PAIR FORMATION, MATING SYSTEM, AND WINTER PHILOPATRY IN HARLEQUIN DUCKS.

by

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Abstract

Current theory suggests that mating systems influence the direction of a sex-bias in philopatry. Most bird species form pair bonds on the breeding grounds and exhibit a resource based mating system, leading to the evolution of male-biased breeding philopatry. Males returning to familiar territories are expected to have a competitive advantage. In contrast, many waterfowl species form pair bonds during the non-breeding season and their mating system at the time of pair bond formation is not known. In this thesis, I studied the Harlequin Duck *Histrionicus histrionicus*, to determine: which factors (such as feather moult) influence when pair bonds form, the mating system and to test whether this species follows the predicted sex-bias in philopatry given the observed mating system.

A moulting and wintering population of about 100 Harlequin Ducks was studied from 1994 to 1997 in coastal southwestern British Columbia. Harlequin Ducks formed pair bonds in October and November and pairs reunited. Males immediately began their feather moult after they returned from the breeding grounds. Males tended to clump into groups while they were moulting and grew in a set of bright white tertial feathers while they were in their basic plumage. Males may use these feathers as a badge to assess the timing and speed of moult of others. Males that moulted slowly were shown to be at a disadvantage when attempting to attract a mate and were likely to be low quality individuals. Harlequin Ducks form pair bonds as soon as possible, after the annual body moult is complete.

Males did not isolate themselves from other males and did not exhibit conspecific aggression along spatial boundaries, suggesting that Harlequin Ducks are not territorial during the winter. They did behave aggressively towards males that approached their mate. These observations suggest that Harlequin Ducks have a mate-defense mating system, and should exhibit a female-biased philopatry. However, both sexes show equally high levels of winter return rates (females: 62%, males: 77%). The mating system was not successful in predicting a sex-bias in winter philopatry, probably because the benefits of returning to familiar habitat are high for both sexes.

Acknowledgments

This journey began in the summer of 1990. Although the work I did at La Pérouse Bay has absolutely nothing to do with this thesis, it is the place where I became a field biologist. Matt, James, Rocky and all the other bozos I worked with up there played a role in teaching me this business, thanks guys.

Fred has freely given me his very precious time for endless discussions about Harlequin Duck biology and waterfowl ecology. His input and ideas are present throughout this thesis. Thank you Fred, for making it all possible. Tony was the first person to teach me how to write science, among many, many other things. More importantly he has always been a close friend. Tony, Karen and Natasha, I wish you all the best in the future. Besides the obvious statistical guidance I have received from Evan, he also taught me how to teach it to others. I shall remember our discussions about all sorts of issues, the politically correct ones and the others. Dov taught me how to think critically and that intimidating equations and graphs can be understood. He also gave me the opportunity to play trucker for a week with all of his worldly possessions.

Brett introduced me to the wilds of British Columbia, spoiling me forever. Eric and I learned how to bag ducks together. Standing in the middle of Boundary Bay at 0530h, in the pouring rain, are some of my best memories in the last 5 years. Pat let me take his bike and boat apart, leaps of faith that I appreciate. Bill just tried to kill me, but we had a great time. Sean, Howie, Dave, Yo, Andrew, Tom, Brent, Chris, Don, Steph, Irene and all the others, thank for your friendship.

I would like to thank the dozens of people who have assisted us in collecting Harlequin Duck data. Carl, Jamie, Ned, Ken, Billie, Shawn, Roxana and Joanne deserve special mention. Ian Goudie is responsible for initiating the Harlequin Duck research effort in British Columbia, a huge, and by all accounts, successful undertaking. Sean Boyd, has spent many hours observing Harlequin Ducks and made the initiative to use radio telemetry with this species. Ian and Sean's contribution to this thesis is invaluable, more importantly, they are extremely easy and enjoyable people to work with. It has been a pleasure. Billie Gowan's work, although, not directly part of this thesis is a key component of our current understanding of Harlequin Ducks. Discussions with Roxana Torres, Malcolm Coupe, Billie Gowans, Ken Wright, Cyndi Smith, Bill Hunt, and Shawn Ternan about sea ducks and Harlequin Ducks helped to expand and clarify my ideas. Connie, Joanne and Barb, from someone who has dabbled in logistics and accounting, your efforts to keep the ship afloat do not go unnoticed. My committee members, Ron and Nico, provided me with lots of good advice and suggestions.

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Preface

Scientific research does not progress by the work of isolated individuals. Instead, fields are advanced through the interaction and exchange of ideas amongst a community of researchers. This thesis is a product of interactions. Many of the papers in this thesis are going to be published, submitted, or, are already published in peer-reviewed journals. All of the manuscripts in this thesis are co-authored with others. I believe that the involvement of others in this thesis is a strength, rather than a weakness, of this work. The ability to collaborate, especially across agencies, can only improve the breadth and scope of research. There are two aims of this thesis, one is to look at an interesting ecological question, the other is gather information on a species for which there is a serious conservation concern. Input from individuals with strengths in these two fields helped to fulfill these two goals.

Dr. Fred Cooke is included as an author on all the papers arising from this thesis. We have worked very closely together in all aspects of the Harlequin Duck research project, and as my senior supervisor Dr. Cooke's input into my research effort was incalculable. Ian Goudie was a biologist with the Canadian Wildlife Service at the time of the research. Mr. Goudie was responsible for the initial development of the Harlequin Duck research program in British Columbia and establishing a marked population of birds. Sean Boyd, a research scientist with CWS, was heavily involved in establishing the resighting effort at the White Rock study site. All three of these researchers have been involved in designing the research program, providing and organizing logistic support, and revising, commenting and editing all of the manuscripts in this thesis. Finally, a paper which is not included in this thesis, but is a significant part of the Harlequin Duck research effort is Billie Gowans undergraduate research paper. We published this paper as, Gowans, B., Robertson, G. J. & Cooke, F. 1997. Behaviour and chronology of pair formations by Harlequin Ducks

Histrionicus histrionicus in Wildfowl. Mrs. Gowans and I worked very closely together on this paper and I was involved in all aspects of her study.

The input of these individuals was a important in developing this thesis, however, my role was essential. Every aspect including; forming the research questions, collecting data (by myself or organizing others), collating the data, analyzing the data, and writing the papers and thesis, were ultimately my responsibility. As such, I am senior author on all the papers presented in this thesis, save one. This exception is the material in Chapter 3.3. a copy of a paper published in Condor on which Dr. Cooke is first author. Dr. Cooke is first author because he was the first to notice that the white basic tertial feathers fell out before the pre-alternate body moult. He also took the lead in drafting the manuscript. It is included in my thesis because I played a key role in writing this paper. I analyzed all of the data, edited the entire manuscript numerous times and wrote significant portions of the text. I also contributed the analysis of grouping behaviour and sexual segregation of the ducks during moult. This insight is an equally important finding in this paper and was discovered by my work.

Chapter 1

General introduction

1.1. Introduction to the thesis

1.1.1. The research question

How individuals distribute themselves across habitats is a fundamental ecological question. Factors that can influence the distribution of individuals include the presence and quality of biotic and abiotic requirements, such as food and nesting sites (Cody 1985), the patchiness of these resources (Wiens 1976), the risk of predation (Lima & Dill 1990), and the presence or absence of conspecific (Rubenstein & Wrangham 1986, Milinski & Parker 1991) or interspecific individuals (Rosenzweig 1985). An important aspect of how animals distribute themselves is the degree to which they can use their knowledge and experience in a local area to their advantage when extracting resources, hiding from predators and looking for mates. If individuals can use this knowledge to their benefit it would be expected that individuals would prefer to occupy familiar habitats. However, there may be costs associated with occupying a familiar habitat, for example, habitats may degrade in quality after being utilized for a period of time (Cooch et al. 1993), predators may be attracted to patches with high densities of individuals (Pulliam & Caraco 1984) and mating opportunities may be restricted to related individuals (Moore & Ali 1984). Similarly, there are benefits and costs of moving away from familiar habitats. Better foraging conditions, safer habitats and mating opportunities may be present in other habitat patches. However, moving across unfamiliar habitat may increase the risks of starvation, predation and becoming isolated from conspecifics (Bernstein et al. 1991). The relative costs and benefits of remaining in familiar habitats and moving across unfamilar habitats will, in part, determine the distribution of animals across a landscape.

A large body of literature has shown that many birds, both adults and juveniles, are philopatric (the tendency to return to, or remain at, a given location) to their breeding grounds (Greenwood 1980, Greenwood & Harvey 1982, Johnson & Gaines 1990, but see Weatherhead & Montgomerie 1994). Generally, adults show higher philopatry than juveniles (Johnson & Gaines 1990). In many species of birds males show a higher return rate to breeding grounds than females (Greenwood & Harvey 1982, Clarke et al. 1997). This sex bias has been explained as being a consequence of the resource defense monogamy mating system exhibited by most birds (Greenwood 1980). Males return to familiar territories where they have an advantage because they have local knowledge of the area (Greenwood 1980). A major exception to this pattern was found in the waterfowl, where females show much higher philopatry to the breeding grounds than males (Cooke et al. 1975, Johnson & Grier 1988, Anderson et al. 1992). This exception to the pattern was explained by the fact that waterfowl breeding habitat is so expansive and ephemeral that it is probably not economically defendable by male waterfowl and subsequently a mate defense mating system evolved (Rohwer & Anderson 1988). However, an important aspect of waterfowl biology has been overlooked in this explanation for why waterfowl are different from other birds. Many species of waterfowl, most notably the ducks, pair during the winter months and not during the breeding season (Rohwer & Anderson 1988). Thus, the location of pair formation and therefore the mating system is independent of the breeding grounds. The relationship between the mating system and sex-biased philopatry has not been considered during the winter period for waterfowl. In general, philopatry is expected to evolve when habitats are stable and predictable (Lima 1984). In this thesis, it is proposed that waterfowl species which utilize stable wintering habitat could show a resource defense mating system and subsequently exhibit the predicted male-biased philopatry not to the breeding grounds, but rather to the wintering grounds. Hence, waterfowl may not be an exception to the pattern Greenwood

(1980) described for birds after all, when the appropriate time of year is examined. The Harlequin Duck *Histrionicus histrionicus* was chosen as the species in which to test this idea.

Some authors have considered a stricter definition of philopatry and restrict its use only to natal philopatry (e.g. Oring & Lank 1984). Adult individuals that return to the same areas year after year were termed to show site fidelity. In this thesis we use Greenwood's (1980) definitions, as adapted by Anderson et al. (1992): philopatry, both natal and to locations used by the birds in their lifetimes (e.g. breeding, moulting, migratory stopover or wintering) is the tendency of individuals to return to these sites year after year.

1.1.2. The study species

Harlequin Ducks are members of the sea duck tribe (Mergini). Sea ducks typically dive for food, spend considerable portions of their life in saltwater, are long-lived, and experience low and variable annual productivity (Goudie et al. 1994). Harlequin Ducks are basal in sea duck phylogenies, the only resolution is that they are more closely allied with the mergansers, scoters and goldeneyes than the eiders (Livezey 1995). Harlequin Ducks have many specializations because their breeding habits are unique among the sea ducks. They are the only species to feed in, and nest along, fast flowing streams and rivers. Preferred food items during the breeding season include simulid and chironomid larvae (Bengtson 1972) and the roe of salmonids and catostomids (Dzinbal & Jarvis 1984). Their breeding range extends from Iceland, southern portions of Greenland, parts of northern Labrador, Baffin Island and northern Quebec in the Atlantic. Along the eastern Pacific rim they breed from northern California and Wyoming north through Washington, Idaho, Montana and Oregon, throughout most of British Columbia and the Rocky Mountains of Alberta, and up into Alaska, including the Aleutians. On the western rim of the Pacific they breed along the Kamchatka peninsula and throughout the Okhotsk drainages (Palmer 1976).

The wintering range of the Harlequin Duck are usually towards the nearest coastline and sometimes south of their breeding range. Harlequin Ducks winter along rocky coast lines, where they forage for a variety of intertidal and shallow subtidal food items. Preferred food items include mollusks (limpets, snails, chitons), crustaceans (small crabs, amphipods and isopods), small fish and roe (Cottam 1939, Vermeer 1983, Gaines & Fitzner 1987). They are shallow divers and prefer to remain close to shore (Goudie & Ankney 1986).

The breeding ecology of Harlequin Ducks is not well documented because they nest in remote locations difficult to access. Breault & Savard (1991) provide a summary of current information as of the late 1980s. The information presented here is a synthesis of the most relevant details. Most work has been carried out in Iceland (Bengtson 1966, 1972, Inglis et al. 1989). When birds arrive on the breeding grounds males vigorously defend their mates from bachelor males (Inglis et al. 1989). Breeding begins relatively late and Harlequin Ducks spend considerable amounts of time feeding before egg-laying (Bengtson & Ulfstrand 1971). Clutch size averages 5 to 6 eggs and incubation lasts approximately 28 days (Bengston 1972). After incubation males depart for the coast. Hatching success is generally high (87%), probably a function of the relatively predator free habitat Harlequin Ducks use to nest (Bengtson 1972). Duckling survival is also high (52 to 58%) with most mortality occurring in the first 2 weeks after hatch, a typical pattern in ducks (Sedinger 1992). Ducklings fledge at about 5 to 9 weeks of age (see Breault & Savard 1991). Some females depart for the coast before, and others after, the brood has fledged (Kuchel 1977, Wallen 1987).

A substantial proportion of the female breeding population may not attempt breeding in any given year, and this proportion is related to the food supply on the breeding grounds (Bengtson & Ulfstrand 1971). Although females are reproductively mature at 2 years of age, they have very low rates of attempted and successful breeding until they are at least 5 years of ~~age~~ (Reichel et al. 1997).

Aspects of their biology during the non-breeding season are even less well known. Males are known to moult on the coast after they return from the breeding grounds (Palmer 1976). Females are assumed to moult at some time during the fall, although the exact timing is not clear. It is known that individuals are paired before they arrive at the breeding grounds and that many pair bonds remain intact from previous years (Bengston 1972). These bonds are thought to form sometime in the winter (Fleishner 1983). Movements and migrations of moulting and wintering birds are not well understood.

The North American east coast population of Harlequin Ducks was listed as endangered in Canada in 1990 (Goudie 1991) and is currently being reviewed for the same status in the United States of America (Carlton & Roy 1995). Current estimates suggest that there are 1000 to 2000 Harlequin Ducks remaining on the east coast (Montevecchi et al. 1995). A large portion of this population winters in a single location on the south side of Isle au Haut, Maine (Mittlehauser 1992), making it vulnerable to a single environmental catastrophe. Populations on the west coast of North America are healthier, although the species has been extirpated from the southern end of its breeding range (Palmer 1976). Recent estimates suggest that Harlequin Ducks may be declining in the Strait of Georgia, British Columbia (R. I. Goudie, pers. comm.). Threats to wintering Harlequin Ducks on the west coast include oil spills, human disturbance, and inshore development. Logging, mining, and human disturbance pose threats to breeding Harlequin Ducks. In response to these threats there are research efforts to understand the basic biology and monitor populations of Harlequin Ducks in every state and province along the Pacific coast of North America that have resident wintering or breeding populations.

1.1.3. Outline of the thesis

The are two main objectives of this thesis. The first and foremost is to understand the relationships between the habitat use, mating system, site fidelity and philopatry in a species that forms pair bonds away from the breeding grounds. The second objective is to provide some basic information on the moulting and wintering ecology of a species for which there is a serious conservation concern.

In the second half of Chapter 1 I present a theoretical framework for studying philopatry away from the breeding grounds, with a particular emphasis on waterfowl. This framework is lacking in the literature and needs to be established before continuing with the research question. Information on winter philopatry was gathered and summarized for a variety of waterfowl taxa. Chapter 2 describes the pairing chronology of Harlequin Ducks. This information was previously not available and it was necessary to know whether Harlequin Ducks do indeed pair in the winter period before a test of whether the mating system has an influence on patterns of philopatry was possible. I also summarize available data for the timing of pairing for the entire sea duck tribe and present an explanation for the patterns documented within the tribe by relating the time of pairing to foraging methods and body size. Chapter 3 is presented in three major parts in which I examine the influence of the annual body, wing, and tail feather moult on the timing and success of pair formation in Harlequin Ducks. In the first section the actual timing of arrival from the breeding grounds and the moult chronology are documented and related to the timing of pair formation. In the second section I describe the social organization of Harlequin Ducks while they are moulting and explore the function of conspicuous white feathers that are present during the basic plumage of the males. In the third and final section I evaluate the role of the speed and timing of the moult on the success of individual males attempting to obtain a mate. In chapter 4, I directly test Greenwoods' hypothesis that the mating system will predict the direction of a sex bias in philopatry.

First, I describe the mating system of Harlequin Ducks at the time when pair formation occurs. I then describe the patterns of philopatry seen with reference to the mating system. Chapter 5 represents a change in emphasis and asks the question of how philopatry influences the demography of a population. Using stage-based projection matrices and data gathered from other researchers I model populations with different exchange rates between wintering grounds that vary in quality. I also explore the effect that annual variation in vital rates has on population growth rate. In chapter 6 I summarize the most important findings of this thesis and discuss the conservation implications of this research.

1.2 Winter philopatry in migratory waterfowl[1]

1.2.1 Abstract

The degree of philopatry influences the genetic structure of populations, but only at the stage of the annual reproductive cycle when pair formation and gene exchange occurs. Since most pair formation in birds occurs in the breeding area, philopatry has been examined mainly through breeding studies. Waterfowl (Anseriformes) are a major exception to this pattern, in that pair formation often occurs during the winter months. A robust framework for the study of philopatry outside the breeding season has not been offered for waterfowl. We present a number of genetical and ecological hypotheses and provide examples from studies supporting or refuting these hypotheses. Sex-biases in philopatry are common throughout the avian taxa. We outline ecological conditions and life history traits that will, or will not, predict a sex-biased winter philopatry in waterfowl species. We summarize winter philopatry rates presented in the literature for a variety of waterfowl taxa. Our review shows a paucity of data and generalizations were difficult to make. It was apparent from these data that geese and swans (Anserini), and probably sea ducks (Mergini) exhibit relatively high levels of winter philopatry. Dabbling ducks (Anatini), however, show much lower levels of winter philopatry. No taxa exhibited absolute philopatry to their wintering grounds. A fruitful approach to studies of wintering waterfowl is in the context of population structure and philopatry. We suggest some possible directions for future research and a standardized way of reporting the data.

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[1] This section (1.2) has been submitted for publication as Robertson, G.J. & Cooke, F. Winter philopatry in migratory waterfowl, to the *Auk*.

1.2.2 Introduction

Philopatry, defined as a tendency of a migratory animal to return to a particular location, has been in observed in many species (Mayr 1963). Two types of philopatry to the breeding grounds have been recognized, natal philopatry where a juvenile animal returns to breed at its place of birth and breeding philopatry where an animal returns to breed at the site of a previous attempt (Greenwood 1980). Philopatry has significant implications for genetic structure of populations. When there is little movement of individuals among populations then significant genetic population sub-structure can arise (Wright 1969, Rockwell & Barrowclough 1987, Chesser 1991). Philopatry increases the isolation of populations, making local population extinctions more likely (Levins 1970, Gadgil 1971).

A number of hypotheses have been put forth to explain why individuals are philopatric, or conversely, dispersive. Hypotheses based on kin selection, mating systems, coloniality, inbreeding and familiarity with local environments have all been advanced (Johnson and Gaines 1990). In the case of non-migratory species most of the focus is on why individuals disperse into unfamiliar habitats. For migratory species the question is generally reversed; why do individuals make the effort to return to a specific breeding location, instead of simply attempting to breed in the first piece of suitable habitat they encounter? High levels of natal and breeding philopatry have been documented in many bird species (Greenwood & Harvey 1982, Rohwer & Anderson 1988). However, Weatherhead & Forbes (1994) point out that most studies in passerines that show a high breeding philopatry are with resident species, whereas migratory species tend to have much lower levels of breeding philopatry. In contrast, other families of migratory birds show high levels of breeding philopatry (Greenwood & Harvey 1982, Sandercock & Gratto-Trevor 1997).

A focus on breeding philopatry may not lead to a complete picture in some species. Migratory species utilize a variety of habitats throughout the year, including breeding, molting, wintering, and, migratory stopover locations. Each of these habitats is important in the life history of the species. Significant mortality can occur at any of these stages, and philopatry or dispersion at these sites can have significant effects on population regulation. Furthermore, genetically based arguments for the evolution of philopatry suggest that some amount of genetic isolation among populations is advantageous. The physical location where gene flow occurs (likely determined by the mating system) is the relevant location for evaluating this set of hypotheses for the evolution of philopatry.

Waterfowl (Anatidae) are a group where an emphasis only on breeding philopatry leads to an incomplete understanding of the life history of a species. For this group, philopatry to the location where pair formation occurs, not necessarily breeding philopatry, may be critical in understanding population structure. Waterfowl often pair in the winter, hence, gene flow and population structure will be defined during this period. Breeding philopatry is female-biased in migratory waterfowl, a pattern which is opposite from that seen in most birds. As such, much attention has been focused on sex-biases in breeding philopatry of waterfowl (see Rohwer & Freeman 1988; Anderson et al. 1992 for reviews). Within species there might be different selective forces that lead to sexual biases in breeding as opposed to wintering philopatry. Futhermore, selection pressures leading to winter philopatry might be different than those that lead to breeding philopatry in waterfowl species.

The objectives of this review are to: 1) review current hypotheses regarding philopatry and apply them to winter philopatry in waterfowl, 2) summarize existing data on patterns of winter philopatry in waterfowl and evaluate these patterns with respect to current hypotheses, and 3) outline future research needs.

1.2.3 Hypotheses and Mechanisms

Two main sets of hypotheses have been proposed to explain why individuals are philopatric. One set (broadly ecological or somatic) proposes that individuals returning to familiar sites are able to use their prior local knowledge of the area to their advantage. The other set (broadly genetic) suggest that individuals are philopatric to ensure that individuals mate with other individuals that have some level of genetic relatedness to themselves. In the following section hypotheses falling in these two categories, which are not necessarily mutually exclusive, are described and interpreted in the context of winter philopatry in waterfowl. Evidence for, or against, these hypotheses from the waterfowl taxa are presented, if available, for each hypothesis.

Ecological (or somatic) mechanisms

There are a number of hypotheses that fall within an ecological or somatic benefit framework. All of these models predict that individuals that are philopatric have a higher lifetime reproductive success than dispersers. Quantifiable benefits of philopatry should be apparent in the current generation.

Local knowledge. - Individuals that return to the same region year after year will become familiar with an area and will be able to use this knowledge to their advantage. Philopatric individuals have a selective advantage over dispersers because they are not continually confronted with novel environments. Potential benefits include knowledge of; patchy food resources, location of conspecifics, location of predator refugia and predator movements and habits. This hypothesis is commonly used to explain the high levels of female breeding philopatry seen in waterfowl (Rohwer & Anderson 1988).

Wintering waterfowl that return to a known location may be able to use their local knowledge to avoid predators and exploit known food resources to increase their overwinter survival. However, overwinter survival is not the only fitness component for wintering waterfowl that needs to be maximized. Good foraging conditions on the wintering grounds can increase the reproductive success of females in the subsequent breeding season (Ankney & MacInnes 1978, Nichols & Hines 1987, Raveling & Heitmeyer 1989). For waterfowl which pair in winter, both sexes have an enhanced fitness if they succeed in finding a suitable mate (Wishart 1983, Rohwer & Anderson 1988). Males and females in good body condition pair earlier than those in poor body condition (Brodsky & Weatherhead 1985, Hepp 1988, Pattenden & Boag 1989). This allows individuals in good condition not only to find a mate, but a higher quality mate as well (Heitmeyer 1995). There should be strong selection to choose high quality wintering areas to maximize survival, subsequent reproductive success and obtaining a quality mate. Additionally, if philopatric individuals have local knowledge about where conspecifics tend to congregate, they may have an advantage in finding a suitable mate.

If local knowledge is useful for individuals it suggests that the local habitat is predictable at some level. Models of dispersal and philopatry have long recognized the importance of habitat stability on the evolution of philopatry (Johnson & Gaines 1990 and references therein). Clearly, philopatry will not be favored in ephemeral habitats. Species which use more ephemeral habitats would be expected to be less philopatric than species using stable habitats. Similar patterns should be seen among populations of the same species. Coastal habitats tend to be more stable than inland sites because they generally remain ice and snow free throughout the winter Northern Pintail *Anas acuta* and Black Duck *A. rubripes* wintering in coastal habitats show a lower tendency to disperse than their counterparts wintering in inland habitats (Hestbeck 1993, Diefenbach et al. 1988a). Overall, habitat stability may have a role in determining how dispersive a species will be during the winter.

Social grouping. - This hypothesis proposes that philopatry has evolved as a mechanism for individuals to maintain some sort of social bonds with other individuals.

Maintaining a cohesive family unit might be one reason for individuals to keep social bonds intact. In species with long-term pair bonds and extended parental care (geese and swans) individuals which are separated would be able to re-unite at common wintering ground. Raveling (1969) suggested one function of the use of traditional roost sites by

Canada Geese *Branta canadensis* was so that family groups that had become separated could reunite.

Another version of a social cohesion hypothesis is related to the mating system. Species that exhibit long-term pair bonds but do not remain together for the entire year can reunite if they share a common wintering ground. In seaducks where males leave the breeding grounds while the females are incubating the clutch. Barrow's Goldeneye *Bucephala islandica* (Savard 1985), Bufflehead *B. albeola* (Gauthier 1987), Oldsquaw *Clangula hyemalis* (Alison 1975), Common Eider *Somateria mollissima* (Spurr & Milne 1976) and Harlequin Duck *Histrionicus histrionicus* (Bengston 1972) individuals have all been seen with the same mate on the breeding grounds in subsequent years (see also Anderson et al. 1992). Direct observations of pairs reuniting on the wintering grounds have been observed in Common Eider (Spurr & Milne 1976), Barrow's Goldeneye (Savard 1985) and Harlequin Ducks (Chapter 2, Gowans et al. 1997). Therefore, it is clear in these species that males and females do reunite on a common wintering ground. Males that mate with the same female should follow her year after year to her natal breeding grounds. Seaduck males do show high levels of breeding philopatry, with levels approaching that of females (Anderson et al. 1992). In these species philopatry to a common wintering ground may have evolved to allow individuals to reunite and obtain the benefits of retaining the same mate (for examples see Black 1996). However, philopatry in this group may have evolved for other reasons, and pair reunion has subsequently evolved because high levels of winter philopatry makes pair reunion a viable option.

Genetic mechanisms

Individuals which mate with very close relatives may have offspring which suffer from inbreeding depression (Greenwood et al. 1978), on the other hand, individuals which mate with highly unrelated individuals may also have offspring with a reduced fitness, due to the breakup of co-adapted gene complexes. Theoretically, a level of inbreeding should evolve that maximizes an individual's fitness (optimal outbreeding; Bateson 1983, Greenwood 1987). Some level of inbreeding allows gene combinations that are particularly adaptive in a local site to remain together and not be disrupted by random mating (optimal inbreeding; Shields 1982, 1983). In the genetic hypotheses, philopatry increases an individual's fitness not in the current generation but in subsequent generations; the philopatric individuals will have offspring which are genetically superior. When evaluating genetic hypotheses this must be borne in mind; studying a single generation will not provide any conclusive evidence to evaluate a genetically based hypothesis on the evolution of philopatry.

Local inbreeding may be selected for because it keeps co-adapted gene complexes together, resulting in an optimal level of inbreeding (Shields 1982, 1983). Shields noted that waterfowl presented a potential problem to this interpretation, because male waterfowl are highly dispersive when following their mate. The females' breeding grounds are usually at a site very different from the natal area of the male (Rohwer & Anderson 1988, Anderson et al. 1992). This introduces substantial amounts of gene flow among breeding sub-populations (Cooke et al. 1975, Rockwell & Barrowclough 1987), suggesting that optimal inbreeding would be difficult to achieve in waterfowl. Shields (1982, 1983) noted that waterfowl mate on the wintering grounds, and that the arguments could be still valid if populations are isolated on the wintering grounds.

Genetic differentiation occurs in some winter populations of waterfowl. Rhodes et al. (1993) documented some genetic sub-structure of American Wigeon *Anas americana* populations wintering in Texas. Novak et al. (1989) present electrophoretic data suggesting that Brant *Branta bernicla* wintering on the North American east coast also show some level of local philopatry, although the magnitude was small. The presence of a variety of races in many goose species also suggests that there is genetic isolation among different populations (Owen 1980, Van Wager & Baker 1986). However, this genetic sub-structure cannot be used to support or reject a genetically based hypothesis for the evolution of philopatry. If philopatry has evolved for purely somatic reasons (see above) some level of genetic sub-structure will arise as a consequence, rather than the cause, of the philopatry.

An interesting case is short-stopping, where geese and swans winter in more northerly locations when habitat conditions are favorable. Short-stopping has been documented in Canada Geese and changes in the winter distributions of European geese have been well documented (Owen 1980, Hestbeck et al. 1991). Short-stopping would not be predicted under a genetically based hypothesis for the evolution of philopatry, birds should always return to the same wintering grounds to maintain the genetic isolation of the flock. However, if movements of flocks of waterfowl involve the same birds every time (see Percival 1991), genetic isolation of flocks could still be maintained. In this case it is not philopatry itself that is maintaining the isolation but rather the social integrity of flocks. Snow Geese *Anser caerulescens*, on the other hand, do not maintain flock integrity on their wintering grounds because interchanges of individuals among flocks were very frequent (Schroer & Chabreck 1974).

Some species of ducks are known to segregate sexually on the wintering grounds, including most pochards, some seaducks and some dabblers. Generally, higher proportions of males are found in more northerly locations (e.g. Owen & Dix 1986, Carbone & Owen 1995). Local sexual segregation of species has also been documented (Nichols & Haramis 1980). Philopatry to areas where pairing does not occur cannot be explained by genetic mechanisms. Thus, if philopatry to wintering locations occurs even when the sexes are segregated, hypotheses other than genetically based ones must be sought.

For a genetic model to provide an adaptive explanation for the evolution of philopatry in waterfowl, a mechanism must exist for juveniles to go to the same mate-choosing location as their parents. If not, gene flow would be widesread as juveniles disperse and incorporate into wintering flocks randomly. A mechanism which locates juveniles in the same wintering location as their parents exists for geese and swans; they exhibit extended parental care so that broods follow their parents to the wintering grounds. Duck broods, however, are usually abandoned by the female parent before they leave for their wintering grounds. Although mechanisms have evolved for female ducks to home to their natal breeding grounds, for optimal inbreeding hypotheses to be relevant in birds which pair in the winter, juvenile ducks must be able to "home" to a wintering location where they have never been. Young birds could conceivably migrate on their own and attempt to find their parents on the wintering grounds. In many other bird species mechanisms have evolved for juveniles to migrate for the first time south, after the parents have left, to suitable wintering quarters (Berthold 1996). Evidence from Mallards *Anas platyrhynchos* and Black Ducks suggests that juveniles leave the breeding grounds after their mothers and associate with later migrating adults (probably from more northerly locations). They subsequently migrate south with these other adults and incorporate into these flocks (Bellrose & Crompton 1970, Hopper et al. 1978, Nichols & Hines 1987). Additionally, within a season some species are highly mobile in response to poor weather conditions (Bennett & Bolen 1978, Jorde et al. 1984, Nichols et al. 1983), possibly disrupting flock integrity. Thus, the likelihood of juvenile dabbling ducks joining the same wintering flocks as their parents is small; more research on this topic is clearly needed.

Sex biases in philopatry

Given that winter philopatry occurs, there are some circumstances in which a sex-bias in winter philopatry would be predicted. Sex biases can evolve for a number of reasons, and once again, these reasons can be broadly classified as ecologically or genetically (or eco-genetically) based. For the ecologically based models, the somatic advantages of philopatry, or dispersal, are different for each sex. These advantages can be based on natural (different ecological requirements for each sex) or sexual (the mating system favors different patterns of philopatry in the two sexes) selection pressures. For the eco-genetically based arguments, it is assumed that philopatry is advantageous for both sexes, however, at the cost of extensive inbreeding. Slight differences in the ecological advantages of philopatry for one sex will predict which sex will become more dispersive than the other.

Mating system. - The costs and benefits of philopatry may differ between the two sexes depending on the mating system. In general, male birds are more philopatric than females, both in terms of natal and breeding philopatry (Greenwood 1980, Greenwood & Harvey 1982). Male birds tend to defend territories on the breeding grounds. By returning to a familiar territory they have advantages over competitors (a local knowledge based benefit). Mobile females are then able to choose the best quality male and/or territory for breeding (somatic reasons), or disperse to avoid high levels of inbreeding (genetic reasons) (Motro 1991). When males can economically defend an essential resource, male-biased philopatry should predominate. If critical resources cannot be defended, a mate-defense type of mating system should evolve (Emlen & Oring 1977); females remain in familiar areas while males roam to find available females (Greenwood 1980, Greenwood & Harvey 1982). The major prediction from these hypotheses is that the magnitude and direction of the sex-bias will depend on whether resources can be economically defended by males. If males can defend a critical resource a male-biased philopatry is predicted. If males cannot find a critical resource and the number of females is limited (or females vary in quality), a female-biased philopatry is predicted.

