

**TIMING OF PAIRING IN HARLEQUIN DUCKS: INTERACTION OF SPACING
BEHAVIOUR, TIME BUDGETS, AND THE INFLUX OF HERRING SPAWN**

by

Michael S. Rodway

B.Sc., Simon Fraser University, 1979

M.Sc., Memorial University of Newfoundland, 1994

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

in the Department

of

Biological Sciences

© Michael S. Rodway 2003

SIMON FRASER UNIVERSITY

September 2003

All rights reserved. This work may not be
reproduced in whole or in part, by photocopy
or other means, without permission of the author.

APPROVAL

Name: Michael S. Rodway

Degree: Doctor of Philosophy

Title of Thesis:

Timing of pairing in Harlequin Ducks: interactions of spacing behaviour, time budgets, and the influx of herring spawn.

Examining Committee:

Chair: Dr. R. Nicholson, Associate Professor

Dr. F. Cooke, Professor Emeritus, Senior Supervisor
Department of Biological Sciences, SFU

Dr. L.M. Dill, Professor
Department of Biological Sciences, SFU

Dr. R.W. Elner, Research Scientist
Canadian Wildlife Service

Dr. D. Esler, Research Associate
Department of Biological Sciences, SFU

Dr. B.D. Roitberg, Professor
Department of Biological Sciences, SFU
Public Examiner

Dr. M.G. Anderson, Director
Institute for Wetland and Waterfowl Research
External Examiner

Date Approved: 16 September 2003

PARTIAL COPYRIGHT LICENCE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

Timing of pairing in Harlequin Ducks: interactions of spacing behaviour, time budgets, and the influx of herring spawn.

Author:

(signature)

Michael Stephen Rodway

(name)

10 December 2003

(date)

ABSTRACT

This thesis had two major objectives. The first was to test predictions of previous and new theories to explain variation in the timing of pair formation in waterfowl by investigating how several aspects of the winter ecology of Harlequin Ducks, including distribution and spacing behaviour, time-activity budgets, and the use of herring spawn, may be related to the process of mate choice and the timing of pair formation. The second was to identify and address some of the gaps in our knowledge of the winter ecology and demography of Harlequin Ducks that currently handicap effective conservation action. Previous theory to account for variation in the timing of pairing, that primarily considered how phenotypic, social, and ecological factors affect male costs, poorly predicted pairing behaviour in Harlequin Ducks and other waterfowl. Female Harlequin Ducks invested considerable time and energy into selecting a mate, and decisions by females about how much time and energy to allocate to the pairing process appeared to be the main factor controlling the timing of pairing. Those decisions were affected by age, previous pairing experience, time required for other activities due to seasonal differences in day-length and food availability, and group spacing that affected the availability and likely the costs of mate sampling and in turn was also related to food availability. Spacing behaviour supported the hypothesis that unpaired birds will show adaptive changes in their spacing to reduce the costs of mate sampling. Aggregating at herring spawning sites in March provided birds with both direct nutritional benefits and indirect benefits related to changes in time budgets and spacing behaviour. Male and female interests necessarily interacted and a comprehensive theory to predict variation in pairing behaviour in waterfowl and other species requires consideration of benefits, costs, and conflicts of interest among individuals engaged in pairing decisions. The process of making mate-choice decisions, how the interactions of phenotypic, social, and ecological conditions affect that process, and how individuals integrate that process with other requirements of their life history are essential to consider in order to understand variation in the timing of pairing events.

To R. Wayne Campbell
for caring

ACKNOWLEDGMENTS

Most importantly, I want to thank my senior supervisor Fred Cooke for accepting me as a student, for tolerating, encouraging, and defending my need to work independently off-campus, for trusting and inspiring me to excel, for many insightful discussions and reviews, for his constant efforts to provide funding for me, and for extending his care of me long past his retirement. If I am a better scientist, it is largely due to Fred's influence. I hope that I have gained some measure of his keen knack for pinpointing a problem and identifying the next step required to answer a question. I am grateful and privileged to have been one of his last students at the Centre for Wildlife Ecology at Simon Fraser.

Many thanks to my committee members, Larry Dill, Bob Elner, and, for the latter part of my program, Dan Esler. They were instrumental in helping me focus my thesis questions and ensuring that I obtained an adequate background to effectively tackle those questions. This thesis is much more than it would have been without their help and guidance. I am grateful for their concern for my success throughout the program. Thanks also to Bob for help identifying faecal remains in the diet study.

This study would not have been possible without the marking of large numbers of Harlequin Ducks. The banding project has been ongoing and I am grateful to Ian Goudie for having the foresight to begin the project in 1993 and to Fred Cooke for securing funding and keeping the project alive through the period of my study. I stepped into the program in 1998 and I am indebted to Ken Wright, Pete Clarkson, and Stuart Jackson for inducting me into the team and showing me the ins and outs of working with Harlequin Ducks. Many individuals have helped with capturing, marking, and resighting Harlequin Ducks. I especially thank Brian Arquilla, John Ashley, Sean Boyd, Lynn Campbell, Pete Clarkson, Fred Cooke, Frank Elkins, Mary Jane Elkins, Dave Genter, Ian Goudie, Janet Hardin, Stuart Jackson, Heidi Regehr, Greg Robertson, Cyndi Smith, Richard Swanston, and Ken Wright.

Thanks to Brian Arquilla, Heidi Regehr, Jennifer Shore, and Jason Smith for assistance with behavioural observations, and to Sylvia Foran, Judy Higham, Margo Moore, Marlene Nguyen, Faith Rapchuk, Barbara Sherman, and Connie Smith for administrative and logistic assistance. Special thanks to Connie Smith for all her efforts procuring permits, managing the unwieldy capture and resighting data-bases, and ensuring that field equipment was operable and available. Canadian Wildlife Service provided the boat and associated gear used for winter surveys. I am most grateful to Moira Lemon for help in procuring and organising that equipment. Steve Holford kindly lent a stereoscopic microscope to use for the duration of the study. Many thanks to Martin Regehr for help with Visual Basic programming to manipulate large data files.

I want to thank my family, Arleigh Rodway, Don Rodway, Colleen Moore, Dan Rodway, Deva Rodway, and Christine Kravac for putting up with over five years of hectic and infrequent visits and for always giving me a place to stay when I needed to work at the university. Also, I thank Mary Jane and Frank Elkins' for their frequent hospitality and enthusiasm for the project on Hornby Island.

I am very grateful to the agencies that made this study possible. Funding was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, the British Columbia Waterfowl Society, the Institute of Waterfowl and Wetlands Research, and the James L. Baillie Memorial Fund. Various parts of the thesis were much improved by comments from my supervisor and committee, as well as by Michael Anderson, Sean Boyd, Julian Fischer, Heidi Regehr, Bernie Roitberg, Jean-Pierre Savard, and several anonymous reviewers. I especially want to thank Sean Boyd for his interest and detailed comments on most chapters. Thanks to Alton Harestad for moral support and encouragement throughout the program.

As always, I cannot adequately thank Heidi Regehr for sharing and help with virtually every aspect of the field study, for being a constant source and critic of ideas and motivating countless discussions that extended and refined my thinking, for making the entire program exponentially more enjoyable than it would have been otherwise, and for loving the storm-force seas.

TABLE OF CONTENTS

Title Page.....	i
Approval Page.....	ii
Abstract.....	iii
Dedication.....	iv
Acknowledgments.....	v
Table of Contents.....	vii
List of Tables.....	x
List of Figures.....	xii
Chapter 1: General Introduction.....	1
The Research Questions.....	1
Outline of the Thesis.....	3
Literature Cited.....	5
Chapter 2: Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates.....	8
Abstract.....	8
Introduction.....	8
Methods.....	9
Surveys.....	9
Sex and age ratios.....	10
Habitat associations.....	11
Statistical analyses.....	11
Results.....	12
Surveys.....	12
Sex and age ratios.....	13
Habitat associations.....	16
Discussion.....	17
Acknowledgments.....	23
Literature Cited.....	23
Chapter 3: Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site.....	33
Abstract.....	33
Introduction.....	33
Methods.....	35
Results.....	36
Discussion.....	38
Acknowledgments.....	41
Literature Cited.....	41
Chapter 4: Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia.....	48
Abstract.....	48
Introduction.....	48
Methods.....	50
Direct counts.....	50
Population estimates from mark-recapture analyses.....	50

Movement of birds.....	52
Distance travelled.....	53
Duration of stay.....	53
Consumption of spawn	54
Results	54
Locations and timing of spawning aggregations.....	54
Size of spawning aggregations.....	55
Origin of birds aggregating for spawn	55
Effect of travel distance	57
Duration of stay during spawning.....	57
Where birds went after spawning.....	58
Consumption of spawn	58
Discussion	59
Acknowledgments	62
Literature Cited	63

Chapter 5: Effect of food availability on arrival and departure decisions of Harlequin

Ducks at diurnal feeding grounds	75
Abstract	75
Introduction	75
Methods.....	77
Results	78
Discussion	79
Acknowledgments.....	81
Literature Cited	81

Chapter 6: Timing of pairing in waterfowl.....

Introduction	84
Male-costs hypothesis.....	85
Mutual-choice hypothesis	89
How do we measure timing of pairing?.....	90
Mate choice in waterfowl	92
Mating tactics and choosiness	94
Social and ecological factors	98
Harlequin Ducks	102
Methods.....	103
Marking and ageing	103
Pairing chronology.....	104
Behavioural observations.....	105
Spacing behaviour.....	107
Sex and age ratios	108
Inter-specific comparisons	108
Analyses.....	109
Results	109
Pairing chronology measured by pair-date	109
Sex and age differences	109
Re-uniting and re-pairing birds.....	110
Court-time and court-rate.....	111
Start and duration of courtship	111
Pair-date and pairing success in relation to court-rate.....	112
Evidence of trial liaisons	113

Length of time taken to re-pair	114
Time-activity budgets	114
Comparing 5 and 30 minute observation sessions.....	114
Seasonal changes and herring spawn.....	114
Differences by age	115
Differences by sex and paired status	116
Frequency of agonistic interactions	117
Do females control whether courtship occurs?.....	118
Pair-bond defence	120
Spacing behaviour.....	121
Group size.....	121
Courting arenas.....	123
Herring spawn	124
Time budgets	124
Sex ratio.....	124
Pair status.....	125
Mate sampling	125
Inter-specific comparisons	126
Discussion	128
Pairing in Harlequin Ducks.....	128
Timing of pairing in waterfowl.....	137
Conclusion	142
Acknowledgments.....	143
Literature Cited	144
Chapter 7: Summary and conclusions.....	184
Timing of pairing	184
Winter ecology and conservation implications	186
Literature Cited	190

LIST OF TABLES

Table 2.1. Mid-winter populations of Harlequin Ducks (<i>Histrionicus histrionicus</i>) in the northern Strait of Georgia, British Columbia, 1999-2000.....	27
Table 2.2. Logistic regression model relating presence or absence of Harlequin Ducks to shoreline habitat characteristics in the northern Strait of Georgia, winter 1999-2000.....	29
Table 2.3. Habitat use by wintering Harlequin Ducks in relation to shoreline complexity, substrate, and width of intertidal habitat in the northern Strait of Georgia, British Columbia, 1999-2000.....	30
Table 3.1. Prey types identified from remains found in Harlequin Duck feces (n = 202) at Hornby Island, British Columbia, 1998-1999.....	45
Table 3.2. Percent occurrence of prey remains in Harlequin Duck feces during four seasons at Hornby Island, British Columbia, 1998-1999.....	46
Table 4.1. Comparison of counts of Harlequin Ducks (<i>Histrionicus histrionicus</i>) during winter (January-February.), spawning (March), and spring (April) in sampling areas in the Strait of Georgia, British Columbia, 1998-2001.....	66
Table 4.2. Mean wintering numbers and maximum aggregations of Harlequin Ducks during herring spawning at four sites on the northeast side and four sites on the south and west sides of Hornby Island, British Columbia, in 1998-2002.....	67
Table 4.3. Numbers of Harlequin Ducks at Hornby Island during herring spawning, estimated by direct counts and by proportions of banded birds, in 1995-2002.....	68
Table 4.4. Proportions of marked wintering populations of Harlequin Ducks in the northern Strait of Georgia that moved to Hornby Island during herring spawning in 1999 and 2000.....	69
Table 6.1. Predictions of the female benefits-male costs hypothesis and the female-biased choice hypothesis to explain variation in the timing of pairing in waterfowl.....	164
Table 6.2. Monthly changes in the percentage (n) of marked, first-, second-, third-, and after-third-year female and male Harlequin Ducks that were identified as paired in the Strait of Georgia, British Columbia, 1995-2001.....	168
Table 6.3. Proportions of time and absolute amount of time spent during diurnal periods in various activities by wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000.....	169
Table 6.4. Proportion of time and absolute amount of time spent during diurnal periods in various activities by wintering Harlequin Ducks in relation to sex and paired status.....	170
Table 6.5. Agonistic interactions among wintering Harlequin Ducks in relation to sex and paired status.....	171

Table 6.6. Relative frequencies of different aggressive displays performed by wintering Harlequin Ducks in relation to their sex, age [hatch-year (1Y) and after-hatch-year (A1Y)], and paired status, and to the target of the display.....	172
Table 6.7. Aggression by female and male partners of Harlequin Duck pairs in relation to the recipient of the aggressive signal.	173
Table 6.8. Frequency of aggressive displays by female and male partners of Harlequin Duck pairs in relation to the age of the paired female.....	173
Table 6.9. Changes in group sizes of wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000.	173
Table 6.10. Variables used to analyse differences in the timing of pair formation among northern hemisphere species of the waterfowl subfamily Anatinae.....	174
Table 6.11. Differences in pairing chronology among waterfowl tribes in the subfamily Anatinae in the northern hemisphere.....	177

LIST OF FIGURES

Figure 2.1. Location of area surveyed for Harlequin Ducks (<i>Histrionicus histrionicus</i>) in the northern Strait of Georgia during the winter of 1999-2000.....	31
Figure 2. 2. Upper and lower 95% confidence limits of estimates of male age ratios of Harlequin Ducks from different-sized random samples of km-sections of shoreline that contained birds (A) and in relation to the total number of males sampled in those shoreline sections (B) in the northern Strait of Georgia during winter, 1999-2000.....	32
Figure 3.1. Changes in relative abundance scores of algae, herring eggs, and all other animal prey type remains found in Harlequin Duck feces over 10-day intervals after herring first spawned on Hornby Island, British Columbia, 1998-1999.	47
Figure 4.1. Locations of study areas and movement of Harlequin Ducks (<i>Histrionicus histrionicus</i>) from their wintering areas to Pacific herring (<i>Clupea pallasii</i>) spawning grounds in the Strait of Georgia, British Columbia in March of 1999 and 2000.	70
Figure 4.2. Box plots showing band-reading effort over the herring spawning period on Hornby Island, British Columbia, in 1998-2001.	71
Figure 4.3. Location of herring spawning and Harlequin Duck aggregations in the Hornby Island and Denman Island area, British Columbia, in March 1998.	72
Figure 4.4. Timing of Harlequin Duck aggregations relative to herring spawning at sites on Hornby Island, British Columbia, in March 1998.....	73
Figure 4.5. Percentages of wintering Harlequin Duck populations in the Strait of Georgia, British Columbia, that moved to Hornby Island for herring spawn in 1999-2000 in relation to the distance the birds had to travel.	74
Figure 5.1. Timing of arrival and departure of Harlequin Ducks at nearshore, diurnal feeding areas on Hornby Island, British Columbia during winter, herring spawning, and spring, 1998-2000.....	83
Figure 6.1. Age-related pairing chronology of Harlequin Ducks in the Strait of Georgia, British Columbia, 1995-2001.	178
Figure 6.2. Mean proportion of Harlequin Duck females paired in different sized groups during January, February, and March 2000 in the Strait of Georgia, British Columbia.	179
Figure 6.3. Comparison of seasonal trends from October to April in the amount of diurnal time spent in courtship by unpaired, greater-than-one-year-old Harlequin Ducks between locations where herring spawned in March and locations where herring did not spawn, in the Strait of Georgia, British Columbia, 1998-2001.	180
Figure 6.4. Allocation of time to different behaviours by unpaired, greater-than-one-year-old Harlequin Ducks during March at locations where herring did and did not spawn, in the Strait of Georgia, British Columbia, 1998-2001.....	181

Figure 6.5. Comparison of trends in Harlequin Duck sex ratios (upper lines) and male age ratios (lower lines) between locations where herring spawned and locations where herring did not spawn in the Strait of Georgia, British Columbia, 1998-2001..... 182

Figure 6.6. Comparison of absolute (a) and relative (b) ages when females first begin courtship (circles), median age of first pairing (squares), and median age of first breeding (triangles) among representative species of waterfowl tribes Cygnini (Mute Swans *Cygnus olor*), Anserini (Snow Geese *Anser caerulescens*), Tadornini (Paradise Shelducks *Casarca variegata*), Anatini (Mottled Duck *Anas fulvigula*), and Mergini (Harlequin Duck *Histrionicus histrionicus*)..... 183

CHAPTER 1

GENERAL INTRODUCTION

THE RESEARCH QUESTIONS

Pair bonds in many species of waterfowl are formed often several months or even years prior to breeding, in contrast to the more common avian pattern of pair formation just prior to breeding (Lack 1968). Pairing in most northern-hemisphere waterfowl occurs during the winter, and timing of pairing varies among and within species (Weller 1965, Paulus 1983, Wishart 1983, Hohman et al. 1992). Pairing occurs well in advance of the actual period of fertility, in some species when gonadal regression is maximal (Bluhm 1988). Timing of pairing is not correlated with the timing of reproduction (Rohwer and Anderson 1988) and differences are unlikely to be related to variation in female reproductive physiology. Waterfowl lay eggs at 1-2-day intervals, and eggs are fertilized from sperm stored in the female's reproductive tract after the laying of one egg and during about a 1-hr window after the ovulation of the next egg (Cheng et al. 1982, Alisauskas and Ankney 1992, McKinney and Evarts 1997). In Mallards (*Anas platyrhynchos*), stored sperm within the female reproductive tract remains viable for up to 17 d (Elder and Weller 1954), and though sperm from any male has a chance of fertilizing the next egg when multiple males inseminate the female in close succession, there is a last-male priority if inseminations occur more than 6 h apart (Cheng et al 1983). Though not well studied in other waterfowl, these physiological patterns are unlikely to vary by more than hours among or within species and thus cannot be linked to variation at scales of weeks or months in the timing of pairing.

Current theory to explain variation in the timing of pairing in waterfowl suggests that early pairing benefits both females, through male defence and vigilance that increases nutrient acquisition and survival, and males, through mate acquisition and improved female condition, but is delayed by trade-offs to males of the costs of courtship and mate defence (Rohwer and Anderson 1988, Owen and Black 1990). Several common features of waterfowl courtship behaviour are inconsistent with this idea. Courtship is often intense for extended periods before pair formation occurs, pair bonds in some species are formed during mid-winter when time and energy constraints should be most severe, and paired males frequently have time and energy to participate in social courtship groups (Hepp and Hair 1983, Williams 1983, Hohman et al. 1992, McKinney 1992). In addition, females often are unreceptive to male advances (Johnsgard 1960, Weller 1965, Hepp and Hair 1983), suggesting that there must be trade-offs of early pairing for females as well as males.

I propose that it is the process of mate choice that determines timing of pairing in waterfowl, and that variation in the costs, benefits, and tactics of mate choice for males and females results in variation in timing of pairing. In most migratory ducks, males outnumber females, and females provide all parental care (Oring and Saylor 1992). This should lead to greater female choosiness and control of the pairing process (Gowaty 1996, Jennions and Petrie 1997). There is ample evidence of female choosiness in waterfowl (Choudhury and Black 1993, Sorensen and Derrickson 1994, Omland 1996), and free choice of a mate and a strong pair bond appear to be prerequisite to successful egg production (Bluhm 1985, 1988).

How individuals are distributed may affect mate choice and timing of pairing (Jennions and Petrie 1997). Most waterfowl are gregarious on their wintering grounds, but some are widely scattered in small groups (e.g., species in tribe Mergini). Individuals looking for mates in dispersed populations will incur greater movement costs and may find it difficult to compare the quality of potential partners. As in lek-mating systems, females may prefer larger aggregations where potential mates can be sampled concurrently (Lank and Smith 1992). This could lead to aggregations of unpaired birds at specific locations that would serve as courting arenas (Johnsgard 1994). Winter spacing patterns of waterfowl may thus be partially shaped by sexual selection.

Mate-choice copying has been demonstrated and may be a means for inexperienced or more energetically constrained individuals to reduce sampling costs (Dugatkin 1992). Previous experience also has been shown to change mate-choice decisions (Bakker and Milinski 1991, Dugatkin and Godin 1992, Collins 1995). This suggests that learning may be important to young individuals. In many colonial-nesting marine birds, immature individuals visit breeding grounds, presumably to develop skills to increase their future reproductive success (e.g., Harris 1984). I propose that young waterfowl may aggregate in areas where they could gain exposure to and experience in courtship and mate choice.

Individuals searching for mates could benefit from localized food abundance that attracts aggregations of conspecifics. Individuals of many species often show adaptive changes in their distribution and spacing behaviour, and time their life history events to coincide with predictable but ephemeral food abundance (e.g., Botton et al. 1994). Benefits of exploiting such resources are generally assumed to be nutritive, whether for foraging animals themselves or for their offspring. Little attention has been paid to possible indirect benefits of ephemeral food abundance that may be associated with changes in time budgets and the reduction or elimination of intra-specific competition for food. Superabundant and easily exploitable food should decrease the time required for foraging and allow individuals to allocate more time to other behaviours that affect

their fitness. In addition, lack of competition for food may change a population's social structure by allowing individuals to join optimal sized groups for reasons unrelated to finding food.

Herring (*Clupea pallasii*) spawn provides a predictable, superabundant food that is available to waterfowl for three-to-four weeks in March-April (Haegele 1993). Spawning occurs at few locations, and in the Strait of Georgia, large aggregations of waterfowl gather at the main spawning area in the vicinity of Hornby Island and the adjacent Vancouver Island shore. Some or most individuals of a number of waterfowl species, including Harlequin Ducks (*Histrionicus histrionicus*), form pair bonds at this time (Rohwer and Anderson 1988, Robertson et al. 1998). Moving to herring spawning sites may be cost effective only for birds within a certain distance of those sites because of movement costs and possible mortality risks. This balance of costs and benefits may predict different mate choice strategies for birds that do and do not move to spawning sites, such as lower mate-sampling rates or threshold criteria (Janetos 1980) for birds that stay in small, dispersed groups than those that aggregate at spawning sites. This presents a conservation issue because herring spawning sites were more widespread in the past than they are at present in the Strait of Georgia.

Harlequin Ducks winter along marine rocky shores, generally in small groups of 2-20 birds. Their distribution in the Strait of Georgia changes in the spring when a large segment of the population travels unknown distances to be at Hornby Island when herring traditionally spawn. They have a mate-defence mating system with a male-biased sex ratio, form multi-year pair bonds on the wintering grounds, and show age-specific differences in the timing of pairing (Robertson et al. 1998). Feeding takes a large proportion of their time during winter months (Goudie and Ankney 1986, Torres et al. 2002). They are easy to observe and can be captured during their fall moult period so that individuals can be uniquely marked for behavioural observations. They are thus an appropriate species on which to test hypotheses about mate choice and timing of pairing, including the effects of spacing behaviour, time budgets, and seasonal food abundance in a natural population.

OUTLINE OF THE THESIS

The thesis had two major objectives. The first was to investigate how several aspects of the winter ecology of Harlequin Ducks, including distribution and spacing behaviour, time-activity budgets, and the use of herring spawn, may be related to the process of mate choice and the timing of pair formation. Four main hypotheses were developed: 1) timing of pair formation is primarily determined by female mate-choice decisions; 2) pairing individuals will aggregate to reduce costs of mate sampling; 3) immature (hatch-year to second-year) birds benefit from

observing the courtship behaviour and mate choices of older birds; and 4) herring spawn will provide indirect benefits to pairing birds through associated changes in time budgets and spacing behaviour. My approach to evaluating these hypotheses was to consider multiple alternative hypotheses (Chamberlain 1897). Acknowledging the problems in interpreting observational data, because of the complex interactions of environmental and social factors in uncontrolled, natural populations, I tried to identify specific, competing and falsifiable predictions that would discriminate among alternative hypotheses. I used those predictions to focus my research design. Although the scale of this study of a wild population mitigated against experimental manipulation, the spring influx of herring spawn constituted a natural experiment that increased food abundance and changed spacing behaviour and time budgets. This natural manipulation provided an opportunity to test a number of predictions about the effects of spacing and time budgets on courtship, mate choice, and timing of pairing.

The second objective was to identify and address some of the gaps in our knowledge of the winter ecology and demography of Harlequin Ducks that are prerequisite to effective conservation action in the face of rapidly escalating development in the Strait of Georgia, British Columbia. Their nearshore habits and low reproductive rate make Harlequin Ducks particularly vulnerable to increasing human activity (Goudie et al. 1994, Robertson and Goudie 1999). Basic information on distribution, abundance, and habitat use, including the use of herring spawning sites, was lacking. Estimates of recruitment are poor and it is uncertain whether recruitment is sufficient to balance adult mortality (Cooke et al. 2000, Smith et al. 2001). Many of the data required to fill some of these knowledge gaps were required before I could answer my research questions related to the timing of pair formation. I have thus included some chapters that present basic information on the winter ecology of Harlequin Ducks and provide a logical background for more detailed analyses that directly answer my research questions.

I review what is known about mate choice and pairing in waterfowl, evaluate current theories to explain variation in the timing of pairing, develop the theory that timing is primarily determined by female mate-choice decisions, and test predictions of previous and new theory in Chapter 6. Chapters 2-5 were prerequisite to accomplishing that task. Chapter 2 presents, from a conservation perspective, information on sex- and age-specific distribution, abundance, and habitat use that was prerequisite to evaluating, in Chapter 6, the hypotheses that unpaired birds will aggregate to reduce costs of mate sampling and immature birds will join such aggregations and participate in courtship activities to increase their future prospects of obtaining a mate.

Because little was known about the use of herring spawn by Harlequin Ducks, I first had to determine whether they fed on spawn when it was available (Chapter 3), whether and at what

spatial scale they aggregated at spawning sites, and, if they did aggregate, where they came from and how far they were willing to travel (Chapter 4), before I could address hypotheses relating pair formation to indirect benefits of feeding on spawn. Chapter 5 investigates how food abundance during spawn affects arrival and departure times of birds at diurnal feeding grounds, and provides necessary information for determining changes in time budgets during spawn. This set the stage for testing the hypothesis that feeding on herring spawn would have indirect benefits to pairing birds because of changes in time budgets and spacing behaviour. Finally, the conclusions presented in Chapter 7 integrate the various findings of the study.

LITERATURE CITED

- Alisauskas, R.T., and C.D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pp. 30-61 *in* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Bakker, T.C.M., and M. Milinski. 1991. Sequential female choice and the previous male effect in Sticklebacks. *Behavioral Ecology and Sociobiology* 29:205-210.
- Bluhm, C.K. 1985. Mate preferences and mating patterns of Canvasbacks (*Aythya valisineria*). *Ornithological Monographs* 37:45-56.
- Bluhm, C.K. 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. *Current Ornithology* 5:123-185.
- Botton, M.L., R.E. Loveland, and T.R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of Horseshoe Crab (*Limulus polyphemus*) eggs. *Auk* 111:605-616.
- Chamberlain, T.C. 1897. The method of multiple working hypotheses. *Journal of Geology* 5:837-848.
- Cheng, K.M., J.T. Burns, and F. McKinney. 1982. Forced copulation in captive Mallards. II. Temporal factors. *Animal Behaviour* 30:695-699.
- Cheng, K.M., J.T. Burns, and F. McKinney. 1983. Forced copulation in captive Mallards. III. Sperm competition. *Auk* 100:302-310.
- Choudhury, S., and J.M. Black. 1993. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour* 46:747-757.
- Collins, S.A. 1995. The effect of recent experience on female choice in Zebra Finches. *Animal Behaviour* 49:479-486.
- Cooke, F., G.J. Robertson, C.M. Smith, R.I. Goudie, and W.S. Boyd. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. *Condor* 102:137-144.

- Dugatkin, L.A. 1992. Sexual selection and imitation: females copy the mate choice of others. *American Naturalist* 139:1384-1389.
- Dugatkin, L.A., and J-G.J. Godin. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London Series B: Biological Sciences* 249:179-184.
- Elder, W.H., and M.W. Weller. 1954. Duration of fertility in the domestic Mallard hen after isolation from the drake. *Journal of Wildlife Management* 18:495-502.
- Goudie, R.I., and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475-1482.
- Goudie, R.I., S. Brault, B. Conant, A.V. Kondratyev, M.R. Petersen, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 59:27-49.
- Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. Pp. 21-52 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press. Oxford.
- Haegele, C.W. 1993. Seabird predation of Pacific Herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73-82.
- Harris, M.P. 1984. *The puffin*. T & A D Poyser, Calton.
- Hepp, G.R., and J.D. Hair. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. *Wilson Bulletin* 95:675-682.
- Hohman, W.L., C.D. Ankney, and D.H. Gordon. 1992. Ecology and management of postbreeding waterfowl. Pp. 128-189 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Janetos, A.C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology* 7:107-112.
- Jennions, M.D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* 72:283-327.
- Johnsgard, P.A. 1960. Pair-formation mechanisms in *Anas* (Anatidae) and related genera. *Ibis* 102:616-618.
- Johnsgard, P.A. 1994. *Arena birds: sexual selection and behavior*. Smithsonian Institution Press, Washington.
- Lank, D.B., and C.M. Smith. 1992. Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behavioral Ecology and Sociobiology* 30:323-329.
- McKinney, F. 1992. Courtship, pair formation, and signal systems. Pp. 214-250 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu

- (eds.). Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.
- McKinney, F., and S. Evarts. 1997. Sexual coercion in waterfowl and other birds. *Ornithological Monographs* 49:163-195.
- Omland, K.E. 1996. Female mallard mating preferences for multiple male ornaments. *Behavioral Ecology and Sociobiology* 39:353-360.
- Oring, L.W., and R.D. Saylor. 1992. The mating systems of waterfowl. Pp. 190-213 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.
- Owen, M., and J.M. Black. 1990. Waterfowl ecology. Blackie, Glasgow.
- Paulus, S.L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947-952.
- Robertson, G.J., and R.I. Goudie. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill (eds.). The birds of North America, No. 466. The Birds of North America, Inc., Philadelphia, PA.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1998. The timing of pair formation in Harlequin Ducks. *Condor* 100:551-555.
- Rohwer, F.C., and M.G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- Smith, C.M., R.I. Goudie, and F. Cooke. 2001. Winter age ratios and the assessment of recruitment of Harlequin Ducks. *Waterbirds* 24:39-44.
- Sorenson, L.G., and S.R. Derrickson. 1994. Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology* 35:389-400.
- Torres, R., F. Cooke, G.J. Robertson, and W.S. Boyd. 2002. Pairing decisions in the Harlequin Duck: costs and benefits. *Waterbirds* 25:340-347.
- Weller, M.W. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). *Auk* 82:227-235.
- Williams, D.M. 1983. Mate choice in the Mallard. Pp. 297-309 in P. Bateson (ed.). Mate choice. Cambridge University Press, Cambridge.
- Wishart, R.A. 1983. Pairing chronology and mate selection in the American Wigeon (*Anas americana*). *Canadian Journal of Zoology* 61:1733-1743.

CHAPTER 2

SEX AND AGE DIFFERENCES IN DISTRIBUTION, ABUNDANCE, AND HABITAT PREFERENCES OF WINTERING HARLEQUIN DUCKS: IMPLICATIONS FOR CONSERVATION AND ESTIMATING RECRUITMENT RATES

Rodway, M. S., H. M. Regehr, and F. Cooke. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates. *Canadian Journal of Zoology* 81:492-503.

Reprinted with permission (© NRC Canada).

ABSTRACT

We determined sex- and age-specific distribution, abundance, and habitat preferences of wintering Harlequin Ducks (*Histrionicus histrionicus*), and evaluated potential biases in measuring ratios of immature males to adult males to estimate recruitment rates. A comparison of the occurrence of birds with habitat availability at the 1-km scale indicated a preference for wide intertidal habitat with cobble-gravel or bedrock-boulder substrates, small offshore islets and shoreline with attached or nearby reefs and islets, areas without streams, and areas with greater historical abundance of herring spawn. Where the substrate was bedrock-boulder, birds preferred areas with tidal rapids. Densities of birds were highest along linear and complex shorelines with reefs or islets where intertidal habitat was >100 m wide and substrate was cobble-gravel or bedrock-boulder. Patterns of habitat use among sex and age classes were the same at the 1-km scale but differed at smaller scales, with adult and immature males occurring further offshore than females. Age ratios varied among areas and were biased by survey method and misidentification of distant birds. Correcting for detected biases gave an estimated male age ratio of 9.8%. Calculated estimates of female recruitment suggest a declining population, but it is necessary to incorporate emigration in estimates of adult survival before demographic trends can confidently be inferred.

INTRODUCTION

Information on distribution, demographics, and habitat use is vital in the conservation and management of any species. Many species show sex and age differences in habitat use that are related to differences in body size or dominance status (Fretwell 1972, Calder 1974, Gauthreaux

1978). In northern migratory waterfowl, females and immatures often winter farther south than males (Nilsson 1970, Nichols and Haramis 1980, Alexander 1983), or are relegated to lower quality patches at the local scale (Hepp and Hair 1984, Alexander 1987). Dominance behaviour of paired birds may exclude unpaired birds from preferred habitats (Boyd 1953, Paulus 1983). Habitat segregation can bias estimates of sex and age ratios used in demographic studies to determine effective population size and recruitment (Cowardin and Blohm 1992). Information on sex and age differences in habitat use allows the correction of biased estimates and the generation of unbiased sampling designs.

The sheltered marine waters, shorelines, and estuaries of the Strait of Georgia, British Columbia provide winter refuge for regionally and globally significant populations of numerous waterbird and shorebird species (Butler and Vermeer 1989, Campbell et al. 1990a,b). Since the area is also attractive to people, it has a burgeoning human population whose habitat use often directly conflicts with that of other species (Vermeer and Butler 1994). Management of these conflicts to ensure co-existence requires good information on population size, habitat use, and demographics of sensitive species (Savard 1989). Our goal in this study was to provide some of this information for Harlequin Ducks (*Histrionicus histrionicus*), because their nearshore habits and low reproductive rate make them particularly vulnerable to the adverse effects of increasing human activity (Goudie et al. 1994).

Our specific objectives were to: (i) determine the distribution and abundance of Harlequin Ducks wintering in the northern Strait of Georgia and identify areas of concentration; (ii) measure habitat preferences by relating the occurrence and abundance of birds to habitat availability; (iii) compare distributions and habitat use between sexes and between immature males and adult males; (iv) assess the potential for misidentification of immature males; (v) evaluate the potential bias in estimating age-ratios caused by differences in distribution or habitat use and by misidentification; and (vi) consider the implications of these factors and make recommendations for protecting habitat and conducting surveys to estimate age-ratios.

METHODS

Surveys

The study was conducted in the northern Strait of Georgia (Fig. 2.1) during winter 1999-2000, i.e., from 20 November to the end of February. All shorelines within boundaries of the study area were surveyed once for Harlequin Ducks. We surveyed areas sequentially so that little time elapsed between surveys of adjacent areas, reducing the likelihood that birds would have moved. Also, our study area was large so that even if a few birds did move, this was unlikely to

create directional bias in our population estimates or bird-habitat associations. Surveys were conducted from land whenever possible by one observer walking along the shore and scanning for birds with binoculars or a 20-60X spotting scope. In areas where the shoreline could not be walked, surveys were conducted by two observers (M.S. Rodway and H.M. Regehr) travelling along the shore in a 16' inflatable Zodiac. Often, one observer was set ashore to walk short accessible sections of shoreline, or just to obtain a solid platform from which to scan for birds. Surveys were not conducted in rough weather, when wind or rain might have reduced our ability to detect birds. We scanned as far as we could with a 60X spotting scope to be sure we were not missing birds that were unusually far offshore. We estimated the distance of a bird offshore from the current waterline within four categories: 1 (<10 m), 2 (10-50 m), 3 (50-300 m), and 4 (>300 m). Because the waterline changed with the tide, these distances did not correspond to any particular tide level.

Sex and age ratios

We classified birds as female, adult male, or immature male based on plumage characteristics (Smith et al. 1998). The sex ratio equalled the ratio of the total number of males to the total number of females. The male age ratio equalled the ratio of immature males (first winter) to adult males (second winter and older) expressed as a percentage. This differs from the age ratios calculated by Smith et al. (2001), who used the ratio of immature males to the total number of males, but is similar to fall age ratios commonly calculated for waterfowl species as the ratio of fledgling females to adult females (Cowardin and Blohm 1992). The alternate I plumage of immature males varies among individuals from female-like to male-like and for a particular individual appears to remain similar throughout the winter (Smith et al. 2001, M.S. Rodway and H.M. Regehr, unpublished data). We described immature-male plumage using a subjective 5-point scale, where 1 was female-like and 5 was adult male-like. Immature males received a score of 1 if they were indistinguishable from females except for crescent-shaped loreal patches and faint traces of white neck or chest stripes. Birds given a score of 5 differed little from adult males except they had a whitish belly and their neck collar was incomplete. We calculated overall sex and age ratios and compared ratios among areas to assess their geographic variability. Male age ratios and the relative frequencies of the different plumage codes for immature males were compared between surveys conducted by boat and from shore. We also compared these proportions among the four categories used for the distance birds were observed from the waterline to determine whether young males were more frequently misidentified when they were farther away. Proportions of birds in different-sized groups were determined to assess whether

immature males tend to be isolated and thus more easily missed. Birds were considered to be in separate groups if they were separated by ≥ 10 m.

Habitat associations

We estimated distances between all groups of birds to the nearest 10 m and noted prominent landmarks in order to map the number of birds occurring within each kilometre of shoreline. Kilometre divisions were marked on the largest scale (ranging from 1:10,000 to 1:80,000) marine charts available from the Canadian Hydrographic Service. The following habitat characteristics were described for each kilometre-section (km-section): (i) the width of intertidal habitat over most of the km-section, measured from the marine chart and coded 1 (<10 m), 2 (10-100 m), 3 (100-500 m), or 4 (>500 m); (ii) the substrate over most of the km-section as indicated on marine charts or based on our observations, coded 1 (bedrock or large boulder), 2 (cobble or gravel), or 3 (sand or mud); (iii) shoreline complexity, coded 1 (linear at the 1 km scale), 2 (convoluted with bays or points at the 1 km scale), 3 (reefs or islets <1 km long either connected to or within 1 km of shore), or 4 (islet or islet clusters >1 km offshore, the largest <1 km long); (iv) the presence of a stream, coded 1 (present within the km-section) or 2 (absent); (v) the presence of tidal rapids, coded 1 (present within the km-section) or 2 (absent); and (vi) a measure of the historical (1928-2000) abundance of herring (*Clupea pallasii*) spawn, using the cumulative herring spawn habitat index for each kilometre of shoreline, taken from Fisheries and Oceans Canada (DFO 2001). We included abundance of herring spawn because we hypothesised that intertidal productivity may be higher in areas where spawning occurs (Hay and Fulton 1983). Although exposure to wind and waves was related to Harlequin Duck densities in other studies (Esler et al. 2000, Mittelhauser 2000), we did not consider exposure because the entire Strait of Georgia is semi-protected and there was high redundancy in measures of exposure, intertidal width, and substrate.

Statistical analyses

We used *G* tests to analyse differences in sex and age ratios between land and boat surveys and among habitat categories. Because we surveyed the entire study area rather than sampling it, our age ratio estimate for the Harlequin Duck population in the northern Strait of Georgia has no sampling error associated with it. It was biased as a result of errors such as misidentification. We made adjustments based on our results in an attempt to correct some of these biases. To help with future study design, we used a randomization procedure to generate confidence limits for estimates of age ratios based on different sampling regimes. Random

samples were drawn from the km-sections of shoreline that contained Harlequin Ducks. The estimated age ratio was the ratio of the total number of immature males to the total number of adult males occurring in each random sample. Simulations were repeated 1000 times for each sample size. The 95% confidence limits were taken as the 2.5 and 97.5 percentiles of the randomly generated age-ratio estimates.

To relate habitat use to habitat availability at the 1-km scale, we entered all habitat variables into a logistic regression model in SPSS 8.0 with the presence or absence of Harlequin Ducks as the dependent variable. We set the reference categories with which others were compared in the logistic model to be <10 m for intertidal width, sand-mud for substrate, linear for shoreline complexity, absent for rapids, and absent for streams. To determine which habitat variables were related to Harlequin Duck abundance, we considered only km-sections where birds were encountered, and entered all habitat variables into a hierarchical analysis of covariance (ANCOVA) model. Duck numbers were natural log transformed to satisfy assumptions of normality and homoscedasticity. Interactions were tested in initial models and were dropped from final models if they were not significant.

We used a hierarchical model with Type I sums of squares because we formulated a priori hypotheses that width and substrate of intertidal habitat were the variables most related to bird density, and because we were concerned that relationships between duck numbers and historical abundance of herring spawn may have been spurious, being simply the result of similar use of habitat rather than an effect of herring spawn on intertidal productivity. The spawn index was entered last into this model, which allowed us to determine whether Harlequin Duck numbers were positively related to spawn abundance after all other habitat effects had been accounted for. Tolerance for Type I error was set at 5% for all tests.

RESULTS

Surveys

We surveyed 2289 km of shoreline (Fig. 2.1) and counted 6825 Harlequin Ducks in the northern Strait of Georgia (Table 2.1). Birds were present in 18% of the km-sections surveyed: 75% of the 191 km-sections surveyed from land, and 13% of the 2098 km-sections surveyed by boat. Concentrations occurred along the Vancouver Island shoreline, around Denman and Hornby islands, on the southern ends of Quadra, Marina, Cortes, Hernando, and Savary islands, among the Gillard and Dent islands, and along a short stretch of the mainland coast south of Powell River (Fig. 2.1).

Sex and age ratios

The overall sex ratio was 1.51 males per female, and the age ratio of immature males to adult males was 8.4% (Table 2.1). Sex ratios did not vary significantly among locations (only locations with ≥ 100 birds: $G_{13} = 13.4$, $P = 0.4$) but male age ratios did ($G_{13} = 31.1$, $P = 0.003$).

Age ratio differed between boat surveys (7.0%, immature males : adult males = 99:1409) and land surveys (9.2%, immature males : adult males = 218:2376) ($G_1 = 4.62$, $P = 0.032$). This suggested that we were misidentifying immature males during boat surveys. Misidentification seemed more likely around wide intertidal habitats, where we could not boat close to shore. Age ratios did not vary among intertidal-width categories for land surveys ($G_2 = 1.30$, $P = 0.5$; there were no land surveys of intertidal habitat < 10 m wide), but did differ for boat surveys ($G_3 = 13.9$, $P = 0.003$), declining with increasing intertidal width (14.3%, immature males : adult males = 4:28 for < 10 m; 9.2%, immature males : adult males = 61:666 for 10-100 m; 5.2%, immature males : adult males = 33:634 for 100-500 m; and 1.2%, immature males : adult males = 1:81 for > 500 m). Age ratios determined from all land surveys, including all intertidal-width categories, did not differ from those determined on boat surveys of intertidal habitats < 10 m wide ($G_1 = 0.61$, $P = 0.4$) or 10-100 m ($G_1 = 0.00$, $P = 1.0$), but were significantly greater than those from boat surveys of intertidal habitats widths 100-500 m ($G_1 = 9.83$, $P = 0.002$) and > 500 m wide ($G_1 = 8.20$, $P = 0.004$). This indicated that we were underestimating age ratios during boat surveys only in wider intertidal habitats. If we considered only data from boat surveys of intertidal habitats ≤ 100 m wide, then the male age ratio was 9.3% (immature males : adult males = 65:696), very similar to that calculated from land surveys only.

We considered that the bias in data from boat surveys might have been due to our missing birds with less conspicuous female-like plumage. However, the ratio of females to adult males did not differ between boat (0.70, females : adult males = 992:1409) and land (0.73, females : adult males = 1731:2376) surveys ($G_1 = 0.43$, $P = 0.5$). It is thus most likely that we simply misidentified some immature males as either females or adult males, and were not missing female-like birds during boat surveys.

Proportions of immature males assigned to each plumage category did not differ between boat and land surveys ($G_4 = 3.73$, $P = 0.4$) and overall were 6.4, 43.4, 33.1, 16.4, and 0.7%, for plumage scores 1 through 5, respectively ($n = 281$). Proportions did differ by distance offshore, and immatures with female-like or adult-male-like plumage (scores 1 and 5) were proportionately less frequent at distances > 50 m (3.5%, $n = 115$) than at distances < 50 m (9.6%, $n = 166$) offshore ($G_1 = 4.25$, $P = 0.039$).

Proportions of birds <10, 10-50, 50-300, and >300 m offshore from the waterline were 27, 45, 20, and 8%, respectively ($n = 6210$), and differed among females, adult males, and immature males ($G_6 = 44.5, P < 0.001$). Proportions at those distances were 29, 46, 18, and 7%, respectively, ($n = 2485$), for females, 26, 45, 21, and 9%, respectively ($n = 3433$), for adult males, and 24, 34, 29, and 13%, respectively ($n = 292$), for immature males. Proportions of birds occurring farther from the waterline were higher for immature males than for adult males ($G_3 = 21.0, P = 0.001$), and for immature males ($G_3 = 36.5, P < 0.001$) and adult males ($G_3 = 16.5, P = 0.001$) than for females. Differences in sex and age distributions resulted in higher sex ratios at greater distances offshore (1.33, 1.43, 1.74, and 2.02, respectively; $G_3 = 23.6, P < 0.001$), and higher age ratios at greater distances offshore (7.9, 6.5, 12.0, and 12.6%, respectively; $G_3 = 21.0, P < 0.001$). Trends in age ratios occurred despite the fact that immatures with female-like or adult-male-like plumage were less frequently identified at greater distances from shore, and thus the trends are conservative.

There were no trends in the relationship between sex ratio ($G_3 = 0.4, P = 0.9$) or age ratio ($G_3 = 0.5, P = 0.9$) and number of birds per kilometre. Most females (67%, $n = 1715$), adult males (72%, $n = 2356$), and immature males (69%, $n = 218$) recorded during land surveys occurred in groups of >2 birds. However, the proportion of birds that were alone rather than in groups of 2 was higher for immature males (17 vs. 14%) than for females (4 vs. 29%) or adult males (7 vs. 22%) ($G_2 = 69.5, P < 0.001$).

We adjusted our estimate of the male age ratio (R_{adj}) by considering the biases we found. First, we considered only data from land surveys because of the lower ratios found from boat surveys. Second, we assumed that the proportion of immature males assigned to each plumage category were correct for distances <50 m offshore, and we used these proportions to adjust the numbers of immature males with plumage scores 1 or 5 that might have been misidentified at distances >50 m.

$$R_{adj} = 100 * \left(\frac{J_L + J_L J_{adj}}{M_L - P_{J5}(J_L J_{adj})} \right)$$

where J_L is the total number of immature males identified on land surveys, J_{adj} is an adjustment for the proportion of immatures with plumage scores 1 or 5 missed at distances >50 m offshore, M_L is the total number of adult males identified on land surveys, and P_{J5} is the proportion of birds with plumage scores 1 and 5 that were in fact 5, and thus were likely to be mistakenly called adult males.

$$J_{adj} = \frac{\left[\left(\frac{J_{1,5}}{J_{2-4}} \right)_{<50} (J_{2-4})_{>50} \right] - (J_{1,5})_{>50}}{(J_{1-5})_{Total}}$$

where $(J_{1,5})_{<50}$ is the number of immature males with plumage score 1 or 5 identified <50 m offshore, $(J_{2-4})_{<50}$ is the number of immature males with plumage score 2, 3, or 4 identified <50 m offshore, $(J_{2-4})_{>50}$ is the number of immature males with plumage score 2, 3, or 4 identified >50 m offshore, $(J_{1,5})_{>50}$ is the number of immature males with plumage score 1 or 5 identified >50 m offshore, and $(J_{1-5})_{Total}$ is the total number of immature males scored for plumage. Thus,

$$J_{adj} = \frac{\left(\frac{14}{77} * 99 \right) - 4}{194} = 0.072$$

and

$$R_{adj} = 100 * \left(\frac{205 + 205(0.072)}{2258 - 0.14[205(0.072)]} \right) = 9.8\%.$$

This estimate is likely still somewhat conservative because we only corrected for misidentification of plumage-score 1 or 5 birds at distances >50 m offshore, and assumed that all others were correctly identified.

We randomly sub-sampled our data to simulate 95% confidence limits for age-ratio estimates determined from samples of various sizes. Because of the bias in identifying immature males during boat surveys of areas with wide intertidal habitat, in this simulation we excluded data from boat surveys of intertidal habitats >100 m wide. Results indicate that surveys of 105 random km-sections of shoreline with Harlequin Ducks are required in order to obtain confidence intervals less than $\pm 2\%$ (Fig. 2.2A). If we considered only km-sections that were surveyed from land, confidence intervals less than $\pm 2\%$ could be obtained with a random sample of 60 km-sections. This difference between including or excluding areas surveyed by boat is likely due to the fact that where Harlequin Ducks were present in our study area, densities were higher in areas surveyed from land (30.0 ± 27.9 birds per km) than by boat (9.3 ± 10.3 birds per km; $F_{1,411} = 118.5$, $P < 0.001$). Thus, total numbers of males (including immatures) sampled were similar in 105 random km-sections surveyed from land or boat (range in 1000 simulations: 726-1444; mean = 1057) and in 60 random km-sections surveyed only from land (range in 1000 simulations: 745-1452; mean = 1078). Simulations indicate that samples of random km-sections of shoreline

containing 1000 males in total will serve to provide age-ratio estimates with confidence intervals less than $\pm 2\%$ (Fig. 2.2B).

Habitat associations

There was a high correlation between abundances of females and males ($r = 0.95$, $P < 0.001$) and between abundances of immature males and adult males ($r = 0.65$, $P < 0.001$) within km-sections, and trends in relation to habitat variables were the same for females, adult males, and immature males. We therefore present statistical results for all males and females combined.

Logistic regression analyses indicated that intertidal-habitat width and substrate, shoreline complexity, the presence of streams, and the historical abundance of herring spawn were significant predictors of the occurrence of Harlequin Ducks (Table 2.2). The presence of ducks was positively related to the width of intertidal habitat: ducks were present in 2, 18, 54, and 33% of km-sections with <10 m ($n = 880$), 10-100 m ($n = 977$), 100-500 m ($n = 369$), and >500 m ($n = 63$) of intertidal habitat, respectively. Ducks were more likely to be present when the substrate was cobble-gravel (42%, $n = 584$) than when it was bedrock-boulder (10%, $n = 1490$) or sand-mud (8%, $n = 215$), and more likely to be present when it was bedrock-boulder than sand-mud. Differences between bedrock-boulder and sand-mud were most pronounced in wider intertidal habitats (Table 2.3). For example, along linear shorelines where the intertidal habitat was >100 m wide, birds were present in 100% of km-sections with bedrock-boulder substrate but in only 14% of km-sections with sand-mud substrates. The presence of birds was positively related to the historical abundance of herring spawn and negatively related to the occurrence of streams: birds were present in 10% ($n = 249$) of km-sections with streams compared to 19% ($n = 2040$) of km-sections without streams. Birds were more likely present on offshore islet clusters (41% of km-sections, $n = 167$) and along shorelines with nearby reefs or islets (21%, $n = 309$) than on linear (19%, $n = 1222$) and convoluted (7%, $n = 591$) shorelines. The differences between linear shorelines and shorelines with nearby reefs or islets were not large and were most apparent where intertidal habitat was narrower (Table 2.3).

The presence of birds was not significantly related to presence of tidal rapids. However, tidal rapids were present in only 3.3% ($n = 2289$) of km-sections, and occurred only in the channels among the northern Discovery Islands, mainly in the Settlers Group and Gillard and Dent islands (Table 2.1, Fig. 2.1). Shoreline in these areas was mostly steep rock with narrow intertidal habitat. Few Harlequin Ducks were encountered in these areas except in those with tidal rapids. If we considered only shoreline with bedrock-boulder substrate, Harlequin Ducks were

more likely present in areas where tidal rapids occurred (23% of km-sections, $n = 64$) than where they did not (9%, $n = 1426$; $G_1 = 10.3$, $P = 0.001$).

When we considered only km-sections where Harlequin Ducks occurred, a hierarchical ANCOVA model indicated that numbers of Harlequin Ducks per km-section were related to the width ($F_{3,399} = 88.2$, $P < 0.001$) and substrate ($F_{2,399} = 14.8$, $P < 0.001$) of intertidal habitat, shoreline complexity ($F_{3,399} = 3.8$, $P = 0.01$), the intertidal width x presence of streams interaction ($F_{2,399} = 6.2$, $P = 0.002$), and the historical abundance of herring spawn ($F_{1,399} = 11.8$, $P = 0.001$). Numbers were not significantly related to the presence of streams ($F_{1,399} = 0.0$, $P = 0.9$) or tidal rapids ($F_{1,399} = 0.7$, $P = 0.4$). For the overall model, $r^2 = 0.44$. Tukey post-hoc tests showed that ducks were more abundant in wider intertidal habitats (unadjusted means \pm SD were 4 ± 3 , 7 ± 6 , 21 ± 16 , and 60 ± 54 birds per km-section for intertidal-width categories 1, 2, 3, and 4, respectively) for every pairwise comparison between width categories (all $P < 0.001$). Numbers of ducks were higher over cobble-gravel (21 ± 24 birds per km-section) than over bedrock-boulder (9 ± 11 birds per km-section; $P < 0.001$) and sand-mud (11 ± 12 birds per km-section; $P = 0.001$) substrates. Numbers were higher along linear shorelines (21 ± 21 birds per km-section) than for all other complexity categories (all $P < 0.001$), and were higher where there were reefs or islets nearby (15 ± 30 birds per km-section) than along convoluted shorelines (6 ± 5 birds per km-section; $P = 0.012$). The intertidal width x presence of streams interaction was significant because duck numbers were higher at wider intertidal habitats where streams were absent but were lower at habitat widths >500 m than at widths 100-500 m where streams were present.

Densities of birds were highest along linear and complex shorelines with reefs or islets where intertidal habitat was >100 m wide and the substrate was cobble-gravel or bedrock-boulder (Table 2.3). Densities in occupied km-sections ranged from 2 to 108 birds/km, and averaged 17 birds/km. Over 60% of Harlequin Ducks occurred along linear shorelines where the intertidal habitat was >100 m wide with cobble-gravel substrate. Offshore islets with wide intertidal habitat were uncommon but were used by Harlequin Ducks wherever they occurred (Table 2.3).

DISCUSSION

Habitat and population management is often crippled by a lack of adequate information on basic aspects of species' ecology and demography (Doak and Mills 1994). This may be because species are difficult to study, funds for studies have not been committed, or inappropriate methodologies were used. Dedicated methodologies are required for a census of Harlequin Ducks because conventional aerial or boat surveys of waterfowl do not adequately detect Harlequin

Ducks (Savard 1989, Breault and Savard 1991). In our study area, some important wintering areas along the east coast of Vancouver Island were previously recognised (Mitchell 1952, Campbell et al. 1990a), but many areas of concentration had not been identified prior to our study. The large reef systems at the south ends of Quadra, Marina, Cortes, Hernando, and Savary islands support high densities of Harlequin Ducks. In those areas of extensive intertidal habitat, Harlequin Ducks were foraging as far as 2 km offshore. This contrasts with the previous perception that they forage very close to shore (Vermeer 1983, Robertson and Goudie 1999, Esler et al. 2000). Harlequin Ducks are best surveyed from land or a small boat that can closely approach shallow intertidal habitat.

We counted almost 7000 Harlequin Ducks in the northern Strait of Georgia. Based on numbers of birds wintering in other parts of British Columbia (Savard 1989, Campbell et al. 1990a, Breault and Savard 1991, Smith et al. 2001, K.G. Wright unpublished data, M.S. Rodway and H.M. Regehr, unpublished data), the total known wintering population is 8000-10 000 in the Strait of Georgia, and 12 000-15 000 in British Columbia. Overall numbers are probably higher because many coastal areas remain unsurveyed.

We found no evidence of habitat segregation between the sexes or ages at the 1-km scale. Numbers of males and females and immature males and adult males were highly correlated and their patterns of habitat use were similar. However, variation among locations found in this study and other studies (Smith et al. 2001) indicates that estimates of population sex and age ratios may be biased if only a few areas are surveyed.

