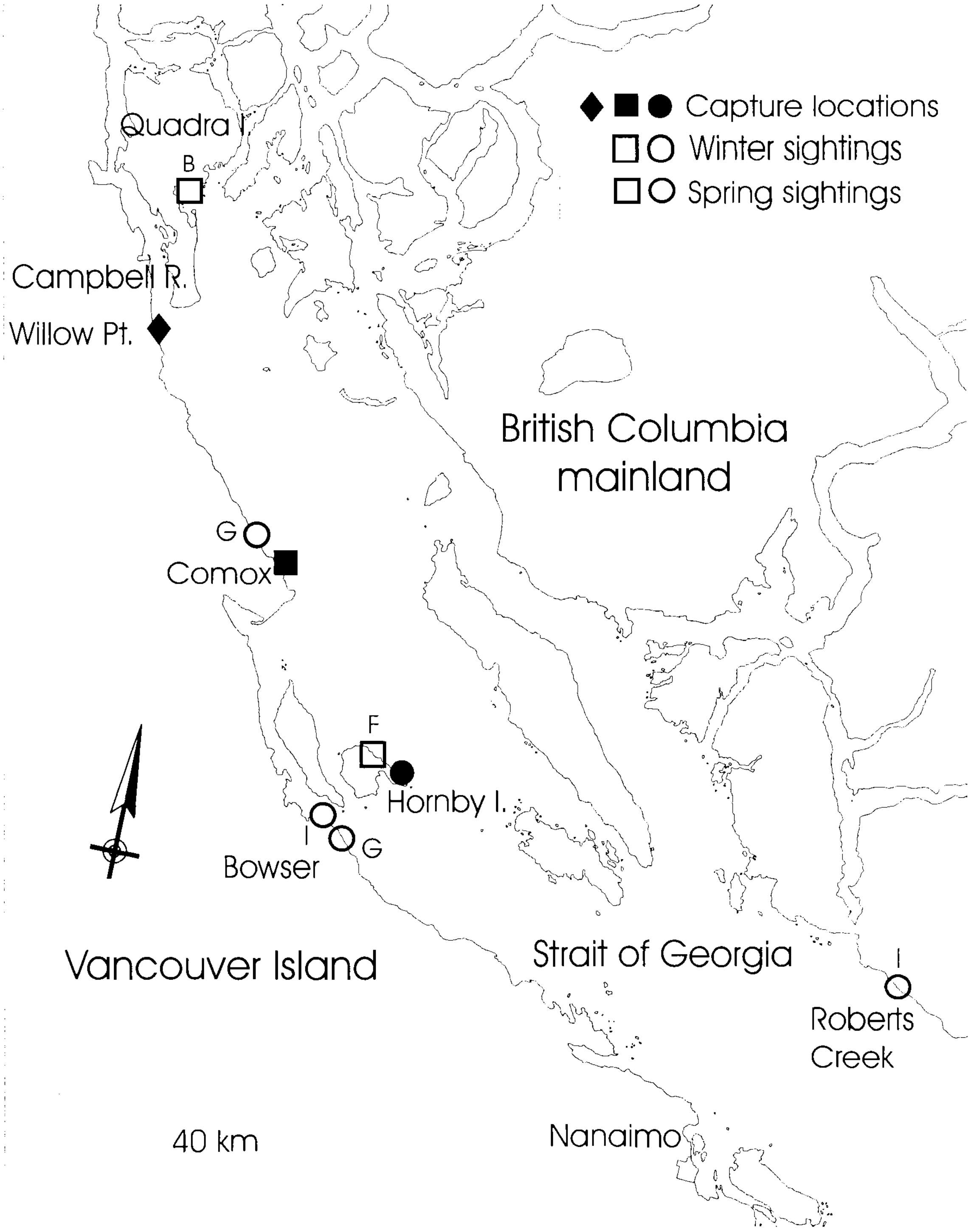

Figure 4.1. Four of eight juvenile radio-marked Harlequin Duck females moved > 10 km from their capture location in the Northern Strait of Georgia, British Columbia, Canada, 2000-2001. Capture locations are shown as solid symbols; winter (mid-October through February) and spring (March) sighting locations of females that moved > 10 km are shown as partially filled and unfilled symbols, respectively, with the type of symbol indicating the capture location from which the individual originated. Individual females are identified with letters (see also Table 4.2).

CHAPTER 5

MOVEMENT PATTERNS AND POPULATION STRUCTURE OF HARLEQUIN DUCKS WINTERING IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

Unpublished manuscript.

ABSTRACT

Movements of individuals from their place of birth to their place of reproduction or pairing determine the relatedness of potential mates and the genetic and demographic relationships of subpopulations. This, in turn, has implications for many aspects of a species' biology, including social structure, degrees of genetic and phenotypic differentiation found throughout the species' range, and ability to persist through time. I investigated movement patterns and population structure in the Harlequin Duck (*Histrionicus histrionicus*). Recent evidence suggested that juvenile Harlequin Ducks migrate to the coast with their mothers, which, in combination with winter pairing and strong philopatry to wintering areas in this species, may result in populations becoming genetically and demographically isolated. Movement patterns at wintering areas determine demographic and genetic connections among groups of wintering birds. Due to delayed maturation, long-term pair bonds, and winter pairing, it is particularly the movement patterns of young birds that have not yet paired that are important to genetic population structure. Gene flow models that can be used to evaluate genetic population structure from movements of individuals include the isolation by distance and stepping stone models, both of which assume that individuals move with highest probability to adjacent areas, and the island model, in which migrants are equally likely to come from any sub-population.

I tested hypotheses that 1) movement rates and distances of Harlequin Ducks differ by sex, as predicted by theories of male-biased dispersal for waterfowl, and by age, as is typically observed for many species, 2) movement rates are related to distance between locations, an important assumption of gene flow models, and 3) wintering populations of Harlequin Ducks are physically isolated to an extent that may imply genetic and demographic isolation. I used resightings of nasal-marked individuals to determine movement distances, and multi-stratum models in capture-mark-recapture analyses to estimate movement rates among locations. I found that movement distances and rates did not differ by sex, likely due to extreme philopatry of paired males, slightly reduced philopatry of unpaired males, and intermediate philopatry of paired females. Movement rates and distances were related to age, with individuals in their first and second winters moving farther and with higher probability than older ones. Movement rates were negatively related to the distance between locations, indicating that the isolation by distance and stepping stone gene flow models were the most appropriate. These models generated estimates of the among population component of genetic variance of less than 1% for the Strait of Georgia, indicating that, due to dispersal of young individuals, populations of Harlequin Ducks are unlikely to be genetically distinct at this scale, and that dispersal distances and effective population sizes are not unusual compared to other avian species. Estimates from the stepping stone model for an increased number of colonies did suggest that, due to their linear distribution along the west coast of North America, genetic differences could develop over their entire west coast range. Between and within year movement rates suggested that groups of wintering birds in the northern Strait of Georgia were unlikely to be demographically independent; however, low movement rates between the northern and southern strait suggested that populations may be demographically independent at this scale. Dispersal by both sexes indicated that there is potential for rescue or recolonization of declining or extinct groups. High movement rates and large dispersal distances of young birds relative to older birds suggest that survival rates of young birds are particularly vulnerable to underestimation. Emigration of some previously paired females indicates that female survival may have been underestimated in previous studies and that our concerns about population declines may have been overly pessimistic.

INTRODUCTION

Movement patterns of individuals are an important component of population dynamics that have ecological, evolutionary, and conservation implications (Mayr 1970, Wilson 1975, Clobert and Lebreton 1991, Nichols 1996, Simberloff 1988, 1998). From a demographic perspective, movement rates affect the likelihood of extinction, rescue, and recolonization of sub-populations (MacArthur and Wilson 1967, Levins 1969, 1970, Lande 1988, Hanski 1991). From a genetic perspective, movement of individuals from their place of birth to their place of pairing or reproduction determines the relatedness of potential mates and the genetic relationships of populations (Shields 1982, Slatkin 1985, Rockwell and Barrowclough 1987), which in turn has implications for the evolution of social behaviour, for potential genetic and phenotypic differentiation, and for the conservation of evolutionary potential (Mayr 1970, Frankel and Soulé 1981, Greenwood 1983, Barton 1992, Brandt 1992). Thus, an understanding of dispersal rates and distances relative to spatial distribution is important in determining the genetic and demographic connectedness, or structuring, of populations and the viability of populations and species over time.

Gene flow, defined as the movement and incorporation of alleles between populations, can be expected to counteract the diverging forces of genetic drift, mutation, and selection for local adaptation, which can act to produce local genetic differentiation (Mayr 1970, Slatkin 1985, 1987, Rockwell and Barrowclough 1987). Thus, it is the dispersal of individuals and their incorporation into new populations through pairing and reproduction that constitute gene flow, and the amount of gene flow among populations relative to the effects of diverging forces that determines genetic population structure. Natural populations typically show some degree of genetic structuring, ranging from total isolation to connection by regular and high rates of gene flow. Quantification of the distribution of genetic variation at the level of the species or a part of its range has been accomplished by partitioning the total genetic variation into within and among population components. The proportion of genetic variance found among populations (F_{ST}) is a frequently used measure of genetic population structure (Wright 1969, Slatkin 1985, Rockwell and Barrowclough 1987).

Estimates of gene flow are typically generated using either the direct approach, in which movements of individuals are directly measured, or the indirect approach, in which gene flow is inferred from genetic differences among populations assessed from analysis of genetic markers (Quinn and White 1987, Utter et al. 1987, Mitton 1994). Both approaches have strengths and weaknesses (reviewed by Slatkin 1985, 1987). The direct approach measures movement directly, but conclusions may be specific to the study area, simplifying model assumptions may limit usefulness of the estimates, and time scale of studies are typically short resulting in a potential for biased conclusions. In addition, because movement alone indicates only potential gene flow, assumptions may be needed that pairing and breeding follow dispersal, that is, that dispersal is effective. The indirect approach requires no assumptions about pairing and often it is possible to generate results applicable to large geographic areas; however, bias may result if the number of loci sampled are small or if allele frequencies are not in equilibrium. In addition, the genome reflects not only current conditions, but also those of the past. To what degree forces that operated on populations in the past are still in effect may be difficult to determine without other information. Ideally, both direct and indirect approaches are used to complement each other (Cooke 1987, Slatkin 1987, Avise et al. 1992, Whitlock and McCauley 1999, Scribner et al. 2001).

The relationship between spatial distribution and genetic and demographic population structure is more complex for species that have separate breeding and wintering distributions than for non-migratory species, and for those that pair at wintering areas rather than at breeding areas (Syroechkovsky et al. 1994, Cooke et al. 1995, Esler 2000, Scribner et al. 2001). Among birds, waterfowl are a case in point. Many species migrate from wintering to breeding areas, and many pair during winter (Bellrose 1980, Rohwer and Anderson 1988). Thus, for many species of waterfowl, effective management requires that demographic population structure needs to be defined for breeding and wintering areas separately (Esler 2000). Due to winter pairing, however, genetic mixing likely occurs primarily at wintering areas, either through movement during the wintering season, or through movement to new wintering locations following breeding (Syroechkovsky et al. 1994, Cooke et al. 1995). Although focus has been placed primarily on philopatry to breeding areas (Anderson et al. 1992), an understanding of the genetic population structure of many waterfowl species must be based on an understanding of distribution and movement patterns at wintering areas (Robertson and Cooke 1999). For species that pair at breeding area or during migration (e.g., Oxyurini, Aythya; Johnsgard and Carbonell 1996, Weller 1965), information on distribution and movement patterns at locations where pair formation takes place would be most important to understanding genetic population structure. Additional genetic mixing may occur at breeding areas through events such as extra pair copulation or re-pairing following mate or nest loss, the probabilities of which could vary widely among species and ecological or social conditions.

For conservation and management of populations, is it useful to determine whether population parameters differ among classes of individuals, and if so, to partition them accordingly (Perrins 1991). Movement patterns differ among age classes in many species, with young individuals generally having greatest dispersal tendencies (Dobson 1982, Greenwood and Harvey 1982, Horn 1983). Dispersal rates also frequently differ between sexes, with the pattern of the sex-bias depending on the mating system and the balance of costs and benefits of environmental and genetic factors (Greenwood 1980, 1983, 1987, Shields 1982, Bateson 1983, Pusey 1987). The typical avian pattern is one in which males defend breeding territories and both sexes contribute to parental care, thus the cost of dispersal is greater to males than to females because site familiarity is critical to territory defence, and females typically disperse. However, waterfowl are exceptions among birds. Dispersal from breeding areas is male-biased in many waterfowl species, likely because highly precocial young make male territory defense unimportant during brood rearing, resulting in predominantly female parental care. Thus, females gain greater benefits from philopatry than do males, and due to winter pairing, males follow females to their breeding areas (Greenwood 1980, 1983, Rohwer and Anderson 1988, Anderson et al. 1992). For wintering waterfowl, dispersal should still be male-biased if males cannot defend a critical resource

(Greenwood 1980), although this sex-bias may be confounded by winter sexual segregation or by the reunion of previous mates for species with long-term pair bonds that separate during the breeding season (Robertson and Cooke 1999).

Harlequin Ducks (*Histrionicus histrionicus*), like other sea ducks, have separate breeding and wintering areas and pair during winter. Harlequin Ducks breed at inland streams, winter at coastal areas, show high levels of philopatry to molting and wintering sites, have a male-biased sex-ratio and a mate-defense mating system, maintain long-term pair bonds, and show delayed maturation (Robertson and Goudie 1999). Recent evidence suggests that juveniles arrive at wintering areas in family groups with their mothers, at least when families are intact at the time of fledging (Regehr et al. 2001). Because individuals pair at wintering areas and move paired to breeding areas, and if one could assume that no further mixing occurs at breeding areas, then the geographic location of breeding areas would be unimportant to genetic population structure, whereas the distribution and movement of unpaired individuals at wintering areas would be critical. Strong philopatry to breeding and wintering areas, in combination with patchy habitat suitable to brood rearing during summer and feeding during winter, suggest that populations may be demographically independent and may be spatially connected as metapopulations (Hanski 1991, Esler 2000) during both seasons.

Several life history characteristics suggest that wintering populations of Harlequin Ducks could become genetically differentiated. If juveniles arrive at coastal locations with their mothers, and if their mothers are philopatric to specific coastal sites, then juveniles could winter at the same location as their siblings from multiple breeding seasons, and their mates could therefore be chosen from a subset of the population with a high probability of relatedness. However, genetic studies from populations in western North America have found no apparent fine scale genetic structuring (Scribner et al. 1998, Goatcher et al. 1999, Lanctot et al. 1999). These results caused researchers to postulate that lack of genetic differences among populations could be due either to recent changes in gene flow through processes such as range expansion or habitat alterations, or that more dispersal among wintering populations exists than that implied by reported high levels of philopatry (Lanctot et al. 1999). Dispersal of juveniles or unpaired adults from their initial coastal location would lead to genetic mixing and would counter the isolating effects of family migration and female philopatry.

Objectives of this study were to quantify movement rates and distances at wintering areas for the Harlequin Duck and to test hypotheses about movement that would contribute to our understanding of their genetic and demographic population structure. Unlike some other sea duck species, Harlequin Ducks typically spend their daylight hours during winter near shore and are relatively easy to observe and are therefore are an ideal sea duck for the study of winter movement patterns.

I tested hypotheses that movement rates and distances differed for individuals of different sex and age classes. Based on theories of male-biased dispersal in waterfowl, males were hypothesized to disperse greater distances and with greater rates than females. Movement rates and distances also were predicted to be higher for young than for older individuals based on expected differences in costs and benefits. Although some costs and benefits of philopatry may be equivalent among age groups, given that Harlequin Ducks form long-term pair-bonds and that older birds are more likely to be paired than young birds, younger individuals are less likely than older individuals to be constrained to site faithfulness for the purpose of reuniting with a mate. Young individuals also may gain less from some ecological benefits, such as site familiarity, relative to older individuals that may have invested more time becoming familiar with an area (Nichols and Hines 1987). Tests of these hypotheses are important to the advancement of dispersal theory and to interpretation of movement patterns with respect to demographic and genetic connectedness of populations. The movement of unpaired individuals is most important to genetic population structure, and among species with male-biased sex ratio, long-term pair bonds, and delayed maturation, age and sex are associated with paired status. Partitioning movement rates by sex and age also improves our understanding of the demographic connection among populations and improves our ability to interpret sex and age-specific local survival rates, which tend to be underestimated due to movement out of the study area (Clobert and Lebreton 1991).

The relationship between movement and distance between locations is important to assumptions of demographic and gene flow models. Distances between islands are critical to immigration and colonization rates in demographic models (MacArthur and Wilson 1967, Levins 1970, Hanski 1991). Similarly, gene flow models differ conceptually in the spatial distribution of individuals and in the means by which dispersers are incorporated into recipient populations (Wright 1969, Rockwell and Barrowclough 1987). The isolation by distance and stepping stone models, while differing in the distribution of individuals (continuous or colonial, respectively), both assume that dispersing individuals move with highest probability to adjacent locations. In contrast, the island model assumes that migrants are sampled randomly from the entire population and are therefore equally likely to come from any of the sub-populations. The island model has been used to estimate gene flow for Snow Geese (*Anser caerulescens*) that pair at wintering areas where several breeding colonies aggregate; thus mates can potentially be chosen from all sub-populations (Cooke et al. 1975, Rockwell and Cooke 1977, Rockwell and Barrowclough 1987).

The dispersed wintering distribution of Harlequin Ducks suggests that assumptions for the island model could realistically be met only if individuals disperse widely and randomly among coastal areas on their return from inland breeding areas. I therefore tested the hypothesis essential to the use of demographic and gene flow models that movement rates between years are related to distance between locations.

Lastly, I tested the hypothesis that, given evidence for winter philopatry and family migration, wintering populations of Harlequin Ducks are physically isolated, which would imply that they also are genetically and demographically isolated. This hypothesis addresses the question of whether lack of genetic differentiation in western North American populations are more likely to reflect historical population structure or current movement patterns. I used results from movement analyses in conjunction with gene flow models to estimate the among population component of genetic variance and compared this to what has been estimated for other avian species and to what has been estimated for Harlequin Ducks using the indirect approach. Movement distances and between year movement rates were used to estimate gene flow among wintering populations. Within year movement rates represent a component of between year movement rates and, as such, were not used to estimate gene flow; however, within year movement rates were used to help identify factors that may affect between year movement rates and gene flow. Between and within year movement rates also were used to evaluate the scale of potential demographic independence of populations.

METHODS

Capture and marking of Harlequin Ducks

Capture locations within the Strait of Georgia were White Rock, Hornby Island, Comox, Campbell River, and Quadra Island, British Columbia, Canada, and Point Roberts, Washington, USA (Fig. 5.1). Over 2,500 Harlequin Ducks were captured during their wing molt (July through September) in 1994 – 2000 by corralling them into a drive trap erected along the shoreline (Clarkson and Goudie 1994). All captured individuals were marked with a metal United States Fish and Wildlife Service band on the left tarsus, and a laminated plastic 2-digit alphanumerically encoded color band with code cut out to expose the inner color layer on the right tarsus. Individuals were sexed by plumage and were aged as after-third year (ATY), third year (TY), or second year (SY) by absence or length of the Bursa of Fabricius (Kortright 1942, Mather and Esler 1999), or as hatch year (HY) by plumage (Regehr et al. 2001). Due to low numbers of HY birds captured, 15 additional HY birds were captured in September 2000 using mist nets and decoys.

During August and September 1999, 208 Harlequin Ducks captured in the northern Strait of Georgia were marked with nasal discs in addition to leg bands. HY birds captured in September 2000 also received nasal discs. Discs of four shapes (circle, diamond, rectangle, triangle) and eight colors (aqua, black, blue, green, orange, red, white, yellow) were cut, 9 mm maximum diameter, from Darvic plastic (a PVC plastic resistant to UV light). We attached disks using a 36 kg monofilament fishing line connector and marked each individual with a unique combination of two nasal discs attached on either side of the nares, as described by Bartonek and Dane (1964).

Resighting of marked individuals

Marked individuals were identified with 15-60 X spotting scopes throughout the fall, winter, and spring, from fall 1994 to spring 2001. Most sightings were recorded during July – October, when the annual fall molt takes place, and during March, when large numbers of Harlequin Ducks congregate at Pacific herring (*Clupea pallasi*) spawning sites (Rodway et al. 2003a). During these periods birds spend less time feeding than during winter and frequently haul out on shoreline rocks. Paired status was recorded for marked individuals when possible. Birds were recorded as paired if they remained in close proximity, behaved synchronously, and exhibited defense behaviors such as mate guarding (Gowans et al. 1997).