Dabbling ducks form new pair bonds each year (Bellrose 1980, but see Losito & Baldassarre 1996). Male dabbling ducks engage in active courtship of females during the winter season, the exact timing depending on the species (Hepp & Hair 1983, Rohwer & Anderson 1988). Male ducks generally form a hierarchy amongst themselves before pair formation and then the females tend to choose the highest ranking males first (Hepp 1988, McKinney 1992, Oring & Sayler 1992). A significant male bias in most duck populations results in females being the limiting sex (Bellrose et al. 1961). The mating system in dabblers is based on mate choice and no defensible resources are involved. In this case female-biased philopatry may be expected to evolve, as females are free to stay in familiar habitats while males which are unsuccessful in finding a mate must disperse to find other available females (Greenwood 1980).

In the dabbling ducks there is some evidence for a male-biased dispersal, especially in juveniles. Male Northern Pintails in the Sacramento Valley ($\chi^2 = 11.41$, $P < 0.001$), and the Imperial Valley, ($\chi^2 = 12.76$, $P < 0.001$, our test) (Rienecker 1987) had a lower recovery (bird bands recovered and reported to the authorities) rate in the area they were originally banded than females. Juvenile male Green-winged Teal *Anas crecca* banded in the southern high plains of Texas during winter were 4.2 times more likely to be recovered outside of this area than adults (Baldassarre et al. 1988). Juvenile male Green-winged Teal were also more dispersive than juvenile females (Baldassarre et al. 1988). Within a winter season Jorde et al. (1984) showed that male juvenile Mallards had the largest home ranges, followed by juvenile females and adult males; adult females had the smallest home ranges. Juvenile male Mallards had a lower chance of being recovered in the same area as they were banded in than adult males (Nichols & Hines 1987).

Extended parental care. - Geese and swans bring their broods with them to their wintering grounds. Social interactions in wintering goose and swan flocks are common and a dominance hierarchy is established (Raveling 1970, Owen 1980). Both the male and the female are involved in defending an area around their brood so that the young birds can feed. Pairs with broods are the highest on the hierarchy followed by pairs and then single birds (Raveling 1970, Lamprecht 1986, Black & Owen 1989). Families with high social status tend to feed more and win more encounters with other families (Scott 1980a, Black & Owen 1989). It is largely the male who determines the social status of a pair (Raveling 1970, Scott 1980b, Lamprecht 1986). Males also control, if, and when, any local flights are made by the family (Raveling 1969, Owen 1980). If the male's defense of the brood during winter is important, a young male may be at a selective advantage to return to a familiar area. This knowledge may help to ensure the survival of the brood and his mate over the winter. Thus, in geese and swans male-biased philopatry results not from pair formation, but rather from the extended parental care on the wintering grounds and the advantages for dominant males to bring their mates and broods to a familiar area.

Rees (1987) found that newly paired Bewick's Swans *Cygnus bewicki* moved to the males' previous wintering ground. The male initiated local movements in the fall and on the wintering ground. In the spring it was the female who initiated movement toward the breeding grounds. Yearling male Bewick's Swans had a higher return rate than females to their first wintering grounds (marginally significant, Rees 1987). Two year old male Canada Geese had higher return rates than females to a roost site, but yearlings and adults did not show any sex biases in homing rate (Raveling 1979). Raveling (1979) suggested that the female follows the male to his wintering ground once a pair bond is established.

Timing of pairing. - Even in situations where the mating system would lead to a prediction of a sex-bias in winter philopatry, a sex-bias may not exist. In species where pairing takes place very early in the winter, it may not be advantageous for unpaired males to disperse and attempt to find a mate, as all females in the population will be paired. This mechanism was proposed to describe the equal philopatry rates seen in Black Ducks (Diefenbach et al. 1988a). A similar situation will occur if pairing in a species is highly synchronous across its entire range.

Duration of the pair bond. - The duration of the pair bond affects whether sex biases in winter philopatry can exist during certain times during the life of the birds. In the case of geese, swans and at least some seaducks, the pair is together during the winter and both sexes return to the same wintering ground. Only in the unpaired young birds and birds in new pair bonds (where an adult loses a mate or divorces) will evidence of any sex bias be expected. As seen above, most sex-biased philopatry seen in geese and swans is restricted to younger or newly paired birds (Raveling 1979, Rees 1987).

Among the seaducks there is no evidence of a sex bias in winter philopatry. The proportion of Canvasback *Aythya valisineria* males and females banded and then recovered in the same area around San Francisco Bay was the same ($\chi^2 = 2.23$, $P = 0.132$, our test) (Rienecker 1985). Similarly, no sex differences in return rates were seen in other Canvasback (Nichols & Haramis 1980, Haramis et al. 1986), Bufflehead (Limpert 1980, analysis in Anderson et al. 1992) or Harlequin Duck (Chapter 4) populations. A sex bias in winter philopatry would not be expected in adult seaducks since pair reunion is common (see above). If a bias exists, it should only be expected among young birds and birds forming new pair bonds.

Latitudinal segregation. - In many species of ducks the sexes exhibit latitudinal segregation during the non-breeding season, at some level. Generally, males winter at more northerly locations than females. At some time the sexes must overlap in space and time at an area for pair formation to occur. Pair formation can occur on the breeding grounds, as seen in Ruddy Ducks *Oxyura jamaicensis*, but most species which show a sexual segregation during the winter tend to pair in the spring (Weller 1965, Rohwer & Anderson 1988). Philopatry in the two sexes may or may not be different depending on the mechanisms of the sexual segregation in these species. If females are attempting to winter at the more northerly locations with the males, yet are excluded due to male dominance, a female-biased dispersal might been seen. Males have been shown to be behaviorally dominant to females on the wintering grounds (Choudhury & Black 1991) and this dominance has lead to the hypothesis that latitudinal segregation of the sexes is due to males excluding females from high quality areas (intersexual dominance hypothesis). Females may have to disperse when confronted with a large population of males. Alternatively, however, a sex-bias in philopatry would not be expected if females immediately go to marginal, or southerly habitats, instead of confronting the males directly and then dispersing if unsucessful at competing with them. This scenario is also consistent with the intersexual dominance hypothesis of sexual segregation, whereby the very presence of males reduces the quality of the habitat sufficiently that females immediately go to marginal, yet better for them, habitats. Hypotheses that suggest that sexual segregation is based on different habitat requirements of the sexes (such as the cold tolerance, where females winter farther south to avoid cold temperatures, Myers 1981), also predict no sex bias as females and males head for their respective wintering grounds.

1.2.4. Patterns of winter philopatry

Methods

Published data on winter philopatry (between year site fidelity) were obtained for 19 species in four tribes (Anserini - geese and swans; Anatini - dabbling ducks; Aythyini - pochards and Mergini - seaducks) from a total of 28 studies. The study areas ranged from a single pond or field to large continental areas. We restricted ourselves mostly to published information, however, we believe that a large amount of information exists in unpublished documents, which are difficult to obtain.

Quantifying philopatry. - The quantification of philopatry has meaning only in the context of the area to which the animal returns. This could be defined as narrowly as a nest site or as broadly as a major subdivision of an entire range. Using too small an area to define philopatry is not useful but neither is using too large an area. Clearly, the more narrowly the location is defined the lower the frequency of philopatry, all other things being equal. This can make comparisons among studies difficult. Therefore, study area sizes were categorized on a logarithmic scale starting from less than 1 km^2, < 10, < 100, . . . , up to $< 10^5$ km^2.

Return rates are frequently used to quantify philopatry. However, return rate (the number of animals recaptured or resighted in following years as a proportion of the total number of animals marked) is a composite of three different probabilities: the probability that a bird will survive to the following year (survival rate), the probability that a bird will return to the study area, given that it is alive (homing rate), and the probability that a bird will be recaptured or resighted, given that it is alive and has returned to the study area (recapture rate) (Hestbeck et al. 1991, Ebbinge 1992). Homing rate provides a true index of philopatry. Unfortunately, as a composite probability, return rates from different studies are not necessarily comparable. Generally, the recapture/resighting rate is highly variable from one study to the next, and depends on the study design and the nature of the animal. Survival rates can also vary considerably, geese have annual survival rates reported that vary from 0.53 to 0.88, while ducks range from 0.32 to 0.76 (Johnson et al. 1992). Generally, younger birds have higher mortality rates than adults, and females have higher mortality rates than males (at least in ducks).

A method which estimates the homing rate directly is to compare birds which return to a study site to those which go to other areas. Therefore, homing rate is the number of birds returning to the study site divided by the total number of birds resighted anywhere. Because all the birds in the sample have survived, survival is not confounded in this method of estimating homing rate. This method assumes that the resighting rates at all of the study sites are similar, which may or may not be true. Generally, this estimate will be biased high if the effort to resight birds outside of the study area is low.

Statistical methods for concurrently estimating survival, homing and recapture rates are available (Hestbeck et al. 1991, Nichols et al. 1993) as an extension to standard Capture-Mark-Recapture (CMR) methodologies (Lebreton et al. 1992). As researchers become more familiar with these statistical techniques, better estimates of homing rates should be present in the literature.

A further method of estimating levels of winter philopatry in waterfowl is to use data obtained from people reporting bands to the authorities of recovered (usually shot) birds. This method is similar to the method using resightings to estimate a homing rate. The homing rate is the ratio of birds which were banded in one winter and recovered in a subsequent winter in the same area divided by all birds that were recovered anywhere. This method is useful only over a large geographic range to obtain the necessary number of recoveries. An implicit assumption in homing rates derived from recoveries is that the hunting pressure and vulnerability are similar across the range of the species. If certain areas are more heavily hunted then more recoveries will come from that region due to higher mortality and not due to differences in the propensity of birds to return to that area. Differences in the reporting rate between areas could bias the homing rate in a similar way.

Return rates are a composite probability that includes the homing rates, so these two probabilities are presented separately. We emphasize studies reporting homing rates for making comparisons among studies when possible, because survival is not confounded in these values.

Results

Geese and swans show high levels of winter philopatry; homing rates vary from 46 to 89% with a median of 72% (n = 24, Table 1.2.1). For the pochards only data from Canvasback are available. Canvasback show relatively low return rates (3% to 19%) to small study areas (Table 1.2.1). Seaducks show high return rates to small study areas as well. Given that return rates are a minimum estimate for homing rates, it would appear that the seaducks (at least Buffleheads and Harlequin Ducks) may show high levels of winter philopatry. Return rates for dabbling ducks ranged from 0 to 10% with a median of 3% (n = 9, Table 1.2.1). Study areas tended to be very large; most were 10^5 km^2. The proportion of individuals recovered in the same area of banding (homing rate) varied from

Table 1.2.1. Return rates (proportion of all banded individuals returning to a study area) and homing rates (proportion of surviving individuals returning to a study area) of waterfowl to a wintering ground.

Species		Number of banded birds	Number of returns	Return rate	Homing rate	Study location	Return area (km^2)	Source
Bewick's Swan (*Cygnus columbianus*)	1969-73	978	354	36.2		Slimbridge, U.K.	< 1	Evans (1980)
(after first winter seen at study site)	1963-68	1421	304	21.4				
(after second winter seen at study site)	1963-68	354	263	74.3				
	1969-73	304	167	54.9				
	adult male	367			67.8	Slimbridge, U.K.	< 1	Rees (1987)
	adult female	323			66.3			
	adult male (new pair)		167		56.2			
	adult female (new pair)		115		45.5			
	yearling male	98			58.1			
	yearling female	63			49.2			

	cygnet male	181		60.5			
	cygnet female	195		57.0			
Canada Geese (*Branta canadensis*)	adults	271	212	78.2	Rochester,	< 1	Raveling
					Minn.		(1979)
	yearling males	80	64	80.0			
	yearling females	60	46	76.7			
	2-year-old males	52	36	69.2			
	2-year-old females	37	22	48.9			
	adults	Total :		71.0^{a}	Atlantic states	< 10^{5}	Hestbeck
		28 849		88.9^{a}	Chesapeake		(1991)
				56.2^{a}	Carolinas		
Barnacle Geese (*B. leucopsis*)	1984-85	141	104	73.8	Islay, U.K.	< 10	Percival
	1985-86	154	113	73.4			(1991)
	1986-87	245	195	79.6			
Brant (*B. bernicla*)	1994-95	Total:	n/a	74	SW British	< 1	E. Reed
	1995-96	112		86	Columbia		(unpubl.)
White-fronted Geese (*Anser albifrons*)		531		85.1	Wexford Co.,	< 100	Wilson et al.
					U.K.		(1991)

Pink-footed Geese (*A. brachyrhynchus*)	736	559		76	Lancashire, UK	$< 10^5$	Fox et al. (1994)
Snow Geese (*A. caerulescens*)	77	68		88	SE Texas, SW Lousiana, USA	< 1	Prevett & MacInnes (1980)
Bean Geese (*A. fabalis*)	25	15		60	SW Skåne, Sweden	$< 10^2$	Nilsson & Persson (1991)
	35	23		67			
Mallard (*Anas platyrhynchos*)	1929	35 (48)^c	1.8 (2.5)^c		Southern High Plains (Texas)	$< 10^4$	Fedynich et al. (1989)
	16789	1014	6.0^c		southwestern B.C.	$< 10^4$	Munro (1943)^d
	695	66	9.5		Calgary, Alberta	< 1	Sugden et al. (1974)
	n/a	1396		35^b	N.E. North America	$< 10^5$	Diefenbach et al. (1988b)
	n/a	90		54^b	SW British Columbia	$< 10^4$	McKelvey & Smith (1990)

	1231	1014	82[b]			Munro (1943)
adult males	n/a	585	64	Continental	$< 10^5$	Nichols &
			(14 - 87)[b]	USA		Hines (1987)
	n/a	459	72			
			(63 - 83)[b]			
adult females	n/a	112	70			
			(58 - 82)[b]			
	n/a	137	61			
			(38 - 78)[b]			
juvenile males	n/a	458	54			
			(18 - 75)[b]			
	n/a	564	58			
			(25 - 75)[b]			
juvenile females	n/a	107	66			
			(50 - 73)[b]			
	n/a	225	53			
			(17 - 79)[b]			

Black Duck (*A. rubripes*)		n/a	813		50^b	NE North America	$< 10^5$	Diefenbach et al. (1988b)
	coastal	n/a	2035		85^b	NE North America	$< 10^4$	Diefenbach et al. (1988a)
	inland	n/a	1067		55^b			
Northern Pintail (*A. acuta*)		1262	$0\ (1)^c$	0 $(0.01)^c$		southern high plains, Texas	$< 10^4$	Fedynich et al. (1989)
	males	15672	636		44.2^b	Sacramento Valley, CA	$< 10^5$	Rienecker (1987)
	females	8607	223		53.6^b		$< 10^5$	
	males	17538	745		38.9^b	Imperial Valley, CA	$< 10^5$	
	females	13595	385		46.2^b		$< 10^5$	
		6481	186	2.9^c		SW British Columbia	$< 10^4$	Munro (1944)^d
		276	186		67.4^b			Munro (1944)
		954 - 29505	169 - 3651		$5.3 - 81.3^b$	continental United States	$< 10^5$	Hestbeck (1993)

American Wigeon (*A. americana*)		n/a	36		59^{b}	SW British Columbia	< 10^4	McKelvey & Smith (1990)
		726	15 (16)^{c}	1.8 (2.2)^{c}		southern high plains, Texas	< 10^4	Fedynich et al. (1989)
Cinnamon Teal (*A. cyanoptera*)		31	3	9.7		southern high plains, Texas	< 10^4	Fedynich et al. (1989)
Green-winged Teal (*A. crecca*)		820	9 (13)^{c}	1.4 (1.6)^{c}		southern high plains, Texas	< 10^4	Fedynich et al. (1989)
		6432	230	3.6^{c}		SW British Columbia	< 10^4	Munro (1949)^{d}
		314	230		73^{b}			Munro (1949)
Canvasback (*Aythya valisineria*)	adult males	3009	162	5.4		Chesapeake Bay	< 1	Haramis et al. (1986)
	adult females	374	22	5.9				
	juvenile males and females	2741	93	3.4				

		5670	1147	19.2		San Pablo Bay, CA	< 1	Rienecker (1985)
	males		389		68.6^{b}	San Francisco Bay area	< 10^{4}	Rienecker (1985)
	females		178		74.0^{b}			
Harlequin Duck (*Histrionicus histrionicus*)	males	82	63	76.8		Vancouver, BC	< 10	Chapter 4
	females	66	41	62.1				
Bufflehead (*Bucephela albeola*)	males	91	24	26.4 (46.5)^{e}		Chesapeake Bay	< 1	Limpert (1980)
	females	37	4	11.1 (19.5)^{e}				
Oldsquaw (*Clangula hyemalis*)		?	1^{f}	?		Presqu' île P.P.	< 1	Alison (1974)
Barrow's Goldeneye (*Bucephala islandica*)		?	1^{g}	?		Vancouver, BC	< 10	Savard (1985)

[a] these values represent with site transistion probabilities based on CMR models including a transistion probability of moving to the same of different site. As such this value represents a true homing rate.

[b] the proportion of indirect recoveries that occured in same location as the banding.

[c] includes birds found dead or recovered on the study area, in addition to live recaptures.

[d] see also Fedynich et al. (1989).

[e] includes birds only recaptured at a single banding station (Locust Point), value in parentheses represents a corrected return rate removing the recapture probability from this composite (i.e. this value represents homing rate * survival). Recapture probability could be calculated because the entire population size was known (approx. 55% of all birds were caught)

[f] a bird banded in the spring of 1972 was recovered 200 m from the banding site in late Nov, 1972.

[g] a male banded on the breeding grounds was sighted at the same wintering location in two subsequent years.

35% to 85% with a median of 58%, except Northern Pintail which ranged down to 5% (n = 21, Table 1.2.1).

Discussion

Although there are a considerable number of studies that report indices of winter philopatry it is very difficult to compare these data in a meaningful way. The actual size of the study areas vary so widely that comparisons are not possible. Return rates in an area 10^5 km^2 are not very instructive in determining whether an individual is philopatric. The utility of return rates is also highly questionable, and comparing return rates across studies is difficult to justify. Given the large amounts of heterogeneity in these data, are they comparable in any way?

The data do provide us with an ability to make some very coarse comparisons between the taxa, making certain assumptions. Geese and swans show high homing rates to relatively small geographic areas (1 to 10 km^2), although they may use more than one wintering area in a season (Percival 1991, Fox et al. 1994). Dabbling ducks also show relatively high homing rates, yet the study areas are 100-1000 times larger than those used for geese and swans. Assuming that the homing rate would increase as the size of the study area increases, dabbling ducks show a lower homing rate than geese and swans to a range of similar size. However, we do not know if homing rate would increase with study area size or not. For the other duck species only return rates are available. Return rates for pochards and dabbling ducks are low, whereas for seaducks they are relatively high. The size of the study areas for pochards (< 1 km^2) is much smaller than that of dabbling ducks (10^4 to 10^5 km^2). Assuming that the survival and recapture rates are similar for both groups of ducks and the return rate increases with the size of the study area, then seaducks and possibly Canvasback show a higher homing rate than dabbling ducks. Survival rates for all diving ducks are slightly higher than, or similar to that, of dabbling ducks (Johnson et al. 1992), so major survival differences are unlikely to be the reason behind the different homing rates. It is an untested assumption that recapture rates are similar between studies.

A general conclusion that can be drawn from these data is that philopatry is not absolute to small geographic areas in any species. Although philopatry in geese in swans is very high, even small numbers of individuals moving among populations is sufficient to disrupt genetic isolation (Rockwell & Barrowclough 1987). Most dabbling duck species do not appear to be 'philopatric' in a general sense at all, except maybe at the flyway level. Genetic isolation of wintering dabbling duck populations is highly unlikely.

Future directions

Standardized data collecion. - All of the studies reported in this review used individually marked birds to provide measurements of philopatry. Obviously, continued use of individually marked birds, ideally over a long period of time, is the only way to obtain the data necessary to test hypotheses about the evolution of philopatry. For comparisons between studies, better metrics of philopatry need to be established. First and foremost the reporting of return rates should be strongly discouraged. Differences in return rates can reflect differences in survival, study design, resightability of individuals and/or a measure of homing. As argued above very little useful information can be extracted from return rates. Homing rates provide a better index of philopatry. The best method available for estimating homing rates are by using modern capture-mark-recapture methodologies to design and analyse data. Literature is currently available for researchers to use this method, which estimates survival, recapture rate and homing rates simultaneously (Hestbeck et al. 1991, Lebreton et al. 1992, Nichols et al. 1993).

A further refinement in study design might be to standardize what exactly is the minimum distance (or preferably area) before an individual is considered to have dispersed. We suggest reporting on a logarithmic scale as we have done in this review, to facilitate comparisons with future studies. Instead of reporting a single homing rate, a series of homing rates could be reported assuming the study area is 1 km^2, 10 km^2 .. 10^5 km^2. Smaller ranges could be used for species which do not range widely. The mean dispersal distance could also be reported instead. The range considered to be ecologically meaningful for dispersal of a species would be dependent on the authors opinion and knowledge of the species in question. Therefore, studies which compare philopatry patterns within populations at different spatial scales would be most valuable.

Taxonomic gaps .- Currently there are reasonably good data available for the geese and the swans. Although we were able to collect information from a number of studies of dabbling ducks, the utility of the data was questionable, making comparisons difficult. This is not to say these studies were done poorly, but rather obtaining the necessary information to produce a useful homing rate is much harder with the dabblers than with geese and swans. As is generally true for most aspects of waterfowl biology, very little information was available for pochards, seaducks, perching ducks and other groups. An effort should be made to study winter philopatry patterns in these species.

Sex biases. - Comparisons between sexes in future studies will provide insights into the role of mating systems and parental care in shaping the patterns of winter philopatry seen in waterfowl. Waterfowl provide a rich opportunity for interesting studies of winter philopatry because they utilize so many habitats and exhibit a number of mating systems (Oring & Sayler 1992). The study of breeding philopatry has been well formalized into a theoretical framework in waterfowl (Rohwer & Anderson 1988). It is time for winter philopatry to receive the same attention. As pairing occurs on the wintering grounds, all of the predictions of mating system theory can be applied to this period. The main predictions are: 1) if males can defend a critical resource then male-biased philopatry would be predicted, 2) if males cannot defend a critical resource, a female bias is expected (Emlen & Oring 1977, Greenwood 1980). Research should focus on testing these predictions. For example, Goldeneye are territorial on the wintering grounds (Savard 1988). Based on this information a male-biased winter philopatry is predicted in Goldeneye. If so, this is very interesting considering that females are more philopatric than males to the breeding grounds. In those species exhibiting a mate defense type of mating system, we should predict a female-biased philopatry to the wintering grounds. The response of an individual male that cannot find a mate depends on local conditions and the mating system. Does he disperse, or remain at the same site?

The frequency of pairs reuniting in the seaducks will be a very fruitful avenue of research, as well. Although it has been documented that some pairs reunite on the wintering grounds, no research has been done on the frequency of pairs that do reunite. Correlations between the frequency of pairs that reunite and the level of winter philopatry that each species exhibits will provide some insights into the importance of pairing with the same mate and the role of philopatry in facilitating pairing with the same mate.

Importance of juveniles. - A critical gap in our knowledge of philopatry is how juveniles become incorporated into their wintering population. Any test of a genetically based hypothesis of the evolution of philopatry requires knowledge about the juvenile settlement pattern into wintering flocks. Even if adults are completely philopatric, moderate, or even low, levels of juvenile dispersal will result in gene flow. As many other taxa exhibit a juvenile-biased dispersal to the breeding grounds (Greenwood & Harvey 1982) it will be interesting to see if wintering waterfowl show the same pattern. The data for waterfowl suggest that juveniles may be more dispersive, but much more information is needed on this point.

Juveniles also provide interesting insights into the relationship between philopatry and mating systems. In species that exhibit long-term pair bonds, only the younger age classes will be actively involved in mate choice. It is possible that this mating system has led to a strong male sex bias, however this bias is masked by the equal philopatry levels exhibited by the adults in long-term pair bonds.

Even if the species is serially monogamous, juveniles may be under different pressures from adults, and display different levels of philopatry. It is common that individuals of differing condition or quality exhibit different mating tactics (Austad 1984). As an example, adult male dabbling ducks might be better suited to remain at a familiar place where they can obtain good quality resources and actively court females. Juvenile males may be better off to disperse to try and find concentrations of unpaired females, or go to other feeding areas, with no adult males, to ensure survival for their first winter.

More sophisticated reanalysis of existing recovery data by sex and age classes could begin to address some of these questions.

Location and timing of pairing. - Surprisingly, pairing chronologies and the location of pairing are not well documented for many species of waterfowl. The data for philopatry is of the best quality in geese and swans, yet very little is known about exactly when geese form pair bonds (Owen et al. 1988). Obviously, for a test of a genetic hypothesis for the evolution of philopatry in geese and swans to be made, the location where the pair bond is formed is crucial. Indeed, individual geese and swans may begin forming pair bonds at different times of the year at different locations. The exact timing and location of pair bond formation is not well known for species which segregate during the winter. As the mating system is only a factor during pair formation itself, different explanations for the philopatry may be necessary for different areas of a species' range. Finally, although it is largely assumed that pairs observed in the winter are maintained into the breeding period, very little direct evidence exists to corroborate this point. If pairs formed in winter are not relevant to gene exchange, winter is no longer the appropriate time to test genetically based hypotheses.

Physical location and social cohesion. - The predictions of the hypotheses that philopatry evolved because local knowledge is useful is very different for the case of philopatry evolving as a means to maintain group cohesion. In the latter case, the actual environment the birds are in is not as important as being together. Waterfowl are highly social as a group, suggesting that flocking is important for them. It is possible that philopatry in this group is simply a mechanism to ensure that an individual can find a number of conspecifics. In species that are shown to be dispersive, evidence that the same individuals move together to different wintering areas would provide evidence that social cohesion is important.

Habitat stability. - The role of habitat stability in shaping patterns of winter philopatry has not been addressed. Research questions along this line could include: Do species that winter in predictable habitats tend to exhibit higher levels of philopatry. Does this pattern hold within species and between populations? Although habitat predictability is difficult to assess, some generalizations are possible. Marine habitats are considered to be more predictable than freshwater habitats. Shallow freshwater habitats are prone to freezing during cold spells, unlike marine waters. Relatively dry upland habitats are also reasonably stable. Whether patterns of philopatry follow this gradient would be a valuable research direction.

Finally, as is usually the case, a number of these hypotheses and mechanisms may be responsible for shaping the pattern of philopatry seen in waterfowl species. Plenty of opportunities exist for productive studies of winter philopatry in waterfowl. We hope this review provides a useful framework for future studies.

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Chapter 2

The timing of pair formation in Harlequin Ducks[2]

2.1. Abstract

Within and among species of ducks, there is considerable variation in the timing of pair formation. In this study we documented the chronology of pair formation for a population of wintering Harlequin Ducks *Histrionicus histrionicus* in southwestern British Columbia. Harlequin Ducks began forming pair bonds in October, much earlier than other species of similar size (approx. 500 - 700g). A segment of this population was individually marked and we documented the reunion of pairs in subsequent years. In every case where both members of the pair returned to their wintering grounds they reunited in the fall (October - November) (n=11). New pair bonds, involving young females, were formed in the spring (March and April). With this new information on Harlequin Ducks and other species of sea ducks (tribe Mergini) we evaluated the male cost hypothesis for explaining the variation in the timing of pairing in the sea ducks. This hypothesis suggests that males attempt to form pair bonds as early as possible, constrained by their ability to afford the extra energy required for activities associated with courtship and pair bond maintenance. Among the sea ducks, the large species (the two largest eiders) and small species that use stable, predictable food sources and energetically inexpensive foraging techniques (shallow divers) formed pair bonds in the fall. Either of these attributes reduces the costs of foraging during the winter months. Smaller and deeper diving species, or species that forage on ephemeral sources (such as the mergansers which feed on fish) do not pair until the spring. The males in these species possibly pair later because they can not afford to expend the extra energy needed for courtship and pair bond maintenance during the winter

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[2] This chapter has been submitted as Robertson, G.J., Cooke, F., Goudie, R.I. & Boyd, W.S. The timing of pair formation in Harlequin Ducks, to the *Condor*.

period. Thus, the male costs hypothesis for the timing of pairing in the sea ducks is supported by the available data.

2.2. Introduction

In many migratory bird species pair bonds are formed just before the breeding season (Oring 1982). Females arrive at the breeding grounds and select males based on their individual quality and/or on the quality of the territory they hold (Hixon 1987). Waterfowl do not follow this pattern, and pair bonds in ducks are usually formed during the preceding fall, winter or spring, depending on the species (Rohwer & Anderson 1988). In geese and swans the pair bond is maintained throughout the entire year and across years. Pairing well before the breeding season is thought to have evolved in waterfowl because males are unable to defend breeding territories economically, and thus, pairing can occur away from the breeding grounds (Rohwer & Anderson 1988). Intense selection for mates has lead to the evolution of early pairing, sometimes up to seven months before breeding. Males benefit by obtaining a mate, females benefit by being protected by a mate thereby optimizing foraging during the pre-breeding season (Ashcroft 1976, Scott 1980).

There is considerable variation in the timing of pairing, both within and among species (Rohwer & Anderson 1988). Explanations for these differences among species include differences in the timing of breeding, food quality and sex ratio of the species (McKinney 1992). Among species, early pairing tends to be correlated with body size (Rohwer & Anderson 1988). Larger species have a number of energetic advantages that allow them extra time for other activities (Goudie & Ankney 1986), including pairing. Although larger species require absolutely more food they metabolize it at a slower rate, thus they are more efficient with the same amount of relative food (Calder 1974). Additionally, larger species have thermodynamic advantages that slow the rate of body heat loss and lowers their thermoneutral temperature zone (Calder 1974). Therefore, larger species are able to court and maintain a pair bond throughout inclement weather conditions in winter. Males of smaller species are unable to devote the extra energy to courtship and mate guarding until favourable weather during spring (Rohwer & Anderson 1988). This led Rohwer & Anderson (1988) to formulate the male costs-female benefits hypothesis for the timing of pair formation. Pair bonds are predicted to form at a time when the female benefits from being paired, which is assumed to be during the entire non-breeding season, because paired females enjoy a higher dominance status and access to preferred food resources (Ashcroft 1976, Paulus 1983). The costs to males of maintaining the pair bond should not be so high that their own survival is comprised disproportionately from the gains from obtaining a mate. The timing of pair formation depends on the relative benefits and costs for males in maintaining the pair bond. Within species, older males and males in prime condition tend to successfully obtain a mate sooner than young males and males in poor condition (Brodsky & Weatherhead 1985, Hepp 1986, Heitmeyer 1995).

The pairing chronology of the sea ducks is generally not well known, yet they represent a monophyletic clade that exhibits a wide variation in life history characters and body size (Livezey 1995). Pairing begins as early as September in Common Eiders *Somateria mollissima* (Spurr & Milne 1976) and as late as March (possibly even during spring migration) in the mergansers and Buffleheads *Bucephala albeola* (Erskine 1972, Hohman et al. 1992). In some species of sea ducks, individuals are known to regularly reunite with the same mate year after year after a period of separation during brood rearing (Bengtson 1972, Spurr & Milne 1976, Savard 1985)

Harlequin Ducks *Histrionicus histrionicus* represent an interesting case as they are a relatively small sea duck that begins to form pair bonds in October (Gowans et al. 1997). They are also known to reunite with the same mate in subsequent years (Bengtson 1972, Gowans et al. 1997). In this study we identify factors that influence the timing of pair formation among individual Harlequin Ducks. Specifically, the objectives of this study were to; 1) document the pairing chronology of Harlequin Ducks, 2) determine if variation in the timing of pair formation is related to age and/or experience of individuals, 3) discuss how long term pair bonding influences the timing of pair formation, and 4) discuss patterns in the timing of pair formation within the sea duck species.

2.3. Methods

Study area

This study was conducted from August 1994 to May 1997 on a 5.5 km stretch of rocky shoreline near the town of White Rock, in coastal southwestern British Columbia (Figure 2.1). This study area is bounded by mud flats on either side which are not used by Harlequin Ducks. Up to 150 Harlequin Ducks molt and winter at this site (Robertson et al. 1997). Access to the site is provided by a railway line on a dike that runs 2 to 4 m above the intertidal along the entire shoreline.

Methods

Harlequin Ducks were captured annually during the wing molt in July (males) and September (females) since 1994. Flightless individuals were corralled by researchers in sea kayaks into a drive trap placed on the intertidal bench. All individuals captured were sexed and aged (using the depth of the Bursa of Fabricius, Peterson & Ellarson 1978) by cloacal examination. Age was classified as either juvenile (hatched in the same summer as the banding), second year (or yearling), third year (or sub-adult) and after third year (or adults). Each individual was marked with a unique colored tarsal leg band engraved with a 2 digit alpha-numeric code and a standard U.S. Fish and Wildlife Service aluminum band. Birds were released in small groups after processing.