Sex ratios found in this study were similar to those previously reported during winter from large samples of birds in British Columbia (Savard 1989, Campbell et al 1990a, Robertson and Goudie 1999, Smith et al. 2001) and Alaska (Rosenberg and Petrula 1998). Similar sex ratios across broad geographic areas suggest that latitudinal segregation between the sexes does not occur in Pacific Harlequin Ducks. There may be little energetic advantage for Harlequin Ducks in latitudinal segregation related to body size (Nichols and Haramis 1980) because coastal wintering habitats have moderated climates and dependable food resources that are difficult to defend. However, Harlequin Ducks spend a majority of daylight hours feeding during winter, females more than males (Goudie and Ankney 1986, Fischer and Griffin 2000), and time constraints may be more important than food availability (Esler et al. 2000). If so, this would imply an advantage to birds, especially females, in wintering further south, where winter daylight hours are longer. Birds could compensate for shorter day length by feeding nocturnally, but there is as yet no evidence that they do so (Rodway and Cooke 2001). High winter philopatry (Breault and Savard 1999, Robertson et al. 2000), early pairing (Gowans et al. 1997, Robertson et al. 1998), and small

winter ranges (Robertson et al. 1999) suggest that there are benefits to both sexes, especially paired birds, in remaining together in familiar, local habitats.

We did find evidence of small-scale differences in habitat use, with immature and adult males tending to occur farther offshore than females. Robertson et al. (1999) reported that some radio-marked males occasionally move offshore to roost and feed. Birds foraging at greater distances from shore likely incur greater energetic costs from diving in deeper water (Guillemette et al. 1993). Males may be more capable of bearing these costs because of their larger body size, and may gain some benefit from foraging where there are fewer competitors. However, if this were the sole explanation, we would not expect a higher proportion of immature males than adult males to occur farther offshore because young birds often have poorer foraging skills than adults (Burger 1988). Alternatively, segregation by distance offshore may occur because paired birds are dominant to unpaired birds. Greater access to preferred habitat is thought to be one of the benefits of early pairing in Harlequin and other ducks (Rohwer and Anderson 1988, Robertson et al. 1998). Although Harlequin Ducks do not defend feeding areas, paired birds are aggressive towards unpaired birds, particularly males (Robertson and Goudie 1999, M.S. Rodway, unpublished data). Such interference may increase costs in nearshore areas and make foraging offshore more cost-effective for unpaired birds (Sutherland and Parker 1985, Ranta et al. 1993). This could explain the higher proportion of immature males than adult males offshore because all immatures are unpaired, while a large proportion of adult males are paired.

This is the first study of Harlequin Ducks to investigate habitat use in relation to habitat availability. Occurrence of birds indicated a preference for wide intertidal habitat with cobble-gravel or bedrock-boulder substrate, for clusters of small offshore islets and shoreline with attached or nearby reefs and islets, and for areas with greater historical abundance of herring spawn. Birds avoided streams and were least likely to occur where there was minimal intertidal habitat, where the substrate was sand-mud, or where the shoreline was convoluted, with small bays and points. Where little intertidal habitat was available, birds exhibited a preference for areas with tidal rapids. Although birds showed a stronger preference for shorelines with small islets and reefs than for linear shorelines, differences in habitat availability resulted in the majority of the population using linear shorelines with wide cobble-gravel intertidal habitat.

Preferred habitats are generally assumed to be those where resource availability confers the greatest individual fitness (Rosenzweig 1991), but habitat use may reflect trade-offs between feeding, predation risk, and the availability of other resources such as roost sites or mates (Stephens and Krebs 1986, Lima and Dill 1990). Wide cobble or rock intertidal habitat likely provides the greatest availability of benthic invertebrates preyed upon by Harlequin Ducks

(Vermeer 1983, Rodway and Cooke 2002). Small islets and reefs may be most attractive because they provide roost sites and offer protection from terrestrial predators and human disturbance. Previous studies also have reported that reefs are important (Goudie and Ankney 1988, Esler et al. 2000). Our finding that the presence of streams was negatively related to occurrence and not related to abundance of Harlequin Ducks contrasts with that of Esler et al. (2000). Many streams in our study area occurred along steep, rocky shoreline with little intertidal habitat, or, in areas with gentler topography, in small bays along convoluted shorelines with intertidal substrates of sand or mud, habitats that were generally unattractive to Harlequin Ducks. Tidal rapids provide productive upwelling environments used by a variety of waterbirds (Edwards 1965, Campbell et al. 1990a), and likely provide richer foraging habitat for Harlequin Ducks in fjord-like channels generally devoid of extensive intertidal habitat.

The positive association between Harlequin Duck abundance and the historical abundance of herring spawn provides circumstantial evidence to support the hypothesis that spring spawning by herring increases the productivity of inter- and sub-tidal habitats during other times of the year. We think it unlikely that this relationship merely reflects similar habitat use by these species because it was significant after all other habitat effects had been considered. However, an alternate explanation for the association could be that Harlequin Ducks benefit from wintering in proximity to spawning sites so as to more easily access them in the spring (Rodway et al. 2003). The effect of spawn deposition on benthic productivity warrants investigation (Hay and Fulton 1983). Intertidal invertebrates that are the main winter prey of Harlequin Ducks (Rodway and Cooke 2002) are major consumers of herring spawn (Haegele 1993), therefore it is plausible that the massive spring influx of nutrients from herring spawn into the intertidal community (Hay and Fulton 1983) increases prey abundance for Harlequin Ducks during other times of the year. The recent spatial and temporal contraction of spawning in the Strait of Georgia (Hay and McCarter 1999) may be a conservation concern for wintering birds like Harlequin Ducks if the input of spawn is a determinant of benthic productivity.

Variation in male age ratios at large and small spatial scales and biases in age-ratio estimates due to survey method and misidentification have important implications for survey design. Differences among geographic areas indicate that larger scale sampling is required to accurately estimate population age ratios. Where density variation is similar to what we found in the northern Strait of Georgia, random samples of about 100 km-sections of shoreline with Harlequin Ducks will provide age-ratio estimates with 95% confidence limits of $\pm 2\%$. In our study area, similar precision could be obtained with smaller samples (60 km-sections) surveyed from land, and we recommend using only land surveys for monitoring age ratios in that area.

Land surveys were more efficient in that area because densities of Harlequin Ducks were higher along accessible shoreline and more birds were contained in fewer km-sections. Systematic sampling of shoreline habitat where birds are present could provide accurate estimates with similar precision as long as sampling is done over a large portion of the study area. Overall, our simulations indicate that surveys of samples of shoreline habitat need to enumerate about 1000 male Harlequin Ducks, or, in our study area with a sex ratio of 1.51, about 1700 Harlequin Ducks in total, to obtain male age-ratio estimates with 95% confidence limits of $\pm 2\%$.

All birds within sample sections should be identified and included regardless of distance offshore and group composition because age ratios are higher at greater distances offshore and a substantial proportion of immature males occur singly. The greater chances of misidentifying immature males with female- or adult-male-like plumage at greater distances offshore need to be considered and correction factors similar to those used in this study employed. The need to identify more distant birds makes it important to conduct surveys when visibility is good. Boat surveys of wide intertidal areas underestimate age ratios and their use for that purpose should be avoided; however, they can be useful for enumerating all birds using those areas and thus determining habitat use patterns. We found no relationship between age ratios and habitat type or total Harlequin Duck density, and excluding wide intertidal areas where density was often high did not bias age-ratio estimates.

Demographic rates of recruitment of young birds into the breeding population and mortality of breeding adults must balance in order to maintain a stable population. Local survival rates have been estimated as 0.76 for paired females and 0.91 for paired males (Cooke et al. 2000). Our unadjusted estimate of male age ratio of 8.4% was similar to that reported from Alaska (8.8%; Rosenberg and Petrula 1998) and to previous estimates determined on boat surveys of a wide geographic area in the Strait of Georgia (8.9%; Smith et al. 2001). Estimates by Smith et al. (2001) that were based on land surveys of a small number of areas were lower and highly variable. After adjusting for biases, we estimated the male age ratio to be 9.8%. Because females are the limiting sex, we calculated a female age ratio of 15.6% by assuming an equal sex ratio for immature birds and using the overall male-to-female sex ratio of 1.51. Almost all females pair in their second year (Robertson et al. 1998, M.S. Rodway, unpublished data). If we make the assumption that they also start breeding in their second year, which is not always the case (Robertson and Goudie 1999), then the actual recruitment rate of females into the breeding population would be 15.6% times an annual survival rate of 76% (Cooke et al. 2000), or 11.9%. Even if the annual rate of survival of non-breeding females is higher than 76% and actual recruitment rate is higher, it is still clearly insufficient to balance estimated mortality.

Although conservation concern for west coast Harlequin Ducks seems warranted, there is still uncertainty about current estimates of recruitment and survival rates. Our adjusted male age ratio of 9.8% is likely still conservative. While juvenile males may be misidentified as adult males, adults are unlikely to be misidentified as juveniles. We assumed that juveniles with plumage scores 2 through 4 were always identified correctly regardless of their distance offshore, which is unlikely to be so. However, we do not think that further biases in identifying immature males would greatly increase our recruitment-rate estimates. A second consideration is that our recruitment-rate estimate is based on only 1 year of data. Inter-annual variation in male age ratios have been reported (Smith et al. 2001), although our results indicate that such variation would be expected when only a few sites are sampled. Determining inter-annual changes in age ratios is difficult without random large-scale sampling because variation by location and year may be confounded. Further study with adequate sampling is required to determine annual variation.

Estimates of adult survival rates are also likely to be conservative. Although we have considered local survival rates of paired birds, and paired birds are highly philopatric (Robertson et al. 2000), estimates of true adult survival rates are lacking. Emigration needs to be incorporated into demographic models before true survival estimates can be derived.

Industrial, residential, and recreational development by humans is often concentrated along coastlines and competes directly with other species' habitat use. Harlequin Ducks depend on a productive littoral environment that is readily impacted by human activities. Their small body size and high feeding rates suggest that they are living near an energetic threshold during winter and have little flexibility to accommodate increased stress (Goudie and Ankney 1986, Mittelhauser 2000). The rapid expansion of the aquaculture industry in British Columbia is a major concern because of its direct and indirect habitat impacts and the risk of entanglement for marine birds (Vermeer and Morgan 1989). Extensive intertidal and shallow subtidal habitats are attractive for both shellfish tenures and Harlequin Ducks. A further concern comes from our finding that Harlequin Ducks prefer small islet and reef clusters. Both shellfish and finfish operations may usurp small islets for gear storage or residences. The recent lifting of the moratorium on new finfish farms in British Columbia is likely premature. Meeting our responsibilities in ensuring the health of marine bird populations in coastal habitats requires management that is cautious, acknowledges the limitations of our ecological understanding, and has the resources and will to pursue informed decisions.

ACKNOWLEDGMENTS

Funding for this study was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, the British Columbia Waterfowl Society, and the Institute of Waterfowl and Wetlands Research. Thanks are extended to Barbara Sherman and Connie Smith for administrative and logistic assistance. CWS kindly provided the boat and associated gear that we used for our surveys. We are grateful to Moira Lemon for help in procuring and organising that equipment. We were privileged to frequently receive the warm hospitality of Mary Jane and Frank Elkins of Hornby Island during this study. Sean Boyd, Larry Dill, and Jean-Pierre Savard made helpful comments on the manuscript.

LITERATURE CITED

- Alexander, W.C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. *American Birds* 37:26-29.
- Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks (Aythyini). *Wilson Bulletin* 99:38-49.
- Boyd, H. 1953. On encounters between wild white-fronted Geese in winter flocks. *Behaviour* 5:85-129.
- Breault, A.M., and J-P.L. Savard. 1991. Status report on the distribution and ecology of Harlequin Ducks in British Columbia. Technical Report Series Number 110, Canadian Wildlife Service, Delta, BC.
- Breault, A.M., and J.-P.L. Savard. 1999. Philopatry of Harlequin Ducks moulting in southern British Columbia. Pp. 41-44 *in* R.I. Goudie, M.R. Petersen, and G.J. Robertson (eds.). *Behaviour and ecology of sea ducks. Occasional Paper Number 100.* Canadian Wildlife Service, Ottawa. .
- Burger, J. 1988. Effects of age on foraging in birds. *Proceedings of the International Ornithological Congress* 19:1127-1140.
- Butler, R.W., and K. Vermeer. 1989. Overview and recommendations: important bird habitats and the need for their preservation. Pp. 185-186 *in* K. Vermeer and R.W. Butler (eds.). *The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Special Publication.* Canadian Wildlife Service, Ottawa.
- Calder, W.A., III. 1974. Consequences of body size for avian energetics. Pp. 86-151 *in* R.A. Paynter (ed.). *Avian energetics.* Nuttall Ornithological Club 15, Cambridge, MA. .
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990a. The birds of British Columbia. Vol. I. Nonpasserines (Introduction, loons through waterfowl). Royal British Columbia Museum, Victoria.

- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990b. The birds of British Columbia. Vol. II. Nonpasserines (Diurnal birds of prey through woodpeckers). Royal British Columbia Museum, Victoria.
- Cooke, F., G.J. Robertson, C.M. Smith, R.I. Goudie, and W.S. Boyd. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. *Condor* 102:137-144.
- Cowardin, L.M., and R.J. Blohm. 1992. Breeding population inventories and measures of recruitment. Pp. 422-445 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- DFO 2001. Fisheries and Oceans Canada Website: <http://www-sci.pac.dfo-mpo.gc.ca/herspawm> [accessed 12 December 2001].
- Doak, D.F., and L.S. Mills. 1994. A useful role for theory in conservation. *Ecology* 75:615-626.
- Edwards, R.Y. 1965. Birds seen in Active Pass, British Columbia. Pp. EE19-EE22 in *Provincial Museum of Natural History and Anthropology Report for the year 1964*. British Columbia Provincial Museum, Victoria.
- Esler, D., T.D. Bowman, T.A. Dean, C.E. O'Clair, S.C. Jewett, and L.L. McDonald. 2000. Correlates of Harlequin Duck densities during winter in Prince William Sound, Alaska. *Condor* 102:920-926.
- Fischer, J.B., and C.R. Griffin. 2000. Feeding behavior and food habits of wintering Harlequin Ducks at Shemya Island, Alaska. *Wilson Bulletin* 112:318-325.
- Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 in P.P.G. Bateson and P.H. Klopfer (eds.). *Perspectives in ethology*, Vol 3. Plenum Press, New York.
- Goudie, R.I., and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475-1482.
- Goudie, R.I., and C.D. Ankney. 1988. Patterns of habitat use by sea ducks wintering in southeastern Newfoundland. *Ornis Scandinavica* 19:249-256.
- Goudie, R.I., S. Brault, B. Conant, A.V. Kondratyev, M.R. Petersen, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 59:27-49.
- Gowans, B., G.J. Robertson, and F. Cooke. 1997. Behaviour and chronology of pair formation by Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl* 48:135-146.
- Guillemette, M., J.H. Himmelman, and C. Barette. 1993. Habitat selection by Common Eiders in winter and its interaction with flock size. *Canadian Journal of Zoology* 71:1259-1266.

- Haegerle, C.W. 1993. Seabird predation of Pacific Herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73-82.
- Hay, D.E., and J. Fulton. 1983. Potential secondary production from herring spawning in the Strait of Georgia. *Canadian Journal of Fisheries and Aquatic Sciences* 40:109-113.
- Hay, D.E., and P.B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document 99/14, Nanaimo, BC.
- Hepp, G.R., and J.D. Hair. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *Condor* 86:251-257.
- Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Mitchell, G.J. 1952. A study of the distribution of some members of the Nyrocinæ wintering on the coastal waters of southern British Columbia. M.Sc. Thesis, University of British Columbia, Vancouver.
- Mittelhauser, G.L. 2000. The winter ecology of Harlequin Ducks in coastal Maine. M.Sc. Thesis, University of Maine, Orono.
- Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. *Condor* 82:406-416.
- Nilsson, L. 1970. Local and seasonal variation in sex-ratios of diving ducks in south Sweden during the non-breeding season. *Ornis Scandinavica* 1:115-128.
- Paulus, S.L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947-952.
- Ranta, E., H. Rita, and K. Lindstrom. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. *American Naturalist* 142:42-58.
- Robertson, G.J., and R.I. Goudie. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill (eds.). *The birds of North America*, No. 466. The Birds of North America, Inc., Philadelphia, PA.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1998. The timing of pair formation in Harlequin Ducks. *Condor* 100:551-555.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1999. Within-year fidelity of Harlequin Ducks to a moulting and wintering area. Pp. 45-51 in R.I. Goudie, M.R. Petersen, and G.J. Robertson (eds.). *Behaviour and ecology of sea ducks*. Occasional Paper Number 100. Canadian Wildlife Service, Ottawa.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 2000. Spacing patterns, mating systems, and winter philopatry in Harlequin Ducks. *Auk* 117:299-307.

- Rodway, M.S., and F. Cooke. 2001. Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor* 103:870-874.
- Rodway, M.S., and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. *Journal of Field Ornithology* 73:363-371.
- Rodway, M.S., H.M. Regehr, J. Ashley, P.V. Clarkson, R.I. Goudie, D.E. Hay, C.M. Smith, and K.G. Wright. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology* 81:504-514.
- Rohwer, F.C., and M.G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- Rosenberg, D.H., and M.J. Petrula. 1998. Status of Harlequin Ducks in Prince William Sound, Alaska, after the Exxon Valdez oil spill, 1995-97. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 97427), Alaska Dept. Fish Game, Div. Wildl. Conserv., Anchorage, AK.
- Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137(Supp.):S5-S28.
- Savard, J-P.L. 1989. Birds of rocky coastlines and pelagic waters in the Strait of Georgia. Pp. 132-141 in K. Vermeer and R.W. Butler (eds.). *The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia*. Special Publication, Canadian Wildlife Service, Ottawa.
- Smith, C., F. Cooke, and R.I. Goudie. 1998. Ageing Harlequin Duck *Histrionicus histrionicus* drakes using plumage characteristics. *Wildfowl* 49:245-248.
- Smith, C.M., R.I. Goudie, and F. Cooke. 2001. Winter age ratios and the assessment of recruitment of Harlequin Ducks. *Waterbirds* 24:39-44.
- Stephens, D.W., and J.R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton.
- Sutherland, W.J., and G.A. Parker. 1985. Distribution of unequal competitors. Pp. 255-273 in R.M. Sibley and R.H. Smith (eds.). *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford. .
- Vermeer, K. 1983. Diet of the Harlequin Duck in the Strait of Georgia, British Columbia. *Murrelet* 64:54-57.
- Vermeer, K., and R.W. Butler. 1994. The international significance and the need for environmental knowledge of estuaries. Pp. 75-76 in R.W. Butler and K. Vermeer (eds). *The abundance and distribution of estuarine birds in the Strait of Georgia, British Columbia*. Occasional Paper Number 83, Canadian Wildlife Service, Ottawa.
- Vermeer, K., and K.H. Morgan. 1989. Mariculture and bird interactions in the Strait of Georgia. Pp. 174-176 in K. Vermeer and R.W. Butler (eds.). *The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia*. Special Publication, Canadian Wildlife Service, Ottawa.

TABLE 2.1. Mid-winter populations of Harlequin Ducks (*Histrionicus histrionicus*) in the northern Strait of Georgia, British Columbia, 1999-2000.

Location ^a	Length of shoreline (km)	Total ducks	Density per km	Females	Adult males	Immature males	Sex ratio ^b	Male age ratio ^c
Vancouver Island								
Nanoose to French Creek	68	149	2.2	56	84	9	1.66	10.7
French Creek to Deep Bay	34	751	22.1	300	409	42	1.50	10.3
Deep Bay to Comox	44	105	2.4	36	66	3	1.92	4.5
Comox to Oyster R.	41	944	23.0	385	500	59	1.45	11.8
Oyster R. to Campbell R.	30	524	17.5	207	294	23	1.53	7.8
Campbell R. to Chatham Pt.	54	15	0.3	5	6	4	-	-
Strait islands								
Denman I.	49	685	14.0	281	383	21	1.44	5.5
Hornby I.	33	716	21.7	287	399	30	1.49	7.5
Lasqueti I.	118	5	0.0	1	3	1	-	-
Texada I.	127	0	0	0	0	0	-	-
Harwood I.	14	14	1.0	4	8	2	-	-
Savary I.	18	211	11.7	68	127	16	2.10	12.6
Hernando I.	16	234	14.6	101	129	4	1.32	3.1
Mitlenatch I.	3	10	3.3	6	3	1	-	-
Discovery islands								
Quadra I. south end	21	638	30.4	263	355	20	1.43	5.6
Quadra I. north	229	207	0.9	83	113	11	1.49	9.7
Marina I.	13	355	27.3	155	192	8	1.29	4.2
Cortes I. south end	12	262	21.8	90	151	21	1.91	13.9
Cortes I. north	172	253	1.5	106	135	12	1.39	8.9
Read I.	114	175	1.5	69	100	6	1.54	6.0
Settlers Group	19	56	2.9	25	30	1	1.24	3.3
Gillard and Dent Is.	37	94	2.5	36	51	7	1.61	13.7
Nodales Channel	67	31	0.5	16	15	0	-	-

TABLE 2.1. cont'd

Location ^a	Length of shoreline (km)	Total ducks	Density per km	Females	Adult males	Immature males	Sex ratio ^b	Male age ratio ^c
Mainland coast								
Bute to Malaspina Inlets	464	26	0.0	9	15	2	-	-
Malaspina Inlets	91	10	0.1	4	6	0	-	-
Sarah Pt. to Powell R.	54	65	1.2	26	37	2	1.50	5.4
Powell R. to Jervis Inlet	41	201	4.9	72	121	8	1.79	6.6
Nelson and Hardy Is.	169	48	0.3	19	28	1	1.53	3.6
Jervis Inlet to Reception Pt.	137	41	0.3	13	25	3	2.15	12.0
TOTAL	2289	6825	3.0	2723	3785	317	1.51	8.4

^a See Fig. 2.1.

^b Total number of males to total number of females (calculated only for locations with >40 birds).

^c Immature males to adult males as a percentage (calculated only for locations with >40 birds).

TABLE 2.2. Logistic regression model relating presence or absence of Harlequin Ducks to shoreline habitat characteristics in the northern Strait of Georgia, winter 1999-2000.

Variable	Regression coefficient	SE	Wald's Chi-square	df	<i>P</i>	<i>R</i>
Intertidal width (m)			166.2	3	0.0000	0.27
< 10	0.00					
10-100	2.26	0.29	59.8	1	0.0000	0.16
100-500	4.23	0.35	149.4	1	0.0000	0.26
>500	4.51	0.55	67.3	1	0.0000	0.17
Substrate			99.0	2	0.0000	0.21
Bedrock-boulder	2.92	0.41	50.4	1	0.0000	0.15
Cobble-gravel	3.60	0.38	91.2	1	0.0000	0.20
Sand-mud	0.00					
Complexity			100.3	3	0.0000	0.21
Linear	0.00					
Convolute	-0.22	0.21	1.1	1	0.3015	0.00
Nearby reefs/islets	0.55	0.21	6.8	1	0.0091	0.05
Offshore islets	2.20	0.25	79.9	1	0.0000	0.19
Rapids present	0.45	0.34	1.7	1	0.1883	0.00
Stream present	-0.73	0.29	6.4	1	0.0117	-0.04
Herring spawn index	1.03×10^{-6}	1.35×10^{-7}	58.2	1	0.0000	0.16

TABLE 2.3. Habitat use by wintering Harlequin Ducks in relation to shoreline complexity, substrate, and width of intertidal habitat in the northern Strait of Georgia, British Columbia, 1999-2000.

Complexity: Substrate	Width of intertidal (m)	No. of km sections	No. of km with ducks ^a	No. of ducks ^a	Density (ducks/km) ^b
Linear shoreline:					
Bedrock-boulder	< 10	549	1 (0.2)	2 (0.0)	2.0
	10-100	157	16 (10.2)	121 (1.8)	7.6
	100-500	11	11 (100)	294 (4.3)	26.7
	> 500	2	2 (100)	62 (0.9)	31.0
Cobble-gravel	< 10	4	0 (0)	0 (0)	0
	10-100	171	34 (19.9)	269 (3.9)	7.9
	100-500	200	149 (74.5)	3406 (49.9)	22.9
	> 500	12	12 (100)	785 (11.5)	65.4
Sand-mud	10-100	32	0 (0)	0 (0)	0
	100-500	56	9 (16.1)	112 (1.6)	12.4
	> 500	28	3 (10.7)	37 (0.5)	12.3
Convolutated shoreline:					
Bedrock-boulder	< 10	212	5 (2.4)	17 (0.2)	3.4
	10-100	190	21 (11.1)	101 (1.5)	4.8
	100-500	3	2 (66.7)	36 (0.5)	18.0
Cobble-gravel	< 10	1	0 (0)	0 (0)	0
	10-100	89	8 (9.0)	43 (0.6)	5.4
	100-500	16	5 (31.3)	37 (0.5)	7.4
Sand-mud	10-100	26	1 (3.8)	4 (0.1)	4.0
	100-500	38	1 (2.6)	2 (0.0)	2.0
	> 500	16	0 (0)	0 (0)	0
With reefs or islets within 1 km:					
Bedrock-boulder	< 10	59	4 (6.8)	15 (0.2)	3.8
	10-100	146	25 (17.1)	165 (2.4)	6.6
	100-500	4	3 (75.0)	101 (1.5)	33.7
	> 500	1	1 (100)	42 (0.6)	42.0
Cobble-gravel	< 10	1	0 (0)	0 (0)	0
	10-100	54	16 (29.6)	120 (1.7)	7.5
	100-500	21	10 (47.6)	163 (2.3)	16.3
	> 500	4	3 (75.5)	324 (4.7)	108.0
Sand-mud	10-100	6	0 (0)	0 (0)	0
	100-500	13	3 (23.1)	32 (0.5)	10.7
Offshore islets:					
Bedrock-boulder	< 10	53	5 (9.4)	20 (0.3)	4.0
	10-100	97	47 (48.5)	297 (4.4)	6.3
	100-500	6	6 (100)	92 (1.3)	15.3
Cobble-gravel	< 10	1	0 (0)	0 (0)	0
	10-100	10	10 (100)	126 (1.8)	12.6

^aValues in parentheses are percentages.

^bCalculated as the number of ducks per kilometre of occupied shoreline.

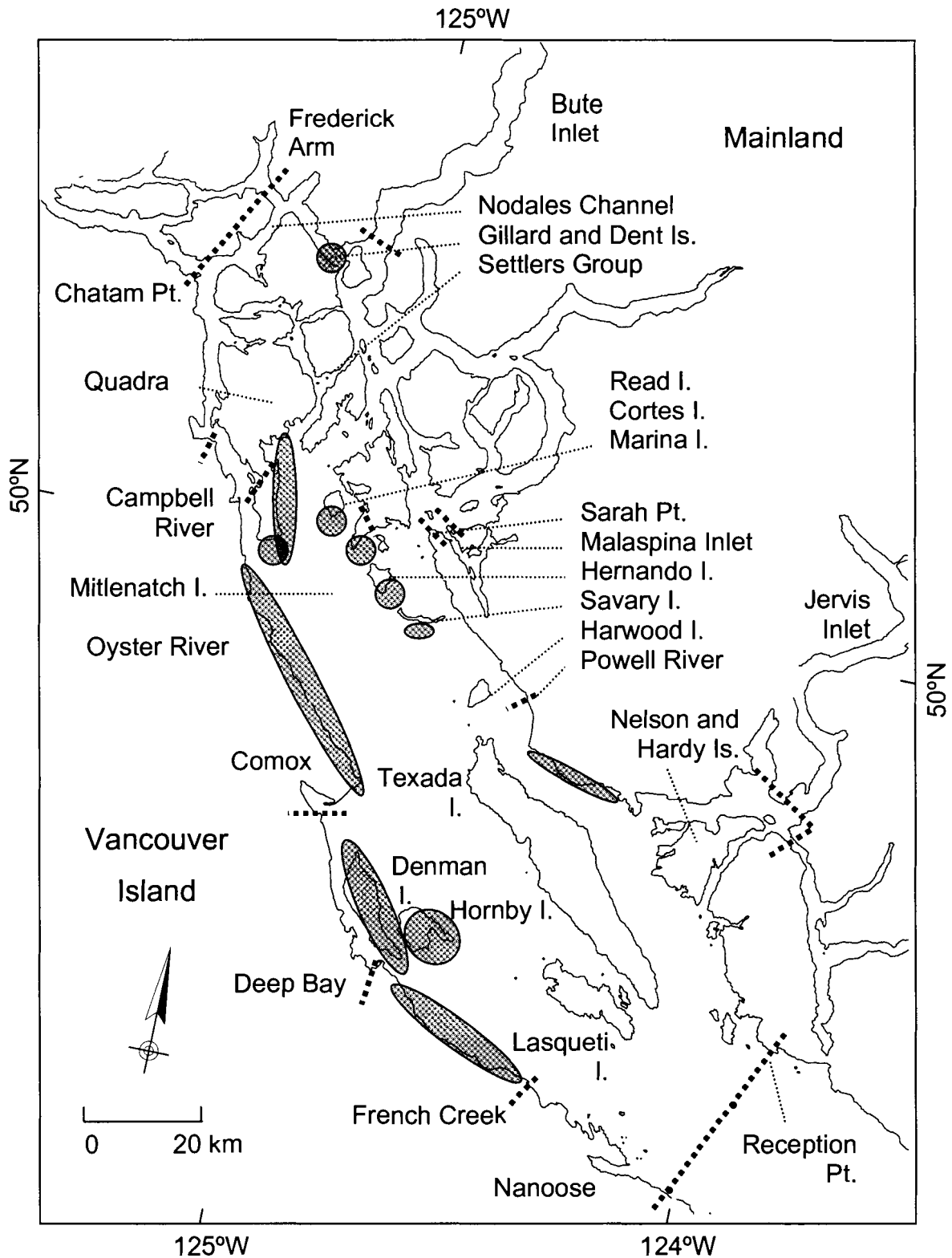


FIGURE 2.1. Location of area surveyed for Harlequin Ducks (*Histrionicus histrionicus*) in the northern Strait of Georgia during the winter of 1999-2000. Thick dotted lines indicate the limits of the survey area and divisions between locations listed in Table 2.1. Shaded areas show locations of major concentrations of ducks.

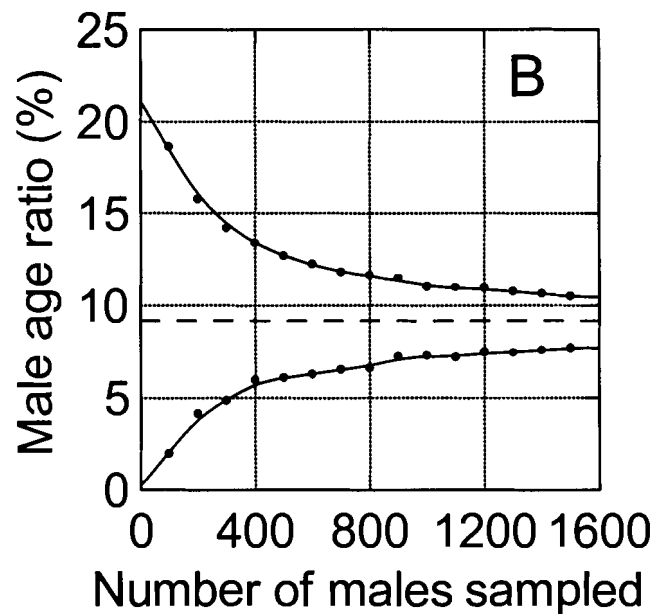
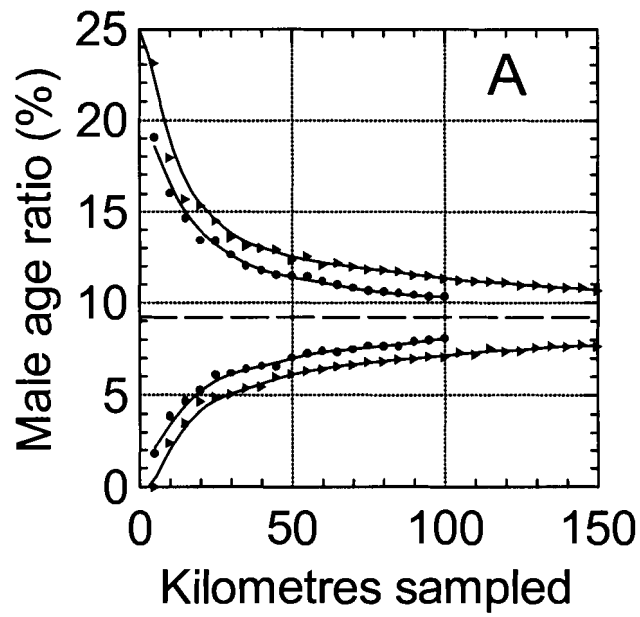


FIGURE 2.2. Upper and lower 95% confidence limits of estimates of male age ratios of Harlequin Ducks from different-sized random samples of km-sections of shoreline that contained birds (A) and in relation to the total number of males sampled in those shoreline sections (B) in the northern Strait of Georgia during winter, 1999-2000. Confidence limits were derived through simulation by drawing random samples from 144 km-sections of shoreline surveyed from land (●) and from 313 km-sections of shoreline surveyed from land or boat (►). Data from boat surveys of intertidal habitats >100 m wide were excluded from the latter simulation because of the bias in identifying immature males during boat surveys of areas with wide intertidal habitat (see the text). Simulations were repeated 1000 times for each sample size. The central broken line indicates the population age ratio from all km-sections sampled.

CHAPTER 3

USE OF FECAL ANALYSIS TO DETERMINE SEASONAL CHANGES IN THE DIET OF WINTERING HARLEQUIN DUCKS AT A HERRING SPAWNING SITE

Rodway, M. S., and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. *Journal of Field Ornithology* 73:363-371.

Reprinted with permission (© Association of Field Ornithologists).

ABSTRACT

Few data are available on seasonal changes in winter diet of Harlequin Ducks (*Histrionicus histrionicus*), especially in relation to their use of Pacific herring (*Clupea pallasii*) spawn. We used fecal analyses to determine seasonal changes in Harlequin Duck winter diet at a site where Pacific herring spawn. We measured frequency of occurrence and relative abundance by volume of prey remains in 202 fecal samples collected during four date periods in 1998 and 1999. These two measures were highly correlated ($r = 0.94$). We identified snails, crabs, limpets, and chitons as the principal animal prey, and ranked relative importance of most prey types in similar order as previous studies using stomach analyses. Crabs parts constituted the majority of prey remains during molt and we concluded that crabs were dominant in the diet during molt because crabs generally have greater organic content and less hard-part remains per unit of body mass than other hard-shelled prey consumed at that time. Snail remains were highest in frequency of occurrence during winter. Herring eggs were not detected in feces until a week after herring spawned, but abrupt changes in other prey types indicated that herring eggs were the principal prey throughout the spawn period. Polychaetes increased in importance in winter and spring, and rated third in frequency of occurrence in spring. We recommend using fecal analyses to determine frequency of occurrence of prey in the diet of other sea-ducks that are known to feed on hard-shelled molluscs and crustaceans. Measures of relative abundance of prey remains can be useful if conversion factors relating hard-part remains to whole-body biomass are available.

INTRODUCTION

Harlequin Ducks (*Histrionicus histrionicus*) are sea-ducks (Mergini) inhabiting nearshore marine waters of the north Pacific and north Atlantic (Robertson and Goudie 1999). Populations

are considered endangered in eastern North America and, along with populations of other sea-duck species, are of special concern in western North America (Goudie et al. 1994). Burgeoning human activity, shoreline development, rapid expansion of aquaculture industries in the nearshore habitat used for foraging, and potential impacts of invasive species such as the Green Crab (*Carcinus maenas*) present management challenges and make it important to understand habitat use and diet requirements. Seasonal changes in diet are important to investigate because of differences in nutritional requirements during annual events such as molt, migration, and reproduction (Hohman et al. 1992).

Detecting seasonal changes requires large sample sizes, making lethal methods of diet analysis unattractive. Although absolute measures of diet composition are sometimes difficult to obtain without sacrificing some individuals to procure stomach samples, such methods need careful justification, and are inappropriate for small or endangered populations. Also, public acceptance increasingly requires stringent rationale for sacrificing animals for scientific knowledge.

Fecal analysis provides a non-intrusive method that is commonly used to investigate diet of mammal and many bird species (e.g., Tigar and Osborne 2000). Such analysis can accurately determine frequency of occurrence of prey types and diet diversity if there are identifiable, undigested remains of all prey types. Accurate measures of diet composition are less feasible because of differences in digestibility and hard-part remains of various prey, although correction factors can sometimes be applied (Owen 1975, Tigar and Osborne 2000). Fecal analysis is an accepted method for diet studies of herbivorous waterfowl and can provide quantitative measures of diet composition of these species because throughput times of vegetative matter are relatively consistent, across the taxa consumed (Owen 1975, Krapu and Reinecke 1992). This is not so for animal prey and the method has rarely been used for carnivorous or omnivorous species (e.g., Wakelin 1993, Veltman et al. 1995, Rodway 1998).

Previous studies using stomach analyses indicate that winter prey of Harlequin Ducks are mainly intertidal and subtidal crustaceans and mollusks (Cottam 1939, Vermeer 1983, Goudie and Ankney 1986, Gaines and Fitzner 1987, Fischer and Griffin 2000). Fish eggs can be important when they are available (Munro and Clemens 1931, Vermeer 1983, Dzinbal and Jarvis 1984, Haegele and Schweigert 1989). All major prey except fish eggs have identifiable hard parts that are voided in the feces. Fecal analysis thus may be an effective method for diet studies in most cases.

Winter diet varies seasonally in the Aleutian Islands, Alaska (Fischer and Griffin 2000), but there is little information on how the diet may vary in other areas (e.g., Vermeer 1983), and no

information on variation during molt or at sites where Pacific herring (*Clupea pallasii*) spawn. Herring eggs are an ephemeral superabundant prey available to waterbirds for 3-4 weeks in late winter-early spring at spawning sites in the northeastern Pacific (Haegele 1993). Harlequin Ducks are known to aggregate at herring spawning sites and have been observed feeding on herring eggs (Munro and Clemens 1931, Bayer 1980, Haegele and Schweigert 1989, Haegele 1993, Vermeer et al. 1997).

Our objective was to determine seasonal changes in Harlequin Duck winter diet at a site where Pacific herring spawn. Concern for the birds, public interest in the Harlequin Duck in the study area, and the large sample size required to detect seasonal changes, precluded collecting specimens for stomach analyses. We investigated diet using fecal analysis, discuss the limitations of the method, and compare our results with those of previous studies that used stomach analyses.

METHODS

The study was conducted on Hornby Island (49°33' N 124°40' W), in the Strait of Georgia, British Columbia during the winters of 1998 and 1999. The area is a molting and wintering site for several hundred Harlequin Ducks, and an important spawning site for Pacific herring. We compared diet during four date periods: molt (August-September), winter (November-February), herring spawn (3-week interval after herring spawn was first deposited in the study area, which occurred on 11 March in 1998 and 5 March in 1999), and spring (April). Timing of spawning was determined by visual inspection; shoreline waters turn milky when spawn is released.

During molt, feces were collected on 7 different occasions from birds that had been captured in drive traps for banding purposes. Individuals often defecated when being handled and feces could be collected from known, banded individuals in those cases. Only one sample was collected from each bird. In winter, spawn, and spring, feces were scraped from tidal rocks where Harlequin Ducks hauled out. Collections were made opportunistically throughout these date periods. Feces were only collected from roosts where Harlequin Ducks had been observed immediately prior to collection and where no other species had been roosting at that time. Care was taken not to contaminate the sample when scraping it off the substrate.

Collected feces were dried or frozen until they could be analyzed. Feces were mixed and carefully rinsed with water to separate prey fragments, which were then examined under a stereoscopic microscope. Prey remains were identified with reference to mollusk and crustacean shell specimens collected at Hornby Island where Harlequin Ducks were feeding, and to Griffith (1967), Ricketts et al. (1968), Kozloff (1983), and Elner et al. (1985). Identification was made to

the lowest taxonomic level possible based on unique indicator fragments. More general prey categories, to which all types of prey fragments could be dependably assigned, were used for quantitative analyses (see Table 3.2). Percent occurrence for each prey category was defined as the percentage of fecal samples in which that particular prey type occurred.

A modified points index (Hyslop 1980, Williams 1981) was developed to estimate relative proportions of different prey types in each fecal sample. Relative abundance by volume was visually estimated and scored: 1 (<1%), 2 (1-10%), 3 (10-50%), 4 (50-90%), or 5 (>90%). Proportion of grit in the sample was scored relative to the volume of total remains, and animal and plant remains were scored relative to total remains minus grit. Fragments of unknown type were rare, formed a tiny proportion of the total, and were ignored.

Likelihood ratio (*G*) tests were used to analyze differences in frequency of occurrence. Differences in relative abundance scores were analyzed using Kruskal-Wallis tests followed by Mann-Whitney U-tests for pairwise comparisons and Bonferroni adjustments for the number of pairwise comparisons. Number of prey types per sample was compared among seasons with ANOVA and Tukey post-hoc tests. Tolerance for Type I error was set at 5%. Means \pm SD are given.

RESULTS

Species of snails were the most easily identified prey in Harlequin Duck feces (Table 3.1). Entire shells of small individuals (1-5 mm) were frequently present and readily identified. With practice, fragments of larger shells could also be identified to species. Numerous operculi were present in many samples, indicating that the snails were an important food source and that their shells were not merely the temporary abodes of hermit crabs. *Littorina scutulata* was the most frequently identified species (Table 3.1). Except for minute (1-2 mm) individuals, limpet shells were always fragmented and only larger fragments could be identified to species. Jaws of nereid and polynoid polychaetes, fragments of mussel, barnacle, and urchin shells, and small plate fragments of the distinctively patterned chiton *Tonicella lineata* were unmistakable. Crabs could be identified to species when claws or peripods were present, but often only comminuted shell remained. Undigested herring eggs and portions of egg membranes were easily recognized when present.

Snails and crabs were the most frequently occurring animal prey in fecal samples (Table 3.2). Limpets, chitons, barnacles, polychaetes, and herring eggs each occurred in more than 20% of samples. Significant seasonal differences in frequency of occurrence were found for polychaetes, chitons, snails, limpets, barnacles, amphipods, crabs, herring eggs, algae, and grit

(Table 3.2; G tests, $P_s < 0.05$). Algae was recorded in more than 80% of feces and was uncommon only during molt. Percent occurrence of snails remained high in all seasons, and was highest in the winter when they occurred in almost all samples. Percent occurrence of crabs was highest during molt and lowest during spawn. Chitons, polychaetes, and amphipods were important only in winter and spring. Algae, snails, barnacles, and herring eggs were the most frequent remains recorded during the spawn period. Grit occurred in most samples with increasing frequency through the winter.

Among the major prey types, percent occurrence was greater for crabs than snails ($G_1 = 5.9$, $P = 0.015$), and limpets ($G_1 = 7.3$, $P = 0.007$) during molt (Table 3.2). During winter, percent occurrence was higher for snails than crabs ($G_1 = 5.7$, $P = 0.017$), limpets ($G_1 = 7.1$, $P = 0.008$), and chitons ($G_1 = 8.5$, $P = 0.004$), and higher for chitons than polychaetes ($G_1 = 18.5$, $P < 0.001$). During the spawning period, percent occurrence was higher for algae than all other prey types ($P_s < 0.001$), higher for snails than spawn and barnacles ($G_1 = 6.6$, $P = 0.010$ for both comparisons), and higher for spawn than crabs ($G_1 = 5.9$, $P = 0.015$). In spring, percent occurrence was higher for algae than all other prey types ($P_s < 0.001$), higher for snails than all other types except algae ($P_s < 0.005$), and not significantly different among crabs, polychaetes, chitons, limpets, spawn, and barnacles ($P_s > 0.05$).

Mean relative abundance scores for prey remains were highly correlated with percent occurrence ($r = 0.94$, $P < 0.001$), and seasonal differences in relative abundance scores matched differences in percent occurrence. Mean relative abundance scores were 4.0 ± 1.4 , 1.8 ± 1.7 , and 1.6 ± 1.2 for crabs, limpets, and snails, respectively, during molt, 2.8 ± 1.3 , 2.3 ± 1.7 , 2.0 ± 1.7 , 1.8 ± 1.2 , and 1.5 ± 0.9 for snails, algae, chitons, crabs, and limpets, respectively, during winter, 4.4 ± 1.1 for algae during spawn, 3.1 ± 1.6 , 1.5 ± 1.3 , and 1.1 ± 1.4 for algae, snails, and crab, respectively, during spring, and < 1.0 for all other prey types in each season. Pairwise comparisons between main prey types within each season showed the same significant differences in relative abundance scores (Kruskal-Wallis tests, followed Mann-Whitney pairwise comparisons, all $P_s < 0.05$) as we found for comparisons of percent occurrence above.

Number of prey types per sample ranged from one to nine, and was lower during molt (2.6 ± 0.7) and spawn (2.7 ± 1.5) than during winter (4.8 ± 1.3) and spring (4.2 ± 1.8 ; $F_{3,198} = 21.6$, $P < 0.001$; Tukey pairwise comparisons, all $P_s < 0.001$). Numbers of species in the diet were greater than these estimates because multiple species were subsumed within most prey type categories.

Herring eggs were not detected in feces until about a week after spawning first occurred (Fig. 3.1). Herring eggs formed the greatest proportion of fecal remains during the second 10-day

interval after spawning, when they occurred in 67% of samples, declined thereafter, and were still present, and last recorded, 32 days after spawning. Algae made up most of the remains during the first 10 days of spawn and decreased afterwards. Remains of all other prey types made up a small proportion of the fecal samples during the first 20 days after spawn, and then increased in abundance.

DISCUSSION

Most prey identified in Harlequin Duck feces have been found in stomach samples in previous studies. Types not formerly reported in the diet include Polynoidae, snails *Amphissa columbiana*, *Bittium attenuatum*, *Cypraeolina pyriformis*, and *Eulima rutila*, crabs *Haplogaster mertensii* and *Lophopanopeus bellus*, coralline algae, and eelgrass. Eelgrass, along with *Fucus* and a variety of unidentified algae were detected in fecal samples only during spawn and likely were incidentally ingested by birds feeding on herring eggs, which are mainly deposited on eelgrass and *Fucus* (Haegele and Schweigert 1985). *Eulima rutila* and *Cypraeolina pyriformis* are tiny and also may have been taken incidentally, although more frequent snail species were often as small. *Eulima* spp. are often commensal or parasitic on echinoderms, polychaetes, or other animals, and *Cypraeolina pyriformis* may occur on the backs of larger shells (Griffith 1967). Algae has not been reported (Kurichi and Yamada 1984, Goudie and Ankney 1986, Gaines and Fitzner 1987, Patten et al. 1998) or has been found with low frequency and considered an incidental item in the diet (Cottam 1939, Palmer 1976, Fischer and Griffin 2000, Robertson and Goudie 1999) in most previous studies of Harlequin Ducks. The high percent occurrence and relative abundance of algae throughout the winter and spring in this study suggest that it may have provided some nutrition, and was not solely incidental. Polychaetes also have been a minor and infrequent prey type in previous studies (Cottam 1939, Gudmundsson 1971, Goudie and Ankney 1986, Fischer and Griffin 2000, Patten et al. 1998). They occurred in 43% of the samples taken in spring in this study and were the third most-frequently-occurring prey type at that time. Barnacles rarely have been reported in diet studies of Harlequin Ducks (Cottam 1939, Vermeer 1983). They occurred in 24% of samples in this study, most frequently during herring spawn and spring.

Previous diet studies using stomach analyses conducted in the Strait of Georgia (Vermeer 1983) and Puget Sound, Washington (Gaines and Fitzner 1987) also identified snails, limpets, crabs, and chitons as the dominant winter prey, and ranked most prey types in similar order to our study. Most differences among the three studies seem to reflect real differences in the diet. Algae and amphipods were more frequent in this study than in Vermeer's, and were not mentioned in Gaines and Fitzner. Polychaetes were also frequent in this study and not mentioned in either of

the other two. Shrimp were the only prey type reported in the other two studies and not identified in this study. Soft-bodied crustaceans, including shrimp, are quickly broken down beyond recognition in a bird's stomach (Cottam 1939), and thus may not be easily detected in fecal samples. However, shrimp may not have occurred in the diet during this study, because amphipods and isopods are also soft-bodied and were identified by exoskeleton remains.

Herring eggs were visible in feces, but not until the second week after spawning, and generally in small quantities. We suspect that herring eggs were the principal prey of most if not all Harlequin Ducks for the first three weeks after spawning occurred. This conclusion is based on the concomitant decrease in other types of animal prey and the increase in the proportion of algal remains, direct observations of birds feeding on eggs, and observed changes in foraging behavior from predominantly diving to dabbling (MSR unpubl. data). If true, this suggests that digestion of herring eggs is complete for the first week of egg development, and is less complete as eggs age or weather. Egg mortality and desiccation can be high in the intertidal zone (Grosse and Hay 1988) where Harlequin Ducks feed, and the increase in undigested egg remains we found in fecal samples may relate to the increase in dead or desiccated eggs over the spawn period. An unlikely, alternative explanation is that birds switch to feeding predominantly on algae when herring spawn. Fecal analysis thus failed to accurately quantify the use and relative importance of herring eggs in the diet, although abrupt changes in percent occurrence and relative abundance of other prey types at that time were indicative of a shift to feeding on herring spawn.

Crabs generally have greater organic content and less hard-part remains per unit of body mass than hard-shelled univalves and bivalves (e.g., see Guillemette et al. 1992). Thus, we can be confident that the high relative abundance of crab remains during molt indicates absolute dominance in the diet at that time. Specialized diet during molt has been reported for Greylag Geese (*Anser anser*; Fox et al. 1998), but not for other waterfowl species (Hohman et al. 1992, Combs and Fredrickson 1996, Thompson and Drobney 1997). Whether Harlequin Ducks were selecting crabs specifically during molt, or whether crabs were the preferred food generally and changes in their relative abundance in the diet through the winter were due to depletion or decreased availability relative to other prey is unknown. Number of different prey types in fecal samples decreased when herring eggs were available and increased again when their availability declined. Similarly, greater numbers of prey types during winter than molt could indicate decreased availability of crabs during winter.

Throughout the winter, Harlequin Ducks depend on access to productive inter-tidal habitats for foraging. The importance in the diet of crabs during molt and herring eggs in the spring pre-migration period indicates specific needs for access to habitats with high crab

productivity and to sites where herring spawn. Displacement of birds or degradation of habitat quality by continually increasing human activity requires monitoring and mitigation. Spatial and temporal contraction of herring spawning (Hay and McCarter 1999) is also a concern because it may be limiting access to herring eggs for birds that winter distant from extant spawning locations. Potential impacts of the northward-spreading Green Crab (McDonald et al. 2001) on native species used by Harlequin Ducks warrant investigation.

We did not collect birds in this study and were unable to determine the relationships between diet measures obtained from fecal samples and those from stomach samples. Comparisons with studies conducted in similar geographical areas suggest that our fecal analyses provided similar quantitative estimates of diet as stomach analyses. Percent occurrence measures from fecal analyses were likely accurate for all taxa that have dependably identifiable hard parts, even if the proportion is small, such as for polychaetes. We undoubtedly underestimated percent occurrence in the diet for herring eggs that have no hard part remains. However, differential digestion and mastication can also reduce the accuracy of quantitative measures from stomach analyses (Hyslop 1980, Williams 1981), and analyses of stomach samples may also underestimate the importance of herring eggs.

We recommend using fecal analyses to determine percent occurrence of prey in the diet of other sea-ducks such as eiders (*Somateria* spp.), scoters (*Melanitta* spp.), and goldeneye (*Bucephala* spp.) that are known to feed on hard-shelled molluscs and crustaceans (Cottam 1939). The method also may be useful for diet investigations of piscivorous species, but experimental work using captive birds is required to determine how otoliths and other identifiable fish remains pass through the digestive tract (Duffy and Jackson 1986). Fecal analysis has been successfully used to determine freshwater invertebrate prey of breeding Harlequin Ducks and other river specialists (Wakelin 1993, Veltman et al. 1995, Rodway 1998), and could be used for other species feeding on such prey. Collecting fecal samples from other sea-ducks would likely require capturing the birds because they rarely roost on shoreline rocks like Harlequin Ducks. Capturing birds has the advantage that samples can be obtained from known individuals, making sex and age comparisons possible.

We also measured relative abundance of prey remains in feces. This measure cannot be used to estimate diet composition without experimental work to calibrate fecal remains to whole body biomass of prey because of differences among prey types in the ratio of hard to soft parts. We were able to use our relative abundance scores to conclude that crabs were the most important prey type during molt only because we had information from other studies on the ratio of hard to soft parts in crabs and hard-shelled molluscs. Additional data calibrating the ratio of hard to soft

parts in the variety of prey used by diving waterfowl would allow conversions of relative abundance of prey remains in feces into estimates of diet composition that could be compared among locations and species.

Appropriate methods for diet studies will depend on objectives and the kind of diet information required. Non-lethal methods can likely provide most information required for management purposes. Observations to identify foraging habitats and handled prey, stable isotope analysis (SIA; Hobson et al. 1994), and stomach pumping are possible alternate or complementary methods to fecal analysis for diet studies of diving waterfowl. Fecal analysis has advantages of being inexpensive compared to SIA and of providing more detailed data on prey types than either SIA or behavioral observations. The shortcomings of fecal analysis are that it cannot provide quantitative estimates of diet composition unless conversion factors are available, and it cannot measure percent occurrence for prey types that have no identifiable parts that are voided in the feces. Stomach pumping has been a successful method for seabird species (Duffy and Jackson 1986), but to date has not been proven effective, and warrants experimentation, for waterfowl.

ACKNOWLEDGMENTS

Funding for this study was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, and the British Columbia Waterfowl Society. We thank Lynn Campbell, Pete Clarkson, Mary Jane Elkins, Frank Elkins, Ian Goudie, Stewart Jackson, Heidi Regehr, and Ken Wright for help capturing birds and collecting samples during molt, and Heidi Regehr for help obtaining samples through the rest of the winter seasons. Steve Holford kindly lent a stereoscopic microscope to use for the duration of the study. Thanks to Barbara Sherman and Connie Smith for administrative assistance, and Bob Elner for help identifying fecal remains. Larry Dill, Bob Elner, Julian Fischer, Heidi Regehr, and an anonymous reviewer made helpful comments on the manuscript.

LITERATURE CITED

- Bayer, R.D. 1980. Birds feeding on herring eggs at the Yaquina estuary, Oregon. *Condor* 82:193-198.
- Combs, D.L., and L.H. Fredrickson. 1996. Foods used by male mallards wintering in southeastern Missouri. *Journal of Wildlife Management* 60:603-610.

- Cottam, C. 1939. Food habits of North American diving ducks. U.S. Department of Agriculture Technical Bulletin 643, Washington.
- Duffy, D.C., and S. Jackson. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds* 9:1-17.
- Dzinbal, K.A., and R.L. Jarvis. 1984. Coastal feeding ecology of Harlequin Ducks in Prince William Sound, Alaska in summer. Pp. 6-10 in D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.). *Marine birds: their feeding ecology and commercial fisheries relationships*. Canadian Wildlife Service Special Publication, Ottawa.
- Elnor, R.W., P.G. Beninger, L.E. Linkletter, and S. Lanteigne. 1985. Guide to indicator fragments of principal prey taxa in the stomachs of two common Atlantic crab species: *Cancer borealis* Stimpson, 1859 and *Cancer irroratus* Say, 1817. Canadian Technical Report of Fisheries and Aquatic Sciences 1403:1-20.
- Fischer, J.B., and C.R. Griffin. 2000. Feeding behavior and food habits of wintering Harlequin Ducks at Shemya Island, Alaska. *Wilson Bulletin* 112:318-325.
- Fox, A.D., J. Kahlert, and H. Etrup. 1998. Diet and habitat use of moulting greylag geese *Anser anser* on the Danish Island of Saltholm. *Ibis* 140:676-683.
- Gaines, W.L., and R.E. Fitzner. 1987. Winter diet of the Harlequin Duck at Sequim Bay, Puget Sound, Washington. *Northwest Science* 61:213-215.
- Goudie, R.I., and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475-1482.
- Goudie, R.I., S. Brault, B. Conant, A.V. Kondratyev, M.R. Petersen, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 59:27-49.
- Griffith, L.M. 1967. The intertidal univalves of British Columbia. Handbook No. 26, British Columbia Provincial Museum, Victoria.
- Grosse, D.J., and D.E. Hay. 1988. Pacific herring, *Clupea harengus pallasii*, in the northeast Pacific and Bering Sea. Pp. 34-54 in N.J. Wilimovsky, L.S. Incze, and S.J. Westrheim (eds.). *Species synopses: life histories of selected fish and shellfish of the northeast Pacific and Bering Sea*. Washington Sea Grant Program, University of Washington, Seattle, WA. 88-2.
- Gudmundsson, F. 1971. Straumendur (*Histrionicus histrionicus*) á Islandi. *Náttúrufræðingurinn* 41:1-28, 64-98.
- Guillemette, M., R.C. Ydenberg, and J.H. Himmelman. 1992. The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. *Journal of Animal Ecology* 61:599-610.
- Haegle, C.W. 1993. Seabird predation of Pacific Herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73-82.