Movement distances of nasal-marked individuals

Movement distances of birds marked with nasal discs in August and September 1999 were assessed during a mid-winter exhaustive shoreline survey in the northern Strait of Georgia (November 1999 – February 2000), and opportunistically in March and April 2000. Mid-winter shoreline surveys covered all shoreline, with the exception of inlets, from Chatham Point in the north to Nanoose in the south (Fig. 5.1; see also Rodway et al. 2003b), and were designed to include shoreline that fell within a minimum of 50 km from all capture locations. Surveys were conducted by walking beaches where Harlequin Duck densities were high or from a Zodiac 16' inflatable boat where densities were low. All Harlequin Ducks found were inspected for nasal discs with binoculars or 15-60 X spotting scope. Because a second exhaustive boat survey was not feasible in winter 2000-2001, I marked HY birds captured in September 2000 with external radio transmitters (in addition to bands and nasal discs) and located them from land, or from the air using fixed-wing aircraft. Three HY birds that were known or suspected to have lost their radios shortly after capture were excluded from the sample (n = 12 remaining). Three telemetry flights were conducted in October and November and the entire area in which boat surveys had been conducted the previous year was covered at least once, and most parts were covered at least twice. Movement distances from capture locations were recorded to the nearest kilometer using a handheld GPS unit or were measured from marine charts. Due to large-scale movements during the Herring spawning period in March (Rodway et al. 2003a), movements during the mid-winter period (November to February) were reported separately from those during the full wintering season (November to April). When more than one sighting was recorded, maximum movement distances from the capture site were used in comparisons.

Although many Harlequin Ducks in western North America molt and winter in the same location, some individuals have separate molting and wintering locations (Breault and Savard 1999, Robertson et al. 1999, 2000). Movement distances of individuals marked with nasal discs during molt therefore could reflect dispersal, but also could reflect regular seasonal movement between separate molting and wintering areas. To test whether differences in movement distances among sex-age classes reflected differences in dispersal tendencies or differences in the tendency to move seasonally between a separate molt and winter location, I compared the proportions of individuals among sex-age classes wintering in a different location than that in which they had molted during two consecutive molt seasons. I included only marked individuals for which at least one set of three consecutive molt-winter-molt locations was known. If differences in movement distances among classes reflected differences in their tendencies to use separate molt and winter locations, proportions of individuals wintering and molting in separate locations would likely differ among classes. Alternatively, if differences in movement distances reflected differences in their dispersal tendencies, then the proportion of birds with separate molt and winter locations should be similar among classes.

Movement rates between and within years

I used sightings and recaptures from 2,550 Harlequin Ducks captured in the Strait of Georgia (243 in the southern Strait of Georgia [White Rock and Point Roberts] and 2,307 in the northern Strait of Georgia [Hornby Island, Cape Lazo, Campbell River, and Quadra Island]) from 1994 to 2000 in multi-stratum models in the CMR program MARK (see below) to determine between and within year movement rates among locations and to test hypotheses that movement rates differed by sex, age, and distance between locations. I estimated movement rates among five locations which were defined based on capture sites within the Strait of Georgia, with capture sites Campbell River and Quadra Island combined into one location (hereafter "Campbell River") (Fig. 5.1). Additionally, these five locations (Campbell River, Comox, Hornby, Point Roberts, and White Rock) were grouped into two regions for some analyses: 1) Southern Strait (SS region), composed of White Rock and Point Roberts, and 2) Northern Strait (NS region), composed of Hornby, Comox, and Campbell River. Fine-scale data collection on Hornby Island, where sightings were recorded at 13 sites around the island, allowed the analysis of shorter-range movements believed to reflect differences in home range size. These sites also were grouped into two regions for between year mark-recapture analyses: the north coast and the south coast of Hornby Island. Movement rates between pairs of locations could either differ depending on direction of movement (direction-specific), or could be constrained to be the same for both directions.

Annual between year movement rates primarily were estimated from sightings and recaptures during the molt period (July – October); thus between year movement rates were generated from one molt period to the next. I also used winter (November – February) sightings to generate between year movement rates from one winter to the next, but because birds rarely haul out during winter, analyses could be conducted for adults only and there was little power to detect differences among sexes. For the estimation of within year movement rates, I present movement rates between locations from the molt to the winter season and from the winter to the herring spawn season (March) within the NS region, and from the molt to the winter season within the SS region. Unequal time intervals were calculated from mid-point to mid-point of the distribution of sightings for each season. When an individual was seen in more than one location in a season (observed for 46 [2%] and 1 [0.04%] of 2,307 individuals in the NS region, and 17 [7%] and 1 [0.4%] of 243 in the SS region, in a total of one and two seasons, respectively), one of the two locations was chosen randomly, weighted by the number of sightings in each location.

Estimation of survival rates was not an objective of this study; however, I estimated survival rates with a multi-stratum approach to allow comparison to survival rates from other studies. I used data from the NS region for the estimation of survival rates, and used data from two seasons, molt (July – October) and herring spawn (March), because this allowed partitioning of annual survival rates into a non-breeding (molt to spawn) and breeding (spawn to molt) component. The use of a multi-stratum analysis allowed incorporation of movement among locations and incorporation of potentially heterogeneous location-specific sighting rates.

Paired status

Sex and age-specific movement rates generated by CMR analyses provided some information on movement patterns in relation to paired status due to associations between paired status and sex and age in Harlequin Ducks. In order to supplement these results and aid in their interpretation, I was able conduct some analyses using information on paired status directly. I included three sex-paired status groups: paired males, unpaired males and paired females. Unpaired females are rare due to the male-biased sex ratio, thus they were not included in these analyses. I first used multi-stratum CMR analyses to estimate movement rates of the three sex-paired status groups. Because CMR analysis requires that each encounter history (one per individual) is assigned to one group entirely, I included only individuals that had been assigned paired status for the majority of years in which they had been sighted and that this was consistent among years. Such individuals generally could be grouped as "paired" or "unpaired". I only considered unpaired records if they were recorded after 31 December. Because individuals sometimes change their paired status and because paired status frequently is not known, sample size for CMR analysis using only individuals that could be grouped as paired or unpaired was small.

Secondly, I supplemented CMR analysis with an examination of the proportion of marked individuals with known paired status for any one year that were detected changing molting or wintering locations. For this comparison, because I evaluated paired status for each individual on a year by year basis, requirements for confirmation of paired status were more stringent than in the above analysis where data from multiple years provided information used to classify individuals into generally paired or unpaired groups. For this year by year analysis, I considered paired status confirmed for an individual for any one year if I had at least two consistent paired status records from opportunistic sightings, or if birds were identified as paired or unpaired during behavioural observations conducted for other research purposes (Rodway 2003). To ensure that paired status was correct for the end of the pairing season, unpaired records were accepted only if they were from 1 March or later. Only one case per individual was accepted, unless paired status changed (e.g., a paired individual became unpaired) or fidelity changed (e.g., a paired individual that had been philopatric once or more often [considered first case], then changed locations [second case]). For between year analyses, I determined the frequency with which individuals were faithful to their molting or wintering locations in two consecutive years, considering their confirmed paired status at the end of the pairing season for the first of the two years. For within year analyses, I determined the frequency with which individuals remained, during winter, in the location in which they had molted, during any one year for which paired status was confirmed. Comparisons among sex-paired status groups were done at the coarse scale of locations within the entire Strait of Georgia and at the fine scale of sites on Hornby Island.

Due to some individuals moving to areas where little or no band-reading took place, and due to the bias inherent in selecting a sample of individuals for which paired status was known for more than one year, proportions of individuals detected changing locations were undoubtedly biased low. However, proportions of individuals changing locations were considered comparable among sex-paired status groups because it seemed reasonable to assume that there was no difference in sighting probability among sex-paired status groups at any of the locations where sightings were recorded.

Statistical analyses

Statistical comparisons

I used Kruskal-Wallis tests to determine the effects of sex and age on movement distances and used *G* tests to compare proportions. Type I error rate at was set at 0.05. I report means ± SE.

Multi-stratum CMR analyses

model notation and assumptions

I used multi-stratum models in the CMR program MARK (Brownie et al. 1993, White and Burnham 1999, Cooch and White 2001) to estimate movement rates. Multi-stratum models permit estimation of movement rates (ψ) in addition to estimates of survival (S) and sighting rates (p) by separating the joint probability of surviving and making a transition between two states into a survival and a movement component. For my purposes, transitions between states represent movement among geographic locations. Following Cooch and White (2001),

p_i^s = the probability that a marked animal alive in location s at time i is recaptured or resighted at time $i+1$,

ϕ_i^{rs} = the probability that an animal alive in location r at time i is alive and in location s at time $i+1$.

The joint probability of surviving from i to $i+1$ and making a transition from r to s, ϕ_i^{rs}, is then decomposed into survival and movement components, such that

$$\phi_i^{rs} = S_i^r \psi_i^{rs}$$

where

S_i^r = the probability that an animal survives in location r from time i to time $i+1$, and

ψ_i^{rs} = the conditional probability that a marked animal alive in location r at time i is in location s at time $i+1$, given that the animal is alive at time $i+1$.

From the above we see that an assumption of multi-stratum models is that survival from time i to $i+1$ depends only on the location in time i. In other words, survival is estimated specific to location r, and an animal is assumed to survive the interval in location r first, then move to location s. Living marked individuals also are assumed to be in one of the locations at all times, i.e., $\sum \psi_i^{rs} = 1$.

Multi-stratum models also share the general assumptions of CMR analyses: all individuals have an equal chance of being captured and all marked individuals have an equal chance of being recaptured or resighted, individuals behave independently of each other, marks are not lost or missed and do not affect behaviour, and all samples are instantaneous. Due to differences in sighting probability between colored leg bands and nasal discs (Regehr and Rodway 2003), all mark-recapture analyses included only sightings from individuals identified by their leg bands. Although leg band wear has been reported for Harlequin Ducks (Regehr and Rodway 2003), and clearly is a concern for the unbiased estimation of survival rates, movement rates are estimated from survivors and, provided that leg band wear does not differ among locations, are not biased. Model notation follows Cooch and White (2001).

model selection and goodness of fit

I developed sets of candidate models that included the effects necessary to test hypotheses of interest and that were based on a-priori biological and sampling information (Lebreton et al. 1992, Anderson and Burnham 1999). Effects included in the estimation of sighting and survival rates were chosen with the objective of maximizing overall model fit; effects included in the estimation of movement rates were those needed to test hypotheses and to generate movement rates of interest. Competing models were ranked using Akaike's Information Criterion (AIC), which is based on the concept of statistical parsimony and is calculated as the best compromise between minimizing the number of parameters while maximizing model fit (Lebreton et al. 1992, Anderson and Burnham 1999, Cooch and White 2001). Because parametric goodness of fit tests have not been developed for multi-stratum models (Cooch and White 2001), randomizations were used to evaluate the G-statistic for model fit (Roff and Bentzen 1989, B. Smith, pers. comm.) and to estimate the variance inflation factor, c-hat, which is a measure of the magnitude of overdispersion (lack of fit of the model to the data). This ensured that models adequately fit the data and that model ranking and measures of confidence were appropriate given model fit. I conducted randomizations to compare observed frequencies of encounter histories to simulated values generated by model parameters and the binomial distribution. C-hat was calculated as the G value from the observed data divided by the average G value from 1,000 randomized values based on simulations. Model fit was adjusted for overdispersion and the Quasi Akaike's Information Criterion ($QAIC_c$) was used to indicate models that were substantially supported by the data. The ratio of $QAIC_c$ weight was used to determine the comparative support received by competing models. When two or more models received very similar support ($\Delta QAIC_c < 2$) this meant that they were fairly similar in their abilities to describe the data in a parsimonious manner. In such cases I drew inferences from this subset of models (Lebreton et al. 1992, Anderson and Burnham 1999) and used model averaging to generate estimates weighted by model support, thus incorporating model selection uncertainty into estimates. Exceptions were the small data sets used for analyses of paired-status effects; for these I present estimates from the most highly parameterized model in a subset of models with similar $QAIC_c$s, because models with few parameters tend to be favored when small sample size is very small.

models including effects of sex and distance between locations

I used data collected during molt from the entire study area (5 locations) to test for sex effects and the effect of distance between locations on annual between year movement rates among molting locations. Effects included in candidate models were time (for survival and sighting rates), sex (for survival and movement rates), location (for survival, sighting and movement rates), and distance between locations (for movement rates). Distances between locations were incorporated into model structure by modifying the design matrix (Cooch and White 2001).

I used data collected during winter and analyzed data from the NS and SS regions separately to test for sex effects on annual between year movement rates among wintering locations. Effects included in candidate models were sex (for survival and movement rates) and location (for survival, sighting and movement rates). Time dependent models had too many parameters for the data and were not included.

For analysis of sex effects on within year movement rates, effects included in candidate models were time (for survival and sighting rates), season (for sighting and movement rates), sex (for survival and movement rates) and location (for survival, sighting, and movement rates).

age models

For the analysis of age effects on between year movement rates I used data from the molt season within the NS region (3 locations) and at the fine scale of regions on Hornby Island (2 locations). Data limitations within the SS region precluded its use for these analyses. Two age categories were defined: "young" (individuals aged two years or less), and "adult" (individuals older than two years). Thus individuals aged HY at capture spent the first two years in the "young" category, those aged SY at capture spent only one year in the "young" category, and those aged TY or ATY at capture spent all years in the "adult" category. Effects included in candidate models were time (for survival and sighting rates), age (for survival and movement rates), and location (for survival, sighting, and movement rates). Analyses of age effects on within year movement rates also were confined to the NS region; candidate models included effects listed for between year models, above, but additionally included effects of season for sighting and movement rates.

models including effect of paired status

Only the NS region was used for multi-stratum CMR analysis on paired-status for between and within year analyses. Molt sightings were used for between year analyses. Effects included in candidate models were sex (for survival and movement rates), location (for sighting, and movement rates), and paired status (for movement rates). Time dependent models had too many parameters for the data and were not included.

Estimating the among population component of genetic variance

I used movement distances and rates for young (HY and SY) Harlequin Ducks to measure gene flow. Only movement for young individuals was considered because, due to delayed maturation and long-term pair-bonds in Harlequin Ducks, only HY and SY individuals can confidently be assigned unpaired status. I then used estimates of gene flow to calculate the among population component of genetic variance (F_{ST}). Based on the relationship of distance between locations and between year movement rates (see Results), and because Harlequin Ducks in the Strait of Georgia have a spatial distribution that can be considered an intermediate between colonial and continuous (see Rodway et al. 2003b), I estimated F_{ST} using both the isolation by distance and stepping stone gene flow models (Wright 1943, 1946, Kimura and Weiss 1964, Rockwell and Barrowclough 1987). Estimates of F_{ST} should be considered rough order of magnitude estimates only, due to simplifying model assumptions (e.g., spatial distribution of Harlequin Ducks does not fit neatly into any model), sampling error inherent in the generation of movement distance distributions and movement rates, limited study time scale, and adjustment of effective population size from census population size by estimation of some life-history parameters that are poorly known (Rockwell and Barrowclough 1987, Bohonak 1999) .

Isolation by distance gene flow model

The isolation by distance model was applied to *Drosophila* (Dobzhansky and Wright 1943, Wright 1943) and modified for avian species by Barrowclough (1980) and Rockwell and

Barrowclough (1987). Because individuals are assumed to be continuously distributed, dispersal distances are used as a measure of gene flow. Neighbourhood size (Ne), defined as the number of individuals within a circle of radius twice the standard deviation of the dispersal distances, represents the effective population size of the area within which individuals can interbreed randomly, and is related to the density of individuals and their dispersal distances. Following adjustment for factors that reduce effective population size (Ne) relative to census population size (N_{census}) (e.g., biased sex-ratio, fluctuating population size; Crow and Kimura 1970), F_{ST} can be estimated from the effective neighbourhood size and the number of demes in the species range.

Following Rockwell and Barrowclough (1987), overall gene flow, also called the root-mean-square dispersal distance, σ_T, was estimated from movement distances of nasal marked birds as $\sqrt{(\frac{1}{2N}\sum_{i=1}^{N} x_i^2)}$, where x_i is the distance moved by individual i from its natal site to its site of reproduction or, in this case, pairing (Wright 1946, Crumpacker and Williams 1973). Neighbourhood size (Ne) was estimated from overall gene flow and the density of individuals, such that $Ne = 4\pi\rho\sigma_T^2$, where ρ is the density of individuals. F_{ST} was then estimated as $(1 - Kt_k)/(1 + Kt_k)$, where Kt_k is defined as the infinite series

$$\begin{aligned} &\exp-[(1/Ne)\times[\ln(K-0.5)+0.5772] \\ &+(1/(2Ne^2))\times[1.6449-2/(2K-1)] \\ &+(1/(3Ne^3))\times\{1.202-2/(2K-1)^2]+....] \end{aligned}$$

and K is the total number of demes in the species' range (Wright 1951).

Barrowclough (1980) calculated the overall gene flow from juvenile and adult dispersal components, however, I used only movement distances from HY and SY individuals to estimate σ_T (see above), and the time factor included by Barrowclough (1980) for the number of times adults breed after moving was omitted. Because some adults are unpaired, omitting all adult movement contributes to overestimation of F_{ST} . I estimated a density of individuals using survey results of 6,825 Harlequin Ducks counted in the northern Strait of Georgia in mid-winter 1999-2000 (Rodway et al. 2003b), and estimating the total survey area at roughly 7,500 km^2. Thus, I estimated a density (ρ) of 0.91 birds per km^2. I estimated the number of demes in the range of the species in western North America based on total estimated numbers of Harlequin Ducks (Robertson and Goudie 1999) divided by neighbourhood size.

Because Ne refers to effective population size, I adjusted the census population size for male-biased sex ratio, variance in offspring number, and overlapping generations (Wright 1938, Nei and Imaizumi 1966, Crow and Kimura 1970). To adjust for a male-biased sex ratio (1.51 males : 1 female; Rodway et al. 2003b), I estimated the effective population size as twice the number of females (Wright 1938). Variance in offspring number is poorly quantified for Harlequin Ducks but is thought to be high because a variable proportion of females appear not to breed each year (Robertson and Goudie 1999). Assuming that roughly two-thirds of females produce no young, and the remainder produce between 1 and 6, I roughly estimated the variance in offspring number ($\sigma^2_{offspring}$) at 3 and calculated Ne as $4N_{census}/(\sigma^2_{offspring}+2)$ (Meffe and Carroll 1994). The effect of overlapping generations on population size was estimated from the equation $Ne = Nm\lambda$, where Nm is the number born per year that are able to reach the mean reproductive age, λ (Nei and Imaizumi 1966, Baker 1981). Making rough assumptions of a stable population, an overall annual mortality of 0.2, and mean reproductive age of 4 years, I estimated overlapping generations to reduce N_{census} by a factor of 0.8. Fluctuations in population size over time also reduce Ne relative to N_{census}, with Ne considered approximately equivalent to the harmonic mean of generation by generation population sizes (Spiess 1989); however, because such data are lacking, I assumed constant population sizes over time. I conducted sensitivity analyses to evaluate the robustness of F_{ST} to factors used in its estimation.

Stepping stone gene flow model

The stepping stone model (Kimura and Weiss 1964) assumes that individuals are distributed in colonies and that migration occurs to adjacent colonies at a certain rate. Thus, the fraction of the total number of recruits in one colony that are from adjacent colonies represents an estimate of gene flow. Following Kimura and Weiss (1964) and Rockwell and Barrowclough (1987), F_{ST} was estimated as $1/[1+2NeC_0]$, where $C_0 = 2[2m_{adj}m_{\infty}]^{0.5}$, Ne is the effective population size of colonies, m_{adj} is the gene flow from adjacent colonies, and m_{∞} is the long-range gene flow, formally equivalent to mutation (10^{-6}; Rockwell and Barrowclough 1987), and defined as the rate at which genes are uniformly spread over the entire species' range. A correction factor used to adjust F_{ST} for a finite number of colonies in a reduced portion of the species range is given in Kimura and Weiss (1964, p. 574).

I estimated F_{ST} for Harlequin Ducks in the Strait of Georgia by dividing the entire area into six colonies (Fig. 5.2). I let each of the areas used as locations for CMR analysis in the northern part of the study area represent one colony (Campbell River, Comox, and Hornby), and took census population sizes for these colonies from Rodway et al. (2003b). The colony surrounding Nanaimo was estimated to contain about 200 birds based on a survey of its northern portion (Rodway et al. 2003b). The Gulf Islands have only been partly surveyed and were estimated to contain 400 birds. White Rock and Point Roberts were combined as the sixth colony with a joint population of 200 birds. I took the harmonic mean of colony population sizes due to differences in population size among colonies (Wright 1969), and made further corrections for effective population size relative to census population size as described for the isolation by distance model above. I used between year movement rates from HY and SY birds among the northern three colonies to represent gene flow. Conversion of annual rates to rates per generation would result in higher movement rates, thus the use of annual rates contributes to overestimation of F_{ST}.