Surveys of the study site were conducted regularly (about once per week) throughout the year. During each survey, observers noted the location and group composition of all Harlequin Ducks present at the study site. Unlike most other sea ducks, Harlequin Ducks

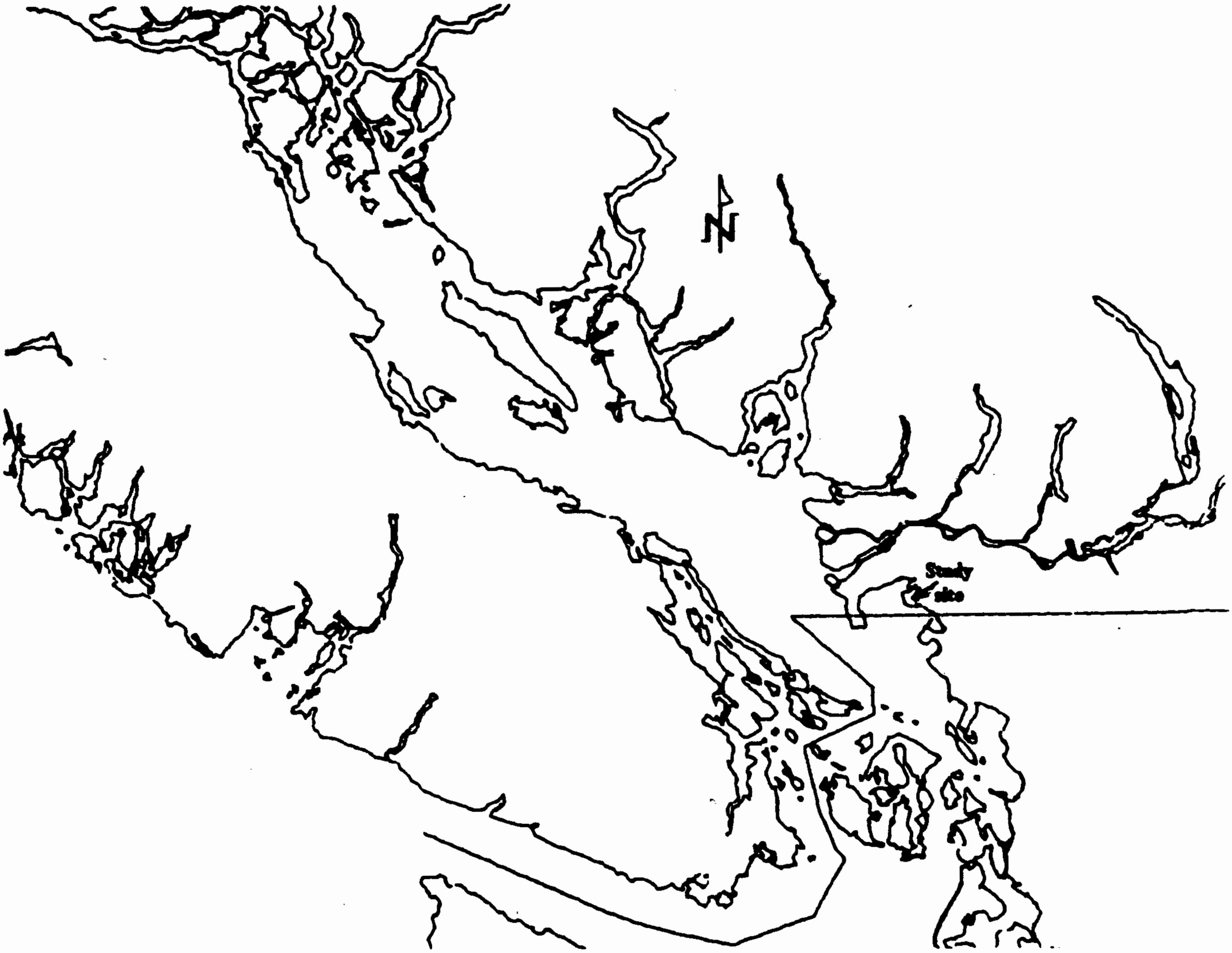

Figure 2.1. Map of southwestern British Columbia and northern Washington State showing the study area.

prefer to remain within about 50 m of the shoreline and accurate population counts are feasible. Harlequin Ducks haul out on to rocks to rest and preen and at this time the tarsal band can be read. Pairs were identified by the methods described in Gowans et al. (1997). Briefly, individuals were considered paired if they behaved synchronously, remained close together and the male was seen to guard the female from other males. A particular emphasis was made to identify pairs in which one, or both, of the members of the pair carried tarsal bands. The first time a pair was observed represents a biased estimate of when the pair bond formed; birds could have been paired for months before they were identified, so our estimate of the timing of pair formation represents the latest possible time a pair bond could have formed. The pairing status of an individual was considered confirmed if they were observed in the same state at least three different times.

The non-breeding season was broadly classified into, molt (June though September, see Robertson et al. submitted), fall (October to mid-December), winter (mid-December to February), and spring (March to mid-May).

2.4. Results

Timing of pairing

The chronology of pair formation was very similar over the three seasons (Figure 2.2). The first pairs were seen in early October and by mid-December approximately 80% of females were paired. A decrease in the number of pairs detected occurred in December and January in 1995-1996 and to ~ 60% of females in pair bonds, this decrease was not apparent in 1994-1995 or 1996-1997. Through March and April the proportion of females paired approached 100% in all years.

Pair reunion

In 1994, six pairs were identified where both the male and the female were banded. Four (67%) of these pairs reunited in 1995, and in all four cases the birds were observed paired

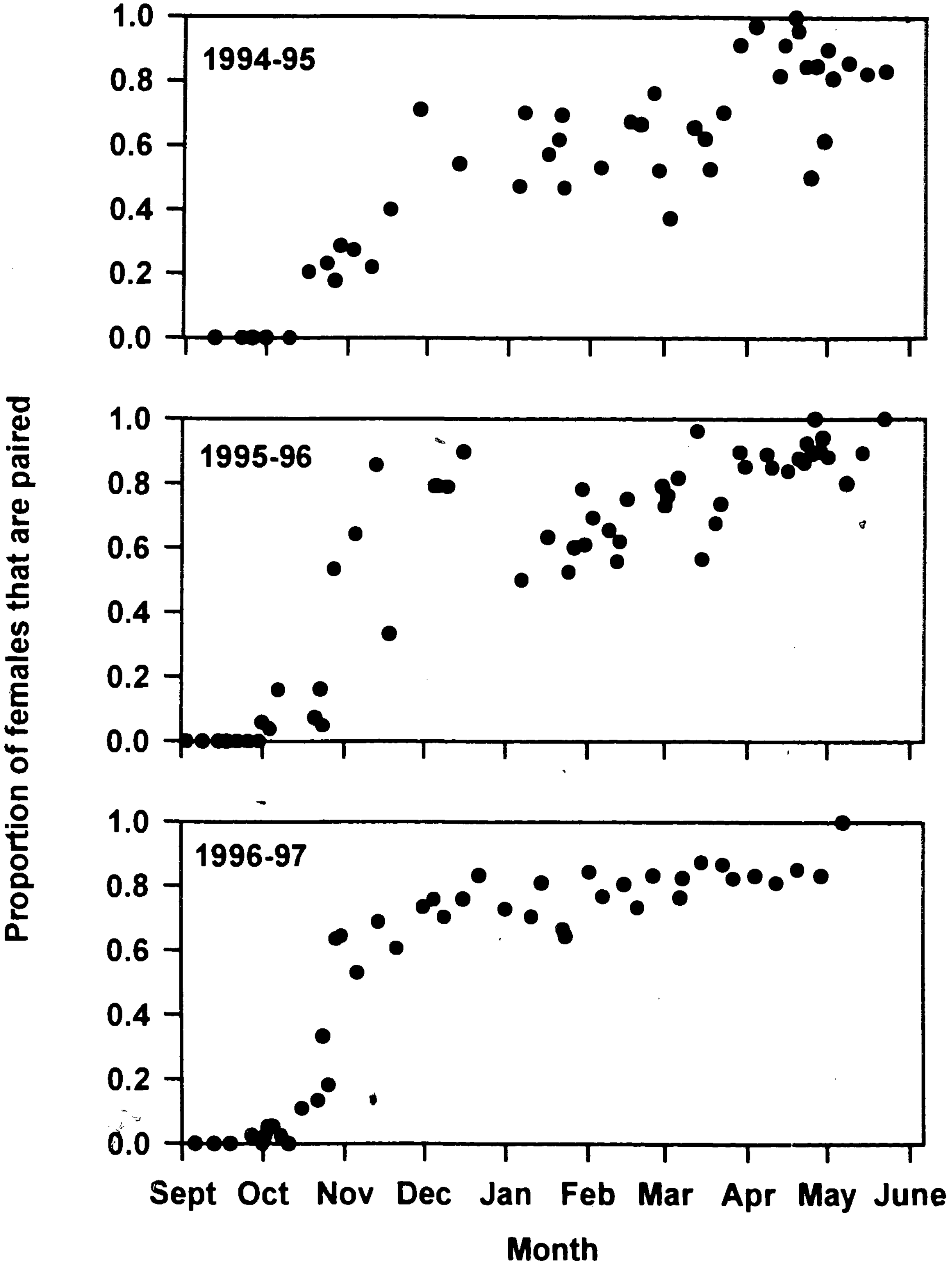

Figure 2.2. Pairing chronology of female Harlequin Ducks at White Rock, BC.

for the first time in the fall. In the other two cases the male returned and the female was never seen. One of these males remained in the study area for the 1995-1996 non-breeding season, and was observed courting other females but was never successful in obtaining a mate. He also returned to the study area to molt in the summer and fall of 1996, but left the study area after the molt. The other male was seen intermittently over the next two non-breeding seasons. He was observed once, possibly paired, in the spring of 1996 and once, apparently unpaired, in the spring of 1997. Only one possible case of pair divorce occurred, where a male was seen with an unmarked bird in 1994-1995 and was seen with a banded female (from the 1994-1995 marked cohort) in the following year.

In 1995, 11 pairs were identified where both the male and the female were banded (including the four that were identified in 1994-1995). Eight of these pairs reunited in 1996-1997. All but 2 (75%) of these pairs were seen for the first time in the fall. Of the remaining 3 pairs the males returned and the females did not. One of these males left the study area after the molt, another male remained in the study area and was seen unpaired in the spring of 1997, and finally, the last male was observed paired with a different female (a sub-adult) in the spring.

Age and timing of pairing

A juvenile female was captured and marked in the fall of 1996. She was observed unpaired in the spring of 1997. Of nine second-year individuals in the banded sample i.e. yearling females, it was possible to identify the pairing status for five, four of which formed pair bonds in the spring. The other female did not obtain a mate and remained on the study area after the pairs had departed for the breeding grounds. Of nine third year females i.e. sub adults, it was possible to determine the pairing status of five of them. All five formed pair bonds, one in the fall and four in the spring. All adult females formed pair bonds (n = 31); 16 (52%) were first seen paired in the fall or winter, 15 in the spring.

Of two second year males, one paired in the spring the other did not obtain a mate. The male that was successful in obtaining a mate reunited with his mate in the following fall. Of two third year males, neither were successful in obtaining a mate. Among the adult males 13 of 40 (33%) did not obtain a mate in the first year after they were banded. Of the 27 males that did find mates 11 (41%) were seen paired for the first time in the fall, 16 were seen for the first time in the spring.

2.5. Discussion

Timing of pair formation in Harlequin Ducks

Harlequin Ducks began to form pair bonds in the fall, with well over half of the females paired by December, and all females paired by April. If both members of a pair return to the wintering grounds they reunited in the fall. Young females (2 and 3 years old) pairing for the first time did so in the spring (February and March). Some young males (2 years old) were able to establish a pair bond.

Harlequin Ducks form pair bonds much earlier than other species of waterfowl of similar sizes. Among dabbling ducks, the larger species tend to form pair bonds in the fall and smaller species in the spring (Rohwer & Anderson 1988). Possibly, males of smaller species are unable to expend extra energy maintaining a pair bond and a balanced energy budget during the cold weather and short days during the mid-winter months. Therefore, they must wait until spring before courting females. All of the pochards form pair bonds in the spring, even the large bodied Canvasback *Aythya valisineria* (Weller 1965). Pochards, in contrast to dabblers, dive for food. In divers it is thought that males cannot efficiently defend the female from harassment or economically defend a food resource, so there are no benefits to pairing for either sex before the spring. Smew *Mergus albellus* (Nilsson 1974), Oldsquaw *Clangula hyemalis* (Alison 1975) and the Bufflehead (Erskine 1972) are sea ducks similar or smaller in size to Harlequin Ducks, and all of these species pair in the spring. Given that Harlequin Ducks are both small and dive for food they would be predicted to pair in the spring, yet this is not the case. Two inter-related factors may explain why Harlequin Ducks pair earlier than other species of similar size. One is that they prefer to forage in relatively shallow waters along the intertidal zone (Goudie & Ankney 1988) and the other is that established pairs reunite every fall.

Male sea ducks abandon their mates while they are incubating and depart to a molting location, which may be a substantial distance from the breeding locations (Salomonsen 1968). Females may join in these migrations at a later date or molt on the breeding grounds. The males and females are separated for at least some period of time. Therefore, individuals must be philopatric to the location where they first formed their pair bond in order for pair reunion to occur. Since pairs are formed in the fall through spring in Harlequin Ducks, they should exhibit philopatry to their non-breeding grounds. Philopatry is also expected to be favored in species that use stable habitats. Harlequin Ducks use a relatively predictable habitat in the winter and are philopatric to their wintering grounds (Chapter 4), allowing pairs to reunite every fall. A potential benefit for early pair reunion is the ability for an individual to determine if their mate has survived the breeding and molting season. Individuals that lose their mate can begin courting another mate as soon as possible.

Pairs that reunite do so in the fall, whereas new pairs (including young females) are established for the first time in the spring. If only new pairs are considered and not pairs that reunite, Harlequin Ducks do follow the predicted pattern for a spring timing of pair formation in a small diving species. Presumably during the winter months, it is not possible for males to attract and effectively defend a new female, and still maintain a balanced energy budget. They may need to forage at such a high rate and cannot budget the time for courtship activities. Indeed foraging rates during December and January are high, over 70% of the days' activity is spent feeding (Goudie & Ankney 1986, unpubl. data, R.

Torres unpubl. data), other sea ducks show increased foraging rates during the mid-winter period as well (Nilsson 1970). Furthermore, even the established pairs tend not to be close to each other during the mid-winter, and in some cases it is not even clear that the pair bond is intact (S. Boyd pers. comm., R. Torres unpubl. data), thus the males are investing little energy in mate guarding.

If the winter period is stressful for Harlequin Ducks why do pairs reunite in the fall? Savard (1985, adapted from Rowley 1983) discussed potential reasons for why pairs reunite, which included; i) obtaining a mate of known abilities, ii) maintaining the same territory, and, iii) reducing the time and energy spent in courtship. Gowans et al. (1997) showed that courtship behaviour increased dramatically in the fall, however they concluded that most of the behaviour was mate guarding by already paired males and courtship by the unpaired males. Mate guarding is probably not as energetically expensive as active courtship, because courting males fly around trying to find females, males that are mate guarding do not need to fly. Very little courtship is seen between pairs that reunite (Gowans et al. 1997). On the other hand, males which are unpaired in the fall and court females are very active in the spring (pers. obs.). By saving time and energy in courtship, males and females are able to reunite in the fall and not have to wait until spring. Even if the costs are reduced for established pairs, they could still reunite in the spring, and not expend energy in any courtship activity and mate guarding. However, one important cost of waiting until the spring for a male may be that his female has found a new mate.

In systems where pairs reunite, the pool of available females is very small. If there is a sex ratio bias for males, as seen in virtually all duck populations (Bellrose et al. 1961, Sargeant & Raveling 1992) including Harlequin Ducks (Bengtson 1972), that bias in the pool of unpaired birds is even higher, as an equal number of males and females make up the pool of paired birds. Only young females and females which have lost a mate are available for pairing. This situation has been taken to the extreme in the Chiloe Wigeon *Anas sibilatrix*. This sedentary species also exhibits long-term pair bonds and available females are sufficiently rare that unpaired adult males will court juvenile females, so as to copulate with them when they are reproductively mature (Brewer 1991). This lack of available females may explain why male Harlequin Ducks reunite with the same mate as soon as possible and do not wait until the spring. Females gain by obtaining a mate of known abilities (Savard 1985), and are protected from harassment during the fall and spring (Ashcroft 1976). Therefore, it is possible that early pairing seen in Harlequin Ducks results from the increased sexual selection for available females due to the fact that most pairs reunite at relatively low costs of courtship. Other sea ducks where pairs have been shown to reunite also tend to pair early. Common Eiders begin pairing in September (Spurr & Milne 1976) and Barrow's Goldeneye *Bucephala islandica* (Savard 1985) in November. However, there are documented cases of pairs reuniting in Oldsquaw (Alison 1975) and Bufflehead (Gauthier 1987) yet both of these species pair in the spring. Therefore, pair reunion in a species is not a sufficient condition for early pair formation.

Timing of pairing in the sea ducks

There are two characteristics shared by the five species of sea ducks that have been documented to pair in the fall. The Common Eider and King Eider *Somateria spectabilis* are the largest sea ducks (Table 2.1). They dive for benthic prey in relatively deep water. Barrow's Goldeneye, Harlequin Ducks and Hooded Mergansers *Lophodytes cucullatus* are smaller and they all forage in relatively predictable, stable and shallow habitats. Harlequin Ducks are inshore coastal foragers (Goudie & Ankney 1988) as are Barrow's Goldeneye, while Hooded Mergansers forage for invertebrates and small fish in shallow freshwater ponds and estuaries (Palmer 1976, M. Coupe pers. comm., Dugger et al. 1994). In contrast, the later pairing species tend to be smaller and/or deeper divers (Steller's Eider *Polystitca stelleri*, Black and Surf Scoters *Melanitta nigra*, *M. perspicillata*, Oldsquaw

Table 2.1. Body mass, winter foraging habits, and timing of pairing in sea ducks.

Species	Body mass of males (g)[a]	Dive depth and food[b]	Timing of pairing[c]	Pair reunion (number of cases)	Source[d]
Somateria mollissima	2218	Deep / benthic	Fall	Frequent	1,2
S. spectabilis	1668	Deep / benthic	(Fall)	?	1
S. fischeri	1432	Deep / benthic	(Spring)	?	1
Polysticta stelleri	773	Middle / benthic	(Spring)	?	1
Histrionicus histrionicus	687	Shallow / benthic	Fall	Frequent	1,3
Clangula hyemalis	932	Deep / benthic	Spring	Yes (1-2)	1, 4
Melanitta nigra	1100	Middle / benthic	(Spring)	?	1
M. perspicillata	1000	Middle / benthic	(Spring)	?	1
M. fusca	1500	Deep / benthic	(Winter)	?	1
Bucephala clangula	1000	Middle / benthic	Winter	?	1, 5
B. islandica	1090	Shallow / benthic	Fall	Yes (1)	1, 6
B. albeola	473	Middle / benthic	Spring	Yes (1)	1, 7, 8
Mergellus albellus	652	Shallow / fish	Spring	?	1, 9
Lophodytes cucullatus	680	Shallow / pelagic invertebrates and small fish	Fall	?	1, 10, 11
Mergus serrator	1135	Shallow / fish	Spring	?	1, 10

M. merganser	1709	Shallow / fish	Spring	?	1, 10

[a] body mass data from Dunning (1993)

[b] adapted from Nilsson (1972), Palmer (1976) and Goudie et al (1994). Dive depths broadly classified into most dives regularly occurring at shallow (1 to 3 m), middle (3 to 6 m) or deep (< 6 m) depths.

[c] due to regional and annual variation grouped into fall (September to November), winter (December and January) and spring (February to April). Reflects timing of when the first pair bonds are formed in the population. Information in parentheses represent cases where a dedicated study for the timing of pair formation has not been done and only anecdotal information is available.

[d] for timing of pairing and the frequency of pair reunion; 1) Hohman et al. 1992; (2) Spurr & Milne (1976); (3) this study; (4) Alison (1975); (5) Afton & Sayler (1982); (6) Savard (1985); (7) Erskine (1972); (8) Gauthier (1987); (9) Nilsson (1974); (10) M. Coupe, unpubl. data; (11) Dugger et al. (1994).

and Bufflehead), or forage on more ephemeral or patchily distributed foods such as benthic or schooling fish (Common Merganser *Mergus merganser*, Red-breasted Mergansers *M. serrator*, and Smew *Mergullus albellus*) (Palmer 1976, Nilsson 1974). It appears that early pairing can be accomplished by species that are either very large or forage in very stable and predictable habitats. Deeper diving species that are not as large as eiders or species that feed on ephemeral sources are not able to maintain a pair bond through the winter and do not pair until spring. White-winged Scoters *Melanitta fusca* and Spectacled Eiders *Somateria fisheri* present a challenge to the general trend, both are large-bodied sea ducks that apparently pair in the winter or spring (Table 2.1). Data for both species are sparse and no formal studies for the timing of pair formations have been dedicated to these species. Observations of pairing behavior in the fall have been observed in White-winged Scoters (R. I. Goudie pers. comm.), further observations should resolve these issues.

The balance between male costs and females benefits are thought to be the main determinants of the pairing chronology in species (Afton & Sayler 1982, Rohwer & Anderson 1988). Evidence from the sea ducks supported this hypothesis. Generally, large body size enables males to devote more of their activity budget to behavior other than foraging because they are able to maintain homeothermy more efficiently. Hence, eiders, like the large bodied Mallards *Anas platyrhynchos* and Black Ducks *A. rubripes* are able to maintain a pair bond throughout the winter period. However, resource use also plays a role in the cost to the male of maintaining a pair bond. Males which use reliable food sources should be able to spend more time and energy on courtship than males using ephemeral food sources or foods that are energetically expensive to obtain. The shallow diving sea ducks, Harlequin Ducks, Hooded Mergansers and Barrow's Goldeneye also form pair bonds relatively early. Gadwall *Anas strepera* and Wigeon *A. americana* are dabblers that pair early for their body size (Paulus 1983, Wishart 1983), they also forage on vegetation, a very reliable food source.

The ability for the males to maintain the pair bond through the winter determines the timing of pairing, although the benefits for females to establish a pair bond must also be considered. Dabbling ducks wintering in Mexico form pair bonds much later than those wintering in the United States (Thompson & Baldassarre 1992, Migoya et al. 1994). Due to ameliorated climates, females wintering further south may not need the benefit from being paired with a male. In fact, one prediction of the male cost - female benefit hypothesis for the timing of pair formation is that across the wintering range of a species pair bonds would be formed earliest in the middle of the species wintering range. In northern wintering populations males may not be able to afford to maintain a pair bond through the winter and in the southern populations, females would not be interested in pair bonding as they gain no benefit.

The next direction for research on pairing chronology in the sea ducks would be to study the extent of pair reunion in the poorly studied species. Evidence for pair reunion in Oldsquaw and Bufflehead suggest that early pairing and pair reunion are not completely linked, although the clearest evidence for pair reunion comes from the earlier pairing species. When data for the other species are available, especially the mergansers and scoters, the hypothesis that winter philopatry and pair reunion leads to intense sexual selection for the few available females and subsequently early pair formation can be tested. Alternatively, the data may show that pair reunion among the sea ducks is prevalent throughout the tribe and the costs of foraging and body size are the most important determinants of the timing of pairing in the tribe.

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Chapter 3

The influences of moult on pair bond formation in Harlequin Ducks

3.1. General introduction

Harlequin Ducks form pair bonds relatively early compared to many other duck species (Chapter 2). Apparently, male Harlequin Ducks are not energetically constrained from forming pair bonds, and selection has favoured males that attempt to establish pair bonds as soon as possible (Chapter 2). If energetic constraints are not limiting the timing of pair formation then another factor must limit the ability of male Harlequin Ducks to begin courtship before October. A likely constraint is that all waterfowl species undergo an annual moult and regrowth of their entire plumage at some point of time during the year (Hohman et al. 1992). Waterfowl moult all of their remiges simultaneously, rendering them flightless for a period of time. Hence, the physiological stress of regrowing feathers and/or the inability to fly may make the moulting period a stressful time for waterfowl and preclude courtship and pair formation (Hohman et al. 1992).

Among the ducks, males generally leave the breeding grounds and migrate to another location to moult (Salomonsen 1968). The males begin moulting before or soon after they have arrived at these locations. Females on the other hand moult on the breeding grounds. Males tend to undergo the entire moulting process, consisting of two contour body feather moults (the pre-basic and pre-alternate moult) and a single wing (remiges: the primaries and secondaries) and tail (rectrices) moult in one continuous effort. Females also undergo the remige and rectrix moult after breeding, but the two body moults are spread out over much more of the rest of the year (Hohman & Crawford 1995). The plumage of the basic and alternate plumage of females is difficult to differentiate. The male basic plumage is a brown, cryptic, plumage which is very 'female like'. However, the alternate plumage is a showy plumage containing a variety of colour patterns and textures. The males are in the basic body plumage while they are moulting their wing feathers, thus a proposed function of the basic plumage was to provide the males a cryptic plumage while they were flightless. The showy alternate plumage is worn by males while courting and for most of the year (Johnsgard 1965).

Male Harlequin Ducks (Gowans et al. 1997) and other species (Wishart 1983) appear to wait until they have attained their alternate plumage until they begin courtship. Therefore, the length of the moulting period may play a role in limiting the ability of male Harlequin Ducks to begin courtship. In the first section of this chapter the general arrival patterns, moulting chronologies and length of time for visually identifiable periods of the moult are presented and compared with the timing of pairing in this species. The beginning of courtship behaviour is closely tied with the completion of the female wing moult and the male pre-alternate body moult. The second section challenges the idea that the basic plumage of male Harlequin Ducks is maintained to provide crypticity to the males. A conspicuous set of white tertials is grown while the males are in the basic plumage. Evidence is presented that males are already beginning to establish a dominance hierarchy amongst themselves in anticipation of the arrival of the females from the breeding grounds. The final section shows how the speed and timing of the entire moulting sequence of individual males affects their subsequent success in obtaining a mate. Slow moulting males are shown to be at a considerable disadvantage when courting females, however, the timing of moult has no effect on the success of a male. Therefore, good quality males are able to moult quickly and obtain a mate and it is concluded that the moult speed is an honest signal reflecting male quality.

3.2. The timing of arrival and moult chronology of Harlequin Ducks *Histrionicus histrionicus*[3]

3.2.1. Abstract

The timing of arrival and moulting chronology of a population of post-breeding Harlequin Ducks *Histrionicus histrionicus* was studied over a three year period in south-western British Columbia. Males first arrived on the moulting and wintering grounds in mid-June and most had returned from the breeding areas by the end of July. Females first arrived in late July and continued to arrive until the end of September. The flightless period for the males ranged from late July to late August. Flightless females could be seen throughout August and September. Wings took 30-31 days to regrow, compared to 26 days for tails. Assuming birds can fly at 70% remex growth this corresponds to a flightless period of about 21 days. Yearlings of both sexes exhibited moulting chronologies similar to adult males. All birds initiated moulting as soon as they arrived on the non-breeding grounds, suggesting an advantage for early moulting. The reasons for this are likely to be different for the two sexes. Males probably initiate moult quickly to be able to return to their alternate plumage and begin courting females. Females may moult early to complete wing growth before the onset of winter.

3.2.2. Introduction

The post-breeding period is important in the life history of waterfowl (Hohman et al. 1992). After breeding, birds must undergo a number of activities before the onset of winter. These include recovering from the stress of breeding, possibly migrating to a

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[3] This section (3.2) has been accepted for publication as Robertson, G.J., Cooke, F., Goudie, R.I. & Boyd, W.S. 1997. The timing of arrival and moult chronology in Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl*, 48.

moulting location, undergoing at least one body moult, a wing moult and a tail moult, and migrating to the wintering grounds.

Compared to other holarctic waterfowl very little is known about Harlequin Ducks *Histrionicus histrionicus*. Most studies of this species have been carried out during the breeding season (Bengtson 1966, 1972, Inglis et al. 1989), with the exception of some non-breeding studies of their diet composition and foraging behaviour (Vermeer 1983, Goudie & Ankney 1986, Gaines & Fitzner 1987). After breeding, little is known of their migration pattern and habitat use. Most information on post-breeding movements and behaviour comes from the well studied populations in Iceland, where the breeding grounds are adjacent to their coastal wintering areas and the birds can simply swim down the rivers to reach the non-breeding grounds (Bengtson 1966, 1972). In western North America, where over half of the Harlequin Duck population resides, some birds breed hundreds of kilometres away from their non-breeding grounds, so substantial migrations must occur in these populations (Palmer 1976).

A detailed account of the moulting chronology for Harlequin Ducks is not available. Wing moult is an important activity for seaducks. They often take part in extensive migrations to moulting grounds, which are thought to allow the ducks to moult in isolated and, presumably, safe locations (Salomonsen 1968). Sometime after the body and wing moult is complete courtship begins. Harlequin Ducks (Gowans et al. 1997), along with other duck species (Wishart 1983), do not initiate vigorous courtship until they have completed moulting. Therefore, the moult chronology and the timing of pair bond formation could be related.

In this study we describe the annual return of a population of Harlequin Ducks to their non-breeding grounds on the west coast of North America. We also describe the chronology of their subsequent moult, in both sexes, and in yearling and adult birds. Finally, we calculate the length of time for the wing and tail to be shed and regrown.

3.2.3 Methods

This study was carried out from August 1994 to November 1996 near White Rock, in coastal south-western British Columbia. A population of about 100 Harlequin Ducks moult and winter along a 5.5 km stretch of rocky shoreline. Once or twice a week the study area was surveyed and the sex and age composition of all groups of Harlequin Ducks were recorded. A proportion of this population is marked with individually coded leg rings (see Cooke et al. 1997 for details), and an effort was made to read the code for all ringed individuals. While the ducks were moulting all individuals were visually assessed to determine their moult status. For the body moult, males were categorized as either: still in old alternate plumage, undergoing pre-basic moult, in basic body plumage, undergoing pre-alternate moult or in full alternate plumage. Body moult in females could not be identified as most feathers are not visibly different in basic and alternate plumages. For males and females the wing (remex) and tail (rectrix) moults were classified as either: feathers old and present, feathers not present, feathers visible but not yet full grown, or feathers new and full grown. Observations of all ducks were made from close distances (< 50 m) and individuals were observed intently to determine the stage of their moult (see Cooke et al. 1997 for details). This method allowed us to identify moult in only those feather tracts that were visible to observers.

Harlequin Ducks tend to haul out onto rocks, enabling observers to read the rings and identify individuals. Observations on these individually marked birds were used to calculate the total length of time individuals took to shed and regrow their wings and tails. Sufficient data were available only for 1995, from the birds that were marked in 1994 and returned in 1995. Harlequin Ducks exhibit high levels of winter philopatry, so many of the birds marked in 1994 returned in 1995 (we did not have a sufficient number of sightings in 1996 to perform the following analysis). The method used to calculate these periods relied on estimating the minimum and maximum length of time the bird could have been undergoing a particular moult. For each individual the interval in which a particular moult sequence began (e.g. the last day the bird was seen with their old remiges to the first day the birds was sighted after it lost its remiges) and ended (similar calculation) was determined. The minimum and maximum number of days a moulting sequence spanned was calculated with these intervals. This information was summarized for all birds and a probability density function was derived to estimate the most likely number of days a particular moulting sequence took for the population (see Cooke et al. 1997 for further details). The 95% confidence intervals were extracted from this probability density function. Errors around these estimates are quite large and reflect variation from: 1) sampling, because birds were not seen every day so the exact day of shedding or complete regrowth of feathers was not known, and, 2) to a lesser extent, natural variation among birds in the time it takes them to shed and regrow different feather tracts.

3.2.4. Results

Timing of arrival and moult

Males began returning to White Rock in June and most males had returned by late June. Males started to enter the pre-basic body moult almost as soon as they arrived (Figure 3.2.1). Some males were flightless by the end of July, with most able to fly again by early September. The entire moult (the pre-basic and pre-alternate body moults, and the wing and tail moult) was complete by the end of September for most males (Figure 3.2.1). Arrival and moulting chronologies appear similar in the two years, 1995 and 1996, for which we have complete data.