- Haegele, C.W., and J.F. Schweigert. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behaviour. *Canadian Journal of Fisheries and Aquatic Sciences* 42 (Supplement 1):39-55.
- Haegele, C.W., and J.F. Schweigert. 1989. Egg loss from Pacific Herring spawns in Barkley Sound in 1988. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2037.
- Hay, D.E., and P.B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document 99/14, Nanaimo, BC.
- Hobson, K.A., J.F. Piatt, and J. Pitochelli. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63:786-798.
- Hohman, W.L., C.D. Ankney, and D.H. Gordon. 1992. Ecology and management of postbreeding waterfowl. Pp. 128-189 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Hyslop, E.J. 1980. Stomach content analysis - a review of methods and their application. *Journal of Fish Biology* 17:411-429.
- Kozloff, E.N. 1983. *Seashore life of the northern Pacific coast*. University of Washington Press, Seattle.
- Krapu, G.L., and K.J. Reinecke. 1992. Foraging ecology and nutrition. Pp. 1-29 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Kurechi, M., and K. Yamada. 1984. Foods in the gizzard of a male Harlequin Duck. *Tori* 33:78-80.
- McDonald, P.S., G.C. Jensen, and D.A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology* 258:39-54.
- Munro, J.A., and W.A. Clemens. 1931. Waterfowl in relation to the spawning of Herring in British Columbia. *Bulletin of the Biological Board of Canada* 17:1-46.
- Owen, M. 1975. An assessment of fecal analysis technique in waterfowl feeding studies. *Journal of Wildlife Management* 39:271-279.
- Palmer, R.S. 1976. *Handbook of North American Birds, Vol. 3. Waterfowl*. Yale Univ. Press, New Haven, Connecticut.
- Patten, S.M., Jr., T. Crowe, R. Gustin, R. Hunter, P. Twait, and C. Hastings. 1998. Assessment of injury to sea ducks from hydrocarbon uptake in Prince William Sound and the Kodiak archipelago, Alaska, following the Exxon Valdez oil spill. Exxon Valdez Oil Spill Natural Resource Damage Assessment Final Report, Bird Study 11. Alaska Dept. Fish Game, Anchorage.

- Ricketts, E.F., J. Calvin, and J.W. Hedgpeth. 1968. *Between Pacific Tides*. Stanford University Press, Stanford.
- Robertson, G.J., and R.I. Goudie. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill (eds.). *The birds of North America*, No. 466. The Birds of North America, Inc., Philadelphia, PA.
- Rodway, M.S. 1998. Activity patterns, diet, and feeding efficiency of Harlequin Ducks breeding in Labrador. *Canadian Journal of Zoology* 76:902-909.
- Thompson, J.E., and R.D. Drobney. 1997. Diet and nutrition of male canvasbacks during postreproductive molts. *Journal of Wildlife Management* 61:426-434.
- Tigar, B.J., and P.E. Osborne. 2000. Invertebrate diet of the Houbara Bustard *Chlamydotis (undulata) macqueenii* in Abu Dhabi from calibrated faecal analysis. *Ibis* 142:466-475.
- Veltman, C.J., K.J. Collier, I.M. Henderson, and L. Newton. 1995. Foraging ecology of blue ducks *Hymenolaimus malacorhynchos* on a New Zealand river: implications for conservation. *Biological Conservation* 74:187-194.
- Vermeer, K. 1983. Diet of the Harlequin Duck in the Strait of Georgia, British Columbia. *Murrelet* 64:54-57.
- Vermeer, K., M. Bentley, K.H. Morgan, and G.E.J. Smith, 1997. Association of feeding flocks of Brant and sea ducks with herring spawn at Skidegate Inlet. Pp. 102-107 in K. Vermeer and K.H. Morgan (eds.). *The ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands*. Canadian Wildlife Service Occasional Paper No. 93, Ottawa.
- Wakelin, M.D. 1993. Contents of blue duck faeces from the Tongariro river. *Notornis* 40:205-212.
- Williams, M.J. 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology* 52:103-113.

TABLE 3.1. Prey types identified from remains found in Harlequin Duck feces (n = 202) at Hornby Island, British Columbia, 1998-1999. The number of fecal samples in which a prey type was identified is given in parentheses.

Bryozoan (2)	Mussel
Polychaete	<i>Mytilus edulis</i> _(26)
<i>Nereis</i> spp. (22)	Urchin
Polynoidae (5)	<i>Strongylocentrotus</i> spp. (12)
Chiton	Barnacle
<i>Mopalia</i> spp. (13)	<i>Balanus</i> spp. (49)
<i>Tonicella lineata</i> (39)	Isopod (3)
Snail	Amphipod (26)
<i>Amphissa columbiana</i> (14)	Crab
<i>Bittium attenuatum</i> (22)	<i>Cancer</i> spp.(7)
<i>Calliostoma ligatum</i> (9)	<i>Haplogaster mertensii</i> _(1)
<i>Cypraeolina pyriformis</i> _(4)	<i>Hemigrapsus nudus</i> (31)
<i>Eulima rutila</i> (1)	<i>Lophopanopeus bellus</i> _(4)
<i>Lacuna variagata</i> _(13)	<i>Pagurus</i> spp. (21)
<i>Lirularia lirulata</i> (9)	Fish
<i>Littorina scutulata</i> _(61)	<i>Clupea pallasii</i> _(eggs) (43)
<i>L. sitkana</i> _(15)	Algae
<i>Margarites helycinus</i> (1)	<i>Corallina</i> spp. (3)
<i>Mitrella gausapata</i> (2)	<i>Fucus</i> spp. (3)
<i>Nassarius mendicus</i> _(3)	<i>Ulva</i> spp. (14)
<i>Nucella emarginata</i> _(4)	Eelgrass
Limpet	Zosteraceae (2)
<i>Notoacmaea scutum</i> (12)	
<i>N. persona</i> (8)	
<i>Collisella pelta</i> (19)	

TABLE 3.2. Percent occurrence of prey remains in Harlequin Duck feces during four seasons at Hornby Island, British Columbia, 1998-1999. "Spawn" was defined as a three-week period after herring spawn was first deposited in early March.

Prey	Season (number of samples)				Total (202)
	Molt (25)	Winter (33)	Spawn (61)	Spring (83)	
Bryozoan	0.0	3.0	1.6	0.0	1.0
Polychaete	0.0	21.2	0.0	43.4	21.3
Chiton	0.0	72.7	11.5	37.3	30.7
Snail	72.0	97.0	54.1	65.1	67.8
Limpet	68.0	75.8	8.2	28.9	35.1
Mussel	8.0	12.1	11.5	15.7	12.9
Urchin	0.0	12.1	1.6	8.4	5.9
Barnacle	4.0	18.2	31.1	27.7	24.3
Isopod	4.0	0.0	1.6	1.2	1.5
Amphipod	0.0	12.1	6.6	21.7	12.9
Crab	96.0	78.8	13.1	43.4	46.5
Fish	4.0	3.0	0.0	0.0	1.0
Herring eggs	0.0	0.0	31.1	28.9	21.3
Algae	4.0	75.8	98.4	92.8	80.7
Grit	12.0	54.5	73.8	90.4	69.8

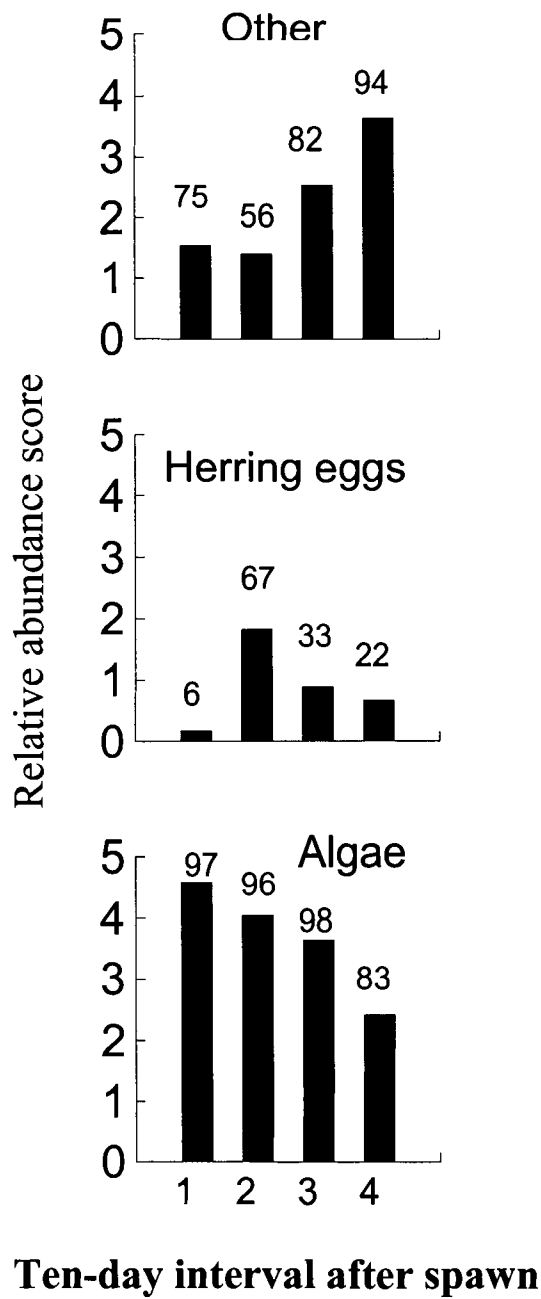


FIGURE 3.1. Changes in relative abundance scores of algae, herring eggs, and all other animal prey type remains found in Harlequin Duck feces over 10-day intervals after herring first spawned on Hornby Island, British Columbia, 1998-1999. Percent occurrence of each prey category per 10-day period is given above each bar.

CHAPTER 4

AGGREGATIVE RESPONSE OF HARLEQUIN DUCKS TO HERRING SPAWNING IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

Rodway, M. S., H. M. Regehr, J. Ashley, P. V. Clarkson, R. I. Goudie, D. E. Hay, C. M. Smith, and K. G. Wright. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology* 81:504-514.

Reprinted with permission (© NRC Canada).

ABSTRACT

We determined the scale of aggregative response of Harlequin Ducks (*Histrionicus histrionicus*) to seasonally and locally superabundant prey at Pacific herring (*Clupea pallasii*) spawning sites in the northern Strait of Georgia, British Columbia, 1995-2002. Aggregations of 3400-5500 birds gathered at a small number of sites along the same 8-km stretch of shoreline each year spawn was available there. Aggregations occurred in only a small fraction of the habitat area where spawn was available. Duration of stay at spawning sites averaged 2-3 weeks and many birds returned to their wintering grounds afterwards. Birds moving to spawning sites represented 55-87% of the total wintering population. The proportion of local wintering populations that moved to spawning sites was negatively related to the distance that they had to travel and few birds travelled farther than 80 km. The decline in proportions moving with increasing distance suggest that more distant individuals may be constrained by lack of information or that there are trade-offs between the benefits of exploiting spawn and the costs of movement. This raises a conservation concern because the temporal and geographic range of herring spawning in British Columbia is contracting and some wintering waterbird populations may be losing access to this important late-winter food.

INTRODUCTION

Many animals exhibit an aggregative response to the abundance of an ephemeral resource and may depend on seasonally superabundant prey for fueling migration or reproduction or for survival (Botton et al. 1994, Hilderbrand et al. 1999, Restani et al. 2000). Determining or predicting consequences to predator populations of changes in abundance or distribution of such prey requires an understanding of the scale of the aggregative response in terms of the proportion

of the population involved and the distances over which they move to exploit the prey. “Ideal-free” models of habitat selection assume that individuals are free to aggregate at a highly profitable resource (Fretwell and Lucas 1970), but more realistic models admit that individuals may suffer movement costs and be constrained by imperfect information (Stephens and Krebs 1986, Kennedy and Gray 1997). Such costs may limit access to superabundant food supplies and may mean that some individuals lose access to the resource when its availability changes.

The Pacific Herring (*Clupea pallasii*) is an important prey species for marine birds in southern British Columbia (Hay et al. 1989), and consumption of herring eggs is intense during spawning periods. Herring spawn mainly in protected inter- and shallow sub-tidal waters in the late winter and spring (Grosse and Hay 1988). Large spawns can be many kilometres long, with egg depositions of 10^6 eggs/m² or more - the equivalent of 2-3 kg/m² of eggs. Spawning is usually a conspicuous event: the water turns milky white from milt and the activity may attract thousands of marine mammals and seabirds to feed both on spawning fish and spawned eggs. Aggregations of 50 000-300 000 waterbirds, mostly gulls (*Larus* spp.), seaducks, and other diving species, have been observed at annual herring spawning events in British Columbia (Campbell et al. 1990, Haegele 1993).

Other than counts of bird aggregations and dietary data showing consumption of spawn (Haegele 1993, Vermeer et al. 1997, Rodway and Cooke 2002) there is little detailed information on the use of herring spawn for any marine bird species. This is surprising given that herring spawning is such a conspicuous event. Also, the high energy content of eggs may provide substantial benefits by increasing survival rates and fuelling migration and reproduction (Munro and Clemens 1931, Bayer 1980, Vermeer 1981). Therefore the consequences for marine birds of the recent spatial and temporal contraction of spawning (Hay and McCarter 1999), and of the periodic fisheries-related collapse of herring stocks, are unknown. Sea ducks in the North Pacific Ocean are the focus of recent management concern (Goudie et al. 1994), and there is a need for studies of marked birds to determine how individuals use spawn and the proportion of total populations that use it, whether movements to herring spawning sites are part of the migration to the breeding grounds, and whether access to spawn increases survival rates and breeding success. In this paper we examine the use of herring spawn by Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia.

Our specific objectives were to determine: (i) if Harlequin Ducks aggregate at herring spawning grounds, and if so, at which locations, (ii) the proportion of the Harlequin Duck wintering population that uses spawn, (iii) the origin of aggregating birds and the distances over which they move, (iv) the duration of individuals' stay at spawning sites, (v) whether moving to

herring spawn is part of the migration to the breeding grounds or is simply a shift in winter habitat use, and (vi) annual consumption of herring spawn by Harlequin Ducks in the northern Strait of Georgia.

METHODS

Direct counts

The study was conducted throughout the northern Strait of Georgia and at White Rock (Fig. 4.1) during winter and spring, 1998-2001, at Hornby Island during spawning (March) in 1995-1997, and at Hornby Island and the adjacent Vancouver Island shore in March 2002. Numbers of Harlequin Ducks wintering in the study areas were determined during a complete survey of the northern Strait of Georgia and White Rock conducted during the winter (November-February) of 1999-2000 (Rodway et al. 2003, MSR unpubl. data). Repeated counts at sampling areas that were accessible by road were used to determine changes in numbers of birds before (January and February), during (March), and after (April) herring spawning. The occurrence and timing of herring spawning was determined during our shoreline surveys, complemented with data from Fisheries and Oceans Canada (DFO 2002).

Counts of small flocks of Harlequin Ducks were straightforward and are likely quite accurate because we did not conduct counts in compromising weather or sea conditions and birds generally were close to shore. Large flocks that aggregated at Hornby Island during spawning were more difficult to count and numbers were usually estimated by counting by 10s. In 1998-2001, we calculated the maximum flock size for these aggregations by averaging repeated estimates made at the time the flock was judged to be at its largest. Sample sizes for these mean counts were thus the number of estimates made of the same flock. Standard deviations for these maximum counts indicates the variation in our estimates and should not be misconstrued as indicating variation in the numbers of birds present. In 1995-1997, and in 2002 only one estimate was made of the maximum numbers at Hornby Island during spawning in each year.

Population estimates from mark-recapture analyses

Since 1993, about 3500 Harlequin Ducks have been captured during their post-breeding moult in the Strait of Georgia or on their breeding streams. Beginning in 1994, captured birds were leg-banded with two-digit alpha-numeric colour bands and standard U.S. Fish and Wildlife Service (USFW) metal bands. Birds captured in 1993 received colour bands without an identifiable code. Nasal tags with unique colour-shape combinations were also put on 457 birds in 1997-2000. The main coastal banding locations have been Hornby Island, Comox, Campbell

River, Quadra Island, and White Rock (Fig. 4.1). Since 1995, and especially from 1998-2001, a great effort has been made by numerous persons to resight marked birds on Hornby Island during herring spawning (Fig. 4.2). Harlequin Ducks spend more time hauled out on shoreline rocks at this time, and there is a high probability of a banded bird being identified if it is present (see below).

Maximum counts at Hornby Island during spawning did not indicate total numbers of birds moving there for herring spawn because there was a turnover of birds due to variation in when individuals arrived and how long they stayed. We followed Jolly (1965) to estimate this total population (\hat{N}_t) during each annual spawning period t , using the relationship,

$$\hat{N}_t = \frac{\hat{M}_t}{\hat{\alpha}_t}$$

where \hat{M}_t is the size of the marked population and $\hat{\alpha}_t$ is the proportion of birds marked.

$$\hat{M}_t = m_t + u_t$$

where m_t is the number of marked birds actually resighted, which was simply the number of banded individuals identified; and u_t is the number of marked birds present but not resighted. We could not estimate u_t using conventional mark-recapture methods (Seber 1982) because we were unable to assume that individuals not sighted at time t but sighted after time t were actually present at Hornby Island at time t , either between years or within years. To obtain an estimate of u_t we fit the regression,

$$\ln Y = b_0 + b_1(X)$$

where X is the number of sightings per bird, and Y is the frequency of birds with that number of sightings. The estimate of u_t , the frequency of birds with zero sightings (i.e., when $X = 0$), is then given by $\exp(b_0)$. Linear regression lines were fit to the log-transformed Y -values in SPSS 8.0. We determined $\hat{\alpha}_t$ by scanning groups of birds whose legs were visible. We only included in the sample those birds for which the tarsi of both legs were entirely visible because it is easier to see that a bird is banded than confirm that it has no band when only part of the tarsi is seen. Scans were conducted throughout the spawning period.

We tested our assumption that most birds with identifiable bands present at Hornby Island during spawning were actually identified. We first determined the proportion of colour bands that were unreadable (B_w) in 2000 and 2001 by telescopic inspection of samples of birds whose bands

were visible at close range. Unreadable colour bands included those that were too worn to allow their alphanumeric code to be read, those without a code, and those that birds had lost. We then compared B_w with our estimate of u_i . These two measures should be similar if most readable bands were being identified.

Movement of birds

Movements of birds to herring spawning sites were determined through resightings of marked individuals. Two of us (M.S. Rodway and H.M. Regehr) spent much of the winters of 1998-1999 and 1999-2000 identifying marked birds throughout the northern Strait of Georgia. We combined data from those two years to determine where birds wintered that came to feed on herring spawn in the spring, what proportion of these wintering populations moved to spawning sites, and how this proportion related to the distance birds had to travel. The high cost in labour and time of collecting these data made it impractical to obtain enough data to be able to estimate annual movement probabilities among all our study locations using multi-stratum mark-recapture analyses (Brownie et al. 1993). We were able to directly estimate parameter values typically obtained from capture-mark-recapture analyses in order to answer these questions, but were unable to determine error rates associated with these values. However, the proportional values generated are comparable among areas and to future data using analyses of frequencies.

We estimated the numbers of birds moving to location A from wintering area C:

$$[1] \quad \hat{N}_{C \rightarrow A} = N_C \left(\frac{m_{C \rightarrow A}}{m_C R_A} \right)$$

where N_C is the total number of wintering birds at location C, determined during our winter surveys, m_C is the number of marked individuals identified at location C during the winter, $m_{C \rightarrow A}$ is the number of marked individuals identified at location C during the winter that were identified at location A during spawning, and R_A is the probability of resighting a marked bird at location A during spawning.

$$R_A = \frac{m_A}{\hat{M}_A - B_w \hat{M}_A}$$

where m_A is the number of banded birds identified at location A, \hat{M}_A is the total number of birds predicted to have bands at location A, and B_w = the proportion of bands that were unreadable (see above). At all locations other than Hornby Island,

$$\hat{M}_A = N_A \hat{\alpha}_A$$

where N_A is the total number of birds present and $\hat{\alpha}_A$ is the proportion of birds with bands at location A, which we determined at each location as described above for Hornby Island. We had to subtract $B_w \hat{M}_A$ from \hat{M}_A in the above equation to calculate R_A because $\hat{\alpha}_A$ included bands that were not readable. We could not use this method at Hornby Island because the number of bands identified was higher than the number predicted, owing to birds moving through the area. At Hornby Island,

$$\hat{M}_A = m_A + u_A$$

where u_A is the number of marked birds present but not resighted, and is calculated as described above.

Equation 1 gives an accurate estimate of the total number of birds moving only if banded and unbanded birds are equally likely to move. We determined whether this was so by comparing, at each wintering location, the proportions of birds with bands in winter and during spawning. Proportions should remain the same if banded and unbanded birds were moving with equal probability. We also compared proportions of birds with bands at Hornby Island during winter and spawning to estimate what proportion of birds were coming from marked populations.

Distance travelled

The distance from each location to Hornby Island that birds had to travel was taken as the shortest path over water between the mid-point on the northeast shore of Hornby Island and the mid-point of the respective location. Distances were measured to the nearest kilometre on a 1:80,000 scale marine chart .

Duration of stay

We subtracted the dates of first and last sightings (+1) in March and April to obtain the number of days that individuals were present at Hornby Island during spawning. We calculated duration of stay only for birds marked with nasal tags because they were the most readily identified. We confined our analysis to 1999 and 2000, when we had large samples of birds marked with nasal tags and our resighting efforts spanned the spawning period (Fig. 4.2). We identified nasal-tagged birds that were winter residents on Hornby Island in those two years, and separated residents from immigrants in the analyses. Two-way ANOVA was used to test for differences between years and between residents and immigrants. Tolerance for Type I error was set at 5%. Values are given as the mean \pm SD.

Consumption of spawn

Daily consumption of herring spawn was estimated using the equation

$$F = 0.51 * W^{0.85}$$

where F is daily food consumption (g), and W is bird mass (g) (Nilsson and Nilsson 1976, Haegele 1993). Weighting by a male:female ratio of 1.51 (Rodway et al. 2003), we calculated the mean mass of adult Harlequin Ducks to be 611 g from a sample of 586 females (569 ± 31 g) and 1204 males (638 ± 37 g) captured during their post-breeding moult in the Strait of Georgia. Total spawn consumed was given by F times the number of days that birds fed on spawn times the total number of birds present.

RESULTS

Locations and timing of spawning aggregations

Harlequin Ducks in the northern Strait of Georgia aggregated in only a small portion of the area where herring spawn was available. In the years 1998-2001, increases in numbers of Harlequin Ducks during herring spawning occurred mainly at Hornby Island (Table 4.1). Numbers at other Harlequin Duck wintering sites in the northern Strait of Georgia declined, even at Comox, Denman Island, Baynes Sound, and Qualicum where herring also spawned. There were brief increases at other spawning locations if spawning occurred there earlier than at Hornby Island. For example, herring spawned near Comox on 6 March and at Hornby Island on 7 March in 2001. Numbers of Harlequins in the Comox area increased from 433 to 578 on 6 March, then declined to 347 on 7 March coincident with increased numbers at Hornby Island. In 2002, herring did not spawn at Hornby Island and spawned mainly along the Vancouver Island shore (DFO 2002). Compared to wintering populations, there was no increase in Harlequin Duck numbers at Hornby Island or elsewhere that year, and the largest aggregation we found at other sites where herring did spawn was 156 Harlequin Ducks near Qualicum on 30 March.

At a smaller scale at Hornby Island, birds also aggregated in only a portion of the habitat where spawn was available (Fig. 4.3). Most birds present during spawning aggregated into one or two large flocks (Table 4.2). The location of those aggregations varied among years and was related to the location and timing of spawning. Aggregations occurred only at sites where spawn was available. Again, similar to events at the larger geographic scale, there were brief increases at some sites where spawning occurred first. For example, numbers increased at Grassy and Phipps when spawning occurred there on 5 March 1999, but decreased again after herring spawned nearby at Squeaker on 6 March (Table 4.2). The largest, persistent aggregations were seen at Squeaker, Anderson, or Helliwell in all years, but did not necessarily occur at all those

sites in any one year, even if spawn was available at all of them. Among those sites, numbers first increased where herring first spawned. In 1998, herring spawned at Squeaker on 7 March and at Anderson and Helliwell on 11 March. Numbers initially increased at Squeaker to a maximum of 1650, then gradually declined at Squeaker and increased at Helliwell during the two weeks after 11 March (Fig. 4.4). Smaller aggregations on the south and west sides of the island generally occurred later, often in April after most herring eggs would have hatched, except in 2000, when spawning was less extensive along the northeast side (Table 4.2).

The aggregative response by Harlequin Ducks was immediate, numbers often increasing at a particular location the same day spawning occurred, but maximum flock sizes were not reached until several days after spawning (Fig. 4.4). In no cases did we witness birds aggregating prior to herring spawning.

Size of spawning aggregations

Direct counts gave maximum estimates of between 2114 and 5000 birds at Hornby Island during spawning over the years 1995-2001 (Table 4.3). Fitting the regression, $\ln Y = b_0 + b_1(X)$ to estimate the number of banded birds missed (u_t) gave r^2 values of 0.88, 0.95, 0.96, 0.86, 0.96, and 0.95 for consecutive years 1996-2001, respectively. Estimates for the total number of birds that used Hornby Island during spawning in the years 1996-2001 ranged from 3400 to 5500 (Table 4.3).

The proportion of bands that were unreadable (B_w) was 15.1% ($N = 152$) and 15.8% ($N = 133$) in 2000 and 2001, respectively. Using these proportions and the number of banded birds identified (Table 4.3) we calculated that 126 and 88 birds present at Hornby Island during spawning had bands that were unreadable in 2000 and 2001, respectively. These estimates of the number of bands that were unreadable were only slightly lower than the estimates made using regression analysis of the number of banded birds that were present but not identified (u_t) in 2000 and 2001 (Table 4.3). This increased our confidence that most marked birds with readable bands present on Hornby Island during spawning were identified in those years and, by extension, in other years.

Origin of birds aggregating for spawn

The majority of marked birds seen at Hornby Island during spawning in 1999 and 2000 came from nearby wintering areas on Denman Island, Comox, Qualicum, and Baynes Sound (Table 4.4). Some marked birds travelled 64 km from Quadra and Cortes islands in the north, and

a single bird travelled 150 km from White Rock in the south (Fig. 4.1). Estimated numbers of birds coming from marked populations made up 68% of the numbers of birds present at Hornby Island for spawn. On Hornby Island, birds that wintered on the south and west sides moved to the northeast side during spawning more frequently (58% of known banded birds, $n = 53$) than the reverse (12%, $n = 82$; $\chi^2_1 = 32.6$, $P < 0.001$).

There were also movements to areas other than Hornby Island during spawning (Fig. 4.1). We calculated resighting probabilities (R_A) during spawning of 48% ($n = 58$), 65% ($n = 65$), 95% ($n = 77$), 47% ($n = 71$), and 44% ($n = 109$) for Quadra Island, Campbell River, Comox, Denman Island, and Qualicum, respectively. Using these probabilities, we estimated movements of over 50 birds to Campbell River from Quadra Island, to Denman Island from Qualicum, and to Qualicum from both Comox and Denman Island. We estimated that 10 winter residents from Hornby Island moved to Denman Island and Comox during spawning, and 24 birds from Hornby Island moved back and forth between Hornby Island and Qualicum, Comox, or Denman Island.

The accuracy of our calculations of the number of birds that moved from each wintering location during spawning depends on the assumption that banded and unbanded birds were equally likely to move. Combined data from 1998-2001 indicate that proportions that were banded did not vary among winter, spawning, and spring at locations other than Hornby Island, and averaged 12.9% at Quadra Island ($\chi^2_2 = 2.5$, $P = 0.3$, $n = 263$), 19.9% at Campbell River ($\chi^2_2 = 0.6$, $P = 0.7$, $n = 533$), 19.0% at Comox ($\chi^2_2 = 1.4$, $P = 0.5$, $n = 1028$), 20.3% at Denman Island ($\chi^2_2 = 0.8$, $P = 0.7$, $n = 128$), 15.5% at Qualicum ($\chi^2_1 = 3.4$, $P = 0.07$, $n = 142$; no spring samples were obtained), and 3.2% ($n = 248$; numbers of banded birds were too small for chi-square tests) at all other areas in the northern Strait of Georgia. The overall average proportion of birds with bands at Quadra Island, Campbell River, Comox, Denman Island, and Qualicum was 19.6% ($n = 832$) in winter and 18.3% ($n = 847$) during spawning ($\chi^2_1 = 0.5$, $P = 0.5$). These similar proportions in winter and spawning indicate that banded and unbanded birds were equally likely to move from these locations.

In contrast, seasonal changes in proportions of birds with bands on Hornby Island suggest that banded birds were more likely to move there during spawning than unbanded birds. On Hornby Island, proportions with bands differed among seasons and were 30.7% ($n = 758$), 21.7% ($n = 5045$), and 24.8% ($n = 290$) in winter, spawning, and spring, respectively ($\chi^2_2 = 16.3$, $P < 0.001$). Considering that 30.7% of the 706 wintering birds that stayed at Hornby Island for spawn, and 19.6% of the 2,291 birds wintering at other study locations that came to Hornby Island for spawn in 1999-2000 (Table 4.4) were banded, the number of banded birds from those locations that came to Hornby Island for spawn would have been 666. This would equal 15.0% of

the average number of birds (4429) estimated to come for spawn in 1999 and 2000 (Table 4.3). The observed proportion of birds with bands for those two years (21.2%; Table 4.3) was significantly higher ($\chi^2_1 = 57.6, P < 0.001$). Balancing this discrepancy would require that 19.2% of the birds that came to Hornby Island from areas other than those accounted for in Table 4.4 were banded. Our data indicate that only 3.2% of birds were banded in other parts of the northern Strait of Georgia.

The above results suggest that banded and unbanded birds were equally likely to come to Hornby Island for spawn from study locations where birds have been captured and banded during their post-breeding moult, but that banded birds were more likely than unbanded birds to come to Hornby Island for spawn from other locations where we have not banded birds. Because banded birds wintering at those other areas must have been banded at one of our study sites, it is possible that birds that disperse from the banding sites where they moulted are more likely to return for spawning than those that moult elsewhere. We could not test this idea for birds from these distant areas, but did have sufficient data to test it for birds that wintered at Comox and Campbell River. Birds wintering at Comox and Campbell River that moulted at Hornby Island were more likely to come to Hornby Island for spawn (83%, $n = 24$) than those that moulted at Comox and Campbell River (63%, $n = 78$; one-sided test: $\chi^2_1 = 3.53, P = 0.030$).

Effect of travel distance

The proportion of different Harlequin Duck wintering populations that moved to Hornby Island during herring spawning was strongly dependant on the distance birds had to travel. The relationship between proportion of birds moving to Hornby Island and the distance they had to travel was quadratic and indicated that percent moving would approach zero at a distance of about 80 km (Fig. 4.5).

Duration of stay during spawning

The estimated number of days that immigrant birds stayed at Hornby Island during spawning ranged from 1 to 55 and averaged 22 ± 13 ($n = 81$) in 1999 and 11 ± 8 ($n = 106$) in 2000. Birds that spent the winter on Hornby Island were observed present for longer periods of time during spawning: 32 ± 15 d ($n = 37$) in 1999 and 18 ± 10 d ($n = 81$) in 2000. A two-way ANOVA indicated that differences were significant between years ($F_{1,301} = 84.5, P < 0.001$) and between resident and immigrant birds ($F_{1,301} = 44.5, P < 0.001$). The difference between years may partially be attributable to lower resighting effort in 2000 than 1999 (Fig. 4.2), but the difference in length of stay was much greater than difference in effort and we are confident that

difference in estimated lengths of stay was real. The longer duration of stay detected for resident birds also increases our confidence that the length of stay measured for immigrant birds was accurate.

Where birds went after spawning

Repeated counts at sample areas (Table 4.1), plus resightings of banded birds, indicate that many birds return to their main wintering ground after coming to Hornby Island for spawn and prior to departing for breeding streams. Twenty-two birds that came to Hornby Island for spawn were resighted in April: 73% had returned to their winter residence, the rest were still on Hornby Island. Of 63 winter residents of Hornby Island resighted in April, 58 (92%) were still on Hornby Island, 2 were sighted at Comox, and 3 were seen inland.

Consumption of spawn

We calculated the amount of spawn consumed by Harlequin Ducks at Hornby Island in 1999 and 2000 and in the total spawning area in that vicinity in 1995-2001. Harlequin Ducks at Hornby Island appear to feed almost exclusively on herring spawn for 20 d and then partially on spawn for another 10 d after it is first deposited (Rodway and Cooke 2002). We thus assumed that birds fed entirely on spawn for an average of 25 d, which is similar to the average length of time Haegele (1993) estimated spawn was available to marine birds in the area. Though the mean length of stay of immigrant birds at Hornby Island during herring spawning was less than this, we assumed that birds that moved away from Hornby Island went to other spawning locations as long as spawn was available. This assumption was justified because all movements from Hornby Island that we detected during the spawning period were to Denman Island, Qualicum, and Comox, where spawning also occurred. Consumption on Hornby Island was based on the numbers of resident and immigrant birds (Tables 4.3 and 4.4) and their respective mean durations of stay, to a maximum of 25 d, during spawning. Consumption in the entire area was based on the total numbers of birds that moved to Hornby Island for spawn (Table 4.3) plus the numbers at spawning locations on Denman Island, Baynes Sound, Qualicum, and Comox that did not move to Hornby Island (Table 4.4). Daily food consumption (F) per duck was calculated to be 119 g. Extrapolating gave estimates of 12.4 and 6.2 t of herring spawn consumed on Hornby Island in 1999 and 2000, respectively, and 16.2, 13.3, 17.8, 13.2, 15.1, 13.9, and 11.3 t of spawn consumed in the entire area in the years 1995-2001, respectively.

DISCUSSION

We found large aggregations of several thousand Harlequin Ducks gathering at few locations on the northeast side of Hornby Island during herring spawning. Aggregations occurred in only a small portion of the total spawning area. The northeast side of Hornby Island was not included in Haegele's (1993) study area, which would explain why he failed to detect an increase in Harlequin Duck numbers during spawning. Our results indicate that 49-81% of the mid-winter population in the northern Strait of Georgia (Rodway et al. 2003) spent time at Hornby Island during herring spawning. The presence of Harlequin Ducks at other spawning sites suggest that 55-87% of the mid-winter population exploited herring spawn in the northern strait in the years 1995-2001. Clearly herring spawn is an important late-winter food for Harlequin Ducks in this area and probably throughout their Pacific range.

Birds aggregating at Hornby Island consumed an estimated 12.4 and 6.2 t of herring spawn in 1999 and 2000, respectively. In total, Harlequin Ducks consumed between 11.3 and 17.8 t of spawn annually in the larger spawning area between Comox and Qualicum. Haegele (1993) estimated annual consumption of spawn by all waterbirds gathering along Denman and Hornby islands to be 198-216 t, representing 3-4% of the spawning biomass of herring in that area. Consumption by Harlequin Ducks is a small proportion of this total, but aggregation of Harlequin Ducks along northeast Hornby Island may have a greater local impact.

Maximum counts of Harlequin Ducks at Hornby Island during spawning underestimated total numbers coming there because there was a turnover of birds throughout the herring spawning period. The length of time that immigrant birds stayed at Hornby Island averaged 2-3 weeks, but varied considerably among individuals and between years. In the Hornby Island area, spawning is typically concentrated over a period of several weeks and eggs hatch within 2-3 weeks, making them available in large numbers to predators for 3-4 weeks (Haegele 1993). The difference between calculated estimates and maximum counts of numbers of birds was greater in 2000 than 1999. This was related to a shorter residence time for birds in 2000. Lower numbers, a shorter stay, and larger flocks on the south side of Hornby Island during spawning in 2000 were associated with less extensive herring spawning along the northeast shore of Hornby Island than in 1999 (DFO 2002). Fewer bands read and lower numbers estimated in 2001 were also associated with less extensive spawning on Hornby Island, but may also have been partially due to lower band-reading effort that year. In 2002, when herring did not spawn on Hornby Island, there were no large aggregations of Harlequin Ducks at Hornby Island or at other sites, even those where herring did spawn. Herring spawned extensively along the Vancouver Island shoreline that year (DFO 2002) and it is likely that Harlequin Duck populations from those areas that

aggregated at Hornby Island in previous years remained dispersed in 2002. A number of birds from Hornby Island may have moved elsewhere for spawn in 2002 because the maximum count on Hornby Island during the spawning period was considerably lower than wintering numbers (see Tables 4.3 and 4.4).

Sixty-eight percent of birds at Hornby Island during spawning originated from study areas where birds were marked. The remainder probably came from populations wintering in the north and eastern strait and in the area south of Qualicum. Our data indicate that banded and unbanded birds were equally likely to come to Hornby Island for spawn from locations where Harlequin Ducks have been banded, but banded birds were more likely than unbanded birds to come from locations where we did not band. This apparent discrepancy can be explained by our finding that birds which moulted in the Hornby Island area were more likely to return there for spawn than those which moulted elsewhere. This tendency would result in more banded birds coming from more distant areas because the only banded birds present in those areas must have moulted elsewhere, at one of our banding sites. In contrast, marked birds in wintering populations at our banding locations included both birds that moulted there and those that moulted at one or more of the other banding sites. Overall proportions of birds with bands did not change at those sites when birds moved to Hornby Island for spawn because proportions of banded birds were similar in those two groups.

Harlequin Ducks migrate to their inland breeding grounds in late March, April, and May (Robertson and Goudie 1999). Counts at sample areas, and sightings of banded birds revealed that the majority of the wintering population is still at coastal habitats through much of April. Thus, for many or most Harlequin Ducks, moving to herring spawning grounds is not a way stop en route to the breeding grounds, but is a shift in winter habitat use to exploit a valuable, short-term resource. Aggregations of a few hundred birds on the south and west sides of Hornby Island, which generally occurred in April after most herring eggs would have hatched, may have been associated with movements back to wintering grounds to the south of Hornby Island.

Aggregating Harlequin Ducks did not behave as ideal-free predators. The proportion of birds that moved to Hornby Island for spawn from other locations was strongly related to the distance birds had to travel. Few birds travelled more than 80 km. Why only some birds came and how they knew to go to Hornby Island is unknown, although our finding that birds which moulted on Hornby Island were more likely to return there during spawning identifies a possible mechanism for some birds. Declining proportions moving with increasing distance may result from differences in information among local populations. The activity of foraging flocks and the movement of birds to and from their nocturnal roosts several kilometres offshore (Rodway and

Cooke 2001) may facilitate information transfer among adjacent populations. The time lag and reduced effectiveness of information transfer with increasing distance may explain why flock sizes increased for several days after spawning occurred and why the proportions of birds moving declined as travel distance increased. Alternatively, the trade-off between the costs of moving and the benefits of being at Hornby Island during spawning may vary among individuals.

Reductions in the number of herring spawning locations in the northern, eastern, and southern Strait of Georgia (DFO 2002) likely impose costs of greater movement distances or loss of access to spawn for Harlequin Ducks and other waterbirds wintering in those areas. Interestingly, White Rock was the only surveyed location other than Hornby Island where numbers of Harlequin Ducks increased during spawning (see Table 4.1). Herring used to spawn in the White Rock area but have not done so since 1992 (DFO 2002). The potential benefits of feeding on herring spawn to social and pairing behaviour of Harlequin Ducks are currently under study (MSR unpubl. data). Benefits to survival and reproductive success seem likely and warrant investigation for all waterbird species that feed on herring spawn.

Our knowledge of the winter ecology and habitat needs of Harlequin Ducks would be enhanced if we understood why they are particularly attracted to northeast Hornby Island during herring spawning. Reasons may relate to the history of spawning in that area in recent years, accessibility of spawn in relation to depth and substrate type, roosting habitat, disturbance, or competition with other marine bird species. Birds may traditionally gather at locations where spawn has been most abundant and most consistently deposited over recent years. The accessibility of spawn to Harlequin Ducks may vary among areas because of differences in substrate type or depth of spawning. The littoral substrate along northeast Hornby Island is mainly a mix of cobble and bedrock, whereas there is more sand and gravel along much of the Vancouver Island and Denman Island shorelines, where herring also spawn. Our observations in intertidal habitat suggest that spawn may weather differently on these different substrates, tending to mix in with a gravel substrate when impacted by wave action. This may reduce the accessibility of spawn to Harlequin Ducks, which feed mainly in shallow intertidal and subtidal habitat. Other seaduck species that were seen in large flocks in other areas fed in slightly deeper waters, where spawn may be less likely to be weathered by wave action. The northeast shore of Hornby Island provides some shelter from prevailing winds and wave action, but not more than other nearby areas where spawn is deposited. In fact, we have seen rafts of several thousand Harlequin Ducks riding out waves in gale-force winds along the northeast shore of Hornby Island when just around the corner were sheltered waters and abundant herring spawn.

The quality of roosting habitat may affect habitat choices. The shoreline of Hornby Island, with its sandstone shelves and offshore skerries, may offer more attractive roosting habitat for Harlequin Ducks than other spawning areas. This would not be as pertinent for other sea duck species because they do not haul out on shoreline rocks like Harlequin Ducks do. Disturbance of roosting birds by humans and dogs may be less on Hornby Island than on the extensive beaches of Vancouver Island, which are closer to larger human populations and easily accessible. Activity of the fishery, which during the years of this study occurred along Vancouver Island and along the south and west but not the northeast side of Hornby Island, may also disturb feeding and roosting birds, but only for short periods, as the fishery generally lasts only a few days.

Finally, competition with other marine birds may be a factor. We saw up to 300 Harlequin Ducks in mixed-species flocks with several thousand other sea ducks, and small numbers of Harlequin Ducks were frequently observed in multispecies flocks at herring spawn in the Queen Charlotte Islands (Vermeer et al. 1997). However, the large aggregations of Harlequin Ducks along northeast Hornby Island were primarily single-species flocks. Dense flocks of gulls often excluded or displaced Harlequin Ducks from roosting areas, and also foraged in the same intertidal habitat, but this seemed to be as common on Hornby Island as elsewhere. Competitive exclusion seemed unlikely to be operating because of the extent of unused habitat where herring spawn was available.

Conservation of marine birds in increasingly populated and exploited environments like the Strait of Georgia requires careful management of the resources and habitats essential to their continued survival. Most Harlequin Ducks, and likely a majority of the wintering populations of other sea ducks (Vermeer 1981), undertake seasonal movements to feed on herring spawn. It will thus be prudent to integrate the management of sea ducks with that of the herring fishery, as well as the management of any other extraction industry that affects the food supply or foraging habitat of waterbirds. Understanding the importance of herring spawn to wintering birds will help us predict the potential impacts of natural or human-induced climatic changes that may reduce the abundance of herring in these waters (Schweigert 1995, Alheit and Hagen 1997).

ACKNOWLEDGMENTS

Funding for this study was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, the British Columbia Waterfowl Society, the Institute of Waterfowl and Wetlands Research, and the James L. Baillie Memorial Fund. Many individuals helped with capturing, marking, and resighting Harlequin Ducks. We especially thank

Brian Arquilla, Sean Boyd, Lynn Campbell, Fred Cooke, Frank Elkins, Mary Jane Elkins, Dave Genter, Janet Hardin, Stewart Jackson, Greg Robertson, and Richard Swanston. Thanks are extended to Fred Cooke for continued support and insightful discussion and to Barbara Sherman and Connie Smith for administrative and logistic assistance. We often had the pleasure of Mary Jane and Frank Elkins' hospitality while working on Hornby Island. Sean Boyd, Larry Dill, and Jean-Pierre Savard gave us helpful comments on the manuscript.

LITERATURE CITED

- Alheit, J., and E. Hagen. 1997. Long-term climate forcing of European herring and sardine populations. *Fisheries Oceanography*. 6:130-139.
- Bayer, R.D. 1980. Birds feeding on herring eggs at the Yaquina estuary, Oregon. *Condor* 82:193-198.
- Botton, M.L., R.E. Loveland, and T.R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. *Auk* 111:605-616.
- Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock, and J.B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173-1187.
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990. The birds of British Columbia. Vol. I. Nonpasserines (Introduction, loons through waterfowl). Royal British Columbia Museum, Victoria, Canada.
- DFO 2002. Fisheries and Oceans Canada Website: <http://www.pac.dfo-mpo.gc.ca/sci/herring/bulletin.htm>. [accessed 15 December 2002].
- Fretwell, S.D., and H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16-36.
- Goudie, R.I., S. Brault, B. Conant, A.V. Kondratyev, M.R. Petersen, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 59:27-49.
- Grosse, D.J., and D.E. Hay. 1988. Pacific herring, *Clupea harengus pallasii*, in the northeast Pacific and Bering Sea. Pp. 34-54 in N.J. Wilimovsky, L.S. Incze, and S.J. Westrheim (eds.). Species synopses: life histories of selected fish and shellfish of the northeast Pacific and Bering Sea. Washington Sea Grant Program, University of Washington, Seattle, WA. 88-2.
- Haegle, C.W. 1993. Seabird predation of Pacific Herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73-82.

- Hay, D.E., and P.B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document 99/14, Nanaimo, BC.
- Hay, D.E., M.C. Healy, L.J. Richards, and J.B. Marliave. 1989. Distribution, abundance, and habitat of prey fishes in the Strait of Georgia. Pp. 37-49 in K. Vermeer and R.W. Butler (eds.). The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Special Publication, Canadian Wildlife Service Ottawa.
- Hilderbrand, G.V., C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132-138.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and dilution – stochastic model. *Biometrika* 52:225-247.
- Kennedy, M., and R.D. Gray. 1997. Habitat choice, habitat matching, and the effect of travel distance. *Behaviour* 134:905-920.
- Munro, J.A., and W.A. Clemens. 1931. Waterfowl in relation to the spawning of Herring in British Columbia. *Bulletin of the Biological Board of Canada* 17:1-46.
- Nilsson, S.G., and I.N. Nilsson. 1976. Numbers, food consumption, and fish predation by birds in Lake Moeckeln, southern Sweden. *Ornis Scandinavica* 7:61-70.
- Restani, M., A.R. Harmata, and E.M. Madden. 2000. Numerical and functional responses of migrant bald eagles exploiting a seasonally concentrated food source. *Condor* 102:561-568.
- Robertson, G.J., and R.I. Goudie. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill (eds.). The birds of North America, No. 466. The Birds of North America, Inc., Philadelphia, PA.
- Rodway, M.S., and F. Cooke. 2001. Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor* 103:870-874.
- Rodway, M.S., and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. *Journal of Field Ornithology* 73:363-371.
- Rodway, M.S., H.M. Regehr, and F. Cooke. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates. *Canadian Journal of Zoology* 81:492-503
- Schweigert, J.F. 1995. Environmental effects on long-term population dynamics and recruitment of Pacific herring (*Clupea pallasii*) populations in southern British Columbia. *Can. Spec. Publ. Fish. Aquat. Sci.* 121.
- Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Griffin, London.

- Stephens, D.W., and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton.
- Vermeer, K. 1981. Food and populations of Surf Scoters in British Columbia. *Wildfowl* 32:107-116.
- Vermeer, K., M. Bentley, K.H. Morgan, and G.E.J. Smith. 1997. Association of feeding flocks of Brant and sea ducks with herring spawn at Skidegate Inlet. Pp. 102-107 in K. Vermeer and K.H. Morgan (eds.). The ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands. Occasional Paper Number 93, Canadian Wildlife Service, Ottawa.

TABLE 4.1. Comparison of counts of Harlequin Ducks (*Histrionicus histrionicus*) during winter (January-February.), spawning (March), and spring (April) in sampling areas in the Strait of Georgia, British Columbia, 1998-2001.

	Winter	Spawning	Spring
Quadra Island	590 (1)	470 (1)	479 (1)
Campbell River	373 ± 73 (5)	265 ± 52 (4)	358 (1)
Comox	378 ± 101 (7)	298 ± 86 (5)	418 (1)
Denman Island	148 ± 52 (2)	108 (1)	222 (1)
Hornby Island	612 ± 89 (7)	2972 ± 958 (52)	927 ± 442 (6)
Qualicum	751 (1)	505 ± 88 (2)	-
White Rock	61 ± 10 (6)	94 ± 14 (5)	67 ± 24 (5)

Note: The sampling areas where Harlequin Ducks were counted repeatedly were often a subset of the total areas whose winter populations are presented in Table 4.4. Values are given as the mean ± SD with the sample size in parentheses.

TABLE 4.2. Mean wintering numbers and maximum aggregations of Harlequin Ducks during herring spawning at four sites on the northeast side and four sites on the south and west sides of Hornby Island, British Columbia, in 1998-2002.

Location	Winter numbers (mean \pm SD) ^a	Maximum number during March and April ^b				
		1998	1999	2000	2001	2002
Northeast side						
Grassy	48 \pm 27 (9)	97 (11)*	196 (5)*	117 (19)*	14 (10)*	97 (23)
Squeaker	44 \pm 15 (9)	1650 (11)*	3172 (23)*	62 (8)	1140 (15)*	98 (23)
Anderson	25 \pm 13 (10)	548 (13)*	834 (23)*	1110 (19)*	1150 (15)*	74 (24)
Helliwell	96 \pm 53 (10)	2126 (27)*	514 (28)*	67 (8)*	45 (10)	89 (23)
South and west sides						
Sandpiper	129 \pm 44 (6)	281 (45)*	98 (39)*	523 (29)*	50 (10)	82 (28)
Heron	42 \pm 27 (6)	265 (45)*	249 (39)*	212 (19)*	20 (10)*	142 (28)
Ford's	9 \pm 5 (7)	128 (45)*	168 (28)*	178 (19)*	12 (10)*	35 (18)
Phipps	36 \pm 29 (10)	160 (8)*	249 (5)*	34 (19)	61 (10)*	49 (23)

Note: The sites listed from top to bottom are ordered clockwise around the island, beginning at the northeast corner, and encompass similar linear extents of shoreline. Herring first spawned on Hornby Island on 7, 5, 6, and 7 March in 1998-2001, respectively. Numbers in boldface type denote aggregations that persisted at a similar size for a week or more are indicated in bold print. Surveys during spawning were conducted through March and the first half of April in 1998-2000 and ended on 15 March in 2001 and 30 March in 2002.

^aNumbers in parentheses are sample sizes.

^bNumbers in parentheses show the date of maximum count (1 = 1 March). An asterisk indicates that spawning occurred at that site.

TABLE 4.3. Numbers of Harlequin Ducks at Hornby Island during herring spawning, estimated by direct counts and by proportions of banded birds, in 1995-2002.

Year	Max. count during spawning (mean \pm SD)	No. of banded birds identified (m_t)	Estimated no. of banded birds not identified (u_t)	Percentage of birds with bands ($\hat{\alpha}_t$)	Calculated total during spawning ($((m_t + u_t)/\hat{\alpha}_t)$)
1995	5000 (1)	186	-	-	-
1996	2457 (1)	497	474	24.2 (1040)	4007
1997	2375 (1)	679	285	17.5 (905)	5522
1998	2655 \pm 218 (13)	801	258	26.5 (1226)	3995
1999	4277 \pm 545 (16)	821	128	20.5 (2046)	4623
2000	2114 \pm 192 (9)	711	212	21.8 (959)	4235
2001	2325 \pm 180 (14)	467	135	17.9 (814)	3356
2002	519 (1)	110	-	-	-

Note: Herring spawned on Hornby Island in 1995-2001, but not in 2002. Numbers in parentheses are sample sizes.

TABLE 4.4. Proportions of marked wintering populations of Harlequin Ducks in the northern Strait of Georgia that moved to Hornby Island during herring spawning in 1999 and 2000.

Area	Winter population size	Percentage of banded winter residents sighted on Hornby Island during spawning	Estimated total numbers that moved to Hornby Island	Percentage of total number of birds at Hornby Island for spawn
Quadra Island	845	13.6 (22)	141	3.2
Campbell River	524	11.7 (60)	75	1.7
Comox	944	65.1 (129)	754	17.0
Baynes Sound	105	60.0 (5)	77	1.7
Denman Island	685	78.3 (23)	658	14.9
Hornby Island	716	86.1 (238)	706	15.9
Qualicum	751	63.6 (22)	586	13.2
White Rock	65	1.1 (94)	1	0.0

Note: Winter numbers are from a mid-winter survey conducted in 1999-2000 (Rodway et al. 2003). The percentage of birds sighted on Hornby Island during spawning was adjusted by the average estimate (22.7%) of the proportion of marked birds that were present but not identified in 1999 and 2000 (see Table 4.3) in order to estimate total numbers that moved. The calculated average total number of birds at Hornby Island during spawning in 1999 and 2000 (4429; see Table 4.3) was used to estimate the percentage of the total number of birds at Hornby Island. Numbers in parentheses are sample sizes.

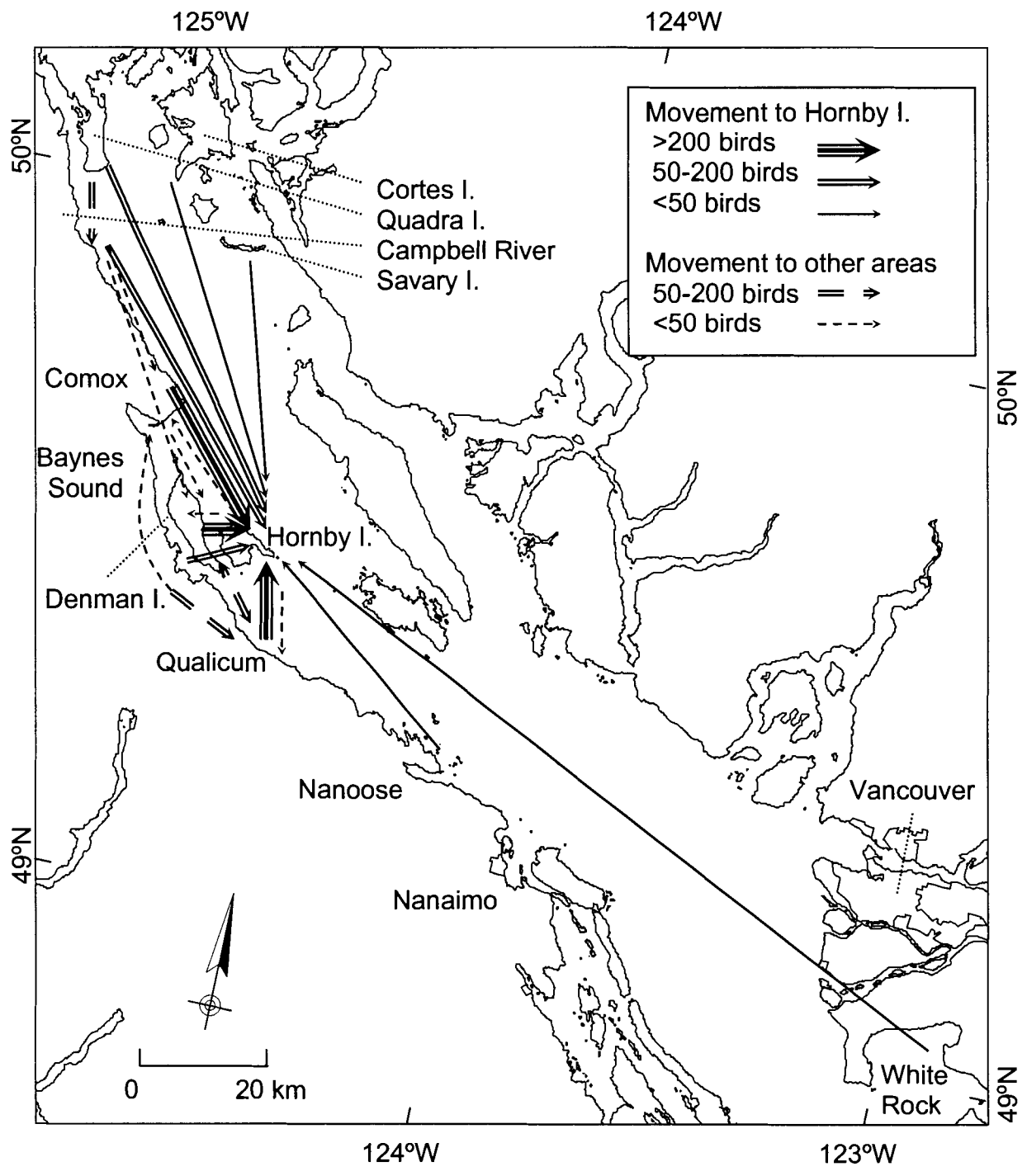


FIGURE 4.1. Locations of study areas and movement of Harlequin Ducks (*Histrionicus histrionicus*) from their wintering areas to Pacific herring (*Clupea pallasii*) spawning grounds in the Strait of Georgia, British Columbia in March of 1999 and 2000.