RESULTS

Movement distances of nasal-marked individuals

Of 220 birds marked with nasal discs in 1999 ($n = 208$) or with external radio transmitters and nasal discs in 2000 ($n = 12$), 193 (88%) were resighted at least once between November and April following marking. Maximum movement distances did not differ by sex but did differ by age, with young birds moving greater distances than older ones (Figs. 5.3 and 5.4). These relationships held whether considering the full wintering season (sex effect: Kruskal-Wallis: $H = 2.52$, $df = 1$, $P = 0.11$; age effect: Kruskal-Wallis: $H = 20.35$, $df = 3$, $P < 0.001$) or the mid-winter period only (sex effect: Kruskal-Wallis: $H = 0.11$, $df = 1$, $P = 0.74$; age effect: Kruskal-Wallis: $H = 10.61$, $df = 3$, $P = 0.014$). Of all sighted individuals, 69% and 78% were never seen more than 20 km from their capture locations, and 13% and 10% were seen more than 30 km from their capture location, during the full winter season and the mid-winter periods, respectively.

I found no evidence that young birds were more likely than were older birds to move seasonally between molt and winter locations. Proportions of individuals that molted in the same location in two consecutive molting seasons but had wintered in a different location in between did not differ among age classes (HY&SY: 3%, $n = 30$; TY: 3%, $n = 35$; ATY: 8%, $n = 200$; $G_2 = 1.86$, $P = 0.39$) and averaged 6% for all age classes combined. Proportions that had molted and wintered in the same location also did not differ among age classes (HY&SY: 83%, $n = 30$; TY: 80%, $n = 35$; ATY: 86%, $n = 200$; $G_2 = 0.85$, $P = 0.65$).

Movement rates between years

Sex and distance between locations

Between year movement rates estimated from sightings of leg-banded birds during the molt season were similar for males and females and including a sex effect in the estimation of movement rates did not improve model fit; however including a distance effect in the estimation of movement rates did improve model fit indicating that movement rates declined with increasing distance. The highest ranking model (lowest $QAIC_c$) included the effect of sex in the estimation of survival rates, location and time in the estimation of sighting rates, and distance between locations in the estimation of movement rates (Table 5.1). This model received 6 times the support of the next best model (ratio of $QAIC_c$ weights) which included the effect of sex in the estimation of movement rates in addition to distance. Thus I was able to reject the null hypothesis of no distance effect, but not the null hypothesis of no sex effect. Movement rates ranged from 5 in 100 individuals per year for locations separated by 15 km, to 1 in 1,000 individuals per year for locations separated by over 200 km (Table 5.2). Sex-specific movement rates generated by the second best model indicated that although point estimates were very similar among the sexes, rates for males were consistently higher than those for females for all distance classes (Table 5.3).

Between year movement rates estimated from sightings of banded birds during the winter season also were similar for males and females in both the NS and the SS regions, however, power clearly was low. For both regions, a subset of 3 (NS region) or 4 (SS region) models received similar support ($\Delta QAIC_c < 1.60$), and a sex effect was included in the estimation of movement rates for one model within the subset for both analyses (Tables 5.4 and 5.5). Model averaging generated movement rates of 0.009 ± 0.012 and 0.006 ± 0.009 for males and females, respectively, for the NS region, and movement rates of 0.053 ± 0.042 and 0.070 ± 0.050 from White Rock to Point Roberts for males and females, respectively, and 0.081 ± 0.083 and 0.099 ± 0.086 from Point Roberts to White Rock for males and females, respectively, for the SS region.

Age

Between year movement rates estimated from sightings of leg-banded birds during the molt season were greater for young individuals in their first and second winters than for older individuals at the coarse scale of movement among locations in the NS region. The two highest ranking models received similar support ($\Delta QAIC_c = 0.62$); both models included an age effect in the estimation of movement rates, and any model that did not received virtually no support (Table 5.6). The first of the two models included the effects of age in the estimation of survival rates, location and time in the estimation of sighting rates, and only age in the estimation of movement rates. The second model included the effects of age and of location for the young age class in the estimation of survival rates, location and time in the estimation of sighting rates, and location and age in the estimation of movement rates, with the location effect constrained to be the same regardless of the direction of movement. Model averaging provided age-specific movement rates among locations (Fig. 5.5).

Point estimates of between year movement rates also tended to be higher for young individuals than for older ones at the fine scale of movement between the north and south coasts of Hornby Island, although support for differences between age groups was less at this scale than at the coarse scale of movement within the NS region. At the fine scale of movement between the north and south coasts of Hornby Island, three models received similar support ($\Delta QAIC_c < 1.65$). These included effects of age in the estimation of survival rates, location and time in the estimation of sighting rates, and generated either a single movement rate, an age-specific movement rate, or a location-specific movement rate (Table 5.7). Model averaging provided estimates of movement for both age classes from the north coast to the south coast of Hornby Island (young: 0.078 ± 0.059; adult: 0.047 ± 0.014), and from the south coast to the north coast (young: 0.075 ± 0.059; adult: 0.044 ± 0.012).

Paired status

Seventy-seven males and 156 females had a consistent paired status in a majority of years sighted in the NS region and could be grouped as "paired" (both sexes) or "unpaired" (males only) for comparison of between year movement rates among sex-paired status groups using multi-stratum CMR analysis. I was unable to detect differences in movement rates between the three sex-paired status groups with CMR analysis when c-hat was adjusted for model fit. However, because small sample size tends to favor models with few parameters, I present results from the most highly parameterized model among the four highest ranking models, which had similar $QAIC_c$ values and differed only in the effects included in the estimation of movement rates (Table 5.8). This model, which estimated separate movement rates for each sex-paired status group and was the highest ranking model before c-hat was adjusted, estimated movement rates of 0.000 ± 0.000 for paired males, 0.050 ± 0.055 for unpaired males, and 0.018 ± 0.017 for paired females, for all locations combined.

Comparisons among sex-paired status groups of proportions of marked individuals with known paired status for any one year that were detected changing molting or wintering locations between years gave similar results to those obtained with CMR analysis. Movement rates for unpaired males tended to be highest and those for paired males tended to be lowest, at the coarse scale of movement among locations within the entire Strait of Georgia and at the fine scale of movement among sites on Hornby Island, although differences among sex-paired status groups were rarely significant. Males tended to be seen at a greater number of sites on Hornby Island than females, both during the molt and during the winter seasons, although, once again, differences were not significant.

At the coarse scale of movement among locations within the Strait of Georgia, for marked individuals with confirmed paired status for one year and known molting location for that year and the following one, 0% (n = 51) of paired males, 5% (n = 39) of unpaired males, and 5% (n = 138) of paired females were seen only in a different molting location in the second year (G_2 = 4.66, P = 0.10). Of the 7 females that changed molting locations following a year in which they had been paired, 3 (1 SY, 1 TY, 1ATY in the first of the two years) moved to the location in which they had wintered in the preceding year, 3 (2 SY, 1 ATY) moved to the location in which they had spent one or two of the previous spawning periods (one made the long-distance move from White Rock to Hornby Island), and one (TY) moved to a location in which she had not been seen previously. Of the 2 males that changed molting location following a year of failing to pair, 1 (ATY) moved to the location where he had wintered the previous year, and the other (SY) moved to a location where he had not been seen previously. When only adults (TY or older) were included, proportions known to change molting location dropped slightly for both unpaired males (3%, n = 30) and paired females (3%, n = 123), but proportions remained similar relative to each other. No movement among molting locations was detected for paired males.

At the fine scale of 13 sites on Hornby Island, 15% (n = 13) of paired males, 30% (n = 23) of unpaired males, and 15% (n = 58) of paired females were seen only at a different site during molt in the following year (G_2= 2.32, P = 0.31). Percentages of individuals seen at more than one site during molt on Hornby Island were 38% (n = 13, maximum of 4 sites) for paired males, 30% (n = 23, maximum of 3 sites) for unpaired males, and 16% (n = 58, maximum of 2 sites) for paired females (G_2 = 4.21, P = 0.12).

At the coarse scale of movement among locations within the Strait of Georgia, for individuals with known paired status at the end of the last non-breeding season and known wintering locations for both years, 0% (n = 23) of paired males, 6% (n = 17) of unpaired males, and 3% (n = 60) of paired females (G_2= 1.81, P = 0.41) were seen only in a different wintering location in the second year.

At the fine scale of Hornby Island, of individuals with known paired status at the end of the last non-breeding season, 0% (n = 4) of paired males, 38% (n = 13) of unpaired males, and 7% (n = 28) of paired females (G_2= 7.17, P = 0.028) were seen only in a different wintering site in the second year, and 50% (n = 4, maximum of 3 sites) of paired males, 23% (n = 13, maximum of 2 sites) of unpaired males, and 21% (n = 29, maximum of 2 sites) of paired females (G_2 = 1.45, P = 0.49) were seen at more than one site. For individuals with confirmed paired status within a given year, 16% (n = 31, maximum of 3 sites) of paired males, 39% (n = 31, maximum of 4 sites) of unpaired males, and 23% (n = 81, maximum of 2 sites) of paired females were seen at more than one site (G_2 = 4.36, P = 0.11).

Movement rates within years

Multi-stratum CMR analyses testing for sex and age effects on within year movement rates within the NS region were conducted for 1) movement from the molt to the winter season, and 2) movement from the winter to the spawn season. Within the SS region they were conducted for movement from the molt to the winter season.

Sex

I detected no differences between males and females in movement rates from the molt to the winter season or from the winter to the spawn season in the NS region. The highest ranking model for both molt to winter and winter to spawn analyses included effects of sex in the estimation of survival rates, location and time in the estimation of sighting rates, and location and season in the estimation of movement rates (Tables 5.9 and 5.10). Highest ranking models indicated that movement rates from the molt to the winter season were best estimated as identical regardless of the direction of movement between pairs of locations, whereas movement rates from winter to the spawn season were best estimated as direction-specific for each location pair (Fig. 5.6). For the molt to winter analysis, the highest ranking model received 5 times the support of the highest ranking model that included a sex effect in the estimation of movement rates (Table 5.9). For the winter to spawn analysis, the highest ranking model that included a sex effect in the estimation of movement rates received virtually no support (Table 5.10). When sex-specific movement rates were generated by the highest ranking models including a sex effect, no trend was apparent for either analysis (Table 5.11).

There was some support for sex differences in within year movement rates from the molt to the winter season in the SS region. The two highest ranking models received similar support ($\Delta QAIC_c$ = 1.93), and one of these included the effect of sex in the estimation of movement rates (Table 5.12). Both models included effects of sex in the estimation of survival rates, location and season in the estimation of sighting rates, and generated either a single movement rate or a sex-specific movement rate. However, model averaging provided similar point estimates of 0.053 ± 0.023 and 0.057 ± 0.0324 for movement of males and females, respectively.

Age

Including age effects in the estimation of within year movement rates among locations within the NS region did improve model fit for the molt to winter analysis, but not for the winter to spawn analysis; however, point estimates of movement rates tended to be greater for young than adult birds for both analyses. For the molt to winter analysis, two models received very similar support (Table 5.13). These models included effects of age in the estimation of survival rates, location and time in the estimation of sighting rates, and either age, or location (constrained to be the same regardless of the direction of movement) and season, in the estimation of movement rates. Both models received at least 4 times the support of the next highest ranking model. Model averaging generated age-specific movement rates from the molt to the winter season for each location pair (Fig. 5.7).

For the winter to spawn analysis, the highest ranking model included effects of age in the estimation of survival rates, location and time in the estimation of sighting rates, and location (direction-specific for each location pair) and season in the estimation of movement rates (Table 5.14). This model received 4 times the support of the next highest ranking model. Because the highest ranking model included the same effects in the estimation of movement rates as did the highest ranking model in the analysis testing for sex effects in the winter to spawn analysis (season and direction-specific location, Table 5.10), estimates of movement rates were virtually identical to those generated in the analyses testing for sex effects (Fig. 5.6). Including age effects in the estimation of movement rates did not improve model fit; however, age-specific estimates of movement generated by the highest ranking model that included the effect of age in the estimation of movement rates indicated that point estimates for young birds were greater than those for adults in all but one case where movement was observed (Table 5.15).

Paired status

Similar to the between year analysis above, small sample size precluded detection of differences in movement rates among sex-paired status groups in multi-stratum CMR analysis when c-hat was adjusted for model fit in analyses between molt and winter seasons and between winter and spawn seasons. As for the between year analysis, for both the molt to winter and the winter to spawn analyses I present results from the most highly parameterized model among the four highest ranking models which differed only in the effects included in the estimation of movement rates (Tables 5.16 and 5.17). This model estimated separate movement rates for each sex-paired status group, for all locations combined, of 0.004 ● 0.009 for paired males, 0.037 ● 0.043 for unpaired males, and 0.014 ● 0.012 for paired females for the molt to winter analysis, and movement rates of 0.007 ● 0.013 for paired males, 0.027 ± 0.036 for unpaired males, and 0.013 ± 0.012 for paired females for the winter to spawn analysis.

I also detected no differences among sex-paired status groups in the proportions of marked individuals with known paired status for any one year that were detected wintering at a different location than at which they had molted. At the coarse scale of locations within the Strait of Georgia, 6% (*n* = 64) of paired males, 13% (*n* = 55) of unpaired males, and 8% (*n* = 165) of paired females were seen only in a different wintering location from the location in which they molted, in a year in which paired status was confirmed (G_2 = 1.53, *P* = 0.47). At the fine scale of sites on Hornby Island, 45% (*n* = 20) of paired males, 43% (*n* = 30) of unpaired males, and 26% (*n* = 64) of paired females were seen only in a different wintering site than at which they had molted (G_2 = 3.80, *P* = 0.15).

Survival

Multi-stratum CMR analyses generated separate survival rates for the period from the molt to the spawn season (non-breeding season) and from the spawn to the molt season (breeding season) for both males and females. In the NS region, including data from molt and spawn seasons only, the highest ranking model after adjustment for model fit included effects of sex and season, for females, in the estimation of survival rates, location and time in the estimation of sighting rates, and location and season in the estimation of movement rates (Table 5.18). This model differed only slightly from the next highest ranking model (ΔQAIC$_c$ = 1.60) which differed only in that it included effects of season in the estimation of survival rates for both sexes. The highest ranking model received 4 times the support of the third highest ranking model, which included the effect of sex, and not season, in the estimation of survival rates. Model averaging using the two highest ranking models provided estimates of survival, in annual units, of 0.826 ± 0.030 and 0.804 ± 0.038 for males, and 0.915 ± 0.074 and 0.550 ± 0.082 for females, from molt to spawn (non-breeding season) and from spawn to molt (breeding season), respectively. Annual local survival rates averaged over both seasons were estimated as 0.816 ± 0.018 and 0.754 ● 0.031, for males and females, respectively.

Estimating the among population component of genetic variance

Isolation by distance gene flow model

I used the isolation by distance gene flow model with movement distances of young nasal-marked birds to estimate F_{ST}. The distribution of movement distances of nasal marked HY and SY individuals (Fig. 5.8) generated an estimate for overall gene flow, the root-mean-square dispersal distance (σ_T), of 14 km. With a density (ρ) of 0.91 birds per km^2, this generated an unadjusted N_{census} of 2,241. Adjustment for sex-ratio, variance in offspring number, and overlapping generations resulted in an Ne of 1,143. F_{ST} was calculated to be 0.002 and 0.003 when the number of demes in the range of the species for western North America was set at 100 and 1,000, respectively. An estimate of 1,000 demes was considered maximum given that the number of Harlequin Ducks in western North America is estimated on the order of 200,000 (Robertson and Goudie 1999).

These results indicated that the number of demes, within the range of reasonable estimates, had little impact on the magnitude of F_{ST}. I also evaluated the impact of changes to Ne, the other estimator required to calculate F_{ST}. Because decreases in neighbourhood size result in increases in F_{ST}, and because F_{ST} was estimated as a very low value (indicating that less than 1% of the total genetic variance is found among populations), I evaluated robustness of F_{ST} by considering factors that could cause underestimation of F_{ST} by overestimating Ne. Overestimation of Ne could result from: 1) underestimation of the effects of factors that reduce effective neighbourhood size relative to census neighbourhood size, i.e., variance in offspring number, overlapping generations, biased sex-ratio, and changes in population size over time, 2) overestimation of density of individuals, or 3) overestimation of gene flow (estimated from dispersal distances). I therefore evaluated the sensitivity of Ne and F_{ST} to each these factors in turn.

Varying the four correction factors that could potentially underestimate the reduction of effective neighbourhood size relative to census neighbourhood size indicated that, although I considered extreme examples in correcting for potential overestimation of Ne, F_{ST} reached a maximum of 0.009 when factors were varied separately (Table 5.19). A variance in offspring number of 5, a male-biased sex ratio of 2.0, and a reduction of N_{census} by a factor of 0.5 due to overlapping generations were considered extreme because variance in offspring number is limited by a maximum fledging brood size of 6, the male-biased sex ratio of 1.5 has been well documented with large samples for the western population (Rodway et al. 2003b), and life history schedules for the Lesser Snow Goose (*Anser caerulescens caerulescens*), a species with similar demographic schedules (e.g., similar delayed maturity and survival rates), indicated necessary correction for overlapping generations by a factor of only 0.982 (Rockwell and Barrowclough 1987). The likelihood and magnitude of fluctuations in population size over time are most difficult to evaluate, however, a reduction in population size to 10% of the census number for 20% of all generations over time is also likely an extreme scenario. Among the examples I considered, such strong periodic reductions in population size had greatest impact on F_{ST} (Table 5.19). Combining correction of factors increased F_{ST} to a maximum of 0.03%.

Density of individuals could be overestimated if census counts are biased high or if area estimates are biased low. Although both seem unlikely within the study area (census counts were minimal and area estimation was maximal), density estimates may be higher in the study area than in other areas within the species range. Sensitivity analyses of F_{ST} to decreases in density over an order of magnitude (Table 5.20.) indicated that a very low density of 1 bird in 10 km^2 generates an Ne of 113 and F_{ST} of 0.03.

Maximum dispersal distances of young Harlequin Ducks (Fig. 5.8) could have led to the overestimation of overall gene flow (root-mean-square dispersal distance, σ_T) if maximum movement distances did not reflect actual dispersal distances to a pairing location (effective dispersal distances) or because the distribution of dispersal distances was leptokurtic and not normal (kurtosis = 3.9). Using the relationship between kurtosis and neighbourhood size developed by Wright (1969, p. 304-305), I estimated that a kurtosis of 3.9 would reduce neighbourhood size by a factor of 0.98, resulting in little impact on F_{ST} (Ne reduced from 1,143 to 1,120; F_{ST} unchanged at 0.003). Wright (1951) also noted that the shape of the distribution of dispersal distances, which is usually leptokurtic, has little impact on neighbourhood size. It was not possible to evaluate potential overestimation of gene flow due to differences between maximum movement distance and effective dispersal distances, thus I tested sensitivity of F_{ST} to decreases in overall gene flow by limiting dispersal distances to 50, 30, 20, 10, and 5 km (Table 5.21), thereby simulating possible scenarios in which maximum dispersal distances were greater than effective dispersal distances. Even when all individuals in the sample were limited to a maximum effective dispersal distance of 10 km, F_{ST} only reached 0.02; however, when the maximum effective dispersal distance was limited to 5 km, F_{ST} reached 0.07. Further exploration revealed that a reduction in Ne to 39 and 25 were required to increase F_{ST} to 0.10 and 0.15, respectively, given 1,000 demes in the species range. Such effective neighbourhood sizes could be achieved if, for example, maximum effective dispersal distances remained at or below 5 km and density was reduced to approximately 0.6 birds per km.

Stepping stone gene flow model

The stepping stone gene flow model requires movement rates among adjacent colonies in order to generate estimates of F_{ST}. Point estimates of between year movement rates for young individuals among colonies in the NS region ranged between 0.07 and 0.11 (Fig. 5.5), with the average rate among colonies estimated as 0.081 ± 0.035. Because this rate represents movement to an adjacent colony on only one side, and because each colony has an adjacent colony on either side, approximately twice this rate was taken as the average annual movement into and out of each colony (m_{adj} = 0.16 per year). Assuming that a total of 6 colonies can be assigned to the entire study area (Fig. 5.2), harmonic mean of colony census population size was calculated to be 404, and Ne was estimated at 206 due to male-biased sex ratio, variance in offspring number, and overlapping generations. Before correction for a finite number of colonies in a reduced portion of the species range (i.e., the number of colonies is assumed to be infinite), F_{ST} was estimated at 0.682, however, correction for 6 colonies reduced F_{ST} to 0.005.

I investigated the effect on F_{ST} of varying m_{adj} from 0.10 to 0.22 based on error around the average point estimate (Table 5.22), and increased the number of colonies from 6 to 150 in order to represent the entire species range in western North America, as estimated from the numbers of birds believed to winter along the west coast of North America (Robertson and Goudie 1999) and on the geographical extent of their range. Increasing the number of colonies to 150 resulted in an increase in F_{ST} to 0.09 to 0.14 depending on m_{adj} (Table 5.22). F_{ST} was highly robust to decreases in mean colony effective population size: with an m_{adj} of 0.16 and 150 colonies in the species range, reducing Ne from 206 to 30 only increased F_{ST} from 0.11 to 0.15.