Females began returning in late July or early August (Figure 3.2.2.). The small number of females present during July (approx. 5 birds) were yearling females which may have been present in the area throughout the summer. The flightless period for females began

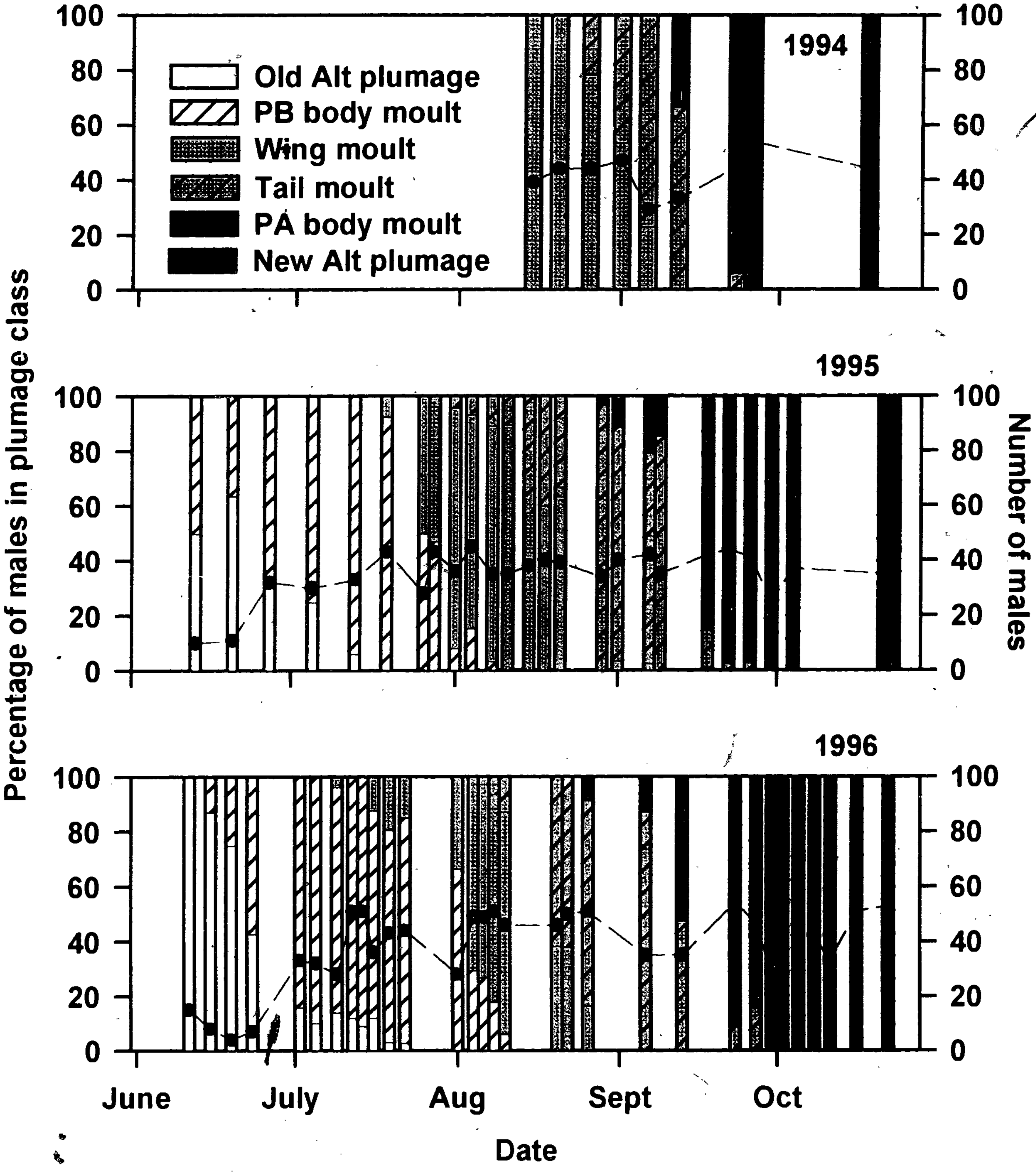

Figure 3.2.1. Percentage of male Harlequin Ducks seen in various plumage classes and the numbers of males present at White Rock, British Columbia.

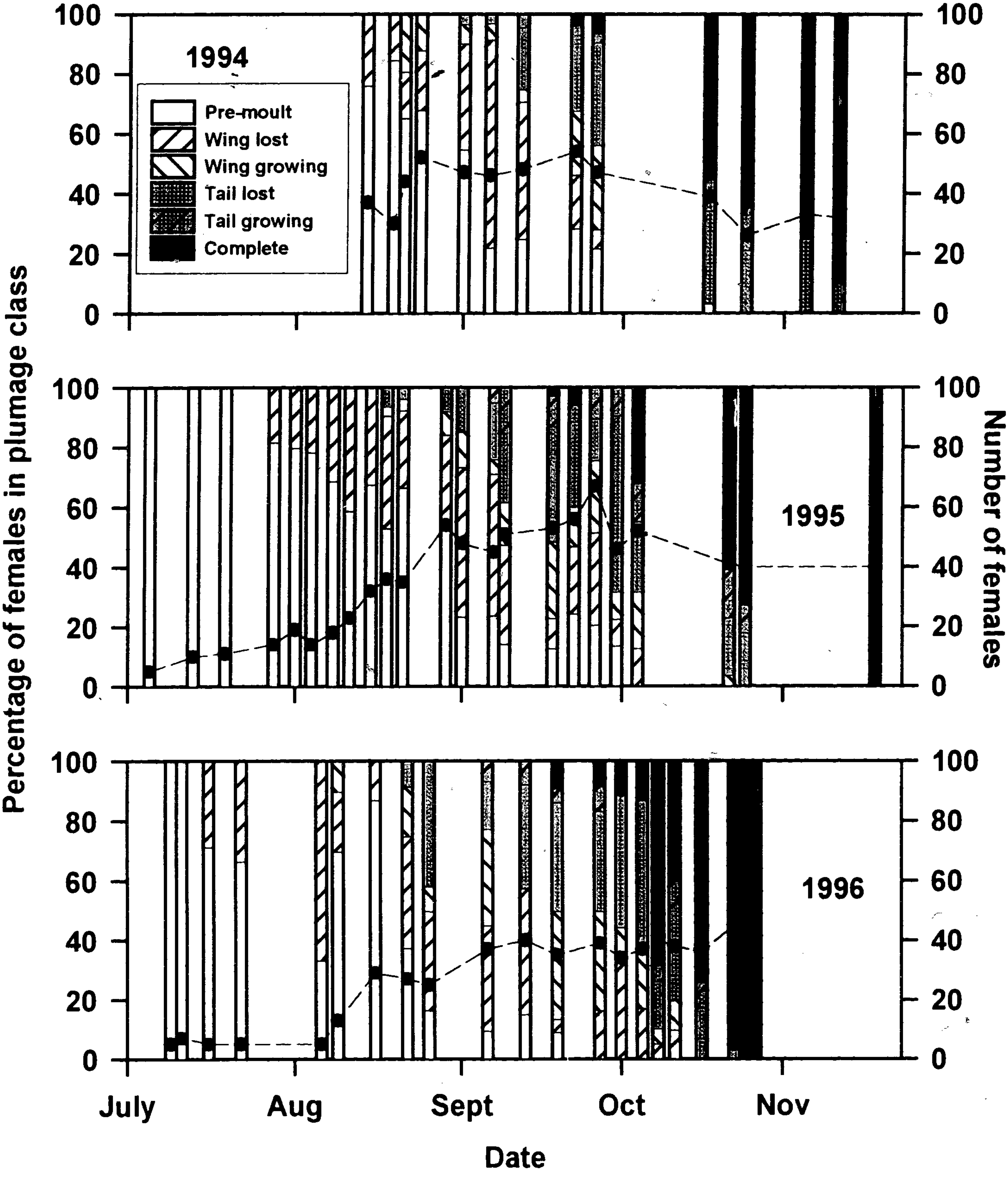

Figure 3.2.2. Percentage of female Harlequin Ducks seen in various plumage classes and the numbers of females present at White Rock, British Columbia.

in August and continued into early October. As a population, females had a longer flightless period than males, a reflection of their more protracted arrival chronology. Females appeared to complete the moult earlier in 1996 (Figure 3.2.2) than in the other two years. Their return to the non-breeding grounds was relatively synchronous in this year with most females returning in the first weeks of August.

Length of wing and tail moult

The estimated length of time for individual males and females to moult their wings and tails were very similar (Table 3.2.1). In both sexes it took, on average, about one month for a complete set of remiges to regrow and 26 days for the tail to regrow, although there is considerable variation in these estimates.

Young birds

A small sample of yearling ducks were caught during moult drives in late July in all 3 years. All of the nine yearling females captured over the three years (2 in 1994, 5 in 1995, 2 in 1996) exhibited a wing and tail moult chronology similar to the adult males. All were flightless by late July and early August, well in advance of the adult females. All three yearling males captured (2 in 1995, 1 in 1996) had moulting chronologies similar to the adult males. Additionally, all three were seen in complete definitive alternate plumage in the following fall, suggesting that males have a full breeding plumage by the beginning of their second pre-alternate moult.

3.2.5. Discussion

Chronology of arrival

Harlequin Ducks show some similarities in arrival patterns to the non-breeding grounds to that seen in most ducks (Palmer 1976, Bellrose 1980). Males arrive first and relatively synchronously, females arrive later and their arrival occurs over a longer time period. Males do show some variation in their timing of arrival, probably due to the fact that the

Table 3.2.1. Estimated times for individual Harlequin Ducks to complete their wing and tail moult in 1995.

	Males		Females	
	n	Estimated number of days (95% C. I.)	n	Estimated number of days (95% C. I.)
Wing moult	26	30 (14-44)	18	31 (12-47)
Tail moult	30	26 (10-47)	16	26 (4-54)

timing of breeding may vary considerably for Harlequin Ducks in a single wintering population. Harlequin Ducks breeding in high elevation streams in the Rocky Mountains may initiate breeding up to six weeks later than birds nesting in low elevation coastal streams. Male Harlequin Ducks abandon their mates once incubation begins and then form 'clubs' on the streams where they breed (Bengtson 1966). They remain in these clubs for only a few days and then migrate to the coast. Females that have failed as nesters, or simply have not bred, also form groups on the breeding grounds, and then migrate to the ocean soon afterward (Bengston & Ulfstrand 1971). Females which successfully hatch their eggs remain with their brood until fledging, at which time they depart for the coast (Bengston 1972). Evidence for whether or not the brood migrates with their mother is ambiguous, and both strategies may exist (Kuchel 1977, Wallen 1987). A protracted chronology in the arrival of breeding females occurs because females may lose their nests or broods to predation at any time during breeding, after which they presumably migrate to the coast.

In some species of ducks, females moult on, or close to, the breeding grounds. In others they join the males on separate moulting grounds (Hohman et al. 1992). Usually it is only young, failed-breeding and non-breeding females that participate in a moult migration and moult with the males at these sites. Female Harlequin Ducks, at least in our population on the west coast of North America, migrate to the moulting grounds before they initiate the wing moult, regardless of their success in rearing young. Female Harlequin Ducks probably moult at the same location as the males because the moulting and wintering grounds overlap in this population. There are a number of reasons why females leave the breeding areas to moult on the coast. Harlequin Ducks are relatively late nesters; pre-fledging broods in western North America are seen well into September (Hunt 1995, Smith 1996). There may not be time, or sufficient food, for females to moult on the breeding grounds before the winter, so they must migrate to the coast before wing moult.

Alternatively, coastal moulting locations may provide better protection from predators during the vulnerable moult period than narrow rivers and streams. Females may also moult on the coast to begin the process of selecting a high quality male before they are all paired or reuniting with her former mate as soon as possible. Pair reunion commonly occurs in Harlequin Ducks (Gowans et al. 1997). Finally, females may moult on the coast so that they can bring their offspring with them to their coastal wintering grounds. Any or all of these explanations could explain why females migrate to the coast to moult.

Timing of moult

Males initiate the pre-basic body moult soon after they arrive on the moulting grounds. This contrasts with patterns seen in King Eiders *Somateria spectabilis* (Frimer 1994) and Steller's Eider *Polysticta stelleri* (Petersen 1980) where males arrive at the moulting grounds undergoing, or already having completed, the pre-basic body moult. In these species, wing moult is initiated soon after they arrive. Harlequin Ducks on the west coast make only one known migration to a coastal location where they moult and spend the winter season, as opposed to making a moult migration and then a second autumn migration to their wintering grounds, such as that exhibited by other sea ducks (Salomonsen 1968). Some individual Harlequin Ducks may move to other sites after the moult, but these movements are not extensive and do not represent a true migration (Robertson et al. in press). Conditions or food resources in western coastal North America may be sufficiently benign during the non-breeding season that a subsequent migration after moulting is unnecessary to avoid harsh conditions. Harlequin Ducks in the Atlantic region of North America do migrate south after moulting (Goudie 1991).

Females also initiate a moulting sequence (wing and tail moult) as soon as they arrive at the non-breeding grounds. For females we cannot visually detect body moult. Unlike males, which tend to undergo the pre-basic moult after breeding, females in other species of ducks initiate the pre-basic moult before breeding (Lovvorn & Barzen 1988, Hohman &

Crawford 1995). The feather tracts in the wing are next to be moulted after the pre-basic body moult, suggesting that females are re-initiating the feather moult as soon as they arrive at the coast.

Females appeared to complete moulting slightly earlier in 1996 than in the other two years, and their arrival was relatively more synchronous than in 1995. In 1995, the number of females gradually increased from mid July to late August, in 1996, a large number of females arrived in the second week of August, and a few more arrived in early September. An earlier arrival and moult of the female population may suggest something about conditions on the breeding grounds. If breeding conditions were good then it would be expected that many females would be successful and all females should return later to the non-breeding grounds after raising their young. Otherwise, if conditions were very poor on the breeding grounds, then many females may fail in their attempt to nest or not attempt at all, leading to an early and synchronous return of females to the non-breeding grounds. Conditions during the spring of 1996 were not favourable for Harlequin Ducks in the Rocky mountains. It snowed periodically during May, temperatures were cold, and the spring run-off was very high (R. I. Goudie, pers. obs.). We suggest that the early and more synchronous return of females in 1996 was a result of a poor breeding effort, where many females did not succeed or did not attempt to nest. Interestingly, the males appeared to follow a similar arrival and moult chronology in all three years. Males return to the coast after the nesting attempt has been made, thus their arrival chronology is not greatly influenced by the reproductive effort or failure made by the females.

Length of wing and tail moult

We estimated that individual Harlequin Ducks require 30-31 days for their remiges to be lost and re-grown. For male Harlequin Ducks the ninth primary is the longest (Cramp & Simmons 1977) and grows to a length of about 130 mm; female primaries are slightly shorter at about 120 mm (G. J. Robertson, unpubl. data). Assuming a constant growth rate this feather is growing at 4.33 mm/day (or 3.33 % of remex length/day) for males and 3.87 mm/day (or 3.23% of remex length/day) for females. These values are slightly faster than the average of 2-3% of remex length/day reported for other species of waterfowl (Hohman et al. 1992). This consistency among species in remex growth rates lead Owen & King (1979) to speculate that 2-3% remex/day may be the physiological maximum for waterfowl and all species are regrowing their remiges as fast as they can. Given the disadvantages to waterfowl in remaining flightless (predation risk, the inability to quickly change location if resources become depleted, and/or search for mates) it would be expected that birds would regrow their flight feathers as fast as possible.

Assuming that Harlequin Ducks can fly at about 70% wing regrowth (Hohman et al. 1992) we calculate a flightless period of 21-22 days. This period is relatively fast for waterfowl which have flightless periods from about 20 to over 49 days (Hohman et al. 1992). Smaller species, such as the Wood Duck *Aix sponsa* (Bellrose 1980) and Green-winged Teal *Anas crecca* (Sjöberg 1988), have estimates of 21 days for the flightless period (Hohman et al. 1992), so our values do not appear unreasonable for Harlequin Ducks. Additionally, seaducks and pochards have shorter wing feathers relative to body size so they may not take as long to grow as in the dabbling ducks. Our estimate of 21-22 days may be biased low if 70% wing growth is not valid for Harlequin Ducks. Seaducks have a high wing loading capacity and shorter remiges. They may need a more developed wing before being able to fly again. Unfortunately, information on the true duration of flightlessness for seaducks is not available.

The tail moult took an estimated 26 days to complete, shorter than the wing moult. The seventh and the eighth rectrices are the longest at 70 mm in males and 65 mm in females. Considering that there are only 14 tail feathers, compared to 40 primaries and secondaries which are much longer, tail feathers grow much slower than remiges. This suggests that regaining flight capability is important and has led to selection for growing remiges as fast as physiologically possible. Not having a complete tail for a period of time is not as crucial. The rate of rectrix growth is much slower than the rate of remex growth. The nutritional cost of moulting rectrices is spread over a longer period of time and is possibly coupled with simultaneous moulting of other feather tracts.

The importance of rapid moulting

Males moulted through the pre-basic body moult, remex, rectrix, and, pre-alternate body moult within a 3 month period with no obvious breaks between the different body, wing, and tail moults. They also moulted as soon as they arrived on the moulting grounds and regrew their wing feathers relatively quickly. This information suggests that males are moulting as rapidly as possible. Harlequin Ducks pair very early compared to most ducks, beginning in late September, and over 50% of adult females are paired by December (Gowans et al. 1997). Although males which have not completed the pre-alternate body moult do engage in some courtship behaviour, it is less than males which have completed this moult (Gowans et al. 1997). No male still in pre-alternate body moult was seen successfully paired; pairing began soon after this moult was completed. This suggests that selection may favour those males which leave the breeding site early and complete moult quickly, as it would allow them to compete more effectively for females.

Females may initiate their wing moult rapidly and immediately when they arrive at the coast to avoid being flightless during the approaching winter. Although recent opinion suggests that the nutritional costs of moulting are not very high (Hohman et al. 1992), it may be disadvantageous to moult wing feathers during the short, cold days of winter for a number of reasons. If local conditions become unsuitable then late-moulting females may not be able to fly to another location. Additionally, Harlequin Ducks feed almost continuously during the winter period (G.J. Robertson & R. Torres, unpubl. data), the further nutritional demands of wing moult may not be tolerable at this time of year.

3.3. Molt and the Basic Plumage of Male Harlequin Ducks[4]

3.3.1. Abstract

Using observations on 28 individually marked male Harlequin Ducks from mid-June until late November, we describe plumage changes which occur as individuals proceed from the alternate plumage through basic to the return of the new alternate plumage. We also describe the timing of these events, at the individual and population level. Conspicuous white tertial feathers which become visible early in the period of the basic plumage present a challenge to existing theories to explain the function of the drab basic plumage. We hypothesize that these feathers act as a badge of quality and are used as a sexual signal to other birds. Intra-sexual competition among males to assess the quality of rival males prior to subsequent pair formation is a proposed function of this feather badge.

3.3.2. Introduction

The males of most species of holarctic Anatidae show two distinct adult plumages each year, a basic plumage, which is relatively inconspicuous, and an alternate plumage which is often brightly coloured (Palmer 1976). The dull basic plumage is also referred to as the eclipse plumage (Witherby et al. 1939), and closely resembles the body plumage of the female. The change from alternate to basic and from basic to alternate involves two replacements of body feathers. While drakes are in basic plumage, a complete molt of remiges and rectrices occurs and birds become flightless for a period of several weeks. They usually move to specific, often secluded locations before the prebasic molt. These places are usually distinct from both breeding and wintering locations (Salomonsen 1968).

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[4] This section (3.3) is published as Cooke, F., Robertson, G.J., Goudie, R.I. & Boyd, W.S. 1997. Molt and the basic plumage of male Harlequin Ducks. *Condor* 99:83-90.

Because of the cryptic features of the male eclipse plumage, its association with the flightless period and the utilization of secluded locations during this period, it has usually been assumed that the main function of the basic plumage is to reduce detection by predators during a period of increased vulnerability (Hochbaum 1944, Owen & Black 1990, Hohman et al. 1992). However, other hypotheses have been proposed. Bailey (1981) questioned the value of cryptic plumages for diving ducks which spent much time on open water where they could escape predators by diving. He proposed that a dark colored basic plumage may confer a thermal advantage by reducing the temperature gradient between skin and plumage and potentially reducing heat loss. A third explanation could be referred to as the default hypothesis. We might expect feathers to be without conspicuous markings unless there were some selective advantage for conspicuous plumage. The selective pressure for bright alternate plumages in many holarctic waterfowl is presumed to be a result of strong directional sexual selection. During the time when birds are in basic plumage this selection is presumably absent and based on the assumption that elaborate plumage patterns are energetically more expensive than simple ones, one might expect feathers to be simple, lighter, cheaper to produce and lacking in color variety (Wielecki 1987).

The generally short, 3 to 6 month duration in which drakes are in basic plumage, relative to the time in alternate plumage has been broadly interpreted in terms of sexual selection (Anderson et al. 1992). Pressure on males to acquire a mate prior to arrival on the breeding grounds and the advantages for females to have a male guarding her from conspecific disturbance during the winter so she can forage efficiently can lead to directional selection for earlier and earlier pair formation. This gives a selective advantage to drakes that develop a bright alternative plumage as soon as possible (Rohwer & Anderson 1988). Under this scenario the relative duration of the basic and alternate plumages in the drakes can be thought of as being determined by the fitness advantages associated with crypticity during the basic plumage period relative to the fitness advantages associated with attracting a high quality mate during the alternate plumage period. Although the relative fitness of these countervailing pressures has not been measured, Owen & Black (1990) argue that reduced predation pressure on seaducks might increase the length of the molting period, and presumably increase the duration of the period when the birds are in basic plumage.

In this study, we: (1) describe the changes in conspicuous body plumage of individual male Harlequin Ducks *Histrionicus histionicus* from early June until early October, during which time the birds progress from the alternate plumage, through pre-basic molt into the basic plumage and then through the pre-alternate molt into their new alternate plumage. We concentrate on those visible features of the plumage which might provide signals to predators (crypticity or not) or to conspecifics (allowing species, sex or individual recognition) insofar as these might give us clues to the possible function of the plumage patterns; (2) record behavioral changes during this period associated with the plumage changes, which may provide hints as to the function of the plumages; and (3) examine the basic plumage of male Harlequin Ducks in light of three hypotheses outlined above a) crypticity; b) thermal advantage and c) default, which have been proposed to explain the lack of conspicuous markings and color in the basic plumage of ducks.

3.3.3. Methods

Unlike several recent molt studies in waterfowl (Hohman & Crawford 1995, Thompson & Drobney 1995) that follow the methodology of Billard & Humphrey (1972) in collecting large samples of birds at intervals through the appropriate time of year, our approach relies instead on observing individually marked live birds frequently through the period. The advantages of this latter method is that it allows us to (1) observe the plumage changes of known individuals which are relevant to the questions on the function(s) of the basic plumage which we posed above (2) examine the timing and duration of the plumage changes and (3) observe the behaviors of the birds during this period in order to investigate behavioral correlates of the plumage patterns.

A molting and wintering population of Harlequin Ducks comprising between 100 and 150 birds occurs on a 5.5 km stretch of rocky waterfront of the Pacific Ocean between the communities of Crescent Beach and White Rock in southwest British Columbia (Savard 1988). On 26 July 1994, 43 Harlequin Ducks from this population were captured during the flightless period using kayaks and a drive-trap (Clarkson & Goudie 1994). Each bird was aged, sexed and marked with an individually identifiable colored tarsal band with 2 alphanumerics on the band. Tarsal bands allow identification of individuals as Harlequin Ducks often haul out on to rocks.

Adult males that returned to the molting area the following year were closely monitored from 9 June 1995 until early November 1995. At about three day intervals an observer walked along the study site with a 15-60X telescope to assess the population. Sex, age, group structure, behavior, and location of all ducks present were recorded. Additionally several plumage features which change during the molt period were recorded. Individuals were classified as being in alternate plumage, basic plumage or transitional (either pre-basic or pre-alternate molt). It was always possible to determine whether a bird was in pre-basic or pre-alternate molt by the timing of the event and the presence of intermediate plumages. Evidence of feather on any tract loss or gain indicated that a bird was undergoing a molt. Observations of the birds were from within 50 meters and we are confident that birds in any stage of an intermediate plumage could be identified. Furthermore, birds were observed intensively (approximately 10 to 15 minutes) until all aspects of their plumage could be seen before the assessment of their molt status was made. All birds were seen a minimum of six, and up to 23 times during the course of the study. Additionally, the stage of the rectrial and remigial molt was assessed by observation.

Timing of molt

Unfortunately the molt stage of each and every individual could not be assessed daily. Available data can only provide a range of dates within which the various molt stages were initiated or completed. We used a method assessing daily probabilities of individuals starting or finishing various stages of the molt in order to estimate the length of time for completion of the various stages. For example, a bird seen in alternate plumage on 10 June and first seen undergoing the pre-basic molt on 13 June could have initiated the pre-basic molt on any one of the days within that time period. We conservatively estimate that this bird had equal probabilities of initiating the pre-basic molt on any one of the 4 days during that interval. Similarly if this hypothetical bird was last seen undergoing pre-basic molt on 26 June and seen in basic plumage on 3 July, we have minimum and maximum estimates for the length of time for the pre-basic molt. For this bird the maximum length of time for the pre-basic molt to be completed is 23 days (10 June to 3 July), the minimum period is 13 days (13 June to 26 June). Each day within this period was assigned an equal probability that the pre-basic molt took that length of time. In this case 13 to 23 days would be given a probability of 0.0909 (1/11) and lengths of time outside that period would be given 0 probability. These probabilities were then summed up for all birds for which there was available data, resulting in a probability density function (pdf) for the length of time each stage needed to be completed. The median of this distribution was taken as the best estimate of the length of time to complete each stage of the molt. This method is entirely analogous to maximum likelihood estimation, except that we used the median value from the pdf and not the highest value, as our pdfs contained occasional outlying values, probably due to low sample size. Ninety-five percent confidence limits were obtained directly from the pdfs. The strength of this method is that it gives higher weights to birds that were seen frequently since the range for the intervals are smaller, and the associated daily probabilities are larger. Taking means of ranges provides a biased estimate, as birds not seen for long periods artificially extended the length of the estimate.

Assessment of groups

Groups of Harlequin Ducks were defined as a set of individuals present in a restricted section of the study area and generally interacting with each other in some way or performing similar behaviors. The study area was divided into 39 sections of equal length approximately 160 m along the shoreline that we surveyed. To assess how ducks grouped themselves over the whole study area, we recorded the number of birds, including zero values, in each of the 39 sections. We then calculated the variance-to-mean ratio of group sizes seen over the study area as a whole. Variance-to-mean ratios of 1 indicate that group sizes are following a Poisson distribution, suggesting that birds are distributing themselves independently of local habitat differences and/or the presence of other birds. Values less than 1 indicate that birds are actively avoiding one another, and values above 1 suggest that birds are clumping at some sites and not using others (Sokal & Rohlf 1981).

Spearman rank correlations were used to ascertain whether there was a positive, negative, or no association between the sexes in all of the groups seen on a given survey. Spearman rank correlations were used instead of parametric Pearson correlations to avoid overweighting observations with many birds in a single group. One large grouping of males and females is sufficient to provide a positive Pearson correlation, even if all of the rest of the smaller groups in the study area are showing a negative association between the sexes.

3.3.4. Results

Chronology of Returning Males

Of 37 adult males which were color banded in 1994, 28 returned after breeding to molt at the study site in 1995. The dates on which individual males were first seen ranged from 9 June to 19 July, a period of 40 days. Half of the birds (14) were first seen in alternate plumage, one quarter (7) were seen just after they had begun the pre-basic molt; five of the birds were well into their pre-basic molt and two birds were first seen already in their basic plumage. Recognizing that birds were not necessarily observed immediately after they arrived, these data suggest that most birds arrived at the molting area in alternate plumage and soon began molting body feathers.

Molt Chronology

Table 3.3.1 presents the estimated number of days that male Harlequin Ducks spent in each stage of the molt. Pre-basic molt of the conspicuous body feathers lasted an estimated 20 days. We have divided the period when males are in their full basic plumage into two stages. One is the period when males showed no conspicuous body plumage, having dropped all conspicuous body feathers. They were very similar to females except for darker feathers on the belly and a general richer brown for the body plumage. This plumage fits the description by Johnsgard (1965). The length of this stage is estimated to be about 18 days. Old remiges are dropped at this time. The second stage is when two white-centered tertials become clearly visible on each side of the lower back. The visibility of these tertial feathers is enhanced by the loss of the remiges. These feathers are the new basic plumage tertials, which are part of the body feathers rather than the remiges (Stresemann & Stresemann 1966). Old rectrices were dropped early in this stage and new remiges began to grow. This stage was estimated to last an average of 34 days and is illustrated in several standard field guides and handbooks (e.g., Witherby et al. 1939). Males were much more conspicuous and distinct from the females during this plumage,

Table 3.3.1: Estimated number of days male Harlequin Ducks spent in various plumage stages at White Rock, BC, 1995.

Molt stage	*n*	Estimated number of days (95 % C. I.)
Undergoing pre-basic	15	20 (7-32)
Basic (cryptic)	26	18 (3-41)
Basic (white tertials visible)	8	34 (22-54)
Undergoing pre-alternate	24	15 (1-35)

because of the white tertials. The total time that birds are in basic plumage as detected from the visual characters which can be identified in the field is on average 52 days.

The white tertials are shed at the beginning of the pre-alternate molt, these feathers lasted slightly more than 34 days allowing for some days of growth before they are visible in the field. At the early stages of the pre-alternate molt, males again are relatively inconspicuous, due to the absence of the white tertials but the plumage patterns of the alternate plumage reappear quickly and synchronously. Included in the alternate plumage pattern is a new set of three white tertials on each side. These are larger and have a different shape from those that preceed them, and they are the last of the alternate plumage body feathers to re-appear. Pre-alternate molt lasts an average of 15 days.

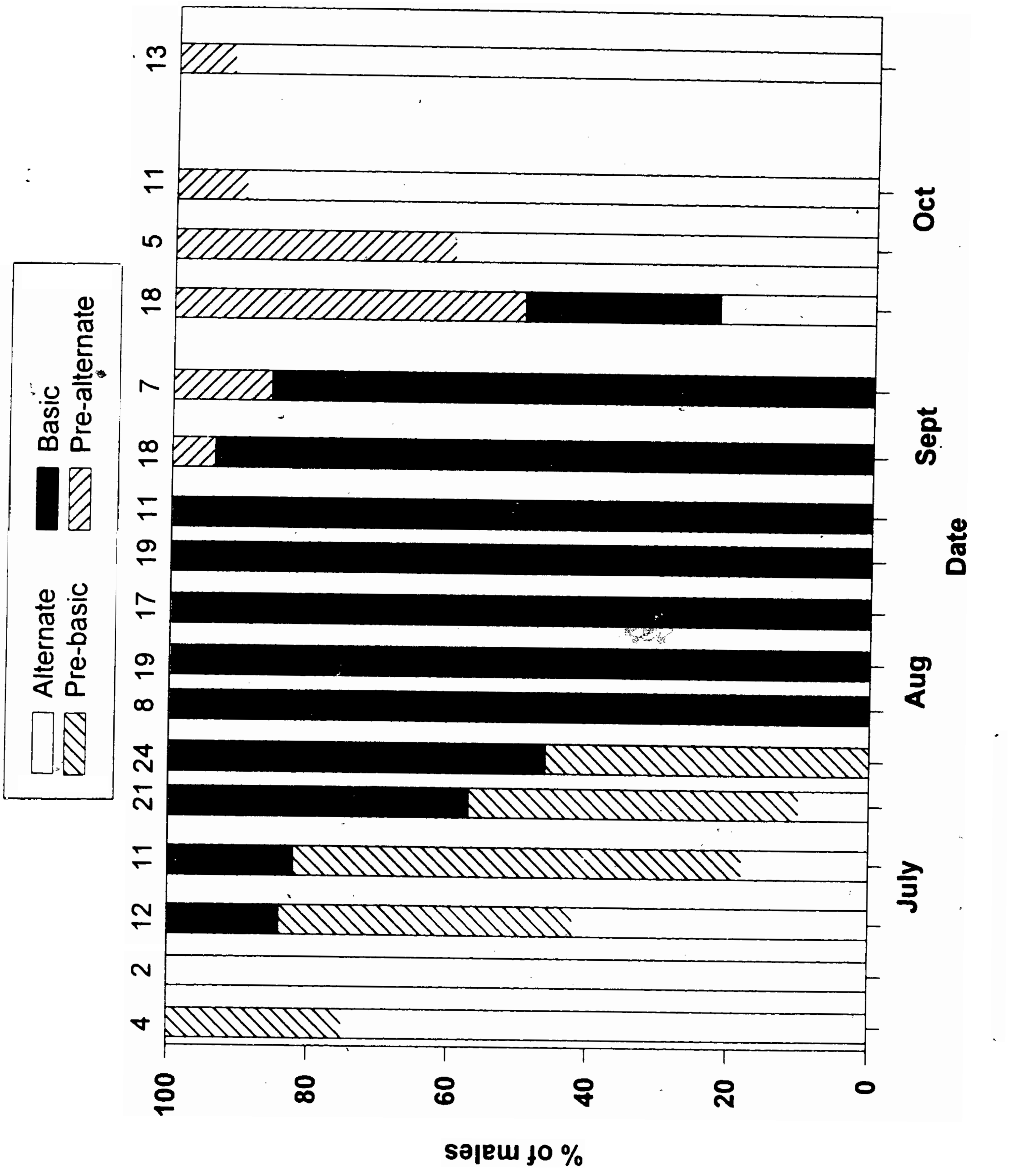
At the population level, although the sample size is small, males began the pre-basic molt in mid-June (Figure 3.3.1). All males were in basic plumage during the last week of July through most of August. The first males began the pre-alternate molt in early Sept. and the last male still with signs of molt was seen in mid-October.

The total estimated period for a male Harlequin Duck from the start of the conspicuous stage of the pre-basic molt to the return to his visible alternate plumage feathers is 87 days or approximately three months.

Distributional Patterns

Male Harlequin Ducks were highly clumped from their arrival in June and July through the end of September (Fig. 3.3.2). In October and November, when molting was completed, the birds tend to disperse throughout the habitat and the coefficient of dispersion approached 1 (Fig. 3.3.2). In August and September there was a tendency for the ducks to segregate into same sex groupings (Fig. 3.3.3) as evidenced by the negative correlation coefficients. In October and November, the correlations between the number of males and females in any given group became positive, suggesting pairing among the birds.

Figure 3.3.1. Proportion of banded male Harlequin Ducks in each of the four plumage stages at White Rock, BC., 1995.