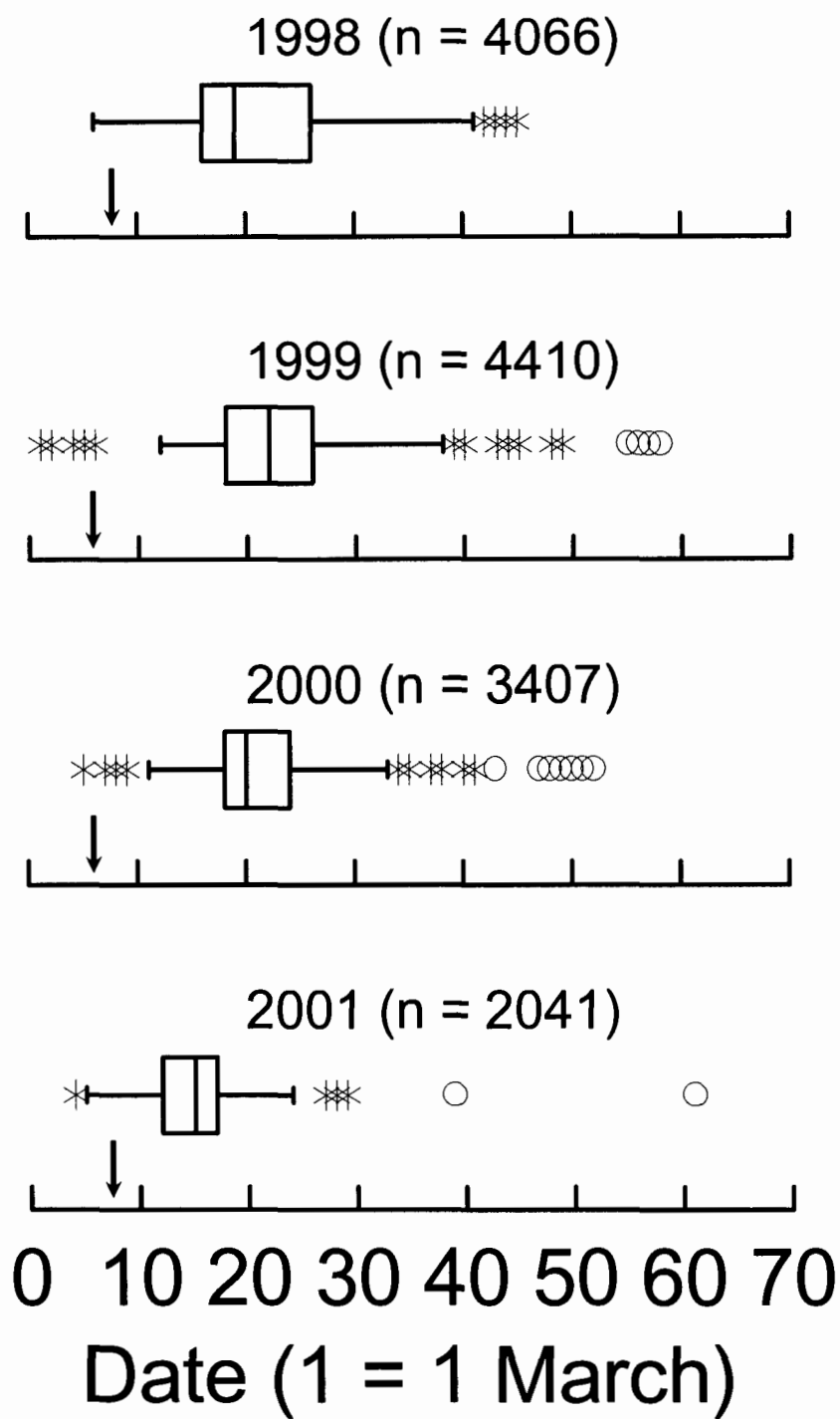


FIGURE 4.2. Box plots showing band-reading effort over the herring spawning period on Hornby Island, British Columbia, in 1998-2001. The arrow on the x-axis shows the date of first spawning. The total number of resightings of marked Harlequin Ducks is given in parentheses.

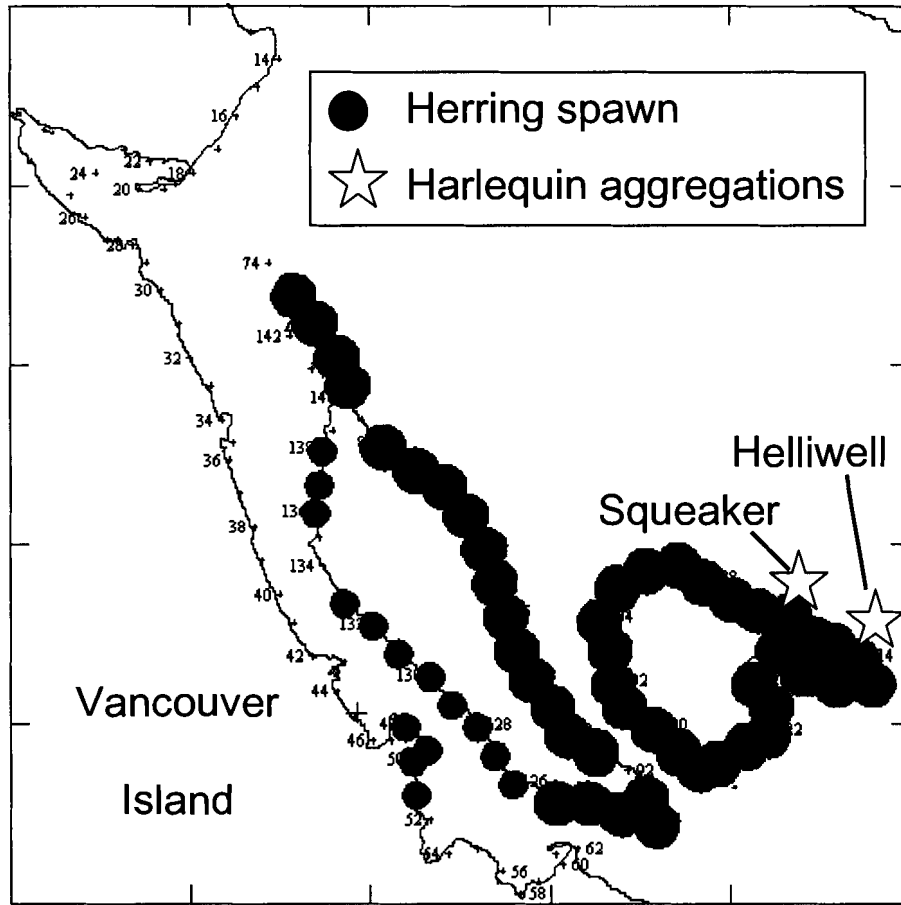


FIGURE 4.3. Location of herring spawning and Harlequin Duck aggregations in the Hornby Island and Denman Island area, British Columbia, in March 1998. Herring spawning data are from DFO (2002).

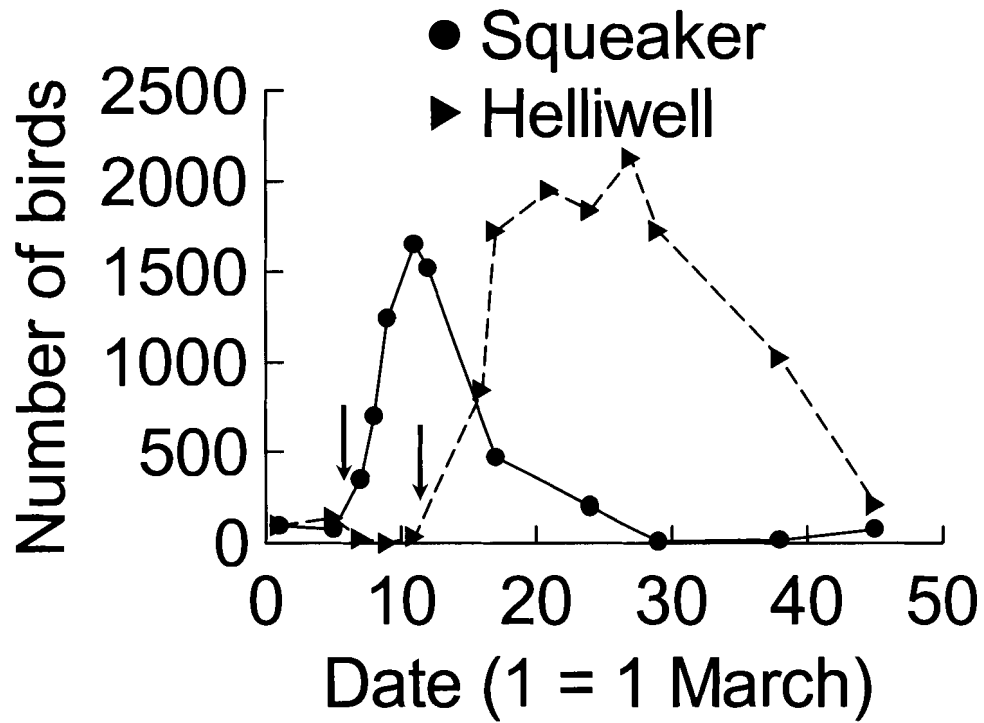


FIGURE 4.4. Timing of Harlequin Duck aggregations relative to herring spawning at sites on Hornby Island, British Columbia, in March 1998. The arrows indicate the dates when herring spawned at the two locations.

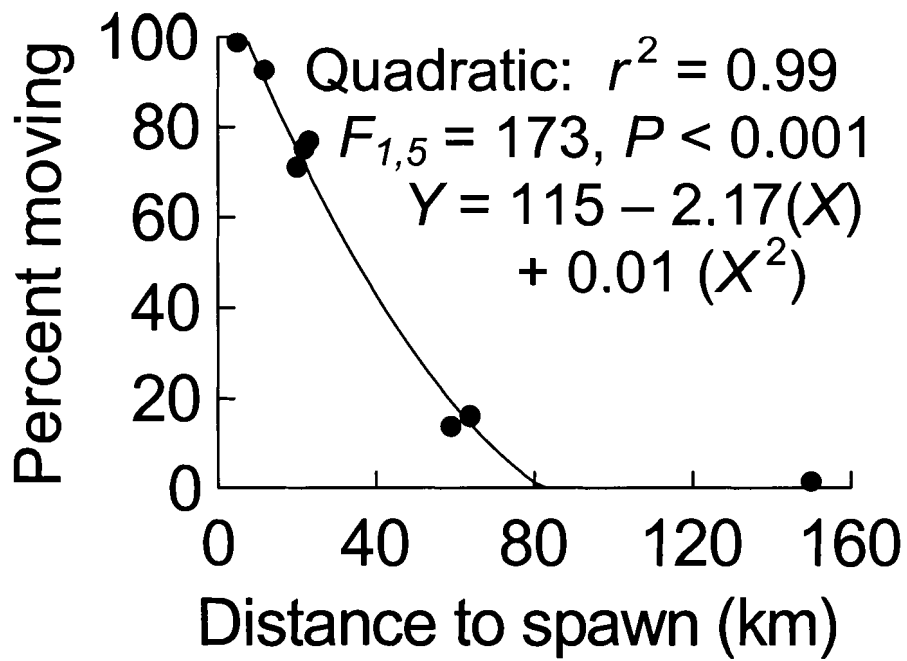


FIGURE 4.5. Percentages of wintering Harlequin Duck populations in the Strait of Georgia, British Columbia, that moved to Hornby Island for herring spawn in 1999-2000 in relation to the distance the birds had to travel.

CHAPTER 5

EFFECT OF FOOD AVAILABILITY ON ARRIVAL AND DEPARTURE DECISIONS OF HARLEQUIN DUCKS AT DIURNAL FEEDING GROUNDS

Rodway, M. S., and F. Cooke. 2001. Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor* 103:870-874.

Reprinted with permission (© Cooper Ornithological Society).

ABSTRACT

We investigated three types of decisions made by Harlequin Ducks (*Histrionicus histrionicus*) in moving between nearshore feeding and offshore resting areas: when to move, whether to move synchronously, and whether to form dense flocks on the roosting grounds. We used the spawning of Pacific herring (*Clupea pallasii*) as a natural food-supplementation experiment. Birds arrived at nearshore feeding areas a few minutes later and departed almost an hour earlier relative to sunrise and sunset when spawn was available than before and after. Cloud cover and high winds resulted in earlier departures, especially during spawning. Arriving, departing, and offshore groups consisted most frequently of two ducks, and birds showed little tendency to synchronize movements or to form dense flocks when resting. Results indicate that Harlequin Ducks avoid crepuscular and nocturnal periods near shore when not constrained by food availability and the length of daylight in which to feed.

INTRODUCTION

Individuals may trade off predation risk against nutritional state when making foraging decisions (Lima and Dill 1990). Changes in food availability can alter cost-benefit ratios and make animals more or less willing to risk predation. Reducing predation risk is thought to explain why many waterfowl species undertake daily movements between feeding and safer resting grounds, and why they often form dense flocks on roosting grounds (Fox et al. 1994, Cox and Afton 1996). Decisions of when and how to move to and from feeding areas are likely affected by a suite of factors, including foraging method, prey type, nutritional state, food availability, environmental conditions, and predation risk (Nilsson 1970, Miller 1985, Cox and Afton 1996). Effects of food availability have not previously been investigated.

For diurnal foragers in northern latitudes, decreased daylight during winter exerts constraints on time budgets that can affect survival, habitat use, and winter distribution (Goudie and Ankney 1986, Guillemette et al. 1992). In addition, prevalent cloudy conditions in winter reduce light levels, further limiting diurnal time available for feeding. Birds may compensate for shorter daylight by increasing the proportion of the day spent feeding (Nilsson 1970, Goudie 1999) and increasing the rate of food processing (Guillemette 1998). They may also extend the time available for feeding by arriving earlier, leaving later, or feeding nocturnally (Nilsson 1970, Brown and Fredrickson 1997).

Studies investigating daily movements are generally observational because it is difficult to manipulate factors affecting movements under natural conditions. Spawning by Pacific herring (*Clupea pallasii*) along the British Columbia coast provides a superabundant food resource available to waterbirds for about three weeks in late winter-early spring (Haegerle 1993). We used it as a natural food-supplementation experiment to investigate how arrival and departure behavior of Harlequin Ducks (*Histrionicus histrionicus*) is affected by food availability.

Harlequin Ducks forage diurnally along rocky, marine shorelines and move to offshore waters at night (Phillips 1925, Fleischner 1983). During winter they spend the majority of daylight hours feeding (Goudie and Ankney 1986). The influx of herring spawn relaxes constraints on foraging time, and birds spend less than half as much time foraging when spawn is available than during the months before and after (MSR, unpubl. data).

We investigated three types of decisions made by Harlequin Ducks in moving between feeding and resting areas: when to move, whether to move synchronously, and whether to form dense flocks on the roosting grounds. We hypothesized that arrivals near shore should be later and departures earlier during herring spawning if offshore resting areas offer decreased predation risk and are preferred by satiated birds. Secondly, if birds are at risk from aerial predators during flights onshore and offshore, then synchronicity in behavior may be important (Gochfeld 1980). Reasoning that if differences in foraging efficiency among birds are minimized when food is abundant, then arrivals and departures should be more synchronous during spawning than at other times. Finally, we hypothesized that birds will form dense flocks offshore at all times if there is predation risk there. We compared arrival and departure behavior before, during, and after the herring spawning period. Effects of weather were investigated to ensure that seasonal differences were not simply due to different weather conditions (Cox and Afton 1996).

A secondary objective of this study addressed a widely accepted assumption in time-budget methodology. Activity budgets are usually determined by scan or focal animal sampling from which proportions of time spent in various activities can be estimated (Altmann 1974).

Multiplying the proportion of time spent by total time available then provides estimates of absolute times spent in specific behaviors. The hours between sunrise and sunset are often used as a reasonable surrogate for the time available for feeding by diurnally foraging birds (e.g., Guillemette 1998). We determined seasonal changes in arrival and departure times relative to sunrise and sunset, and whether Harlequin Ducks ever foraged at night, to evaluate the accuracy of using daylight hours as a measure of the time available for feeding.

METHODS

The study was conducted along the northeast shore of Hornby Island (49°33'N 124°40'W), an important molting and wintering site for Harlequin Ducks and part of the main spawning grounds for herring in the Strait of Georgia, British Columbia, Canada (Haegele 1993). Open water extends 16 km northeast and over 30 km northwest and southeast off the study area. Evening and morning observations were made during February through April in 1998 and 1999 and from November 1999 to April 2000. Observations of offshore groups were made by telescope from shore at dusk and dawn when the sea was calm and visibility was good, and by binoculars from a kayak at sea in the evening and after dark under starlight or moonlight when birds were visible at close range. Distances offshore were estimated by comparison to landmarks.

We determined whether birds stayed into the night or were present before dawn on 88 and 71 days, respectively. Arrivals and departures were determined during 36 observation sessions, 2-4 hr long, usually paired on the same day or night. Flock size and number were counted during each minute interval between the times of the first and last flocks to arrive or depart. Group sizes near shore were much larger during spawning than at other times, and numbers of birds sampled per observation session ranged from 4-58 during winter, 1656-3172 during spawning, and 14-283 in spring. Birds on the water were considered members of different groups if >10 m separated them. Percent cloud cover was recorded. We estimated wind speed using the Beaufort scale of wind force. Sunrise and sunset times for the study area were obtained from the US Naval Observatory Astronomical Applications Data Services (US Navy 2000).

Data were compared among three date categories, winter (November to February), spawning (the three week period after herring first spawned in early March), and spring (April), two cloud categories (0-89 and $\geq 90\%$ cloud cover), three wind direction categories (no wind, southerly winds, and northerly winds), and three wind speed categories (0-14, 15-29, and ≥ 30 km hr⁻¹). Statistical comparisons were made on mean arrival or departure times per session using a three-way ANOVA without interactions, followed by Tukey post-hoc tests. Means were considered the best estimate of central tendency for small numbers of departing birds, especially

if the majority of birds left at one time and the rest left after a lapse of several minutes. We used hierarchical Type I sums of squares because weather was somewhat dependent on time of year (e.g., more cloudy days in winter), and we wished to determine the effect of date on mean arrival and departure times after the effects of cloud cover and wind had been considered. Interactions could not be included in the model because not all wind and cloud categories occurred within each date category. Tests were performed using GLMs in SPSS 8.0. Residuals were inspected for deviations from normality and homoscedasticity. Tolerance for type one error was set at 5%. Average times that birds spent at nearshore feeding areas were calculated by adding mean arrival and departure times relative to sunrise and sunset to the median number of daylight hours during each date period. Means \pm SD are given.

RESULTS

Harlequin Ducks were never seen near shore during the night. Around sunset, birds in small flocks flew or infrequently swam 1-3 km offshore, where they spent the night scattered in small groups over an area at least 1 km wide and 10 km long parallel to the shore of the Hornby Island study area. Mean sizes of departing (3.2 ± 2.5), offshore (3.7 ± 3.5), and incoming (2.8 ± 1.5) flocks were slightly, though highly significantly different due to large sample sizes ($F_{2,2675} = 22.5$, $P < 0.001$, $r^2 = 0.02$; all Tukey post-hoc tests, $P < 0.01$). The frequency of larger flocks was greater in offshore than departing groups (comparing frequencies of flocks < 10 and ≥ 10 : $\chi^2_1 = 13.5$, $P < 0.001$), and greater in departing than arriving groups ($\chi^2_1 = 12.1$, $P = 0.001$). Two was the most frequent ($> 50\%$) flock size in all cases, and 95%, 90%, and 85% of incoming, departing, and offshore flocks, respectively, were composed of five birds or less.

The earliest arrival time recorded was 32 min before sunrise on 2 November. Latest departure time was 32 min after sunset on 16 December. Feeding occurred as early as 11 min before sunrise and as late as 27 min after sunset. Offshore birds were not observed feeding during dawn or dusk, but were observed preening.

Mean arrival time did not vary significantly in relation to cloud cover or wind, but differed among date categories ($F_{2,17} = 3.8$, $P < 0.05$, $r^2 = 0.26$; Fig. 5.1). Mean arrival times per observation session averaged 12 min before sunrise, 1 min after sunrise, and 3 min before sunrise during winter, spawning, and spring, respectively (Tukey post-hoc tests were not significant). Departure times were affected by percent cloud cover ($F_{1,13} = 6.9$, $P < 0.03$), wind speed ($F_{2,13} = 5.9$, $P < 0.02$), and date ($F_{2,13} = 5.4$, $P < 0.02$, overall $r^2 = 0.58$). Wind direction was not important ($P > 0.5$). Departure times averaged 21 min earlier on cloudy than clear days, and 41 and 37 min earlier in winds ≥ 30 km hr⁻¹ than in winds 0-14 (Tukey post-hoc: $P < 0.02$) and

15-29 km hr⁻¹ ($P < 0.05$), respectively. Mean departure times were 1 min after sunset during both winter and spring, and 56 min before sunset during spawning ($P < 0.05$ for post-hoc comparisons between spawning and other seasons; Fig. 5.1).

The effects of wind and cloud cover on departure times were most pronounced during spawning. Birds left 72 min earlier on days with $\geq 90\%$ cloud cover than on clearer days during spawning, compared to 12 min earlier on cloudy days in winter. The effect of wind speed was seen only during spawning. Departure times during spawning were 100 min earlier in winds ≥ 30 km hr⁻¹ than in winds 0-14 km hr⁻¹. Average departure times showed no trends in relation to wind during other seasons. Effects of cloud cover and wind were partially confounded because strongest winds came from the southeast and tended to be associated with cloudy weather.

Variance of arrival and departure times differed significantly by direction (arrival or departure; $F_{1,22} = 167.7$, $P < 0.001$), date category ($F_{2,22} = 124.7$, $P < 0.001$; all Tukey pairwise comparisons, $P < 0.001$), and the interaction of direction and date ($F_{2,22} = 80.9$, $P < 0.001$). The interaction was significant because departure times were more variable than arrival times during spawning and spring, but not during winter.

Median times spent at nearshore feeding areas were 8 hr 30 min, 11 hr 12 min, and 13 hr 48 min during winter, spawning, and spring, respectively.

DISCUSSION

Arrival and departure times of Harlequin Ducks were influenced by food availability and the associated temporal constraints on foraging time caused by limited day length. Birds extended the time available for foraging by arriving about 10 min earlier during winter. Arrival and departure times were more synchronous, and were little affected by cloud and wind during the winter, suggesting that most birds required the full daylight period to meet their daily energy requirements at that time. Greater variation in arrival and departure times during spring than winter suggests a relaxation of time constraints as day length increased.

There was no evidence of nocturnal foraging, although some individuals in winter fed near shore until almost half an hour after sunset, when it was getting quite dark. Unlike nocturnally feeding species which may compensate for increased thermoregulatory costs and decreased foraging efficiency during stormy weather by moving earlier to feeding areas (Cox and Afton 1996, Green et al. 1999), diurnal foragers may be constrained by the length of daylight, beyond which they cannot see to feed. However, it is not always clear why some diurnally foraging species with diets similar to some nocturnal feeders do not also feed nocturnally (Nilsson 1970).

Birds responded to the input of abundant food during herring spawning by arriving at feeding areas near shore a few minutes later and departing almost an hour earlier than before and after spawning. More similar arrival than departure times may have been due to energy constraints of fasting through the night. Ease of meeting daily energy requirements likely contributed to the highly variable arrival and especially departure times, and the greater response to cloudy and windy weather during spawning. However it is interesting that Harlequin Ducks did not move offshore even earlier than they did during spawning, when only 16% of their time was spent feeding (MSR, unpubl. data). This may suggest that predation risk near shore was low during daylight hours, especially during spawning, when there were large groups of birds effecting vigilance. Alternatively, digestive constraints (Guillemette 1998) may mean that birds have to spend a majority of the day at the feeding grounds, even though feeding bouts are short. The fasting period also may prove limiting if birds move offshore too early.

Arriving and departing groups were small, and birds showed little tendency to synchronize movements. Contrary to our predictions, times were least synchronous during herring spawning when birds should have had the temporal flexibility to coordinate their movements. Offshore groups also were small and showed no tendency to coalesce into rafts. There were significantly greater proportions of larger groups in departing and offshore than in arriving flocks, but all groups were composed of less than 30 birds, and the vast majority of groups were of less than five birds.

Overall, Harlequin Ducks adjusted their activity patterns to avoid crepuscular and nocturnal periods near shore, unless constrained by food availability and the length of daylight. Whether they chose not to feed at night because predation risk near shore was high or because they could not see to feed is unknown. Some nocturnal feeding observed in other seaducks, and suspected in Harlequin Ducks elsewhere (Bengtson 1966), suggests that Harlequin Ducks may be capable of feeding after dark. Predation risk at night may be high from mammalian predators such as mink (*Mustela vison*) which were common on shore.

The methodological implications of the study for time budget analysis indicate that using time between sunrise and sunset would provide a reasonably accurate surrogate for the time available for foraging during spring, but would be less accurate during winter and spawning. Average total time that birds were near shore was 13 min longer, 57 min shorter, and 4 min longer than the time between sunrise and sunset, during winter, spawning, and spring, respectively. These differences represent error rates for the three periods of -2.5%, 7.8%, and -0.5%. Birds were not observed feeding offshore, but observations of birds preening offshore reveals that studies of time budgets at shoreline feeding areas will underestimate total time spent in

maintenance activities, and suggests that birds may defer some activities until night to increase the time available for foraging during the day.

A question not answered by this study was whether individuals differed in the length of time they stayed at the feeding grounds. Known pairs always departed together, and the high frequency of flocks of two birds suggests that times for paired males and females would be the same. Whether young or unpaired birds differ in the length of time they stay near shore is unknown. During herring spawning, social courtship groups of a number of males pursuing one female were often seen near shore after the majority of birds had left for the night. The time between the first and last arrivals and departures indicates that the potential for differences among birds is large and should be considered in studies comparing activity budgets among birds differing in age, sex, or pairing status.

ACKNOWLEDGMENTS

Funding for this study was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, and the British Columbia Waterfowl Society. We are grateful to Heidi Regehr for help collecting arrival and departure data. Thanks to Barbara Sherman for administrative assistance. Mary Jane and Frank Elkins generously shared their hospitality during the senior author's stay on Hornby Island. Two anonymous reviewers made helpful comments on the manuscript.

LITERATURE CITED

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-265.
- Bengtson, S.-A. 1966. Field studies on the Harlequin Duck in Iceland. *Wildfowl Trust Annual Report* 17:79-94.
- Brown, P.W., and L.H. Fredrickson. 1997. White-winged Scoter (*Melanitta fusca*). In A. Poole and F. Gill (eds.). *The birds of North America*, No. 274. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Cox, R.R., Jr., and A.D. Afton. 1996. Evening flights of female Northern Pintails from a major roost site. *Condor* 98:810-819.
- Fleischner, T.L. 1983. Natural history of Harlequin Ducks wintering in northern Puget Sound. M.Sc. Thesis, Western Washington University, Bellingham, WA.
- Fox, A.D., A.D. Green, B. Hughes, and G.M. Hilton. 1994. Rafting as an antipredator response in wintering White-headed Ducks *Oxyura leucocephala*. *Wildfowl* 45:232-241.

- Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pp. 207-270 in J. Burger, B.L. Olla, and H.E. Winn (eds.). Behavior of Marine Animals Vol. 4. Plenum Press, New York.
- Goudie, R.I. 1999. Behaviour of Harlequin Ducks and three species of scoters wintering in the Queen Charlotte Islands, British Columbia. Pp. 6-13 in R.I. Goudie, M.R. Petersen, and G.J. Robertson (eds.). Behaviour and ecology of sea ducks. Canadian Wildlife Service Occasional Paper No. 100, Ottawa, Canada.
- Goudie, R.I., and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475-1482.
- Green, A.J., A.D. Fox, B. Hughes, and G.M. Hilton. 1999. Time-activity budgets and site-selection of White-headed Ducks *Oxyura leucocephala* at Burdur Lake, Turkey in late winter. Bird Study 46:62-73.
- Guillemette, M. 1998. The effect of time and digestion constraints in Common Eiders while feeding over blue mussel beds. Functional Ecology 12:123-131.
- Guillemette, M., R.C. Ydenberg, and J.H. Himmelman. 1992. The role of energy intake rate in prey and habitat selection of Common Eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. Journal of Animal Ecology 61:599-610.
- Haeghele, C.W. 1993. Seabird predation of Pacific herring, *Clupea pallasii*, spawn in British Columbia. Canadian Field-Naturalist 107:73-82.
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.
- Miller, M.R. 1985. Time budgets of Northern Pintails wintering in the Sacramento Valley, California. Wildfowl 36:53-64.
- Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145-154.
- Phillips, J.C. 1925. A natural history of the ducks. Vol. 3. Houghton Mifflin, Boston, MA.
- US Navy. 2000. Website: <http://riemann.usno.navy.mil/AA/data/>. [accessed 15 September 2000].

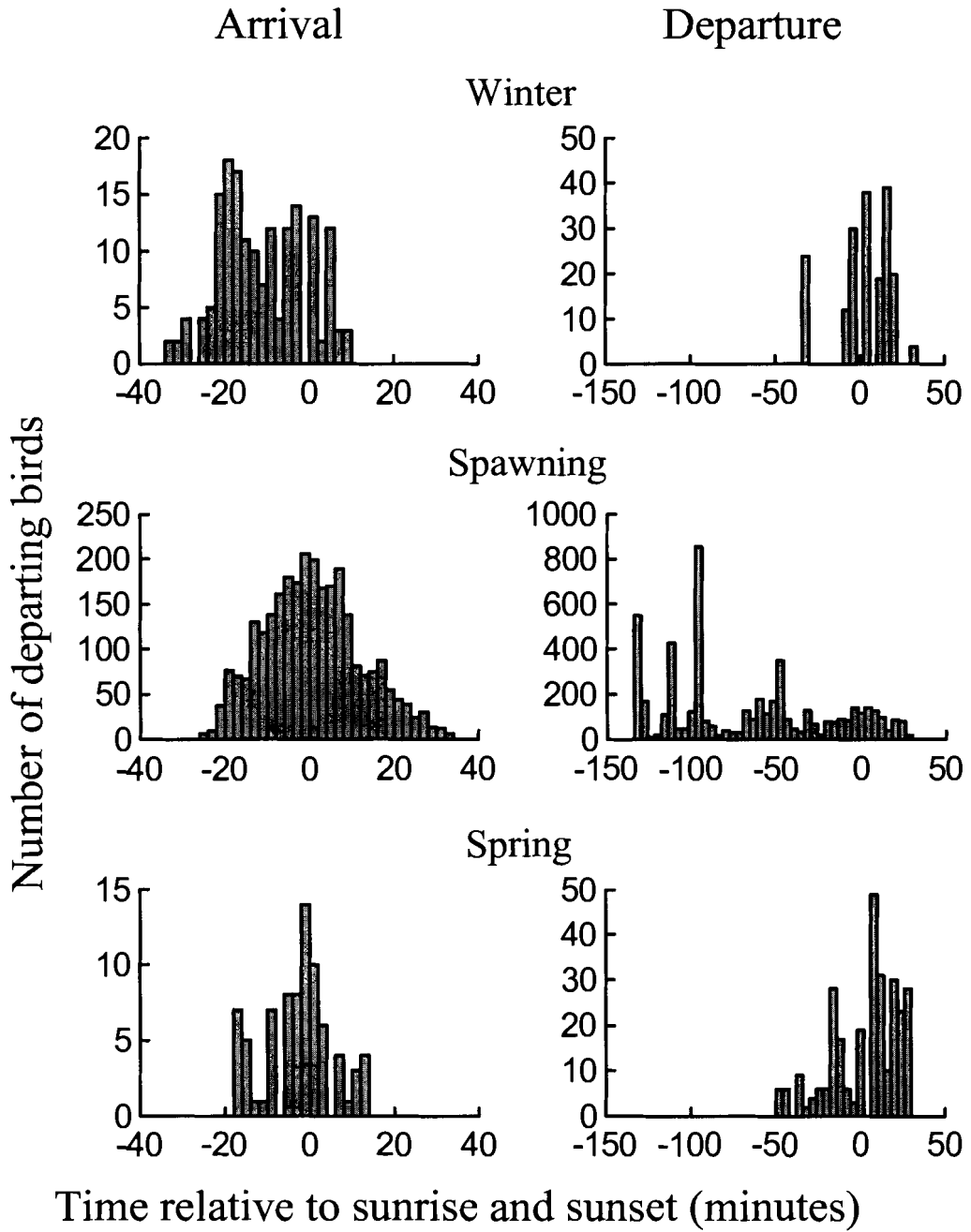


FIGURE 5.1. Timing of arrival and departure of Harlequin Ducks at nearshore, diurnal feeding areas on Hornby Island, British Columbia during winter, herring spawning, and spring, 1998-2000.

CHAPTER 6

TIMING OF PAIRING IN WATERFOWL

Unpublished manuscript.

INTRODUCTION

Mating systems theory has largely concentrated on relationships among males and females during reproductive periods and has progressed from population-level classifications of apparent social relationships (Wynne-Edwards 1962, Lack 1968) to a complex Darwinian theory (Darwin 1871) incorporating adaptive individual variation in behavioural decisions (Orians 1969), conflicts of interest between males and females (Trivers 1972, Maynard-Smith 1977, Johnson and Burley 1997), interaction between social and ecological factors (Crook 1964, Emlen and Oring 1977, Oring 1982), and differences between social and genetic relationships (Parker 1970, Smith 1984, Birkhead and Møller 1998). Focus has been on functional and, more recently, mechanistic explanations for observed mating behaviour. In many animal taxa, males and females form and maintain relationships outside breeding seasons (Lack 1940, 1968). Male-female partnerships during non-reproductive seasons may be unrelated to reproduction (Erickson 1978), but commonly are extensions of monogamous sexual relations that lead to mating and offspring production during reproductive periods. Other than investigation into the timing and extent of precopulatory mate guarding, common in crustaceans, insects, arachnids, and frogs (Grafen and Ridley 1983, Ridley 1983, Brown et al. 1997), questions of why individuals form partnerships when they do has not been prominent in the development of mating systems theory.

Several aspects of the sexual behaviour of waterfowl (Anatidae) are unusual and, despite long-term interest (Darwin 1871, Heinroth 1910, 1911, Lorenz 1941, Johnsgard 1965, Lack 1968), remain poorly understood (McKinney 1986). Males of most migratory ducks do not participate in incubation and brood rearing, yet contrary to theoretical expectations that such male emancipation should lead to polygynous mating systems (Orians 1969, Emlen and Oring 1977), most ducks are seasonally or perennially monogamous. Though socially monogamous, the degree of sexual dichromatism and diethism is more typical of lek-mating species with pronounced polygyny (Skutch 1992, Johnsgard 1994). One of the most intriguing questions is why pair bonds in many species of waterfowl are formed well in advance of the actual period of fertility (Bluhm 1988), often several months or even years prior to breeding, in contrast to the more common avian pattern of pair formation just prior to breeding (Lack 1968), and why the timing of pairing varies

among and within waterfowl species (Weller 1965, Paulus 1983, Wishart 1983, Hohman et al. 1992). Though a variety of hypotheses have been generated and the topic has motivated numerous studies (reviewed in Rohwer and Anderson 1988, Oring and Saylor 1992), many phenotypic, social, and ecological factors that likely influence pairing chronology have not been adequately considered and progress in understanding the behaviour has been slow. My objectives in this paper are to 1) evaluate extant hypotheses to explain variation in the timing of pairing in waterfowl, 2) develop a new hypothesis applicable to all waterfowl and other species of birds that form and maintain monogamous pair bonds outside the breeding season, 3) identify phenotypic, social, and ecological factors that are likely to influence pairing chronology but have not been adequately considered, 4) test predictions of previous and new hypotheses using data on Harlequin Ducks (*Histrionicus histrionicus*), and 5) broadly test the new hypothesis and consider the phylogeny of pairing behaviour using comparative data from all waterfowl.

Male-costs hypothesis

Current theory to explain variation in the timing of pairing in waterfowl suggests that early pairing benefits both females (through increased foraging efficiency and survival due to male defence and vigilance) and males (through mate acquisition and improved female condition) but is constrained by costs to males of courtship, mate defence, and vigilance (Rohwer and Anderson 1988, Owen and Black 1990, Oring and Saylor 1992). There are four main problems with this *female benefits-male costs hypothesis* (hereafter *male-costs hypothesis*): 1) the hypothesis focuses on the state of being paired and ignores the mate-choice process and how individuals integrate that process with other requirements of their life history, 2) trade-offs to females are largely ignored, 3) the criterion used to measure timing of pairing is inadequate, and 4) many available data are inconsistent with the hypothesis and limited tests of some aspects of the hypothesis have largely been unsupportive (Table 6.1).

The reason that current theory largely ignores the process of becoming paired and ascribes little importance to mate choice (particularly female choice) in determining the timing of pairing can be revealed by retracing the main steps in the evolution of thinking on the subject. Lack (1968) suggested that males control the time of pairing and will pair well in advance of breeding to obtain a mate. He developed this theory primarily in relation to northern, migratory ducks, and assumed that males can sequester females through mate-guarding behaviour. Males may obtain a mate through scramble competition or male-male competition with success related to dominance status (Wynne-Edwards 1962). Male-biased sex ratios in these species (Bellrose et al. 1961) has likely resulted in directional selection on males, but not females, to pair as early as

possible, and variation in the timing of pairing was thought to be due to inter-male competition and the trade-offs between male costs of maintaining a pair bond if pairing occurs early, and the risk of failing to obtain a mate or obtaining a low-quality mate if pairing is delayed. Lack (1968) gave little import to the role of female choice, surprisingly, because ethologists had long recognized the importance of female choice in pairing waterfowl, especially in species with sexually-selected, dichromatic plumage and male-biased sex ratios (Lorenz 1941, Johnsgard 1960a), and because the operation and fitness consequences of female choice had been clearly demonstrated (Bateman 1948, Maynard Smith 1956).

Since Lack (1968), the functional significance of female choice has been accepted and recent authors agree that in most waterfowl species, relative parental investment and intra-sexual competition among males for females place females in control of pairing (Trivers 1972, McKinney 1986, Black and Owen 1988, Oring and Saylor 1992). Ironically however, because female migratory ducks are thought to benefit from early pair formation, it has been assumed that they should be willing to pair whenever males are energetically capable, and thus *ipso facto* the control of the timing of pairing still devolves to the males (Rohwer and Anderson 1988). Little consideration has been given to cost-benefit trade-offs and decision-making by females, nor to the actual process of mate choice, and how different social and ecological factors may affect that process to result in variation in the timing of pairing.

The main premise of the male-costs hypothesis, that females gain benefits of increased foraging efficiency by being paired, is poorly founded. Rohwer and Anderson (1988, p. 209) state that, "...selection for enhanced effectiveness of nutrient storage seems to be the major factor driving winter pair formation". Justification for this conclusion comes from pivotal studies demonstrating that mate guarding and vigilance by their partner may increase foraging efficiency for paired females by protecting them from harassment and reducing their need for vigilance (Milne 1974, Ashcroft 1976, Scott 1980, Sorenson 1992). However, these studies did not compare paired and unpaired females but investigated differences in mate performance among paired females. This detail has gone largely unremarked by subsequent researchers and the results of these studies in relation to the benefits of being paired have been misrepresented. Ashcroft (1976) and Scott (1980) showed that feeding rates of paired females were related to the attentiveness of their mates; feeding rate was higher and number of interactions with other birds was lower when males were close than far away. In fact, in Common Eiders (*Somateria mollissima*), very few paired males consistently defended their females, most only responded to threatening and inciting behaviour by the female (Ashcroft 1976). Sorenson (1992) described a similar situation for White-checked Pintails (*Anas bahamensis*): "few males followed their mate

closely and provided strong mate defence, [others] provided little or no defence even when their mate was being harassed". In Bewick's Swans (*Cygnus bewickii*) both males and females benefited from mate proximity, and dominant males kept closer proximity to their mate than subordinate males (Scott 1980). Results of these studies provide evidence for differences in mate quality and indicate likely benefits of mate choice rather than benefits of being paired *per se*.

The male-costs hypothesis predicts that **paired** females will spend more time feeding, suffer less harassment, and spend less time in vigilant behaviour than **unpaired** females. Studies comparing time spent in these activities during winter by paired and unpaired females report little difference (Jorde 1981, Paulus 1984, Paulus 1988a,b, Rave and Baldassarre 1989, Migoya et al. 1994, Lee 1997, Nakamura and Atsumi 2000, Torres et al. 2002).

Foraging efficiency may also improve for paired females (and males) because they can gain access to higher quality food patches due to the increased behavioural dominance of paired to unpaired birds (Paulus 1983). Dominance of paired to single birds has been found in many waterfowl groups, including swans (Scott 1980), geese (Boyd 1953, Hanson 1953, Raveling 1970, Lamprecht 1986, Black and Owen 1989a, Rylander 1993, Stahl et al. 2001), shelducks (Patterson 1982), dabbling ducks (Jorde et al. 1983, Paulus 1983, 1988b, Hepp and Hair 1984, Heitmeyer 1988, Hepp 1989, Thompson and Baldassarre 1992), pochards (Lovvorn 1989), and sea-ducks (Inglis et al. 2000). In geese, families are dominant to pairs without young (Rylander 1993), and large families are often (Boyd 1953, Hanson 1953, Raveling 1970, Gregoire and Ankney 1990, Black and Owen 1989a, Loonen et al. 1999) but not always (Lamprecht 1986, Mulder et al. 1995, Siriwardena and Black 1998) dominant to smaller families. Dominant birds monopolise access to preferred food patches (Black and Owen 1989a, Hupp et al. 1996, Siriwardena and Black 1998, Stahl et al. 2001), may spend less time feeding (Hupp et al. 1996), and, for family groups, show increased survival of young and increased survival or no apparent fitness costs to parents (Black and Owen 1989b, Williams 1994, Loonen et al. 1999). In ducks, the hypothesis that increased dominance status provides access to preferred food supplies or results in improved body condition for paired birds has frequently been postulated (Paulus 1983, Heitmeyer 1988, Baldassarre and Bolen 1986, Pattenden and Boag 1989, Hanson et al. 1990, Demarest et al. 1997), but has little support (Combs 1987, Hepp 1989, Hohman 1993, Hohman and Ankney 1994, Hohman and Weller 1994, Marsden and Sullivan 2000), although further critical testing of this hypothesis is warranted.

These data in relation to the foraging benefits of being paired reveal two important points. For northern, migratory ducks, there is as yet no evidence that females gain nutritional benefit during the winter by becoming paired, either through male protection or through increased

dominance status of the pair. Benefits of increased foraging efficiency is not supported as an explanation for early pair formation in these species. In contrast, single geese are lowest in dominance hierarchies and young birds could benefit from becoming paired after leaving their family or sibling groups. That yearling and older geese often remain single in winter flocks (Boyd 1953, Raveling 1970, Lamprecht 1986, Black and Owen 1989a, Gregoire and Ankney 1990, Stahl et al. 2001, Ganter et al. in prep), even after they have begun courting and have had temporary liaisons with prospective partners (Raveling 1969, Prevett and MacInnes 1980), indicates that increased dominance status and access to better food supplies provides insufficient benefit to young, single birds to select for acceleration of the mate choice process.

The premise that females gain nutritional benefit from being paired and prefer to pair as early as possible creates a need for hypotheses to then explain why all waterfowl do not pair early (Oring and Sayler 1992). The male-costs hypothesis has been the one most frequently advanced (McKinney 1986, Rohwer and Anderson 1988, Owen and Black 1990, Oring and Sayler 1992) and is interpreted by the main architects of the hypothesis to mean that greater energy constraints on males will tip the cost-benefit balance of maintaining a pair bond to favour later pairing (M. Anderson pers. comm.). However, if females are willing to pair early, as is assumed by this hypothesis, then the fitness costs to males of obtaining a low-quality mate, or, in male-biased duck populations, of failing to obtain a mate, should result in all males attempting to pair as early as possible unless they are absolutely time or energy limited (Oring and Sayler 1992). Also, as male time constraints increase, then harassment by courting males and thus the costs to paired males (and benefits to females) of mate-defence should decrease. This makes it difficult to predict how the cost-benefit balance will change. Evidence that males in better condition or at better food supplies pair earlier than conspecifics in poorer condition (Wishart 1983, Brodsky and Weatherhead 1985, Hepp 1986, but see below), and a positive correlation inter-specifically between body size (assuming greater energy constraints with smaller body size) and early pairing among North American dabbling ducks (Rohwer and Anderson 1988) lend support to this hypothesis. There are considerable data inconsistent with this hypothesis. Timing of pairing is not correlated with body size inter-specifically among Western Palearctic dabbling ducks (Rohwer and Anderson 1988) nor among North American Mergini (Coupe and Cooke 1999). Male courtship is often intense for extended periods before pair formation occurs, pair bonds in some small-bodied species (e.g., Hooded Merganser *Lophodytes cucullatus*; Dugger et al. 1994, Coupe and Cooke 1999) are formed during mid-winter when time and energy constraints should be most severe, and paired males frequently participate in social courtship groups indicating that energetic costs of mate defence are not limiting (Hepp and Hair 1983, Williams 1983, Hohman et

al. 1992, McKinney 1992). In addition, females may perform as much or more pair-bond maintenance and defence as males (Weller 1967, Anderson 1984, Lovvorn 1989), and females often are unreceptive to male advances (Johnsgard 1960a, Weller 1965, Hepp and Hair 1983), suggesting that there must be trade-offs of early pairing for females as well as males.

The male-costs hypothesis assumes that males that pair can better afford the costs of mate defence than unpaired males (assuming that there are unpaired females available), and thus predicts that unpaired males will require more time for foraging than paired males, and will spend less time courting than paired males spend in mate defence. The female-choice hypothesis would expect unpaired males to spend as much or more time in courtship than paired males spend in mate defence. Studies comparing time budgets of paired and unpaired males during the winter pair formation period have shown little difference in time spent feeding, and a trend for unpaired birds to allocate more time to courtship and agonistic behaviour than paired males spend in mate defence, although total time devoted to these latter activities was generally small (Jorde 1981, Paulus 1984, 1988a,b, Rave and Baldassarre 1989, Migoya et al 1994, Torres et al. 2002).

Mutual-choice hypothesis

I propose that a more heuristic approach to the study of pairing chronology is to consider pairing as the culmination of the mate choice process by females and males. Three components of the pairing process, each with associated costs and benefits, then become important to consider: the process of choosing a mate, the mate chosen, and the state of being paired. The first two components correspond, respectively, to choosiness and preference functions in mate choice theory (Jennions and Petrie 1997). The third component at least partially reflects the realized fitness benefits of a particular mate choice, but also may function to enhance the benefits of that choice through experience and familiarity gained with a partner (Rowley 1983). The three components are not independent because mate choosing can continue after pairing occurs. Variation in the timing of pairing then depends on variation in and trade-offs among the benefits and costs of these three components, and results from variation in individual life-history decisions about the allocation of time and energy to the mate choice process, i.e., when to begin, how much time and energy to allocate to search and assessment, and when to make the choice. Phenotypic, social, and ecological conditions will influence optimal pairing decisions for an individual through their effects on the various benefits and costs of the pairing process and thus on the tactics of mate choice (Parker 1983, Real 1990). Female and male interests necessarily interact and likely partially conflict (Trivers 1972), and optimal decisions on the timing of pairing will depend on the behaviour of others due to competition and changes in mate availability as pairing

occurs (Real 1991, Johnstone 1997). I call this state-dependent, game-type theory to explain variation in the timing of pairing the *mutual-choice hypothesis*.

Applied to waterfowl, this hypothesis may aptly be named the *female-biased choice hypothesis* (hereafter *female-choice hypothesis*) because, though there is evidence for choice by both female and male waterfowl (Wishart 1983, Bossema and Roemers 1985, Choudhury and Black 1993), differences in parental investment (Trivers 1972, Oring and Saylor 1992), greater female natal philopatry in most species (Anderson et al. 1992), and male-biased sex-ratios in most migratory ducks (Bellrose et al. 1961), predict generally greater female choice and control of the pairing process. Also, physiological studies have demonstrated that pair formation is associated with cybernetic, hormonal-behavioural changes that affect courtship and aggression in males and that those changes are mediated by female response (Sorenson et al. 1997, Davis 2002).

The female-choice and male-costs hypotheses are not mutually exclusive, inasmuch as female benefits and male costs of being paired are component considerations of both hypotheses, but they do make some contrasting predictions. Deriving testable predictions (Table 6.1) that will allow us to distinguish between the two hypotheses, as well as to further develop the female-choice hypothesis, requires consideration of mate choice behaviour, the potential benefits and costs of the three components of the pairing process, and how these may relate to the mating tactics used by waterfowl. Recent theoretical and empirical progress in our understanding of mating tactics will be most relevant to developing predictions of the female-choice hypothesis. First, however, we need to better define the kind of data we can collect in field and experimental studies to measure timing of pairing so that we can then make predictions about how we expect those measures to vary.

How do we measure timing of pairing?

The interacting components of the pairing process indicate that we need to better define how we measure timing of pairing. In their review, Rohwer and Anderson (1988) defined timing of pair formation as the winter month when a majority of birds (75-80%) are observed in conspicuous pair bonds. Such population-level measures were all that were available at that time and, with few exceptions, are still the only kind of data we have to test hypotheses. However, there are four problems with this kind of measure if we attempt to build a more comprehensive theory. First, no distinction is made among individuals of different status. The benefits, costs, and tactics of mate choice leading to pair formation likely differ among individuals that are reuniting, re-pairing (*sensu* Rowley 1983), or forming their first pair bond. An individual's age and previous paired experience and the population demographic structure are important to consider.

Age and previous experience are important because young, newly-pairing individuals likely have less complete knowledge about mate-quality distributions than older, experienced individuals, and because such knowledge can affect the costs of mate sampling and thus the tactics of mate choice used by these different individuals (Dombrovsky and Perrin 1994). In waterfowl, previously paired individuals likely retain some knowledge about mate-quality distribution, especially considering the fact that re-uniting individuals recognize each other after separations of several months. Mate sampling for re-pairing individuals thus probably involves some form of information updating (McNamara and Houston 1980). Demographics are important because the proportion of birds paired at any one time will be affected by the proportion of young birds in the population if new recruits pair at different times than experienced breeders. If young birds generally pair later than older birds, then species with higher mortality rates will appear to pair later only because of the greater proportion of new recruits. For similar reasons, populations under greater hunting pressure may appear to pair later due to disruption of existing pair bonds and a greater proportion of birds re-pairing. Second, no consideration is given to when individuals pair relative to when they begin breeding. This is especially relevant to long-lived birds that may form initial pair bonds one or more years before they first breed, and to non-migratory and tropical species that may breed at irregular times. Third, no measure of the process of pair formation is included. If individuals of one species are more choosy (*sensu* Jennions and Petrie 1997) in selecting a mate, then they may pair later even though they may have begun courtship and mate sampling at the same or even earlier time than a less choosy species. Finally, pair bonds may not always be conspicuous (Armbruster 1982, Green and Hamzaoui 2000). Costs may outweigh the benefits to paired birds of maintaining a pair-bond structure through the winter, for example in diving species that forage in dense flocks. Non-conspicuous pair bonds may exist in such flocks and may explain the rapid rate of “apparent” pair formation that occurs during late spring migration (e.g., Austin et al. 1998). Determining whether pair bonds exist can be difficult for species that forage in flocks and requires detailed observations of marked birds (e.g., Smith 1991).

For future studies I recommend five measures of the timing of pairing: 1) the age at which young individuals first begin courtship (court-age), 2) the number of days or months that newly-pairing or re-pairing individuals are engaged in courtship activity and mate sampling, including trial liaisons, before pairing (court-time), 3) the amount of time per day allocated to courtship (court-rate), 4) the calendar date that pairing occurs (pair-date), and 5) the number of days or months between pair formation and nesting (pair-time). The product of measures #2 and #3 reflects the total time investment into mate sampling, except it ignores mate search and

assessment that may occur during other behaviours (e.g., flying alone, feeding) that are difficult to assign unequivocally to this function, at least in waterfowl. These measures are likely subject to different selection pressures and may require different hypotheses to explain their inter- and intra-specific variation. They are also inter-related and may entail trade-offs, for example between investing in the mate choice process so as to obtain a higher quality partner, and early pairing to reap possible benefits of mate defence during winter or to gain familiarity with a partner prior to breeding.

Mate choice in waterfowl

Do we expect mate choice to be important in waterfowl? Ample evidence from many taxa confirms that mate choice can affect fitness (Andersson 1994, Ligon 1999). Numerous studies have demonstrated direct environmental or phenotypic benefits of mate choice, such as greater nutritional rewards (Thornhill and Alcock 1983), superior breeding territories (Searcy and Yasukawa 1995), lower risk of mortality (Borgia 1981) or parasite infection (Møller 1994), better fertilization abilities (Robertson 1990), better parental abilities (Downhower and Brown 1980), or improved mate co-ordination (Coulson and Thomas 1983). Indirect genetic benefits of greater offspring viability (Reynolds and Gross 1992) or attractiveness (Hedrick 1988) have proved more difficult to demonstrate (Johnstone 1995). Individuals may differ in their optimal mate choices through variation in both direct (e.g., mate compatibility) and indirect (e.g., optimal outbreeding, heterozygosity) benefits (Bateson 1983, Coulson and Thomas 1983, Brown 1997, Jennions and Petrie 1997, Wedekind and Furi 1997). Though there are few data to evaluate the fitness consequences of mate choice in waterfowl (Cooke and Davies 1983), free choice of a mate and a strong pair bond are prerequisite to successful egg production in some species (Bluhm 1985, 1988, McKinney 1992), and patterns of pairing are consistent with theories of optimal outbreeding in a number of studies (Sherrod 1974, Cooke and McNally 1975, Cheng et al. 1979, Kruijt et al. 1982, Bluhm 1985, Owen et al. 1988).

There is abundant evidence that mate choice occurs in waterfowl (Choudhury and Black 1993, Sorensen and Derrickson 1994, Omland 1996), and though there is evidence of choice by both females and males (Wishart 1983, Bossema and Roemers 1985, Choudhury and Black 1993), theory, as described above, predicts generally greater female choice and control of the pairing process, especially in species lacking paternal care and with male-biased sex ratios. Male dominance rank has been correlated with pairing success, suggesting that male-male competition may sometimes constrain female choice (Brodsky et al. 1988), but more often male dominance has been unrelated to female choice (Bossema and Roemers 1985) and high dominance rank has

been a consequence of pairing success rather than a cause (Raveling 1970, Patterson 1977, Lamprecht 1986, Sorenson and Derrickson 1994, Omland 1996, Sorenson et al. 1997, but see Hepp 1989). Observations of mate take-overs by usurping males that successfully drive out previous males (Minton 1968, Ball et al. 1978, Williams and McKinney 1996, van der Jeugd and Blaakmeer 2001) also suggest subversion of female choice. However, even though females in these cases appeared to passively accept the winner of the male-male conflict, usurping males were typically familiar to females and the possibility that females 'invited' the challenging males could not be ruled out (Ens et al. 1996). The most convincing evidence that males can sometimes undermine female choice are the frequent observations of forced extra-pair copulations (FEPC), although fertilization rates from FEPC are low (Dunn et al. 1999), and some authors suggest that females feign resistance to attract and incite competition among males, an unlikely supposition given the high costs to females of resistance (McKinney et al. 1983, McKinney and Evarts 1997).

Potential benefits of mate choice in waterfowl will vary depending on the mating system and type of parental care. Likely evolving from an ancestral mating system of biparental care and perennial monogamy, the family now exhibits a diverse range of mating systems, including perennial, seasonal, and serial monogamy, bigamy, resource- and non-resource-based polygyny, and promiscuity, with variable biparental, uniparental, or, in the case of one parasitic species, no parental care (Kear 1970, Oring and Saylor 1992). As males of most migratory ducks (Anatinae) generally do not participate in parental care nor provide other resources to females, possible benefits of female choice in those species will relate directly to male phenotypic traits such as parasite load, competence in copulation, and quality of mate defence on breeding and wintering grounds, and indirectly to male genotype. In other groups, direct benefits may also include paternal care (Anseranatinae, Anserinae, some Anatinae) and defended resources on breeding or wintering territories (Tadornini, Tachyerini, river ducks, *Bucephala* spp.). Secondary reproductive strategies of FEPCs are pursued by paired males of many monogamous species, but females are not known to solicit EPCs, suggesting that benefits of protecting their chosen pair bond outweigh benefits of amending or complementing their mate choice decisions through EPCs (McKinney et al. 1983, McKinney 1985, McKinney and Evarts 1997). Direct and indirect fitness benefits for females of most species are thus almost entirely dependent on their choice of mate prior to the breeding season, except for re-pairing on the breeding ground that may occur when females re-nest after male desertion (McKinney 1986).