Summary of major findings

The distances that nasal-marked Harlequin Ducks moved did not differ between males and females, but did differ by age, with young birds generally moving farther than adults. Similarly, between year movement rates were greater for young birds than adults, and although there was a consistent trend for slightly higher point estimates of movement rates for males than females, including the effect of sex in the estimation of movement rates in multi-stratum CMR analysis did not improve model fit. Including the effect of distance between locations in the estimation of movement rates did improve model fit, indicating that movement rates declined with increasing distance between locations. Unpaired males tended to have higher between year movement rates than paired males, and movement rates of paired females tended to be intermediate between movement rates of unpaired and paired males. This pattern was observed at the coarse scale of movement among locations within the Strait of Georgia and at the fine scale of movement among sites on Hornby Island, however, differences were generally not statistically significant.

No effects of sex were detected for within year movement rates between the molt and winter seasons or between the winter and spawn seasons. Including the effect of age in the estimation of movement rates did improve model fit for the molt to winter analysis, with young birds moving at higher rates than adults, but did not improve model fit for the winter to spawn analysis. However, age-specific point estimates of movement rates between the winter and spawn seasons also tended to be higher for young individuals than for adults. No differences in within year movement rates were detected among sex-paired status groups, although, similar to the between year analyses, unpaired males tended to have highest rates and paired males tended to have lowest rates, at least for analyses at the coarse scale of locations within the Strait of Georiga. Survival rates, which were estimated from a multi-stratum CMR approach that incorporated movement among locations between the molt and spawn seasons and location-specific sighting rates, were greater from the molt to the spawn season (non-breeding season) than from the spawn to the molt season (breeding season).

The isolation by distance and stepping stone gene flow models both estimated low values of F_{ST} for the Strait of Georgia, ranging from a minimum of 0.002 to a maximum of 0.006. Estimates of F_{ST} generated by the isolation by distance model were robust to increases in number of demes and decreases in effective population size, however, for the stepping stone model, increases in the number of colonies resulted in increases in F_{ST}.

DISCUSSION

Potential for genetic isolation of wintering populations has been postulated for Harlequin Ducks based on fidelity to molting and wintering sites and on migration of juveniles in family groups to their mothers' wintering location (Lanctot et al. 1999, Cooke et al. 2000, Regehr et al. 2001). Results of this study suggest that movement at wintering areas by young individuals in their first and second winter counteracts the isolating effects of philopatry and family migration and that dispersal is sufficient to explain lack of genetic differences found among Harlequin Duck populations in genetic studies in western North America (Lanctot et al. 1999, Scribner et al.

1998). No significant population structuring (and an F_{ST} of zero) was found between wintering populations in Prince William Sound and the Kodiak Archipelago in Alaska (Lanctot et al. 1999), two regions separated by about 450 km, a distance about twice the length of this study area. Based on movement distances and rates of young individuals in this study, both isolation by distance and stepping stone gene flow models predicted that the proportion of genetic variance found among populations in the Strait of Georgia is small. I judged these gene flow models to be the most appropriate because the negative relationship between movement rates and distance between locations indicated that migrants come with highest probability from adjacent locations.

The isolation by distance gene flow model generated estimates of the among population component of genetic variance (F_{ST}) of less than 0.01, and increases above this magnitude could only be generated experimentally when rather unrealistic assumptions about possible causes of underestimation were made. Estimates of F_{ST} generated by the stepping stone gene flow model also were less than 0.01 when the number of colonies was on the order of what had been roughly assigned to the entire Strait of Georgia, even when a movement rate of 0.10 was employed. As the number of colonies in the stepping stone model was increased, however, the estimate for genetic variance among populations also increased (Table 5.22). If, for example, a similar distribution of colonies as were defined for the Strait of Georgia were assumed to stretch along the coast of North America for the entire range of the western population, and roughly 150 such colonies were to exist from northern California to Alaska, each with an effective population size of 206, and each exchanging young individuals with adjacent colonies at the rate of 0.16 per generation, then the among population component of genetic variance would be estimated on the order of 0.10.

Among vertebrates, birds typically have low values of F_{ST}, likely due to their extensive dispersal capabilities and their resultant large effective population sizes and high levels of gene flow between sub-populations (Barrowclough 1980, Buckley 1987, Evans 1987). An example of an avian species with relatively high F_{ST} is the Red-cockaded Woodpecker (*Picoides borealis*) that has an estimated 14% of total its genetic variation distributed among populations (Stangel et al. 1992). For this species, high among population divergence is thought to be related to social structure, non-migratory habits, and habitat fragmentation. Barrowclough (1980) found that among avian species he examined, the single species with a one-dimensional stepping stone distribution (the Silver Gull, *Larus novaehollandiae*, distributed along the Australian coastline) was the most likely to show any genetic differentiation, and suggested that significant differentiation might develop if such a species were distributed in a very extensive string of colonies along a single dimension. Results of the stepping stone model applied to Harlequin Ducks in this study similarly suggest that, because they are distributed along the western coastline of North America, genetic differences could develop over a large geographic range. Nevertheless, results of this study suggest that dispersal distances and effective population sizes for Harlequin Ducks in the Strait of Georgia are not unusual compared to other avian species (Barrowclough 1980). It is their distribution in space, in combination with their life history characteristics of philopatry and family migration, that could theoretically be responsible for genetic differences over their entire west coast range.

Analyses of sensitivity indicated that F_{ST} estimated for Harlequin Ducks was highly robust to changes in number of demes and to changes in all factors used in the estimation of effective neighbourhood size for the isolation by distance model, and neighbourhood sizes needed to be decreased to well below 100 before F_{ST} approached a value that would be considered high for an avian species. Sensitivity analyses also suggested that neighbourhood sizes under 100 are extremely unlikely for Harlequin Ducks and such small effective population sizes could only be experimentally generated when maximum dispersal distances were assumed to overestimate effective dispersal to a great extent. Demographic modeling (Barrowclough 1980), electrophoretic surveys (Barrowclough 1983), and analyses based on rates of karyotypic change (Barrowclough and Shields 1984) all concur that effective population sizes are moderate to relatively large for bird species, which is consitent with results obtained demographically for Harlequin Ducks in this study. Barrowclough and Shields (1984) report that fixation rates of chromosomal changes implicate long-term average effective population sizes for avian species on the order of 100, but because long-term averages are biased towards population size at bottlenecks, effective population sizes are typically somewhat larger.

Estimates of F_{ST} also were found to be robust to decreases in mean colony size in the stepping stone model, however, F_{ST} was sensitive to changes in movement rates among adjacent colonies and to increases in the number of colonies in the species range. The stepping stone model predicted that as much as 73% of the total genetic variance could be found among populations if the number of colonies was assumed infinite. However, adjustment for a finite number of colonies reduced F_{ST} substantially. A dramatic decrease in F_{ST} due to adjustment from an infinite to a finite number of one-dimensional colonies was also reported for the Silver Gull (Barrowclough 1980). Kimura and Weiss (1964, p. 570) demonstrated the rapid decrease of genetic correlation with distance for one dimension relative to two and three dimensions. Thus populations diverge relatively rapidly with increasing number of steps (colonies) in a single dimension, and F_{ST} estimated for a relatively small, finite number of colonies can be expected to be substantially lower than that estimated for a large or infinite number of colonies. Although assumptions of an infinite number of colonies may be appropriate for some species, most avian populations are not so extensive and correction of a finite number of colonies is necessary (Barrowclough 1980). Extreme sensitivity of F_{ST} to the number of one-dimensional colonies indicates that careful consideration is needed of the spatial scale of interest and the number of colonies likely to exist within this area, and emphasizes the importance of demonstrating the potential range in the magnitude of F_{ST}. Clearly, extrapolation of estimates of gene flow among adjacent colonies and mean colony size to geographical areas that extend beyond the study area must also be done with care.

There were several possible causes of overestimation of F_{ST} in this study, and potential for genetic differentiation likely is even less than that estimated. For the isolation by distance model, gene flow was not corrected for dispersal that may have taken some individuals outside of the study area. For the stepping stone model, annual rates were not converted to rates per generation, which, due to delayed maturation in Harlequin Ducks, would likely be greater than annual rates. In addition, F_{ST} estimated in this study was based on assumptions that no further mixing occurs at breeding areas, that individuals pair for life, and that all juveniles migrate to their mother's wintering location, then disperse from there. Gene flow that could occur at breeding areas includes re-pairing following mate or nest loss, or extra pair fertilization (e.g., Syroechkovsky et al. 1994). Mate change at wintering areas, through death or divorce of a mate, can result in gene flow of previously paired individuals if movement precedes pairing. Juveniles migrating to the coast without their biological mother, potentially due to death of the mother, adoption, or brood amalgamation (Bengston 1966, Rodway et al. 1998, Regehr et al. 2001), are less likely to arrive at the wintering location of their biological mother and their introduction into wintering populations could have a homogenizing effect on population structure similar to winter dispersal. Furthermore, F_{ST} may generally be overestimated when the direct method is used to quantify gene flow because observed movement patterns may not represent average rates over evolutionary time. The evolutionary effect of gene flow can be greatly enhanced by a few long-range migrants and by extreme environmental conditions that can temporarily cause unusually high levels of gene flow (Slatkin 1985). A record of one SY male from the White Rock population reported in Duluth, Minnesota (Cooke et al. 2000) suggests that very long-range migration does occur in Harlequin Ducks.

An assumption critical to the estimation of gene flow, that individuals that move also pair in their new location (Endler 1977, Whitlock and McCauley 1999), was not evaluated in this study. However, this assumption likely was justified, at least for females, because virtually all females pair by the end of their second winter (Rodway 2003). In contrast, due to the male-biased sex ratio in Harlequin Ducks, about one third of males do not pair. Thus, greater potential exists for males than females that dispersing individuals never pair, or that they move again to a new or to their original location before forming a pair bond, and thus, the male component of gene flow could have been overestimated. Evaluation of pairing success of dispersing males would be a useful future topic of investigation.

Although pair bond formation occurs during the winter months in Harlequin Ducks, I used sightings from the molt season to quantify the proportion of individuals migrating among locations each year. Between year movement rates estimated from molt sightings, as opposed to those estimated from winter sightings, likely are an appropriate measure of annual rates of gene flow among locations for several reasons. First, many individuals molt and winter in the same location (Breault and Savard 1999, Robertson et al. 1999, this study) and movement among molting sites therefore is likely to approximate movement among wintering sites. Results from this study indicated that movement rates between the molt and winter season were low, with approximately 5% of individuals moving out of each location. Similarly, Breault and Savard (1999) found that 96% ($n = 23$) of marked males molting at their White Rock study area also wintered there or at an adjacent area. In contrast, Robertson et al. (1999, 2000) found higher proportions of marked individuals departing from the White Rock study area following molt. This discrepancy among studies may be partly explained by differences in scale. The size of the search area in the study of Robertson et al. (1999, 2000) was small compared to that of each location within this study, and Breault and Savard (1999) surveyed an adjacent wintering area in addition to the White Rock study area. Thus, if Harlequin Ducks spread out over a wider area following molt (Breault and Savard 1999), it is possible that individuals that molted at White Rock but wintered elsewhere in the study of Robertson et al. (1999, 2000) did not move far, and that if individuals moved similar distance in this study they would have had a higher probability of remaining within the boundaries of a designated location and of being detected. In this case, my estimates of gene flow would be appropriate for the scale of this study.

Secondly, movement of some individuals from a molting location to a different wintering location is problematical only with respect to estimating gene flow from annual movement rates between molt seasons if individuals were either to molt at the same location and winter at different locations each year, or if they were to molt in a different location each year and return to the same wintering location. In these cases, gene flow estimated from molt sightings would be under and overestimated for the first and second case, respectively. However, such movement patterns likely are uncommon given the scale of this study. More likely, movement detected between molt and winter seasons reflects either a regular annual pattern or dispersal. If individuals move annually from a regular molt to a regular wintering location, then no annual movement at the molting location would be detected, a conclusion which would be equally appropriate to the wintering location. If movement from the molt to the winter season represents dispersal, that is, if an individual moves between the molt and the winter season and then returns to its last wintering location for molting in the following year, then this movement will be detected in the estimation of movement rates from molt sightings. Such a dispersal pattern may be relatively common, given that 6 of 7 paired females and 1 of 2 unpaired males that were observed to change molting locations in this study moved to locations in which they had spent at least part of the non-breeding season in the previous year.

Third, because individuals are marked during the molt season, any movement immediately following marking would be missed if winter sightings were used to assess annual gene flow. An example of the type of movement that would be detected using molt sightings and would be missed using winter sightings is when juveniles disperse following migration to the coast with their mothers. If such juveniles dispersed shortly after being marked and then remained in their new location, a comparison of molt sightings between years would indicate movement and gene flow, but a comparison of winter sightings would not. In cases where movement to the new location does not occur until at least the second winter for which sightings are available, such dispersal would be detected whether analyses used either molt or winter sightings. Annual movement rates estimated from winter sightings were very similar to those estimated from molt sightings for the SS region. In the NS region, slightly lower movement point estimates from winter sightings than from molt sightings are likely attributable to the small size of the winter data set and its restriction to adults only.

The lack of difference in movement distances and rates between the sexes was unexpected, based on theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992, Robertson and Cooke 1999). Although the logistics of reuniting at wintering areas for species that maintain long-term pair bonds requires philopatry of both sexes and thus confounds the predicted male-bias in dispersal among waterfowl (Savard 1985, Robertson and Cooke 1999, Robertson et al. 2000), unpaired males are predicted to disperse and, due to a male-biased sex-ratio, their dispersal could be expected to drive an overall difference among the sexes. An observed trend of slightly but consistently higher point estimates for between year movement rates for males than females suggested that some dispersal of unpaired males may have been occurring, but that the net effect of this was small. Analyses of movement rates and frequencies among sex paired-status groups did reveal a consistent non-significant trend of higher movement rates for unpaired males than for paired males or females. However, although paired males were philopatric in the extreme, with not one change in molting or wintering location observed, unpaired males also showed surprisingly high rates of philopatry. In addition, in contrast to the extreme philopatry of paired males, several paired females were observed to change molting or wintering locations. Thus, the lack of difference in movement rates between the sexes may have resulted from the combined fidelity of paired and unpaired males, the first being very high and the second lowest, almost balancing the intermediate fidelity of paired females.

A significant effect of age on between year movement rates was observed for the NS region and, although inclusion of age effects in the estimation of movement rates did not improve model fit for all other between year and within year analyses, in virtually all cases young individuals had higher point estimates for movement rates than did adults. Higher mobility of young than older individuals has been observed among birds in general (Greenwood and Harvey 1982) and among some species of waterfowl at breeding (Anderson et al. 1992) and wintering (Nichols and Hines 1987, Baldassarre et al. 1988, Rienecker 1987, Mittlehauser in prep.) areas. Combined results of movement analyses focused on age, sex, and paired status therefore suggest that young individuals are most mobile, and that following this initial mobility, individuals of both sexes tend to become site faithful regardless of whether or not they have succeeded in pairing.

Females represent a valuable resource to male Harlequin Ducks and philopatry is required to maintain a pair bond, thus results of 100% philopatry for paired males to molting and winter locations were not too surprising. However, reasons for high philopatry rates among unpaired males are less obvious. High philopatry for male Harlequin Ducks with unknown paired status has been previously reported (Breault and Savard 1999, Robertson et al. 1999), as has similar levels of philopatry between paired and unpaired males (Robertson et al. 2000). Although philopatry likely has significant ecological benefits for all individuals (Greenwood 1987, Anderson et al. 1992, Robertson et al. 1999, 2000), site fidelity also may be a viable strategy for establishing a pair bond, and may not necessarily represent a conflict of interest between survival and pairing. One strategy for obtaining a mate may be to search widely for unpaired females; however, another strategy may be to remain faithful to one location and to court familiar females persistently. Philopatric males were observed to form pair bonds following 1 to 3 years of being unpaired (6 cases) and to form a pair bond with another female following loss of a previous mate (2 cases). Thus, persistent courtship or attention directed at familiar females may eventually result in pairing, possibly when a female becomes widowed or divorced and may be most likely to chose a new mate familiar to her (Anderson 1985, McKinney 1986, 1992). Development of liaisons in order to improve chances of future pairing has been suggested for males in other waterfowl species (McKinney and Stolen 1982, Anderson 1985). Courtship of paired females by unpaired males is common in Harlequin Ducks (Rodway 2003), indicating that unpaired males engage in regular social contact with females regardless of their paired status, and that this confers benefits to them, likely in the form of increased probability of future pairing success. It is also possible that by remaining site faithful an unpaired male may increase his dominance relative to other unpaired males (Cooke et al. 1997), thereby increasing his chances for pairing when an opportunity arises.

Results also suggested that paired females may be somewhat less philopatric than paired males. Because a mate is likely less valuable to a female than to a male, paired females may forego reuniting with a previous mate more readily. One mechanism for females initiating divorce may be to move to a new location because such a strategy may facilitate separation from a mate that could otherwise be difficult to dislodge (Rodway 2003). For females, mate loss through death would not be predicted to lead to movement because philopatry has ecological benefits in addition to its importance in allowing the reunion of mates following separation during the breeding season. However, movement could be a mechanism facilitating divorce, and thus may play a role in population mixing mediated by previously paired individuals.

Greater winter home ranges of unpaired males relative to paired males has been reported previously for Harlequin Ducks (Robertson et al. 1999) and presumably is related to the search for available mates. In this study, movement among sites at the fine scale of sites on Hornby Island was expected to reveal differences in home range sizes among sex paired-status groups. However, few significant differences in site changes during molt or winter, or in the frequency of individuals sighted at more than one site, were observed, although males tended to switch sites more frequently and to visit more sites than females. These results were unexpected given previous research (Robertson et al. 1999) and sample size likely was inadequate in this study to detect significant differences among sex paired-status groups. Unpaired males spend more time moving (flying and swimming) than all other sex-paired status groups (Rodway 2003), which is consistent with larger home range size.

For pre-breeding juveniles, explanations other than those of reuniting with previous mates, mating system, or mate-following also may predict a lack of sex-bias in dispersal. Both sexes may gain equally from the ecological benefits of philopatry, and would be penalized equally by the costs of dispersal, such as unfamiliarity with their new environment and mortality risks associated with movement (Greenwood 1987, Weatherhead and Forbes 1994). Other factors may predict sex-biased dispersal of either sex. Females are expected to gain more from the benefits of optimal genetic mixing due to their greater investment in offspring (Pusey 1987), and males may be more likely to disperse due to intrasexual competition for mates (Dobson 1982) or due to a longer non-reproductive period relative to that of females (Johnson 1986, Rodway 2003).

Quantification of intra-annual movement rates is important for investigation of the factors that may contribute to gene flow among populations. Movement between the winter and herring spawn seasons resulted in a great deal of intra-annual mixing among locations within the northern Strait of Georgia, especially due to congregation at Hornby Island. Intra-annual movement rates represent a component of inter-annual movement rates and, as such, are not used to estimate gene flow among populations, however, movements to herring spawning sites may contribute to genetic mixing if pairing individuals originated from different populations. Half of all second year females pair during March and April when congregation at spawning site occurs (Rodway 2003), thus, seasonal movement at the time of pair formation may provide an important mechanism for gene flow. Because virtually all females pair by the end of their second winter and because pair bonds are long-term, this implies that up to half of the population pairs at the time when such congregation occurs. Identifying the factors that may affect the inter-annual movement rates used to estimate gene flow has implications for the generalization of results to other wintering areas. One might predict that frequencies of migrants among populations could be elevated at wintering areas where individuals congregate at spawning sites relative to those where no such intra-annual mixing occurs.

Although annual movement rates indicate a genetically panmictic population within the study area, this may not necessarily imply that Harlequin Ducks within this area also are demographically panmictic. However, high annual movement rates, especially of young individuals in the northern Strait of Georgia, suggest that groups of wintering Harlequin Ducks within this region are likely connected demographically. Seasonal mixing that occurs due to intra-annual movements such as movements to herring spawning sites also may have important implications for demographic connectivity among populations. Demographic independence implies no correlation in vital rates among populations (Hanski 1991). If otherwise spatially separate individuals mix at some time during the wintering period then the potential for demographic independence is reduced. When individuals congregate, vital rates are less likely to remain independent because factors that can affect them and that may be specific to the location where congregation occurs, such as food supply, predation pressure, or the occurrence of disasters, act on all congregating individuals equally for a period of time. Harlequin Ducks in the Strait of Georgia spend two to three weeks of their non-breeding period at herring spawning sites (Rodway et al. 2003a), and given that herring spawn likely is an important late winter food source (Rodway and Cooke 2002), survival rates and the use of herring spawn may be correlated. Both between and within year movement rates therefore suggest that demographic independence of wintering Harlequin Ducks in the northern Strait of Georgia is unlikely.