Alternate
Basic
Pre-basic
Pre-alternate
% of males
100
80
60
40
20
0
4
2
12
11
21
24
8
19
17
19
11
18
7
18
5
11
13
July
Aug
Sept
Oct
Date

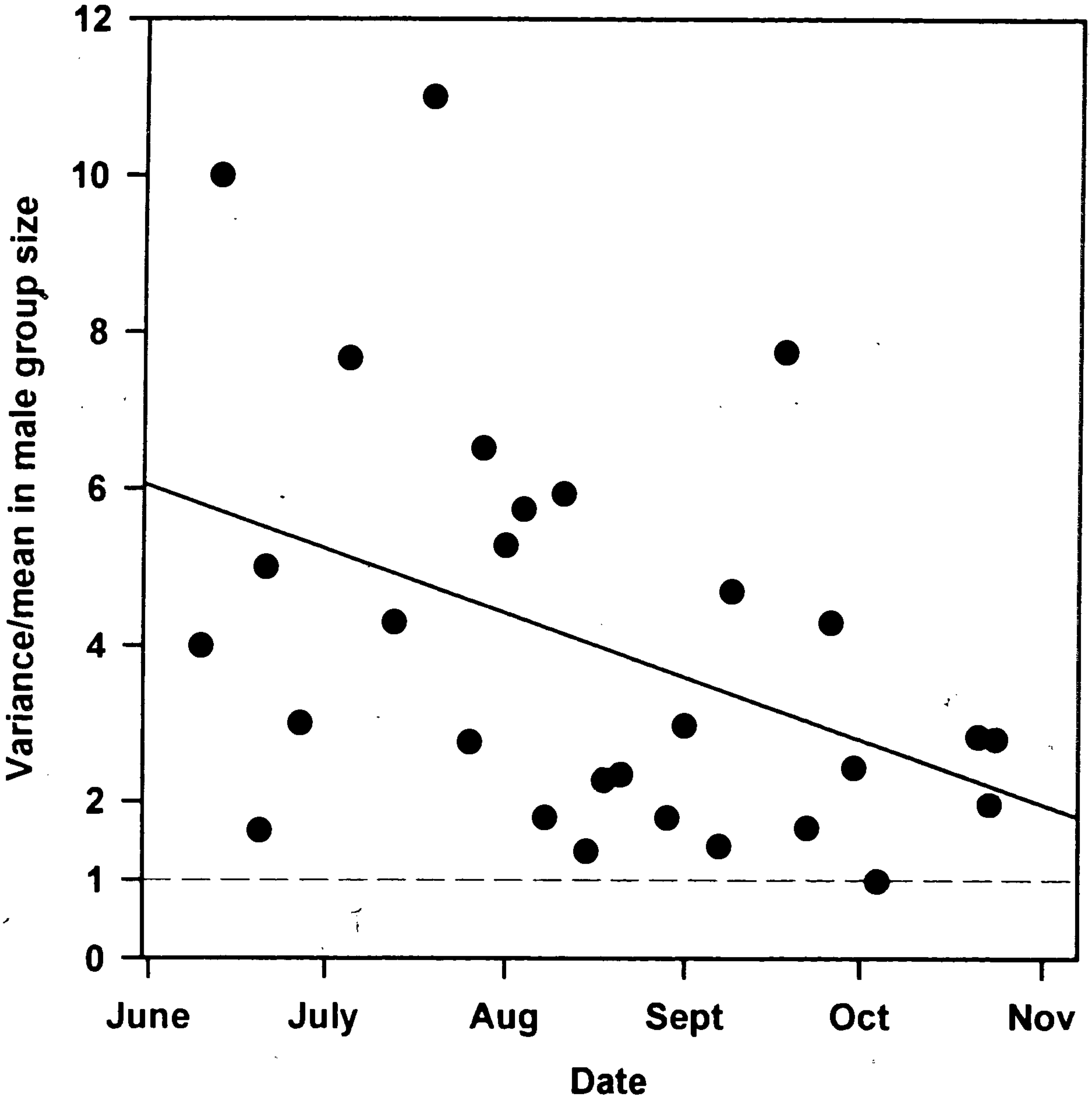


Figure 3.3.2. Coefficients of dispersion (CD; variance/mean ratio) in male Harlequin Duck group size over the moulting season at White Rock, BC., 1995. Values of 1 indicate random distribution of individuals over the available habitat. There is a significant decline in the CD over the season ($F_{1,27}$ = 5.6 , P = 0.025).

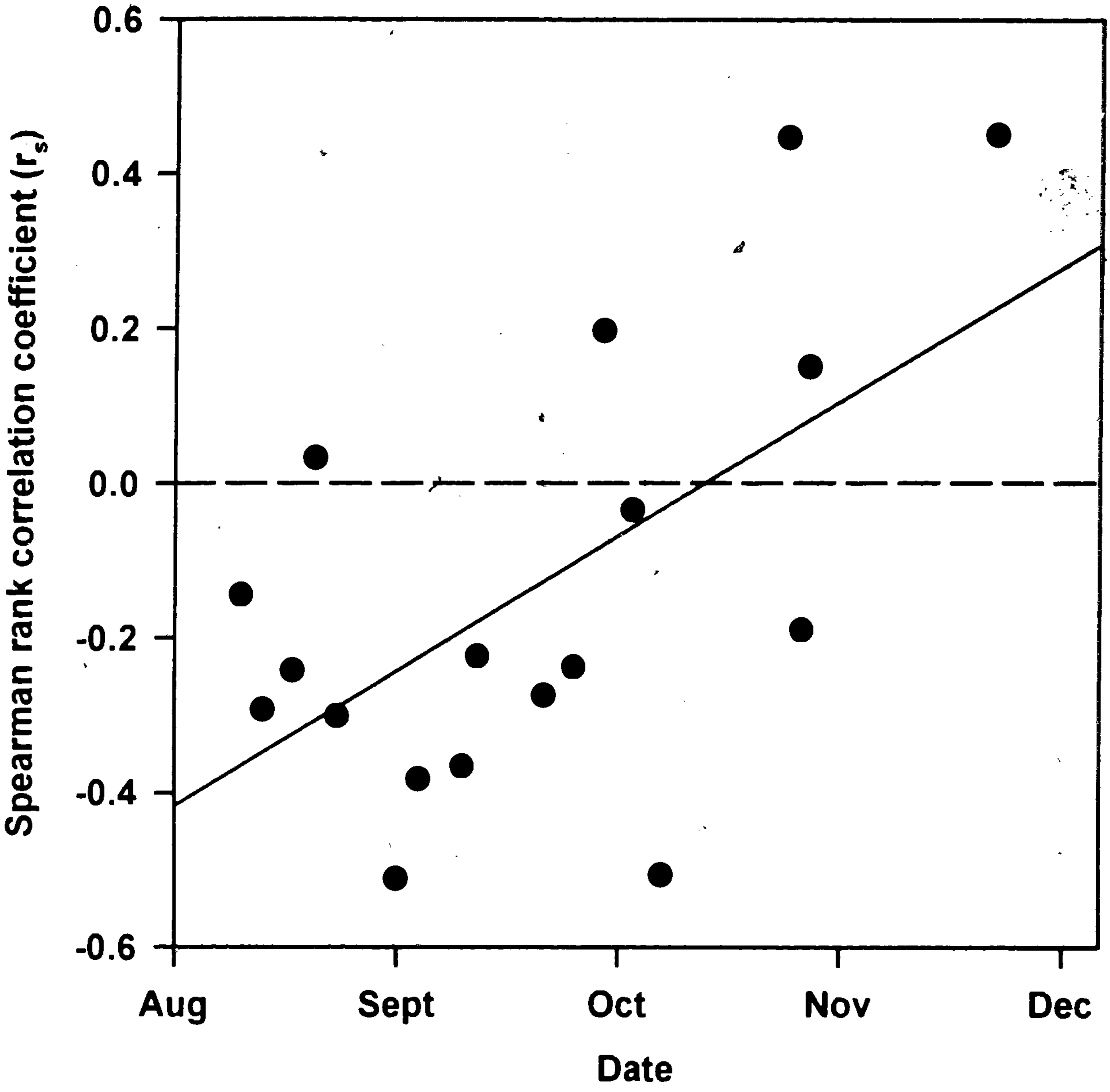


Figure 3.3.3. Spearman rank correlations between the number of males and females Harlequin Duck in individual groups over the moulting and post-moult season at White Rock, BC., 1995. There is a significant increase in the correlations over the season ($F_{1,16}$= 8.63, $P < 0.001$).

3.3.5. Discussion

Male Harlequin Ducks returned to the study location prior to molt, and began to lose body feathers soon after arrival. They hauled out frequently, allowing us to recognize them individually. Because birds were individually color banded we were able to follow the progress of the molt from alternate to basic and back to alternate in 28 individuals, and at the same time observe distributional patterns during the process. Such an analysis has rarely, if ever, been possible in holarctic Anatidae because of the difficulty of following known individuals and the inaccessibility of most molting locations.

A description of the basic plumage does not necessarily allow us to infer function associated with the two stages. Although non-adaptive explanations cannot be refuted, the basic plumage patterns described above allow us to explore the hypotheses described earlier. At the beginning of the basic plumage, the males are indeed female like and cryptic apart from the facial markings which both sexes carry. Throughout the period and in contrast to their distribution during most of the winter, the males form into groups and tend to keep separate from the females. They spend more time hauled out on rocks than they do at any other time of year (F. Cooke & G. J. Robertson, unpubl. data). Clumping may provide increasing protection from predators. If birds are more vulnerable to predators while on the water than on the land, then hauling out may be an anti-predator mechanism. On one occasion three birds were seen to suddenly and rapidly scoot across the water towards the land, as if in response to an underwater threat. However, in general, Harlequin Ducks, in common with other diving ducks respond to land based and aerial predators by heading to open water and diving if attacked (Bailey 1981). It has even been suggested that the alternate plumage of the drake Harlequin Duck is cryptic when the birds are swimming in rough water or bobbing around in high seas (Fleischner 1983).

There are better and more obvious explanations for an increasing tendency to haul out during molt. There is a strong correlation between preening and hauling out (B. Gowans, unpubl. data), and the enhanced preening required during the molt of body feathers is probably easier to perform on land than in the water. Moreover hauling out remains a frequent activity during October when birds have re-acquired their alternate plumage (B. Gowans, unpubl. data). Evidence that the basic plumage acts as an anti-predator mechanism during the first stage of the basic plumage is weak at best. Similarly there is little evidence for the heat loss hypothesis. Harlequin drakes are in basic plumage during June, July and August, the three warmest months of the year. Furthermore, there is no clear relationship in the heat retention capabilities of different plumage colors (Walsberg 1982, Beasley & Ankney 1988).

In the second stage of the basic plumage there is even less evidence for the crypticity hypothesis and considerable evidence against it. The appearance of the white tertial feathers during the basic stage of the body plumage is a puzzle, if one is seeking adaptive explanations for the plumage patterns. These feathers detract from the crypticity of the birds at least to human eyes. Perhaps it could be argued that cryptic plumage is no longer necessary since the birds regain flight capability in this second stage. Nevertheless this does not provide an explanation as to why the feathers should be white rather than dark brown like the others, nor the fact that the conspicuous tertials appear well before the birds can fly again. Neither the heat loss nor the default hypothesis provide an explanation for the white tertials and we must seek an explanation elsewhere.

We theorize that the white tertials serve as a badge of quality. The function of a badge is to provide a recognizable character indicating the quality of individuals in the population (Rohwer & Ewald 1981). To explore this idea further it is necessary to know more about the role of the white tertials in birds with complete alternate plumage. As the new alternate plumage develops, new white tertials appear later than the other visual plumage characters and when the feathers are fully grown they are larger than the ones present in the basic plumage. Initially they have a dark border around the white inner parts of the feather but from a limited examination of museum specimens (F. Cooke, unpubl. data), this border may erode away during the winter. Another unique feature of these feathers is that they may be absent or present dependent on the age of the male. Immature and sub-adult birds either do not have them, or they are small and inconspicuous. A detailed study of the relationship between age and extent of white tertials has not been carried out, but would be most valuable. The white tertials could also provide evidence to other birds of the timing of molt. Those birds which enter molt early display the feathers earlier than those which begin later and this may provide important information to potential competitors later when active competition occurs among males for mates (Hepp 1988). Males are generally not able to successfully attract a mate until they have completed the pre-alternate molt (Wishart 1983).

The variability of the tertials, both in terms of the bird's age and as a signal of the timing of molt could provide a good indicator to other birds of the condition or quality of the bird. If this information is important in assessing other birds in the population, then one can understand why such an apparently unnecessary feature should become conspicuous in the middle of the period when birds are in basic plumage. Badges indicating quality may be important either in terms of intra- or inter-sexual interactions.

Our behavioural data provide evidence that when birds are in basic plumage they associate in predominantly male groups which suggests that the white feathers are providing information to members of the same sex. Birds which molt in the area remain in the area afterwards and actively compete for females as soon as they regain their alternate plumage (F. Cooke & G. J. Robertson, unpubl. data). Advanced knowledge of the quality of rival males could well be useful for the individuals who are competing. Drakes in other duck species are known to sort themselves into a dominance hierarchy before pairing. Males at the top of the hierarchy pair first and so on down the hierarchy (McKinney 1992). The white tertials may be a major clue in the establishment of this hierarchy.

We proposed three hypotheses to explain the drab coloration of basic plumaged drakes. While our data provided little support for the hypotheses, none of them could explain the presence of white tertial feathers in the basic plumage. We theorize that these feathers act as a badge of quality, which may be useful during intra-sexual competition among males during later pair formation.

3.4. Moult speed predicts pairing success in male Harlequin Ducks[5]

3.4.1. Abstract

The bright plumage of male ducks in sexually dichromatic species is thought to have evolved through intense sexual selection. This study examined the role of the timing and speed of moult into this bright plumage on the subsequent mating success of male Harlequin Ducks *Histrionicus histrionicus*. Males which moulted relatively slowly had a lower chance of establishing a pair bond than others. The timing of moult did not have an effect on whether a male obtained a mate, after we controlled for the effects of moult speed. Moult speed and timing were not correlated within individual males. Both moult speed and moult timing were significantly repeatable in individual males over two years. Moulting speed probably reflects the condition of the males, whereas the timing of moult is more likely related to the distance to the individual's breeding areas, which determines the timing of arrival of males to the moulting grounds. In waterfowl species that have been studied, males usually form dominance hierarchies before pairing and females tend to chose dominant males. We suggest that male Harlequin Ducks which moulted slowly were likely to be poor quality individuals and, as such, were relegated to subordinate status and unable to attract a mate in the following fall.

3.4.2. Introduction

The conspicuous plumage of males ducks in sexually dichromatic species has been cited as an example for sexual selection for bright colouration (Darwin 1871, Lack 1974). Waterfowl species showing life long pair bonds are generally monochromatic, whereas serially monogamous species are highly dichromatic (Scott & Clutton-Brock 1989). It is

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[5] This section (3.4) has been submitted for publication as Robertson, G.J., Cooke, F., Goudie, R.I. & Boyd W.S. Moult speed predicts pairing success in male Harlequin Ducks, to *Animal Behaviour*.

thought a significant male biased sex ratio in duck populations (Sargeant & Raveling 1992) has lead to strong sexual selection and the subsequent evolution of bright plumages.

Ducks tend to form pair bonds well in advance of the breeding season (Rohwer & Anderson 1988) and the pair bond ends sometime during incubation, after which the males depart to initiate their moult. Males do not provide any parental care except for some Southern Hemisphere species (McKinney 1985). Thus, females are likely choosing males based on phenotypic qualities that reflect either their genetic quality which can be passed on to the offspring, or the males' quality as a mate, such as their ability to protect females from other males allowing her to feed uninterrupted during the winter and spring period. Paired females have been shown to be harassed less by males than unpaired females and are able to increase their foraging rates (Ashcroft 1976). High quality males are also able to defend their female from harassment during nesting which leads to more successful nesting (Sorenson 1992).

In waterfowl, as in many birds species, females prefer brightly adorned males (see Andersson 1994), perhaps because males with the brightest plumages are in the best condition (Hill & Montgomerie 1994). Female ducks also prefer males that have all of their alternate (breeding) plumage characters fully developed (Klint 1980, Weidmann 1990, Omland 1996a). Paired males collected in the wild have a more complete development of their alternate plumage than unpaired males (Hohman & Ankney 1994). Furthermore, adult males tend to have fully developed alternate (breeding) plumages whereas yearling males sometimes do not completely develop this plumage or the development is delayed until courtship has already begun, putting them at a disadvantage (Wishart 1983, Hepp 1988). Therefore, the timely acquisition of a complete alternate plumage is important for male ducks attempting to find a mate.

We initiated a study to determine the effect of the speed (or rate) and timing (or onset) of moult in a population of male Harlequin Ducks *Histrionicus histrionicus* on the subsequent pairing success of these males. In this study we have sufficient observations of known individuals to document the relative speed and timing of their wing, tail, and pre-basic and pre-alternate body feather moult; and, their subsequent pairing success in the following fall. Moulting early or moulting quickly are two means to complete a moulting sequence as soon as possible, however, few studies have been able to distinguish between these two processes Specifically, our objectives were to: (1) examine any relationship between the independent effects of moulting speed and moulting timing on the mating success of male Harlequin Ducks; (2) discuss the possible underlying factors that influence moulting speed and timing, and (3) discuss why females may be choosing these characters given the life history of this species.

3.4.2. Methods

Study species

Harlequin Ducks are small (500-700g) sea ducks which nest along lowland, sub-alpine and alpine streams and winter on coastal rocky shorelines (Palmer 1976). This species is highly dimorphic, with the males having a variety of striking plumage characters. The general body plumage for the males is a dark blue merging to a slate grey on the belly. They also have: large white crescents behind the bill and on the neck, two large white bands bordered by black under the neck and chest, white tertials and scapulars, rich navy blue secondaries and chestnut coloured feathers on the flanks. Females, on the other hand, are generally brown with white bellies streaked with brown. Both sexes have a white patch behind the bill and a circular white patch behind the eye.

Males return to the non-breeding grounds beginning in mid-June through to July, the females return in August through until September (Chapter 3.2). Pair bonds form in the fall and are maintained through the following spring when the pairs migrate to breeding locations (Gowans et al. 1997). Pairs tend to reunite (as defined in Rowley 1983) if both members of the pair return from the breeding grounds to the same wintering location (Gowans et al. 1997). Harlequin Ducks will sometimes moult and over-winter at the same location, an uncommon trait among the waterfowl.

Study Area and Field Methods

This study was conducted from early June 1995 to May 1997 near White Rock, in coastal southwestern British Columbia. The study site comprised a 5.5 km stretch of rocky shoreline where up to 150 Harlequin Ducks spend the non-breeding season. Beginning in 1994, ducks were captured while they were flightless (late July for males, September for females). The birds were rounded up with sea kayaks and corralled into funnel traps. Individuals were sexed and aged (yearling or adult) by measuring the depth of the bursa of Fabricius during cloacal examination (Peterson & Ellarson 1978). All birds were measured, weighed and banded with standard USFWS bands and a tarsal band with a unique two letter-number code. Individuals were released in small groups after processing.

Observations of marked birds were carried out throughout the non-breeding season. During the moulting period (June to September) observations were made once or twice a week, weather and human activity permitting. Harlequin Ducks often haul out on to rocks to preen and rest, and at this time the leg bands are clearly visible. Individual males were seen between 3 and 17 times during the moulting period. When an individual male was identified, an assessment of the stage of his moult was made. Drakes undergo two body moults and one wing (primaries and secondaries) and tail moult per year. The first body moult after breeding (pre-basic) leads into a basic (eclipse) plumage in which the male is generally drab and female like. While in basic body plumage the remiges (wing feathers) and rectrices (tail feathers) are moulted and replaced. Males remain in basic plumage for an average of 52 days (Cooke et al. 1997), then undergo pre-alternate body moult during which males acquire a new alternate (breeding) plumage. Tertial feathers in waterfowl are moulted as body feathers and are replaced twice a year (Stresemann & Stresemann 1966).

Basic tertials have white ovals on them that are visible in the field. They are grown and then lost just before the pre-alternate moult begins. Tertials in the alternate plumage are the very last visible feathers to grow in and their length can be visually assessed at the end of the pre-alternate moult (Cooke et al. 1997). For the purposes of this paper we define the moulting period as the time when males begin the pre-basic moult to the time they complete the pre-alternate moult. This entire moulting sequence lasts approximately 3 months in Harlequin Ducks (Cooke et al. 1997).

Males were categorized into a sequence of stages during moult. These stages were: (i) still in their old alternate plumage; (ii) just beginning the pre-basic body moult; (iii) undergoing the pre-basic body moult; (iv) just finishing the pre-basic body moult; (v) in basic plumage; (vi) in basic plumage with no primaries; (vii) in basic plumage with their primaries and basic tertials 1/4, 1/2, 3/4 or full grown; (viii) in basic plumage with no basic tertials; (ix) just beginning the pre-alternate body moult; (x) undergoing the pre-alternate body moult; (xi) just finishing the pre-alternate body moult; and finally (xii) in alternate body plumage with their alternate tertials 1/4, 1/2, 3/4 and full grown. It was not necessary to use the tail moult to identify moult stages as tail feather regrowth matches the initiation of the pre-alternate moult. This entire sequence of moulting is consistent among all Harlequin Ducks studied to date (Robertson, unpublished data), and follows the general pattern seen in ducks (Palmer 1976).

The population was monitored throughout the following winter and spring to determine whether males were successful in obtaining a mate. Pairs were easily identified after observing individuals for 5 to 10 minutes. Generally, pairs moved synchronously and males vigorously defended their mates from intruding males (Gowans et al. in press). Unpaired males generally associate together and are seen over a wider range of sites in the study area. The pairing status of an individual was considered confirmed if it was seen in that state more than three times. Some males that moult at the study site depart after moulting and for them it was not possible to determine whether they paired or not in the subsequent winter, although it was possible to assess the relative speed and timing of their moult.

Statistical analyses

To partition moult into its two temporal components (timing and speed) and to cope with the problem of not sighting all males on any given survey we chose a method of analysis that compares the moult stage of each and every male to all the other males seen on the same survey day. For each survey day, each male was ranked by his stage of moult and this rank was subtracted from the rank of all of the other males seen that day. These differences in ranks were entered into a matrix that included all males compared to all other males for each survey day. To compare the relative moult speeds of males, all data matrices where a particular male was seen were analyzed in a repeated measures design (PROC MIXED, SAS Institute Inc. 1996), the repeated measure being all of the other males a particular male was compared to. Date was treated as a continuous variable, and regressed in this design with the difference in ranks between males as the dependent variable. A significant positive regression slope indicated that a male was gaining rank over time as compared to the other males in the data set. These males were identified as 'fast' moulting males. Similarly, males with significant negative slopes were identified as 'slow' moulters. All other males were identified as 'average' speed moulters. This method does not give an actual rate of moulting in terms of feather growth per day, but rather an index of moult speed relative to all other males.

To estimate the relative timing of moult we used the least-squares mean rank calculated from the above analyses as in index of relative timing of when males began moulting. Since males arrive and begin moulting at different dates a least-squares mean rank controls for this variation and calculates an expected mean rank at the same date for all males. Once again this value does not describe an actual date when moult was initiated but rather provides a comparison among males of their overall timing of moult relative to each other. Positive values reflect earlier moulting males, negative values represent later moulting males.

Repeatabilities for the moult speed and the moult timing were calculated following Lessells and Boag (1987). Non-parametric tests were used for comparing moulting speeds and timing because the data for these variables were limited and generally not normal. Many of the same males were used in the analyses in both years (n = 13), and pairs tend to reunite if both members return to the study site (Gowans et al. 1997). Therefore, the data between the two years is pseudoreplicated for a portion of the males. As such, the analyses for the two years should not be considered two independent tests, but neither are they completely pseudoreplicated, and three males changed pairing status from one year to the next.

3.4.4. Results

Moulting Speed and Pairing Success

Some males moulted significantly slower or faster than other males in the population. Of 35 males identified during the moult in 1995, 13 had significant positive slopes, (they gained rank over time), 14 had slopes not significantly different from zero, and eight had significant negative slopes. We were able to determine if 26 of these males were subsequently paired in the following spring. Seven of eight fast moulting males (87.5%) successfully paired, 10 of 12 average speed moulting males (83.3%) successfully paired and only two of six slow moulting males (33%) were able to successfully attract mates. Hence, fewer slow moulting males were successful in obtaining a mate (P = 0.028, Fisher's exact test). Additionally, the mean moult speed index for paired males (mean ± 1 S.D., 0.0057 ± 0.0355) was significantly faster than that for unpaired males (-0.0282 ± 0.0229) (Z_{approx} = 2.17, df = 19,7, P = 0.030, Wilcoxon paired rank test).

Of 38 males identified in 1996, 10 males moulted faster than the others, 19 moulted at average speeds and nine moulted slower than the other males. Twenty of these males were subsequently sighted and we were able to determined if they were paired. Seven of eight fast moulting males (87.5%) successfully paired, four of six average speed moulting males (66.6%) successfully paired and only one of six slow moulting males (16.6%) were able to successfully attract mates. Fewer slow moulting males were successful in obtaining a mate ($P = 0.018$, Fisher's exact test). Additionally, the mean moult speed index for paired males (mean ± 1 S.D., 0.0245 ± 0.0378) was significantly faster than that for unpaired males (-0.0196 ± 0.0229) ($Z_{\text{approx.}} = 2.04$, $df = 11,7$, $P = 0.041$, Wilcoxon paired rank test).

Moulting Timing and Pairing Success

In 1995 males which were successful at obtaining a mate (mean rank = 0.17 ± 1.62) moulted earlier than unsuccessful males (mean rank = - 0.55 ± 0.60) ($Z_{\text{approx.}} = 2.02$, $n = 20, 8$, $P = 0.043$, Wilcoxon paired rank test). There was no significant difference in 1996 (mean rank paired males 0.57 ± 2.5, unpaired males - 0.21 ± 1.56) ($Z_{\text{approx.}} = 1.20$, $n = 12, 8$, $P = 0.23$, Wilcoxon paired rank test). Slow moulting males also moult later by virtue of being slow. In a stepwise logistical regression with pairing status (paired and unpaired) as the dependent variable, moult speed entered and remained in the model as a significant explanatory variable (1995: $Wald\ \chi^2 = 3.86$, $df = 1$, $P = 0.049$; 1996: $Wald\ \chi^2 = 3.98$, $df = 1$, $P = 0.046$). Moult timing did not enter the model in either year ($P > 0.05$).

Repeatabilities and Correlations between Moult Speed and Timing

Both the speed of moulting (*repeatability* = 0.35, $F = 2.06$, $df = 25,26$, $P = 0.036$) and the timing of moulting (*repeatability* = 0.51, $F = 3.06$, $df = 25,26$, $P = 0.004$) were significantly repeatable within males over the two years. However, moulting speed and timing were not significantly correlated in either year (1995: $r = -0.034$, $n = 26$, $P = 0.87$; 1996: $r = -0.21$, $n = 25$, $P = 0.30$; Spearman rank correlations).

3.4.5 Discussion

Wild male Harlequin Ducks which moulted more slowly than other males were less likely to obtain a mate in the subsequent winter. Although the timing of moult also covaried with mating success, this was simply an artifact of slow moulting individuals also moulting later.

Speed of Moult

Moult speed may reflect an individual's body condition or phenotypic quality. Plumage quality has been shown to be positively related to nutritional condition and moulting speed in house finches *Carpodacus mexicanus* (Hill & Montgomerie 1994) and barn swallows *Hirundo rustica* (Møller et al. 1994). Furthermore, plumage quality is related to mating success in these species (Hill 1990, Møller 1994). This evidence indirectly suggests that moulting speed may be a good indicator of condition in birds. Murphy et al. (1988) documented that white-crowned sparrows *Zonotrichia leucophrys* fed poor quality diets regrew their feathers more slowly, moulted fewer feather tracts simultaneously and developed a poorer quality plumage at the end of the moult. Male mallards *Anas platyrhynchos* fed on low protein diets did not moult their remiges more slowly than mallards fed a high quality diet, however, their new wing feathers were shorter (Pehrsson 1987). These two findings are not necessarily contradictory since there are two methods for a bird to increase the speed of its moult. One is to grow individual feathers faster, the other is to moult more feather tracts at the same time. We believe that the second method is probably more likely to explain the increased speed of the moult seen in Harlequin Ducks, because studies of waterfowl show that feather growth rates are remarkably constant, probably at a physiological maximum (Hohman et al. 1992). Birds appear to have more flexibility in the number of feather tracts they can moult simultaneously

(Newton 1967, Murphy & King 1984), rather than feather growth rates *per se*, although adjustments to both can occur in some species (Hahn et al. 1992)

Plumage quality has been shown to be correlated with dominance in some male ducks (Brodsky et al. 1988, Holmberg et al. 1989). Both female choice and male-male competition appear to play a role in pair formation in duck populations (McKinney 1987). In most duck species studied to date, males form dominance hierarchies amongst themselves (Hepp 1988) and then females subsequently choose among these males (Wishart 1983), although Sorenson & Derrickson (1994) showed that males become dominant after they were chosen by a female. Males which were restricted in their access to food were less active in courtship activities (Brodsky & Ankney 1985, Hepp 1988, Holmberg et al. 1989), therefore males in good condition may be able to display more and achieve a higher dominance ranking. Generally, female ducks preferred males that courted at the highest rate, had a high dominance ranking, and had the best quality plumages and ornaments (Holmberg et al. 1989; Sorenson & Derrickson 1994; Omland 1996b).

We suggest that male Harlequin Ducks which can readily meet the nutritional requirements and/or metabolic costs of moulting do so quickly. These males could be vigorous in establishing themselves in the dominance hierarchy and better able to attract females. We were not able to quantify differences in plumage quality, since most males appeared to us to be very similar in plumage. We did notice two second year birds that had poorly coloured chestnut flanks, the major red/orange portion of the plumage. Neither was successful in obtaining a mate. However, one second year male was successful in finding a mate, he also moulted quickly, so our anecdotal observations do not appear to be simply an age effect.

The repeatability of moult speed is interesting as it may reflect some inherent physiological differences in the ability of males to moult. Alternatively, it may be a function of the fact that males tend to achieve the same body condition each summer and fall during the moult due to behavioural interactions. Male Harlequin Ducks form large groupings during the moulting period and we have postulated that males may be establishing a hierarchy amongst themselves during this period (Cooke et al. 1997), as observed in many other duck species (McKinney 1992). Since males are philopatric to their moulting sites (Chapter 4) many of the same individuals are interacting year after year. Males that are low in status in one year may be unable to rise in status in the hierarchy and will remain in low status year after year. Unlike the well studied ducks in the genus *Anas* (McKinney 1992) behavioural interactions among Harlequin Ducks are relatively rare and non-aggressive. Very little agonistic behaviour among males is apparent during the moulting period (Robertson, unpublished data). Furthermore, males feed very little during this time, and appeared not to be under any great nutritional stress. Finally, foraging habitat, at least at this study site, is distributed more or less evenly, making it very difficult for dominant males to restrict the foraging opportunities of other birds. Unfortunately, behavioural interactions among males are so rare it would be very difficult to assess the dominance ranking of males directly.

Timing of Moult

The timing of moulting had a marginal effect on the pairing success of male Harlequin Ducks and could be explained by the fact that, all other things being equal, slow moulting males finish moulting later. There is considerable variation in the arrival times of Harlequin Ducks to the non-breeding grounds (Robertson et al. 1997). As males begin moulting as soon as they arrive on the non-breeding grounds (Cooke et al. 1997), the timing of moult is probably an indicator of arrival time. Individuals from the same wintering grounds breed at many different locations (Goudie, unpublished data). Males whose mates breed in the coastal mountain streams potentially initiate nesting almost six weeks before females nesting in the Rocky Mountains. Moult timing in this wintering population is probably a better indicator of breeding location rather than male quality in Harlequin Ducks. This is an interesting observation as its contrasts with observations for house finches and barn swallows that early moulting males (independent of moulting speed) tended to moult into showier plumages and to subsequently achieve a higher mating success (Hill & Montgomerie 1994, Møller et al. 1994). Additionally, mallards fed high protein diets moulted into their basic plumage moult earlier than birds fed low protein diets (Pehrsson 1987). Since the entire moulting process takes a long time (3 months) in Harlequin Ducks, all males begin moulting immediately on their return to the non-breeding grounds to be ready for courtship in September and October. Therefore, there is no variation, that is unconstrained by breeding location, in the timing of moult available for selection. The high repeatability of moult timing is a function of the high female breeding philopatry of Harlequin Ducks (Bengtson 1972) and the tendency of pairs to re-unite year after year (Gowans et al. 1997), so males are returning to the same breeding location year after year.

Conclusion

We have documented a relationship between pairing and moulting speed in Harlequin Ducks. Moulting speed probably reflects some intrinsic qualities of the male, and males that are able to moult faster are chosen by females. Most females are not present while the males are moulting intensively (Chapter 3.2), so females are not assessing male moult speed directly. Females are probably choosing one or more other characters also correlated with male quality, possibly the dominance of the male with respect to others, plumage quality and/or the quality of the male display. Since females are choosing a male that will remain with them for at least 7 months, and probably for a number of years, they would be expected to choose the best quality males possible. Females choosing good quality males may be choosing good genes for their offspring via honest advertisement (Pomiankowski 1987) and/or choosing a male who will actively rebuke suitors and allow the female to feed undisturbed, this latter choice being a case of the good parent process of sexual selection (Hoelzer 1989).