Although theory and empirical evidence suggest greater female than male choosiness and thus control of pairing decisions, benefits to males and potential conflicts of interest between males and females also need to be considered (Trivers 1972, McKinney 1975). Male behavioural

differences and evidence of choosiness by females implies variance in male mate quality and, because there is known variance in female mate quality in relation to age and other phenotypic traits (Rohwer 1992), theory predicts male as well as female choosiness and mate preference functions that are relative to an individual's own quality and expectations of pairing (Parker 1983). Timing of pairing and behaviour after pairing, such as relative defence of pair bond by male and female partners, courtship, divorce, and search for EPCs, may in part relate to the match between preferred and realized mate choice for each partner (Petrie and Hunter 1993, Choudhury 1995, Ens et al. 1996). Variation in that match likely predicts variation in behaviour among pairs, such as higher mate attendance by some males (Ashcroft 1976, Scott 1980). Whereas the male-costs hypothesis assumes that males will incur most of the cost of defence, the female-choice hypothesis expects variation among pairs in the relative share that males and females engage in aggression and defence of the pair bond, and predicts that a male will assume a greater share of defence when paired to a relatively high than low quality female.

Mating tactics and choosiness

Theoretical models of optimal sampling tactics and decision rules used by individuals choosing mates (Janetos 1980, Wittenberger 1983, Real 1990, Johnstone 1997) lead to a number of testable predictions about how timing of pairing in waterfowl will vary in response to variation in phenotypic, social, and environmental factors. Recent empirical studies have demonstrated the relevance of these models (Choudhury and Black 1993, Forsgren 1997, Rasa 1997), and have confirmed that mate choice tactics are responsive to costs (Milinski and Bakker 1992, Slagsvold and Dale 1994, Backwell and Passmore 1996). Variation in the benefits or costs of being choosy thus may affect timing of pairing by influencing the effort females and males are willing to expend pursuing their mate preferences (Jennions and Petrie 1997, Widemo and Sæther 1999).

Under conditions of costless sampling, absolute recall, and an infinite time horizon, individuals should sample all potential mates and choose the best (Janetos 1980). More realistically, mate sampling entails direct costs in terms of time and energy requirements and predation risk, and indirect, opportunity costs of losing access to higher-quality mates (Real 1990). Also, individuals have imperfect knowledge and operate under finite time horizons constrained by optimal times for commencing reproduction (Sullivan 1994, Johnstone 1997). Models of single-sex (Real 1990) and mutual (Johnstone et al. 1996) discrimination indicate that tactics are most responsive to changes in sampling costs and variance in mate quality, and predict greater choosiness as sampling costs decrease or variance in mate quality increases. Duration of searching is expected to increase as individuals become more choosy (Real 1990).

There are several reasons to suspect low sampling costs and high choosiness in waterfowl, especially for females. First, time constraints are minimized by pairing during non-reproductive periods. Unlike many resource-based mating systems where time for mate-choice decisions may be constrained to only minutes or hours (Dale and Slagsvold 1996, Reid and Stamps 1997), waterfowl may take months or even years to choose a mate. Second, in most waterfowl, males bear most search and advertising costs, reducing the costs to females of mate sampling. Third, choosiness is density-dependent (Real 1990), favouring high female choosiness in male-biased populations. Fourth, mate preference functions vary among females, likely increasing the variance in male mate quality and the benefits of choosiness for a particular female, though this has yet to be modeled. Finally, a prolonged period for mate choice decreases the costs of learning and increases the benefits of adaptive search relative to a fixed threshold for mate choice (Mazalov et al. 1996). It also facilitates accurate assessment of specific males relative to overall variation in male quality, and predicts assessment based on traits that vary over time such as behavioural performance or social status rather than fixed morphological traits (Sullivan 1994, Jennions and Petrie 1997). Waterfowl studies have found that both morphological and behavioural criteria are used in female mate choice, but male courtship activity and attentiveness appear to be most important (Cheng et al. 1978, 1979, Bossema and Kruijt 1982, Kruijt et al. 1982, Bossema and Roemers 1985, Klint 1985, Holmberg et al. 1989, Klint et al. 1989, Sorenson and Derrickson 1994). Winter pairing thus may be partially an adaptation to reduce time constraints on mate choice that has been selected because of the benefits of accurately assessing variation in male behavioural characteristics.

What then do mating-tactics models imply for variation in the timing of pairing in waterfowl? I first will consider variation in relation to phenotypic traits and then proceed to consider social and ecological factors. Under time constraints and competition for mates, choosiness is generally predicted to decrease as the time horizon approaches (Real 1990). An interesting exception is that models of mutual choice predict that low-quality individuals will show initial increases in choosiness as the season progresses due to the declining choosiness of high-quality individuals (Johnstone 1997). Assuming that individuals have *a priori* perfect knowledge of the distribution of mate qualities, these models also predict that high-quality individuals will pair earlier and that mating will be closely assortative early in the season, unless costs are high, and less assortative later. It thus may pay low-quality individuals to delay pairing because they may be accepted by higher-quality mates towards the end of the season when higher-quality individuals can no longer afford to be choosy. Models of Johnstone (1997) assume a 1:1 sex ratio, and benefits of delaying pairing by low-quality individuals will be greater for the

limiting sex when sex ratios are biased. In waterfowl, the assumption that individuals have *a priori* knowledge is likely most true for previously paired individuals that have been through the mate choice process at least once, and least true for young, newly pairing birds. Models of adaptive search predict that naive individuals will spend considerable time gaining information about mate-quality distribution before beginning to select a mate (Dombrovsky and Perrin 1994). Assuming that young, naïve individuals are also low-quality individuals, then the models of Johnstone (1997), that assume perfect knowledge, and the models of Dombrovsky and Perrin (1994), that do not, both make similar predictions about the relative chronology of pairing for birds with different experience. If we assume that individuals that are re-uniting represent the highest-quality mate for each other (Rowley 1983, Black 1996), then the models of Johnstone (1997) predict that they should pair as soon as they re-encounter each other. The female-choice hypothesis thus predicts that re-uniting pairs that have previously completed the mate choice process will pair earliest, as measured by pair-date, while young individuals will require time for mate sampling and pair later. Experienced birds that have lost a mate should require less time for mate assessment than young birds because they have already been through the mate choice process and will pair at intermediate dates. The corollary to this prediction is that court-time will be greatest for young birds and least for re-uniting birds.

What are the predictions of the male-costs hypothesis in relation to individual experience? For males, predicted trends would be similar, though the mechanism would differ, to those of the female-choice hypothesis, i.e., young males would pair later than experienced males because they are less able to afford the costs of mate defence. This trend for males would translate into a similar trend for females when sex ratios are balanced, assuming that mating is assortative, but predictions of the male-costs and female-choice hypotheses differ when sex ratios are male biased. Some interpretation is required to see why this is so. If the cost-benefit balance favours later pairing by some males (e.g., young or low-quality individuals), in male-biased populations of most migratory ducks it is variation in the timing of pairing of the limiting sex that we need to explain. If females obtain benefits of increased foraging efficiency and survival due to male vigilance and defence, then young females should be willing to pair earlier than, or at least at the same time as, experienced females because young females likely have poorer foraging skills than older females and thus would gain greater benefit by increased foraging efficiency. When sex ratios are male biased, there should be a pool of previously paired males, whose mates have died, that are as equally capable of pairing early to young females as those that are re-pairing or re-uniting with surviving, experienced females. This situation should pertain if rates of female recruitment and adult female mortality are similar, which we can assume if populations are stable,

and given higher female than male mortality for breeding birds, which is generally thought to account for male-biased sex ratios in waterfowl (Sargeant and Raveling 1992, Cooke et al. 2000). Thus, the male-costs hypothesis predicts that young females will pair at the same time as experienced females when sex ratios are male biased. All studies that have investigated age-related differences in pairing chronology have found that young females pair later than older females, even in species with male-biased sex-ratios (Stotts 1958, Stotts and Davis 1960, Spurr and Milne 1976, Blohm 1982, Wishart 1983, Heitmeyer 1988, 1995), though it is unknown how this trend relates to female or male choosiness.

Early authors suggested that possible benefits of early pairing were to give birds time for mate testing (Weller 1967, McKinney 1975, Afton and Sayler 1982, Wishart 1983) or to gain familiarity with a partner (Gorman 1970, Milne 1974, Choudhury et al. 1996). Rohwer and Anderson (1988) rejected mate testing as a hypothesis to explain variation in timing of pairing because they reasoned it predicted early pairing for all birds. However, the benefits of mate testing likely vary in relation to relative parental investment by the two sexes and duration of the pair bond. More importantly, if mate testing is viewed as part of the mate choice process, then extended periods required for mate testing may delay rather than accelerate pairing chronology. Variance in male mate quality increases with increasing parental investment by males, favouring greater choosiness by females (Parker 1983). Choosiness by males likely also increases with increased male parental investment. The benefits of choosiness likely increase for both sexes with increasing duration of the pair bond because the fitness benefits of mate choice accrue over multiple breeding seasons. The female-choice hypothesis thus predicts greater investment in the mate-choice process (higher court-time and/or court-rate) with increasing paternal care or increasing duration of the pair bond. Time spent gaining familiarity with a partner (pair-time) also should increase with increasing paternal care because the benefits of mate co-ordination are likely greater when parental care is shared. Though individuals may have to trade-off benefits of increased court-time and increased pair-time if constrained by an approaching breeding season, both measures can be increased by beginning the pairing process earlier in the non-breeding season or at a younger age (i.e., reducing court-age), or by deferring breeding one or more years, as do swans and geese with biparental care, and most other species of waterfowl with long-term pair bonds.

Because court-time and court-rate are component measures of the total time invested into courtship and mate sampling, we might expect an inverse relationship between them prior to pairing if the optimal level of investment into courtship was similar for all individuals. More likely, optimal time investment differs among individuals, and higher quality individuals may be

able to afford a higher court-rate, as suggested by Rohwer and Anderson (1988). However, this would still result in an inverse relationship between court-time and court-rate if individuals begin courtship at the same time and if high-quality individuals pair earliest as predicted by Johnstone (1997). The female-choice hypothesis thus predicts that court-time and pair-date of females, but not necessarily males, will be negatively related to the amount of time per day that they allocate to courtship and mate sampling, i.e., females that engage in courtship at a higher rate will have shorter court-time and will pair earlier. The male-costs hypothesis predicts the same relationship for males but not for females, because all females are assumed to be willing to pair as early as males are capable.

Social and ecological factors

Approaching the study of pairing chronology from a mate choice perspective leads to a number of hypotheses that relate timing of pairing to social and ecological factors, and a reinterpretation of previous results showing that timing of pairing is responsive to variation in ecological conditions. Studies demonstrating that decreased food availability and increased energetic costs due to cold weather delay pairing chronology (Brodsky and Weatherhead 1985, Hepp 1986, Pattenden and Boag 1989, Demarest et al. 1997) generally have been interpreted as support for the male-costs hypothesis (Rohwer and Anderson 1988). As pointed out by Pattenden and Boag (1989), an alternative explanation is that decreased food availability affects pairing because males in poorer body condition are less attractive to females choosing mates. This assumes that females have additional information on male mate-quality distribution, and would explain why pair formation in Mallards and Black Ducks was later and more liaisons were temporary for birds on restricted than *ad libitum* diets even though the amount of courtship by males did not differ (Hepp 1986, Pattenden and Boag 1989). Reduced courtship activity in poorer habitats reported by Brodsky and Weatherhead (1985) may also have been associated with female mate choice, if the quality of males differed among habitats, which seems likely (Fretwell 1972), and because male courtship intensity is in large part governed by female response (Weidmann and Darley 1971, McKinney 1992), although cessation of most activity during extreme conditions at the poorest habitat was likely due to thermoregulatory costs (Brodsky and Weatherhead 1985). Similar differences in male quality may occur whenever habitat or latitudinal segregation occurs (Gauthreaux 1978, Nichols and Haramis 1980, Alexander 1983, Ketterson and Nolen 1983) and may partly explain why pairing chronology was delayed and dominance relations were reversed, with females dominant to males, for dabbling ducks wintering at milder, southern latitudes (Thompson and Baldassarre 1992).

Sex-segregation at local or latitudinal scales due to behavioural dominance (Gauthreaux 1978, Alexander 1983) or habitat specialization (Marsden and Sullivan 2000, Iverson 2002) has been considered as a reason for late pairing in some waterfowl species (Oring and Sayler 1992, Kahlert et al. 1998, Coupe and Cooke 1999). However, sex-segregation is never complete and we need an explanation for why pairing does or does not occur among the males and females that do winter together. Also, individual decisions about habitat use and timing of pairing are likely inter-related and should be considered together. As suggested above, differences in age, body size, or competitive ability of males wintering farther south or in poorer habitats (Anderson and Timken 1972, Nichols and Haramis 1980, Nichols et al. 1983, Hepp and Hines 1991) may account for delayed and low rates of winter pairing in those areas because such males are less attractive to females. This does not explain why, in some Aythyini and Mergini species, males and females in northern areas also pair late (Weller 1965, Kahlert et al. 1998, Coupe and Cooke 1999), a question I will return to in the light of comparative data. In general, the above considerations suggest that if environmental conditions or differences in habitat use reduce the phenotypic quality of potential mates in an area then pairing will be delayed because individuals will find it more costly to satisfy their mate preferences and may be unwilling to pair if there are better options elsewhere or at a later date. This assumes that individuals use either a fixed threshold tactic or that they have prior information on the distribution of mate quality.

Population social structure may influence timing of pairing. Previous theories on the timing of pairing that focused on trade-offs to males (Afton and Sayler 1982) predicted that greater male-biased sex ratios would lead to earlier pairing because of increased male-male competition (Rohwer and Anderson 1988). The female-choice hypothesis makes the opposite prediction. The degree of female or male control of pairing chronology will vary depending on the relative benefits and costs of mate choice, particularly opportunity costs, to each sex or individual. Individuals may incur opportunity costs of losing access to high-quality mates by exercising choice and delaying pairing. Male-biased sex ratios reduce opportunity costs to females, resulting in greater female control and choosiness (Real 1990, Jennions and Petrie 1997) and thus greater investment in courtship and mate sampling, and, for species on similar seasonal cycles, later pair dates, with increasing male bias in the sex ratio. Hepp and Hair (1984) found just such a relationship in their study of six Anatini species. Data used by Rohwer and Anderson (1988, p. 208, Table 5), which included data from Hepp and Hair (1983, 1984), to test the relationship between sex ratio and pairing chronology are also consistent with predictions of the female-choice hypothesis. Considering *Anas* and *Aythya* species separately, Rohwer and Anderson found non-significant, negative correlations between sex-ratio and rank pairing order.

Combining these groups results in a significant, negative correlation ($r_s = 0.58$, $P = 0.02$, $n = 16$), suggesting that pairing is later in species or populations with greater male-biased sex ratios.

Up to this point I have considered how ecological and social conditions affect an individual's pairing decisions. We should also expect individuals to show adaptive changes in behaviour that partially shape their social and ecological environment to facilitate pairing (Møller 1994, Höglund and Alatalo 1995). How individuals are distributed may affect the costs of choosing a mate and consequently the timing of pairing (Jennions and Petrie 1997). Most waterfowl are gregarious on their wintering grounds, but some are widely scattered in small groups (e.g., species in tribe *Mergini*). Individuals looking for mates in dispersed populations will incur greater movement costs and may find it difficult to compare the quality of potential partners. This will be especially true in species with long-term pair bonds and late in the pairing season because as established pairs are removed from the mating pool the number and density of potential partners declines. As in lek-mating systems, females may prefer larger aggregations where potential mates can be sampled concurrently (Emlen and Oring 1977, Bradbury 1981, Lank and Smith 1992). This could lead to aggregations of unpaired birds at mobile courting arenas (Johnsgard 1994) or at specific locations that would serve as "lekking" sites (Petrie 1988). Winter spacing patterns of waterfowl thus may be partially shaped by sexual selection.

If birds do aggregate in courting arenas to reduce sampling costs, then the ratio of unpaired to paired birds and, in populations with male-biased sex ratios, the ratio of males to females, will be greater in larger groups at courting arenas than in other groups. Male bias in the sex-ratio will be higher at courting arenas because the ratio of males to females that are aggregating at these arenas will correspond to the operational sex ratio (Emlen and Oring 1977), and, if some females are paired in male-biased populations, and all unpaired birds are part of the pool of potential mates, then the operational sex ratio will always be greater than the population sex ratio. The operational sex ratio is unlikely to vary among groups or sites unless unpaired females are assorted according to their attractiveness to males. If larger groups or "lekking" sites do function as courting arenas, and because we expect increased choosiness with decreased search costs (Real 1990), the female-choice hypothesis also predicts that courtship by unpaired birds will be more frequent in larger groups at courting arenas than in smaller groups, and unpaired birds will spend more time in courtship and will sample more potential mates at 'lekking' sites than elsewhere. If 'lekking' occurs at fixed sites, then unpaired birds will come to those sites primarily for the purposes of mate sampling and not for feeding.

Adaptive changes in spacing behaviour related to pairing have not specifically been investigated in waterfowl. However, some support for the idea comes from studies of Wood

Ducks (*Aix sponsa*), that are typically dispersed in small groups, showing that group size and male bias in the sex ratio were greater for courting groups in the fall (Armbruster 1982). Northern Pintails (*Anas acuta*) also exhibited greater courtship in larger groups, but at a much larger scale, with most courtship occurring in groups >5,000 birds (Miller 1985, Migoya et al. 1994).

Individuals searching for mates could benefit from localized food abundance that attracts aggregations of conspecifics. Individuals of many species often show adaptive changes in their distribution and spacing behaviour, and time their life history events to coincide with predictable but ephemeral food abundance (e.g., Botton et al. 1994). Benefits of exploiting such resources are generally assumed to be nutritive, whether for foraging animals themselves or for their offspring. Little attention has been paid to possible indirect benefits of ephemeral food abundance that may be associated with changes in time budgets and the reduction or elimination of intra-specific competition for food. Superabundant and easily exploitable food should decrease the time required for foraging and allow individuals to allocate more time to other behaviours that affect their fitness such as courtship and mate sampling. In addition, lack of competition for food may change a population's social structure by allowing individuals to join optimal sized groups for reasons unrelated to finding food.

Culture can have important influences on mate choice decisions. The role of imprinting and early social experience in determining mate choice preferences has long been recognized (Cooke and McNally 1975, Todd and Miller 1993). Recent social experience also has been found to influence mate choice preferences (Bakker and Milinski 1991, Dugatkin and Godin 1992, Collins 1995). Models of adaptive search suggest that when there is spatial or temporal variation in mate quality, individuals choosing mates benefit from a learning strategy, unless sampling costs or time constraints are high (Mazalov et al. 1996). Mate-choice copying has been demonstrated in a number of fish and bird species (Andersson 1994, Patriquin-Meldrum and Godin 1998) and may be a means for inexperienced or more energetically constrained individuals to reduce sampling costs (Dugatkin and Godin 1992). Displays of young male waterfowl are less developed than adults (Dane and Van der Kloot 1964, Korschgen and Fredrickson 1976, Afton and Sayler 1982) and young waterfowl may accompany adult courting birds to gain exposure to and experience in courtship so as to improve their courtship skills, as well as to gain the benefits of learning about mate-quality distributions to improve future mate-choice decisions (Mazalov et al. 1996). If these are benefits, we should expect immature birds to be involved in courtship and to show similar adaptive changes in spacing behaviour as those predicted above for unpaired, courting adults.

Harlequin Ducks

I investigated several aspects of the female-choice hypothesis using data on Harlequin Ducks. Harlequin Ducks winter along marine rocky shores, generally in small groups of 2-20 birds (Robertson and Goudie 1999). They have a monogamous mating system with no paternal care, male desertion during incubation, form multi-year pair bonds on the wintering grounds (Gowans et al. 1997, Smith et al. 2000), show age-specific differences in the timing of pairing (Robertson et al. 1998), have a male-biased sex ratio of 1.5:1 in the Pacific Northwest (Rodway et al. 2003a), and, in males, have a distinct Alternate I plumage that makes males identifiable as first-year birds throughout their first winter (Smith et al. 1998). Feeding takes a large proportion of their time during winter months (Goudie and Ankney 1986, Torres et al. 2002). Their distribution on the Pacific coast changes in the spring when a large segment of the population aggregates at sites where Pacific herring (*Clupea pallasii*) spawn (Rodway et al. 2003b). Herring spawn provides a predictable, superabundant food that is available to waterfowl for three-to-four weeks in March-April (Haegele 1993). Pair bonds are often formed at this time in a number of waterfowl species, including Harlequin Ducks (Rohwer and Anderson 1988, Hohman et al. 1992, Robertson et al. 1998). Harlequin Ducks are easy to observe and can be captured during their fall moult period so that individuals can be uniquely marked for behavioural observations. They are thus an appropriate species on which to test hypotheses about mate choice and timing of pairing, including the effects of spacing behaviour, time budgets, and seasonal food abundance in a natural population.

The study will address four inter-related aspects of the female-choice hypothesis that have been developed above. Alternative working hypotheses (Chamberlain 1897) are considered in each case.

1) Timing of pair formation is primarily determined by female mate-choice decisions. This should be particularly true of Harlequin Ducks because of their male-biased sex ratio and lack of paternal care. The main alternative hypothesis is the male-costs hypothesis reviewed above. Predictions of the two hypotheses will be tested by comparing pairing chronologies by sex, age, and previous pairing history, and by comparing time-activity budgets and rate of aggressive interactions in relation to sex, age, and paired status. Predicted conflict of interest between pair members will be assessed by considering possible reasons for divorce and by measuring variation in the relative share of pair-bond defence performed by female and male partners. As a logical extension of the male-costs hypothesis I also consider potential benefits to females of being paired, other than nutritional benefits and reduced harassment, including more time for feather maintenance and resting. Costs to males may also include less time for maintenance and resting.

2) Pairing individuals aggregate in a fashion similar to 'lekking' to reduce costs of mate sampling. Aggregations may occur at mobile arenas (Johnsgard 1994) or at fixed sites. Alternative hypotheses are that the distributions of unpaired and paired birds differ because unpaired birds are excluded from preferred areas by higher-quality or more dominant, paired birds (Fretwell and Lucas 1970), and that there is neither aggregation nor dispersion of unpaired birds. Other reasons for aggregation (e.g., predator avoidance, Wittenberger and Hunt 1985) would not predict segregation based on paired status and will not be considered.

3) Immature birds benefit from observing the courtship behaviour and mate choices of older birds and will be involved in courtship and show similar aggregative behaviour for courting and mate sampling as unpaired adults. Alternatively, immature birds will show no interest in courting birds or will be excluded from courtship groups by adult birds.

4) Herring spawn will be attractive to pairing birds because it provides abundant food, reducing the time required for foraging and allowing birds to allocate more time to pairing behaviour, and eliminates intra-specific competition for food, allowing birds to join larger groups for the purpose of mate sampling. Joining larger groups at this time may also reduce predation risk associated with courtship activity. An alternative hypothesis is that birds come to herring spawn solely for nutritional benefit. Time spent feeding may be less but time spent courting and the number of potential mates sampled will not differ between sites with and without spawn if birds come solely for nutritional benefit. If coming to spawn provides more than nutritional benefits to unpaired birds then unpaired birds will be more likely to move to spawning sites than paired birds, and the ratio of unpaired to paired birds and the ratio of males to females will initially increase at sites with spawn, and will be higher at sites with than without spawn at that time (operational sex ratio will not differ among sites). Other reasons unpaired birds may be more likely than paired birds to move to herring spawning sites will be considered in the Discussion. If aggregating for mate sampling is an indirect benefit of herring spawn, then unpaired birds will be more aggregated than paired birds (I assume that other benefits to aggregation would be similar).

METHODS

Marking and ageing

Harlequin Ducks have been caught in drive traps during moult in August and September and individually marked at five locations in the Strait of Georgia in 1993-2000 as part of a joint effort between Canadian Wildlife Service and Simon Fraser University (details in Robertson et al. 1998, Wright and Clarkson 1998, Rodway et al. 2003b). Some birds wintering in the Strait of Georgia have been banded as adults or young by various researchers working on breeding streams

in British Columbia, Alberta, Washington, and Montana (e.g., Smith et al. 2000). About 3500 birds have been marked. Since 1994, all captured birds have been marked with unique, alphanumeric coloured leg bands. Captured birds were sexed and aged by plumage, cloacal examination, and the depth of the Bursa of Fabricius (Kortright 1942). Four age classes were discriminated: first, second, and third year, and after third year (Smith et al. 1998, Mather and Esler 1999). Birds were considered first- (1Y), second- (2Y), and third-year (3Y) throughout their first, second, and third winters, respectively, and after-third-year (A3Y) afterwards. In some cases I distinguish between first-year (1Y) and after-first-year (A1Y) birds.

Unique, shape-colour-combination nasal disks were also put on 457 birds, most in 1998-99 at three banding sites in the northern Strait of Georgia, plus a few in 1997 and 2000. Nasal tags decreased pairing success of males and increased mate change in previously paired females but did not affect timing of pairing or other behaviours (Regehr and Rodway 2003). I thus used all marked birds to determine pairing chronology. I assumed that effects of nasal tags on males would not affect pairing success of females because sex ratios in this large study population are biased 1.5:1 in favour of males (Rodway et al. 2003a) and thus effects would be entirely compensatory. Effects on females may have increased the divorce rate observed in this study.

Pairing chronology

Pair status was judged based on observed behaviour. If a male and female remained in close proximity, behaved synchronously, and exhibited defensive reactions to intruders they were called paired (Gowans et al. 1997). Individuals alone or that showed no particular association with a potential partner were called unpaired. Pair status was considered confirmed for an individual if it was behaving paired or unpaired for most of an observation session of 30 min or more, or if it appeared consistently paired or unpaired at least twice when it was observed for shorter periods of time. An exception was made for birds re-uniting with a known mate that they had been seen paired with in the previous year. Only one observation of being paired was required in that case. Status was called unknown if behaviours did not clearly indicate paired status during an observation. For birds that were confirmed paired, the timing of pair formation (pair-date) was taken as the first date on which they were observed paired. Individuals were included in the sample used to determine pairing chronology if they paired before November, or, if they paired later, only if they were observed not paired no more than 30 d prior to when they were first observed paired. This method ensured that estimates of pairing chronology were not biased by birds that were first seen paired later in the winter but could have paired much earlier. All birds pairing before November were included because females are completing their post-

breeding moult during September and October (Robertson et al. 1997), few initiate pairing until October (Gowans et al. 1997, Robertson et al. 1998), and many of those pairing in late September and October were not observed prior to when they were first seen paired. I thus assumed that my estimates for timing of pair formation were accurate within 30 d for all birds.

Proportions of various sex- and age-classes paired at the end of winter were determined using the same criteria listed above for confirming pair status but including only observations made in March, April, and May, which is when birds are leaving for the breeding grounds (Robertson and Goudie 1999). Not including observations earlier than March avoided biases caused by the fact that my criteria make it is easier to be sure that a bird is paired than not paired at the end of the season. Even so, some birds called unpaired may still have paired that spring and my estimates of proportion paired are conservative.

For birds in each age-sex class, I used the pairing chronology determined as described above, adjusted by the total proportion paired at the end of the winter, to estimate the relationship between proportion paired and date. This method would accurately portray this relationship as long as I was equally likely to detect pairing events throughout the winter. Fewer observations made during inclement winter weather may have reduced my chance of confirming pair status, but on the other hand birds are more dispersed in small flocks during winter, making it easier to confirm pair status than when they are in large roosts for extended lengths of time as often occurs in spring. I used a second method to determine proportions of known-aged birds paired at different times during the winter to help corroborate that the patterns I was observing were unbiased. For each month I compared total numbers of marked birds identified as paired or not paired within that month. I relaxed the criteria for confirming paired status to obtain adequate sample sizes, accepting one or more consistent observations of pair status per individual. Requiring only one observation made it more likely that errors were made in assigning pair status, but I assumed that within a month biases towards more paired or more unpaired birds were unlikely, especially because pair status was typically quite obvious.

Behavioural observations

Continuous observations of focal birds (Altmann 1974) were conducted throughout daylight hours to determine time budgets, type and frequency of social interactions, number of potential mates sampled, and group sizes and composition. Thirty-minute observation sessions were conducted on random marked and unmarked individuals in two areas, Hornby Island (49°33'N 124°40'W), in the northern Strait of Georgia, and White Rock (49°01'N 122°51'W), in the southern Strait of Georgia, in February, March, and April of 1998 and 1999 and at White

Rock from October 1999 to April 2000. Between October 1999 and April 2000 at >20 locations in the northern Strait of Georgia, I shortened observation sessions to 5 min to make it logistically practical to monitor pairing chronology and behaviour of randomly chosen birds as well as a large number of young birds that were caught and nasal-tagged in August and September 1999.

Behaviour of nasal-tagged birds did not differ from that of unmarked birds (Regehr and Rodway 2003) and observations of both marked and unmarked birds were combined to determine daily time-activity budgets. I scored the Alternate I plumage of a small sample of 1Y males on a 5-point scale from juvenile-like to adult-like (details in Rodway et al. 2003a), to determine whether birds in more adult male-like plumage were more likely to engage in courtship than birds with more juvenile-like plumage.

Behavioural observations were initially categorized into two location categories and seven date categories. Location categories included two areas where spawning by herring occurred, Hornby and Denman Islands and the Vancouver Island shoreline from Qualicum to Little River (WITH), and two areas where herring spawning did not occur during the study, White Rock and the Vancouver Island shoreline from Little River to Campbell River plus the south end of Quadra Island (WITHOUT) (locations described in Rodway et al. 2003a,b). Date categories were October, November, December, January, February through to the beginning of herring spawning in early March each year (February), the 3-week period in March after herring spawning began each year (March), and from the end of the spawning period at the end of March through April (April). Preliminary analyses indicated no consistent differences among location categories except during herring spawning. For subsequent analyses I thus combined data from all locations for all date categories except during herring spawning, and used a single date-location variable with 8 categories: October, November, December, January, February, March without spawning, March with spawning, and April. For analyses where sample sizes were reduced (e.g., comparisons among known-age birds) I collapsed data into fewer date-location categories: 1) October and November (FALL), 2) December and January (WINTER), 3) February through to the beginning of herring spawning in early March each year (BEFORE), 4) the 3-week period after herring spawning began each year but at sites where herring spawning did not occur (DURING-WITHOUT), 5) the 3-week period after herring spawning began each year at sites where herring spawning did occur (DURING-WITH), and 6) from the end of the spawning period through April (SPRING).

Duration to the nearest second of feeding (diving, dabbling, and surface feeding), moving (swimming and flying except during courtship), preening (preening, bathing, and wing flaps), resting (on the water or on land), courtship (on water or land, or in flight), predator avoidance

(alert posture with extended neck, flushing in response to predators or other disturbance, and fleeing from other, non-predatory species), and agonistic (chasing, fleeing, mate-guarding, and any other aggressive interactions that lasted for 1 s or more) behaviours, and frequency of agonistic interactions were recorded during each observation session. Mate-guarding included times when a paired male actively placed himself between his mate and approaching males, and times when a paired male followed his mate as she was being pursued by other males but was not always between his mate and the courting males. I defined five types of agonistic displays in order of increasing intensity (modified from Inglis et al. 1989, 2000): the *head-nod* (elliptical upward and forward movement of the head), the *bill-poke* (neck extended horizontally with bill closed), the *bill-gape* (neck extended horizontally with bill open), the *chase* (neck extended plus rush across the water at the target), and the *trounce* (jumping on the target bird and usually driving it under the water). I excluded low-intensity, intra-pair displays (head-nods and slight head-jerks) that were used during copulation and during times when pairs were initiating different behaviours, such as leaving a roost or taking flight, and included only aggressive displays (chases) between mates that were used in relation to other birds (typically the male chasing his mate away from other males).

I present both the proportion of diurnal time and the absolute amount of time per day spent in each behaviour, because proportion of time best indicates time constraints relative to time required for feeding, while absolute amount of time best indicates seasonal changes in total time spent in each activity. Absolute amount of time that birds spent in different behaviours per day was calculated by multiplying proportions of time spent in those behaviours during observation sessions by the estimated number of daylight hours that birds were present in nearshore habitat. Numbers of daylight hours per day that birds were present was calculated as the time between sunrise and sunset adjusted by the median arrival or departure times relative to sunrise or sunset determined by Rodway and Cooke (2001) for each relevant date category. Sunrise and sunset times for the study area were obtained from the US Naval Observatory Astronomical Applications Data Services (US Navy 2000).

Spacing behaviour

Repeated surveys of birds throughout my study areas (methods described in Rodway et al. 2003a,b) were used to determine variation in group size and sex ratio. Birds were considered to be in separate groups if they were separated by ≥ 10 m. I assessed changes in overall group size using unweighted means, and also using means weighted by the number of birds in each group to

better reflect the proportion of total birds in each group size. Behaviour of birds in different groups was determined by instantaneous scan sampling (Altmann 1974).

Systematic sampling of females was used to compare proportions of females that were paired among different sized groups and between locations where herring did and did not spawn. Group size for these females was determined when they were first sighted and thus females that were alone sometimes turned out to be paired. I attempted to determine pair status of all females in small groups containing no more than 5 or 6 females, but in larger groups I used systematic sampling with a random start, varying the interval between females sampled according to the size of the group. For example, for a large group of 2000 birds aggregated at herring spawn, I first drew a random number between 1 and 5 to select the first female, then, scanning across the group with a telescope, sampled every 5th female encountered in the scope field after the first, aiming for a sample size of about 100 females. For a smaller group of about 30 birds I sampled every 2nd female. I observed each female selected until I was confident of their pair status or until I had observed them for 5 min. Females that I lost track of before I could determine their pair status, or those that I was uncertain about after 5 min, were excluded from the sample.

Sex and age ratios

Sex ratio was defined as the ratio of total males to total females. To analyze the relationship between sex ratio and group size, I converted sex ratio to the proportion of birds in a group that were male because sex ratio is constrained by group size. Male age ratio was the ratio of first-year to after-first-year males (Rodway et al. 2003a). I counted birds at locations where herring did and did not spawn (see above) during 2-week intervals from 4 weeks before to 8 weeks after herring spawning began to compare changes in sex and age ratios associated with herring spawn. I considered counts from different years, 1998-2001, to be independent and combined them for analyses (*G*-tests). Conclusions were the same if years were considered separately.

Inter-specific comparisons

I compiled available data on pairing chronology in waterfowl by searching BIOSIS Previews 1969-2003, and by tracking down published and unpublished literature referenced within major works on the subject and within those found by searching BIOSIS.

Analyses

Kruskal-Wallis and Mann-Whitney *U*-tests were used to compare pairing chronologies among different classes of birds. Proportional data were arcsine transformed to satisfy assumptions for parametric tests, except proportion of males in groups, which did not require transformation. Variances of mean statistics from 5 min and 30 min behavioural observation sessions were compared using *F*-tests to determine the appropriateness of combining those data for analyses. *F*-values were calculated as the quotient of 5-min over 30-min variances because I expected variances to be greater from 5 than 30 min sessions. Variation in activity budgets was analyzed using full factorial ANOVA. Interaction terms were dropped from final models if they were not significant. The date-location variable was included in all analyses comparing time budgets among different classes of birds to control for differences due to date and the availability of herring spawn. I combined sex and paired status into a single variable (sex-pair) with four classes to test for differences among unpaired and paired females and males. Unadjusted means \pm SE are reported for date-location categories, and adjusted means from a 2-way ANOVA including date-location are reported for sex-pair classes. Tolerance for Type I error was set at 5% for all tests.

RESULTS

Pairing chronology measured by pair-date

Sex and age differences

There was good agreement between my two measures of pairing chronology (Table 6.2, Fig. 6.1) except when I had sample sizes too small to adequately assess proportions of different age classes paired within a month (Table 6.2). Some females formed initial pair bonds in the spring of their first year and almost all paired by March and April of their second year. No males were observed paired in their first year ($n = 109$). A few males began pairing in March of their second year but the majority did not pair until they were >3 yr old. Older females formed or re-established pair bonds earlier than younger females (Kruskal-Wallis $H_3 = 35.4$, $P < 0.001$; all pairwise comparisons: $P < 0.05$ with Bonferroni corrections). Most females >2 yr old and most males >3 yr old, many of which would be re-uniting birds (see below), formed pair bonds in October and November. About 40% of 2Y females paired during mid-winter from November to February and 50% paired in March and April.

Re-uniting and re-pairing birds

Mate fidelity from year to year was high. For pairs for which I knew the identity of both partners, and both were known to be still alive the next year, I had 4 records of divorce and 126 records of re-uniting, representing a divorce rate of 3.1% per year. Most records were of A3Y birds, but I did have 3 records of females and 1 record of a male paired as 2Y birds and re-uniting with their mates the next year. Some pairs were known to be together for at least 5 years. Divorced pairs were known to have been together for at least 1 (2 pairs) or 2 (2 pair) years before divorcing. Females of the former two pairs were 4 yr old, the latter were at least 6 yr old, and all males were at least 7 yr old when they divorced. Though I could not determine the cause of divorce or which partner initiated the divorce, the subsequent history of the birds involved provided some clues and suggested that either females or males may initiate divorce. Two of the divorced females and none of the divorced males were marked with nasal disks. Nasal disks had been on one younger and one older female for over a year, and thus, if the disks were responsible for divorce, their effect was delayed one year. Also, the older female lost her nasal disks before divorcing, and, in contrast to the rest of the individuals that remained in their same wintering location following divorce, moved to a different wintering site 150 km away. The former mate of this female consorted with two other females within the 3-week period after being left in mid-March but remained unpaired the next winter. This suggests that this female initiated divorce by moving to a different wintering location. My finding that one member of a former pair may move to a different wintering area suggests that some divorces may have been undetected because one partner may have moved outside my study areas and thus was not known to be alive. One male that was at least 8 yr old and had been paired to a no-nasal, 3Y female for one year, was, following divorce, paired for at least two consecutive years to a female that also was at least 8 yr old. Assuming that reproductive success increases with female age (Rohwer 1992), this suggests that this male may have secured a better mate and may have been the partner that initiated the divorce.

Re-uniting pairs re-established pair bonds in late September, October, and early November, suggesting that those that paired later (Fig. 6.1) were birds that were finding new mates. There were few cases in which I could be sure a bird had lost its mate, so I compared pair dates for birds known to be re-uniting and birds for whom I did not know the fate of their former mates. This latter group included previously paired birds that had lost or divorced their mates and were re-pairing with new partners, but also may have included re-uniting birds whose mates were not marked or that I had not observed previously. I therefore assume that differences between the two groups were due to later pairing of birds re-pairing with new mates. Estimated differences

will be conservative because some re-uniting birds may have been included in the latter group. Mean (\pm SD) pair dates of A3Y females (17 Oct \pm 12 d, $n = 39$) that were re-uniting with former mates were earlier than pair dates of A3Y females (16 Nov \pm 47 d, $n = 57$) and 3Y females (26 Nov \pm 50 d, $n = 13$) for whom I did not know the fate of their former mates, and of 2Y females (19 Feb \pm 57 d, $n = 13$) that were pairing for the first time (Kruskal-Wallis $H_3 = 35.4$, $P < 0.001$; pairwise comparisons: $P_s < 0.003$, except $P = 0.2$ for 3Y vs A3Y females for whom I did not know the fate of their former mates). Mean pair dates of A3Y males (17 Oct \pm 14 d, $n = 32$) that were re-uniting with former mates were also earlier than pair dates of A3Y males (3 Dec \pm 66 d, $n = 30$) for whom I did not know the fate of their former mates ($H_1 = 9.8$, $P = 0.002$).

Estimated differences in pair-dates of re-uniting and re-pairing birds may be conservative because there was evidence that some established pairs re-unite, at least briefly, before moult has been completed. One known pair, last seen together on their wintering ground in April, were seen acting paired again on 26 July. At this time the male was in basic plumage and was flightless, and the female had just returned to the coast and had not yet initiated moult. After this brief rejoining, these birds remained in the same general area but behaved unpaired until 14 October, after which they behaved paired for the rest of that winter.

Court-time and court-rate

Start and duration of courtship

I was unable to confidently estimate the dates when particular individuals began courtship because observations were infrequent and courtship was intermittent. As a surrogate I estimate population-level trends for different sex and age classes. To estimate this I first determine at what age birds began courtship, and then consider whether for each class of birds the frequency of courtship changed through the winter, which should indicate whether courtship was a continuous process after it began or whether it was interrupted during some part of the winter.

Earliest observations of 1Y females being courted were in March. Three of 7 first-year females observed in March were being courted and it is likely that a majority were courted at this time because observations of specific individuals were infrequent. Frequency of courtship by 1Y males increased through the winter: proportion of observation sessions with courtship was greater during February-April than October-January ($G_2 = 4.2$, $P = 0.04$); and 1Y males comprised 1.3% ($n = 468$), 1.7% ($n = 595$), 4.8% ($n = 207$), 4.5% ($n = 374$), and 4.5% ($n = 161$) of all males observed courting during the date periods fall, winter, before, during, and spring, respectively ($G_4 = 14.5$, $P = 0.006$). I could not determine whether differences by date were due to increasing frequency of courtship by all 1Y males or by increasing proportions of 1Y males engaging in

courtship. Number of 1Y males for which I scored plumage and that engaged in courtship (2 birds each with scores 2, 3, and 4) was too small for analyses, but trends suggested that plumage did not affect whether a 1Y male participated in courtship.

Courtship by all sex and age classes, except 1Y females, was observed in all months of the study beginning in October. Although the amount of time spent in courtship varied among date categories (see below), there was no indication, except for 1Y birds, that the likelihood of engaging in courtship varied through the winter. The proportion of observation sessions during which an unpaired individual engaged in some courtship was less for 1Y (9%, $n = 47$) than 2Y (32%, $n = 71$), 3Y (34%, $n = 47$), and A3Y (45%, $n = 67$) females ($G_3 = 19.7$, $P < 0.001$), and less for 1Y (9%, $n = 68$) than 2Y (65%, $n = 17$), 3Y (54%, $n = 46$), and A3Y (52%, $n = 208$) males ($G_3 = 61.5$, $P < 0.001$). There were no significant differences in these proportions among unpaired 2Y, 3Y, and A3Y females ($G_2 = 2.5$, $P = 0.3$) and unpaired 2Y, 3Y, and A3Y males ($G_2 = 2.2$, $P = 0.3$). Excluding 1Y birds, I found no differences in the proportion of observation sessions with courtship among the months October – April for unpaired females ($G_6 = 3.0$, $P = 0.8$), unpaired males ($G_6 = 4.6$, $P = 0.6$), paired females ($G_6 = 6.6$, $P = 0.4$), or paired males ($G_6 = 1.2$, $P = 1.0$). Excluding 1Y birds and combining months, the proportion of observation sessions during which courtship occurred was greater for unpaired (37%, $n = 185$) than paired (21%, $n = 406$) females ($G_1 = 15.7$, $P < 0.001$), for unpaired (58%, $n = 246$) than paired (7%, $n = 115$) males ($G_1 = 100.7$, $P < 0.001$), for unpaired males than unpaired females ($G_1 = 17.8$, $P < 0.001$), and for paired females than paired males ($G_1 = 12.8$, $P < 0.001$).

Thus, on average, courtship by males and females began in October and March, respectively, of their first year and continued until pair bonds were formed, although courtship was less intense by 1Y than older males (see below) and individual 1Y males may have begun courting at different times through the winter. Courtship was a continuous process for older unpaired and paired birds, occurring at similar frequencies throughout the winter for each class of bird, but at highest and lowest frequencies for unpaired and paired males, respectively.

Pair-date and pairing success in relation to court-rate

There was evidence that time spent in courtship differed among individuals, although there were few birds for which I had adequate data to test for differences. Three unpaired 2Y females that I observed at least 5 times during November-February were courted during 0 of 6 (binomial $P = 0.001$, given a probability of being courted of 0.32, see above), 1 of 5, and 6 of 6 ($P = 0.1$) observation sessions, and differed in the mean time spent in courtship during that period (Kruskal-Wallis $H_2 = 9.02$, $P = 0.01$). As mentioned above, I was unable to confidently estimate

court-time for individuals, but some 2Y females were known to have been courted at least 3 months before pairing.

Pair-date was negatively related to the amount of time spent courting per observation session for 2Y (Spearman correlation: $r_s = -0.55$, $P_{1\text{-tailed}} = 0.008$, $n = 19$) and 3Y ($r_s = -0.54$, $P_{1\text{-tailed}} = 0.02$, $n = 14$) females but not for A3Y females ($r_s = 0.0$, $P = 1.0$, $n = 30$) or A3Y males ($r_s = 0.42$, $P = 0.2$, $n = 13$). Considering only behaviour prior to pairing, and effects of nasal tags (Regehr and Rodway 2003), there was no significant difference in the court-rate of A3Y males who successfully paired (adjusted mean from a 2-way ANOVA including date-location: 61 ± 36 min d^{-1}) and those who failed to pair (74 ± 13 min d^{-1}) within that year ($F_{1,101} = 0.0$, $P = 1.0$).

Evidence of trial liaisons

Four first-year females appeared paired during extended observations and subsequently were seen unpaired. These temporary pairs were seen between 1 March and 4 May; first-year females were not seen paired during observations before March. The two other first-year females that were identified as paired (Fig. 6.1) also may have been engaged in trial liaisons because all second-year females that I observed early in the fall were unpaired (Table 6.2). If so, then 55% of first-year females for which I had pair status data during March or later ($n = 11$) were observed in temporary liaisons. This underestimates the rate of trial liaisons in first-year females because my observations of these birds were infrequent.

Two second-year females were seen in sequential liaisons with two different males, one marked and one unmarked in each case, and then seen unpaired. Three additional second-year females were observed paired, then unpaired, then paired again, in all cases to unmarked males. It is possible that females seen with unmarked males may have consorted with only one male, but this appeared unlikely because, of five marked males observed paired and then unpaired, four did not pair again within the same year. Initial liaisons were observed between 21 November and 23 January. These five females represented 13% of the second-year females for which I had pair status data during that period ($n = 38$), which again, because of infrequent observations, underestimates the rate of trial liaisons. Because most males involved in temporary liaisons were unmarked, females may have formed liaisons with more males than indicated. Also, because almost all second-year females formed pair bonds by April (Fig. 6.1, Table 6.2), it is likely that the two females that were seen with two different males and then seen unpaired formed a liaison with at least one more male. Male mortality possibly could have been responsible for some temporary liaisons but is insufficient (Cooke et al. 2000) and unlikely to account for many.

Length of time taken to re-pair

There were few birds for which I had adequate data to determine time taken to re-pair after the apparent disappearance of a previous mate. If a mate did not return after the breeding season, I calculated the time taken to re-pair as the number of days or months after the end of September until re-pairing occurred. Two A3Y females re-paired 12 and 20 d after their previous mate disappeared in March, and two other A3Y females were known to remain unpaired for 3 and 5 months during the early part of winter. After-third-year males that were successful in forming another pair bond averaged 10 months (range: 4 – 14 mo, $n = 6$) to re-pair, others were known to remain unpaired for at least 4 months ($n = 1$), 6 months ($n = 2$), 2 years ($n = 1$), and 4 years ($n = 1$) after losing their mate.

Time-activity budgets

Comparing 5 and 30 minute observation sessions

Variances around means estimated from 5 min sessions were not significantly higher than those estimated from 30 min sessions for feeding ($F_{727,1068} = 0.94$, $P = 0.8$), resting ($F_{727,1068} = 0.42$, $P = 1.0$), preening ($F_{727,1068} = 1.07$, $P = 0.15$), agonistic behaviour ($F_{727,1068} = 0.22$, $P = 1.0$), and predator avoidance ($F_{727,1068} = 0.43$, $P = 1.0$), and were higher for moving ($F_{727,1068} = 1.25$, $P < 0.001$) and courtship ($F_{727,1068} = 2.87$, $P < 0.001$). I combined data from 5 and 30 min sessions for subsequent analyses presented here because differences in variances were inconsistent, sample sizes were large, no differences in estimated time budgets were detected among years, and preliminary, separate analyses yielded similar results.

Seasonal changes and herring spawn

I found significant seasonal changes in the proportions of time spent, and in the absolute amount of time spent per diurnal day, for all major behaviours that I observed (Table 6.3). Percent of the day devoted to feeding peaked in January and February, but the amount of time spent feeding per day peaked in March at sites where herring spawn was not available. In March, birds fed during only 16% of the day at herring spawning sites compared to 56% of the day at locations where herring did not spawn. Proportion and amount of time spent feeding in March where spawn was available was less than during all other months (Tukey post-hoc tests: $P_s < 0.05$). Birds spent more time resting, moving, and courting at spawning sites than elsewhere in March, and than during all other months ($P_s < 0.05$) except April for resting, October for moving, and October, November, and December for courting. Proportion and amount of time spent preening was less during December, January, and February than during all other months ($P_s <$

0.05) except October, and did not differ between spawning sites and elsewhere in March ($P > 0.05$). In all months birds spent only a few minutes of their day in aggressive interactions and predator avoidance behaviours (Table 6.3). Post-hoc tests showed that time spent in aggressive interactions was generally greater during February-April than November-January (February $>$ January; March without spawn $>$ November and January; March with spawn $>$ November, December, and January; and April $>$ November and January; $P_s < 0.05$). Frequency of aggressive interactions was highest during March at herring spawning sites than all other date-location categories (Table 6.3; $P_s < 0.05$) and did not differ between other date-location categories ($P_s > 0.05$).

Differences by age

Before proceeding to compare time budgets of paired and unpaired birds it was important to determine whether age affected time budgets because unpaired birds tend to be younger birds and effects of pair status and age may be confounded. Also, I wished to use data from all randomly-sampled birds that I had observed, but except for 1Y males that could be identified by plumage, I only knew age for birds that had been captured for marking. Determining effects due to age allowed me to either use data from all birds if no differences by age were found, or, when effects of age were found, to consider age classes separately when possible or to consider how the effects of age may influence results when I could not separate pertinent age classes.

Proportion of time spent in courtship differed among age groups for unpaired females ($F_{3,223} = 4.6, P = 0.004$) and unpaired males ($F_{3,305} = 13.5, P < 0.001$), and was less for 1Y females ($0.4 \pm 0.2\%$) than older females (older ages combined: $9.5 \pm 0.9\%$) and less for 1Y males ($0.6 \pm 0.3\%$) than older males ($10.2 \pm 0.8\%$; Tukey post-hocs, $P_s < 0.05$). Proportion of time spent preening differed among age groups for unpaired males ($F_{3,305} = 5.8, P = 0.001$) but not females ($F_{3,183} = 0.6, P = 0.6$), and was greater for 1Y males ($26.8 \pm 3.8\%$) than older males ($12.5 \pm 1.0\%$; Tukey post-hocs, $P_s < 0.05$). Proportion of time spent moving differed among age groups for unpaired males ($F_{3,305} = 6.9, P < 0.001$) but not females ($F_{3,183} = 1.1, P = 0.4$), and was less for 1Y males ($13.2 \pm 2.2\%$) than older males ($27.2 \pm 1.6\%$; Tukey post-hocs, $P_s < 0.05$). There were no significant differences by age of unpaired females or males in proportions of time spent feeding ($F_{3,183} = 0.1, P = 1.0$ and $F_{3,305} = 1.2, P = 0.3$, respectively), resting ($F_{3,183} = 1.0, P = 0.4$ and $F_{3,305} = 0.3, P = 0.8$, respectively), being vigilant and avoiding predators ($F_{3,183} = 0.9, P = 0.5$ and $F_{3,305} = 0.6, P = 0.6$, respectively), being aggressive ($F_{3,183} = 0.3, P = 0.8$ and $F_{3,305} = 0.2, P = 0.9$, respectively), and being a recipient of aggression ($F_{3,183} = 0.4, P = 0.8$ and $F_{3,305} = 0.1, P = 1.0$, respectively).

Differences by sex and paired status

Considering both sexes together, a 2-way ANOVA of the proportion of time spent feeding indicated significant effects due to date-location (Table 6.3), sex-pair (Table 6.4), and the date-location*sex-pair interaction ($F_{21,2563} = 2.1, P = 0.002$). Differences by sex and paired status were due to lower feeding rates by unpaired males than other birds. Feeding rates by paired and unpaired females were similar (Table 6.4). I performed separate analyses for the two sexes to help interpret the significant interaction effect. For females, I found no effect due to paired status ($F_{1,1234} = 0.2, P = 0.7$), but the interaction of paired status*date-location was significant ($F_{5,1234} = 2.3, P = 0.04$), and the proportion of time spent feeding in March at herring spawning sites was greater by unpaired ($25 \pm 4\%$, $n = 49$) than paired ($13 \pm 1\%$, $n = 106$) females ($P = 0.03$), while no differences were found between unpaired and paired females during other date categories ($P_s > 0.05$). I found a significant effect of paired status for males ($F_{1,1337} = 5.1, P = 0.02$), but again the interaction of paired status*date-location was significant ($F_{5,1337} = 2.5, P = 0.03$). Time spent feeding was less for unpaired ($46 \pm 2\%$, $n = 349$) than paired ($55 \pm 2\%$, $n = 399$) males during fall and winter (October to January), was greater for unpaired ($20 \pm 3\%$, $n = 70$) than paired ($12 \pm 1\%$, $n = 98$) males in March at herring spawning sites ($P_s < 0.05$), and did not differ between unpaired and paired males during other date categories ($P_s > 0.05$).

Paired birds of both sexes spent more time resting than unpaired birds (Table 6.4). I excluded 1Y males from analyses comparing time spent preening and time spent moving among sex-pair classes because proportion of time spent in those behaviours differed significantly between 1Y and older males (see above). When 1Y males were excluded, amount of time, but not proportion of time spent preening differed significantly among sex-pair classes (Table 6.4). No significant differences were apparent if 1Y males were included. Females tended to preen more than males, but post-hoc tests indicated only that unpaired females spent more time preening than unpaired and paired males. Time spent moving was greater for males than females, and greater for unpaired males than paired males (Table 6.4). Significant differences were the same and trends were only slightly less pronounced if 1Y males were included in the analysis of moving behaviour.

Due to their lower rates of courtship than older birds, I excluded 1Y males and known 1Y females from the analysis of the proportion of time spent in courtship and found significant effects due to date-location (Table 6.3), sex-pair (Table 6.4), and the date-location*sex-pair interaction ($F_{21,2488} = 4.0, P < 0.001$). Estimates of time spent in courtship by unpaired females were likely biased low relative to unpaired males because I was unable to exclude unmarked 1Y

females from the analysis. Time spent in courtship was greater for unpaired than paired birds of both sexes, and was greater for paired females than paired males (Table 6.4). Separate analyses of paired and unpaired birds indicated that the significant interaction effect was due to greater time spent in courtship by paired females than paired males during October to January and during March at herring spawning sites ($P_s < 0.05$), while there was little difference between paired females and males during February to April at sites without herring spawn ($P_s > 0.05$). Greatest differences were seen in October and in March at spawning sites when paired females and males were involved in courtship for 4.6 vs. 0.3% and 3.7 vs. 0.5% of their day, respectively. When paired females were being courted their mates attended them and were always part of the courting group, but the activity of males at those times was considered part of mate defence rather than courtship (see below).

Paired males spent more time being aggressive to others and less time as the recipient of aggression than all other sex-pair classes, while unpaired females spent more time as the recipient of aggression than all other sex-pair classes (Table 6.4). In addition to the amount of time spent being aggressive to others listed in Table 6.4, paired males also spent 8 ± 1 min d⁻¹ on average attending their mates but not behaving aggressively to other males when their mates were being courted. Time spent vigilant and in other predator avoidance behaviours was greater for unpaired males than paired females and paired males, and did not differ between paired males and females (Table 6.4).

Frequency of agonistic interactions

Data on the frequency of agonistic displays revealed a likely bias in the method of focal individual sampling used to measure behaviour. The data incongruously suggested that in almost all cases displays directed at others were more frequent than displays received (Table 6.5). This clearly cannot be true for all individuals, and I suspect reflects the fact that when observing a focal individual, displays performed by that individual will be detected with high probability, while displays directed at that individual by others have a lower probability of being detected, especially if there is no response from the focal individual. Because these two measures were analyzed separately, this bias is unlikely to affect comparisons among sex-pair classes.

Many agonistic displays were associated with courtship and sex-pair differences in the frequency of interactions varied depending on whether courtship behaviour was included or excluded. Paired males directed aggressive signals at others more frequently and received aggressive signals less frequently than all other sex-pair classes if courtship behaviour was excluded (Table 6.5). However, aggressive displays directed at others were more frequent by

unpaired than paired males if signalling to females during courtship was included, although the number of aggressive displays directed at males was still higher for paired than unpaired males. Unpaired males were the recipients of aggressive displays more frequently than paired males, regardless of whether courtship behaviour was included or excluded. Unpaired females received aggressive signals more frequently than paired females, but again these differences were due to interactions during courtship; outside of courtship there was little difference between unpaired and paired females in the number of aggressive interactions they initiated or received. Unpaired females and males were the recipients of aggressive acts by other species more often than paired females and males. In total, unpaired birds were involved in more interactions than paired birds if courtship behaviour was included, whereas males were involved in more interactions than females if courtship behaviour was excluded (Table 6.5).