Populations in the northern parts of the Strait of Georgia may, however, be demographically independent from those in the southern part. Between year movement rates between the northern and southern regions were low, ranging between 1 in 1,000 and 4 in 1,000. These rates appear small enough to maintain demographic independence, but large enough to provide some connection, likely sufficient for recolonization or rescue of reduced or damaged populations. In addition, results indicate that dispersal is not limited to males. Because females are needed to found new colonies, dispersal by males would, on its own, not lead to successful recolonization of extinct subpopulations (Avise 1995). Thus, given low movement rates between the northern and southern Strait of Georgia and dispersal by both sexes, it seems plausible that a metapopulation distribution may function for Harlequin Ducks at a larger scale within the pacific coast of North America, with the northern and the southern Strait of Georgia each representing separate sub-populations within this larger system. Population modeling, using methods such as stochastic simulations and spatially explicit population models (Dunning et al. 1995, Simberloff 1988, Hoopes and Harrison 1998), and making use of current survival (Cooke et al. 2000, Goudie et al. in prep) and movement (this study) rates, may be a future research direction that could contribute to our understanding of the potential for metapopulation structuring in wintering Harlequin Ducks.

Movement patterns have implications for the estimation of survival rates. Because the confounding of emigration with mortality results in an underestimation of survival in CMR analyses, knowledge of movement rates can be used to aid our interpretation of local survival rates. Multi-stratum models can be used to correct survival rates for movement (e.g., Spendelow et al. 1995); however, the degree of correction is dependent on the degree to which movement is detected. In this study, individuals did not necessarily move only among locations, but likely also moved to areas where they would have remained undetected, thus survival rates would still have been underestimated to some degree. Furthermore, survival rates would have been underestimated due to leg band wear and loss (Regehr and Rodway 2003).

Survival rates estimated by multi-stratum models in this study were similar to, though slightly lower than, those obtained for the northern Strait of Georgia by Goudie et al. (in prep), and for the White Rock population by Cooke et al. (2000). Goudie et al. (in prep) attempted to correct for emigration by limiting estimation of survival rates to resident individuals, and report survival rates, with adjustment for leg band loss, of 0.86 for males and 0.81 for females. Another approach used to correct for emigration was to estimate survival rates separately for paired individuals, which are most likely to be philopatric, and this resulted in estimates of 0.91 and 0.76 for paired males and females, respectively, for the White Rock population (Cooke et al. 2000). The possibility that unpaired or non-resident individuals may be more likely to die than paired or resident individuals remains a recognized potential bias for such methods (Cooke et al. 2000). My results indicated that paired males are highly philopatric, whereas a small proportion of paired females move, thus survival estimates generated from paired males are likely to be accurate, whereas those estimated for paired females are likely underestimated. Slightly lower survival estimates from this study than from Cooke et al. (2000) and Goudie et al. (in prep) support the assumption that some emigration would have remained unaccounted for and that leg band wear and loss biased estimates. In addition, high c-hat values, likely caused by non-independence of movement among individuals to herring spawning sites (Rodway et al 2003a), resulted in loss of power. However, the data nevertheless supported two seasonal survival rates for females, providing further support that, at least in some areas, survival rates are lower for the breeding than the non-breeding season (Sargeant and Raveling 1992, Cooke et al. 2000, Mittlehauser in prep).

Results of this study suggest that movement rates are especially high for young birds, thus young birds are particularly vulnerable to underestimation of survival rates due to emigration. Survival estimates for young individuals therefore are best generated from studies using radio-marking or from those with large search areas (Regehr submitted). These results also emphasize the importance of separating age classes when estimating survival rates because differences in movement rates among age classes will cause local survival to be underestimated by emigration to different degrees.

Many sea duck species are of conservation concern due to apparent or suspected population declines (Goudie et al. 1994, Petersen and Hogan 1996). For Harlequin Ducks, conservation concern is based on an apparent imbalance between recruitment and mortality. Conspicuous plumage of first year males allows visual determination of population age structure in Harlequin Ducks (Smith et al. 2001, Rodway et al. 2003b). These age-ratio data in combination with estimates of survival suggest that production of juveniles is insufficient to compensate for adult mortality; however, some uncertainty remains as to the accuracy of survival estimates due to emigration (Rodway et al. 2003b). Results from this study indicate that at least 6% of individuals migrated annually from any location in the Strait of Georgia (Table 5.2) and that local survival estimates for any one location would be underestimated by at least this amount. However, adjusting current survival estimates by this amount would not be appropriate because estimates were generated for individuals suspected to be highly philopatric (Cooke et al. 2000, Goudie et al. in prep) or using methods that already incorporated this movement (this study). My movement estimates for different age classes and among locations differing in their distances apart may be useful in correcting local survival rates due to emigration in future studies. However, distance alone may be insufficient to predict movement rates because the relationship between distance and movement is likely specific to the scale and distribution of habitat and, possibly, to the density of individuals (Dobzhansky et al. 1979, Greenwood et al. 1979, Slatkin 1985, Paradis et al. 1998, Wiens 2001), both of which may differ substantially among regions and study areas. More complex population models may help to determine population stability by incorporating age-specific movement, leg band wear and loss, and recruitment. Another approach may be to radio-mark individuals and thereby gain age and sex-specific estimates of survival that are not confounded by emigration (e.g., Esler et al. 2000). My results suggest that female survival has been underestimated in previous studies due to emigration. In combination with the additional underestimation of recruitment due to juvenile males that are missed during surveys (Rodway et al. 2003b), this suggests that our concerns about population declines may be overly pessimistic.

Waterfowl are unusual among birds in that many species pair during winter. This difference in their life history strategy indicates that a different approach to evaluating genetic and demographic population structure is needed, and emphasizes the importance of quantifying movements during the wintering season. Three areas of knowledge are critical in the assessment of population structure for waterfowl that pair during winter using the direct method: 1) the manner in which juveniles are incorporated into wintering populations, 2) movement rates and distances of unpaired birds at wintering areas, and 3) sources and frequencies of genetic mixing at locations other than wintering areas. For most waterfowl species, little is known about the way in which juveniles are incorporated into wintering populations or about movement patterns at wintering areas (Anderson et al. 1992, Robertson and Cooke 1999). For Harlequin Ducks, previous research suggests that juveniles migrate to the coast with their mothers in family groups (Regehr et al. 2001) and, although data are scarce, their dispersed distribution along streams (Goudie and Robertson 1999) suggests that their breeding season component of gene flow is likely to be small. In this study I therefore have attempted to assess movement at wintering areas and have concluded that movement rates of young individuals are high enough to substantially negate the isolating forces of philopatry and family migration.

For other duck species, juveniles are thought to be typically abandoned by the female before migration (Afton and Paulus 1992), and because many species winter at interior wetlands that are more variable and unstable than coastal waters, they exhibit flexibility in wintering sites among years (Baldassarre et al. 1988, Diefenbach et al. 1988, Nichols et al. 1983, Hestbeck 1993). Thus, because juveniles are unlikely to migrate to wintering areas in family groups, and because wintering areas are not conducive to philopatry, most duck populations are thought to be relatively panmictic. However, although Harlequin Ducks may be unique among ducks in their ability to migrate in family groups because they molt and winter in the same location (Regehr et al. 2001), there may be mechanisms other than family migration that could result in offspring wintering in the vicinity of their parents. For example, ducks are known to follow traditional migration routes (Bellrose 1980), which could serve to funnel juveniles into wintering locations near their parents and could lead to less extensive population mixing than has been previously believed (Anderson et al. 1992). To my knowledge, this study is the first to estimate winter movement rates and distances, and attempt a first estimate of gene flow using direct methods, for a waterfowl species with dispersed and separate breeding and wintering distributions. Research aimed at determining how juveniles are incorporated into wintering populations and at quantifying movement patterns at wintering areas for other waterfowl species would improve our understanding of their demographic and genetic population structure and aid in their management and conservation.

ACKNOWLEDGEMENTS

This study was possible only with the efforts of many individuals too numerous to list entirely. I extend special thanks and gratitude to the following people. Brian Arquilla, John Ashley, Sean Boyd, Pete Clarkson, Fred Cooke, Frank Elkins, Mary Jane Elkins, Ian Goudie, Stuart Jackson, Greg Robertson, Michael Rodway, Cyndi Smith, Richard Swanston, and Ken Wright captured, marked, and sighted Harlequin Ducks. Ian Goudie initiated the banding project. Michael Rodway devoted months of his time to the search for marked birds by boat and on foot. Carl Schwarz and Barry Smith provided generous advice on multi-stratum mark-recapture analyses; I am especially grateful to Carl Schwarz for helping me with design matrices and to Barry Smith for providing me with a method for testing goodness of fit in multi-stratum models. Mary Jane Elkins and Frank Elkins provided generous hospitality on Hornby Island. Connie Smith provided data and equipment management, Martin Regehr helped with programming, and

Barb Sherman and Judy Higham provided financial administration. Sean Boyd, Felix Breden, Fred Cooke, Dan Esler, and Michael Rodway provided helpful discussion and critical reviews essential to the development of this manuscript. Helpful reviews were also provided by Alan Afton, Glen Mittelhauser, and Arne Mooers. Funding was provided by the National Science and Engineering Research Council (NSERC) of Canada, Centre for Wildlife Ecology, Simon Fraser University, British Columbia Waterfowl Society, Institute of Waterfowl and Wetlands Research (IWWR), and the Canadian Wildlife Service.

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Table 5.1. Candidate model set, ranked in order of increasing QAIC$_c$, used to determine effects of sex and distance between locations on between year movement rates among molt locations for leg-banded Harlequin Ducks in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, sex, location, and distance between locations are indicated in parentheses by *t*, *sx*, *l*, and *d*, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction. AIC$_c$ values were adjusted for c-hat of 3.32.

Model	No. of parameters	QAIC$_c$	Delta QAIC$_c$	QAIC$_c$ weight
$\phi(sx)p(l*t)\psi(d)$	34	2713.45	0.00	0.7763
$\phi(sx)p(l*t)\psi(sx*d)$	36	2716.87	3.43	0.1400
$\phi(l*sx)p(l*t)\psi(d)$	42	2718.24	4.79	0.0707
$\phi(l*sx)p(l*t)\psi(sx*d)$	44	2721.78	8.33	0.0121
$\phi(sx)p(l*t)\psi(l)$	52	2727.93	14.48	0.0006
$\phi(sx*t)p(l*t)\psi(d)$	44	2729.60	16.15	0.0002
$\phi(l*sx)p(l*t)\psi(l)$	60	2732.46	19.01	0.0001
$\phi(sx*t)p(l*t)\psi(sx*d)$	46	2733.05	19.61	0.0000
$\phi(sx)p(l*t)\psi(l_c*sx)$	52	2738.98	25.54	0.0000
$\phi(sx*t)p(l*t)\psi(l)$	61	2741.76	28.31	0.0000
$\phi(l*sx)p(l*t)\psi(l_c*sx)$	60	2744.14	30.69	0.0000
$\phi(sx*t)p(l*t)\psi(l_c*sx)$	61	2753.24	39.80	0.0000
$\phi(sx)p(l*t)\psi(l*sx)$	72	2763.71	50.27	0.0000
$\phi(sx)p(l*t)\psi(sx)$	34	2768.42	54.98	0.0000
$\phi(l*sx)p(l*t)\psi(l*sx)$	80	2768.48	55.03	0.0000
$\phi(l*sx)p(l*t)\psi(sx)$	42	2771.64	58.20	0.0000
$\phi(sx)p(l)\psi(d)$	9	2776.68	63.23	0.0000
$\phi(sx*t)p(l*t)\psi(l*sx)$	81	2777.80	64.35	0.0000
$\phi(sx*t)p(l*t)\psi(sx)$	43	2782.10	68.66	0.0000
$\phi(sx)p(l)\psi(l)$	27	2792.62	79.17	0.0000
$\phi(sx)p(l)\psi(sx)$	9	2836.23	122.78	0.0000

Table 5.2. Between year movement rates in relation to distance between five locations (White Rock [WR], Point Roberts [PR], Hornby [HO], Comox [CX], Campbell River [CR]) for Harlequin Ducks in the Strait of Georgia, British Columbia. Estimates are equal for both directions of movement and were generated from data collected during the molt season by the model with lowest $QAIC_c$: ϕ (sex) p (location*time) ψ (distance), where survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. C-hat was adjusted to 3.32.

Location #1	Location #2	Distance apart (km)	Estimate	SE	Lower CI	Upper CI
WR	PR	15	0.046	0.009	0.031	0.066
HO	CX	30	0.034	0.006	0.024	0.047
CX	CR	35	0.031	0.005	0.022	0.042
HO	CR	65	0.017	0.003	0.012	0.023
PR	HO	140	0.004	0.001	0.002	0.007
WR	HO	155	0.003	0.001	0.001	0.006
PR	CX	170	0.002	0.001	0.001	0.005
WR	CX	180	0.002	0.001	0.001	0.004
PR	CR	210	0.001	0.000	0.000	0.003
WR	CR	220	0.001	0.000	0.000	0.002

Table 5.3. Sex-specific between year movement rates in relation to distance between five locations (White Rock [WR], Point Roberts [PR], Hornby [HO], Comox [CX], Campbell River [CR]) for Harlequin Ducks in the Strait of Georgia, British Columbia. Estimates are equal for both directions of movement and were generated from data collected during the molt season by the highest ranking model that provided sex-specific movement rates: ϕ (sex) p (location*time) ψ (sex*distance), where survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. C-hat was adjusted to 3.32.

Location #1	Location #2	Distance apart (km)	Males		Females	
			Estimate	SE	Estimate	SE
WR	PR	15	0.048	0.011	0.040	0.015
HO	CX	30	0.036	0.007	0.029	0.001
CX	CR	35	0.032	0.006	0.026	0.008
HO	CR	65	0.018	0.003	0.013	0.005
PR	HO	140	0.004	0.002	0.002	0.002
WR	HO	155	0.003	0.001	0.002	0.002
PR	CX	170	0.002	0.001	0.001	0.001
WR	CX	180	0.002	0.001	0.001	0.001
PR	CR	210	0.001	0.001	0.000	0.001
WR	CR	220	0.001	0.001	0.000	0.001

Table 5.4. Candidate model set, ranked in order of increasing QAIC$_c$, used to determine the effect of sex on between year movement rates among winter locations for leg-banded adult Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of sex and location are indicated in parentheses by *sx* and *l*, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction. AIC$_c$ values were adjusted for c-hat of 1.77.

Model	No. of parameters	QAIC$_c$	Delta QAIC$_c$	QAIC$_c$ weight
$\phi(sx)p(l)\psi()$	6	226.25	0.00	0.3618
$\phi()p()\psi()$	3	227.07	0.83	0.2394
$\phi(sx)p(l)\psi(sx)$	7	227.84	1.60	0.1628
$\phi()p()\psi(sx)$	4	228.66	2.41	0.1082
$\phi(sx)p(l)\psi(l_c)$	8	229.96	3.71	0.0565
$\phi()p()\psi(l_c)$	5	230.38	4.13	0.0458
$\phi(l*sx)p(l)\psi(sx)$	11	233.67	7.42	0.0088
$\phi(sx)p(l)\psi(l)$	11	234.75	8.50	0.0052
$\phi()p()\psi(l)$	8	234.83	8.58	0.0050
$\phi(l*sx)p(l)\psi(l_c)$	12	235.74	9.49	0.0031
$\phi(sx)p(l)\psi(l_c*sx)$	11	235.90	9.65	0.0029
$\phi(l*sx)p(l)\psi(l)$	15	239.99	13.74	0.0004
$\phi(l*sx)p(l)\psi(l_c*sx)$	15	241.82	15.57	0.0002
$\phi(sx)p(l)\psi(l*sx)$	17	245.21	18.97	0.0000
$\phi(l*sx)p(l)\psi(l*sx)$	21	252.45	26.20	0.0000

Table 5.5. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of sex on between year movement rates among winter locations for leg-banded adult Harlequin Ducks in the SS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of sex and location are indicated in parentheses by *sx* and *l*, respectively. AIC_c values were adjusted for c-hat of 3.28.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi()p()\psi()$	3	167.20	0.00	0.3080
$\phi()p()\psi(sx)$	4	168.14	0.94	0.1920
$\phi()p()\psi(l)$	4	168.23	1.03	0.1836
$\phi(sx)p(l)\psi()$	5	168.68	1.49	0.1463
$\phi(sx)p(l)\psi(sx)$	6	169.91	2.71	0.0795
$\phi(sx)p(l)\psi(l)$	6	170.66	3.46	0.0546
$\phi(l*sx)p(l)\psi(sx)$	8	173.52	6.33	0.0130
$\phi(sx)p(l)\psi(l*sx)$	8	173.74	6.55	0.0117
$\phi(l*sx)p(l)\psi(l)$	8	174.20	7.00	0.0093
$\phi(l*sx)p(l)\psi(l*sx)$	10	177.18	9.99	0.0021

Table 5.6. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of age on between year movement rates among molt locations for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, age, and location are indicated in parentheses by *t*, a, and *l*, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction and l_j indicates that the location effect on survival rates are specific to the young age class. The '/' notation separates time effects in survival rates for juvenile and post-juvenile birds, respectively, with '*t*' indicating time dependence and "*c*" indicating time held constant. AIC_c values were adjusted for c-hat of 2.87.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi(a-c/c)p(l*t)\psi(a)$	22	2614.25	0.00	0.5609
$\phi(l_j*a-c/c)p(l*t)\psi(l_c*a)$	28	2614.87	0.62	0.4124
$\phi(a-c/t)p(l*t)\psi(a)$	26	2620.99	6.74	0.0193
$\phi(l_j*a-c/c)p(l*t)\psi(a)$	23	2622.91	8.65	0.0074
$\phi(l*a-c/t)p(l*t)\psi(l_c)$	34	2639.45	25.20	0.0000
$\phi(l*a-c/t)p(l*t)\psi(l_c*a)$	41	2639.82	25.57	0.0000
$\phi(a-c/c)p(l)\psi(l)$	11	2700.41	86.16	0.0000
$\phi(a-c/c)p(l)\psi(l_c)$	8	2703.87	89.61	0.0000
$\phi(a-c/c)p(l)\psi(a)$	7	2707.17	92.91	0.0000
$\phi(l*a-c/t)p(l*t)\psi(a)$	34	2735.05	120.80	0.0000
$\phi(l_j*a-c/t)p(l*t)\psi(l_c)$	29	2746.91	132.66	0.0000
$\phi(l_j*a-c/t)p(l*t)\psi(a)$	27	2750.87	136.62	0.0000
$\phi(l_j*a-c/c)p(l*t)\psi(l_c)$	24	2763.16	148.91	0.0000
$\phi(l*a-c/c)p(l*t)\psi(l_c*a)$	29	2800.70	186.45	0.0000
$\phi(l*a-c/c)p(l*t)\psi(l_c)$	25	2805.05	190.80	0.0000
$\phi(a-c/c)p(l*t)\psi(l_c)$	22	2807.84	193.59	0.0000
$\phi(a-c/c)p(l*t)\psi(l_c*a)$	25	2810.53	196.28	0.0000
$\phi(l*a-c/c)p(l*t)\psi(a)$	25	2812.67	198.41	0.0000
$\phi(a-c/c)p(l*t)\psi(l*a)$	29	2813.00	198.74	0.0000
$\phi(l_j*a-c/t)p(l*t)\psi(l_c*a)$	32	2815.49	201.24	0.0000
$\phi(a-c/t)p(l*t)\psi(l*a)$	33	2835.05	220.80	0.0000
$\phi(a-c/t)p(l*t)\psi(l_c)$	25	2838.39	224.14	0.0000
$\phi(a-c/t)p(l*t)\psi(l_c*a)$	29	2846.74	232.49	0.0000

Table 5.7. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of age on between year movement rates between molt locations on the north and south coasts of Hornby Island, for leg-banded Harlequin Ducks in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, age, and location are indicated by *t*, a, and *l*, respectively. The '/' notation separates time effects in survival rates for juvenile and post-juvenile birds, respectively, with '*t*' indicating time dependence and "*c*" indicating time held constant. AIC_c values were adjusted for c-hat of 2.41.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi(a-c/c)p(l*t)\psi()$	15	1380.55	0.00	0.4177
$\phi(a-c/c)p(l*t)\psi(a)$	16	1381.19	0.64	0.3032
$\phi(a-c/c)p(l*t)\psi(l)$	16	1382.20	1.65	0.1830
$\phi(a-c/c)p(l*t)\psi(l*a)$	18	1384.70	4.14	0.0526
$\phi(a-c/t)p(l*t)\psi()$	20	1386.76	6.21	0.0187
$\phi(a-c/t)p(l*t)\psi(a)$	21	1387.41	6.86	0.0135
$\phi(a-c/t)p(l*t)\psi(l)$	21	1388.28	7.73	0.0088
$\phi(a-c/t)p(l*t)\psi(l*a)$	23	1390.76	10.21	0.0025
$\phi(a-c/c)p(l)\psi()$	5	1439.62	59.06	0.0000
$\phi(a-c/c)p(l)\psi(a)$	6	1440.56	60.01	0.0000
$\phi(a-c/c)p(l)\psi(l)$	6	1441.41	60.85	0.0000

Table 5.8. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of paired status on between year movement rates among molt locations for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of sex, location, and paired status are indicated in parentheses by *sx*, *l*, and *ps*, respectively. AIC_c values were adjusted for c-hat of 2.60.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi()p()\psi()$	3	211.03	0.00	0.4382
$\phi()p()\psi(ps)$	4	212.33	1.29	0.2293
$\phi()p()\psi(sx)$	4	213.09	2.06	0.1568
$\phi()p()\psi(ps * sx)$	5	213.55	2.52	0.1244
$\phi(sx)p(l)\psi(ps)$	7	217.58	6.55	0.0166
$\phi()p()\psi(l)$	8	217.82	6.79	0.0147
$\phi(sx)p(l)\psi(sx)$	7	218.47	7.44	0.0106
$\phi(sx)p(l)\psi(ps * sx)$	8	218.82	7.79	0.0089
$\phi(sx)p(l)\psi(l)$	11	224.15	13.12	0.0006

Table 5.9. Candidate model set, ranked in order of increasing QAIC$_c$, used to determine the effect of sex on within year movement rates from the molt to the winter season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, sex, location, and season are indicated in parentheses by t, sx, l, and s, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction. AIC$_c$ values were adjusted for c-hat of 4.23.