In waterfowl, female body condition during the winter and especially in the spring is important in determining subsequent reproductive success in the following summer (Alisauskas & Ankney 1992). Paired birds are dominant to single birds (Paulus 1983) and paired females are able to forage at a higher rate than unpaired females (Ashcroft 1976). Females selecting dominant males as mates will have better access to resources during a time when nutrients for reproduction are being accumulated. Thus a females' fecundity is determined, in part, by the quality of her male. Females selecting males that possess traits that reflect good body condition and vigour will be at an advantage, leading to female choice for these traits. The variation in the male traits need not have a genetic basis (Hoelzer 1989); females are simply selecting for good quality males that will protect them during the winter and increase her ability to acquire nutrients that can be subsequently used to lay a clutch size greater than the population mean and achieve the a higher reproductive success (Hepp 1984).

3.5. References

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Chapter 4

Site fidelity, mating systems, and winter philopatry in Harlequin Ducks *Histrionicus histrionicus*[6]

4.1. Abstract

Many waterfowl species form pair bonds during the non-breeding season, yet current descriptions of the mating system focus on the breeding grounds. Harlequin Ducks wintering in southwestern British Columbia were studied to test the hypothesis that mating systems cause a sex-bias in philopatry. The numbers of male Harlequin Ducks at our study area were far more variable than that of females. Males that were unsuccessful in obtaining a mate were observed over a larger area than paired males. Unpaired males appeared to roam about the available habitat, and behaved as floaters.There was considerable overlap in habitat use among paired males and no obvious boundaries were formed. Therefore, Harlequin Ducks did not appear to form territories in winter, but rather exhibited a mate-defense mating system. Annual return rates to the non-breeding grounds were high (62-77%) and similar for both sexes when probable differences in survival were accounted for. Individuals not only returned to the study area but to specific sections within the study area. Males that lost their mates returned to the study area in the subsequent year with the same frequency as other males, however, they tended to leave the study area prior to courtship. We suggest that both males and females returned the study area for reasons beyond those than just forming a pair bond. There are likely to be survival advantages for both sexes to be philopatric. High levels of philopatry exhibited by both sexes also allows

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pairs to re-unite each fall. Thus, the mating system failed to predict the direction of the sex-bias in philopatry seen in this species because other factors were important.

4.2. Introduction

A relationship between resource dispersion and mating systems occurs due to the dichotomy between male and female reproductive strategies (Emlen & Oring 1977). In general, male reproductive output is limited by the number of females he is able to fertilize while female reproductive output is limited by the amount of resources for reproduction she can acquire (Trivers 1972). Therefore, female dispersion across a landscape should be influenced by the distribution of resources and conspecifics (Fretwell & Lucas 1970), while males should distribute themselves to be able to encounter and fertilize as many high quality females as possible (Davies 1991). Two general types of mating systems have evolved for males to attempt to secure matings. Males may defend critical resources needed by the females and a territorial (or resource-defense) system evolves. The resource that is defended must be critical to the females' survival or reproductive success (Emlen & Oring 1977) and economically defensible (Brown 1964, 1969). Critical resources to breeding females include food (either energy or specific nutrients), and/or safe or suitable sites for reproduction and survival (e.g. nest sites, roosts). If males cannot defend a critical resource males compete amongst themselves for access to, or search for, females and a mate-defense mating system evolves (Oring 1982).

A relationship between mating systems and sex-biased philopatry (the tendency to return to, or remain at, the same place) was first highlighted by Greenwood (1980) and Greenwood & Harvey (1982), who showed that, in species which exhibit resource-defense based mating systems, males tend to return to the breeding grounds with a higher frequency than females. The explanation for this pattern was that males that return to the same territory year after year are thought to be at an advantage in establishing and maintaining their territory. Presumably, they could use their prior knowledge of the local area to their advantage. This situation is typified by birds (Greenwood & Harvey 1982, Clarke et al. 1997). In contrast, in mate-defense based mating systems females tend to return to, or remain at, the same areas with a higher frequency. Females in these systems are free to stay at preferred locations while males must roam to find potential mates. Mammals tend to exhibit this pattern of female-biased philopatry (Greenwood 1980).

Waterfowl exhibit a female-biased philopatry to the breeding grounds (Greenwood & Harvey 1982, Johnson & Grier 1988, Rohwer & Anderson 1988, Anderson et al. 1992) and generally exhibit a mate-defense mating system at this time (McKinney 1986, Oring & Sayler 1992). However, pairing in many species of migratory ducks occurs during the non-breeding season, well before migration to the breeding grounds (Rohwer & Anderson 1988). Therefore, the mating system of many duck species must be defined during the winter period, and not the breeding season. For many species, however, there is very little information on their habitat use patterns during the time of pair formation and how the habitats they use influence their mating system. Species where winter territoriality could be possible are those that utilize relatively stable habitats and sessile food resources, whereas species using ephemeral resources would not be territorial (Lima 1984). If a waterfowl species is territorial in winter then a male-biased philopatry would be predicted, if a species showed a mate-defense mating system female-biased philopatry would be expected.

Breeding waterfowl show a wide range of spacing behaviour during the breeding season (Anderson & Titman 1992). Some species do not show any evidence of territorial behaviour (northern pintail *Anas acuta*, Titman & Seymour 1981 and colonial nesting arctic breeding geese) while others show highly aggressive behaviour and strong territoriality e.g. steamer ducks (Livezey & Humphrey 1985), river ducks (Eldridge 1986), goldeneyes (Savard 1984, Gauthier 1987, Savard 1988a) and swans (Kear 1972). It is likely that wintering waterfowl could show any pattern within the range of spacing behaviour and aggression that is seen during the breeding season. Territorial behaviour in other bird species is not restricted to the breeding grounds. Wintering shorebirds (Myers et al. 1979a, McNeil & Rompré 1995, Turpie 1995) and passerines (Salomonson & Balda 1977, Rappole & Warner 1980, but see Lefebvre et al. 1994) have been shown to form territories. Furthermore, there appears to be some evidence that passerines that show winter territoriality have relatively high return rates to their wintering grounds (McNeil 1982, Faaborg & Arendt 1984).

Therefore, unlike the situation on the breeding grounds, it is possible that some waterfowl species could exhibit a resource-defense based mating system and demonstrate a male-biased philopatry to the wintering grounds, similar to other bird species (Clarke et al. 1997). A likely group of waterfowl where this situation may occur is the sea ducks; many of these species winter in marine waters and consume sessile benthic prey, a stable and predictable food source (Palmer 1976). Harlequin Ducks *Histrionicus histrionicus* are small sea ducks that forage along linear sections of intertidal habitat (Goudie & Ankney 1986). Such linear sections of habitat, especially intertidal communities, have been shown to be economically defensible in other bird species (Weller 1975, Ens et al. 1992). Harlequin Ducks are also known to form pair bonds during the winter (Gowans et al. 1997), thus predictions about a sex-biased philopatry based on the mating system are relevant during the winter season in this species.

The main objectives of this paper were twofold. The first objective was to determine if Harlequin Ducks exhibit a mate-defense or a resource-defense based mating system by studying the movement patterns of males and females during the non-breeding season. The stability of a population of males was examined to detect the presence of floaters, and movements of individual males were examined to determine whether they shared sections of habitat or whether the habitat was partitioned into territories. The second objective was to test the prediction that the mating system exhibited by a species will predict the direction of any sex bias in philopatry (Greenwood 1980, Greenwood and Harvey 1982). Philopatric behaviour of successful and unsuccessful males was examined to explicitly test whether the sexual selection can influence the philopatric behaviour of an individual.

4.3 Methods

Study area and methods

This study was carried out between July 1994 and May 1997 in coastal southwestern British Columbia. The study site comprised of 5.5 km stretch of rocky shoreline bounded by mud flats. Mud flats are not used by Harlequin Ducks and effectively delimit the study area. Large boulders are scattered across the entire study site. Continuous access to the site is provided by a railway line on a 2-4 m high dike which is marked with mile markers every tenth of a mile (160 m).

In the late summer and fall of each year, flightless moulting Harlequin Ducks were captured for ringing. Researchers in sea kayaks rounded up the ducks and corralled them into a drive trap placed on the intertidal bench. All birds were sexed and aged by cloacal examination. Birds which still possessed a bursa of Fabricius were classified as young birds (either in their second or third calendar year, Peterson & Ellarson 1978). Each bird was marked with a standard U.S. Fish and Wildlife Service ring and a plastic tarsal ring engraved with a unique two-character alphanumeric code.

We attempted weekly surveys of this population of Harlequin Ducks. The numbers of each sex, the pairing status of the individuals and the location of the sighting (to the nearest 160 m) were recorded. Pairs were identified by synchronous behaviours and mate guarding by the male (Gowans et al. 1997). Harlequin Ducks frequently haul out onto rocks to rest and preen. At this time the tarsal rings can be deciphered, and as many rings as possible were read during each survey.

Male Harlequin Ducks began arriving at the study area in June and July and immediately began their pre-basic body moult (Robertson et al. 1997). They continued moulting and were flightless by early August. They finished their final moult (pre-alternate) by the end of September. Females began to arrive in August and early September, and were flightless during September (Robertson et al. 1997). Pair bond formation began in October, and most females were paired by December (Gowans et al. 1997).

Statistical analyses

To assess the movements of individuals within a non-breeding season a metric of site tenacity was needed. Complex home range estimators seemed unnecessary as our study area was linear. The variance in the sighting locations was used as a metric of within site movements. The variance was preferred over methods using the range of observations or quantiles of the range of sighting. Estimates of home range size based on ranges are highly influenced by extreme values, while the variances are not. Parametric comparison tests (t - tests) were used to compare the distribution of variances among groups because we wished to test for a difference between means and not for a difference between distributions (Stewart-Oaten 1995). An $\alpha = 0.10$ was used, to strike a better balance between Type I and Type II errors (Lebreton et al. 1992). Retrospective power analyses were not presented as we have no *a priori* expectation of what is a biologically meaningful difference in return rates. Furthermore our sample size could not be controlled for and was limited by the number of individuals we could catch and the size of our study population. Confidence intervals were presented where possible to allow readers to draw their own conclusions about the power of tests (Steidl et al. 1997). The repeatability of mean sighting location between years was calculated from equations in Lessells & Boag (1987).

Return rates are presented as the percentage of the marked sample that returned in the next year. Return rates presented in this study are a true return rate and are not confounded by the probability of detecting individuals (Pollock et al. 1990, Lebreton et al. 1992). The probability of detecting an individual at least once during the year approached 1.00 (G.J. Robertson unpubl. data), because of the high frequency of our visits to the study area and the regularity with which birds hauled out and their rings could be deciphered.

4.4. Results

Population structure

The numbers of males present at the study site was more variable from one survey to the next than the number of females (F ratio of Mean Squared Residuals from the cubic splines, $F_{172.9,175.3} = 3.11$, $P < 0.0001$) (Figure 4.1) Similar to previous analyses (Chapter 4) males began returning from the breeding grounds in June and July, females in August and September. The number of females at the study area peaked in September, possibly representing a population of females that moults at the study area and then departs. Large numbers of males were observed occasionally in April. This surplus of males were largely unpaired birds which did not moult at the study area (i.e. none were marked). Pairs departed for the breeding grounds beginning in April, and by mid-May most birds were gone.

Within-season movements

Before pair bond formation, males tended to be seen over a greater area than females (Table 4.1). Again, before pair bond formation, males that were eventually successful in obtaining a mate were seen over a larger area than males that did not subsequently find a mate only in 1995, there was no difference in 1994 and 1996 (Table 4.2). After pair bond formation, males that were unsuccessful in obtaining a mate were seen over a larger area than the paired males (Table 4.2). Males known to be paired in one year and unpaired in the next were used to test whether the difference in movement patterns between paired

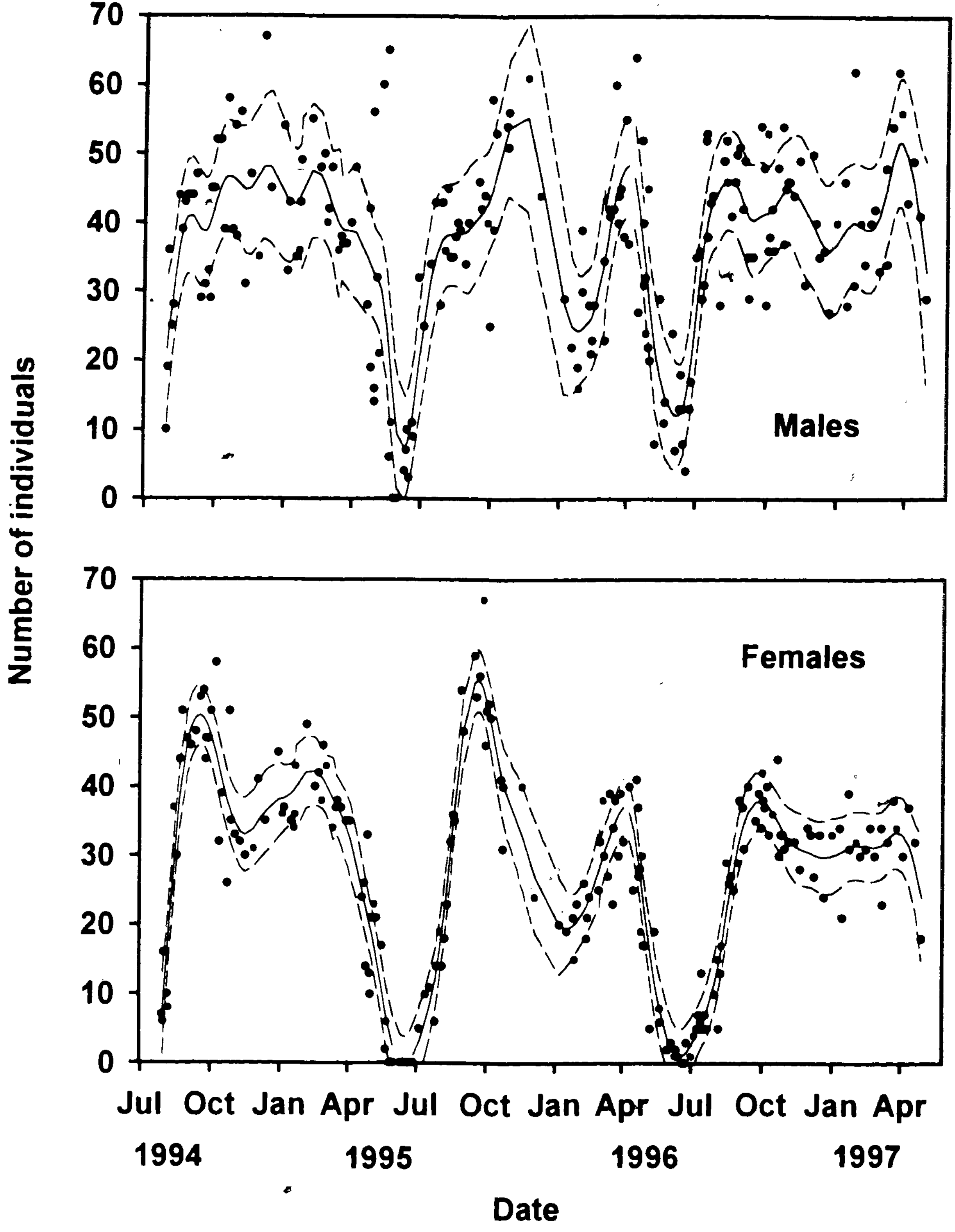

Figure 4.1. Numbers of male and female Harlequin Ducks present at White Rock, BC. Lines represent cubic smoothing splines and associated 95% confidence intervals.

Table 4.1. Mean variance (90% CL in parentheses km) in the locations where individually marked Harlequin Ducks were seen within the study area before pair formation occurs.

	Males		Females		*t*	*P*
	n		*n*			
1994	39	5.2 (0.0 - 17.2)	15	0.8 (0.0 - 3.6)	3.68[a]	0.0006*
1995	35	5.2 (0.0- 13.1)	35	0.9 (0.0 - 7.1)	3.27	0.0017*
1996	38	4.5 (0.0 - 10.4)	22	1.2 (0.0 - 3.5)	5.26[a]	0.0001*

* significant after sequential Bonferroni adjustment at $\alpha = 0.10$ (Rice 1989).

[a] t value adjusted for unequal variances between groups ($P < 0.0001$).

Table 4.2. Mean variance (90% confidence limits in parentheses, km) in the locations where individually marled male Harlequin Ducks were seen within the study area. Harlequin Ducks begin forming pair bonds at the beginning of October.

	Paired		Unpaired		*t*	*P*
	n		*n*			
Before Oct 1						
1994	18	6.5 (0.0 - 23.6)	7	3.5 (0.0 - 10.1)	1.18[a]	0.248
1995	19	6.4 (0.0 - 16.7)	7	2.4 (0.9 - 3.9)	3.10[a]	0.006*
1996	13	5.1 (0.0 - 13.9)	8	3.4 (0.0 - 9.9)	0.87	0.395
After Oct 1						
1994	21	2.2 (0.0 - 7.2)	7	6.2 (0.0 - 12.8)	3.23	0.003*
1995	22	3.8 (0.0 - 12.7)	5	7.4 (0.0 - 12.8)	1.75	0.091*
1996	16	3.1 (0.0 - 10.9)	9	9.5 (0.0 - 19.9)	3.20	0.004*

* significant after sequential Bonferroni adjustment at $\alpha = 0.10$ (Rice 1989).

[a] *t* value adjusted for significantly unequal variances between groups ($P < 0.026$).

and unpaired males was a result of a difference between the males in these two groups, or whether a males' success in finding a mate subsequently influenced his movement patterns. Individual males that were paired in one year and not paired in the next year were seen over a larger area in the next year (year paired: mean (90% C.I.), 2.6 (0 - 11.9), year not paired: 9.2 (0.1 to 18.3), $t = 2.43$, $P = 0.04$, $n = 5$).

Habitat use overlap

If individual males were defending territories one might expect that they would distribute themselves over the available habitat with little or no overlap The distribution of sightings for all paired males after 1 October are presented in Figure 4.2. Although males were segregated across the habitat, a number of males used any given section of shoreline. A further example of the movements of four paired males in the 1995-1996 winter season are presented in Figure 4.3. The overlap in the location of the sightings of these males is considerable. These four males were chosen because they had a large number of sightings (over 27) and they concentrated their activities in the middle of the study area.

Annual patterns of return: winter philopatry

No annual differences could be detected in return rates within each sex for 1995 and 1996 (Fisher's exact test, $P > 0.10$), so all data were pooled for these two years. Within the sexes there were no detectable difference in the propensity for the different age classes to return from one year to the next (males: young (2/4 or 50%), old (61/78 or 78.2%), Fisher's exact test, $P = 0.23$; females: young (10/16 or 62.5%), old (31/50 or 62.0%), Fisher's exact test, $P = 1.00$). Males (63/82 or 76.8%) tended to return to the study area, on an annual basis, with a greater frequency than females (41/66 or 62.1%) (Fisher's exact test, $P = 0.07$).

Paired males (37/43 or 86.1%) returned to the study area in the next year with the same frequency as unpaired males (10/15 or 66.7%) (Fisher's Exact test, $P = 0.13$). However, paired males stayed in the study area until the spring (36/37 or 97.3%) with greater

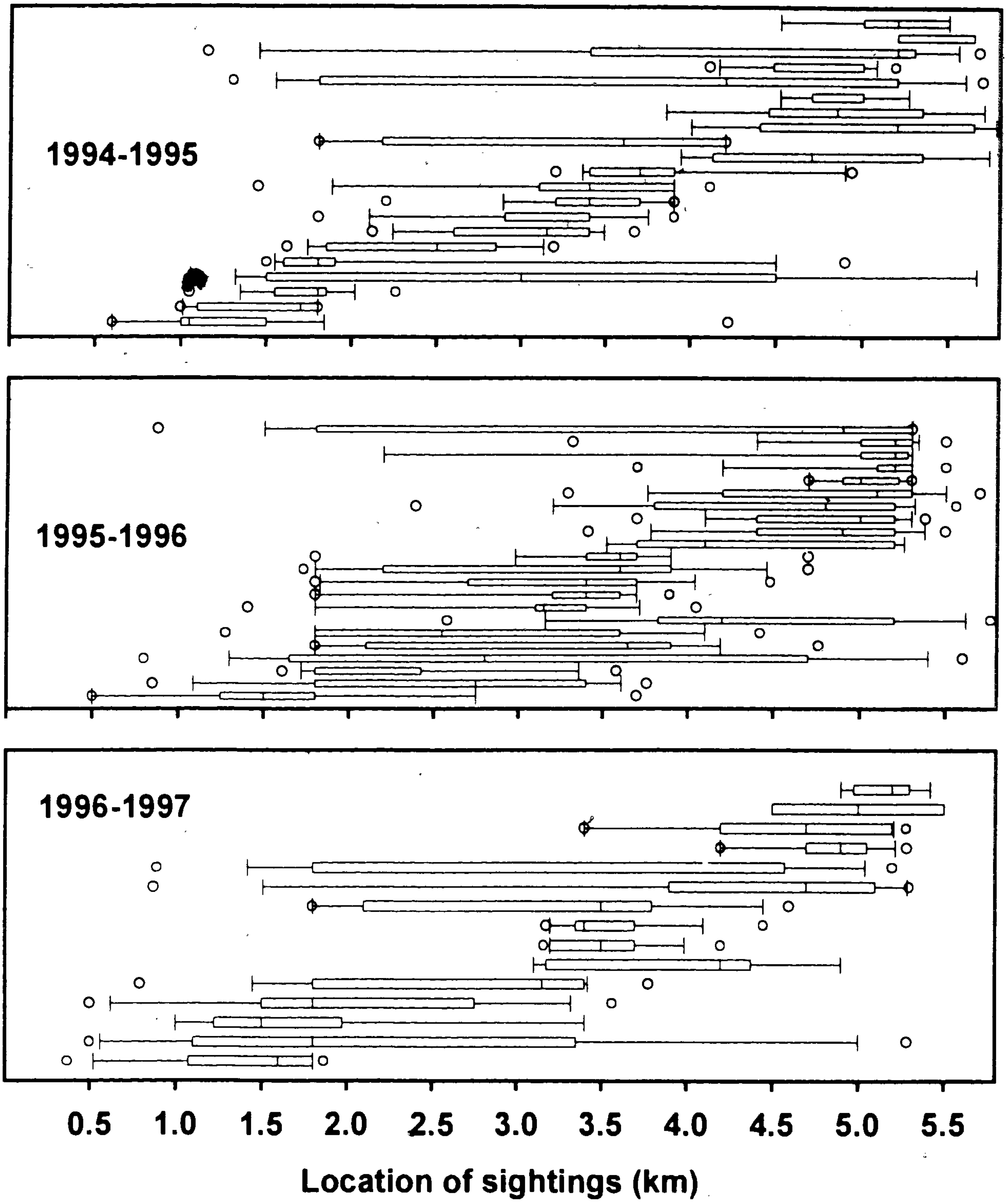

Figure 4.2. Sighting locations along a 5.5 km rocky shoreline for all paired male Harlequin Ducks from 1 Oct. until 1 June. Circles represent the 5th and 95th percentiles, outer box edges represent the 25th and 75th percentiles and the centre line in the box represents the median.

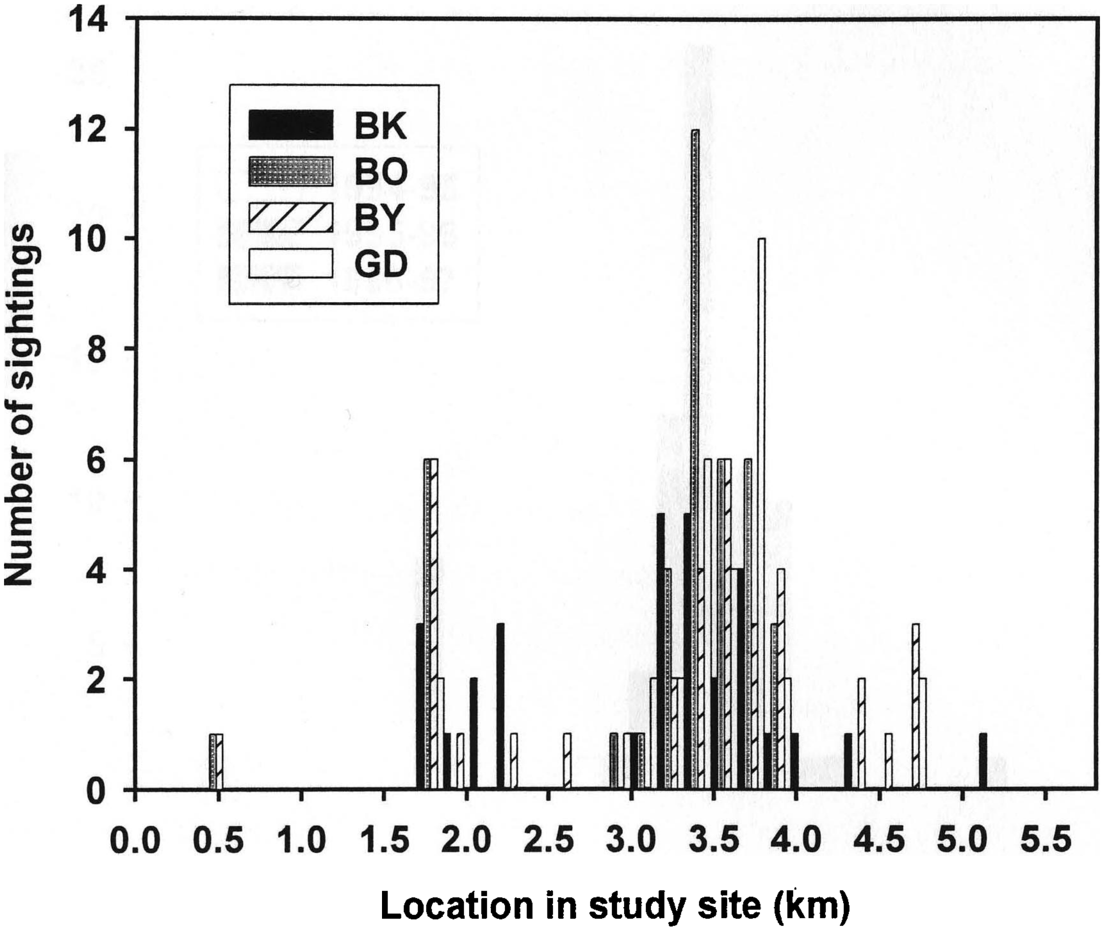

Figure 4.3. Sighting locations along a 5.5 km rocky shoreline for four male Harlequin Ducks from 1 June 1995 to 1 May 1996 at White Rock, BC.

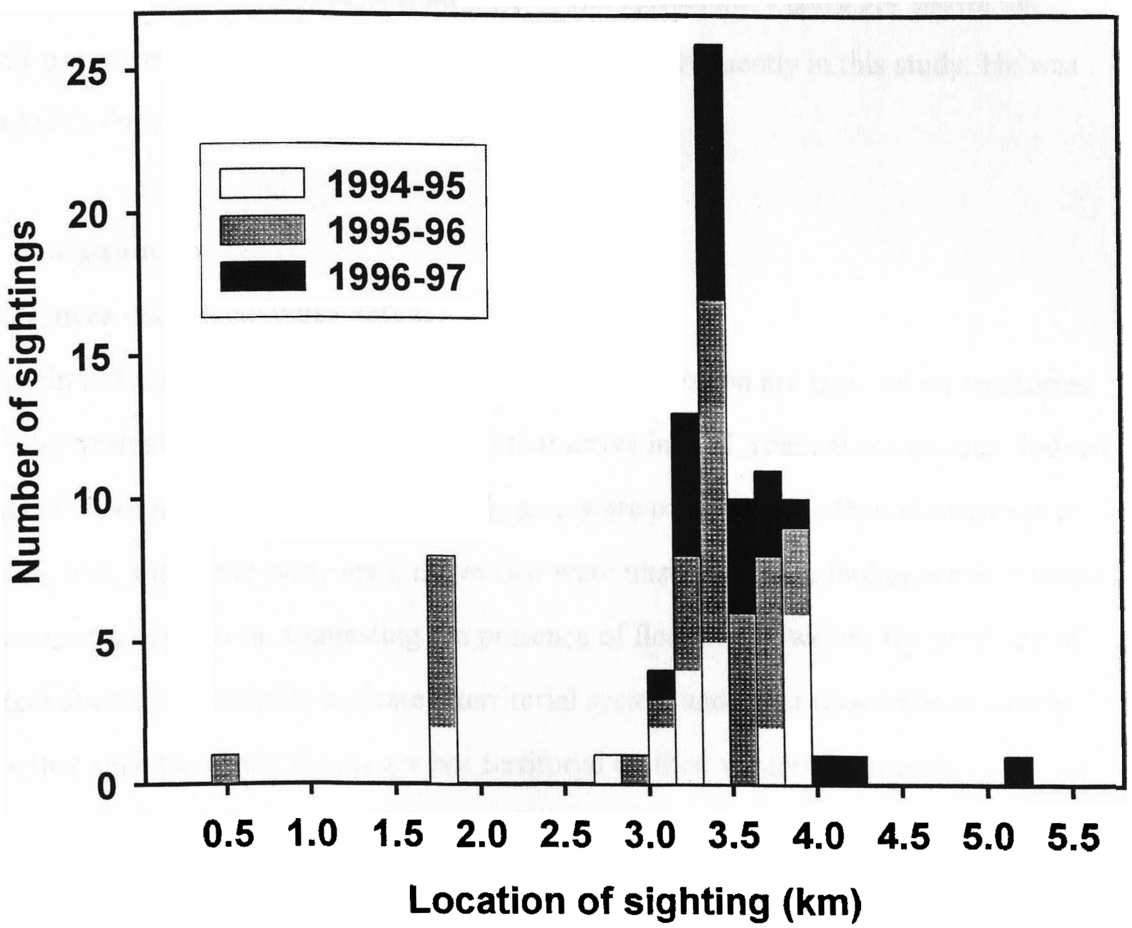

Figure 4.4. Sighting locations along a 5.5 km rocky shoreline for a male Harlequin Duck over the three years of the study.

propensity than the previously unpaired males (3/10 or 30%), seven of which left after they moulted in the fall (Fisher's exact test, $P = 0.0001$).

Individuals were not only philopatric to the study area but they tend to use the same section of shoreline within the study area as well. Repeatabilities for the annual mean location for each bird were all high, ranging from $r = 0.744$ to $r = 0.976$, ($P < 0.0001$ in all cases) for the two sexes, before, and after pair bond formation. Figure 5.4 shows the habitat use pattern for the male that was observed most frequently in this study. He was paired with the same female in all three years.

4.5. Discussion

Resource defense or mate defense

In certain territorial systems some of the males in a population are resident on territories and other males are floaters (Brown 1969) that arrive in, and, roam about an area. Indeed, the numbers of males observed at the study area were more variable than the number of females, and, within the study area, males that were unsuccessful in finding a mate were a seen across a larger area, suggesting the presence of floaters. However, the presence of floaters does not necessarily indicate a territorial system and other observations clearly show that male Harlequin Ducks are not territorial on their wintering grounds.

Before pair bond formation, all males exhibited similar patterns of movement, contrary to what would be expected if some male were territorial while others were floaters. However, it is possible that all males form territories before pair bond establishment, and males that are unsuccessful in attracting a mate become floaters and begin moving about the habitat. Alternatively, males may form territories just before pair bond formation begins. The observation that a number of paired males used the same sections of habitat is the most compelling evidence that males are not territorial. Thus, a basic condition for territoriality is not met, insofar as males are not excluding other males from a specific area

(Brown 1969). Although males may be avoiding each other on a temporal scale and the spatial overlap of habitat use occurs because the males are moving about the habitat, this behaviour is not strict territoriality. Furthermore, behavioural observations revealed that paired males were aggressive towards other males, only when unpaired males approached his female and began courting her (Gowans et al. 1997). This is consistent with mate guarding rather than territoriality. Aggressive behaviour between males along boundaries was never observed. In fact, males tend to be clumped into groups during the period before pair formation (Cooke et al. 1997) and very little agonistic behaviour is seen at this time (G. J. Robertson, unpubl. obs.). Observations of Harlequin Ducks suggest that they exhibit a mate-defense mating system and not a resource-based defense mating system, in contrast to the typical pattern birds.

Why are male Harlequin Ducks not territorial?

For a resource-defense based mating system to evolve the resource must be economically defensible (Brown 1964) and critical to the female's survival and/or reproduction (Emlen and Oring 1977). Costs of territorial behaviour increase with the number of competitors (Myers et al. 1979b). The relative benefits of territorial behaviour decrease if food in the territory is very sparse or of very low quality, or, if food is widely available for all individuals (Carpenter 1987). Harlequin Ducks forage for intertidal invertebrates by diving or by pecking them off rocks at the waterline (Goudie & Ankney 1986). For a sea duck species of their body size Harlequin Ducks spend comparatively little time foraging (Goudie & Ankney 1986), probably because they forage in shallow waters. Food may be widely and inexpensively available, so there may be no advantage to being territorial in this species. Large numbers of waterfowl, including other sea ducks with similar diets, winter in the general region of Boundary Bay that encompasses the study area (Savard 1988b). The cost of defending territories from conspecifics and other larger species may prove too great to make territoriality a viable option for Harlequin Ducks. Barrow's goldeneye

Bucephala islandica make an interesting comparison with Harlequin Ducks as they do form winter territories (Savard 1988a), utilize similar intertidal habitats, yet they are about twice the size of Harlequin Ducks. Female common goldeneye *B. clangula* are known to forage at very high rates in winter (Nilsson 1970), and males of this species have been shown to defend territories for short periods of time (Sayler & Afton 1981). Barrow's goldeneye may be able to economically defend territories in winter because the benefits for exclusive access to food resources are greater due to their requirement for more food and their large size and aggression enables them to defend their territories successfully against conspecific and interspecific rivals (Savard & Smith 1987). Whether winter territory formation is critical to mate acquisition and retention in Barrow's goldeneye has yet to be addressed and should prove to be an interesting research question.