Do females control whether courtship occurs?

An important assumption of the female-choice hypothesis is that males are unable to coercively sequester females. I thus consider whether females can control when courtship occurs. First-year females interacted little with males through most of the winter. During 29 observation sessions conducted October-February, I observed 1Y females mostly in all-female groups (55% of sessions), female-biased groups (28%), or alone (10%). Aggressive interactions involving 1Y females were first observed during observation sessions on 17 February and were common in March and April (7.2 ± 2.2 interactions h^{-1} , no. of observation sessions = 18), but not as common as those that involved all other unpaired females (25.2 ± 5.2 interactions h^{-1} , no. of observation sessions = 79; *t*-test, equal variances not assumed: $t = 3.19$, $P = 0.002$). Before March, unpaired males appeared uninterested in 1Y females and seemed to ignore them. Although I cannot rule out subtle or infrequent signals by 1Y females that discouraged courtship by males and that I did not detect during October-February, available evidence suggests that 1Y females were unattractive to courting males during that period. Four interactions involving 1Y females that I witnessed between 17 February and 5 March, were of 1Y females being chased away by paired females (2), a paired male, and an unpaired male. Many interactions occurring after I first observed 1Y females being courted on 6 March were associated with courtship (41%, no. of interactions = 71), and during March and April, 1Y females performed more aggressive displays to other birds (5.3 ± 2.0 h^{-1}) than they received (1.9 ± 0.6 h^{-1} ; Wilcoxon Signed Ranks Test: $Z = -2.1$, $P = 0.04$).

It was often difficult to determine the intention of various displays by 1Y females. Displays sometimes deterred males that were showing an interest: *bill-pokes* at an approaching

unpaired male resulted in him turning away, and a *bill-poke* followed by a *chase* deterred a 1Y male that was following. At other times, similar displays (*bill-pokes* and *bill-gapes*) were performed to passing males that were not showing obvious interest, and I could not tell whether the female was attempting to deter or to invite male interest in those situations. During courtship, *bill-pokes* appeared to sometimes incite competition among courting males and sometimes deter males. Thus, many displays performed during March and April by 1Y females may have been associated with signalling preference or rejection of specific males rather than attempts to deter courtship *per se*.

Considering all ages, unpaired females frequently displayed aggressively at males (Table 6.5), and they used a greater proportion of higher intensity displays to A1Y males than did all other sex-paired-status classes, including paired females (Table 6.6; *chases* and *trounces* combined into one category: $G_3 = 18.6, P < 0.001$), 1Y males ($G_3 = 47.5, P < 0.001$), unpaired A1Y males ($G_3 = 87.8, P < 0.001$), and paired males ($G_3 = 259.9, P < 0.001$). Unpaired females also used higher intensity displays proportionately more often to A1Y males than to females ($G_3 = 7.6, P = 0.05$). The *trounce* was mostly used by females, especially to deter A1Y males, and I never observed it used by unpaired 1Y or A1Y males (Table 6.6). As with 1Y females, aggressive displays sometimes deterred approaching or courting males and sometimes acted to incite courting males. Even the most aggressive *trounce* varied in its effect, sometimes deterring a party of courting males and ending courtship, and sometimes deterring only the specific male attacked. Thus it appeared that females were at times unwilling to engage in courtship and could effectively signal that unwillingness to approaching males, while at other times her displays were intended to communicate mate-choice preferences.

As mentioned above in relation to 1Y females, it was likely that males exhibited mate-choice preferences, and that the amount of courtship received by particular females was in part due to male preferences. Male preferences may explain my observations described above of an unpaired 2Y female that was courted during 6 of 6 sessions while another was never seen courted during 6 sessions, and also my observations of an unpaired A3Y female that was courted during each of 7 sessions (Binomial test, $P = 0.004$, given a probability of being courted of 0.45). It was not uncommon to see a large party of males courting a female while nearby another unpaired female was unattended. During March at herring spawning sites, I witnessed as many as 18 males courting a female while other nearby females were unattended. Some of these events may not have indicated male preferences because courting parties of males often shifted their attention *en masse* from one female to another, but in some cases particular females were courted more frequently than others.

Pair-bond defence

Paired comparisons between females and males in pair bonds indicated that males overall performed more aggressive displays in defence of the pair bond than females (Table 6.7), but that displays by females were more frequently of higher intensity than those of their mate (Table 6.6; *chases* and *trounces* combined into one category: $G_3 = 336.8, P < 0.001$), and that the relative share of pair-bond defence varied between females and males depending on the target of the aggressive display (Table 6.7). Aggression directed at A1Y males was more frequent by males than females, aggression to 1Y males was more frequent by females than males, and there were no significant differences between female and male partners in the number of aggressive displays directed at other females or at other species. Based on the male age ratio in the population (9.8%, Rodway et al. 2003a) and the total number of displays directed at males (Table 6.6), 1Y males were the target of aggressive displays less frequently than would be expected from paired males ($G_1 = 96.0, P < 0.001$) and not different from that expected from paired females ($G_1 = 0.1, P = 0.7$). Paired females were often recipients of aggressive *chases* by their mates (Table 6.7), which accounted for most of the aggressive signals they received from males (Table 6.5).

The types of display used by female and male partners also varied in relation to the target of the display (Table 6.6). The most intense displays of *chases* and *trounces* comprised 37, 46, and 19% of all displays directed by paired females, and 39, 29, and 6% of all displays directed by paired males, at females, 1Y males, and A1Y males, respectively. For paired females, higher intensity displays formed a similar proportion of the displays directed at females and 1Y males ($G_3 = 2.8, P = 0.4$), and a lower proportion of the displays directed at A1Y males than at females ($G_3 = 26.4, P < 0.001$) and 1Y males ($G_3 = 22.9, P < 0.001$), opposite to the trend found above for unpaired females. For paired males, higher intensity displays also formed a greater proportion of the displays directed at females than at A1Y males ($G_3 = 89.0, P < 0.001$; there were insufficient data to test for differences involving 1Y males). *Head-nods* were the most frequent display performed by paired males, especially to other males (Table 6.6).

The relative share of pair-bond defence performed by females and males varied in relation to the age of the female. For pairs involving 2Y, 3Y, and A3Y females, the number of aggressive displays directed at other birds was higher for 2Y than 3Y and A3Y females, but did not differ among their mates (Table 6.8). Paired *t*-tests indicated that the number of aggressive displays directed at others did not differ significantly between partners for pairs involving 2Y and 3Y females, but for pairs involving older females, males performed more displays in defence of the pair bond than their A3Y mates (Table 6.8). Paired 2Y females also were recipients of aggressive

displays by others more often ($4.2 \pm 1.6 \text{ h}^{-1}$) than 3Y ($1.2 \pm 0.4 \text{ h}^{-1}$) and A3Y ($1.5 \pm 0.3 \text{ h}^{-1}$) females ($F_{2,343} = 4.8$, $P = 0.009$; post-hoc: $P_s < 0.05$), while no significant differences were detected in the number of aggressive displays received by their mates ($0.5 \pm 0.5 \text{ h}^{-1}$, $0.3 \pm 0.2 \text{ h}^{-1}$, and $0.6 \pm 0.1 \text{ h}^{-1}$, for the mates of those same 2Y, 3Y, and A3Y females, respectively; $F_{2,343} = 0.4$, $P = 0.7$). Some of the difference in the number of interactions that paired 2Y, 3Y, and A3Y females were involved in may have been related to the amount that they were courted (20 ± 6 , 10 ± 4 , and $8 \pm 2 \text{ min d}^{-1}$, respectively), although differences in courtship time were not significant ($F_{2,343} = 2.1$, $P = 0.1$).

Further evidence that pairs varied in the relative share of pair-bond defence assumed by each partner came from observations of paired females being courted. Of the few observation sessions during which paired females were courted and I kept track of the position of their mate, the mate was always closest to the female in 8 sessions and was not always closest in 3 sessions. In one example, the female was courted by 3-6 males and performed numerous aggressive displays at these males throughout the 5-min session while her mate swam just ahead, seeming to pay little attention. Pair-bond defence performed only by the female was observed during several other observation sessions.

Spacing behaviour

Group size

Both unweighted and weighted mean group size differed dramatically between March at spawning sites and all other date-location categories (Table 6.9). I excluded March at spawning sites from the ANOVA model to test for differences among other date-location categories because variances for group size were extreme during that period. Excluding March at spawning sites, mean group size was larger during April than during March at sites without spawning and than during all other months, October to February (unweighted means: $F_{6,5706} = 25.6$, $P < 0.001$, $r^2 = 0.03$; weighted means: $F_{6,5706} = 180.2$, $P < 0.001$, $r^2 = 0.07$; Tukey post-hocs: all $P < 0.001$). Weighted mean group size was also larger during March at sites without spawning than during the months October to February ($P_s < 0.05$).

Different sex-paired-status classes of birds were found in different-sized groups during January-February prior to herring spawning ($F_{4,2037} = 58.3$, $P < 0.001$, $r^2 = 0.10$), but not during March at herring spawning sites ($F_{4,484} = 1.5$, $P = 0.2$) or during April and March at sites without spawning ($F_{4,1236} = 2.0$, $P = 0.1$). During January-February, mean group size that individuals were found in was larger for unpaired females (6.0 ± 3.6 , $n = 221$), unpaired A1Y males (5.7 ± 3.8 , $n = 553$), and unpaired 1Y males (5.2 ± 4.2 , $n = 100$) than for paired females and males

(3.6 ± 2.5 , $n = 584$; Tukey post-hoc: all $P < 0.001$). Although group size differed between unpaired and paired females only prior to herring spawning, the proportion of females that were unpaired differed among group-size categories in all months that it was measured, including January ($F_{4,590} = 79.0$, $P < 0.001$, $r^2 = 0.34$), February ($F_{5,1011} = 129.4$, $P < 0.001$, $r^2 = 0.39$), March at sites without spawning ($F_{5,210} = 13.1$, $P < 0.001$, $r^2 = 0.24$), March at spawning sites ($F_{7,108} = 8.2$, $P < 0.001$, $r^2 = 0.35$), and April ($F_{4,74} = 10.0$, $P < 0.001$, $r^2 = 0.35$). Except for single birds, highest proportions of females that were unpaired occurred in groups of 6-10 and 11-20 birds (Fig. 6.2). Tukey post-hoc tests indicated that, in all months, proportions that were unpaired were higher for single birds than all other group sizes, lower for groups of 2 than all other group sizes, and higher for groups of 6-10 than groups of 3-5, and, in February, higher for groups of 11-20 than groups of 3-5 (all $P < 0.05$). My finding that mean group sizes did not differ between unpaired and paired females in March and April likely occurred because larger group sizes were more common at that time (Fig. 6.2), while the proportion of females that were unpaired was highest in medium-sized groups.

The size of group an individual was in was related to its behaviour during October-March, excluding sites in March with herring spawning (ANOVA model including date and location: $F_{3,6504} = 37.1$, $P < 0.001$, $r^2 = 0.10$), but not during March at spawning sites ($F_{3,676} = 2.1$, $P = 0.1$). During October-March, groups in which an individual was courting were larger (7.7 ± 0.3 , $n = 492$) than feeding (4.7 ± 0.2 , $n = 1665$) and random (4.7 ± 0.2 , $n = 1986$) groups, but not than roosting groups (7.1 ± 0.3 , $n = 410$), which were also larger than random and feeding groups (Tukey pairwise: all $P < 0.001$). Trends were the same for both unpaired and paired birds. Though not differing in mean size, the composition of roosting groups differed from courting groups. Considering only groups > 2 birds, the proportion of females that were unpaired was greater in groups of 6-10 than 3-5 for courtship ($F_{3,77} = 3.3$, $P = 0.03$, $r^2 = 0.08$; post-hoc: $P < 0.05$) but not for roosting ($F_{3,71} = 1.0$, $P = 0.4$) behaviour. Sex-ratio (analyzed as the proportion of males in a group) also differed among group sizes for courtship ($F_{3,228} = 4.7$, $P = 0.003$, $r^2 = 0.04$; post-hoc: $P < 0.05$) but not for roosting ($F_{4,203} = 0.3$, $P = 0.9$) behaviour, nor for random groups ($F_{4,2921} = 0.6$, $P = 0.7$). When an individual was courting, the proportion of males in the group was greater for groups of 6-10 birds (0.75 ± 0.02 ; sex ratio = 3.0 ± 0.1) than 3-5 birds (0.69 ± 0.02 ; sex ratio = 2.2 ± 0.1 ; $P < 0.05$). The operational sex ratio (analyzed as the proportion of unpaired birds that were males) increased from January to April ($F_{4,639} = 7.9$, $P < 0.001$), and did not differ among group-size categories for random groups ($F_{5,639} = 1.7$, $P = 0.1$), nor for groups related to specific behaviours (e.g., courtship: $F_{3,62} = 0.2$, $P = 0.9$).

There was no evidence that spacing was a result of agonistic interactions. Following an aggressive display, recipients generally moved not at all or only a small distance and remained within the same group, except for courting males that often left a group to pursue other females. First-year males did not appear to be excluded from courtship or other groups, and in fact may have been more tolerated than A1Y males. As shown for paired males above, unpaired males also directed aggressive displays at 1Y males less frequently than would be expected ($G_1 = 12.6$, $P < 0.001$), based on the male age ratio in the population (9.8%, Rodway et al. 2003a) and the total number of displays directed at males (Table 6.6). Expected and observed frequencies of displays directed at 1Y and A1Y males by unpaired females did not differ ($G_1 = 0.9$, $P = 0.3$).

Courting arenas

Courtship occurred throughout the study area and throughout the day, but there was evidence of spatial and temporal differences in courtship rates. There were 20 sites for which I had at least 50 observation sessions per site. A 3-way ANOVA ($r^2 = 0.17$), including date-location, time of day, and site, indicated that birds spent more time courting at some sites than others ($F_{19,2379} = 4.5$, $P < 0.001$) and during the morning prior to 10:00 than later in the day ($F_{4,2379} = 4.5$, $P = 0.001$; post-hoc: $P_s < 0.05$), although the interaction of time*site was also significant ($F_{69,2379} = 2.0$, $P < 0.001$) and some sites had higher rates of courtship at midday or later in the afternoon. Adjusted mean percent of time that birds spent courting at the different sites ranged from 0.6 ± 1.6 to $9.0 \pm 0.9\%$. Post-hoc tests showed that 4 sites had significantly higher rates of courtship than other sites ($P_s < 0.05$). One site in particular, Grassy Point on Hornby Island, had significantly higher rates of courtship than over 50% of the other sites.

I first noticed high rates of courtship at Grassy Point in fall 1999 and visited the site 16 times after that to determine how birds were using the site. Unpaired birds appeared to use Grassy Point as a rendezvous point in the morning, and unpaired females seemed to visit the site to attract a party of courting males, which they then led off in flight to other locations. My observations of 7 December were typical. The first birds to arrive were males, beginning at 07:30, and by 07:51 there were 13 males, including 2 1Y males, and 1 female roosting together on the point. By 08:10, a total of 25 males and 8 females had arrived, including 3 pairs which tended to remain separate from the large group of unpaired birds. The unpaired birds separated into courtship groups and by 08:23 the 5 unpaired females had flown off in courtship flights with 4 or 5 males each in tow, leaving only paired birds behind. Unpaired birds did not feed while they were at Grassy Point. I witnessed this pattern of behaviour on 10 of 11 visits to Grassy Point at daybreak, during October-February. On one occasion, gale-force winds were buffeting the point

and no birds arrived. Sex ratio at Grassy Point in these early-morning flocks (3.1 ± 0.3 , $n = 8$) was higher than expected (based on a population sex-ratio of 1.51; combined probability, $\chi^2_{16} = 33.6$, $P = 0.006$), and higher than later in the day (1.5 ± 0.1 , $n = 8$), and number of birds present was higher in the morning prior to 08:00 (36 ± 9) than at other times of day after 10:00 (12 ± 3 ; $t_{14} = 3.5$, $P = 0.004$).

I did not witness this type of phenomenon at 15 other sites visited at daybreak. Concurrent observations, with the help of an assistant, at Grassy Point and a nearby site called “Squeaker” on 29 October highlighted the differences in behaviour at these sites. By 08:30 that morning, 32 males and 9 females, one of which was paired, had congregated at Grassy Point, and 7 males and 5 females, 4 of which were paired, had gathered at Squeaker. Except for the 1 paired female, all the females at Grassy Point flew off in courtship groups with 3-7 males. First feeding at Grassy point began at 09:19 after the initial courting groups had left and 6 new birds were present, while all the birds at Squeaker were feeding by 08:35 and, with the addition of one male, were still present at 10:00.

Herring spawn

Time budgets

Analyses of time budgets above showed the expected decline in feeding behaviour and increase in courtship behaviour associated with feeding on herring spawn (Table 6.3). However, overall means (Table 6.3) underestimated the seasonal differences in courtship behaviour for unpaired birds, especially during March at herring spawning sites. Time spent courting in March at spawning sites was higher than during all other date-location categories when only unpaired, A1Y birds were considered ($F_{7,872} = 8.8$, $P < 0.001$; post-hoc: $P_s < 0.05$; Fig. 6.3). Those birds also allocated more time to resting and moving, but not to preening, during March at spawning sites in comparison with birds at sites where herring did not spawn (Fig. 6.4).

Sex ratio

Male bias in the Harlequin Duck sex ratio increased during March at spawning sites when herring spawn became available (Fig. 6.5). Sex ratio was higher during the first 2-week interval of the spawn period than during the previous 2-week interval at locations where herring spawned ($G_1 = 6.05$, $P = 0.007$) but not at locations where herring did not spawn ($G_1 = 0.21$, $P = 0.65$). Male bias in the sex ratio was greater at locations where herring spawned than where herring did not spawn during the first ($G_1 = 3.42$, $P = 0.032$) and second ($G_1 = 7.94$, $P = 0.003$) 2-week intervals after herring first spawned. Increased male-biased sex ratios associated with herring

spawn were not due to increases in the proportion of immature males because male age ratios did not increase until after the spawn period (Fig. 6.5).

Pair status

Proportions of females that were unpaired were similar at locations where herring did and did not spawn in the periods 3-4 weeks (19.5%, $n = 493$ vs. 20.9%, $n = 230$; $G_1 = 0.2$, $P = 0.7$) and 1-2 weeks (10.9%, $n = 46$ vs. 11.3%, $n = 115$; $G_1 = 0.01$, $P = 0.9$) before spawning began, but were greater at locations where herring did than did not spawn in the period 1-2 weeks after spawning began (11.6%, $n = 432$ vs. 5.6%, $n = 142$; $G_1 = 4.65$, $P = 0.016$). Proportions were not significantly different at locations with and without spawn in the period 3-4 weeks after spawning began (10.2%, $n = 127$ vs. 8.0%, $n = 176$; $G_1 = 0.5$, $P = 0.5$).

Mate sampling

Number of males courting a female at any one time differed among date-location categories ($F_{7,662} = 6.1$, $P < 0.001$), and was higher during March at spawning sites (5.0 ± 0.3 , $n = 31$) than during January (3.6 ± 0.1 , $n = 200$), February (3.3 ± 0.2 , $n = 136$), and April (3.1 ± 0.4 , $n = 22$; $P_s < 0.05$), but not than during March at sites without spawning (4.3 ± 0.3 , $n = 44$), nor during October (3.7 ± 0.3 , $n = 29$), November (4.1 ± 0.2 , $n = 116$), or December (4.3 ± 0.2 , $n = 92$; $P_s > 0.05$). Because relatively few males were marked, I could not determine how many males in total courted a female per day. A maximum of 18 males courting a single female was observed during March at spawning sites, but as many as 10 males pursuing a female was seen in all months of the study.

Number of females courted by an unpaired male during an observation session (there was no difference between 5 and 30 min sessions; $F_{1,203} = 0.5$, $P = 0.5$) also differed among date-location categories ($F_{7,203} = 3.7$, $P = 0.001$), and was higher during March at spawning sites (2.2 ± 0.2 , $n = 30$) than during all other date-location categories ($P_s < 0.05$; overall mean = 1.4 ± 0.1 , $n = 182$). Focal males courted as many as 5 different females during a single, 5-min observation session. During March at spawning sites, 81% ($n = 42$) and 100% ($n = 17$) of females courted by unpaired and paired males, respectively, were paired, although per encounter during a 5 min observation session, unpaired males spent longer courting unpaired females (4.2 ± 0.4 min) than paired females (0.7 ± 0.2 min; $t_{12} = 2.8$, $P = 0.02$).

Inter-specific comparisons

Age- and sex-specific pairing chronologies were available for few species. I found adequate data to estimate timing of first pairing for females from representative species of five waterfowl tribes (Fig. 6.6). Differences in pairing chronology among these species was related primarily to differences in age of first breeding. Timing of pairing events were similar when standardized to age of first breeding (Fig. 6.6).

I compiled available information on population-level pairing behaviour in 26 North American and 12 Western Palearctic species of waterfowl in the subfamily Anatinae, and attempted to relate that behaviour to a number of variables predicted to influence pairing chronology (Table 6.10). I had sufficient data to test for differences in the calendar date that courtship began (population court-start), the calendar date that 80% of females were paired (population pair-date), and the length of time between those two dates (population court-time). Specifically, I tested predictions of the male-costs hypothesis that pair-date will be earlier with increasing male-bias in sex ratio and with increasing body mass, and predictions of the female-choice hypothesis that pair-date will be later with increasing male-bias in sex ratio, and that court-time will be greater with increasing survival and duration of pair bonds. Differences among tribes were considered first to assess the influence of phylogeny. Only northern hemisphere species are represented because I could find few quantitative data on pairing chronology for southern hemisphere species. Analyses based on these data must be considered exploratory because of the lack of independence in data for related species (Felsenstein 1985, Harvey and Pagel 1991), because where there were several studies of a particular species, I subjectively chose one to include, and because with such a small sample size it was necessary to use a stepwise procedure to determine the relative importance of the different explanatory variables. When there were multiple studies of a species I chose either the one where several species were compared (e.g., Hepp and Hair 1983) or the one I considered the most complete (i.e., presented information on both courting and pairing times).

Different studies of the same species often showed considerable latitudinal variation in pairing chronologies, and a different choice of studies to include may have yielded different conclusions. However, intra-specific trends by latitude were inconsistent. In North America, studies indicated earlier pairing at higher latitudes for Northern Shoveller (*Anas clypeata*; Hepp and Hair 1983, Thompson and Baldassarre 1992), Northern Pintail (Hepp and Hair 1983, Miller 1985), Green-winged Teal (*Anas carolinensis*; Hepp and Hair 1983, Miller et al. 1988, Rave and Baldassarre 1989), and Canvasback (*Aristonetta valisineria*; Smith 1946, Weller 1965), later pairing at higher latitudes for Black Duck (*Anas rubripes*; Johnsgard 1960b, Hepp and Hair 1983)

and Redhead (*Aristonetta americana*; Low 1945, Weller 1965), and no difference by latitude for Gadwall (*Mareca strepera*; Hepp and Hair 1983, Paulus 1983), Mallard (*Anas platyrhynchos*; Johnsgard 1960b, Heitmeyer 1988), and Lesser Scaup (Weller 1965, Austin et al. 1998). For American Wigeon (*Mareca americana*), two studies conducted at middle latitudes showed that 80% of females were paired by November (Hepp and Hair 1983, Heitmeyer 1995), while three other studies conducted at more southern and northern latitudes showed that 80% of females were not paired until March or later (Soutiere et al. 1972, Wishart 1983, Thompson and Baldassarre 1992). In the western Palearctic, Mallard also paired later at higher (Raitasuo 1964) and lower (Green and Hamzaoui 2000) latitudes than at middle latitudes (Bezzel 1959, Lebret 1961). Eurasian Green-winged Teal (*Anas crecca*) showed no difference by latitude (Bezzel 1959, Lebret 1961, Green and Hamzaoui 2000). Studies of American Wigeon in North America and of Mallard in Europe suggest that pairing may be earlier in the middle of a species' range and later at both southern and northern extremes.

The start of courtship, pair-date, and court-time differed significantly among tribes (Table 6.11). Anatini and Mergini species began courtship earlier than Aythyini and Oxyurini species, and Anatini species paired earlier than Aythyini and Mergini species, resulting in longer court-times for Mergini than either Anatini or Aythyini species. No other variables added significantly to explained variation for start of courtship or pair-date after effects of tribe were included. For court-time, a model including only the effect of long-term pair bonds ($r^2 = 0.61$, $F_{1,27} = 44.4$, $P < 0.001$) was superior to the one with tribe (Table 6.11). No other variables added significantly to explained variation for court-time after effects of long-term pair bonds were included. Court-time averaged 2.4 ± 0.3 months ($n = 19$) and 5.4 ± 0.4 months ($n = 9$) for species with annual and long-term pair bonds, respectively. This conclusion is tentative because I assumed that all Mergini species have long-term pair bonds, and this has only been confirmed in some species (Bengston 1972, Allison 1975, Spurr and Milne 1976, Savard 1985, Gauthier 1987a, Savard et al. 1998) and suspected in others (Eadie et al. 1995, Brown and Fredrickson 1997, Mallory and Metz 1999). I also considered most Anatini and Aythyini to have annual pair bonds, even though instances of long-term bonds have been confirmed (Lebret 1961, Dwyer et al. 1973, Palmer 1976a, p. 338, Bluhm 1985) or suspected (Bezzel 1959, Paulus 1988b) in some northern hemisphere species and are more common in tropical or southern hemisphere Anatini species (Sorenson 1991, Williams and McKinney 1996, Port 1998). However, high mortality rates likely constrain the possible frequency of multi-year pair bonds and the proportion of birds possibly involved would be small in most northern, migratory and hunted Anatini species.

I re-analyzed the data excluding tribe from the models to determine what other variables may account for the differences seen among tribes. Start of courtship was later with increasing male-bias in the sex ratio ($F_{1,28} = 12.6, P = 0.001$) and for sexually segregated species ($F_{1,28} = 7.6, P = 0.01$; total $r^2 = 0.36$). Pair-date was similarly related to sexual segregation ($F_{1,25} = 10.2, P = 0.004$) and sex ratio ($F_{1,25} = 4.5, P = 0.04$) and also was later for species with long-term pair bonds ($F_{1,25} = 5.1, P = 0.03$; total $r^2 = 0.36$) when tribe was excluded. Court-time was positively related to female annual survival ($r^2 = 0.26, F_{1,24} = 9.7, P = 0.005$) if duration of pair bond was excluded from the model.

DISCUSSION

Pairing in Harlequin Ducks

The picture of the pair formation process in Harlequin Ducks that emerges from this study reinforces previous perceptions that pair formation in waterfowl is complex, involving the interaction of phenotypic, social, and ecological conditions and the balance of benefits and costs to males and females (McKinney 1986, 1992, Rohwer and Anderson 1988, Oring and Saylor 1992). However, theory to account for variation in the timing of pairing, that primarily considered how phenotypic, social, and ecological factors affects male costs (Rohwer and Anderson 1988), poorly predicted pairing behaviour in Harlequin Ducks. Many recent advances in our thinking about animal social systems have come from greater focus on female perspectives (Gowaty 1996, 1997, Jennions and Petrie 1997, Birkhead and Møller 1998), and in birds recent evidence suggests that resolution of reproductive conflicts between males and females favours female interests (Hughes 1998). Greater insight into the pairing process in waterfowl can be obtained by focusing more attention on female perspectives. Decisions by females about how much time and energy to allocate to the pairing process appeared to be the main factor controlling the timing of pairing in Harlequin Ducks. Those decisions were affected by age, previous pairing experience, time required for other activities due to seasonal differences in day-length and food availability, and group spacing that affected the availability and likely the costs of mate sampling and in turn was also related to food availability. Decisions by males were similarly affected and female and male behaviour necessarily interacted to affect the time required for both sexes to balance the benefits of satisfying their mate preferences and the costs of pursuing those preferences.

Results provided little support for the two main premises of the female benefits-male costs hypothesis. Pair formation was protracted and there was no evidence that females preferred to pair as early as possible, except perhaps for individuals that had already been through the mate

choice process and were re-uniting with their former mate, or that pairing was delayed because males could not afford the costs of courtship or mate defence. Females began courtship and mate sampling, forming liaisons with older males, at the age of 9 months. Many females formed temporary liaisons and almost all formed more lasting pair bonds during their second winter, however some of those pair bonds also may have been temporary because some two-year-old females are seen unpaired on breeding streams (C.M. Smith pers. comm.). Thus, some females engaged in courtship and trial liaisons with several males over a period of 1-2 years. Males began the process earlier than females at only four or five months of age, though they were unlikely to pair for several years. One male was known to pair at the end of his second winter, but few paired before their fourth winter. Timing of first pairing was highly variable among second-year females, occurring throughout the winter from October to April. Mate fidelity from year to year was high as found in previous studies (Gowans et al. 1997, Robertson et al. 1998, Smith et al. 2000) and divorce rate was estimated to be 3.1%. Established pairs re-united in September, October, and early November, and birds that had lost or divorced a mate re-paired at variable times throughout the winter, on average later than re-uniting birds and earlier than first-time pairing females, consistent with predictions of the female-choice hypothesis. Early pair dates for re-uniting birds likely reflects the benefits to individuals of determining whether or not their mate is still alive, so they can protect their pair bond with a compatible and experienced partner if they are, or can begin the re-pairing process in ample time if they are not (Rowley 1983). Robertson et al. (1998) reported later pairing dates for all age groups than found in this study, but differences were likely due to larger sample sizes and more stringent requirements used in this study for estimating pair dates.

Paired females were the recipient of aggressive displays less frequently than unpaired females, but these interactions occupied only about 1 min per day for unpaired females and the benefit for paired females was likely trivial, unless it was associated with a change in habitat use due to despotic behaviour (Fretwell and Lucas 1970). This was unlikely because recipients of aggressive displays were not displaced from their immediate group, and because the greater frequency of interactions experienced by unpaired females was entirely due to their greater involvement in courtship and was not related to feeding or roosting habitats. The same argument applies to unpaired males, and contrary to speculations by Rodway et al. (2003a), despotic behaviour by paired birds was unlikely to account for small-scale differences in habitat use by males found in that study. It was very common in this study to observe unpaired males and females feeding in a group with paired birds for extended periods of time. For Harlequin Ducks

we can safely reject the hypothesis that birds pair early to gain access to preferred food supplies through increased dominance status (Paulus 1983).

Females exhibited flexible time budgets (Herbers 1981) and unpaired females allocated time to courtship and mate choice without sacrificing feeding time. Time budgets were constrained by day-length and less time was allocated to courtship during mid-winter when daylight was shortest and proportion of diurnal time required for feeding was highest. Time spent feeding by unpaired and paired females did not differ except during March at herring spawning sites when unpaired females spent more time feeding than paired females. The only other differences in their time budgets were that paired females spent more time resting and unpaired females spent more time in courtship. Lack of difference in time spent preening, and no increase in the allocation of time to preening by unpaired females during March at spawning sites, also indicated that unpaired females were satisfying their requirements for body maintenance before allocating time to courtship. Unpaired females were capable of deterring courting males and there was no evidence that interference from males or requirements for vigilance reduced feeding efficiency or increased predation risk for unpaired females. Time spent in vigilance and predator escape behaviours differed neither between paired and unpaired females, nor between paired females and their mates. Thus, in terms of time budgets, costs to females of remaining unpaired appeared to be minor, and immediate benefits of becoming paired were not apparent beyond the obvious consequence that less investment in courtship was required.

However, greater feeding by unpaired than paired birds during March at spawning sites could indicate higher energy costs for unpaired birds. More time allocated to courtship and moving could explain higher energy costs at that time (Ricklefs 1974). Alternatively, unpaired birds may have been in poorer body condition as a result of increased costs of courtship that were not offset by higher feeding rates through the winter. This latter explanation seems more likely true for unpaired males whose rate of feeding from October to January was reduced compared to paired males. At that time, unpaired males appeared to allocate time to courtship and moving, likely in search of potential mates, partially at the expense of feeding time.

As measured by changes in time budgets, males stood to gain more from becoming paired than females. Unpaired males spent less time feeding and resting and more time moving, courting, as the recipient of aggressive interactions, and in predator avoidance behaviours than paired males. Although paired males spent more time being aggressive to others than unpaired males, on average this only amounted to 4 min per day. Including as part of mate defence all the time paired males spent being aggressive to others, plus the time they spent attending their mates but not behaving aggressively to other males when their mates were being courted, still indicates

that unpaired males spent much more time in courtship than paired males spent in mate defence. This was true in all winter months, even during mid-winter when time constraints were most severe. Constraints on male time and energy budgets is thus not a plausible reason for delayed and protracted pairing of young and re-pairing females in this species.

Many aspects of the pairing behaviour of Harlequin Ducks were consistent with predictions of the female-choice hypothesis (Table 6.1). Newly-pairing females spent an extended period of time in courtship and mate sampling, and their date of pairing was related to the amount of time per day that they allocated to courtship. Pairing success of males was not related to the amount of time that they devoted to courtship, and female choice was likely based on more specific male traits and behaviours than just the total amount of time males had available for courtship. Mate choice criteria were not specifically investigated, but this study did reveal that male age and the possession of nasal tags (Regehr and Rodway 2003) affected female mate choice. Unpaired females frequently rejected the advances of courting males and through agonistic displays were able to at least partially control whether and by whom they were courted. However, amount of courtship directed at particular females, especially first-year females, also appeared to be partially a function of male mate-choice preferences, and female and male preferences likely interacted to regulate courtship behaviour, number of potential mates sampled, and ultimately pair formation.

Relative roles of females and males in defence of their chosen pair bond varied among pairs and also suggested that pair bonds were a compromise between female and male mate-choice preferences and their attendant costs of exercising those preferences. Although on average males performed more aggressive display in defence of the pair bond than did females, displays by females were of higher intensity than those of their mate, and it is difficult to compare the costs of mate defence for the two sexes without some measure of the cost of each type of display. In some pairs females performed virtually all defensive displays and obviously bore the main cost of pair-bond defence. Even when sex ratios are male-biased, differences in male quality may make some females willing to protect a pair bond with a high-quality male. Differences among pairs may reflect the degree to which each partner's realized choice matched their preference. This could explain why younger females performed a greater share of pair defence and were recipients of aggressive interactions more frequently than older females, and why males as well as females may initiate divorce if a better option is available (Ens et al. 1996). Willingness to invest in pair-bond defence also may depend on the confidence each partner has in the security of the pair bond and their past investment in the pair bond. Females and males shared equally in pair-

bond defence in new pairs involving young females, while males assumed a greater share of defence when paired to an older female.

Patterns of defence exhibited by female and male partners observed in this study indicate that describing mating systems of Harlequin Ducks and similar species as “female-defence monogamy” (Wittenberger 1979, Wittenberger and Tilson 1980), a “mate-defence mating system” (Oring 1982, Anderson et al. 1992, Robertson et al. 2000) or as “monogamy through coercion” (Johnson and Burley 1997) is overly simplistic. Once formed, the pair bond is perhaps best considered as a resource held with varying value by each partner, and entailing conflicts of interest between the two participants in relation to its maintenance and defence. Mutual defence was the basic pattern observed in Harlequin Ducks with each sex more likely to address aggression towards certain types of individuals, perhaps related to their relative dominance status or to perceived risk to the pair bond. The majority of displays performed by both partners were directed towards intruding, adult males, but partner males performed more of these than their mates. Females were more likely than their partners to display aggressively at immature males, while defence directed at females or other species was performed at similar rates by each partner. Though paired males at times guarded their mates from harassment by other males, in fact, outside of courtship activities, paired and unpaired females received similar amounts of aggression from males, and for paired females most of this aggression came from their mates. By becoming paired, a female was by and large trading aggression from all males for aggression from a particular, chosen male. Paired-male behaviour in this regard could be interpreted as “mate-defence”, but, because *system* means *the connection of parts to make a whole*, our definition of a mating system should reflect the strategies of males *and* females. For Harlequin Ducks, I suggest that the mating system would more appropriately be labelled “pair-bond defence” rather than “mate-defence”. This terminology focuses attention on the interests of both partners, recognizes variation among pairs in the relative roles of the two sexes, and avoids *a priori* connotations of male control (Gowaty 1996) or male protection (Rohwer and Anderson 1988) of the female.

It is puzzling why female and male partners used higher intensity displays more frequently to females and immature males than to adult males. Higher intensity interactions between closely-matched opponents is predicted by game theoretic models of fighting (Maynard-Smith and Parker 1976), contrary to what was observed here because there is a clear asymmetry between males and females and between older, paired females and younger, unpaired females. Game theory predictions would be supported if, for females, such interactions occurred primarily between paired females. Aggression between paired females might have been expected because both paired and unpaired males frequently courted paired females, but was rarely observed. More

commonly, a paired female simply waited for her partner while he was courting another paired female, and frequently males of two or three pairs would group together to court each other's mates in turn, suggesting that inter-pair courtship was not perceived as a threat to current pair bonds and may provide some benefit to both sexes in relation to possible future pairing opportunities if a partner dies. Most high-intensity, female-oriented aggression performed by paired birds was directed at unpaired females, who typically retreated. It is likely that display function varied depending on context (Bradbury and Vehrencamp 1998), and a possible explanation for this behaviour by paired females may be that they perceived a greater risk to the pair bond from intruding females than males, while paired males used high-intensity displays to intruding unpaired females to signal their intentions of fidelity to their mate.

Spacing behaviour of Harlequin Ducks supported the hypothesis that unpaired birds will show adaptive changes in their spacing to reduce the costs of mate sampling. Unpaired birds occurred in larger groups than paired birds during October-February, and as discussed above, this pattern could not be explained by exclusion of unpaired birds by more dominant pairs. Behaviour suggested that there was an optimal group size for pairing birds, in the order of 6-20 birds, and a greater proportion of females were unpaired in those sizes of groups in all months that it was measured, even during March and April when mean group sizes were much larger. Birds gathered in larger groups for courtship and roosting than for other behaviours, but the reasons for larger group sizes likely differed for courtship and roosting behaviour because the proportion of females that were unpaired and the male-bias in the sex ratio were greater in larger groups when a focal bird was courting but not when it was roosting, suggesting that unpaired birds were aggregating specifically for courtship. As predicted, operational sex ratio did not vary among group sizes, even for courtship, suggesting that unpaired males were distributed in an ideal-free fashion (Fretwell and Lucas 1970) with respect to unpaired females.

Behaviour seemingly motivated by the need to compare possible mates (in some ways similar to lekking but without reproductive activities) was observed early in the morning at one location. Males gathered at this site at daybreak, unpaired females visited the site each apparently to attract a group of courting males that she could then evaluate as potential mates, and females came for no other obvious purpose because these courting groups left the site without feeding. It was not clear to me why this behaviour occurred at this specific location, but the behaviour was observed at this site during two winters, indicating that there was something unique about the site and that the behaviour was not just a temporary habit of a few birds. Such behaviour may be more widespread and additional sites will need to be discovered before we can determine what location features serve to attract courting birds.

Spacing behaviour of immature males was similar to that of other unpaired birds, and immature males participated in courtship throughout their first winter, though at a lower rate than adult males. I did not evaluate whether early involvement in courtship improved a male's chances of future pairing, but the hypothesis that they improve their display skills and benefit from participation in courtship groups is plausible. Stage of their Alternate I plumage did not seem to affect whether a first-year male participated in courtship, though the small sample size makes this conclusion tentative. Involvement of immature males in courtship, even those with female-like plumage, and lower-than-expected rates of aggression directed at first-year males from adult paired and unpaired males, provide some support for the hypothesis that delayed plumage maturation acts as an honest signal of subordination that minimizes aggressive interactions with adult males and allows young males to gain experience in courtship (Lyon and Montgomerie 1986). Young females were not involved in courtship until their first spring, and perhaps there was little advantage to females of engaging in courtship during their first fall because they would not choose a mate for at least another year. Although I know of no other studies to investigate sex differences in the age when courtship activities are initiated, male-biased sex ratios in many duck species may result in directional selection on males to begin courtship as early as possible if participating in courtship increases the probability that a young male will pair successfully later in life.

Aggregating at herring spawning sites in March provided birds with both direct nutritional benefits and indirect benefits related to changes in time budgets and spacing behaviour. Nutritional benefits for all birds were apparent because a majority of the wintering population of Harlequin Ducks in the northern Strait of Georgia aggregated at herring spawning sites (Rodway et al. 2003b) and birds switched to feeding almost exclusively on spawn (Rodway and Cooke 2002) when it was available. Unpaired birds appeared to benefit from changes in time budgets and spacing behaviour that facilitated courtship and mate sampling and were more likely to come to herring spawning sites than paired birds. Time required for feeding was dramatically reduced for all birds feeding on spawn and unpaired birds allocated much of their spare time to courtship and moving, likely in search of potential mates. Proportion of females that were unpaired was higher at herring spawning sites than elsewhere during the first but not the second two-week interval that spawn was available, and male bias in the sex ratio was higher at spawning sites throughout the time spawn was available. These patterns would be expected if unpaired birds were coming to spawning sites at the start of the spawning period and then forming pair bonds while they were there.

Alternative explanations for the change in proportions of unpaired and paired birds at herring spawn are that unpaired birds may be more likely to visit spawn areas because paired birds are generally more attached to their traditional wintering grounds and are less liable to move (Robertson et al. 1999, 2000, Cooke et al. 2000), or that paired birds are in better condition and need to feed less than unpaired birds. The former explanation seems least plausible because most of the wintering population moves to herring spawning sites (Rodway et al. 2003b) and the vast majority of birds moving are paired. The latter explanation gains some support from the fact that unpaired birds spent more time feeding than paired birds at spawning sites. Another possible benefit of herring spawn, especially for unpaired males, may be that it enabled them to recover from an energy deficit incurred over the winter for the purpose of increasing their chances of pairing. These alternative reasons for the differential movement of paired and unpaired birds do not affect the likelihood that unpaired birds gain indirect benefits from herring spawn, especially because most of the winter population aggregates at spawning sites.

Contrary to predictions, I did not find unpaired birds to be more aggregated than paired birds, and courtship groups were similar in size during March at spawning sites as elsewhere at that time and as during October through December. However, the proximity of large numbers of birds at spawning sites (Rodway et al. 2003b) would have decreased sampling costs for birds searching for mates, and may have functioned analogously to the “lekking” site that unpaired birds used through the winter as a rendezvous point from which they departed in social courtship groups. Decreased costs were most apparent for unpaired males who had higher rates of mate sampling during March at spawning sites than during any other date-location category. Most of the females courted by males were paired at this time, but unpaired males spent only brief intervals courting paired females and focused most of their courtship on unpaired females. This may suggest that males required a brief assessment period to determine that a female was paired, or that potential benefits from spending time courting paired females (i.e., future pairing opportunities if she lost or divorced her mate) warranted less investment in courtship than those from courting unpaired females. Some support for the former possibility comes from frequent observations throughout the winter of flying, unpaired males alighting and briefly courting a paired female that was diving a small distance away from her mate. Such unpaired males generally ceased courting the female and often flew off again when the paired male intervened, although it was not uncommon for an unpaired male to stay and feed with a pair for a while. On several occasions I also witnessed flying, unpaired males perform similar behaviour with single female Surf Scoters, flying away again after a brief assessment, as if realizing their mistake. This behaviour was more costly away from spawning sites because of the greater travel distance

between females. Although numbers of males courting a female at any particular time was not exceptional during herring spawning, I suspect that females also had higher rates of mate sampling at herring spawning sites, due to a greater turnover of males in courting groups.

More time for mate sampling and coincidental access to large numbers of potential partners that could be readily compared at herring spawning sites likely increased the quality and compatibility of mates obtained by pairing birds (Real 1990, Sullivan 1994, Mazalov et al. 1996, Jennions and Petrie 1997, Johnstone 1997). Although most females were paired before March, 50% of second-year females forming their first pair bonds and a small proportion of older, re-pairing females formed pair bonds during or after the herring spawning period. Because pair bonds are long-term, herring spawn may thus provide important indirect benefits that increase the fitness of over 50% of the population through its effects on individual mate choice opportunities and decisions. However, it is possible that herring spawn may be a poor time for mate assessment because differences in male quality will be less apparent when time and energy budgets are relatively unconstrained. Knowledge of the mate-choice criteria used by Harlequin Ducks will be required before we can evaluate this possibility.

This study has demonstrated that female Harlequin Ducks invest considerable time and energy into selecting a mate, and has indicated that the primary benefits of that investment do not accrue during winter. Similar results have been obtained in studies of other migratory ducks (see Introduction) and, although we cannot rule out possible benefits during the winter that have not been measured (species that maintain winter territories [Savard 1988] seem the most likely candidates for demonstrating winter benefits of early pairing, and warrant investigation), the apparent conclusion is that direct benefits of female mate choice in these species relate to improved mate co-ordination through time spent together on the wintering grounds, and to male behaviour during migration or on the breeding ground. Indirect genetic benefits may also be important. Direct benefits may include hormonal synchrony and readiness for breeding (Bluhm 1984, 1988, Hirschenhauser et al. 1999), co-ordination of activities leading to successful migration, copulation, and fertilization, male defence and vigilance that increases foraging efficiency during the period of nutrient acquisition for egg-laying and incubation (Milne 1974, Ashcroft 1976, Sorenson 1992), establishment of a nesting site, and, in some species, defence of a nesting or foraging territory (Stewart and Titman 1980, Savard 1984, Gauthier 1987b). Harlequin Ducks may have improved their co-ordination at copulation as paired birds copulated throughout the winter (October-April) on average once every 2-3 days (M. Rodway unpubl. data), though this behaviour also may have functioned in pair bond maintenance. I never observed copulation, attempted copulation, or female solicitation to copulate by unpaired birds, suggesting that

copulation did not serve in mate assessment, although I cannot rule out the possibility that some copulating pairs may have separated at some future time. Males benefit from these behaviours through indirect parental investment in improved female condition and through paternity assurance. Potential benefits indicate that quality of mate and familiarity with mate may both be important.

Timing of pairing in waterfowl

Having found substantial agreement between predictions of the female-choice hypothesis and observed pairing behaviour in Harlequin Ducks and several inconsistencies with the male-costs hypothesis (Table 6.1), the next step is to ask how well the theory performs when we apply it generally to all waterfowl species. Adequate evaluation of the theory is currently handicapped by a paucity of data on age- and sex-specific pairing chronology of marked birds with known pairing histories. However, some inter-specific comparisons were possible that provide support for the theory and direct us to future research needs.

We first need to consider the phylogeny of pairing behaviour in waterfowl in order to better interpret available comparative data. As noted in the Introduction, the ancestral waterfowl mating system was likely one of biparental care and perennial monogamy (Kear 1970, Oring and Saylor 1992). If we seek an adaptive explanation for variation in timing of pairing among waterfowl, it is thus appropriate to begin with consideration of pairing behaviour in species whose behaviour likely most resembles the ancestral condition (Kear 1970). In geese and swans, young birds generally begin the mate choice process and engage in trial liaisons by the spring or summer of their first year, form permanent pair bonds by the time they are two or three, and first breed at the age of two to four (Raveling 1969, Minton 1968, Owen 1980, Prevet and MacInnes 1980, Owen et al. 1988, Cooke et al. 1995, Mowbray et al. 2000). Geese that have lost or divorced a mate usually take 3-9 months to re-pair (Owen et al. 1988). One-or-more-year intervals between the beginning of mate sampling and pairing, and between pairing and nesting, implicate benefits of both a prolonged period for mate selection and for gaining familiarity and experience with the chosen partner. The relative importance of these two aspects of pairing will likely predict the relative amounts of time that individuals spend in the mate choice process (court-time) and between pairing and breeding (pair-time), and likely also relates to whether or not pair bonds are maintained from year to year.

I have discussed above the potential benefits of a protracted mate choice process. There is evidence that mate familiarity and co-ordination also can contribute to fitness (Ens et al. 1996). Lifetime reproductive success has been related to pair-bond duration in several waterfowl species

(Owen et al. 1988, Black et al. 1996, Rees et al. 1996, Williams and McKinney 1996, Black 2001), and although Cooke et al. (1981) did not find within-season differences in reproductive success for Snow Geese (*Anser caerulescens*) that kept or changed mates between years, they did observe improved behavioural co-ordination between mates with increasing duration of the pair bond. Time to gain familiarity may be important to re-pairing geese as well, as birds that re-pair in autumn are more likely to breed than those re-pairing in spring, who rarely breed the next season (Owen et al. 1988). However, pairing behaviour suggests that beyond the 1-2-year court-time and pair-time intervals, additional investment in court-time has greater fitness returns than additional investment in pair-time. Court-time varies more than pair-time among individuals and some females have been known to take 14 or 15 years to find a suitable mate (Choudhury et al. 1996, Banko et al. 1999). Such delays in breeding after finding a mate are unknown. This reveals the importance and perhaps partially stochastic nature of the mate-choice process and suggests that court-time will be more responsive than pair-time to variation in social and environmental conditions. This appears to be true for Snow Geese. Wrangell Island birds delay pairing and breeding 1-2 years compared to mid-continent birds, possibly as a result of more severe nesting conditions and greater costs of early reproduction at high- than low-arctic colonies (Ganter et al. *in prep*). Thus it appears that these birds extended court-time rather than pair-time when there was selection for later age of first breeding. Alternatively, young birds may have just delayed the start of the pairing process, but this seems unlikely given the generally protracted nature of the process, and because, although some young birds re-formed sibling groups in their second year, most unpaired birds were alone (Ganter et al. *in prep*) and thus could have benefited from the rise in dominance status associated with becoming associated with a potential partner (Black and Owen 1987). In Barnacle Geese (*Branta leucopsis*), earlier mate choice leads to earlier recruitment (van der Jeugd and Blaakmeer 2001), and although earlier recruitment may not increase fitness (Viallefont et al. 1995), it does suggest that pairs allocate similar amounts of time to gaining familiarity before breeding, regardless of when they pair.

Comparisons of pairing chronology for young females revealed markedly similar patterns among representatives of five waterfowl tribes for which such data were available (Fig. 6.6). Differences among taxa suggest that selection has acted primarily to accelerate life history events related to pair formation. Similar relative patterns of pair formation may result from independently-derived, analogous behaviours, but a parsimonious explanation suggests that the pattern of an extended court-time followed by an extended pair-time has been maintained within the relative timeframe of each species' life history and in the context of associated changes in age at maturity, reproductive rate, survival rate, parental care patterns, and mating system (Kear 1970,

Laurila 1988, Oring and Saylor 1992). Changing degree of association between mates and duration of the pair bond has not altered the basic pattern of pair formation for the species represented in Fig. 6.6.

The pattern of pair formation does appear to change in some Anatinae species that form pair bonds shortly before or during migration to the breeding ground (Table 6.10), and more obviously changes in a number of Oxyurini species that form weak pair bonds or lack pair bonds entirely (Siegfried 1976, Johnsgard and Carbonell 1996), but a clear understanding of these differences awaits detailed studies of marked, known-age birds. For example, Lesser Scaup (*Aythya affinis*) are one of the latest of the northern, migratory Anatinae to form pair bonds (Austin et al. 1998), and it appears that selection has acted to reduce pair-time, suggesting that time to become familiar with a mate is less important in this species. However, most Lesser Scaup females probably pair in their first year but do not breed until their second year (Trauger 1971, Johnsgard 1978). What happens to pair associations made in the first year? Are they maintained or renewed? Could they account for the small percentage of females that are paired during mid-winter (Weller 1965), long before most females appear paired? How important are such temporary liaisons to future mate choice and breeding performance? Until we can answer these questions we cannot determine just how the pairing pattern in such species deviates from the likely ancestral pattern depicted in Fig. 6.6.

Population level patterns of pairing measured within a single wintering season, though they obscure differences among individuals and fail to detect behaviours that extend over more than one year, were still useful to summarize and did provide important insights in relation to the hypotheses addressed in this study. Results of exploratory analyses suggested that phylogenetic relationships account for a substantial proportion of the variation in pairing chronologies among species of northern Anatinae. Unfortunately, comparative approaches to understanding the evolution of pairing behaviour among these species are currently handicapped because systematic relationships among tribes within the Anatinae and among subtribes within the Anatini are unresolved (Livezey 1997). Pairing chronology would suggest that Mergini species like Harlequin Ducks with long-term pair bonds have maintained the ancestral pattern, as have some Anatini species (Fig. 6.6). Divergence may then have occurred within the Anatini, Aythyini, and Oxyurini. This evolutionary sequence is supported by the apparent primitive position of long-term pair bonds and bi-parental brood care in Anatini (Livezey 1991). Similar court-time but later pair-date in Aythyini than Anatini support the proposal that selection has acted to shorten relative pair-time but not court-time in Aythyini. This also appears to be true for late-pairing Anatini species (Table 6.10). Both court-time and pair-time have been reduced in Oxyurini, but again the

greatest relative decrease has been in pair-time, especially in promiscuous species (Johnsgard and Carbonell 1996).

Results support previous perceptions that diving ducks pair later than dabbling ducks (Rohwer and Anderson 1988), but suggest that the reasons for later pairing in diving ducks differ between Aythyini and Mergini. Late pairing in Mergini is associated with an early start to courtship and an extended courtship time. Extended courtship probably relates to their higher survival, delayed maturity, and long-term pair bonds, and meets predictions of the female-choice hypothesis that birds with long-term pair bonds will invest more in the mate-choice process. However, this may only apply to young birds because if in most Mergini the majority of females are paired early in the winter, as in Harlequin Ducks, then late pairing simply reflects the time when young females form their first pair bonds and is an artefact of using the time when 80% of females are paired as the measure of pairing date. If most Mergini follow the pattern determined in this study for Harlequin Ducks, then young females are engaged in courtship and trial liaisons for a year or more before they pair, while older females are re-uniting or re-pairing more rapidly.

In contrast, Aythyini species have annual pair bonds, generally pair in their first year, and invest less time than Mergini in the mate-choice process. However, as noted above for Lesser Scaup, the mate-choice process may be more protracted for some young females, especially when breeding conditions are unfavourable (Austin et al. 1998). Also, pair-formation behaviour of pochards has rarely been investigated at northern latitudes early in the winter and thus we still need to know whether females wintering in northern parts of a species' range begin the mate-choice process earlier than those in more southern areas. For example, over 70% of the Atlantic Flyway population of Canvasbacks winter in the Chesapeake Bay area (Lovvorn 1989), but we have little data on pairing activities in that area through the winter. Prolonged court-time in Canvasbacks may be expected given their high selectivity in choosing a mate (Bluhm 1985). Weller (1965) made a visit to Chesapeake Bay in February and observed much more courtship activity by Canvasbacks there than in Texas, and M. Anderson (pers. comm.) reported <10% of Canvasbacks paired there at that time. Canvasbacks arrive paired at their breeding grounds (Anderson 1985) and estimates that the majority of females pair during migration are difficult to interpret without winter data from areas where large proportions of their populations occur. Changes in proportions of females paired at migratory stopovers (Smith 1946) could occur because females are pairing at these sites at these times or could be due to differential arrival of paired and unpaired birds from different wintering areas. The latter scenario may more easily explain observed changes in proportions paired from 10% to 65% to 18% within a one-week interval during the passage of about 50,000 Canvasbacks (Smith 1946).

The issue of whether inconspicuous pair bonds may exist in densely flocking populations also needs to be resolved before confident conclusions can be reached about differences in pairing chronology among species. Returning to the Lesser Scaup example, these ducks are highly gregarious during winter and on migration (Austin et al. 1998), and it is possible that inconspicuous pair bonds exist in such large flocks that do not become apparent until birds approach breeding areas. In other species, established pairs are known to join flocks, at which time their relationships are less obvious (Armbruster 1982, Savard 1988, Green and Hamzaoui 2000). In dense flocks of geese it can be almost impossible to determine pair status unless both members are marked (Prevett and MacInnes 1980). Two different aspects of this issue require investigation. First, paired birds may be closely associated in dense flocks and be difficult for human observers to detect. Careful observations of marked birds can relatively quickly reveal if this so. A second possibility is more difficult to resolve. Birds may be paired but not maintain proximity in dense foraging flocks, only re-uniting at some later time. Longer term observations will be required in this case. This latter scenario seems most likely for some Mergini species like scoters that probably have multi-year pair bonds and forage in dense flocks (Brown and Fredrickson 1997, Savard et al. 1998), and also is relevant to suggestions that pochards pair later than dabbling ducks because the costs to partners of keeping track of each other when diving (Rohwer and Anderson 1988) or during flock reactions to predation risk (Lovvorn 1989) outweigh the benefits of being paired.

Analyses without tribe in the model suggested that start of courtship and pair-date were delayed in species' populations with more male-biased sex ratios. This agrees with the conclusions reached by Hepp and Hair (1984) and with predictions of the female-choice hypothesis, and provides additional evidence that male-male competition is not an important determinant of pairing chronology. Secondary analyses also suggested that sexual segregation delayed pairing, but effects of sexual segregation are difficult to interpret. Much of this effect was likely due to later pairing in Mergini, which as discussed above was probably mostly a function of prolonged court-time. Most Aythyini show sexual segregation during winter, but there is little evidence of segregation in Lesser Scaup, the latest pairing species. We probably need better sampling of pairing behaviour throughout the winter range of segregated and non-segregated species before we can evaluate the importance this factor. Inconsistent latitudinal trends among species discussed above, and inter-annual variation in pairing chronology within species possibly due to changing climatic conditions and habitat quality (Raitasuo 1964, Wishart 1983, Kozulin 1995, Migoya et al. 1994) emphasize the importance of adequate sampling in different parts of a species' range and over several years.