Model	No. of parameters	QAIC$_c$	Delta QAIC$_c$	QAIC$_c$ weight
$\phi(sx)p(l*t)\psi(l_c*s)$	47	2599.29	0.00	0.6254
$\phi(sx)p(l*t)\psi(l*s)$	53	2602.33	3.04	0.1371
$\phi(sx)p(l*t)\psi(sx)$	43	2602.49	3.20	0.1261
$\phi(sx)p(l*t)\psi(l_c*sx)$	47	2603.11	3.82	0.0926
$\phi(l*sx)p(l*t)\psi(l_c*s)$	51	2607.18	7.89	0.0121
$\phi(l*sx)p(l*t)\psi(sx)$	47	2610.33	11.04	0.0025
$\phi(l*sx)p(l*t)\psi(l*s)$	57	2610.35	11.06	0.0025
$\phi(l*sx)p(l*t)\psi(l_c*sx)$	51	2611.06	11.77	0.0017
$\phi(sx*t)p(l*t)\psi(l_c*s)$	70	2637.25	37.96	0.0000
$\phi(sx*t)p(l*t)\psi(l*s)$	76	2639.93	40.64	0.0000
$\phi(sx*t)p(l*t)\psi(sx)$	66	2640.45	41.16	0.0000
$\phi(sx*t)p(l*t)\psi(l_c*sx)$	70	2641.08	41.79	0.0000
$\phi(sx*t)p(l*t)\psi(l*sx*s)$	88	2662.82	63.53	0.0000
$\phi(sx)p(l*s)\psi(l_c*s)$	14	2751.35	152.06	0.0000
$\phi(sx)p(l*s)\psi(sx)$	10	2754.65	155.36	0.0000
$\phi(sx)p(l*s)\psi(l*s)$	20	2755.81	156.52	0.0000
$\phi(sx)p(l*s)\psi(l_c*sx)$	14	2832.82	233.53	0.0000
$\phi(sx)p(l)\psi(l_c*s)$	11	2944.63	345.33	0.0000
$\phi(sx)p(l)\psi(sx)$	7	2947.66	348.37	0.0000
$\phi(sx)p(l)\psi(l*s)$	17	2949.74	350.45	0.0000

Table 5.10. Candidate model set, ranked in order of increasing QAIC_c, used to determine the effect of sex on within year movement rates from the winter to the herring spawn season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, sex, location, and season are indicated in parentheses by t, sx, l, and s, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction. AIC_c values were adjusted for c-hat of 3.78.

Model	No. of parameters	QAIC_c	Delta QAIC_c	QAIC_c weight
$\phi(sx)p(l*t)\psi(l*s)$	52	2408.13	0.00	0.8783
$\phi(l*sx)p(l*t)\psi(l*s)$	56	2412.11	3.97	0.1205
$\phi(sx)p(l*t)\psi(l*sx)$	53	2421.62	13.49	0.0010
$\phi(l*sx)p(l*t)\psi(l*sx)$	57	2425.25	17.12	0.0002
$\phi(sx*t)p(l*t)\psi(l*s)$	75	2443.61	35.48	0.0000
$\phi(sx*t)p(l*t)\psi(l*sx)$	76	2457.50	49.36	0.0000
$\phi(sx*t)p(l*t)\psi(l*sx*s)$	87	2465.12	56.99	0.0000
$\phi(sx)p(l*s)\psi(l*s)$	20	2466.82	58.68	0.0000
$\phi(sx)p(l*s)\psi(l*sx)$	20	2480.02	71.89	0.0000
$\phi(l*sx)p(l*t)\psi(sx)$	47	2501.55	93.42	0.0000
$\phi(sx*t)p(l*t)\psi(l_c*s)$	70	2526.21	118.08	0.0000
$\phi(sx*t)p(l*t)\psi(sx)$	66	2534.60	126.47	0.0000
$\phi(sx)p(l)\psi(l*s)$	17	2571.32	163.18	0.0000
$\phi(l*sx)p(l*t)\psi(l_c*s)$	51	2680.92	272.79	0.0000
$\phi(sx)p(l*t)\psi(l_c*s)$	47	2731.69	323.56	0.0000
$\phi(sx)p(l*s)\psi(l_c*s)$	14	2735.57	327.44	0.0000
$\phi(sx)p(l*t)\psi(sx)$	43	2830.57	422.44	0.0000
$\phi(sx)p(l*s)\psi(sx)$	10	2844.14	436.00	0.0000
$\phi(sx)p(l)\psi(l_c*s)$	11	2884.39	476.26	0.0000
$\phi(sx)p(l)\psi(sx)$	7	3146.21	738.08	0.0000

Table 5.11. Sex-specific within year movement rates in the NS region for Harlequin Ducks in the Strait of Georgia, British Columbia, between the molt and winter seasons, and the winter and spawn seasons, as estimated by highest ranking models that included a sex effect in the estimation of movement rates. Only one movement rate for each sex was estimated for movement between the molt and the winter seasons (c-hat adjusted to 4.23); a separate rate was estimated for each direction of movement between locations (Hornby [HO], Comox [CX], Campbell River [CR]) between the winter and the spawn seasons (c-hat adjusted to 3.78). Survival, sighting, and movement rates are denoted in models by ϕ, p, and ψ, respectively.

Location #1	Location #2	Males		Females	
		Estimate	SE	Estimate	SE
Molt - winter		model: ϕ(sex) p(location*time) ψ(sex)			
–	–	0.017	0.003	0.017	0.005
Winter - spawn		model: ϕ(sex) p(location*time) ψ(location*sex)			
HO	CX	0.033	0.013	0.045	0.017
CX	HO	0.500	0.120	0.604	0.137
HO	CR	0.011	0.007	0.007	0.007
CR	HO	0.079	0.073	0.126	0.082
CX	CR	0.000	0.000	0.000	0.000
CR	CX	0.035	0.046	0.027	0.037

Table 5.12. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of sex on within year movement rates from the molt to the winter season for leg-banded Harlequin Ducks in the SS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, sex, location, and season are indicated in parentheses by *t*, *sx*, *l*, and *s*, respectively. AIC_c values were adjusted for c-hat of 7.27.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi(sx)p(l*s)\psi()$	7	337.53	0.00	0.4790
$\phi(sx)p(l*s)\psi(sx)$	8	339.47	1.93	0.1821
$\phi(sx)p(l*s)\psi(s)$	8	339.55	2.02	0.1747
$\phi(l*sx)p(l*s)\psi()$	9	341.54	4.00	0.0647
$\phi(sx)p(l*s)\psi(l*s)$	10	342.00	4.47	0.0513
$\phi(l*sx)p(l*s)\psi(sx)$	10	343.47	5.93	0.0247
$\phi(l*sx)p(l*s)\psi(s)$	10	343.56	6.03	0.0235
$\phi(sx)p(l*t)\psi(sx)$	30	362.42	24.89	0.0000
$\phi(sx)p(l*t)\psi(s)$	30	362.52	24.99	0.0000
$\phi(sx)p(l*t)\psi(l*s)$	32	364.93	27.40	0.0000
$\phi(sx)p(l*t)\psi(l*sx)$	32	366.25	28.72	0.0000
$\phi(sx)p(l)\psi()$	5	377.27	39.73	0.0000
$\phi(sx)p(l)\psi(sx)$	6	378.90	41.37	0.0000
$\phi(sx)p(l)\psi(s)$	6	379.12	41.58	0.0000

Table 5.13. Candidate model set, ranked in order of increasing $\mathrm{QAIC_c}$, used to determine the effect of age on within year movement rates from the molt to the winter season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, age, location, and season are indicated by *t*, a, *l*, and *s*, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction and l_j indicates that the location effect on survival rates are specific to the young age class. The '/' notation separates time effects for juvenile and post-juvenile birds, respectively, with '*t*' indicating full time dependence, "*s*" indicating time constrained by season, and "*c*" indicating time held constant. $\mathrm{AIC_c}$ values were adjusted for c-hat of 4.17.

Model	No. of parameters	$\mathrm{QAIC_c}$	Delta $\mathrm{QAIC_c}$	$\mathrm{QAIC_c}$ weight
$\phi(a-c/c)p(l*t)\psi(a-c/c)$	43	2602.85	0.00	0.4280
$\phi(a-c/c)p(l*t)\psi(l_c*s)$	47	2603.50	0.65	0.3092
$\phi(l_j*a-c/c)p(l*t)\psi(a-c/c)$	45	2606.14	3.29	0.0826
$\phi(a-c/c)p(l*t)\psi(l*s)$	53	2606.56	3.71	0.0669
$\phi(l_j*a-c/c)p(l*t)\psi(l_c*s)$	49	2607.01	4.16	0.0533
$\phi(l_j*a-c/c)p(l*t)\psi(l_c*a-c/c)$	49	2607.24	4.39	0.0477
$\phi(l_j*a-c/c)p(l*t)\psi(l*s)$	55	2610.09	7.24	0.0114
$\phi(a-c/c)p(l*t)\psi(l_c*a-c/c)$	47	2615.73	12.88	0.0007
$\phi(a-c/t)p(l*t)\psi(a-c/c)$	55	2621.58	18.73	0.0000
$\phi(a-c/t)p(l*t)\psi(l_c*s)$	59	2622.31	19.46	0.0000
$\phi(a-c/t)p(l*t)\psi(l_c*a-c/c)$	59	2662.55	19.70	0.0000
$\phi(a-c/t)p(l*t)\psi(l*s)$	65	2625.18	22.34	0.0000
$\phi(a-c/t)p(l*t)\psi(l*a-s/s)$	77	2645.39	42.54	0.0000
$\phi(a-c/c)p(l*s)\psi(a-c/c)$	10	2754.17	151.32	0.0000
$\phi(a-c/c)p(l*s)\psi(l_c*s)$	14	2754.56	151.71	0.0000
$\phi(a-c/c)p(l*s)\psi(l_c*a-c/c)$	14	2755.43	152.59	0.0000
$\phi(a-c/c)p(l*s)\psi(l*s)$	20	2758.87	156.02	0.0000
$\phi(a-c/c)p(l)\psi(a-c/c)$	7	2949.73	346.88	0.0000
$\phi(a-c/c)p(l)\psi(l_c*s)$	11	2950.40	347.55	0.0000
$\phi(a-c/c)p(l)\psi(l*s)$	17	2955.39	352.54	0.0000

Table 5.14. Candidate model set, ranked in order of increasing QAIC$_c$, used to determine the effect of age on within year movement rates from the winter to the spawn season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, age, location, and season are indicated by *t*, a, *l*, and *s*, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction and l_j indicates that the location effect on survival rates are specific to the young age class. The '/' notation separates time effects for juvenile and post-juvenile birds, respectively, with '*t*' indicating full time dependence, "*s*" indicating time constrained by season, and "*c*" indicating time held constant. AIC$_c$ values were adjusted for c-hat of 3.62.

Model	No. of parameters	QAIC$_c$	Delta QAIC$_c$	QAIC$_c$ weight
$\phi(a-c/c)p(l*t)\psi(l*s)$	52	2474.19	0.00	0.7972
$\phi(l_j*a-c/c)p(l*t)\psi(l*s)$	54	2476.94	2.75	0.2015
$\phi(a-c/t)p(l*t)\psi(l*s)$	64	2488.49	14.30	0.0006
$\phi(a-c/c)p(l*t)\psi(l*a-c/c)$	53	2588.59	14.39	0.0006
$\phi(l_j*a-c/c)p(l*t)\psi(l*a-c/c)$	55	2491.51	17.32	0.0001
$\phi(a-c/t)p(l*t)\psi(l*a-c/c)$	65	2503.44	29.25	0.0000
$\phi(a-c/t)p(l*t)\psi(l*a-s/s)$	76	2511.07	36.88	0.0000
$\phi(a-c/c)p(l*s)\psi(l*s)$	20	2539.19	65.00	0.0000
$\phi(a-c/c)p(l*s)\psi(l*a-c/c)$	20	2555.17	80.98	0.0000
$\phi(a-c/c)p(l*t)\psi(l_c*s)$	47	2561.17	86.98	0.0000
$\phi(l_j*a-c/c)p(l*t)\psi(l_c*s)$	49	2565.04	90.85	0.0000
$\phi(a-c/c)p(l*s)\psi(a-c/c)$	10	2625.65	151.46	0.0000
$\phi(a-c/c)p(l)\psi(l*s)$	17	2648.93	174.74	0.0000
$\phi(a-c/t)p(l*t)\psi(l_c*s)$	59	2813.75	339.56	0.0000
$\phi(a-c/c)p(l*s)\psi(l_c*s)$	14	2815.85	341.66	0.0000
$\phi(a-c/c)p(l)\psi(l_c*s)$	11	2970.77	496.58	0.0000
$\phi(a-c/c)p(l*t)\psi(a-c/c)$	43	3027.56	553.37	0.0000
$\phi(l_j*a-c/c)p(l*t)\psi(a-c/c)$	45	3031.60	557.41	0.0000
$\phi(a-c/t)p(l*t)\psi(a-c/c)$	55	3033.77	559.57	0.0000
$\phi(a-c/c)p(l)\psi(a-c/c)$	7	3242.47	768.28	0.0000

Table 5.15. Age-specific within year movement rates between locations in the NS region (Hornby [HO], Comox [CX], Campbell River [CR]) from the winter to the spawn season for Harlequin Ducks in the Strait of Georgia, British Columbia. Estimates were generated by the highest ranking model that included the effect of age in the estimation of movement rates: ϕ (age-c/c) p (location*time) ψ (location*age-c/c), where survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively, and age effects are constant for both age classes (c/c). C-hat was adjusted to 3.62.

Location #1	Location #2	Young		Adult	
		Estimate	SE	Estimate	SE
HO	CX	0.016	0.028	0.041	0.014
CX	HO	0.615	0.272	0.526	0.095
HO	CR	0.036	0.044	0.007	0.004
CR	HO	1.000	0.000	0.085	0.052
CX	CR	0.000	0.000	0.000	0.000
CR	CX	1.000	0.000	0.014	0.022

Table 5.16. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of paired status on within year movement rates from the molt to the winter season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of sex, location, and paired status are indicated in parentheses by *sx*, *l*, and *ps*, respectively. AIC_c values were adjusted for c-hat of 5.15.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi()p()\psi()$	3	243.75	0.00	0.4596
$\phi()p()\psi(ps)$	4	245.13	1.38	0.2309
$\phi()p()\psi(sx)$	4	245.79	2.04	0.1659
$\phi()p()\psi(ps * sx)$	5	246.83	3.09	0.0982
$\phi()p()\psi(l)$	8	250.34	6.59	0.0170
$\phi(sx)p(l)\psi(ps)$	7	250.85	7.10	0.0132
$\phi(sx)p(l)\psi(sx)$	7	251.64	7.89	0.0089
$\phi(sx)p(l)\psi(ps * sx)$	8	252.57	8.82	0.0056
$\phi(sx)p(l)\psi(l)$	11	256.57	12.82	0.0008

Table 5.17. Candidate model set, ranked in order of increasing $QAIC_c$, used to determine the effect of paired status on within year movement rates from the winter to the spawn season for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ , p , and ψ , respectively. Effects of sex, location, and paired status are indicated in parentheses by *sx*, *l*, and *ps*, respectively. AIC_c values were adjusted for c-hat of 7.33.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi()p()\psi()$	3	185.59	0.00	0.4935
$\phi()p()\psi(ps)$	4	187.34	1.75	0.2056
$\phi()p()\psi(sx)$	4	187.62	2.03	0.1786
$\phi()p()\psi(ps * sx)$	5	189.27	3.68	0.0783
$\phi()p()\psi(l)$	8	190.44	4.85	0.0436
$\phi(sx)p(l)\psi(l)$	11	200.44	14.85	0.0003
$\phi(sx)p(l)\psi(sx)$	7	217.54	31.95	0.0000
$\phi(sx)p(l)\psi(ps)$	7	218.08	32.49	0.0000
$\phi(sx)p(l)\psi(ps * sx)$	8	219.30	33.71	0.0000

Table 5.18. Candidate model set, ranked in order of increasing $QAIC_c$, used to estimate survival rates based on sightings from the molt and spawn seasons for leg-banded Harlequin Ducks in the NS region in the Strait of Georgia, British Columbia, 1994-2000. Survival, sighting, and movement rates are denoted by ϕ, p, and ψ, respectively. Effects of time, sex, location, and season are indicated in parentheses by t, sx, l, and s, respectively; s_f indicates that the season effect on survival rates are specific to females only. AIC_c values were adjusted for c-hat of 7.98.

Model	No. of parameters	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight
$\phi(sx*s_f)p(l*t)\psi(l*s)$	54	2630.99	0.00	0.5945
$\phi(sx*s)p(l*t)\psi(l*s)$	55	2632.60	1.60	0.2668
$\phi(sx)p(l*t)\psi(l*s)$	53	2633.91	2.91	0.1385
$\phi(sx*s_f)p(l*t)\psi(l)$	48	2649.08	18.09	0.0001
$\phi(sx*s)p(l*t)\psi(l)$	49	2650.47	19.47	0.0000
$\phi(sx*s_f)p(l*t)\psi(l*sx*s)$	66	2651.38	20.39	0.0000
$\phi(sx)p(l*t)\psi(l)$	47	2652.44	21.45	0.0000
$\phi(sx*s)p(l*t)\psi(l*sx*s)$	67	2652.94	21.94	0.0000
$\phi(sx)p(l*t)\psi(l*sx*s)$	65	2653.63	22.64	0.0000
$\phi(sx*t)p(l*t)\psi(l*s)$	76	2665.02	34.03	0.0000
$\phi(sx*t)p(l*t)\psi(l)$	70	2683.67	52.68	0.0000
$\phi(sx*t)p(l*t)\psi(l*sx*s)$	88	2685.50	54.51	0.0000
$\phi(sx)p(l)\psi(l*s)$	17	2770.10	139.10	0.0000
$\phi(sx)p(l)\psi(l)$	11	3116.57	485.58	0.0000

Table 5.19. Sensitivity of F_{ST}, as estimated from the isolation by distance model, to changes in factors used to adjust effective neighbourhood size (Ne) relative to census neighbourhood size (N_{census}) for Harlequin Ducks wintering in the Strait of Georgia, British Columbia, for a census neighbourhood size of 2,241 and assuming 1,000 demes in the range of the species in western North America. The first line of the table shows original estimates (see methods) and the remaining lines give results of sensitivity analyses 1 through 5: (1) variance in offspring number was increased to 4 and 5, (2) the effect of overlapping generations was increased by a reduction of N_{census} by a factor of 0.6 and 0.5, (3) male-biased sex ratio was increased to 1.8 and 2.0, (4) neighbourhood size was reduced to 80%, 50%, and 10% of 2,241 in an equivalent of 20% of generations (one out of five) over time, and (5) all factors were combined.

Sensitivity analysis	Variance in offspring number	Effect of overlapping generations[a]	Sex ratio (# of males / # of females)	Population size[b]	Ne	F_{ST}
-	3	0.8	1.51	constant	1,143	0.003
1	4	0.8	1.51	constant	952	0.004
1	5	0.8	1.51	constant	816	0.005
2	3	0.6	1.51	constant	857	0.004
2	3	0.5	1.51	constant	714	0.005
3	3	0.8	1.80	constant	1,024	0.004
3	3	0.8	2.00	constant	956	0.004
4	3	0.8	1.51	reduced to 80%	1,088	0.003
4	3	0.8	1.51	reduced to 50%	953	0.004
4	3	0.8	1.51	reduced to 10%	408	0.009
5	5	0.5	2.00	reduced to 10%	152	0.025

[a] effect of overlapping generations is represented as a reduction of N_{census} by the factor shown.

[b] population size held constant over time (2,241 each generation) or reduced to a specified percentage of the census population size in one out of five generations (20% of generations) over time.