Predation risk can also influence the economics of territory formation (Brown & Orians 1970). By spacing out, individuals lose the advantages of group living, such as increased group vigilance and flocking when predators approach (Rubenstein 1978, Pulliam & Caraco 1984). Flocking is an important anti-predator response of dabbling ducks and shorebirds. Sea ducks tend to dive in response to aerial predation threats, so flocking behaviour may not be as important for sea ducks. Adult sea ducks experience relatively high survival rates (Krementz et al. 1997), therefore predation is likely to be rare and we believe that energetic constraints, and not the costs of spacing out, limits the opportunities for territoriality in sea ducks.

Site fidelity and annual patterns of return

Our data suggest that Harlequin Ducks exhibit a mate-defense type mating system. Male Harlequin Ducks that are unsuccessful in obtaining a mate or lose their mates roam about the study area and join courting parties of bachelor males (Gowans et al. 1997). In mate-defense mating systems females tend to be more philopatric, as they are free to choose where they wish to be and presumably remaining in a familiar area has advantages

(Greenwood 1980). Within years, both sexes tend to remain faithful to specific stretches of coastal shoreline within regions of suitable marine habitat. The reason that males and females exhibit equally high levels of philopatry is probably related to the timing of pair formation and the fact that pairs tend to reunite year after year (Gowans et al. 1997). Pair bonds between reuniting pairs are formed in the early fall, generally in October (Chapter 2). Once the pair bond is re-established the movements of the male and female coincide. Assuming that the males' only concern is maintaining the pair bond, then the high within-season site fidelity exhibited by Harlequin Ducks is likely driven by advantages for site fidelity for the female. Knowledge of localized food resources is a likely reason why females exhibit strong site tenacity. Females may also remain at sites that experience low levels of disturbance from predators and offer good sites to haul out and preen. Conversely, dispersal is thought to be both risky and energetically expensive (Johnson & Gaines 1990). Unless food resources are severely depleted or predation pressure increases there are no reasons for females to move.

Similar reasoning could be applied to explain the annual philopatry exhibited by the females. Female Harlequin Ducks do show high levels of philopatry to their wintering grounds. Interestingly, however, male Harlequin Ducks are equally, and possibly more, likely to return to their non-breeding grounds than females. The difference between male and female return rates seen in this study is probably more a function of survival differences than levels of philopatry. Female ducks generally suffer higher mortality than males during the summer while they are incubating their clutches (Sargeant & Raveling 1992). For a long-lived species (Goudie et al. 1994) knowledge gained in one year at a wintering site could be used in subsequent years. Reproductive advantages of philopatric behaviour have been widely documented for breeding waterfowl (Dow & Fredga 1983, Hepp et al. 1987, Gauthier 1990 but see Hepp & Kennamer 1992, Cooch et al. 1993) and many other species as well (Pärt 1991, 1994).

It is tempting to suggest that males return to the same non-breeding ground year after year to reunite with the same female. However, males whose mate did not return in the fall and were subsequently unable to find a new mate in the following spring, still returned to the same non-breeding ground in the next year to moult. Many of the females have not even arrived at the non-breeding grounds during the moulting period of the males (Robertson et al. 1997). Males may be philopatric to the moulting grounds for reasons other than those related to pairing, i.e. knowledge of food resources and predator habits. However, if males do form dominance hierarchies amongst themselves during the moult, as we have suggested elsewhere (Cooke et al. 1997) then philopatry to the moulting grounds may have been sexually selected as well. These unpaired males departed after they moulted, presumably to search out a new mate. Failing to find a new mate in one year may be a cue for males to move and attempt to find a new mate at another site. The advantages of remaining at the same area were offset by the fact that male needed to find a new mate. Therefore, moulting site philopatry for male Harlequin Ducks may have a more ecological basis, while wintering site philopatry may be a function of the necessity of finding and retaining a mate.

In other species of birds, Greenwood's (1980) predictions are not always met. Male ruffs *Philomachus pugnax* show a high level of philopatry to their leks, this is not predicted for a system where males do not defend any resources. Widemo (1997) showed that the advantage of philopatry for male ruffs was to establish leks with known competitors. Intra-sexual aggression is reduced in leks with familiar rivals and females prefer these leks (Widemo 1997). Reynolds & Cooke (1988) found that adult male and female red-necked phalaropes *Phalaropus lobatus*, a polyandrous species, were equally likely to return to the breeding grounds. Females are not territorial in this species and compete for mates, males provide all of the incubating and brood care, therefore male-biased philopatry would be predicted in this system. Further benefits to the females for returning to the breeding grounds in this system must exist, such as experience with local home ranges to aid in mate competition (Reynolds & Cooke 1988). Although, Greenwood's (1980) general predictions about the direction of sex biases significantly advanced the field of social behaviour and spacing patterns, other aspects of the mating system can clearly modify these basic predictions (Oring & Lank 1984).

In ducks, where males abandon their mates and females incubate the clutch and raise the brood, males and females must be philopatric to the moulting, wintering or breeding grounds to be able to reunite (Savard 1985). Whether winter philopatry has directly evolved as a mechanism to allow pairs to reunite, or, pair reunion evolves after winter philopatry has evolved is not known. There is good evidence in waterfowl that pairs in long term bonds enjoy reproductive advantages over birds in new pair bonds (for examples see Black 1996). Philopatry to the non-breeding ground may have evolved in Harlequin Ducks to allow pairs to reunite and improve their reproductive output. However, the observation that widowed or divorced males still return to moult at the same location suggests that there are benefits to philopatry to the non-breeding grounds above and beyond reuniting with a mate. Females are likely philopatric to be able to return to familiar non-breeding habitats. Philopatry to the wintering grounds (Evans & Pienkowski 1984, Cuadrado et al. 1995) and migration stopovers (Cántos & Tellería 1994) have been seen in other bird species. Philopatry to these areas is related to the survival value of these sites and not to current reproduction and mating systems. The winter period is probably stressful for most bird species as day lengths are short, food is sparse and the weather is generally unfavourable. For species that pair during the winter both survival and pair bond establishment are likely to have influenced their life history strategies at this time of year. Therefore, both sexual and natural selection pressures account for the observed patterns of philopatry seen in these species.

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Chapter 5

The role of variable breeding success and dispersal on the population demography of Harlequin Ducks

5.1. Abstract

In many vertebrate populations the vital rates are not the same for all individuals (i.e. the population is structured). Matrix based population models are powerful tools in evaluating the population dynamics of these structured populations. The Harlequin Duck *Histrionicus histrionicus* is a long-lived sea duck that gains breeding experience as it matures. A four-stage (yearling, non-breeder, inexperienced and experienced breeder) projection matrix was constructed using estimates of vital rates from data on western North American populations. As shown previously for this species, proportional changes in adult survival (elasticity) had the greatest impact on the population growth rate compared to the other parameters. Breeding success and over-winter survival were modeled as stochastic elements in the matrix. As expected, variable vital rates reduced the realized population growth rate. However, the greater natural variation in breeding success compared to over-winter survival resulted in variable breeding success generating a larger decrease in the mean and greater increase in the variance of the realized population growth rate. Two populations, one stable and the other declining, that were connected by dispersal were modeled. An exchange of adults between the two populations had a larger effect on the populations than an equal exchange of juveniles. When connected populations had different survival rates they experienced lower growth rates than populations with the same survival rate.

5.2. Introduction

Matrix-based models are very useful for describing the dynamics of populations whose generations overlap (Caswell 1989). Survival and/or fertility schedules (collectively the vital rates) of individuals that vary with the individuals age (Leslie 1945, 1948) or stage (such as body size) (Lefkovitch 1965) can be modeled with matrix-based models. Important demographic parameters can be derived from matrices, such as population growth rate (λ), stable age (or stage) distribution, and reproductive value of each age or stage class (Caswell 1989, 1997). Furthermore, the sensitivity (or response to change) of the population growth rate to the elements (survival and fertility) of the matrix can be calculated, making it possible to identify the stages in the life history of species that most influence the population growth rate (Crouse et al. 1987).

Matrix-based population models for avian speciesare appearing in the literature (e.g. McDonald 1993, McDonald and Caswell 1993, Brault et al. 1994, Hitchcock & Gratto-Trevor 1997). To date, much of the emphasis has been on examining the sensitivity of the population growth rate to matrix elements so that probable causes of population decline can be identified. Most of these models have used deterministic matrices as it is simpler to extract information from a deterministic matrix than a matrix that contains stochastic elements. However, deterministic projections do not model the annual variation in the survival and productivity rates seen in many species. Monte Carlo simulation is a method to evaluate the influence of stochasticity in matrix element on the dynamics of a population (Tuljapurkar 1989). Although not as elegant as an analytical approach (which is not always possible), it provides easily understood results (Metz et al. 1992). Furthermore, the actual empirical distribution of stochastic parameters can be used in a numerical modeling approach instead of presumed statistical distributions that may not represent the true distribution of stochastic parameters.

Goudie et al. (1994) have already provided a preliminary matrix based population model for Harlequin Ducks *Histrionicus histrionicus*. The information available at that time for this species was relatively sparse, and most parameter estimates were obtained from a coastal breeding population in Iceland (Bengtson 1972). A purpose of this paper is to provide a matrix-based population model using information from western North America. Another purpose is to include more realisitic (and complex) components in the model such as, environmental stochasiticity in vital rates and population connectivity. Specifically, the objectives of this paper are to: 1) provide an updated matrix-based population model for Harlequin Ducks using new information for western North America, 2) calculate the population growth rate (λ), and examine the sensitivity and elasticity of the matrix elements in this deterministic matrix, 3) evaluate the demographic consequences of annual variation in breeding success and survival seen in Harlequin Ducks, and 4) evaluate the role of population connectivity via dispersal on the global dynamics of Harlequin Duck populations.

5.3 Methods

Sources of information

An attempt was made to gather current estimates for survival and productivity for Harlequin Ducks breeding in western North America. Ten years of productivity data were available for western Montana ranging from 1974 to 1996 (Reichel et al. 1997). Estimates for the proportion of young birds not attempting to breed and not breeding successfully were obtained from data on 76 young (two to four years old) females (Reichel et al. 1997). Survival data was gathered from two sources that used radio telemetry data. Daniel Esler, a Wildlife Research Biologist with the Alaska Science Centre, United States Geological Survey - Biological Resources Division, provided an over-winter (1 October 1995 to 16 February 1996) survival estimate of 0.876 (95% C.I., 0.797 - 0.956, n = 38) for females wintering in Prince William Sound, Alaska. Bruner (1997) estimated over-summer survival of females breeding in Oregon at 0.82 (95% C.I., 0.63-1.00, n=34). There were insufficient data in the literature to provide meaningful estimates for juvenile survival (from fall migration to their first summer) and breeding success of inexperienced breeders. For the purposes of this paper juvenile survival was estimated to be 0.67, a value reasonable for waterfowl (Johnson et al. 1992). Breeding success of inexperienced breeders was chosen to be 0.75 times the value for experienced breeders. In some species of waterfowl inexperienced breeders are not as successful as experienced birds, but the degree of the difference between the two groups is generally not known (Johnson et al 1992). This set of parameter estimates modeled a population with a growth rate of nearly 1.00, which is reasonable for a stable population.

Structure of the matrix

A four-stage Lefkovitch (1965) matrix was chosen as the basis for modeling the population demography of Harlequin Ducks. A stage-structure was chosen for two reasons. One is that it is difficult to obtain demographic data for each age class of long-lived species (e.g. Brault & Caswell 1993), and such information is not yet available for Harlequin Ducks. The other reason is that breeding experience may influence the vital rates more than chronological age, thus a stage-structure based on breeding experience may present a better representation of the population structure. Of course, breeding experience and age are correlated, therefore the stages chosen reflect a combination of ages and breeding experience. Four stages were identified: yearlings, females that have never attempted breeding, females that have attempted but not successfully bred, and, experienced breeding females. A pre-breeding season model was chosen to model this population. Pre-breeding matrices project the population vector from spring to spring (in the case of species breeding annually in the summer), unlike post-breeding matrices which project the population from fall to fall, just after the breeding season.

The first stage class in this matrix is yearling individuals just prior to the breeding season. Thus, the survival of juveniles during their first year is incorporated into the fertility row elements (the first row of the matrix) in a pre-breeding matrix. Adult survival is removed from the fertility elements in a pre-breeding matrix, a desirable situation as it simplifies the interpretation of sensitivities in the first row. The structure of the projection matrix **A** used was:

$$\mathbf{A} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & H_2 & G_3 & P_4 \end{bmatrix} \qquad [1]$$

see Brault & Caswell (1993) for a similarly structured matrix. Multiplying **A** by a vector containing the number of individuals in each stage class in the current year will give the a vector containing the number of individuals in each stage class in the next year. The life cycle diagram representing this matrix is presented in Figure 5.1. The fertility elements F represent the number of young females produced by each female in each stage. The survival elements include two components, the probability of surviving and remaining in a particular stage P, and the probability of surviving and moving into the next stage G and H. The matrix elements were calculated from the following expressions, which include fertility m, survival probability ϕ, and transition probability γ terms (Table 5.1):

$$\begin{aligned} F_2 &= m_2\gamma_{24}\phi_{juv}/2 \\ F_3 &= m_3\gamma_3\phi_{juv}/2 \\ F_4 &= m_4\gamma_4\phi_{juv}/2 \\ G_1 &= \phi_1 \\ P_2 &= \phi_2(1-\gamma_{23}-\gamma_{24}) \\ G_2 &= \phi_2\gamma_{23} \\ H_2 &= \phi_2\gamma_{24} \\ P_3 &= \phi_3(1-\gamma_3) \\ G_3 &= \phi_3\gamma_3 \\ P_4 &= \phi_4 \end{aligned} \qquad [2]$$

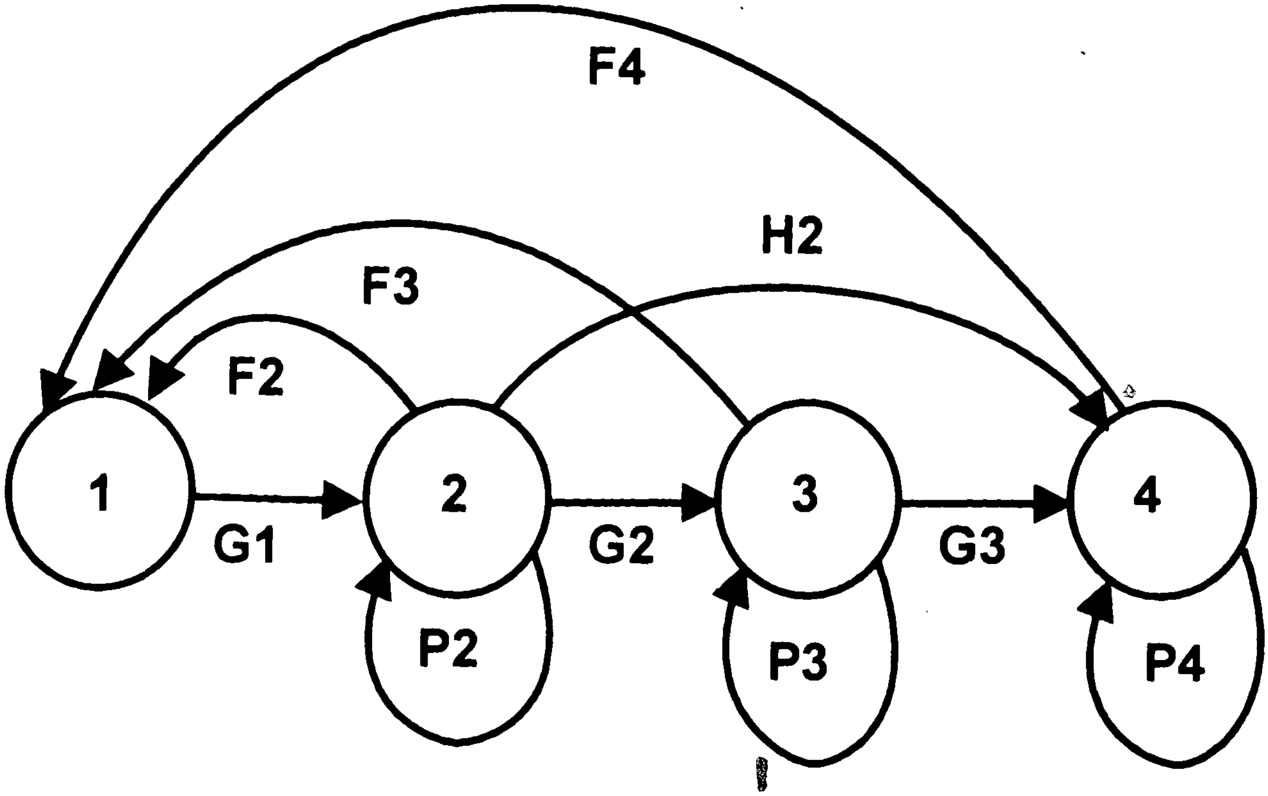

Figure 5.1. Life cycle diagram for Harlequin Ducks (1=yearlings, 2=never attempted breeding birds, 3=inexperienced breeders, 4=experienced breeders).

Table 5.1. Values used to construct a deterministic four-stage (i=stage) matrix based population model for Harlequin Ducks in western North America.

	Yearlings (i=1)	Never attempted breeding (i=2)	Inexperienced adults (i=3)	Experienced adults (i=4)	Source[a]
Number fledged per successful female (m_i)	0	0	3.64	3.64	1
Attempting and succeeding to breed (γ_i)	0	0.04[b] (γ_{24})	0.284[c]	0.378	1
Juvenile survival (ϕ_{juv})	0	0.67	0.67	0.67	2
Annual survival (ϕ_i)	0.876	0.876	0.718 (0.876*0.82)	0.718 (0.876*0.82)	3, 4

[a] Sources of information: (1) Reichel et al. (1997), (2) estimated from other values for waterfowl (Johnson et al. 1992), no data available for Harlequin Ducks, (3) Daniel Esler, unpublished data, (4) Bruner (1997).

[b] attempting and failing to breed ($\gamma_{23} = 27/76 = 0.355$), calculated as the number of young birds present on the breeding grounds, yet unsuccessful. Data from (1).

[c] estimated to be 0.75 of the value for experienced breeders, no data available for Harlequin Ducks.

The population growth rate (λ), the stable stage distribution (**w**) and reproductive value vector (**v**), and the sensitivity and elasticity matrix were calculated using standard equations provided in Caswell (1989). Lower level elasticities were also calculated, via the chain rule, to provide elasticities of elements that are present in more than one cell in the Lefkovitch matrix (e.g. breeding success appears in the fertility elements and the survival elements); these were also calculated following Caswell (1989).

Variable vital rates

A stochastic Monte Carlo simulation was performed to examine the role of variable breeding conditions on the population demography of Harlequin Ducks . Ten estimates for the numbers of young fledged and the breeding success were taken from Reichel et al. (1997) (Table 5.2). This distribution of estimates has a coefficient of variation of 0.608. A population of 10 individuals was projected over 100 years drawing randomly one of the ten estimates for the number of fledged young and breeding success values for each year (projecting the populations for 1000 years produced similar results). These 10 individuals were distributed in proportion to the stable age distribution of the deterministic matrix, the initial structure of the population should not influence the final outcome of the projection as many stochastic matrix projections are ergodic (Tuljapurkar 1997). Thus, the projection matrix $\mathbf{A}_t$ was drawn from a set of ten possible matrices A. In each year of the simulation the current population vector was multiplied by a projection matrix drawn from set A. A statistical distribution was not fitted with these estimates because with only 10 estimates it is difficult to clearly choose an appropriate ditribution. One thousand populations were simulated in this manner to obtain a distribution of final population sizes. A similar simulation was done with variable survival rates. Estimates for natural variation in annual survival rates were not available. Krementz et al. (1996) obtained an annual survival estimate for Common Eider *Somateria mollissima*, another seaduck species, of 0.873 with a 95% confidence interval spanning about 6%. This estimate of variation includes

Table 5.2. Annual productivity estimates for Harlequin Ducks nesting in western Montana. Data from Reichel et al. (1997, Table 6).

Year	Proportion of females successful	Number of young fledged per successful female
1974	0.27	4.00
1975	0.07	2.00
1989	0.54	5.86
1990	0.55	3.82
1991	0.24	3.44
1992	0.55	3.38
1993	0.43	2.81
1994	0.33	4.00
1995	0.23	3.82
1996	0.32	3.44
Mean	0.378	3.64

sampling variance and true biological annual variation, so it overestimates the magnitude of the true natural variation in annual survival rate. An approximate 95% confidence interval spanning 0.1 (or 10%) was used to model natural variation in survival, and likely represents an overestimate of the true natural variation. Thus, in the model runs over-winter survival was chosen from a normal distribution with a mean of 0.876, a standard deviation of 0.025 for a coefficient of variation of 0.0285.

An estimator of stochastic population growth rate ($\hat{a}$) was calculated directly from the distribution of projected population sizes after 100 years by

$$\hat{a} = \mathrm{E}\left(\frac{\ln N_t - \ln N_o}{t}\right) \qquad [3]$$

where E is the expectation (Caswell 1989). The central limit theorem ensures that $\hat{a}$ will approach a given sufficient samples. The stochastic population growth rate (a) is the leading Lyapunov exponent of the random matrix products generated from A and is a generalization of the dominant eigenvalue of a deterministic matrix. As such a essentially encapsulates the same information as λ_1 (Metz et al. 1992). Ln $\hat{a}$ is presented throughout to allow direct comparisons with λ. Stochastic sensitivities and elasticities (Tuljapurkar 1989) were not calculated as their deterministic equivalents tend to give the same qualitative results (Dixon et al. 1997).

Population connectivity

It is possible to model two or more populations simultaneously with matrix-based techniques by building large matrices containing the site-specific projection matrices and matrices containing the transition probabilities of moving between sites. The standard projection matrices are incorporated as sub-matrices along the main diagonal and the transitions sub-matrices are placed along the off diagonals. The population vector includes the number of individuals in all of the stages at the first site followed by the same distribution at the next site. An example with two age classes (juveniles and adults) with two sites is presented in [4].

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ \hline n_3(t+1) \\ n_4(t+1) \end{bmatrix} = \begin{bmatrix} F_1^1 & F_2^1 & 0 & 0 \\ S_1^1 & S_2^1 & M_{2\rightarrow 1} & M_{2\rightarrow 1} \\ 0 & 0 & F_1^2 & F_2^2 \\ M_{1\rightarrow 2} & M_{1\rightarrow 2} & S_1^2 & S_2^2 \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \\ \hline n_3(t) \\ n_4(t) \end{bmatrix} \qquad [4]$$

In this system, only adults move between sites, the M elements in the off diagonal submatrices n_1 and n_2 are the numbers of juveniles and adults in the first site, respectively, n_3 and n_4 are the numbers of juveniles and adults in the second site, respectively. This model assumes that the population is closed within these two sites; i.e. individuals do not leave for, or arrive from, other sites.

A two-site model was constructed to examine the role of dispersal in Harlequin Duck population dynamics. Daniel Esler (pers. comm.) provides an estimate of over-winter survival of 0.876 at a good site and 0.795 (95% C.I. 0.699 - 0.891, n = 46) at an oiled site in Prince William Sound, Alaska. Two different sites were modeled with these two different survival rates, and the rate of exchange between the two sites was varied to examine the effect of different dispersal rates on the global population growth rate of the two sites. Two different models were run, one where the dispersal was one-way only, from the stable (good) site to the declining (sink or oiled) site. The other run allowed for equal exchange rates of individuals between both sites.

Return rates of females to White Rock was 62% (Chapter 4). Assuming true survival to be 0.72 per year (0.876*0.82), then permanent emigration can be estimated as the difference between these two values, or 10% per year. This value was used in a stochastic projection of the same matrix used above with variable breeding conditions (Table 5.2) for each population. It was assumed that each wintering population experienced different subsequent breeding conditions, and exchange between the two populations occurred during the winter. The population was projected over 10 years (projections over 10 years produced large numbers of extinct populations) and this process was repeated 1000 times. To examine if models with wintering sites that differ in quality have different dynamics than populations with wintering sites with the same quality, another model was run that was structured as above. The survival rates at the two wintering grounds were the same, and represented the mean of the two survival rates used ((0.876+0.795)/2=0.8355).

All matrix manipulations, random number generations and populations projections were done using the IML (interactive matrix language) subroutine in SAS (SAS Institute Inc., 1990).

5.4. Results

The deterministic matrix

With the parameter esimates from Table 5.1. the following pre-breeding four-stage matrix was calculated

$$\mathbf{A} = \begin{bmatrix} 0.000 & 0.048 & 0.347 & 0.461 \\ 0.876 & 0.530 & 0.000 & 0.000 \\ 0.000 & 0.311 & 0.514 & 0.000 \\ 0.000 & 0.035 & 0.204 & 0.718 \end{bmatrix} \qquad [5]$$

This matrix has $\lambda = 1.00125$, with the following stable stage distribution and reproductive value vector

$$\mathbf{w} = \begin{bmatrix} 0.194 \\ 0.362 \\ 0.232 \\ 0.211 \end{bmatrix} \qquad \mathbf{v} = \begin{bmatrix} 1.000 \\ 1.142 \\ 1.394 \\ 1.629 \end{bmatrix} \qquad [6]$$

The sensitivity and elasticity matrices of **A** are

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \begin{bmatrix} - & 0.284 & 0.181 & 0.166 \\ 0.175 & 0.325 & - & - \\ - & 0.396 & 0.253 & - \\ - & 0.463 & 0.296 & 0.270 \end{bmatrix} \qquad [7]$$

$$e_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \frac{a_{ij}}{\lambda} = \begin{bmatrix} - & 0.014 & 0.063 & 0.076 \\ 0.153 & 0.172 & - & - \\ - & 0.123 & 0.130 & - \\ - & 0.016 & 0.060 & 0.194 \end{bmatrix} \qquad [8]$$

From [8] only 15.3% of the elasticity of lambda to the matrix elements are present in the fertility row, most of the elasticity, 84.7% is present in the survival elements. The lower level elasticities are presented in Table 5.3. Once again survival is more important than the fertility factors in determining the proportional change in λ.

Projection of a population in stochastic environments

Projecting the simulated population of 10 females for 100 years using the deterministic matrix **A** that contains the mean value for the number of young fledged and the breeding success from Table 5.2 results in a population of 11.209 females. The results from projecting this same population vector 100 years using a random sequence of matrices drawn from $A = \mathbf{A}_1 \ldots \mathbf{A}_{10}$ are presented in Figure 5.2. The mean of this distribution is only 9.707 (95% C.I. 1.099 - 36.029) females after 100 years, for a mean stochastic growth

Table 5.3. Lower level elasticities of the Harlequin Duck projection matrix.

Parameter	Elasticity
Survival of non-breeding young birds	0.3110
Survival of experienced adults	0.1936
Survival of inexperienced adults	0.1902
Survival of yearlings	0.1527
Survival of juveniles	0.1527
Number of young fledged	0.1527
Breeding success of adults	0.0694
Proportion of non-breeders attempting to breed	0.0222
Breeding success of first time breeders	0.0185

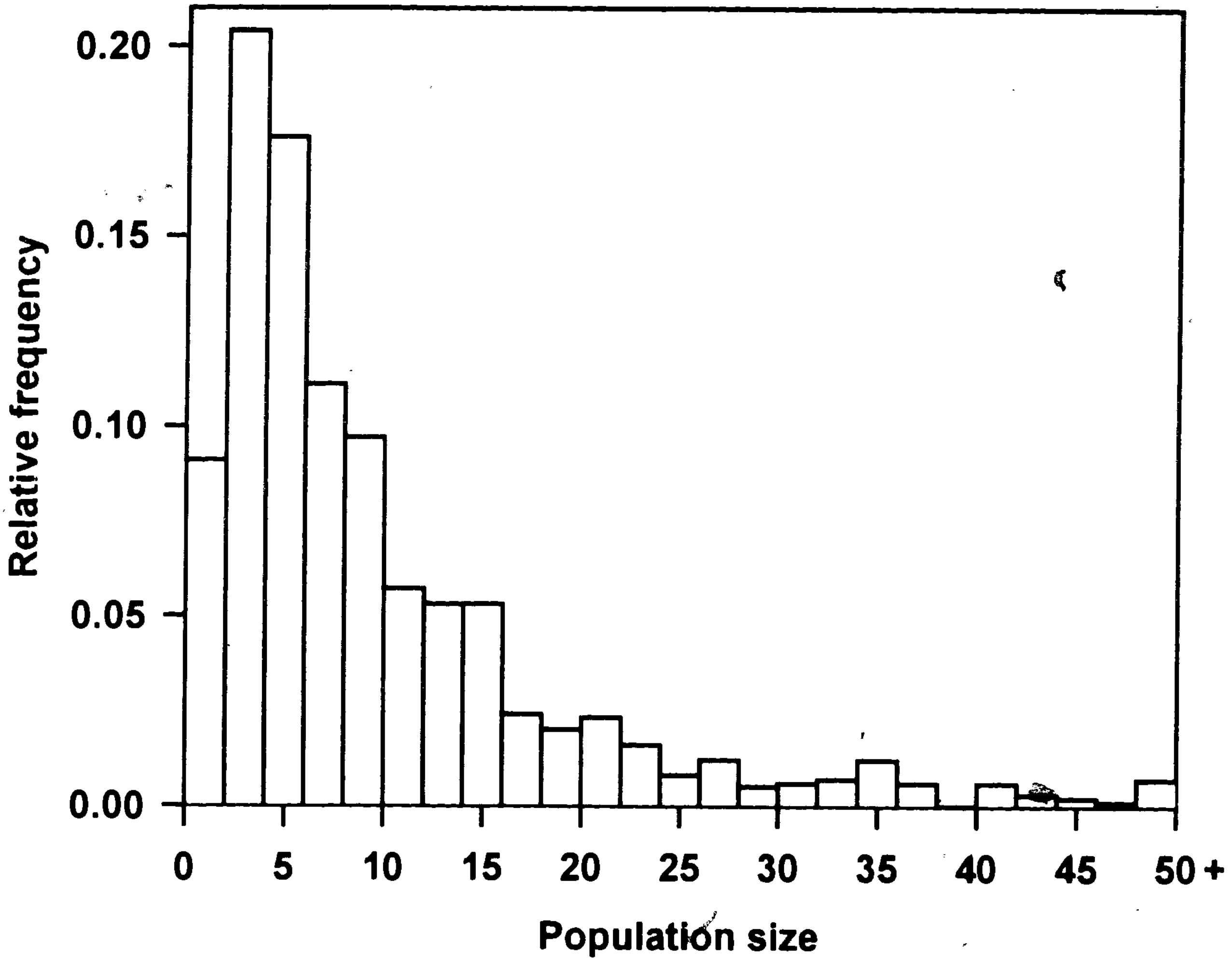

Figure 5.2. Distribution of population sizes after 100 years under variable breeding productivity conditions ($N_0 = 10$).