Conclusion

Greater focus on female perspectives, specifically female mate-choice decisions, has proven to have heuristic value in understanding pairing behaviour in Harlequin Ducks, other waterfowl (Bluhm 1985, Sorenson and Derrickson 1994, Sorenson et al. 1997), and in mating systems research generally (Gowaty 1997, Johnson and Burley 1997, Birkhead and Møller 1998, Hughes 1998). Male and female interests necessarily interact and a comprehensive theory to predict variation in pairing behaviour in waterfowl and other species will require consideration of benefits, costs, and conflicts of interest among individuals engaged in pairing decisions (McKinney 1986, Rohwer and Anderson 1988, Oring and Saylor 1992, Choudhury 1995, Brown et al. 1997). The process of making mate-choice decisions, how the interactions of phenotypic, social, and ecological conditions affect that process, and how individuals integrate that process with other requirements of their life history are essential to consider in order to understand variation in the timing of pairing events.

Such a theory would be a valuable complement to hypotheses regarding temporal, life-history decisions on the age of maturity and the timing of reproduction (Rohwer 1992). The benefits and costs of a protracted mate choice process and time for co-ordination with a mate prior to breeding have yet to be considered in relation to, and ultimately must entail trade-offs with, these other reproductive decisions. Direct fitness consequences of mate choice and familiarity likely affect the costs of reproduction and thus may contribute to variation in the age of first breeding (e.g., up to 15 years in some geese) and the seasonal timing of nest initiation, that are incompletely explained by survival-fecundity trade-offs (Roff 1992) and food limitation hypotheses (Lack 1954, Perrins 1970). In waterfowl, mature females that are not allowed free choice of a mate may not breed, instead deciding to defer breeding even though possible mates are available (Bluhm 1985). Effects of constrained mate choice in wild birds are unknown. Thus, a worthy aim is an integration of hypotheses to explain variation in the timing of pairing, the age of first breeding, and the timing of reproduction.

Mutual mate choice and shared defence of a pair bond indicated that “pair-bond defence” would be a more appropriate label than “mate-defence” for the mating system of Harlequin Ducks and, I suspect, of most waterfowl species. I suggest that we reserve the term “mate-defence” for systems where one sex can completely sequester an opposite-sex individual through mate-guarding (Brown et al. 1997), comparable to “resource-defence” where an individual can sequester space through territorial behaviour. I question whether such a “mate-defence” system ever pertains to birds, and propose that avian monogamy can aptly be divided into “resource-defence” and “pair-bond defence” systems. Under “pair-bond defence” systems we would then

expect intra- and inter-specific variation in the relative roles of female and male partners in defence of the pair bond. This terminology would more explicitly reflect not only conflict of interests but also obvious mutual interests between monogamous partners (Trivers 1972).

Insights gained in this study of Harlequin Ducks would not have been possible without longitudinal data on marked birds. Similar long-term studies of other waterfowl species are needed to further test the hypotheses presented here and to elaborate the phenotypic, social, and ecological factors influencing pairing decisions in waterfowl. We also need comparable data collected from late fall through spring on age- and sex-specific pairing chronologies for a suite of dabbling and diving species so that we can conduct rigorous comparative analyses. These data need to be collected using standardized methods, and using measures of the timing of pairing similar to those recommended in this study. Developing a more comprehensive theory to explain variation in temporal patterns of mate choice and pairing will require broadening our consideration to other groups of birds (e.g., some penguins, corvids, parids) that also form and maintain pair bonds well in advance of breeding and often during non-reproductive periods.

Detailed study of marked Harlequin Ducks has changed our perception of their mating system from seasonal monogamy with pair bonds being formed anew each year (Johnsgard 1975) to long-term monogamy with low divorce rates (Gowans et al. 1997, Robertson et al. 1998, Smith et al. 2000, this study) similar to that of geese and swans, legendary for their mate fidelity (Ens et al. 1996). I expect similar revisions in our understanding of mating systems and pairing behaviour of many waterfowl species as longer-term studies of known-age, marked birds with known pairing histories are conducted. Discovery of perennial pair bonds in highly dichromatic species such as Harlequin Ducks challenges existing sexual-selection theories that relate sexual dichromatism to pair-bond duration (Scott and Clutton-Brock 1989), and future discoveries will undoubtedly continue to challenge evolutionary biologists for some time. Though an intensively studied group, many fundamental questions about waterfowl mating systems remain unanswered and exciting prospects await researchers that tackle them.

ACKNOWLEDGMENTS

Funding for this study was provided by the Natural Sciences and Engineering Council of Canada (NSERC), Canadian Wildlife Service (CWS), the CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University, the British Columbia Waterfowl Society, and the Institute of Waterfowl and Wetlands Research. Many individuals helped with capturing and marking Harlequin Ducks. I especially thank Brian Arquilla, John Ashley, Sean Boyd, Lynn Campbell, Pete Clarkson, Fred Cooke, Frank Elkins, Mary Jane Elkins, Ian Goudie, Stuart

Jackson, Heidi Regehr, Greg Robertson, Cyndi Smith, and Ken Wright. Thanks to Brian Arquilla, Heidi Regehr, Jennifer Shore, and Jason Smith for assistance with behavioural observations, and to Judy Higham, Barbara Sherman, and Connie Smith for administrative and logistic assistance. I thank Mary Jane and Frank Elkins for their frequent hospitality and enthusiasm for the project on Hornby Island. I am most grateful to Fred Cooke for continued inspiration and support and to Heidi Regehr for help with virtually every aspect of the field study. The manuscript was much improved by comments from Michael Anderson, Fred Cooke, Larry Dill, Bob Elner, Dan Esler, Heidi Regehr, and Bernie Roitberg.

LITERATURE CITED

- Afton, A.D, and R.D. Saylor. 1982. Social courtship and pairbonding of Common Goldeneyes, *Bucephala clangula*, wintering in Minnesota. *Canadian Field-Naturalist* 96:295-300.
- Alexander, W.C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. *American Birds* 37:26-29.
- Alison, R.M. 1975. Breeding biology and behavior of the Oldsquaw (*Clangula hyemalis* L.). *Ornithological Monographs* No. 18.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-265.
- Anderson, B.W., and R.L. Timkin. 1972. Sex and age ratios and weights of Common Mergansers. *Journal of Wildlife Management* 36:1127-1133.
- Anderson, M.G. 1984. Parental investment and pair-bond behavior among Canvasback ducks (*Aythya valisineria*, Anatidae). *Behavioral Ecology and Sociobiology* 15:81-90.
- Anderson, M.G. 1985. Variations on monogamy in Canvasbacks (*Aythya valisineria*). *Ornithological Monographs* 37:57-67.
- Anderson, M.G., J.M. Rhymer, and F.C. Rohwer. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pp. 365-395 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Armbruster, J.S. 1982. Wood Duck displays and pairing chronology. *Auk* 99:116-122.
- Ashcroft, R.E. 1976. A function of the pairbond in the Common Eider. *Wildfowl* 27:101-105.
- Austin, J.E., C.M. Custer, and A.D. Afton. 1998. Lesser Scaup (*Aythya affinis*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 338. The Birds of North America, Inc., Philadelphia, PA.

- Backwell, P.R.Y., and N.I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the Fiddler Crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology* 38:407-416.
- Bakker, T.C.M., and M. Milinski. 1991. Sequential female choice and the previous male effect in Sticklebacks. *Behavioral Ecology and Sociobiology* 29:205-210.
- Baldassarre, G.A., and E.G. Bolen. 1986. Body weight and aspects of pairing chronology of Green-winged Teal and Northern Pintails wintering on the southern high plains of Texas. *Southwestern Naturalist* 31:361-366.
- Ball, I.J., P.G.H. Frost, W.R. Siegfried, and F. McKinney. 1978. Territories and local movements of African Black Ducks. *Wildfowl* 29:61-79.
- Banko, P.C., J.M. Black, and W.E. Banko. 1999. Hawaiian Goose (Nene) (*Branta sandvicensis*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 434. The Birds of North America, Inc., Philadelphia, PA.
- Bateman, A.J. 1948. Intrasexual selection in *Drosophila*. *Heredity* 2:349-368.
- Bateson, P. 1983. Optimal outbreeding. Pp. 257-277 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.
- Bellrose, F.C. 1980. *Ducks, Geese and Swans of North America*. Stackpole Books, Harrisburg.
- Bellrose, F.C., T.G. Scott, A.S. Hawkins, and J.B. Low. 1961. Sex ratios and age ratios in North American ducks. *Illinois Natural History Survey Bulletin* 27:391-474.
- Bengtson, S.-A. 1972. Breeding Ecology of the Harlequin Duck *Histrionicus histrionicus* (L.) in Iceland. *Ornis Scandinavica* 3:25-43.
- Bennett, L.J. 1938. *The Blue-winged Teal: its ecology and management*. Collegiate Press, Ames.
- Bezzel, E. 1959. Beiträge zur Biologie der Geschlechter bei Entenvögeln. *Anzeiger der Ornithologischen Gesellschaft in Bayern* 5:269-355.
- Birkhead, T.R., and A.P. Møller. 1998. *Sperm competition and sexual selection*. Academic Press, San Diego.
- Black, J.M. 1996. *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Black, J.M. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioral Ecology* 12:640-645.
- Black, J.M., and M. Owen. 1987. Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour* 102:129-146.
- Black, J.M., and M. Owen. 1988. Variations in pair bond and agonistic behaviors in Barnacle Geese on the wintering grounds. Pp. 39-57 in M.W. Weller (ed.). *Waterfowl in winter*. University of Minnesota Press, Minneapolis.

- Black, J.M., and M. Owen. 1989a. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37:199-209.
- Black, J.M., and M. Owen. 1989b. Parent-offspring relationships in wintering Barnacle Geese. *Animal Behaviour* 37:187-198.
- Black, J.M., S. Choudhury, and M. Owen. 1996. Do Barnacle Geese benefit from lifelong monogamy? Pp. 91-117 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Blohm, R.J. 1982. Differential occurrence of yearling and adult male Gadwalls in pair bonds. *Auk* 99:378-379.
- Bluhm, C.K. 1985. Mate preferences and mating patterns of Canvasbacks (*Aythya valisineria*). *Ornithological Monographs* 37:45-56.
- Bluhm, C.K. 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. *Current Ornithology* 5:123-185.
- Bluhm, C.K., R.E. Phillips, W.H. Burke, and G.N. Gupta. 1984. Effects of male courtship and gonadal steroids on pair formation, egg-laying, and serum LH in Canvasback ducks (*Aythya valisineria*). *Journal of Zoology, London*. 204:185-200.
- Bordage, D., and J.-P.L. Savard. 1995. Black Scoter (*Melanitta nigra*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 177. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Borgia, G. 1981. Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. *Animal Behaviour* 29:71-80.
- Bossema, I., and J.P. Kruijt. 1982. Male activity and female mate acceptance in the Mallard (*Anas platyrhynchos*). *Behaviour* 79:313-324.
- Bossema, I., and E. Roemers. 1985. Mating strategy, including mate choice, in Mallards. *Ardea* 73:147-157.
- Botton, M.L., R.E. Loveland, and T.R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of Horseshoe Crab (*Limulus polyphemus*) eggs. *Auk* 111:605-616.
- Boyd, H. 1953. On encounters between wild white-fronted Geese in winter flocks. *Behaviour* 5:85-129.
- Bradbury, J.W. 1981. The evolution of leks. Pp. 138-169 in R.D. Alexander and D.W. Tinkle (eds.). *Natural selection and social behavior: recent research and new theory*.
- Bradbury, J.W., and S.L. Vehrencamp. 1998. *Principles of animal communication*. Sinauer Associates, Sunderland.
- Brodsky, L.M., and P.J. Weatherhead. 1985. Time and energy constraints on courtship in wintering American Black Ducks. *Condor* 87:33-36.

- Brodsky, L.M., C.D. Ankney, and D.G. Dennis. 1988. The influence of male dominance on social interactions in Black Ducks and Mallards. *Animal Behaviour* 36:1371-1378.
- Brown, J.L. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology* 8:60-65.
- Brown, P.W., and L.H. Fredrickson. 1989. White-winged Scoter, *Melanitta fusca*, populations and nesting on Redberry Lake, Saskatchewan. *Canadian Field-Naturalist* 103:240-247.
- Brown, P.W., and L.H. Fredrickson. 1997. White-winged Scoter (*Melanitta fusca*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 274. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Brown, W.D., B.J. Crespi, and J.C. Choe. 1997. Sexual conflict and the evolution of mating systems. Pp. 352-377 in J.C. Choe and B.J. Crespi (eds.). *The evolution of mating systems in insects and arachnids*. Cambridge University Press, Cambridge.
- Carter, B.C. 1958. The American Goldeneye in central New Brunswick. *Wildlife Management Bulletin*, Series 2, No. 9. Canadian Wildlife Service, Ottawa.
- Chamberlain, T.C. 1897. The method of multiple working hypotheses. *Journal of Geology* 5:837-848.
- Cheng, K.M., R.N. Shoffner, R.E. Phillips, and F.B. Lee. 1978. Mate preference in wild and domesticated (game-farm) Mallards (*Anas Platyrhynchos*): I. Initial preference. *Animal Behaviour* 26:996-1003.
- Cheng, K.M., R.N. Shoffner, R.E. Phillips, and F.B. Lee. 1979. Mate preference in wild and domesticated (game-farm) Mallards: II. Pairing success. *Animal Behaviour* 27:417-425.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour* 50:413-429.
- Choudhury, S., and J.M. Black. 1991. Testing the behavioural dominance and dispersal hypothesis in pochard. *Ornis Scandinavica* 22:155-159.
- Choudhury, S., and J.M. Black. 1993. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour* 46:747-757.
- Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. *Ibis* 138:700-709.
- Collins, S.A. 1995. The effect of recent experience on female choice in Zebra Finches. *Animal Behaviour* 49:479-486.
- Combs, D.L. 1987. Ecology of male mallards during winter in the Upper Mississippi Alluvial Valley. Ph.D. Thesis. University of Missouri, Columbia.
- Cooke, F., and J.C. Davies. 1983. Assortative mating, mate choice and reproductive fitness in Snow Geese. Pp. 279-295 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.

- Cooke, F., and C.M. McNally. 1975. Mate selection and colour preferences in Lesser Snow Geese. *Behaviour* 53:151-170.
- Cooke, F., M.A. Bousfield, and A. Sadura. 1981. Mate change and reproductive success in the Lesser Snow Goose. *Condor* 83:322-327.
- Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. The Snow Geese of La Pérouse Bay: natural selection in the wild. Oxford University Press, Oxford.
- Cooke, F., G.J. Robertson, C.M. Smith, R.I. Goudie, and W.S. Boyd. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. *Condor* 102:137-144.
- Coulson, J.C., and C.S. Thomas. 1983. Mate choice in the Kittiwake gull. Pp. 361-376 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.
- Coupe, M., and F. Cooke. 1999. Factors affecting the pairing chronologies of three species of mergansers in southwest British Columbia. *Waterbirds* 22:452-458.
- Cramp, S., and K.E.L. Simmons. 1977. The birds of the western Palearctic Vol. 1. Oxford University Press, Oxford.
- Crook, J.H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). *Behaviour Supplement* 10:1-78.
- Dale, S., and Slagsvold, T. 1996. Mate choice on multiple cues, decision rules and sampling strategies in female Pied Flycatchers. *Behaviour* 133: 903-944.
- Dane, B., and W.G. Van der Kloot. 1964. An analysis of the display of the goldeneye duck (*Bucephala clangula* (L.)). *Behaviour* 22:282-328.
- Darwin, C. 1871. The descent of man, and selection in relation to sex. Murray, London.
- Davis, E.S. 2002. Female choice and the benefits of mate guarding by male mallards. *Animal Behaviour* 64:619-628.
- Demarest, D.W., R.M. Kaminski, L.A. Brennan, and C.R. Boyle. 1997. Body-mass, survival, and pairing consequences of winter-diet restriction in Wood Ducks. *Journal of Wildlife Management* 61:822-832.
- Dombrovsky, Y., and N. Perrin. 1994. On adaptive search and optimal stopping in sequential mate choice. *American Naturalist* 144:355-361.
- Downhower, J.F., and L. Brown. 1980. Mate preferences of female mottled sculpins, *Cottus bairdi*. *Animal Behaviour* 28:728-734.
- Dugatkin, L.A., and J.-G.J. Godin. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London Series B: Biological Sciences* 249:179-184.
- Dugger, B.D., K.M. Dugger, and L.H. Fredrickson. 1994. Hooded Merganser (*Lophodytes cucullatus*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 98. The

Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.

- Dunn, P.O., A.D. Afton, M.L. Gloutney, and R.T. Alisauskas. 1999. Forced copulation results in few extrapair fertilizations in Ross's and Lesser Snow geese. *Animal Behaviour* 57:1071-1081.
- Dunning, J.B., Jr. 2000. CRC handbook of avian body masses. CRC Press, Boca Raton.
- Dwyer, T.J., S.R. Derrickson, and D.S. Gilmer. 1973. Migrational homing by a pair of Mallards. *Auk* 90:687.
- Eadie, J.M., M.L. Mallory, and H.G. Lumsden. 1995. Common Goldeneye (*Bucephala clangula*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 170. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Eadie, J.M., J.-P.L. Savard, and M.L. Mallory. 2000. Barrow's Goldeneye (*Bucephala islandica*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 548. The Birds of North America, Inc., Philadelphia, PA.
- Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Ens, B.J., S. Choudhury, and J.M. Black. 1996. Mate fidelity and divorce in monogamous birds. Pp. 344-401 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Erickson, C.J. 1978. Sexual affiliation in animals: pair bonds and reproductive strategies. Pp. 697-725 in J.B. Hutchison (ed.). *Biological determinants of sexual behaviour*. John Wiley & Sons, Chichester.
- Erskine, A.J. 1972. Buffleheads. Canadian Wildlife Service Monograph Series No. 4.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1-15.
- Forsgren, E. 1997. Mate sampling in a population of sand gobies. *Animal Behaviour* 53:267-276.
- Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Fretwell, S.D., and H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16-36.
- Ganter, B., W.S. Boyd, F. Cooke, and V.V. Baranyuk. *in prep*. Timing of first pairing in Wrangel Island Snow Geese.
- Gauthier, G. 1987a. Further evidence of long-term pair bonds in ducks of the genus *Bucephala*. *Auk* 104:521-522.

- Gauthier, G. 1987b. The adaptive significance of territorial behaviour in breeding Buffleheads: a test of three hypotheses. *Animal Behaviour* 35:348-360.
- Gauthier, G. 1993. Bufflehead (*Bucephala albeola*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 67. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 in P.P.G. Bateson and P.H. Klopfer (eds.). *Perspectives in ethology*. Vol 3. Plenum Press, New York.
- Gorman, M.L. 1970. Behavioural and physiological adaptations for breeding in the Eider duck, *Somateria m. mollissima* L. Ph.D. Thesis, University of Aberdeen, Aberdeen.
- Gorman, M.L. 1974. The endocrine basis of pair-formation behaviour in the male Eider *Somateria mollissima*. *Ibis* 116:451-465.
- Goudie, R.I., and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475-1482.
- Gowans, B., G.J. Robertson, and F. Cooke. 1997. Behaviour and chronology of pair formation by Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl* 48:135-146.
- Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. Pp. 21-52 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Gowaty, P.A. 1997. *Feminism and evolutionary biology*. Chapman & Hall, New York.
- Grafen, A., and M. Ridley. 1983. A model of mate guarding. *Journal of Theoretical Biology* 102:549-567.
- Gray, B.J. 1980. Reproduction, energetics, and the social structure of the Ruddy Duck. Ph.D. Thesis, University of California, Davis.
- Green, A.J., and M.E. Hamzaoui. 2000. Diurnal behaviour and habitat use of nonbreeding Marbled Teal, *Marmaronetta augustirostris*. *Canadian Journal of Zoology* 78:2112-2118.
- Gregoire, P.E., and C.D. Ankney. 1990. Agonistic behavior and dominance relationships among Lesser Snow Geese during winter and spring migration. *Auk* 107:550-560.
- Haegerle, C.W. 1993. Seabird predation of Pacific Herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73-82.
- Hanson, A.R., C.D. Ankney, and D.G. Dennis. 1990. Body weight and lipid reserves of American Black Ducks and Mallards during autumn. *Canadian Journal of Zoology* 68:2098-2104.
- Hanson, H.C. 1953. Inter-family dominance in Canada Geese. *Auk* 70:11-16.
- Harvey, P.H., and M.D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

- Hedrick, A.V. 1988. Female choice and the heritability of attractive male traits: An empirical study. *American Naturalist* 132:267-276.
- Heinroth, O. 1910. Beobachtungen bei einem Einbürgerungsversuch mit der Brautente (*Lampronessa sponsa* (L.)). *Journal für Ornithologie* 58:101-156.
- Heinroth, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Proceedings of the International Ornithological Congress* 5:589-702.
- Heitmeyer, M.E. 1988. Body composition of female Mallards in winter in relation to annual cycle events. *Condor* 90:669-680.
- Heitmeyer, M.E. 1995. Influences of age, body condition, and structural size on mate selection by dabbling ducks. *Canadian Journal of Zoology* 73:2251-2258.
- Hepp, G.R. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. *Auk* 103:477-484.
- Hepp, G.R. 1989. Benefits, costs, and determinants of dominance in American Black Ducks. *Behaviour* 109:222-234.
- Hepp, G.R., and J.D. Hair. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. *Wilson Bulletin* 95:675-682.
- Hepp, G.R., and J.D. Hair. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *Condor* 86:251-257.
- Hepp, G.R., and J.E. Hines. 1991. Factors affecting winter distribution and migration distance of Wood Ducks from southern breeding populations. *Condor* 93:884-891.
- Herbers, J.M. 1981. Time resources and laziness in animals. *Oecologia* 49:252-262.
- Hirschenhauser, K., E. Möstl, and K. Kotschal. 1999. Within-pair testosterone covariation and reproductive output in Greylag Geese *Anser anser*. *Ibis* 141:577-586.
- Höglund, J., and R.V. Alatalo. 1995. *Leks*. Princeton University Press, Princeton.
- Hohman, W.L. 1993. Body composition of wintering Canvasbacks in Louisiana: dominance and survival implications. *Condor* 95:377-387.
- Hohman, W.L., and C.D. Ankney. 1994. Body size and condition, age, plumage quality, and food of prenesting male Cinnamon Teal in relation to pair status. *Canadian Journal of Zoology* 72:2172-2176.
- Hohman, W.L., and M.W. Weller. 1994. Body mass and composition of Ring-necked Ducks wintering in southern Florida. *Wilson Bulletin* 106:494-507.
- Hohman, W.L., C.D. Ankney, and D.H. Gordon. 1992. Ecology and management of postbreeding waterfowl. Pp. 128-189 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.

- Holmberg, K., L. Edsman, and T. Klint. 1989. Female mate preferences and male attributes in Mallard Ducks *Anas platyrhynchos*. *Animal Behaviour* 38:1-7.
- Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* 79:383-399.
- Hupp, J.W., R.G. White, J.S. Sedinger, and D.G. Robertson. 1996. Forage digestibility and intake by Lesser Snow Geese: effects of dominance and resource heterogeneity. *Oecologia* 108:232-240.
- Inglis, I.R., J. Lazarus, and R. Torrance. 1989. The pre-nesting behaviour and time budget of the Harlequin Duck *Histrionicus histrionicus*. *Wildfowl* 40:55-73.
- Inglis, I.R., J. Lazarus, and R.L.L.F. Torrance. 2000. Breeding status and aggressive communication in the Harlequin Duck *Histrionicus histrionicus*. *Wildfowl* 51:139-153.
- Iverson, S.A. 2002. Recruitment and the spatial organization of Surf Scoter (*Melanitta perspicillata*) populations during winter in the Strait of Georgia, British Columbia. M.Sc. Thesis. Simon Fraser University, Burnaby.
- Janetos, A.C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology* 7:107-112.
- Jennions, M.D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* 72:283-327.
- Johnsgard, P.A. 1960a. Pair-formation mechanisms in *Anas* (Anatidae) and related genera. *Ibis* 102:616-618.
- Johnsgard, P.A. 1960b. A quantitative study of sexual behavior of Mallards and Black Ducks. *Wilson Bulletin* 72:133-155.
- Johnsgard, P.A. 1965. Handbook of waterfowl behavior. Cornell University Press, Ithaca.
- Johnsgard, P.A. 1975. Waterfowl of North America. Indiana University Press, Bloomington.
- Johnsgard, P.A. 1978. Ducks, geese, and swans of the world. University of Nebraska Press, Lincoln.
- Johnsgard, P.A. 1994. Arena birds: Sexual Selection and Behavior. Smithsonian Institution Press, Washington.
- Johnsgard, P.A., and M. Carbonell. 1996. Ruddy Ducks and other stiff-tails: their behavior and biology. University of Oklahoma Press, Norman.
- Johnson, K., and N.T. Burley. 1997. Mating tactics and mating systems of birds. *Ornithological Monographs* 49:21-60.
- Johnstone, R.A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews* 70:1-65.

- Johnstone, R.A. 1997. The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology* 40:51-59.
- Johnstone, R.A., J.D. Reynolds, and J.C. Deutsch. 1996. Mutual mate choice and sex differences in choosiness. *Evolution* 50:1382-1391.
- Jorde, D.G. 1981. Winter and spring staging ecology of mallards in south central Nebraska. M.Sc. Thesis, University of North Dakota, Grand Forks.
- Jorde, D.G., G.L. Krapu, and R.D. Crawford. 1983. Feeding ecology of mallards wintering in Nebraska. *Journal of Wildlife Management* 47:1044-1053.
- Kahlert, J., M. Coupe, and F. Cooke. 1998. Winter segregation and timing of pair formation in Red-breasted Merganser *Mergus serrator*. *Wildfowl* 49:161-172.
- Kear, J. 1970. The adaptive radiation of parental care in waterfowl. Pp. 357-392 in J.H. Crook (ed.). *Social behaviour in birds and mammals: essays on the social ethology of animals and man*. Academic Press, London.
- Ketterson, E.D., and V. Nolan, Jr. 1983. The evolution of differential bird migration. *Current Ornithology* 1:357-402.
- Klint, T. 1985. Mate choice and male behaviour following castration and replacement of testosterone in Mallards (*Anas platyrhynchos*). *Behavioural Processes* 11:419-424.
- Klint, T., L. Edsman, K. Holmberg, and B. Silverin. 1989. Hormonal correlates of male attractiveness during mate selection in the Mallard duck (*Anas platyrhynchos*). *Hormones and Behavior* 23:83-91.
- Korschgen, C.E., and L.H. Fredrickson. 1976. Comparative displays of yearling and adult male Wood Ducks. *Auk* 93:793-807.
- Kortright, F.H. 1942. *The ducks, geese, and swans of North America*. Stackpole, Harrisburg, and Wildlife Management Institute, Washington.
- Kozulin, A. 1995. Ecology of mallards *Anas platyrhynchos* wintering in low temperature conditions in Belarus. *Acta Ornithologica* 30:125-134.
- Krementz, D.G., R.J. Barker, and J.D. Nichols. 1997. Sources of variation in waterfowl survival rates. *Auk* 114:93-102.
- Kruijt, J.P., I. Bossema, and G.J. Lammers. 1982. Effects of early experience and male activity on mate choice in Mallard females (*Anas platyrhynchos*). *Behaviour* 80:32-43.
- Lack, D. 1940. Pair-formation in birds. *Condor* 42:269-286.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.

- Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of Bar-headed Geese (*Anser indicus*). *Behaviour* 96:28-48.
- Lank, D.B., and C.M. Smith. 1992. Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behavioral Ecology and Sociobiology* 30:323-329.
- Laurila, T. 1988. Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size and phylogeny. *Ornis Fennica* 65:49-64.
- Lebret, T. 1950. The sex-ratios and the proportion of adult drakes of teal, pintail, shoveler and wigeon in the Netherlands, based on field counts made during autumn, winter and spring. *Ardea* 38:1-18.
- Lebret, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos* L. *Ardea* 49:7-158.
- Lee, S.-D. 1997. A time-budget study of wintering Mallards on the Southern High Plains of Texas, USA. *Korean Journal of Biological Sciences* 1:571-576.
- Ligon, J.D., and M. Ramos. 1999. The evolution of avian breeding systems. Oxford University Press, Oxford.
- Livezey, B.C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. *Auk* 108:471-507.
- Livezey, B.C. 1997. A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. *Annals of Carnegie Museum* 66:457-496.
- Loonen, M.J.J.E., L.W. Bruinzeel, J.M. Black, and R.H. Drent. 1999. The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. *Journal of Animal Ecology* 68:753-768.
- Lorenz, K.Z. 1941. Vergleichende Bewegungsstudien an Anatinen. *Journal für Ornithologie* 89:194-294.
- Lovvorn, J.R. 1989. Food defendability and antipredator tactics: implications for dominance and pairing in Canvasbacks. *Condor* 91:826-836.
- Low, J.B. 1945. Ecology and management of the Redhead *Nyroca americana*, in Iowa. *Ecological Monographs* 15:35-69.
- Lyon, B.E., and R.D. Montgomerie. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution* 40:605-615.
- Mallory, M., and K. Metz. 1999. Common Merganser (*Mergus merganser*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 442. The Birds of North America, Inc., Philadelphia, PA.
- Marsden, S.J., and M.S. Sullivan. 2000. Intersexual differences in feeding ecology in a male-dominated wintering pochard *Aythya ferina* population. *Ardea* 88:1-7.

- Mather, D.D., and D. Esler. 1999. Evaluation of bursal depth as an indicator of age class of Harlequin Ducks. *Journal of Field Ornithology* 70:200-205.
- Maynard Smith, J. 1956. Fertility, mating behaviour and sexual selection in *Drosophila subobscura*. *Journal of Genetics* 54:261-279.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25:1-9.
- Maynard Smith, J., and G.A. Parker. 1976. The logic of asymmetric contests. *Animal Behaviour* 24:159-175.
- Mazalov, V., N. Perrin, and Y. Dombrovsky. 1996. Adaptive search and information updating in sequential mate choice. *American Naturalist* 148:123-137.
- McKinney, F. 1975. The evolution of duck displays. Pp. 331-357 in G. Baerends, C. Beer, and A. Manning (eds.). *Function and evolution in behaviour*. Clarendon Press, Oxford.
- McKinney, F. 1985. Primary and secondary male reproductive strategies of dabbling ducks. *Ornithological Monographs* 37:68-82.
- McKinney, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pp. 153-171 in D.I. Rubenstein and R.W. Wrangham (eds.). *Ecological aspects of social evolution*. Princeton University Press, Princeton.
- McKinney, F. 1992. Courtship, pair formation, and signal systems. Pp. 214-250 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- McKinney, F., and S. Evarts. 1997. Sexual coercion in waterfowl and other birds. *Ornithological Monographs* 49:163-195.
- McKinney, F., S.R. Derrickson, and P. Mineau. 1983. Forced copulation in waterfowl. *Behaviour* 86:250-294.
- McNamara, J.M., and A.I. Houston. 1980. The application of statistical decision theory to animal behavior. *Journal of Theoretical Biology* 85:673-690.
- Migoya, R.M., G.A. Baldassarre, and M.P. Losito. 1994. Diurnal activity budgets and habitat functions of Northern Pintail *Anas acuta* wintering in Sinaloa, Mexico. *Wildfowl* 45:134-146.
- Milinski, M., and T.C.M. Bakker. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society of London Series B: Biological Sciences* 250:229-233.
- Miller, M.R. 1985. Time budgets of Northern Pintails wintering in the Sacramento Valley, California. *Wildfowl* 36:53-64.

- Miller, M.R., J. Beam, and D.P. Connelly. 1988. Dabbling duck harvest dynamics in the central valley of California - implications for recruitment. Pp. 553-569 *in* M.W. Weller (ed.). *Waterfowl in winter*. University of Minnesota Press, Minneapolis.
- Milne, H. 1974. Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve, Scotland. *Ibis* 116:135-154.
- Minton, C.D.T. 1968. Pairing and breeding of Mute Swans. *Wildfowl* 19:41-60.
- Møller, A.P. 1994. *Sexual selection and the Barn Swallow*. Oxford University Press, Oxford.
- Mowbray, T.B., F. Cooke, and B. Ganter. 2000. Snow Goose (*Chen caerulescens*). *In* A. Poole and F. Gill (eds.). *The Birds of North America*, No. 514. The Birds of North America, Inc., Philadelphia, PA.
- Mulder, R.S., T.D. Williams, and F. Cooke. 1995. Dominance, brood size and foraging behavior during brood-rearing in the Lesser Snow Goose: an experimental study. *Condor* 97:99-106.
- Nakamura, M., and T. Atsumi. 2000. Adaptive significance of winter pair bond in male pintail, *Anas acuta*. *Journal of Ethology* 18:172-131.
- Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. *Condor* 82:406-416.
- Nichols, J.D., K.J. Reinecke, and J.E. Hines. 1983. Factors affecting the distribution of Mallards wintering in the Mississippi alluvial valley. *Auk* 100:932-946.
- Nilsson, L. 1970. Local and seasonal variation in sex-ratios of diving ducks in south Sweden during the non-breeding season. *Ornis Scandinavica* 1:115-128.
- Omland, K.E. 1996. Female mallard mating preferences for multiple male ornaments I. Natural variation. *Behavioral Ecology and Sociobiology* 39:353-360.
- Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589-603.
- Oring, L.W. 1982. Avian mating systems. Pp. 1-92 *in* D.S. Farner, J.S. King, and K.C. Parkes (eds.). *Avian Biology*, Vol. 6 Academic Press, New York.
- Oring, L.W., and R.D. Saylor. 1992. The mating systems of waterfowl. Pp. 190-213 *in* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Owen, M. 1980. *Wild geese of the world: their life history and ecology*. Fakenham Press, Fakenham.
- Owen, M., and J.M. Black. 1990. *Waterfowl ecology*. Blackie, Glasgow.

- Owen, M., J.M. Black, and H. Liber. 1988. Pair bond duration and timing of its formation in Barnacle Geese (*Branta leucopsis*). Pp. 23-38 in M.W. Weller (ed.). Waterfowl in winter. University of Minnesota Press, Minneapolis.
- Palmer, R.S. 1976a. Handbook of North American birds, Vol. 2. Waterfowl. Yale University Press, New Haven.
- Palmer, R.S. 1976b. Handbook of North American birds, Vol. 3. Waterfowl. Yale University Press, New Haven.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45:525-567.
- Parker, G.A. 1983. Mate quality and mating decisions. Pp. 141-166 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.
- Patriquin-Meldrum, K.J., and J.-G.J. Godin. 1998. Do female three-spined sticklebacks copy the mate choice of others? *American Naturalist* 151:570-577.
- Pattenden, R.K., and D.A. Boag. 1989. Effects of body mass on courtship, pairing, and reproduction in captive mallards. *Canadian Journal of Zoology* 67:495-501.
- Patterson, I.J. 1977. Aggression and dominance in winter flocks of Shelduck *Tadorna tadorna* (L.). *Animal Behaviour* 25:447-459.
- Patterson, I.J. 1982. *The Shelduck: a study in behavioural ecology*. Cambridge University Press, Cambridge.
- Paulus, S.L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947-952.
- Paulus, S.L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. *Journal of Wildlife Management* 48:371-380.
- Paulus, S.L. 1988a. Time-activity budgets of nonbreeding Anatidae: a review. Pp. 135-152 in M.W. Weller (ed.). *Waterfowl in winter*. University of Minnesota Press, Minneapolis.
- Paulus, S.L. 1988b. Social behavior and pairing chronology of mottled ducks during autumn and winter in Louisiana. Pp. 59-70 in M.W. Weller (ed.). *Waterfowl in winter*. University of Minnesota Press, Minneapolis.
- Perrins, C.M. 1970. The timing of birds breeding seasons. *Ibis* 112:242-255.
- Petrie, M. 1986. Mating decisions by female Common Moorhens (*Gallinula chloropus*). *Proceedings of the International Ornithological Congress* 19:947-955.
- Petrie, M., and F.M. Hunter. 1993. Intraspecific variation in courtship and copulation frequency: an effect of mismatch in partner attractiveness? *Behaviour* 127:265-277.
- Port, J.L. 1998. Long-term pair bonds and male parental care in Speckled Teal *Anas flavirostris* in eastern Argentina. *Wildfowl* 49:139-149.

- Prevett, J.P., and C.D. MacInnes. 1980. Family and other social groups in Snow Geese. *Wildlife Monographs* 71:1-46.
- Raitasuo, K. 1964. Social behaviour of the Mallard, *Anas platyrhynchos*, in the course of the annual cycle. *Finnish Game Research* 24:1-72.
- Rasa, O.A.E. 1997. Female mate assessment tactics in a subsocial desert beetle: a test of Janetos' models. *Ethology Ecology and Evolution* 9:233-240.
- Rave, D.P., and G.A. Baldassarre. 1989. Activity budgets of Green-winged Teal wintering in coastal wetlands of Louisiana. *Journal of Wildlife Management* 53:753-759.
- Raveling, D.G. 1969. Social classes of Canada Geese in winter. *Journal of Wildlife Management* 33:304-318.
- Raveling, D.G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. *Behaviour* 37:291-319.
- Real, L. 1990. Search theory and mate choice I. Models of single-sex discrimination. *American Naturalist* 136:376-404.
- Real, L. 1991. Search theory and mate choice II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *American Naturalist* 138:901-917.
- Rees, E.C., P. Lievesley, R.A. Pettifor, and C. Perrins. 1996. Mate fidelity in swans: an interspecific comparison. Pp. 118-137 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- 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.
- Reid, M.L., and J.A. Stamps. 1997. Female mate choice tactics in a resource-based mating system: field tests of alternative models. *American Naturalist* 150:98-121.
- Reynolds, J.D., and M.R. Gross. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proceedings of the Royal Society of London Series B: Biological Sciences* 250:57-62.
- Ricklefs, R.E. 1974. Energetics of Reproduction in Birds. p. 52-297 in R.A. Paynter, Jr. (ed.) *Avian Energetics*. Cambridge, Massachusetts.
- Ridley, M. 1983. *The explanation of organic diversity: the comparative method and adaptations for mating*. Clarendon Press, Oxford.
- Robertson, G.J., and R.I. Goudie. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 466. The Birds of North America, Inc., Philadelphia, PA.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1997. The timing of arrival and moult chronology of Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl* 48:147-155.

- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1998. The timing of pair formation in Harlequin Ducks. *Condor* 100:551-555.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 1999. Within-year fidelity of Harlequin Ducks to a moulting and wintering area. Pp. 45-51 in R.I. Goudie, M.R. Petersen, and G.J. Robertson (eds.). Behaviour and ecology of sea ducks. Occasional Paper No. 100. Canadian Wildlife Service, Ottawa.
- Robertson, G.J., F. Cooke, R.I. Goudie, and W.S. Boyd. 2000. Spacing patterns, mating systems, and winter philopatry in Harlequin Ducks. *Auk* 117:299-307.
- Robertson, J.G.M. 1990. Female choice increases fertilization success in the Australian frog *Uperoleia laevis*. *Animal Behaviour* 39:639-645.
- Rodway, M.S., and F. Cooke. 2001. Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor* 103:870-874.
- Rodway, M.S., and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. *Journal of Field Ornithology* 73:363-371.
- Rodway, M.S., H.M. Regehr, and F. Cooke. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates. *Canadian Journal of Zoology* 81:492-503.
- Rodway, M.S., H.M. Regehr, J. Ashley, P.V. Clarkson, R.I. Goudie, D.E. Hay, C.M. Smith, and K.G. Wright. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology* 81:504-514.
- Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.
- Rohwer, F.C., and M.G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- Rohwer, F.C. 1992. The evolution of reproductive patterns in waterfowl. Pp. 486-539 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.
- Rowley, I. 1983. Re-mating in birds. Pp. 331-360 in P. Bateson (ed.). Mate Choice. Cambridge University Press, Cambridge.
- Rylander, M.K. 1993. Observation on the social behaviour of semicaptive Barnacle Geese (*Branta leucopsis*). *Vogelwarte* 37:43-49.
- Sargeant, A.B., and D.G. Raveling. 1992. Mortality during the breeding season. Pp. 396-422 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.

- Savard, J.-P.L. 1984. Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. *Ornis Scandinavica* 15:211-216.
- Savard, J.-P.L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (*Bucephala islandica*). *Auk* 102:389-391.
- Savard, J.-P.L. 1988. Winter, spring and summer territoriality in Barrow's Goldeneye: characteristics and benefits. *Ornis Scandinavica* 19:119-128.
- Savard, J.-P.L., D. Bordage, and A. Reed. 1998. Surf Scoter (*Melanitta perspicillata*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 363. The Birds of North America, Inc., Philadelphia, PA.
- Scott, D.K. 1980. Functional aspects of the pair bond in winter in Bewick's Swans (*Cygnus columbianus bewickii*). *Behavioral Ecology and Sociobiology* 7:323-327.
- Scott, D.K., and T.H. Clutton-Brock. 1989. Mating systems, parasites and plumage dimorphism in waterfowl. *Behavioral Ecology and Sociobiology* 26:261-273.
- Searcy, W.A., and K. Yasukawa. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton University Press, Princeton.
- Sherrod, L. 1974. The role of sibling associations in the formation of social and sexual companion preferences in ducks (*Anas platyrhynchos*): an investigation of the 'primacy versus recency' question. *Zeitschrift für Tierpsychologie* 34:247-264.
- Siegfried, W.R. 1976. Social organization in Ruddy and Maccoa ducks. *Auk* 93:560-570.
- Siriwardena, G.M., and J.M. Black. 1998. Parent and gosling strategies in wintering Barnacle Geese *Branta Leucopsis*. *Wildfowl* 49:18-26.
- Skutch, A.F. 1992. *Origins of nature's beauty*. University of Texas Press, Austin.
- Slagsvold, T., and S. Dale. 1994. Why do female Pied Flycatchers mate with already mated males: deception or restricted mate sampling? *Behavioral Ecology and Sociobiology* 34:239-250.
- Smith, C., F. Cooke, and R.I. Goudie. 1998. Ageing Harlequin Ducks *Histrionicus histrionicus* drakes using plumage characteristics. *Wildfowl* 49:245-248.
- Smith, C.M., F. Cooke, and G.J. Robertson. 2000. Long-term pair bonds in Harlequin Ducks. *Condor* 102:201-205.
- Smith, J.D. 1946. The Canvasback in Minnesota. *Auk* 63:73-81.
- Smith, R.L. 1984. *Sperm competition and the evolution of animal mating systems*. Academic Press, Orlando.
- Smith, S.M. 1991. *The Black-capped Chickadee: behavioral ecology and natural history*. Cornell University Press, Ithaca.

- Sorenson, L.G. 1991. Mating systems of tropical and southern hemisphere dabbling ducks. *Proceedings of the International Ornithological Congress* 20:851-859.
- Sorenson, L.G. 1992. Variable mating system of a sedentary tropical duck: the White-Cheeked Pintail (*Anas bahamensis bahamensis*). *Auk* 109:277-292.
- Sorenson, L.G., and S.R. Derrickson. 1994. Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology* 35:389-400.
- Sorenson, L.G., P.M. Nolan, A.M. Brown, S.R. Derrickson, and S.L. Monfort. 1997. Hormonal dynamics during mate choice in the northern pintail: a test of the 'challenge' hypothesis. *Animal Behaviour* 54:1117-1133.
- Soutiere, E.C., H.S. Myrick, and E.G. Bolen. 1972. Chronology and behavior of American Wigeon wintering in Texas. *Journal of Wildlife Management* 36:752-758.
- Spurr, E., and H. Milne. 1976. Adaptive significance of autumn pair formation in the Common Eider *Somateria mollissima* (L.). *Ornis Scandinavica* 7:85-89.
- Stahl, J., P.H. Tolsma, M.J.J.E. Loonen, and R.H. Drent. 2001. Subordinates explore but dominants profit: resource competition in high Arctic Barnacle Goose flocks. *Animal Behaviour* 61:257-264.
- Stewart, G.R., and R.D. Titman. 1980. Territorial behaviour by prairie pothole Blue-winged Teal. *Canadian Journal of Zoology* 58:639-649.
- Stotts, V.D. 1958. The time of formation of pairs in Black Ducks. *Transactions of the North American Wildlife Conference* 23:192-197.
- Stotts, V.D., and D.E. Davis. 1960. The Black Duck in the Chesapeake Bay of Maryland: breeding behavior and biology. *Chesapeake Science* 1:127-154.
- Sullivan, M.S. 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour* 47:141-151.
- Thompson, J.D., and G.A. Baldassarre. 1992. Dominance relationships of dabbling ducks wintering in Yucatan, Mexico. *Wilson Bulletin* 104:529-536.
- Thornhill, R., and J. Alcock. 1983. *The evolution of insect mating systems*. Harvard University Press, Cambridge, Mass.
- Titman, R.D. 1999. Red-breasted Merganser (*Mergus serrator*). In A. Poole and F. Gill (eds.). *The Birds of North America*, No. 443. The Birds of North America, Inc., Philadelphia, PA.
- Todd, P.M., and G.F. Miller. 1993. Parental guidance suggested: how parental imprinting evolves through sexual selection as an adaptive learning mechanism. *Adaptive Behavior* 2:5-47.
- Torres, R., F. Cooke, G.J. Robertson, and W.S. Boyd. 2002. Pairing decisions in the Harlequin Duck: costs and benefits. *Waterbirds* 25:340-347.

- Trauger, D.L. 1971. Population ecology of Lesser Scaup (*Aythya affinis*) in subarctic taiga. Ph.D. Thesis, Iowa State University, Ames.
- Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179 in B. Cambell (ed.). Sexual selection and the descent of man. Aldine, Chicago.
- US Navy. 2000. Website: <http://riemann.usno.navy.mil/AA/data/>. [accessed 15 September 2000].
- Van der Jeugd, H., and K.B. Blaakmeer. 2001. Teenage love: the importance of trial liaisons, subadult plumage and early pairing in Barnacle Geese. *Animal Behaviour* 62:1075-1083.
- Viallefont, A., F. Cooke, and J.-D. Lebreton. 1995. Age-specific costs of first-time breeding. *Auk* 112:67-76.
- Wedekind, C., and S. Furi. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London Series B: Biological Sciences* 264:1471-1479.
- Weidmann, U., and J. Darley. 1971. The role of the female in the social display of Mallards. *Animal Behaviour* 19:287-298.
- Weller, M.W. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). *Auk* 82:227-235.
- Weller, M.W. 1967. Courtship of the Redhead (*Aythya americana*). *Auk* 84:544-559.
- Widemo, F., and S.A. Sæther. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences.
- Williams, D.M. 1983. Mate choice in the Mallard. Pp. 297-309 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.
- Williams, M., and F. McKinney. 1996. Long-term monogamy in a river specialist - the Blue Duck. Pp. 73-90 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Williams, T.D. 1994. Adoption in a precocial species, the Lesser Snow Goose: intergenerational conflict, altruism or a mutually beneficial strategy? *Animal Behaviour* 47:101-107.
- Wishart, R.A. 1983. Pairing chronology and mate selection in the American Wigeon (*Anas americana*). *Canadian Journal of Zoology* 61:1733-1743.
- Wittenberger, J.F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in P. Marler and J. Vandenberg (eds.). *Handbook of behavioral neurobiology: social behavior and communication*. Plenum, New York.
- Wittenberger, J.F. 1983. Tactics of mate choice. Pp. 435-447 in P. Bateson (ed.). *Mate Choice*. Cambridge University Press, Cambridge.
- Wittenberger, J.F., and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. *Avian Biology* 8:1-78.

- Wittenberger, J.F., and R.L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Sytematics* 11:197-232.
- Wright, K.G., and P.V. Clarkson. 1998. Harlequin Duck moulting ecology and banding synopsis in the strait of Georgia, British Columbia: 1997 Progress Report. Unpublished Report.
- Wynne-Edwards, V.C. 1962. *Animal dispersion in relation to social behaviour*. Oliver and Boyd, Edinburgh.

Table 6.1. Predictions of the *female benefits-male costs hypothesis* and the *female-biased choice hypothesis* to explain variation in the timing of pairing in waterfowl, as measured by the date of pairing (pair-date), the number of days spent in courtship and mate-sampling (court-time), and the amount of time allocated to courtship per day (court-rate), and in relation to time budgets and spacing behaviour during the non-breeding season. Herring spawn is an ephemeral superabundant food available to Harlequin Ducks in March.

Male-costs predictions	Female-choice predictions	Available data (<i>in litt.</i>) ¹	Harlequin Ducks (this study)
<u>Winter time budgets</u>			
Feeding Paired females spend more time than unpaired females	No necessary trend	No difference	No difference except unpaired more during herring spawning
Unpaired males spend more time than paired males	No necessary trend	No difference	Unpaired less through winter; more during herring spawning
Agonistic interactions Paired females receive less than unpaired females	No necessary trend	No difference	Less for paired females but no difference outside courtship
Vigilance Paired females spend less time than unpaired females	No necessary trend	No difference	No difference
Courtship Unpaired males spend less time in courtship than paired males spend in mate defence	Unpaired males spend as much or more time in courtship than paired males spend in mate defence	Unpaired spend more time in courtship than paired spend in defence	Unpaired spend more time in courtship than paired spend in defence
Pair-bond defence Males do most defence	Shared defence relative to mate quality	No data	Shared defence relative to mate quality

Table 6.1 cont'd

Male-costs predictions	Female-choice predictions	Available data (<i>in litt.</i>) ¹	Harlequin Ducks (this study)
<u>Pairing chronology: intra-specific trends</u>			
Pair-date Young, inexperienced males pair later than older males	Young, inexperienced males pair later than older males	Young males pair later	Young males pair later
Young females pair later than old females when sex ratios balanced; at same time when sex ratios male-biased	Young females pair later than previously paired females; re-uniting females pair earliest	Young females later even when sex ratios male-biased	Young females pair later; re-uniting females pair earliest
Court-time			
No necessary trend	Time courting greater for naive than experienced birds	No data	Time courting greater for naive birds
Court-rate			
No trend for females	Female pair-date earlier with higher court-rate	No data	Female pair-date earlier with higher court-rate
Male pair-date earlier with higher court-rate	No necessary trend	No data	No trend for males
<u>Pairing chronology: inter-specific trends</u>			
Pairing earlier with increased body size	No necessary trend	No general trend	n/a
No prediction	Greater time spent in courtship with increasing duration of pair bond	Greater time courting with increasing pair-bond duration	n/a

Table 6.1 cont'd

Male-costs predictions	Female-choice predictions	Available data (<i>in litt.</i>) ¹	Harlequin Ducks (this study)
No prediction	Greater time spent in courtship with increasing paternal care	Greater time courting with increasing paternal care	n/a
Earlier pair-date with increasing male-bias in sex ratio	Later pair-date with increasing male-bias in sex ratio	Later pair-date with increasing male-bias	n/a
<u>Spacing behaviour in dispersed populations</u>			
No predictions	Unpaired birds in larger groups than paired birds	No data	Unpaired birds in larger groups
No predictions	Courtship groups larger than other groups	Courtship groups larger in <i>Aix sponsa</i>	Courtship groups larger than random and feeding but not roosting groups
No predictions	Ratio of unpaired to paired birds greater in larger groups at courting arenas or at "lekking" sites	No data	Ratio of unpaired to paired females greater in larger courting groups and at one "lekking" site
No predictions	Male-bias in sex ratio greater in larger courting groups than other groups and at "lekking" than other sites when population male-biased	Male-bias greater in larger courting groups in <i>Aix sponsa</i>	Male-bias greater in larger courting groups and at one "lekking" site
No predictions	Court-rate greater at "lekking" sites than elsewhere	No data	Court-rate greater at one "lekking" site

Table 6.1 cont'd

Male-costs predictions	Female-choice predictions	Available data (<i>in litt.</i>) ¹	Harlequin Ducks (this study)
<u>Behaviour of immature birds</u>			
No predictions	Immature birds show same spacing as older, unpaired birds	No data	Immature male spacing same as older, unpaired birds
No predictions	Immature birds actively participate in courtship	Immatures in courtship	Immature males courting through winter; females courting in spring
<u>Response to ephemerally superabundant food</u>			
No predictions	Unpaired birds more likely than paired birds to move to exploit food	No data	Ratio of unpaired to paired females greater at herring spawning than elsewhere
No predictions	Male-bias in sex ratio greater where superabundant food available than elsewhere	No data	Male-bias greater at herring spawning
Unpaired males spend more time courting when superabundant food available	Unpaired birds spend more time courting where superabundant food available than elsewhere	No data	Unpaired birds court more at herring spawning
No predictions	Group size of unpaired, courting birds larger where superabundant food available than elsewhere	No data	No difference; all groups larger in size

¹See text for references.

TABLE 6.2. Monthly changes in the percentage (n) of marked, first-, second-, third-, and after-third-year female and male Harlequin Ducks that were identified as paired in the Strait of Georgia, British Columbia, 1995-2001. Percentages within each month are based on the number of birds whose apparent pair status was determined one or more times in that month.

Month	Female age				Male age		
	1	2	3	> 3	2	3	> 3
Sept	0.0 (1)	0.0 (13)	0.0 (14)	2.0 (100)	0.0 (1)	0.0 (7)	1.8 (113)
Oct	0.0 (1)	9.1 (11)	20.0 (20)	51.9 (131)	0.0 (1)	9.1 (11)	39.3 (112)
Nov	0.0 (4)	5.3 (19)	55.6 (18)	77.4 (133)	0.0 (4)	9.1 (11)	54.2 (120)
Dec	0.0 (0)	0.0 (1)	61.5 (13)	98.0 (49)	0.0 (1)	0.0 (4)	52.4 (42)
Jan	0.0 (2)	41.7 (24)	82.1 (28)	94.4 (108)	0.0 (2)	14.3 (7)	51.8 (85)
Feb	0.0 (5)	43.8 (16)	90.0 (20)	92.5 (120)	0.0 (3)	20.0 (10)	59.4 (101)
Mar	20.0 (10)	81.8 (55)	90.6 (64)	96.9 (451)	19.0 (21)	18.2 (33)	65.0 (592)
Apr	33.3 (3)	95.2 (21)	100.0 (36)	99.4 (159)	28.6 (7)	44.4 (9)	75.9 (191)

TABLE 6.3. Proportions of time and absolute amount of time spent during diurnal periods in various activities by wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000. Listed values are means \pm SE, and statistical results for date-location differences are from a 2-way ANOVA model relating time spent to date-location and sex-paired status categories. In all months birds spent <1% of their day in agonistic interactions and predator avoidance and only estimates of the amount of time spent and the frequency of agonistic interactions are given for those activities.

Activity	Oct	Nov	Dec	Jan	Feb	March		Apr	ANOVA results
						without spawn	with spawn		
No. of observations	144	401	247	649	341	216	323	288	
Proportion of time (%)									
Feeding	42 \pm 3	50 \pm 2	59 \pm 2	61 \pm 1	62 \pm 2	56 \pm 2	16 \pm 1	42 \pm 2	49.4
Resting	12 \pm 2	7 \pm 1	6 \pm 1	3 \pm 1	6 \pm 1	10 \pm 1	26 \pm 2	24 \pm 1	87.9
Preening and bathing	13 \pm 2	19 \pm 1	9 \pm 1	9 \pm 1	10 \pm 1	18 \pm 2	23 \pm 1	15 \pm 1	30.6
Swimming and flying	25 \pm 2	19 \pm 1	22 \pm 2	22 \pm 1	20 \pm 1	14 \pm 1	27 \pm 1	17 \pm 1	7.0
Courtship	8 \pm 2	6 \pm 1	5 \pm 1	3 \pm 0	2 \pm 0	2 \pm 0	7 \pm 1	1 \pm 0	8.4
Amount of time per diurnal day (min)									
Feeding	261 \pm 19	280 \pm 11	299 \pm 12	327 \pm 8	374 \pm 10	399 \pm 16	109 \pm 7	346 \pm 15	49.8
Resting	74 \pm 12	38 \pm 5	28 \pm 6	17 \pm 3	36 \pm 5	71 \pm 10	180 \pm 10	199 \pm 15	85.9
Preening and bathing	79 \pm 11	109 \pm 5	47 \pm 7	49 \pm 4	60 \pm 6	132 \pm 11	156 \pm 8	120 \pm 8	32.1
Swimming and flying	157 \pm 13	105 \pm 6	114 \pm 8	119 \pm 5	120 \pm 7	99 \pm 8	185 \pm 9	142 \pm 8	13.6
Courtship	47 \pm 9	33 \pm 4	23 \pm 4	18 \pm 2	15 \pm 2	11 \pm 3	47 \pm 6	6 \pm 2	9.9
Agonistic interactions	1 \pm 0	1 \pm 0	1 \pm 0	<1 \pm 0	2 \pm 0	3 \pm 1	3 \pm 1	2 \pm 0	7.6
Vigilance and escape	1 \pm 0	2 \pm 1	1 \pm 1	0 \pm 0	1 \pm 0	1 \pm 0	3 \pm 1	2 \pm 0	2.5
Frequency of agonistic interactions (no. h ⁻¹)									
All interactions	10 \pm 2	7 \pm 1	6 \pm 2	7 \pm 1	4 \pm 1	3 \pm 2	25 \pm 1	10 \pm 1	25.0

TABLE 6.4. Proportion of time and absolute amount of time spent during diurnal periods in various activities by wintering Harlequin Ducks in relation to sex and paired status. Listed are estimated marginal means \pm SE from a 2-way ANOVA model relating time spent to date-location and sex-paired status categories. Different superscripts indicate significant differences between categories.