Table 5.20. Sensitivity of F_{ST}, as estimated from the isolation by distance model, to a reduction in density of individuals for Harlequin Ducks wintering in the Strait of Georgia, British Columbia, assuming 1,000 demes in the range of the species in western North America, that overall gene flow (root-mean-square dispersal distance) is 14 km, and that effective neighbourhood size (Ne) is reduced relative to census neighbourhood size (N_{census}) using estimates for correction given in the methods.

Density (birds / km^2)	N_{census}	Ne	F_{ST}
0.91	2,241	1,143	0.003
0.50	1,232	628	0.006
0.20	493	251	0.015
0.09	222	113	0.033

Table 5.21. Sensitivity of F_{ST}, as estimated from the isolation by distance model, to a reduction in overall gene flow (root-mean-square dispersal distance, σ_T) for Harlequin Ducks wintering in the Strait of Georgia, British Columbia, assuming 1,000 demes in the range of the species in western North America, a density of 0.91 birds / km^2, and that effective neighbourhood size (Ne) is reduced relative to census neighbourhood (N_{census}) size using estimates for correction given in the methods. The first line of the table shows results when overall gene flow is estimated from maximum movement distances of young birds observed; the remaining lines show results when maximum dispersal distances were limited to a maximum of 50, 30, 20, or 10 km (e.g., second line: any distances greater than 50 km were reduced to 50 km).

Maximum dispersal distance (km)	Overall gene flow (km)	N_{census}	Ne [a]	F_{ST}
-	14.0	2,241	1,120	0.003
50	12.9	1,903	951	0.004
30	10.4	1,237	618	0.006
20	8.5	826	413	0.009
10	5.2	309	154	0.024
5	3.0	103	51	0.073

[a] includes adjustment for kurtosis.

Table 5.22. Among population component of genetic variance (F_{ST}), as estimated from the stepping stone model, for Harlequin Ducks wintering in the Strait of Georgia, British Columbia. Effective mean colony size (Ne) was estimated at of 206 and the rate for long-distance gene flow, m_{∞} , was set at 10^{-6}. Based on movement rates in the northern Strait of Georgia, gene flow from adjacent colonies (m_{adj}) was estimated at 0.16, and the magnitude of m_{adj} also was decreased to 0.10 and increased to 0.22. The number of colonies was estimated at 6 for the Strait of Georgia, and was increased to 50, 150, and infinity.

No. of colonies	m_{adj}	F_{ST}
6	0.10	0.006
	0.16	0.005
	0.22	0.004
50	0.10	0.052
	0.16	0.038
	0.22	0.031
150	0.10	0.139
	0.16	0.106
	0.22	0.087
∞	0.10	0.731
	0.16	0.682
	0.22	0.647

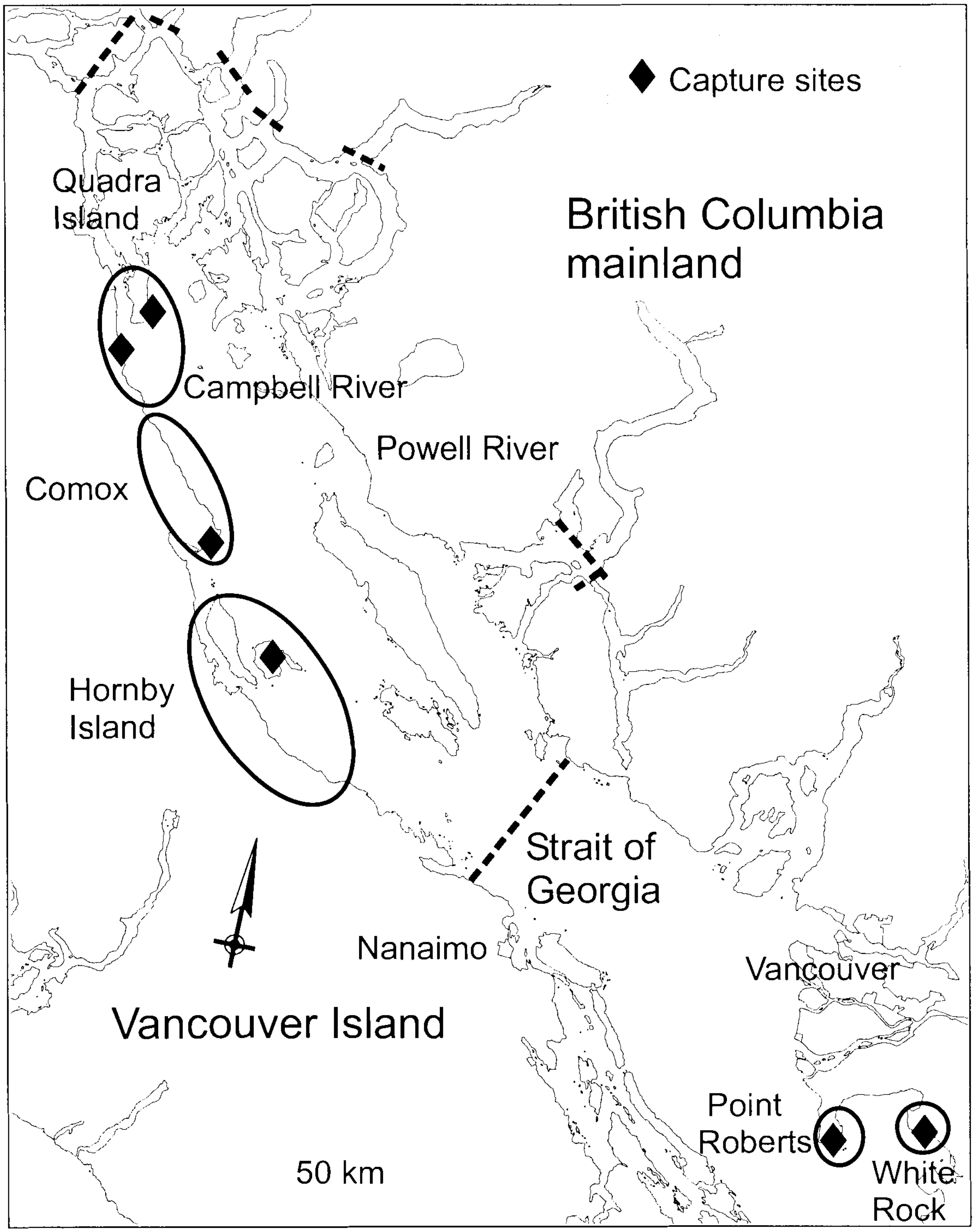

Figure 5.1. Capture sites and areas within which resightings of leg-banded individuals were recorded in the study of Harlequin Duck movement patterns in the Strait of Georgia, British Columbia, Canada, 1994-2001. Boundaries of the five locations (Campbell River, Comox, Hornby Island, Point Roberts, and White Rock) used in the estimation of between location movement rates within the Strait of Georgia are shown as ovals. Bold dotted lines show the limits of shoreline surveys in the search for nasal-marked individuals in the northern Strait of Georgia.

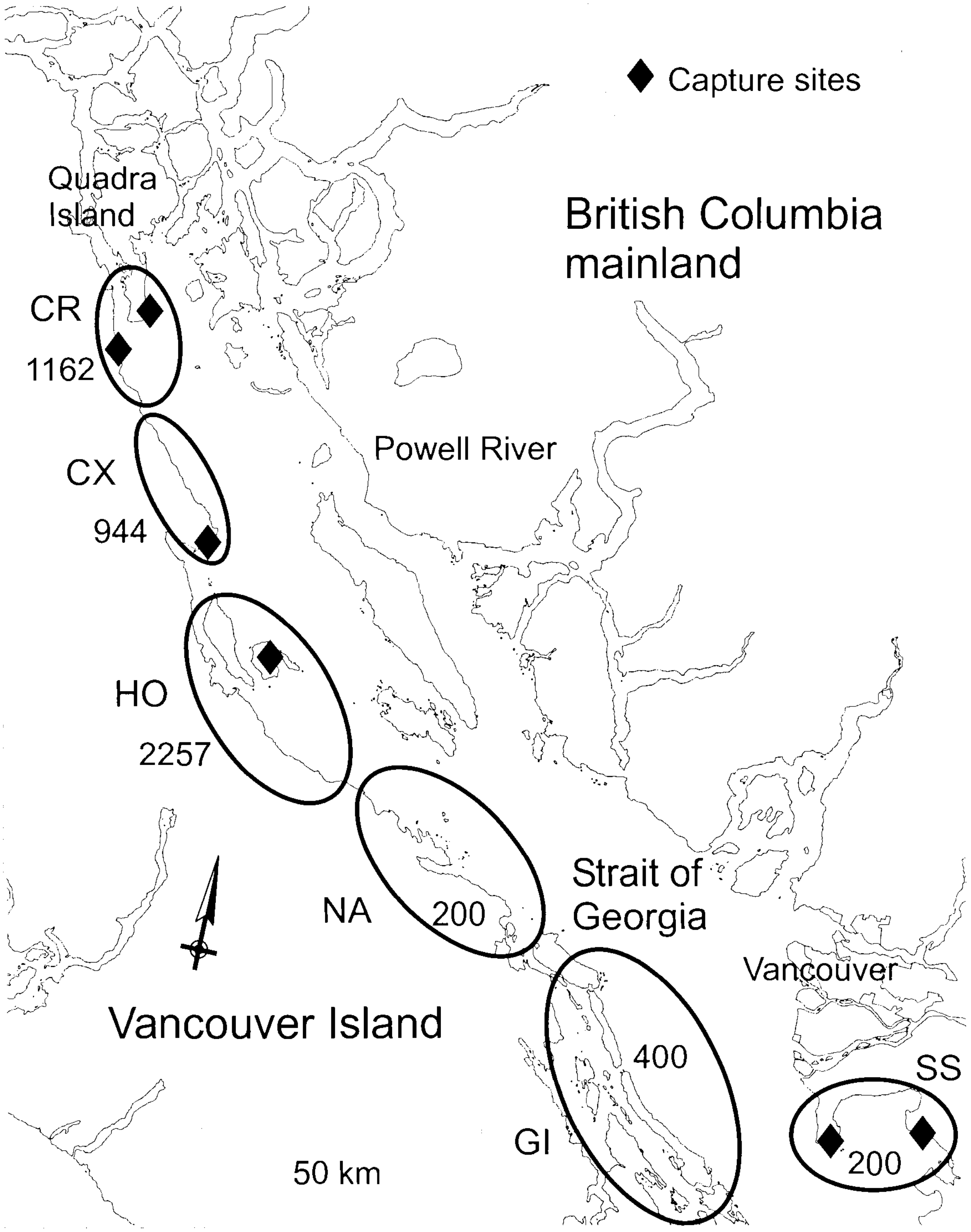

Figure 5.2. The Strait of Georgia subdivided into 6 colonies for use of the stepping stone model to estimate among population component of genetic variance. The six colonies, Campbell River (CR), Comox (CX), Hornby (HO), Nanaimo (NA), Gulf Islands (GI), and White Rock and Point Roberts combined into the Southern Strait (SS), are shown as labeled ovals and estimated numbers of birds within colonies (census population size) are shown within or next to ovals.

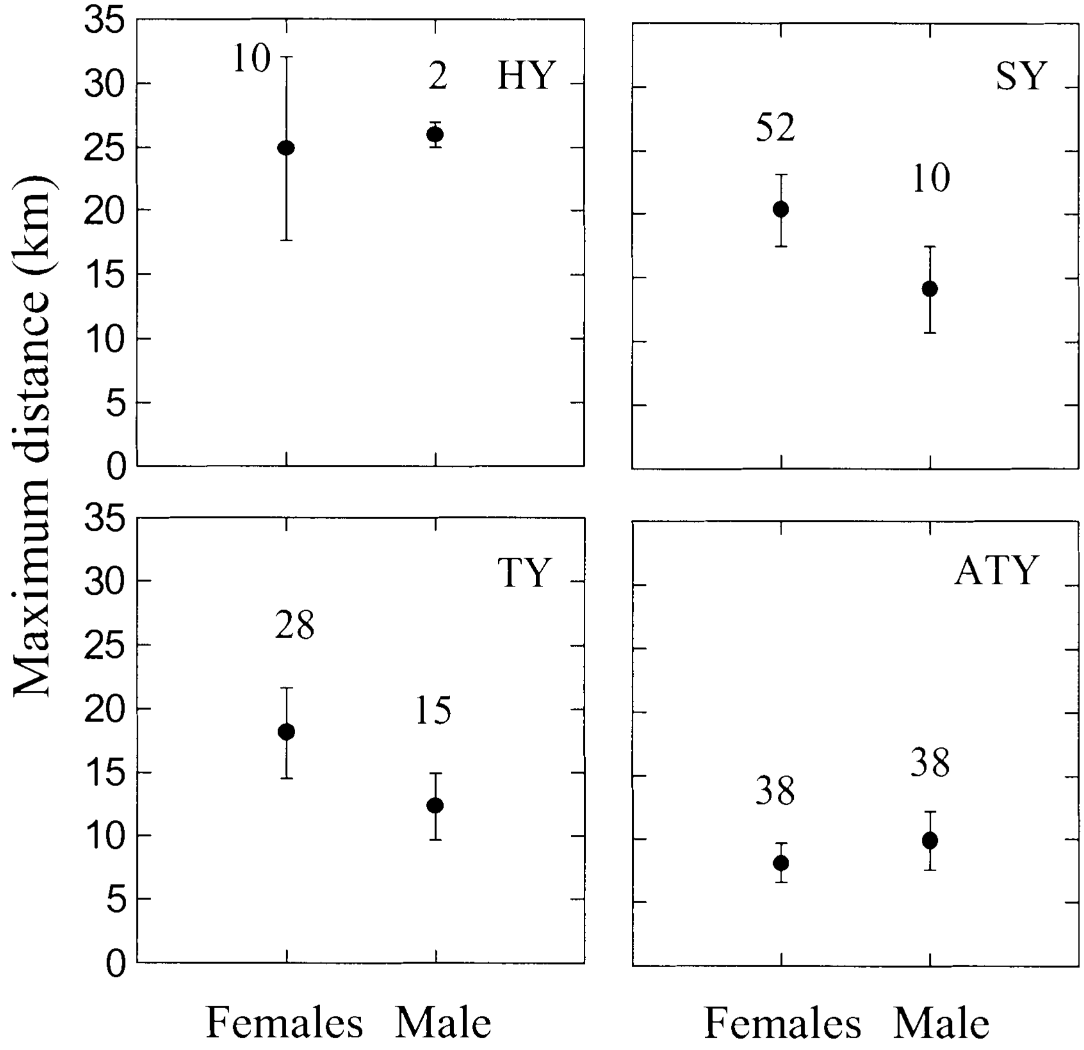

Figure 5.3. Mean maximum movement distances (km ± SE) from capture locations between November and April for male and female hatch year (HY), second year (SY), third year (TY) and after-third year (ATY) Harlequin Ducks in the northern Strait of Georgia, 1999-2001. Sample sizes are shown above points.

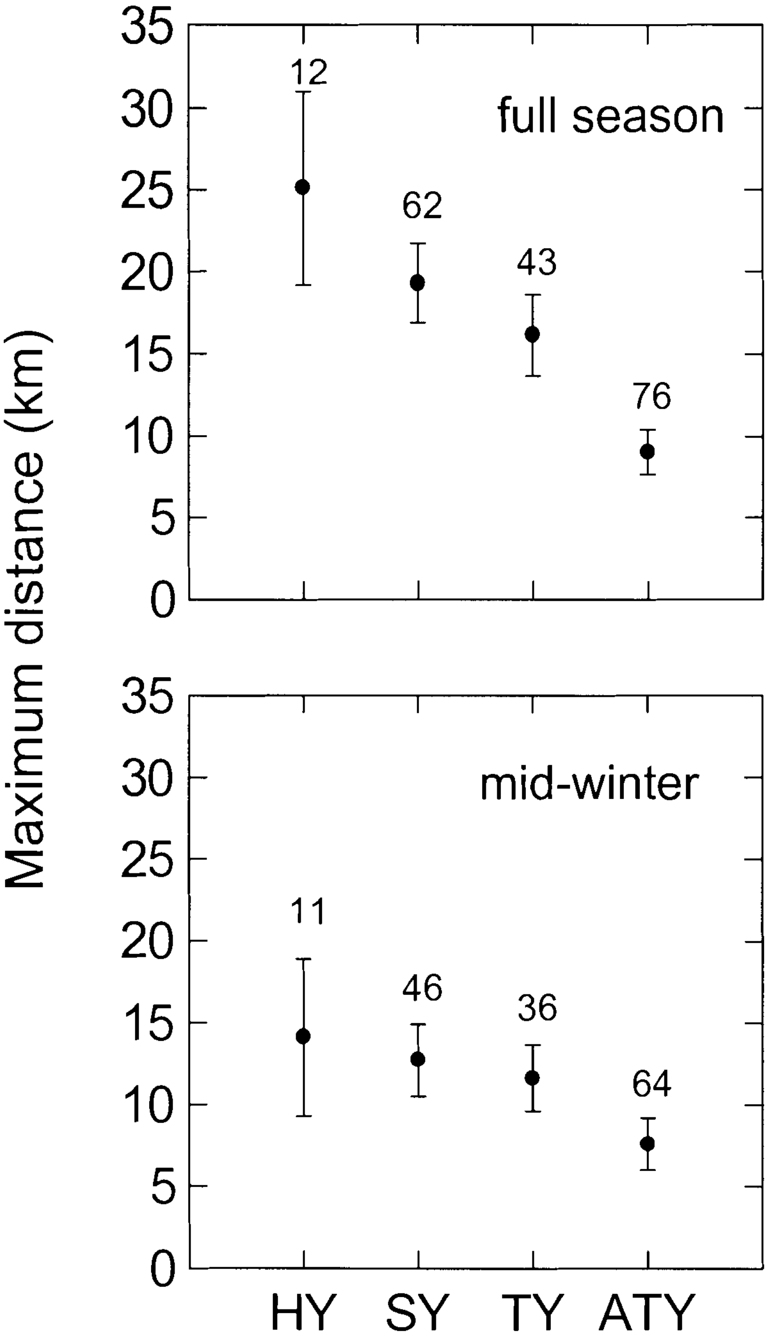

Figure 5.4. Full-season (November to April) and mid-winter (November to February) mean maximum movement distances (km ± SE) from capture locations of hatch year (HY), second year (SY), third year (TY) and after-third year (ATY) Harlequin Ducks in the northern Strait of Georgia, 1999-2001. Sample sizes are shown above points.

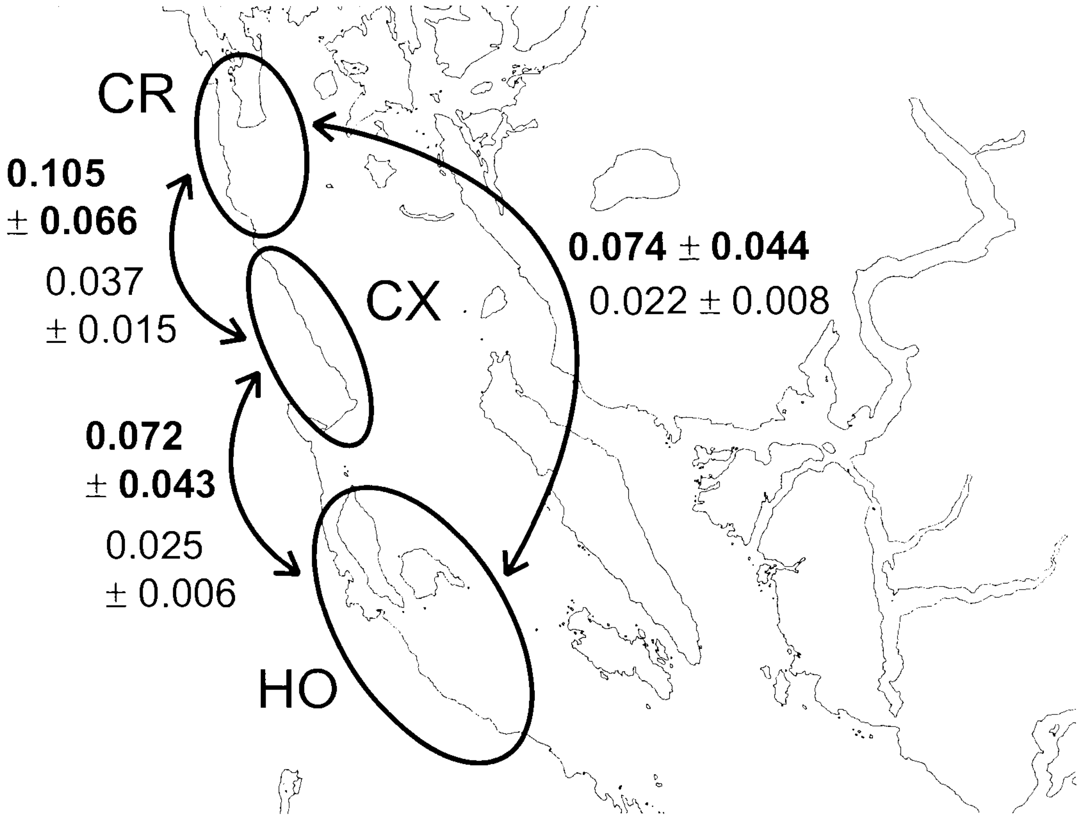

Figure 5.5. Between year movement rates (± SE) between locations in the northern Strait of Georgia (Campbell River [CR], Comox [CX], Hornby [HO]) for young (hatch year and second year) and adult (after-second year) Harlequin Ducks. Movement rates of young birds are shown in bold text and above those of adult birds.

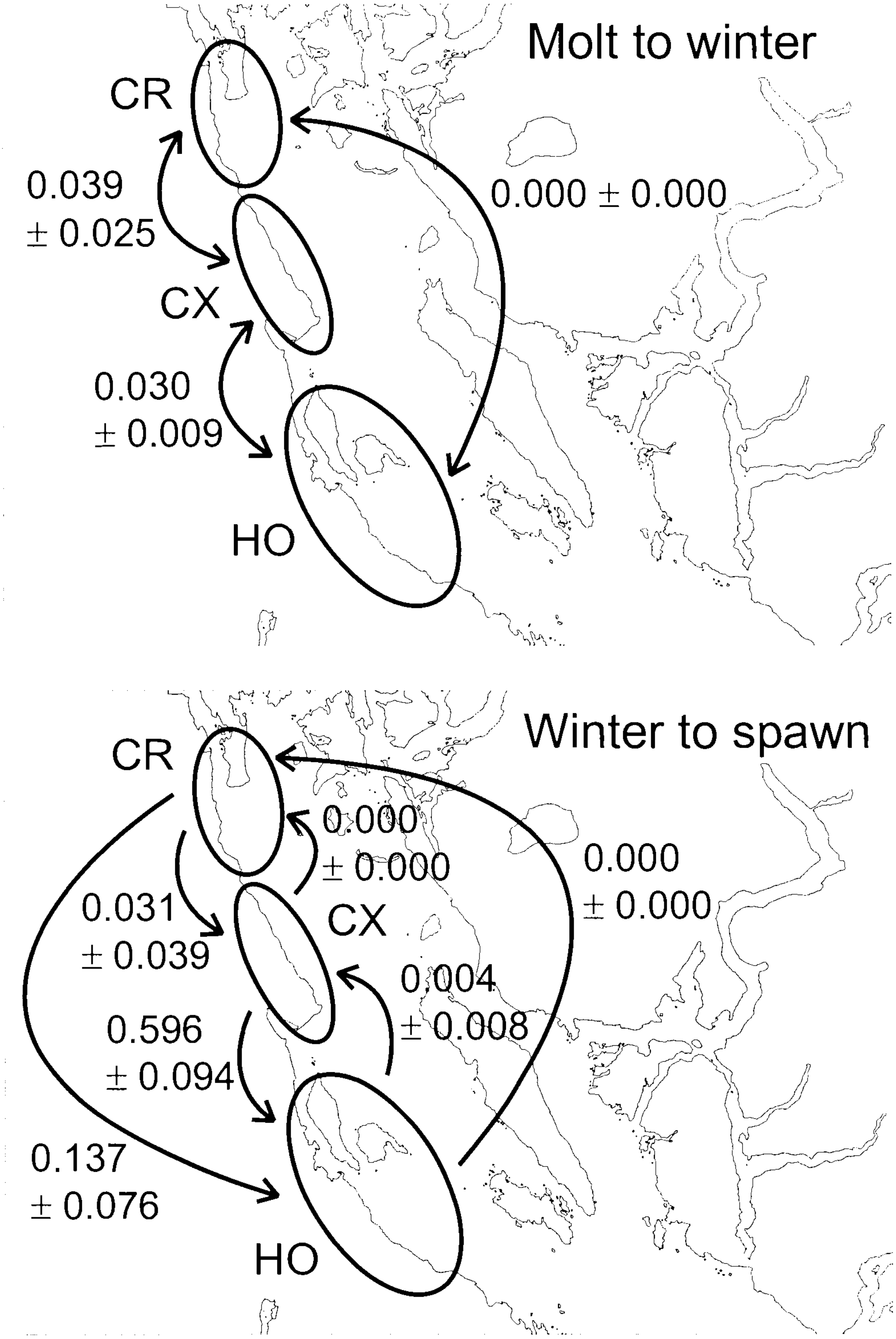

Figure 5.6. Within year movement rates (± SE) between locations in the northern Strait of Georgia (Campbell River [CR], Comox [CX], Hornby [HO]) for movement from the molt to the winter season, and from the winter to the spawn season, for all age groups combined.

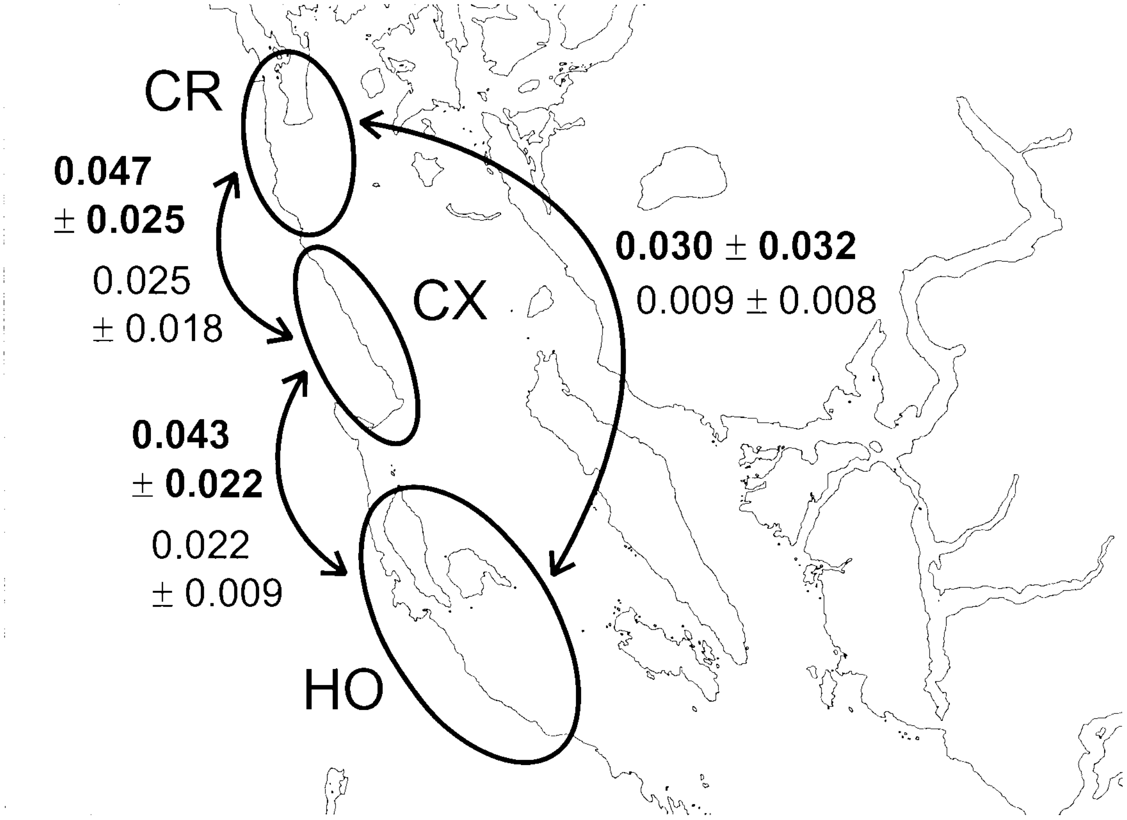

Figure 5.7. Within year movement rates (± SE) between locations in the northern Strait of Georgia (Campbell River [CR], Comox [CX], Hornby [HO]) for movement from the molt to the winter season for young (hatch year and second year) and adult (after-second year) Harlequin Ducks. Movement rates of young birds are shown in bold text and above those of adult birds.

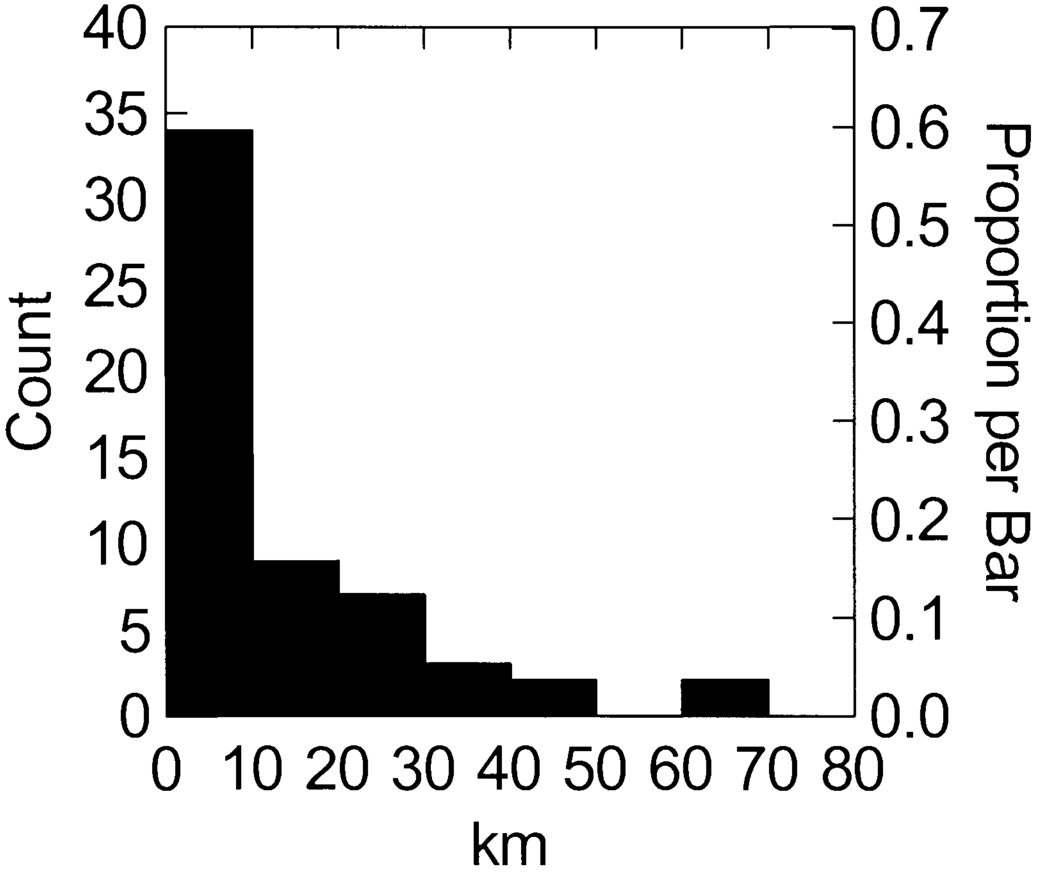

Figure 5.8. Distribution of mid-winter maximum movement distances for hatch year and second year Harlequin Ducks in the northern Strait of Georgia, 1999-2001.

CHAPTER 6

GENERAL CONCLUSIONS

In this thesis, I have investigated two aspects of the population dynamics of Harlequin Ducks important to the evaluation of their population structure. The first was the manner in which juveniles are incorporated into wintering populations (Chapter 2), and the second was the manner in which individuals of different sex and age classes move among wintering locations (Chapters 4 and 5). I also examined survival of juveniles during their first winter (Chapter 4), and evaluated the visibility and life span of two common waterfowl markers for Harlequin Ducks, and the effect of the more intrusive one on their behaviour (Chapter 3). This study took place in the Strait of Georgia, British Columbia, Canada, an important wintering area for Harlequin Ducks in western North America (Robertson and Goudie 1999).

Incorporation of juveniles into wintering populations

Juvenile Harlequin Ducks were observed in family-like associations at the coast following the breeding season. These associations consisted of one adult female and one or more juveniles. Family-like groups that were captured and marked continued to associate afterwards, and defensive and interactive behaviour observed for family groups was consistent with what would be expected for genetic families. Although most family groups seemed to separate soon after arrival at the coast, some family members were seen together as much as six months following capture. Analysis of blood samples provided further support that family groups captured together were genetic families. All juveniles had at least one allele at all of six biparentally inherited microsatellite loci in common with the adult female they were captured with and could therefore have been her genetic offspring. Low variability of alleles meant that about half of other individuals sampled from the population also had at least one allele at all six loci in common with each female captured with juveniles. Nevertheless, for one of the two adult females captured with juveniles, I was able to reject the null hypothesis that other individuals from the population were as likely to be the true offspring of this adult female as were the juveniles captured with her.

Although migration in family groups is common for geese and swans, it is an unusual strategy for ducks (Prevett and MacInnes 1980, Afton and Paulus 1992). Harlequin Ducks likely are unusual among ducks because they molt at the coast and can therefore molt and winter in the same location. This allows them to extend their parent-offspring bond into the wintering season, which likely confers benefits to both mother and young.

Evaluation of markers for Harlequin Ducks

I evaluated the visibility and life span of coloured leg bands and nasal discs for Harlequin Ducks. Nasal discs were more visible than coloured leg bands, thus, individuals marked with nasal discs were seen more frequently. However, nasal discs were lost more rapidly than leg bands. Half of all nasal discs were lost within 13 months, while only 11% of 1-yr-old leg bands on recaptured individuals were replaced due to wear, and some of these would still have been legible when replaced and were not yet lost to the study. Nasal discs therefore were considered inappropriate for long-term studies, however, leg band wear or loss should be considered for demographic studies. Poor nasal disc retention was likely caused by the abrasive action of rocks and cobbles on the nylon monofilament connector during feeding; however, wear of plastic shapes, causing them to become indistinguishable, was also observed, and exposure to sunlight would eventually cause colors to fade.

Nasal discs did not affect time spent in various behaviors, timing of pairing, or female pairing success. However, males with nasal discs had lower pairing success and females with nasal discs were less likely to reunite with previous mates. The fact that nasal discs did not affect time budgets suggests that the effects of nasal discs on pairing success were not attributable to indirect effects, such as a decrease in effort directed towards courtship as has been observed in other waterfowl studies (e.g., Koob 1981), and were more likely attributable to a male-biased sex ratio and sexual selection on male appearance. The impact that nasal discs had on pairing behavior suggests that nasal discs should not be used to study pairing success of males or repairing in either sex. However, nasal discs can be an ideal short-term marker for winter use for some studies because of high visibility during most behaviours. Also, because some aspects of courtship and pairing behavior may be relatively unaffected, and because pairing occurs during winter when birds rarely haul out, some such studies may benefit from nasal markers.

Survival of juveniles in their first winter

Radio-marking of juveniles at the coast allowed me to assess survival of juveniles in their first winter, and capture-mark-recapture (CMR) analysis on all individuals captured as juveniles over the years of the study allowed me to compare local survival among sex and age classes. Survival was higher for female than for male radio-marked juveniles, however, sample size was small and this result must therefore be treated with caution. Female juveniles had very high survival, with at least 89% surviving the winter. CMR analysis suggested that local survival of juvenile males was lower than all other sex-age classes, reflecting a combination of emigration and mortality. Results of this study, in combination with that of Cooke et al. (2000), who primarily included sub-adult (second and third year) and adult (after-third year) females in CMR analyses, suggest that there may be little difference in winter survival rates of female Harlequin Ducks with age, provided that juveniles have completed their first migration, and that these rates can likely be set equal for estimates of recruitment into the breeding population.

Movement at wintering areas

Radio-marking of juveniles allowed me to evaluate movement of Harlequin Ducks during their first winter. Some juvenile females dispersed substantial distances from their coastal capture locations. Due to the small sample of surviving males, I was unable to compare movement distances between the sexes. However, because one of the males may have left the study area, and no female did, it is possible that juvenile males disperse greater distances than do juvenile females. Proportions of male and female juveniles that were resighted at their capture location in their second winter did not differ, suggesting roughly equal dispersal rates between the sexes. Female philopatry for juveniles had been reported in previous studies and male-biased juvenile dispersal has been suggested (Cooke et al. 2000), however, results from this study indicate that both sexes disperse during winter.

Resightings of nasal-marked individuals provided dispersal distances of individuals differing by sex and age. I found no differences in dispersal distances by sex, but did find differences by age, with young individuals moving greater distances than older ones. Multi-stratum CMR analyses indicated that movement rates of young individuals also were greater than those of older ones, and that there was little difference by sex. There was a trend towards slightly higher movement rates by males, and analyses by paired status also revealed a slight non-significant trend of higher movement rates by unpaired males relative to paired males and females.

Movement rates were negatively related to the distance between locations, indicating that the isolation by distance and stepping stone gene flow models were most appropriate. Both models assume that individuals move with highest probability to adjacent areas. These gene flow models generated estimates of the among population component of genetic variance of less than 1% for the Strait of Georgia, indicating that, due to dispersal of young individuals, populations of Harlequin Ducks are unlikely to be genetically isolated and that dispersal distances and effective population sizes are not unusual compared to other avian species. Estimates from the stepping stone model for an increased number of colonies did suggest that, due to the linear distribution of Harlequin Ducks along the west coast of North America, genetic differences could develop over their entire west coast wintering range.

Between and within year movement rates for the northern Strait of Georgia suggested that populations within this area are unlikely to be demographically independent. Within year movement rates were especially high due to congregation at herring spawning sites in spring (Rodway et al. 2003a). However, movement rates between the northern and southern Strait of Georgia were low and these rates appear small enough to maintain demographic independence, but large enough to provide some connection, possibly enough to permit rescue or recolonization following population reductions.

Conclusions

Many sea duck species are of conservation concern due to apparent or suspected population declines (Goudie et al. 1994, Petersen and Hogan 1996). For Harlequin Ducks, available census information is insufficient to evaluate changes in population size and conservation concern is based on an apparent imbalance between recruitment and mortality (Rodway et al. 2003b). Due to low recruitment rates, population stability is highly sensitive to adult mortality (Goudie et al. 1994). In addition, the use of nearshore coastal waters by Harlequin Ducks during winter conflict with ever increasing human disturbance and development. Strong philopatry observed for Harlequin Ducks to molting and wintering sites (Breault and Savard 1999, Robertson et al. 1999, 2000) indicated that it was important to determine the scale at which wintering populations could be considered genetically and demographically distinct and should be managed separately.

Family migration from breeding to wintering areas, in combination with philopatry to wintering sites, would, in the absence of dispersal, lead to juveniles recruiting into the same wintering populations as their close relatives. Thus, results suggesting that juveniles migrate to the coast with their mothers in family groups provided further support for potential isolation of populations. However, radio-marking of juveniles, resightings of nasal-marked individuals of all age classes during extensive shoreline surveys, and age-specific CMR analyses based on sightings of leg-banded individuals, all suggested that young birds disperse substantial distances and at relatively high rates. Use of isolation by distance and stepping stone gene flow models with movement distances and rates suggested that movement at wintering areas by young individuals in their first and second winters counteract the isolating effects of philopatry and family migration and that dispersal is likely sufficient to explain lack of genetic differences found among Harlequin Duck populations in genetic studies in western North America (Scribner et al. 1998, Lanctot et al. 1999).

Movement patterns observed in this study have implications for estimation of survival rates and the evaluation of population stability. The confounding of emigration with mortality typically results in an underestimation of survival in CMR analyses; thus, knowledge of movement rates can be used to aid our interpretation of local survival rates. Relatively high movement rates for hatch year and second year Harlequin Ducks suggest that survival rates of young birds are particularly vulnerable to underestimation. Differences in movement rates by age emphasize the importance of separating age classes when estimating survival rates and suggests that survival estimates for young individuals are best generated from studies using radio-marking or from those with large search areas. My results also indicated that, although paired males are highly philopatric, some paired females emigrate, thus survival estimates generated for paired males are likely to be accurate, whereas those estimated for paired females may be underestimated. Thus it seems likely that estimates of female survival from previous studies have been underestimated due to emigration, and, in combination with the additional underestimation of recruitment (Rodway et al. 2003b), our concerns about population declines may have been overly pessimistic.

My results indicate that the population is relatively panmictic at the scale of this study, suggesting that Harlequin Ducks in the Strait of Georgia are best managed as a single population, especially from a genetic perspective. From a demographic perspective, within and between year movement rates were high within the northern Strait of Georgia, and although rates were much lower between the northern and southern parts of the strait, suggesting demographic independence, these two areas are likely sufficiently connected for movement of young individuals among wintering areas to contribute to recovery from potential population reductions. In addition, because females are required to found new colonies, the discovery that both sexes disperse improves confidence that recolonization or rescue could be successful (Avise 1995). However, there is currently insufficient information to conclude whether or not movement rates are indeed sufficient to connect these two regions in a metapopulation fashion, and population modeling could be attempted to improve predictions. In addition, the amount of time that would be required for recolonization of extinct groups is unknown, and many factors, such as density dependence and potential social requirements for founding groups need to be considered. Population modeling that incorporates survival, age-specific movement, leg band wear and loss, and recruitment, may also help to evaluate population stability.

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