Activity	Unpaired female	Paired female	Unpaired male	Paired male	F	P
No. of observations	435	851	560	789		
Hours of observation	87.2	238.4	119.3	228.6		
Proportion of time (%)						
Feeding	51.0 \pm 2.0 ^a	51.3 \pm 1.3 ^a	43.9 \pm 1.5 ^b	48.5 \pm 1.4 ^a	4.6	0.003
Resting	8.8 \pm 1.0 ^a	12.8 \pm 0.7 ^b	10.0 \pm 0.9 ^a	13.4 \pm 0.8 ^b	6.8	0.000
Preening and bathing ¹	17.0 \pm 1.1	14.6 \pm 0.8	13.3 \pm 1.0	13.1 \pm 0.8	2.2	0.087
Swimming and flying ¹	17.1 \pm 1.1 ^a	19.5 \pm 0.8 ^a	25.8 \pm 1.0 ^b	21.9 \pm 0.8 ^c	16.0	0.000
Courtship ²	9.6 \pm 0.7 ^a	2.0 \pm 0.4 ^b	9.5 \pm 0.6 ^a	0.4 \pm 0.5 ^c	118.1	0.000
Aggression to others	<0.1 \pm 0.1 ^a	<0.1 \pm 0.0 ^a	0.1 \pm 0.0 ^a	0.6 \pm 0.0 ^b	93.0	0.000
Victim of aggression	0.1 \pm 0.0 ^a	<0.1 \pm 0.0 ^b	<0.1 \pm 0.0 ^b	<0.1 \pm 0.0 ^c	23.9	0.000
Predator avoidance	0.2 \pm 0.1 ^{ab}	0.1 \pm 0.1 ^a	0.4 \pm 0.1 ^b	0.2 \pm 0.1 ^a	3.9	0.009
Amount of time per diurnal day (min)						
Feeding	317 \pm 12 ^a	316 \pm 8 ^a	271 \pm 9 ^b	298 \pm 8 ^a	5.4	0.001
Resting	60 \pm 7 ^a	87 \pm 5 ^b	69 \pm 6 ^a	92 \pm 5 ^b	6.2	0.000
Preening and bathing ¹	107 \pm 7 ^a	95 \pm 5 ^{ab}	86 \pm 6 ^b	84 \pm 5 ^b	2.9	0.032
Swimming and flying ¹	106 \pm 7 ^a	122 \pm 5 ^a	161 \pm 6 ^b	137 \pm 5 ^c	14.1	0.000
Courtship ²	59 \pm 4 ^a	12 \pm 3 ^b	59 \pm 3 ^a	2 \pm 3 ^c	88.8	0.000
Aggression to others	<1 \pm 0 ^a	<1 \pm 0 ^a	<1 \pm 0 ^a	4 \pm 0 ^b	49.6	0.000
Victim of aggression	1 \pm 0 ^a	<1 \pm 0 ^b	<1 \pm 0 ^b	<1 \pm 0 ^c	18.5	0.000
Predator avoidance	1 \pm 0 ^{ab}	1 \pm 0 ^a	2 \pm 0 ^b	1 \pm 0 ^a	2.8	0.041

¹ Excluding 1Y males (see text).

² Excluding 1Y males and known 1Y females (see text).

TABLE 6.5. Agonistic interactions among wintering Harlequin Ducks in relation to sex and paired status. Listed are estimated marginal means \pm SE from a 2-way ANOVA model relating number of interactions per hour to date-location and sex-paired status categories. Different superscripts indicate significant differences between categories. Sample sizes are given in Table 6.3. Chases between mates were included but low-intensity, intra-pair displays were excluded (see Methods).

Type of interaction	Unpaired female	Paired female	Unpaired male	Paired male	ANOVA results <i>F</i> <i>P</i>
All agonistic displays including those performed during courtship (no. h ⁻¹)					
Directed at:					
Females	0.7 \pm 0.3 ^{ac}	0.2 \pm 0.2 ^a	7.6 \pm 0.8 ^b	1.6 \pm 0.7 ^c	38.2 0.000
Males	3.7 \pm 0.6 ^{ac}	2.3 \pm 0.4 ^b	3.6 \pm 0.4 ^{ab}	5.1 \pm 0.4 ^c	8.7 0.000
All recipients	5.1 \pm 0.7 ^a	2.8 \pm 0.5 ^b	11.2 \pm 0.9 ^c	7.0 \pm 0.8 ^a	23.5 0.000
Received from:					
Females	0.2 \pm 0.0 ^a	<0.1 \pm 0.0 ^b	2.1 \pm 0.4 ^c	0.1 \pm 0.3 ^{ab}	15.3 0.000
Males	6.0 \pm 0.8 ^a	1.6 \pm 0.6 ^b	1.4 \pm 0.2 ^b	0.2 \pm 0.2 ^c	25.8 0.000
Other species	0.6 \pm 0.1 ^a	0.3 \pm 0.1 ^b	0.8 \pm 0.1 ^a	0.3 \pm 0.1 ^b	7.7 0.000
All sources	6.8 \pm 0.8 ^a	1.9 \pm 0.6 ^b	4.3 \pm 0.5 ^a	0.6 \pm 0.4 ^c	21.2 0.000
Total interactions	11.9 \pm 1.1 ^a	4.7 \pm 0.8 ^b	15.6 \pm 1.2 ^a	7.6 \pm 1.0 ^c	22.3 0.000
Agonistic displays excluding those performed during courtship (no. h ⁻¹)					
Directed at others	2.0 \pm 0.5 ^a	2.6 \pm 0.4 ^a	3.9 \pm 0.4 ^a	5.4 \pm 0.4 ^b	12.9 0.000
Received from others	1.6 \pm 0.2 ^a	1.9 \pm 0.2 ^a	2.6 \pm 0.2 ^a	0.7 \pm 0.2 ^b	16.4 0.000
Total interactions	3.6 \pm 0.6 ^a	4.5 \pm 0.4 ^a	6.5 \pm 0.5 ^b	6.1 \pm 0.4 ^b	5.2 0.001

TABLE 6.6. Relative frequencies of different aggressive displays performed by wintering Harlequin Ducks in relation to their sex, age [hatch-year (1Y) and after-hatch-year (A1Y)], and paired status, and to the target of the display. Displays are listed in order of increasing intensity (see text). All displays between mates were excluded.

Target and type of display	Unpaired female	Unpaired 1Y male	Unpaired A1Y male	Paired female	Paired male
Number of displays	325	108	715	594	1477
Directed at females (%)					
Head-nod	6.5	8.3	22.1	1.2	2.6
Bill-poke	3.1	8.3	1.5	4.0	0.4
Bill gape	5.5	1.9	0.0	0.8	0.8
Chase	1.5	8.3	29.1	3.0	2.4
Trounce	0.0	0.0	0.0	0.5	0.0
Total	16.6	26.9	52.7	9.6	6.2
Directed at 1Y males (%)					
Head-nod	0.9	0.0	0.0	1.0	0.7
Bill-poke	0.9	0.9	0.0	2.0	0.0
Bill gape	1.5	7.4	0.7	1.0	0.1
Chase	2.2	0.9	0.6	3.4	0.3
Trounce	0.0	0.0	0.0	0.2	0.1
Total	5.5	9.3	1.3	7.6	1.2
Directed at A1Y males (%)					
Head-nod	23.4	23.1	30.3	34.3	75.5
Bill-poke	18.8	6.5	7.6	22.4	7.1
Bill gape	18.5	34.3	2.5	10.8	4.3
Chase	16.6	0.0	5.6	14.3	5.7
Trounce	0.6	0.0	0.0	1.0	0.1
Total	77.8	63.9	46.0	82.8	92.7
Total directed all birds (%)					
Head-nod	30.8	31.5	52.4	36.5	78.8
Bill-poke	22.8	15.7	9.1	28.5	7.5
Bill gape	25.5	43.5	3.2	12.6	5.1
Chase	20.3	9.3	35.2	20.7	8.3
Trounce	0.6	0.0	0.0	1.7	0.2
Total	100.0	100.0	100.0	100.0	100.0

TABLE 6.7. Frequency of aggressive displays by female and male partners of Harlequin Duck pairs in relation to the recipient of the aggressive signal. Paired observations ($n = 764$) were compared using 2-tailed, paired t -tests. Chases between mates were included but low-intensity, intra-pair displays were excluded (see Methods).

Recipient	Number of aggressive displays per hour by		t	P
	Female of pair	Male of pair		
Female	0.17 ± 0.05	0.29 ± 0.06	-1.8	0.075
1Y male	0.19 ± 0.05	0.07 ± 0.02	2.4	0.017
A1Y male	2.21 ± 0.30	4.87 ± 0.37	-6.6	0.000
Other species	0.23 ± 0.07	0.31 ± 0.08	-0.7	0.469
Own mate	0.04 ± 0.02	1.32 ± 0.13	-9.8	0.000
Total	2.82 ± 0.33	6.87 ± 0.45	-8.6	0.000

TABLE 6.8. Frequency of aggressive displays to others by female and male partners of Harlequin Duck pairs in relation to the age of the paired female.

Age of female	Number of aggressive displays per hour by		n	Paired t -tests	
	Female of pair	Male of pair		t	P
2Y	7.5 ± 3.5	3.7 ± 1.3	26	1.1	0.301
3Y	0.8 ± 0.4	2.2 ± 0.9	62	-1.7	0.112
A3Y	2.2 ± 0.5	4.5 ± 0.7	258	-3.6	0.000

ANOVA results: $F_{2,343} = 6.4, P = 0.002$ $F_{2,343} = 1.4, P = 0.3$

TABLE 6.9. Changes in group sizes of wintering Harlequin Ducks in relation to date and the availability of herring spawn in the Strait of Georgia, British Columbia, 1998-2000. Means are unweighted and weighted by the number of birds in each group.

Date	No. of groups	Mean \pm SE no. of birds	
		Unweighted	Weighted
Oct-Feb	4008	3.3 ± 0.1	5.9 ± 0.2
March without spawn	904	3.8 ± 0.2	13.3 ± 1.4
March with spawn	708	33.6 ± 7.2	1123 ± 258
April	801	7.5 ± 0.8	73.6 ± 12.5

TABLE 6.10. Variables used to analyse differences in the timing of pair formation among northern hemisphere species of the waterfowl subfamily Anatinae.

Species ¹	Mass (g)		Female survival (%)	Sex Ratio ³	Latitude (°N)	Migr.	Sex segr.	Pair bonds >1 yr	Court start	80% paired	Court time (mo.)	Sources ⁵
	Male	Female										
North America												
Anatini												
<i>Aix sponsa</i>	680	671	48	2.67	37	Y	N	Y	SEP	JAN	4	15,18,25,32
<i>Mareca strepera</i>	966	835	56	1.36	35	Y	N	Y	SEP	NOV	2	15,20,21,32
<i>M. americana</i>	792	719	58	1.85	35	Y	N	Y	SEP	NOV	2	20,21,32,39
<i>Anas rubripes</i>	1252	1111	51	1.32	35	Y	N	Y	SEP	OCT	1	15,20,21,32
<i>A. platyrhynchos</i>	1247	1107	55	1.33	42	N	N	N	SEP	JAN	4	5,15,32
<i>A. fulvigula</i>	1134	1048	46	1.07	30	Y	N	Y	AUG	OCT	2	15,22,32
<i>A. discors</i>	463	376	52	1.50	17	Y	N	Y	DEC	APR	4	1,15,32
<i>A. clypeata</i>	680	635	46	2.02	35	Y	N	Y	DEC	FEB	2	15,20,21,32
<i>A. acuta</i>	1025	866	65	1.81	35	Y	Y	Y	DEC	JAN	1	15,20,21,32
<i>A. carolinensis</i>	322	308	47	2.82	35	Y	Y	Y	DEC	FEB	2	15,20,21,32
Aythini												
<i>Aristonetta valisineria</i>	1252	1157	56	1.94	37	Y	N	Y	FEB	MAY	3	7,15,17,32
<i>A. americana</i>	1107	971	50	1.50	26	Y	Y	Y	DEC	-	-	7,8,15,19
<i>Aythya collaris</i>	744	671	50	1.59	30	Y	Y	Y	JAN	MAY	4	7,15,19,32
<i>A. affinis</i>	826	748	46	2.40	42	Y	N	Y	MAR	MAY	2	7,15,19,33
Mergini												
<i>Histrionicus histrionicus</i>	638	569	76	1.51	49	Y	N	Y	SEP	MAR	6	31,38,42,43,44
<i>Melanitta perspicillata</i>	1050	900	77 ²	2.31	49	Y	Y	Y	OCT	-	-	34,41,45
<i>M. deglandi</i>	1722	1437	77	1.50	52	Y	Y	Y	-	MAY	-	23,30,32
<i>M. americana</i>	1117	987	77	1.67	49	Y	Y	Y	OCT	-	-	13,15,28,45
<i>Clangula hyemalis</i>	932	814	72	0.79	43	Y	Y	Y	OCT	MAY	7	12,14,39
<i>Bucephala albeola</i>	465	337	64	1.50	51	Y	N	Y	OCT	APR	6	10,26
<i>B. clangula</i>	1120	710	61	1.60	45	Y	Y	Y	-	MAR	-	3,29

Table 6.10 cont'd

Species ¹	Mass (g)		Female survival (%)	Sex Ratio ³	Latitude (°N)	Migr.	Sex segr.	Pair bonds >1 yr	Court start	80% paired	Court time (mo.)	Sources ⁵
	Male	Female										
<i>B. islandica</i>	1130	751	66	1.17	49	Y	N	Y	NOV	MAR	4	40
<i>Lophodytes cucullatus</i>	680	540	74	1.85	49	Y	N	Y ⁴	OCT	-	-	15,27,35,39
<i>Mergus merganser</i>	1651	1238	60	1.94	-	Y	Y	Y ⁴	DEC	-	-	13,15,36
<i>M. serrator</i>	1158	925	-	1.62	-	Y	Y	Y ⁴	NOV	APR	5	37
Oxyurini												
<i>Oxyura jamaicensis</i>	590	499	-	4.10	42	Y	N	N	APR	MAY	1	16,39
Western Palearctic Anatini												
<i>Mareca strepera</i>	966	835	56	1.42	48	Y	N	N	JUL	SEP	2	4,15,32
<i>M. penelope</i>	819	724	53	1.08	48	Y	N	N	-	JAN	-	4,14,39
<i>Anas platyrhynchos</i>	1247	1107	55	1.47	48	Y	N	N	SEP	OCT	1	4,15,32
<i>A. acuta</i>	1025	866	65	1.37	48	Y	Y	N	DEC	FEB	2	2,4,9,15,32
<i>A. crecca</i>	364	318	49	1.84	48	Y	Y	N	OCT	MAR	5	2,4,14,39
Aythini												
<i>Aristonetta ferina</i>	849	807	59	1.53	48	Y	Y	N	FEB	MAY	3	4,14,24,32
<i>Aythya fuligula</i>	654	597	71	1.78	48	Y	Y	N	JAN	MAR	2	4,9,14,32
Mergini												
<i>Somateria mollissima</i>	2218	1915	90	-	57	Y	N	Y	SEP	APR	7	11,15,32,39
<i>Bucephala clangula</i>	1120	710	77	0.53	48	Y	Y	Y ⁴	NOV	-	-	4,9,29,32
<i>Mergellus albellus</i>					52	Y	Y	Y ⁴	FEB	-	-	6,9
<i>Mergus merganser</i>	1651	1238	60	-	52	Y	Y	Y ⁴	NOV	APR	5	6,9,13,15
<i>M. serrator</i>	1158	925	-	-	52	Y	Y	Y ⁴	DEC	-	-	6,37

¹Classification after Livezey 1997.²Estimated from other scoters.

Table 6.10 cont'd

³Ratio of males to females during midwinter (Nov.-Jan.) or when the birds were present at the study site. Taken from Bellrose 1980 if not measured at the study site.

⁴Long-term bonds not confirmed; inferred from other Mergimi species.

⁵(1) Bennett 1938, (2) Lebret 1950, (3) Carter 1958, (4) Bezzel 1959, (5) Johnsgard 1960b, (6) Lebret 1961, (7) Weller 1965, (8) Weller 1967, (9) Nilsson 1970, (10) Erskine 1972, (11) Gorham 1974, (12) Alison 1975, (13) Palmer 1976b, (14) Cramp and Simmons 1977, (15) Bellrose 1980, (16) Gray 1980 in *Johnsgard and Carbonell*, (17) Nichols and Haramis 1980, (18) Armbruster 1982, (19) Alexander 1983, (20) Hepp and Hair 1983, (21) Hepp and Hair 1984, (22) Paulus 1988b, (23) Brown and Fredrickson 1989, (24) Choudhury and Black 1991, (25) Hepp and Hines 1991, (26) Gauthier 1993, (27) Dugger et al. 1994, (28) Borage and Savard 1995, (29) Eadie et al. 1995, (30) Brown and Fredrickson 1997, (31) Gowans et al. 1997, (32) Krementz et al. 1997, (33) Austin et al. 1998, (34) Savard et al. 1998, (35) Coupe and Cooke 1999, (36) Mallory and Metz 1999, (37) Timman 1999, (38) Cooke et al. 2000, (39) Dunning 2000, (40) Eadie et al. 2000, (41) Iverson 2002, (42) Rodway et al. 2003a, (43) Rodway et al. 2003b, (44) this study, (45) MSR unpublished.

TABLE 6.11. Differences in pairing chronology among waterfowl tribes in the subfamily Anatinae in the northern hemisphere. Classification after Livezey (1997). Months are numbered 1 to 12 for July to June, respectively. Means \pm SE are given, and sample sizes (number of species) are given in parentheses.

	Anatini	Aythiini	Mergini	Oxyurini	r^2	F	P
Court-start ¹	3.9 \pm 0.4 (15)	7.5 \pm 0.4 (6)	4.7 \pm 0.4 (14)	10.0 (1)	0.51	13.0	0.000
Pair-date ²	6.5 \pm 0.5 (16)	10.3 \pm 0.4 (6)	9.9 \pm 0.3 (9)	11.0 (1)	0.55	13.4	0.000
Court-time ³	2.6 \pm 0.4 (15)	2.8 \pm 0.3 (6)	5.7 \pm 0.4 (7)	1.0 (1)	0.54	12.0	0.000

¹Calendar month that courtship began.

²Calendar month when 80% of females were paired.

³Number of months between start of courtship and pair-date.

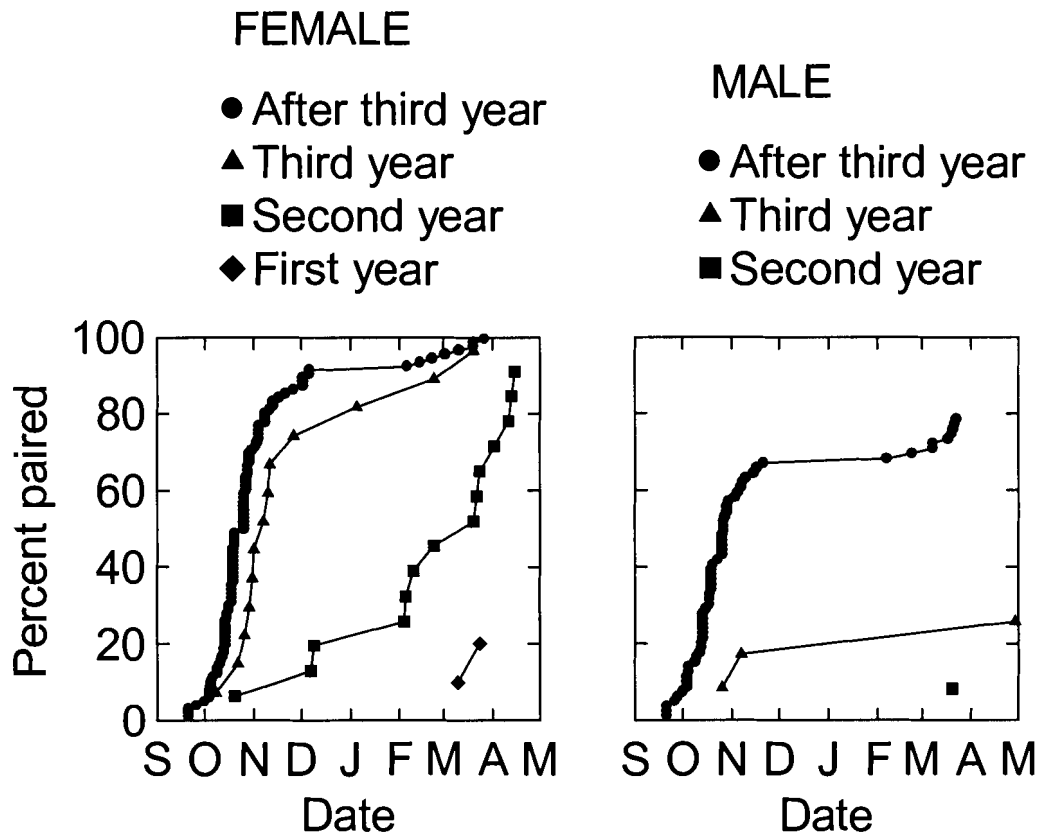


FIGURE 6.1. Age-related pairing chronology of Harlequin Ducks in the Strait of Georgia, British Columbia, 1995-2001. Each point represents the estimated date of pairing of a marked individual and is considered accurate within 30 d. Total percentages of each age class that paired were determined in spring out of samples of 10, 45, 58, and 367 first-, second-, third-, and after-third-year females, respectively, and 3, 8, and 309 second-, third-, and after-third-year males, respectively.

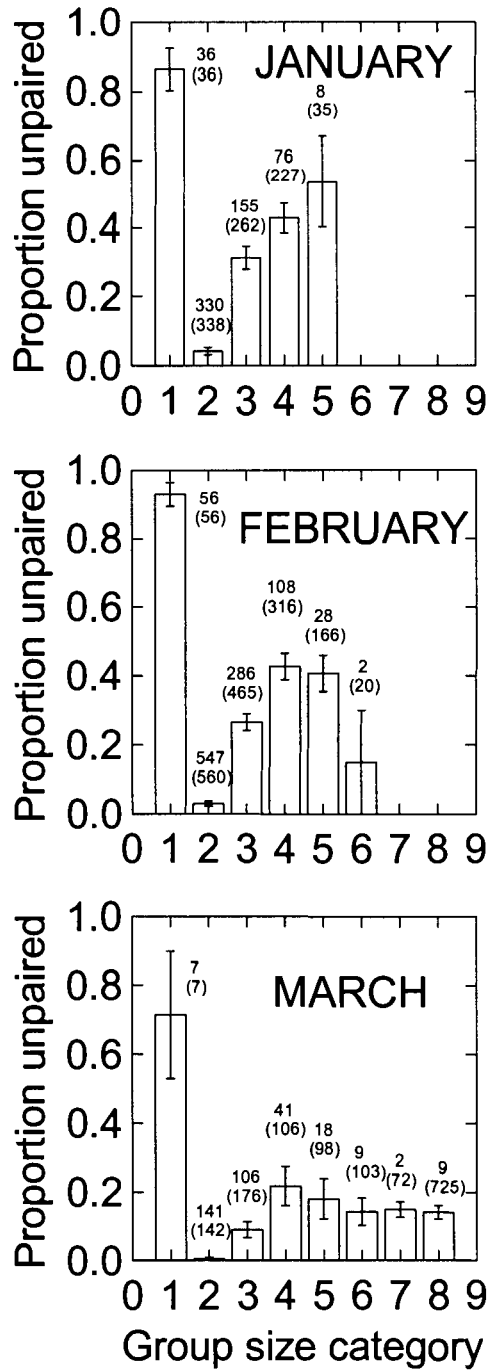


FIGURE 6.2. Mean proportion of Harlequin Duck females paired in different sized groups during January, February, and March 2000 in the Strait of Georgia, British Columbia. Group size categories 1, 2, 3, 4, 5, 6, 7, 8, and 9 represent groups of 1, 2, 3-5, 6-10, 11-20, 21-50, 51-100, and >100 birds, respectively. Standard errors are shown, and above bars are given the number of groups sampled and, in parentheses, the total females in those groups.

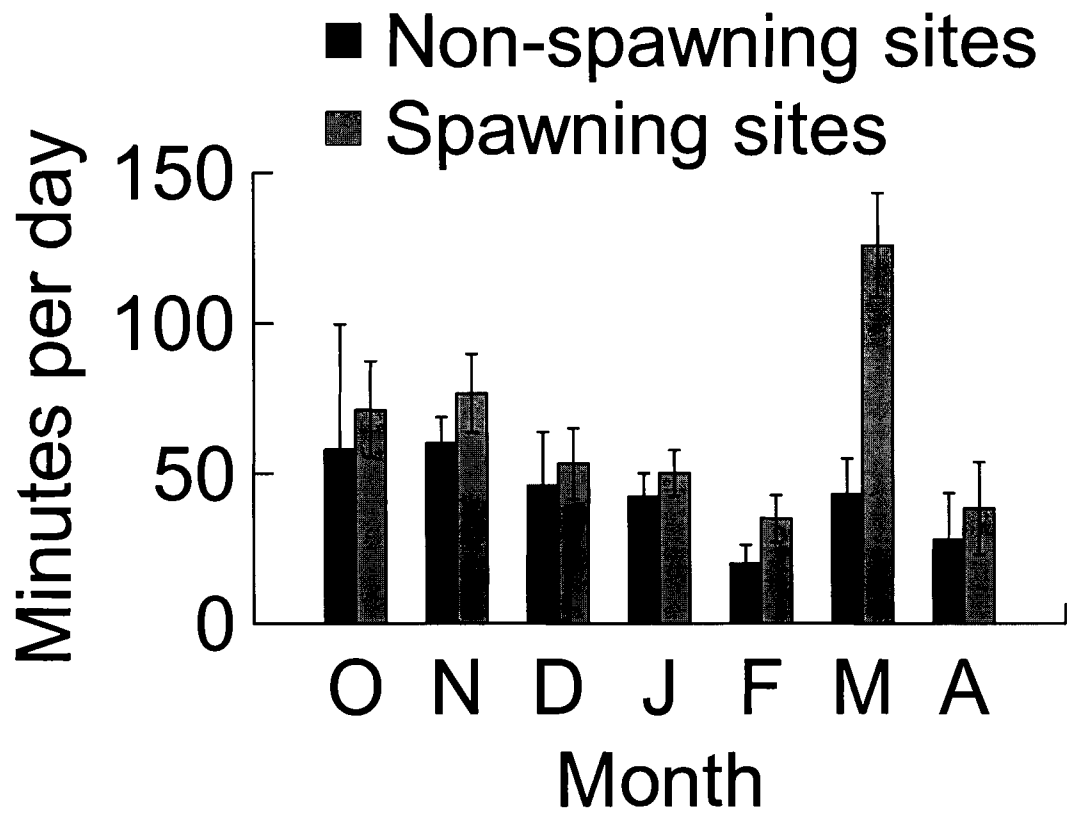


FIGURE 6.3. Comparison of seasonal trends from October to April in the amount of diurnal time spent in courtship by unpaired, greater-than-one-year-old Harlequin Ducks between locations where herring spawned in March and locations where herring did not spawn, in the Strait of Georgia, British Columbia, 1998-2001. Bars depict means \pm SE.

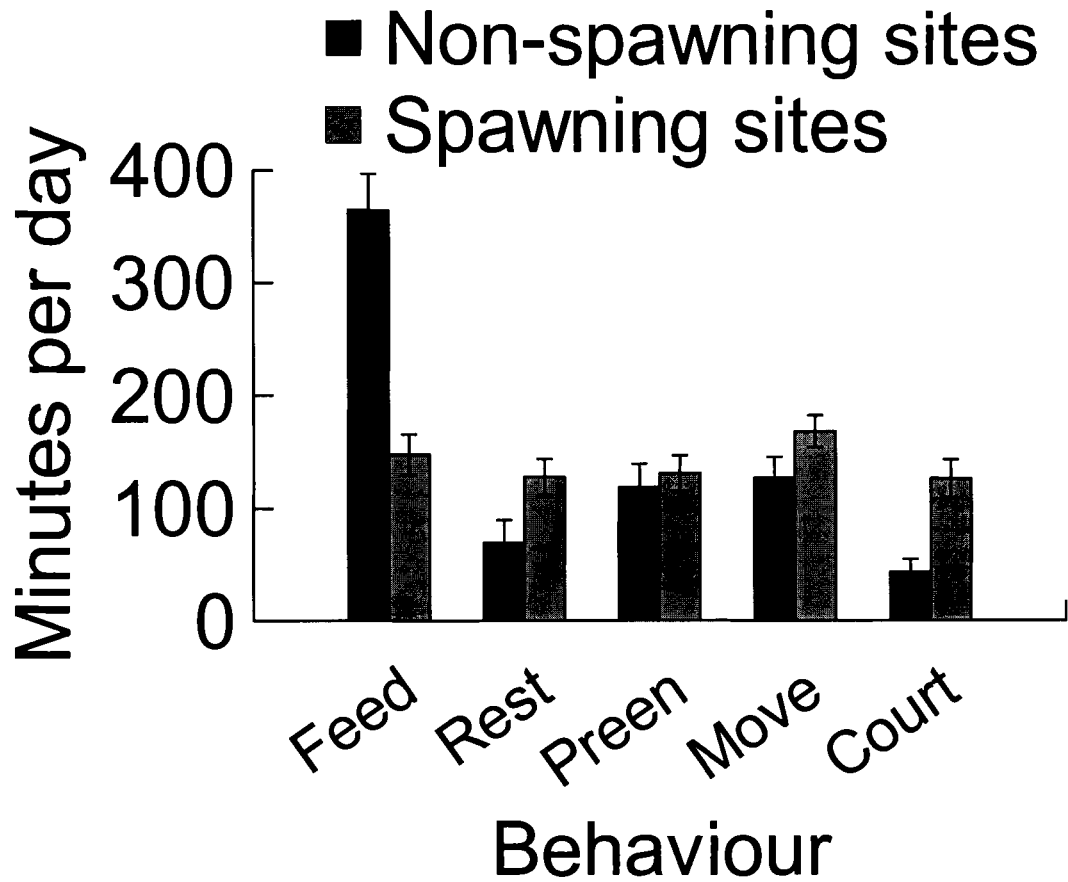


FIGURE 6.4. Allocation of time to different behaviours by unpaired, greater-than-one-year-old Harlequin Ducks during March at locations where herring did and did not spawn, in the Strait of Georgia, British Columbia, 1998-2001. Bars depict means \pm SE.

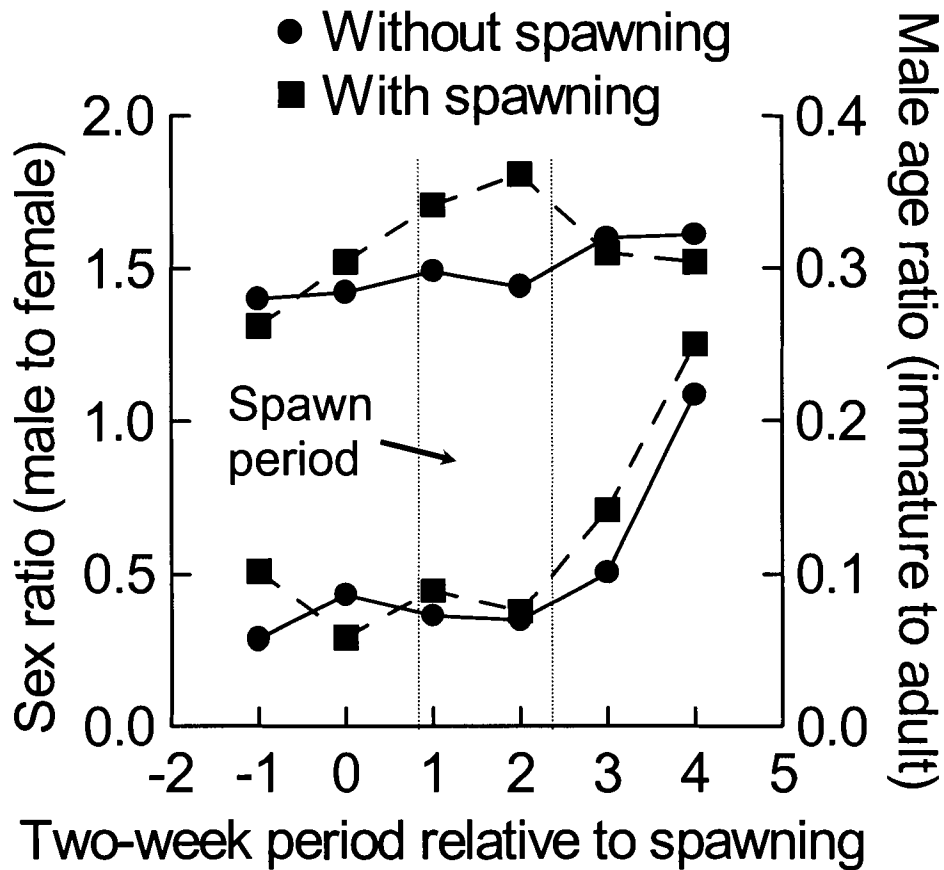


FIGURE 6.5. Comparison of trends in Harlequin Duck sex ratios (upper lines) and male age ratios (lower lines) between locations where herring spawned and locations where herring did not spawn in the Strait of Georgia, British Columbia, 1998-2001. The period when spawn was available to Harlequin Ducks at spawning sites is enclosed in vertical, dotted lines. Sample sizes were 732 and 530, 1241 and 477, 4958 and 428, 1499 and 480, 1988 and 395, and 312 and 434 adult males at locations where herring did and did not spawn, during consecutive, two-week intervals, respectively.

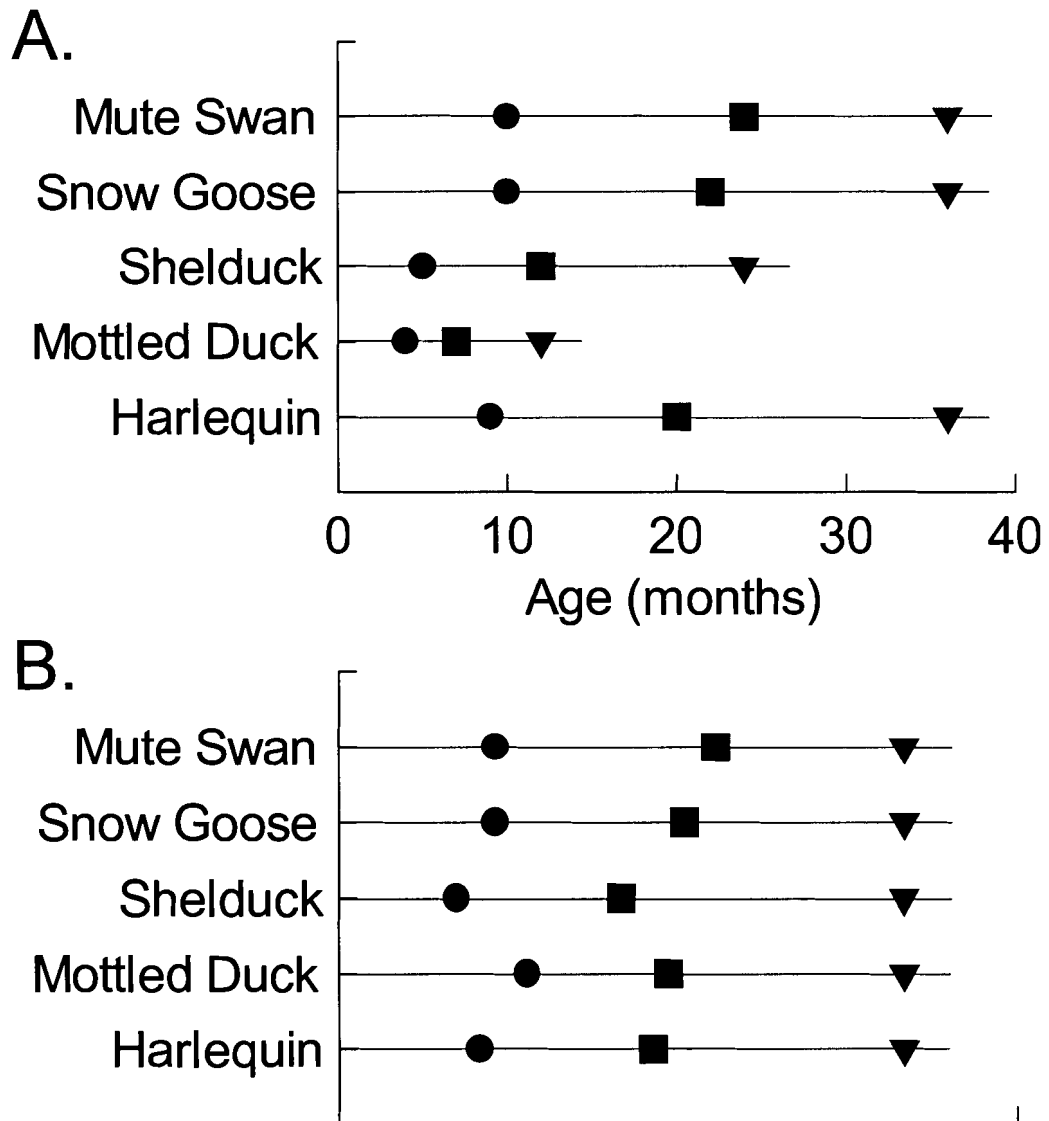


FIGURE 6.6. Comparison of absolute (a) and relative (b) ages when females first begin courtship (circles), median age of first pairing (squares), and median age of first breeding (triangles) among representative species of waterfowl tribes Cygnini (Mute Swans *Cygnus olor*), Anserini (Snow Geese *Anser caerulescens*), Tadornini (Paradise Shelducks *Casarca variegata*), Anatini (Mottled Duck *Anas fulvigula*), and Mergini (Harlequin Duck *Histrionicus histrionicus*). Data from Minton (1968) and Wood and Gelston (1972), Prevett and MacInnes (1980), Williams (1979), Paulus (1988), and this study, respectively, and classification from Livezy (1997).

CHAPTER 7

SUMMARY AND CONCLUSIONS

The studies presented in this thesis would not have been possible without the help and data contributions of many people, some of whom joined me as co-authors on published chapters. However, I will summarize the results of these studies using a first-person point of view because I was responsible for study design, analyses, and writing for all chapters. Studies were conducted in the Strait of Georgia, 1998-2002.

My first objective was to test predictions of previous and new theories to explain variation in the timing of pair formation in waterfowl by investigating how several aspects of the winter ecology of Harlequin Ducks, including distribution and spacing behaviour, time-activity budgets, and the use of herring spawn, may be related to the process of mate choice and the timing of pair formation. My second objective was to identify and address some of the gaps in our knowledge of the winter ecology and demography of Harlequin Ducks that are prerequisite to effective conservation action in the face of rapidly escalating human development. These objectives were complementary because much of the data required to fill some of these knowledge gaps were required before I could answer my research questions related to the timing of pair formation, and because mate choice and pair formation affect fitness and it is important to consider from a conservation perspective how such behaviours may be affected by human perturbation of the winter habitat and ecology of these birds.

Timing of pairing

Previous theory, the *female benefits-male costs hypothesis*, suggested that early pairing in waterfowl benefits both females (through increased nutrient acquisition and survival) and males (through mate acquisition and improved female condition) but is constrained by costs to males of courtship, mate defence and vigilance (Rohwer and Anderson 1988, Owen and Black 1990, Oring and Sayler 1992). I developed a new hypothesis, the *mutual-choice hypothesis*, in which I proposed that a more heuristic approach to the study of pairing chronology is to consider pairing as the culmination of the mate choice process by females and males. Variation in timing of pairing within and among species then depends on variation in the benefits, costs, and tactics of mate choice, and results from variation in individual life-history decisions about the allocation of time and energy to the pairing process. Phenotypic, social, and ecological conditions will influence optimal decisions for an individual through their effects on the benefits, costs, and

tactics of mate choice. Four sub-hypotheses were elaborated in relation to Harlequin Ducks that have a male-biased sex ratio, long-term pair bonds, deferred sexual maturity, and are widely dispersed on wintering grounds: 1) timing of pair formation is primarily determined by female mate-choice decisions; 2) pairing individuals will aggregate in a fashion similar to "lekking" to reduce costs of mate sampling; 3) immature birds benefit from observing the courtship behaviour and mate choices of older birds; and 4) herring spawn will provide indirect benefits to pairing birds through associated changes in time budgets and spacing behaviour. Contrasting predictions of previous and new theories were tested using data on Harlequin Ducks and data compiled from the literature on pairing chronology in other waterfowl species.

The picture of the pair formation process in Harlequin Ducks that emerged from this study reinforced previous perceptions that pair formation in waterfowl is a complex process involving the interaction of phenotypic, social, and ecological conditions and the balance of benefits and costs to males and females (McKinney 1986, 1992, Rohwer and Anderson 1988, Oring and Saylor 1992). However, previous theory to account for variation in the timing of pairing, that primarily considered how phenotypic, social, and ecological factors affects male costs (Rohwer and Anderson 1988), poorly predicted pairing behaviour in Harlequin Ducks and other waterfowl. This study demonstrated that female Harlequin Ducks invest considerable time and energy into selecting a mate, and indicated that the primary benefits of that investment do not accrue during winter. Decisions by females about how much time and energy to allocate to the pairing process appeared to be the main factor controlling the timing of pairing. Those decisions were affected by age, previous pairing experience, time required for other activities due to seasonal differences in day-length and food availability, and group spacing that affected the availability and likely the costs of mate sampling and in turn was also related to food availability. Decisions by males were similarly affected and female and male behaviour necessarily interacted to affect the time required for both sexes to balance the benefits of satisfying their mate preferences and the costs of pursuing those preferences.

Spacing behaviour of Harlequin Ducks supported the hypothesis that unpaired birds will show adaptive changes in their spacing to reduce the costs of mate sampling. Spacing behaviour of immature males was similar to that of other unpaired birds, and immature males participated in courtship throughout their first winter, although at a lower rate than adult males. I did not evaluate whether early involvement in courtship improved a male's chances of future pairing, but the hypothesis that they improve their display skills and benefit from participation in courtship groups was plausible. Aggregating at herring spawning sites in March provided birds with both direct nutritional benefits and indirect benefits related to changes in time budgets and spacing

behaviour. Nutritional benefits for all birds were apparent because a majority of the wintering population of Harlequin Ducks in the northern Strait of Georgia aggregated at herring spawning sites and birds switched to feeding almost exclusively on spawn when it was available. Unpaired birds appeared to benefit from changes in time budgets and spacing behaviour that facilitated courtship and mate sampling and were more likely to come to herring spawning sites than paired birds.

Many recent advances in our thinking about animal social systems have come from greater focus on female perspectives (Gowaty 1996, 1997, Jennions and Petrie 1997, Birkhead and Møller 1998), and in birds recent evidence suggests that resolution of reproductive conflicts between males and females favours female interests (Hughes 1998). Greater focus on female perspectives, specifically female mate-choice decisions, has proven to have heuristic value in understanding pairing behaviour in Harlequin Ducks, other waterfowl (Bluhm 1985, Sorenson and Derrickson 1994, Sorenson et al. 1997), and in mating systems research generally (Gowaty 1997, Johnson and Burley 1997, Birkhead and Møller 1998, Hughes 1998). Male and female interests necessarily interact and a comprehensive theory to predict variation in pairing behaviour in waterfowl and other species will require consideration of benefits, costs, and conflicts of interest among individuals engaged in pairing decisions (McKinney 1986, Rohwer and Anderson 1988, Oring and Saylor 1992, Choudhury 1995, Brown et al. 1997). The process of making mate-choice decisions, how the interaction of phenotypic, social, and ecological conditions affect that process, and how individuals integrate that process with other requirements of their life history are essential to consider in order to understand variation in the timing of pairing events.

Winter ecology and conservation implications

Conservation of marine birds in increasingly populated and exploited environments like the Strait of Georgia requires careful management of the resources and habitats essential to their continued survival. Obviously this is not possible without basic ecological information (Goudie et al 1994). Knowledge of several aspects of the winter ecology and demography of Harlequin Ducks provided by this study will increase our ability to effect that management for this species and, by extension, other species of seaducks.

I determined sex- and age-specific distribution, abundance, and habitat preferences of wintering Harlequin Ducks in the northern Strait of Georgia, and evaluated potential biases in measuring ratios of immature males to adult males to estimate recruitment rates (Chapter 2). Surveys in the northern Strait of Georgia covered all shoreline areas, which provided good estimates of population size and identified important areas of concentration that had not

previously been recognized. A comparison of the occurrence of birds with habitat availability at the 1-km scale indicated a preference for wide intertidal habitat with cobble-gravel or bedrock-boulder substrates, small offshore islets and shoreline with attached or nearby reefs and islets, areas without streams, and areas with greater historical abundance of herring spawn. Where the substrate was bedrock-boulder, birds preferred areas with tidal rapids. Densities of birds were highest along linear and complex shorelines with reefs or islets where intertidal habitat was >100 m wide and substrate was cobble-gravel or bedrock-boulder. Patterns of habitat use among sex and age classes were the same at the 1-km scale but differed at smaller scales, with adult and immature males occurring further offshore than females. Habitat-related densities determined in this study could be used to construct predictive models to estimate population size and distribution in the rest of the Strait of Georgia and in other coastal areas, and thus improve our ability to manage habitat for Harlequin Ducks at a provincial scale.

Age ratios varied among areas and were biased by survey method and misidentification of distant birds. Correcting for detected biases gave an estimated male age ratio of 9.8%, which translated into a female age ratio of 15.6%, and an estimate of female recruitment of 11.9%. Estimated adult female survival of 76% (Cooke et al. 2000) suggests a declining population, but it is necessary to incorporate emigration in estimates of adult survival before demographic trends can confidently be inferred (Regehr 2003). Also, I determined male age ratios during only one season and longer term studies are warranted to determine inter-annual variation and monitor trends in recruitment rates. Variation in male age ratios at large and small spatial scales and biases in age-ratio estimates due to survey method and misidentification have important implications for study design. Differences among geographic areas indicate that larger scale sampling is required to accurately estimate population age ratios. Where density variation is similar to what I found in the northern Strait of Georgia, random samples of about 100 km-sections of shoreline with Harlequin Ducks will provide age-ratio estimates with 95% confidence limits of $\pm 2\%$. In the Strait of Georgia study area, similar precision could be obtained with smaller samples (60 km-sections) surveyed from land, and I recommend using only land surveys for monitoring age ratios in that area. Such a monitoring program has been initiated for Harlequin Ducks and other seaducks in the Strait of Georgia (S. Boyd pers. comm.).

I used faecal analyses to determine seasonal changes in Harlequin Duck winter diet at a site where Pacific herring spawn (Chapter 3). I measured frequency of occurrence and relative abundance by volume of prey remains in 202 faecal samples collected during four date periods in 1998 and 1999. Those two measures were highly correlated ($r = 0.94$). I identified snails, crabs, limpets, and chitons as the principal animal prey, and ranked relative importance of most prey

types in similar order as previous studies using stomach analyses. Crab parts constituted the majority of prey remains during moult and I concluded that crabs were dominant in the diet during moult because crabs generally have greater organic content and less hard-part remains per unit of body mass than other hard-shelled prey consumed at that time. Snail remains were highest in frequency of occurrence during winter. Herring eggs were not detected in faeces until a week after herring spawned, but abrupt changes in other prey types indicated that herring eggs were the principal prey throughout the spawn period. Polychaetes increased in importance in winter and spring, and rated third in frequency of occurrence in spring. I recommend using faecal analyses to determine frequency of occurrence of prey in the diet of other sea-ducks that are known to feed on hard-shelled molluscs and crustaceans. Such non-lethal methods can likely provide most information required for management purposes. The importance in the diet of crabs during moult and herring eggs in the spring pre-migration period indicates specific needs for access to habitats with high crab productivity and to sites where herring spawn. Potential impacts of the northward-spreading Green Crab (McDonald et al. 2001) on native species used by Harlequin Ducks should be investigated.

I determined the scale of aggregative response of Harlequin Ducks to Pacific herring spawning in the northern Strait of Georgia, 1995-2002 (Chapter 4). Aggregations of 3400-5500 birds gathered at a small number of sites along the same 8-km stretch of shoreline each year spawn was available there. Aggregations occurred in only a small fraction of the habitat area where spawn was available. Duration of stay at spawning sites averaged 2-3 weeks and many birds returned to their wintering grounds afterwards. Birds moving to spawning sites represented 55-87% of the total wintering population. The proportion of local wintering populations that moved to spawning sites was negatively related to the distance that they had to travel and few birds traveled farther than 80 km. The decline in proportions moving with increasing distance suggested that more distant individuals may be constrained by lack of information or that there are trade-offs between the benefits of exploiting spawn and the costs of movement. This raises a conservation concern because the temporal and geographic range of herring spawning in British Columbia is contracting (Hay and McCarter 1999) and some wintering waterbird populations may be losing access to this important late-winter food. Geographical contraction of spawning locations is also a concern if, as indicated in the habitat study, the influx of herring spawn is an important determinant of benthic productivity and thus of the quality of habitat for Harlequin Ducks at other times during the winter. The answer to this question has important implications for habitat management and could be readily provided using an experimental approach.

Because most Harlequin Ducks, and likely a majority of the wintering populations of other sea ducks (Vermeer 1981), undertake seasonal movements to feed on herring spawn, it would be prudent to integrate the management of sea ducks with that of the herring fishery, as well as the management of any other extraction industry that affects the food supply or foraging habitat of waterbirds. Though we know that large numbers of waterbirds exploit herring spawn, we have no information on the fitness benefits of doing so. My study on pairing behaviour suggested that feeding on herring spawn may provide birds with indirect benefits that may increase their fitness through facilitating a more optimal mate choice. Benefits to survival and reproductive success seem likely and warrant investigation for all waterbird species that feed on herring spawn. Studies begun on the source of nutrients for egg laying in Harlequin Ducks are good start in that direction (R. Ydenberg pers. comm.). Understanding the importance of herring spawn to wintering birds also will help us predict the potential impacts of natural or human-induced climatic changes that may reduce the abundance of herring in these waters (Schweigert 1995).

I determined how Harlequin Ducks partition their time between nearshore foraging habitat and offshore resting areas, and whether their movement and roosting patterns reflected adaptations to reduce predation risk, by investigating three types of decisions made by moving birds: when to move, whether to move synchronously, and whether to form dense flocks on the roosting grounds (Chapter 5). I also studied how these decisions changed in response to abundant food by using the spawning of Pacific herring as a natural food-supplementation experiment. Birds arrived at nearshore feeding areas a few minutes later and departed almost an hour earlier relative to sunrise and sunset when spawn was available than before and after. Cloud cover and high winds resulted in earlier departures, especially during spawning. Arriving, departing, and offshore groups consisted most frequently of two ducks, and birds showed little tendency to synchronize movements or to form dense flocks when resting. Results indicated that Harlequin Ducks avoid crepuscular and nocturnal periods near shore when not constrained by food availability and the length of daylight in which to feed. Though apparently little threatened at present, nocturnal roosting habitat should be considered as well as diurnal foraging habitat in long-term management plans for this and perhaps other species.

Because Harlequin Ducks depend on a productive littoral environment, any anthropogenic impacts that reduce the availability or productivity of that habitat will likely have effects on Harlequin Duck distribution and, potentially, abundance. Harlequin Ducks are sensitive to disturbance and rapidly flush from roosting or feeding habitat when closely approached by foot or boat traffic along the shoreline. They co-exist with human development in

many areas, but there is evidence that their numbers may be declining in heavily visited areas such as White Rock near Vancouver (M. Rodway unpubl. data, S. Boyd pers. comm.). Studies are warranted on the effects of different kinds of disturbance on movement patterns, foraging, roosting, and pair-formation behaviour, and on long-term distribution and abundance. The burgeoning aquaculture industry poses an obvious conflict for shoreline habitat use and its expansion should be limited until impact assessments are conducted. Unlike larger species of seaducks like scoters that may reap some benefits from shellfish mariculture, Harlequin Ducks are unlikely to exploit shellfish farms for food. Thus, the impacts on Harlequin Ducks of possible habitat loss and contamination from aquaculture development need to be specifically examined. Extensive reef systems at the northern end of the Strait of Georgia that support high densities of wintering Harlequin Ducks are attractive locations for wind turbine installations. Proposed installations plan turbine construction in the intertidal and subtidal zone and so would directly remove habitat used by Harlequin Ducks. Other potential impacts need to be investigated because we do not know whether Harlequin Ducks and other marine birds would avoid turbines, effectively eliminating the availability of that habitat for these birds, or whether they would acclimatize. Mortality to flying birds is also a concern. Proposals to locate a turbine farm at the south end of Quadra Island were recently withdrawn, partly in response to the high densities of Harlequin Ducks wintering there found in this study.

Continued survival of Harlequin Ducks and other marine birds in coastal waters depends on human behaviour, and requires compromise of our seemingly incessant motivation for expansion, development, and profit. Meeting our responsibilities to ensure the health of marine bird populations requires management that acknowledges the limitations of our ecological understanding, has the resources to pursue informed decisions, and is backed by a political will dedicated to conserving a balance between economic prosperity and the quality of the natural world we inhabit, a balance that more and more tips the wrong and irrevocable way.

LITERATURE CITED

- Birkhead, T.R., and A.P. Møller. 1998. Sperm competition and sexual selection. Academic Press, San Diego.
- Bluhm, C.K. 1985. Mate preferences and mating patterns of Canvasbacks (*Aythya valisineria*). Ornithological Monographs 37:45-56.
- Brown, W.D., B.J. Crespi, and J.C. Choe. 1997. Sexual conflict and the evolution of mating systems. Pp. 352-377 in J.C. Choe and B.J. Crespi (eds.). The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge.

- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour* 50:413-429.
- Cooke, F., G.J. Robertson, C.M. Smith, R.I. Goudie, and W.S. Boyd. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. *Condor* 102:137-144.
- Goudie, R.I., S. Brault, B. Conant, A.V. Kondratyev, M.R. Petersen, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 59:27-49.
- Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. Pp. 21-52 in J.M. Black (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, Oxford.
- Gowaty, P.A. 1997. *Feminism and evolutionary biology*. Chapman & Hall, New York.
- Hay, D.E., and P.B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document 99/14, Nanaimo, BC.
- Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* 79:383-399.
- Jennions, M.D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* 72:283-327.
- Johnson, K., and N.T. Burley. 1997. Mating tactics and mating systems of birds. *Ornithological Monographs* 49:21-60.
- McDonald, P.S., G.C. Jensen, and D.A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology* 258:39-54.
- McKinney, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pp. 153-171 in D.I. Rubenstein and R.W. Wrangham (eds.). *Ecological aspects of social evolution*. Princeton University Press, Princeton.
- McKinney, F. 1992. Courtship, pair formation, and signal systems. Pp. 214-250 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Oring, L.W., and R.D. Saylor. 1992. The mating systems of waterfowl. Pp. 190-213 in B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu (eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis.
- Owen, M., and J.M. Black. 1990. *Waterfowl ecology*. Blackie, Glasgow.
- Regehr, H.M. 2003. Movement patterns and population structure of Harlequin Ducks wintering in the Strait of Georgia, British Columbia. Ph.D. thesis, Simon Fraser University, Burnaby.

- Rohwer, F.C., and M.G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- Schweigert, J.F. 1995. Environmental effects on long-term population dynamics and recruitment of Pacific herring (*Clupea pallasii*) populations in southern British Columbia. *Can. Spec. Publ. Fish. Aquat. Sci.* 121.
- Sorenson, L.G., and S.R. Derrickson. 1994. Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology* 35:389-400.
- Sorenson, L.G., P.M. Nolan, A.M. Brown, S.R. Derrickson, and S.L. Monfort. 1997. Hormonal dynamics during mate choice in the northern pintail: a test of the 'challenge' hypothesis. *Animal Behaviour* 54:1117-1133.
- Vermeer, K. 1981. Food and populations of Surf Scoters in British Columbia. *Wildfowl* 32:107-116.