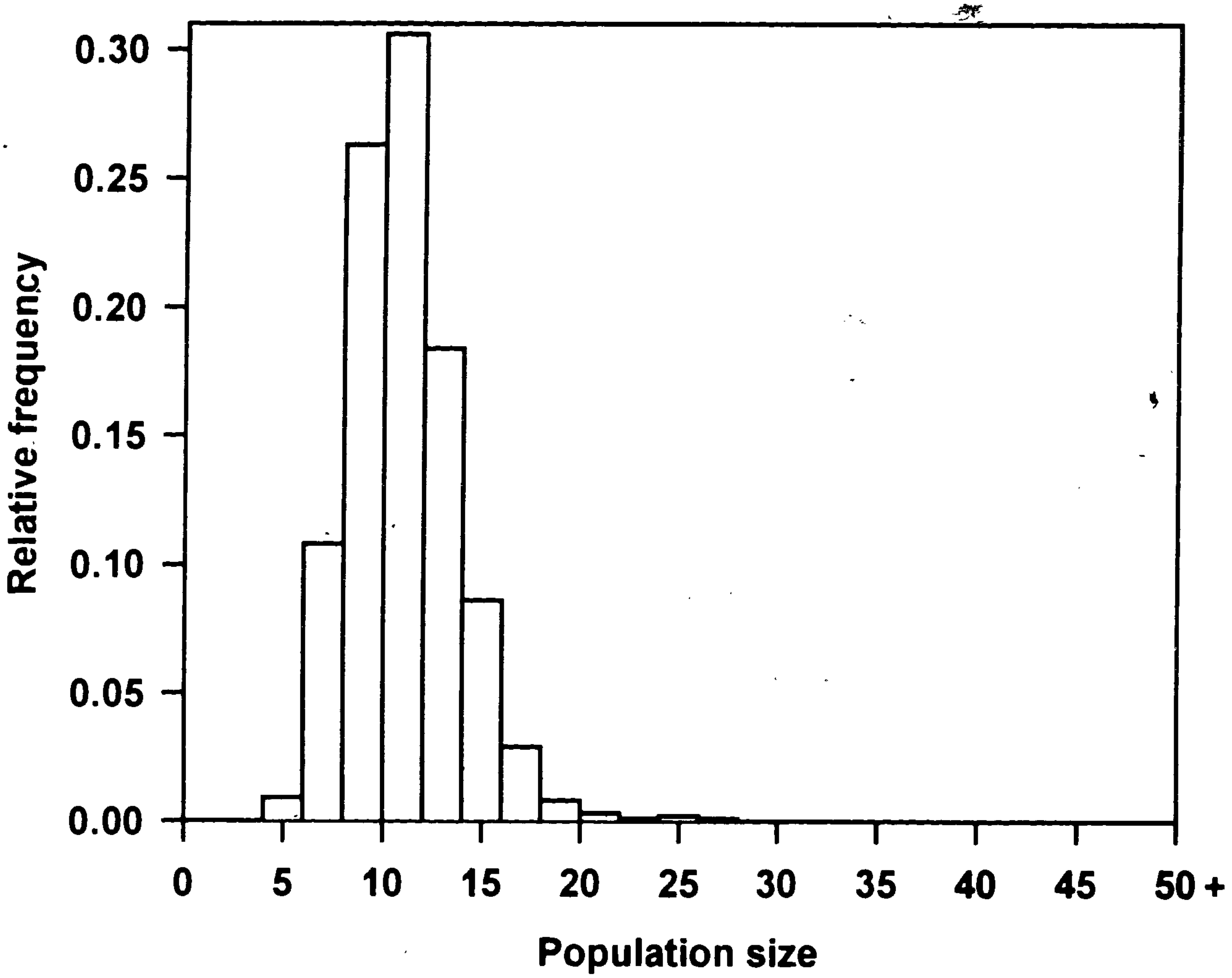

Figure 5.3. Distribution of population sizes after 100 years under variable wintering survival conditions ($N_0 = 10$).

rate $\ln \hat{a} = 0.9997$ (95% C.I. 0.9779 - 1.0130). This distribution is skewed right and the median is 6.500 females after 100 years, resulting in a median $\ln \hat{a} = 0.9957$. The probability of ultimate extinction is 1.00 for these populations because mean $\ln \hat{a} < 1.00$. The mean time to extinction for a population in this stochastic environment is 7674 ± 16252 SD years (equations in Caswell 1989).

The distribution of final population sizes after 100 years with variable over-winter survival rates are presented in Figure 5.3. This distribution had a mean of 11.035 (95% C.I. 6.694 - 17.290) females after 100 years, corresponding to a mean $\ln \hat{a} = 1.00123$ (95% C.I. 0.9960 - 1.0055). The median was 10.713 females after 100 years for a median $\ln \hat{a} = 1.0007$. The probability of extinction for an initial population size of 10 individuals is $3\mathrm{x}10^{-62}$, essentially nil.

Population connectivity in winter

Two populations modeled simultaneously with varying degrees of exchange between the two sites are presented in Figure 5.4. The exchange of adults has a greater effect on the population growth rate than an exchange of juveniles. One-way dispersal out of the sink reduces the population growth rate more than an equal exchange rate between populations. A one-way dispersal of adults into the sink of only 13% is sufficient for the sink population to entirely determine the dynamics of both populations.

The demographic effects on two connected populations in random environments is presented in Table 5.4. Population growth rates were lower when survival rates varied between sites (or within sites) compared to when they were constant with the same mean. Similar population growth rates were seen in all cases when survival was the same in the two sites. In the case where survival differed between sites, the population growth rate was reduced when a two-site model was used rather than in one-site modelwhich had a variable survival rate (Table 5.4)

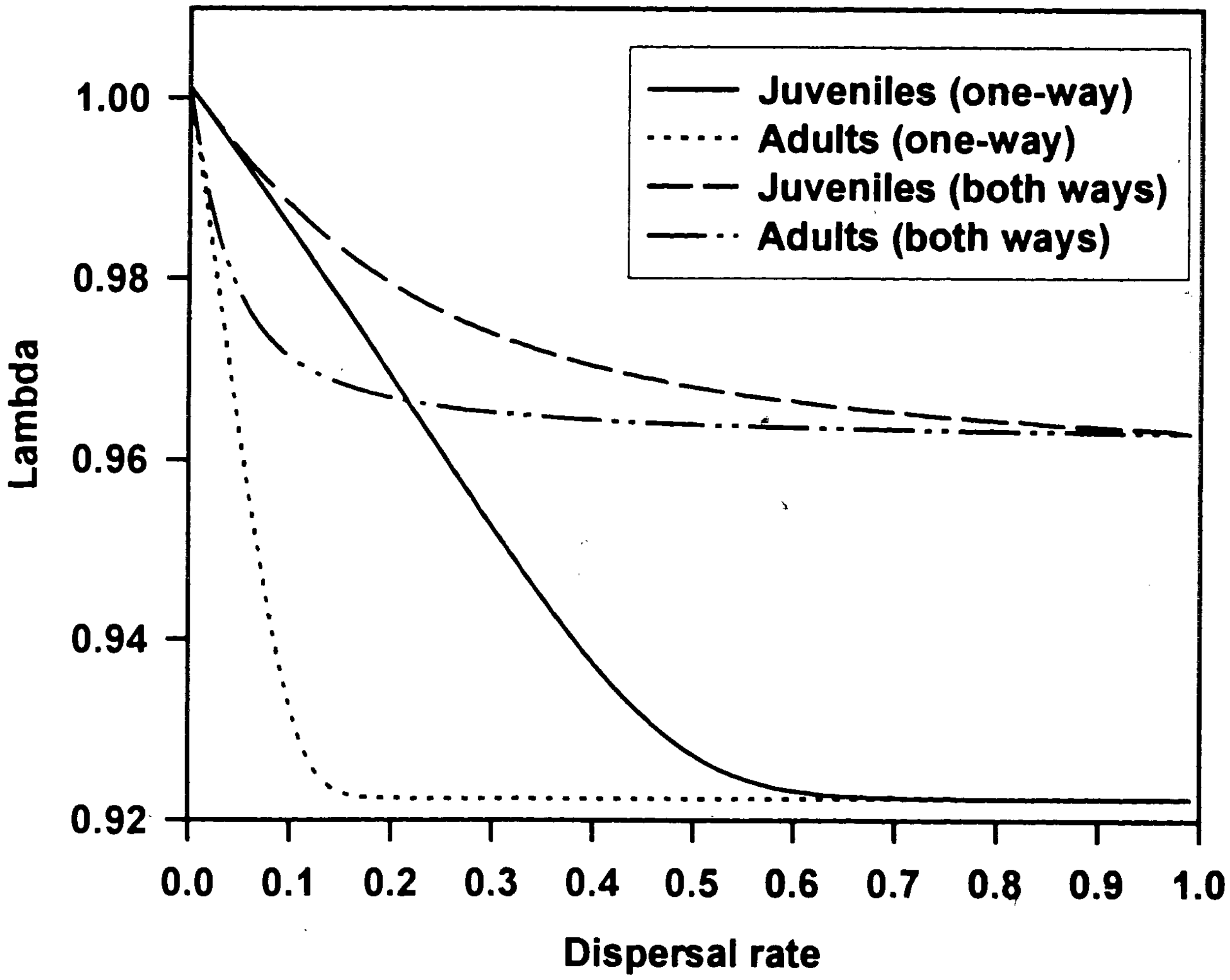

Figure 5.4. Global population growth rates under different rates of exchange of juveniles and adults between two populations. One-way denotes that individuals move out of the stable (λ = 1.0012) population into the sink (λ = 0.9224), both denotes that the exchange occurs both ways.

Table 5.4. Mean population growth rates of 1000 populations after projecting the population for 10 years ($N_0 = 20$). See text for descriptions of λ and $\ln \hat{a}$.

	Over-winter survival different (0.876 or 0.795)	Over-winter survival same (0.8355)
2 sites, breeding constant	$\lambda = 0.9258$	$\lambda = 0.9611$
2 sites, breeding variable	$\ln \hat{a} = 0.9197$	$\ln \hat{a} = 0.9596$
1 site, breeding variable	$\ln \hat{a} = 0.9591$[a]	$\ln \hat{a} = 0.9584$

[a] in this case over winter survival varies randomly as either 0.876 or 0.795 with equal probability

5.5 Discussion

Reliability of parameter estimates

One goal of modeling efforts is to identify parameters for which empirical estimates are not very accurate, or, not available at all. Estimates for survival rates and productivity rates are scarce for Harlequin Duck populations on the west coast of North America. Researchers outside of Montana have also obtained productivity data for a few years (Cassirer & Groves 1992, Hunt 1995, Smith 1996, McCallum 1997). Obtaining a ratio of the number of fledged ducklings per female present on the breeding grounds is reasonably straight forward for Harlequin Ducks. Populations can be surveyed on the breeding stream in the spring to determine the number of females present and surveys can be repeated in the fall to determine the number of fledged broods produced. However, determining why females are not successful in producing broods is much more difficult. Many sources of reproductive failure exist. Some females do not attempt nesting at all, others lose their clutch to predators, and some ducklings die during or after hatching. The influence of each of these sources of failure on productivity is unknown. The rates of reproductive failure may also vary among individuals that have different amounts of breeding experience. Generally, in waterfowl, young birds do not attempt breeding as frequently as adults and those that do so are less successful (see Johnson et al. 1992 for a review). An empirical estimate for the productivity of young females is not known relative to older, experienced birds. Estimating parameters for birds of different ages and experience, requires a marked sample of known-aged individuals. Efforts should be focused on estimating the breeding propensity and productivity of young known-age cohorts, whose breeding experience is known, so a better understanding is obtained. For example, a pure age-based model may better reflect the structure in this population than the stage-structure used in this paper.

Survival rate estimates have recently been obtained for Harlequin Ducks (Bengtson 1972, Cassirer & Groves 1992, Reichel et al. 1997). These were not used, however, as they confound the probability of seeing a marked bird with the probability of a bird surviving and returning to the same study site. Therefore, return rates always provide an underestimate of survival. For the model only survival rate estimates obtained from radio telemetry data were used. Currently, over-winter estimates are available for Alaska and over-summer survival rates are available for birds breeding in Oregon. Further, information from Alaska suggests that female survival may be even lower than the value used in the model. Esler (pers. comm.) estimated overwinter survival from 1 October 1996 to 31 March 1997 to be 0.819 (95% C.I. 0.721-0.916, $n = 43$). Using these lower estimates would produce a model projecting a rapidly declining population. One or more of the estimates used in constructing this current model must be biased, as Harleqiun Ducks populations may be declining, but certainly not rapidly. In fact, Harlequin Duck populations are growing (Esler, pers. comm.) or maintaining themsleves (Murphy et al. 1997) in Prince William Sound. Obviously, the model is not representing Harlequin Duck populations in Alaska very well. A likely source of the error may be from combining survival rates from different areas with productivity estimates from Montana. Clearly, it would be advantageous to obtain the breeding productivity and survival rate information from the same population to produce a more robust model for Harlequin Ducks. However, it should be noted that a site-specific model probably only applies to one site..

A further problem is the complete lack of any information on survival of juveniles and yearlings. In the model juvenile survival was simply a guess that appeared reasonable for waterfowl. Yearling survival was assumed to be the same as for older birds. Interpretations from the model may be suspect if the estimates for juvenile and yearling survival are very different from real values. A final untested, and, unlikely, assumption of the model was that birds that do not breed have an over-summer survival of 1.00. In fact, the survival of non-breeding birds may be even lower than breeders if there are quality differences between the breeding and non-breeding birds. The entire issue of covariance between vital rates was not introduced in this model as no data is available on this point. Anecdotal evidence does suggest that some females are consistently successful in producing broods from one year to the next while other females chronically fail (Harlequin Duck Working Group).

To obtain a demographic model for Harlequin Ducks that can be accepted with confidence, much more information is needed for young birds. Following a marked sample of juveniles followed through time would provide the necessary information.

Elasticity

The ability to extract sensitivities and elasticities from a projection matrix is one of the strengths of matrix based models. The elasticity is particularly useful as it provides the proportional change that a matrix element will make on the population growth rate (de Kroon et al. 1986). In other demographic models, the sensitivity of the parameters of interest to the overall growth rate are usually calculated by changing each of the parameter estimate a certain proportion (10% is commonly used) and calculating the proportional change in λ. There are some limitations to the use of elasticities because they represent the combined effect of the all the individual parameters that comprise a matrix cell. In simple models, cells are usually made of simple expressions, such as a survival rate or total number of eggs produced and surviving. In more complicated systems matrix elements may be complex equations of parameters that are dispersed throughout the matrix. In the Harlequin Duck matrix model, such a case occurs for breeding success as it appears in the expressions for both the fertility and survival elements. In these cases lower level elasticities can be calculated for each parameter to determine its individual effect on λ, although lower level elasticities do not reflect the proportional change in λ in the same way as standard elasticities.

In the model presented, survival rates had much higher elasticities than productivity rates. Therefore, given a similar proportional change in survival rates or productivity rates, a change in survival rates will result in a larger change in λ. This is not a surprising result and has been found for Harlequin Ducks before (Goudie et al. 1994). Among other avian populations, survival, especially of adults, is the most sensitive component of the life history (e.g. geese; Brault et al. 1994, Schmutz et al. 1997; owls; North 1985, Lande 1988, and raptors; Nichols et al. 1980). All of these are larger, and long-lived species of birds. These groups of birds generally experience variable breeding conditions so longevity has been proposed to have evolved as a mechanism for individuals to wait until a good breeding year. Changes in adult survival rate significantly alter the dynamics of populations of these species.

In the model constructed, survival of pre-breeding individuals had the largest impact on the population growth rate. This group of pre-breeders experiences a higher survival rate than the breeding groups in the model raising the elasticity of this stage class. Whether non-breeding individuals do experience a higher survival is not yet known for Harlequin Ducks, nor for many other species. It does raise a potentially interesting demographic consequence. The survival of the pool of non-breeders may be as important as the breeding population for ensuring the health of populations where individuals that do not breed experience a higher survival.

Stochastic breeding conditions

Stochasticity in vital rates are likely to occur for virtually all natural populations of organisms (Tuljapurkar 1989). The most obvious effect of introducing stochasticity into the model is that the population growth rate is lower than a population growth rate calculated from the mean of the stochastic elements in a deterministic model. This is a general result when the environmental variation in stochastic rates are not serially correlated (i.e. do not follow a Markov chain) and the magnitude of the variation is not unreasonably large (Tuljapurkar & Orzack 1980, Nations & Boyce 1997). Another effect of stochastic projections is that large fluctuations in vital rates further reduces the population growth rate.

In the Harlequin Duck model stochastic projections of simulated populations with varying fertility rates resulted in a declining population (on average). Over two-thirds of the simulated populations declined in size. The large variation in breeding conditions encountered by Harlequin Ducks are important in influencing the dynamics of local populations. Variable survival rates also reduced the mean population growth rate, but by very little and the population growth rate was still above 1.00. Although the variance in survival rate was deliberately chosen to be an overestimate of the likely natural variation in survival rate, this variation in survival rate did not cause a decline in the population growth rate nearly as great as that of varying the fertility rates.

In this case the perturbation analysis of sensitivities and elasticities appear to contradict the result of the stochastic projection of a population. The perturbation analysis suggests that survival is the most important parameter, affecting λ, while variation in fertility rates causes the greatest variance and reduction in population growth rate. Dixon et al. (1997), among others, have suggested that population modelers examine the sensitivity of their systems from a variety of approaches. In the case of the Harlequin Duck model this approach has proven valuable. If only the deterministic sensitivities and elasticities were examined then researchers and conservation biologists would correctly conclude that adult survival is the most sensitive vital rate influencing λ. An incorrect conclusion from the deterministic elasticity analysis is that variation in adult survival is currently having the most profound effects on Harlequin Duck population dynamics. From the stochastic projections it is clear that Harlequin Duck productivity is likely causing the variation in λ seen in different populations in different years. Therefore, to conserve Harlequin Duck populations high adult survival must be maintained. However, productivity is probably driving the current population dynamics of Harlequin Ducks, and efforts to reduce variation in productivity, without necessarily increasing the mean productivity, will increase the potential population growth rate of Harlequin Duck populations.

Connectivity and philopatry

Given equal rates of exchange between populations, movement of adults had a greater impact on the population growth rate than juveniles. This is a reasonable result as the reproductive value of adults is greater than that of juveniles [6]. In other words, when an adult moves into the poor quality habitat (a sink, Pulliam (1988)) the overall population growth rate is lowered more than if a juvenile moved into the sink. Relatively low levels of adult dispersal resulted in a population trajectory that follows the sink population trajectory and will lead to population extinction. The implication of this is that given a stable ($\lambda \approx 1.00$) and a declining population ($\lambda < 1.00$) movement of adults into the sink will eventually result in the extinction of both populations. Philopatric behaviour will speed the loss of populations in habitats that result in a $\lambda < 1.00$, but it will also protect healthy populations from going extinct by keeping some individuals in good quality habitat.

Compared to a system where two sites have the same survival rates, in systems where the vital rates differ, but have the same mean as the previous system, the population growth rate is reduced. In some senses, connectivity between populations that have different vital rates is similar to introducing stochasticity. Although the matrix is deterministic, a portion of individuals switch back and forth between high and low survival rates. A management application relevant to this finding is that given the choice between improving one habitat extensively or several habitats a small amount, it may be a better option to upgrade all habitats a smaller amount to maintain the same level of productivity in all habitats.

To conclude, although there are sufficient data available to construct a structured population model for Harlequin Ducks, the accuracy of many of the estimates used are not known. Further research needs to be carried out to obtain demographic information on young cohorts. Introducing stochasticity and population connectivity into models tends to reduce the population growth rate compared to using mean values. In systems with large variation in vital rates, such as Harlequin Duck productivity, ignoring this variation can lead to erroneous conclusions and to overestimate the growth rate of the population, a dangerous conclusion when dealing with threatened populations.

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Chapter 6

Conclusion

6.1. Introduction

The main advantage of writing a thesis in manuscript format is that each chapter is much closer to the style needed for publication in peer-reviewed journals. Peer-reviewed papers receive a much broader readership than theses and publishing a thesis as a series of papers ensures that the ideas and information reach a large audience. However, there are drawbacks to this style of thesis presentation. One of them is that some of the chapters may be written well before other sections of the thesis. For example, Chapter 3.3, was submitted for publication almost one and a half years ago, while other sections were completed within the last few months. As my colleagues and I have uncovered more about Harlequin Ducks our ideas and understanding are changing and becoming more integrative and sophisticated. In some cases, our interpretations of data in papers written at earlier stages have changed. A concluding chapter is valuable to for summarizing the current interpretations of the thesis as a whole.

This thesis, in some senses, is a summary of the ideas and information we have on the wintering life history of Harlequin Ducks as of the spring of 1997. As new ideas emerged over the course of this study, it was clear that new sources of data were necessary to answer new questions. It was impossible for me to pursue all of these new questions and to collect all of the data needed to test all of these new ideas. I decided to maintain my focus on the original question proposed for my thesis: can mating systems predict any sex bias in philopatry at a location other than the breeding ground? I also continued to collect the high quality resighting data needed to address this question. The next avenue of research that was needed to further our understanding was to collect rigourous behavioural observations to obtain a better understanding of the process of pair bond formation and the mating system. Therefore, other researchers were recruited into the Harlequin Duck project to attempt to broaden our understanding of the behavioural patterns and time budgets of these species in winter. Much of this new information has yet to be synthesized and when it is, it may alter our interpretations further, as our understanding broadens.

In this concluding chapter I will summarize my thesis in the context of our current thoughts. I will also outline areas where I have strong data to support hypotheses and the areas where the data is consistent with a number of hypotheses. Next, I will suggest future directions for research to further discriminate between some of the hypotheses that I cannot exclusively dismiss with the current data set. Finally, I present the conservation implications of the findings of the thesis.

6.2. General summary

The central aim of this thesis was to examine some of the factors that shape the patterns of winter philopatry in waterfowl with a focus on predicting sex-biases in philopatry rates from the mating systems (Greenwood 1980). Harlequin Ducks were chosen as the study species because they are a long-lived species that spend the winter along rocky coastlines, a relatively stable habitat (Palmer 1976). Species using stable habitats are expected to return year after year (Johnson & Gaines 1990).

To be able to predict what the sex-bias would be, a number of aspects of Harlequin Duck biology needed to be studied. First of all, it was necessary to determine when the ducks formed pair bonds. Sex-biases in philopatry based on a mating system can only be manifested at the time when individuals chose their mates. Harlequin Ducks form pair bonds early in the wintering season (Chapter 2), thus the wintering ground was the appropriate location to examine the possibility that the mating systems influenced philopatry. Harlequin Ducks formed pair bonds much earlier in the wintering season than others duck species with similar body sizes (Rohwer & Anderson 1988). Although many hypotheses exist to explain the timing of pair formation in waterfowl species, the trade-off between male costs and benefits, coupled with the benefit to females is the hypothesis currently favoured (Anderson et al. 1992). Harlequin Ducks dive for food at very shallow depths compared to many other sea duck species, and this may reduce the relative costs of foraging for this species. Furthermore, many Harlequin Ducks reunite with the same mate, possibly lowering the amount of energetically expensive courtship activity that male Harlequin Ducks must perform to obtain a mate. Although our sample size is small, young individuals pair in the spring, suggesting fundamental differences between the process of pair reunion and new pair bond formation. We do not have data to determine when experienced individuals that lose a mate form their next pair bond. Male Harlequin Ducks reuniting with previous mates may have lower energetic maintenance costs than other sea ducks species during the winter period, allowing them to devote the necessary energy to courtship and pair bond maintenance much earlier than other sea duck species. There may be female benefits for early pair reunion in this species as well, such as having a mate to guard them from other males. We were not able to explicitly assess the relative costs and benefits for pair bond formation and pair bond reunion for the two sexes. Once these costs and benefits are established, the selective forces that determine the timing of pairing can be identified. Furthermore, although different relative costs to males across species can explain the variation in the sparse data available for the timing of pairing in sea ducks species, other explanations, such as relative benefits to females and variation in population sex ratios cannot be ruled until more information is collected.

Since it was discovered that this species forms pair bonds early in the season compared to many other waterfowl species, the factor that limited the initiation of courtship and pair bond formation was explored. Waterfowl, like most bird species, undergo two body moults (a showy breeding plumage and a drab winter plumage), and one wing and tail feather moult every year. Birds renew their feathers through moulting to replace worn and abraded feathers. Most male ducks renew their old breeding plumage sometime after the breeding season (Hohman et al. 1992). Male Harlequin Ducks initiate moulting immediately, or soon after, they arrive at their coastal wintering grounds. They proceed through the entire moulting sequence, with no detectable breaks, until they have acquired a new breeding plumage about three months later. Males that are slow at completing this moulting sequence are at a disadvantage when attempting to find a mate in the fall. Males that have not completed their moult into a new breeding plumage do not engage in as much courtship activity as males that have completed the moult (Gowans et al. 1997). All of this information strongly suggests that male Harlequin Ducks are selected to find a mate as early as possible and the constraint that prevents them forming pair bonds before October is that they must first compete their moult into the breeding plumage. Hypothetically, ancestral male Harlequin Ducks that moulted early would have been selected for, and now all males initiate moult soon after arriving. This directional selection would effectively remove most of the variation for genes that code for the timing of moult in males, and the remaining alleles would code for moulting as soon as possible upon returning from the breeding grounds. The actual timing of the moult would not necessarily provide the female with any information about the quality of the male. Indeed, males that obtained a mate did not moult earlier than males that did not obtain a mate. Directional selection for males to moult quickly would also occur but variation in the phenotypic expression of the moult speed would remain as males in different phenotypic condition would moult at different speeds. This phenotypic variation could have a genetic or environmental basis. Therefore, unlike the timing of the moult, which indicates the seasonal chronology of the breeding area a male went to, moult speed could be correlated with male condition and vigour. Thus, moult speed could be an honest signal of male quality and selected for, used either by males to assess each other or by females to assess the males. Moult speed itself may not be selected for directly, yet may be correlated with another trait that does influence mating success. Since females are not present in great numbers at the study area when males are moulting it is more likely that males are signaling their quality, via the speed of their moult or another correlated trait, to each other. The white tertial feather badge shown by the males at this time may be used as a signal to other males of their quality. Males that do not acquire this badge, such as some first year males, will not be successful in obtaining a mate. Whether or not this white tertial feather badge is used to show the speed of moult to other males is not known Ultimately, however, the initiation of pairing is restricted to when the males have completed their body feather moult and this plumage signal is fully displayed.

Once the location and timing of pair formation was known it was possible to assess the mating system. Evidence for territoriality was not found. True territoriality only occurs when individuals are able to aggressively defend a section of habitat to the exclusion of all other conspecific or intraspecific rivals (Brown 1964, 1969). Harlequin Duck males defended their mates from other male rivals (Gowans et al. 1997), but not along specific boundaries of shoreline. Even though males showed site tenacity to certain sections of shoreline, individuals males did not have exclusive access to sections of shoreline. Males defended a mobile area around their mate instead. Thus, it was concluded that male Harlequin Ducks were displaying a mate defense mating system. Mate defense mating systems occur when males are not able to defend a specific resource needed by females (Emlen & Oring 1977). Females are free to move about suitable habitat and males must roam across the habitat to find these females. Since females were free to select their preferred location it was assumed that females would show a certain degree of philopatry to good patches of habitat. Males would be forced to move about to find these females and a female-biased philopatry would be expected (Greenwood 1980, Greenwood & Harvey 1982). Within each season, females remained at smaller areas within the study site than males, significantly so in one year. Additionally, unpaired males were seen at a greater variety of sites than paired males. Apparently, females do prefer to remain in small areas and males are more dispersive when they are not paired with a females. Our measure of annual philopatry could not control for differences in the survival rate of the two species and may mask a small sex bias in philopatry. However, it is clear from our data that both sexes of Harlequin Ducks exhibited high levels of philopatry to the location of pair formation. Sex-biases in philopatry would be predicted only when the costs and benefits of dispersal are different for each sex. For male Harlequin Ducks the cost of dispersal (increased risk of mortality by moving into unfamiliar areas) may not outweigh the benefits of dispersal (the increased probability of finding an unpaired female). For a long-lived species like the Harlequin Duck, males might not want to take the risk associated with dispersal and may choose to remain in a familiar area, at the cost of not obtaining a mate. Furthermore, for many males, philopatric behaviour will ensure that they will re-unite with a previous mate, if she is alive. Females always formed pair bonds with previous partners if they were present (Chapter 2). In this case, males would not be selected to be dispersive at all, but rather attempt to return to the same wintering grounds to determine if his mate was still alive and reunite with her.

A further evaluation of pairs forming new pair bonds is necessary to determine the impact of pair reunion on the patterns of sex-bias philopatry. As pointed out in Chapter 1, for species which exhibit long term pair bonds, it will only be in new pair bonds that any evidence of a sex bias in philopatry be shown. Unfortunately, our sample of young individuals is too small to assess the relative levels of philopatry in birds forming new pair bonds. Males that are unsuccessful in finding a mate do leave the area after they have moulted, a result in line with the predictions of a mate defense mating system. Even if it is determined that there is female-biased philopatry among birds forming new pair bonds, pair reunion has led to selection for high male philopatry.

Much needs to be known about the life history of a species to understand its philopatric behaviour. All of the needs of the species in the particular habitat they are occupying will influence whether the species will be philopatric. If the species is forming pair bonds in a particular location, then a thorough understanding of the mating system is essential. The requirments of young and old birds are not necessarily the same. In many cases philopatric behaviour may differ among age classes or among individuals with different levels of experience. Species which occupy stable habitats may tend to be philopatric, regardless of the mating system. Strong sexual selection will increase the benefits to males for seeking mating opportunities, whether this leads to male dispersal or philopatry depends on the life history of the species. If researchers have only a vague understanding of the life history of a species, they run the risk of misinterpreting why predictions about philopatric behaviour have failed, or worse, have been met, but for the wrong reason. Long-term studies with marked individuals is a very effective way to obtain this knowledge.

6.3. Future directions

In many ways this thesis is an initial attempt to answer some fundamental questions about the life history of a wintering waterfowl species. As clearly shown in Chapter 1, data on winter philopatry for most waterfowl species is of very poor quality. The importance and general applicability of the hypotheses and mechanisms outlined in Chapter 1 cannot be evaluated until much more data are collected for homing rates in the waterfowl species. Information on the timing of pairing for the sea ducks is also very sparse and unknown in many other waterfowl groups. Once again, much more information is needed on the timing of pairing and the frequency of pair reunion in all waterfowl species before the factors that modify the timing of pairing across species can be identified. It is still unclear whether males costs or female benefits are important in influencing the timing of pairing. As the costs and benefits for the timing of pairing will differ for the two sexes and change depending on when other individuals pair in the population, modeling efforts in a frequency dependent (or ESS) framework may provide further insights into how the timing of pairing is determined. This framework need not be restricted to waterfowl, an exploration of philopatry and the timing of pairing in other species, such as loons and grebes, may add insights as to which factors are important in influencing these traits.

Although we have learned much about the Harlequin Duck in the last 4 years, there is still much more that we need to know. The largest gap in our knowledge is the behaviour and dispersal patterns of young individuals. As mentioned previously, in species that form long-term pair bonds the mating system will only influence the dispersal patterns of birds forming new pair bond. Many of the birds forming new pair bonds will be the younger cohorts. Furthermore, it appears that young birds pair later in the season but the sample size is low. The true timing of new pair formation in Harlequin Ducks is likely to be in the spring, with more information for young birds it will be possible to determine the timing of new pair formation for this group. The importance of experience in pair bond formation is also not yet known. If there is difference in the timing of pair formation between older birds that have lost their mate and young birds then experience is likely to be influencing the timing of pair formation. A rigourous behavioural assessment of the costs and benefits to males and females of being paired should reveal which of these factors is important.

How juveniles incorporate into winter flocks is key to understanding the structure waterfowl populations. Preliminary evidence suggests that in some cases the female parent will bring her offspring to her wintering grounds (F. Cooke, pers. obs.). A quantification of the proportion of both sexes of juveniles that remain at their mother's wintering site will provide a valuable insight into the population structure, and how this population structure is maintained for this species.

The role and quantification of habitat stability is another research direction. A premise of this thesis is that Harlequin Ducks use stable wintering habitat and territorial behaviour could be a feasible option for this species. However, a quantification of the stability of this habitat was not done. A rigourous assessment of the food source available for this species and the variation and predictability of this variation in the food source will give an assessment of the stability of this habitat. Whether habitat stability influences the patterns of philopatry seen across all waterfowl species could be examined once the stability of the habitats used by each species is known.

There are a variety of interesting and diverse research directions that are possible with the waterfowl taxa, generally, and with Harlequin Ducks, specifically. This thesis has attempted to address only a small portion of all of these options, and hopefully points the way to future work.

6.4. Conservation implications

As stated in Chapter 1, the secondary objective of this thesis is to provide some useful information to wildlife managers and conservation biologists about the moulting and wintering ecology of Harlequin Ducks. Precipitous declines of Harlequin Ducks in eastern North America to between 1000 and 2000 individuals has led to a major effort to understand and restore this population. The most important effort was to list the Harlequin Duck endangered on the east coast (Goudie 1991). There is also concern about the Harlequin Duck on the west coast. A major goal of work on the west coast of North America is to obtain good empirical data about their life history, which could be used in the conservation effort in eastern North America. Although the population is much larger, it appears to be declining, similar to many other sea duck populations on the west coast of North America (Goudie et al. 1994). As the west coast continues to be developed and human populations increase, further disturbances and alterations of Harlequin Duck habitat are expected. Although hunting pressure, the main reason for the east coast population decline, is not expected to increase (and will probably decrease in the future) other problems may arise for this species. Chronic disturbance from human activities and habitat alteration or destruction (via development and/or pollution) will be the future threats to Harlequin Duck populations.

When populations decline, the breeding grounds are generally suspected of causing the problem. However, the wintering grounds clearly play an important role as well in the survival of a species and its populations. This shift in concern from the breeding to the wintering grounds is obvious in the research on Neotropical migrant passerines (Rappole 1995). For Harlequin Ducks the moulting and wintering period are particularly important for several reasons. Firstly, moulting and wintering grounds overlap, therefore impacts on wintering sites will also influence the ability of the ducks to moult. Secondly, male Harlequin Ducks spend only six weeks away from the wintering grounds, females spend about three months away, therefore the bulk of the life of a Harlequin Duck is spent on its wintering grounds. Thirdly, the coastal habitats used by Harlequin Ducks are also used for a variety of purposes by humans. Fourthly, unlike many other species, some important life history events of ducks take place during the winter, such as pair bond formation (Anderson et al. 1992) and accumulation of nutrients that will be used in clutch formation (Alisauskas & Ankney 1992). Finally, the legal hunting season occurs during the winter period.

Knowledge of the timing of pair formation and moult may not seem particularly relevant in trying to develop a management plan for a species, but in reality this information leads to a broad conclusion about the importance of the moulting and wintering grounds. The conclusion is that the moulting and wintering sites for Harlequin Ducks cannot be viewed as an area where they are simply waiting out the winter until the important breeding season. Simply ensuring the survival of these wintering populations is insufficient. Harlequin Ducks are under selection pressure all year long to move through their life history stages as quickly as possible. Males moult as soon, and, as fast, as they can, begin courting and pairing as early as possible, vigorously defend their mate all winter long and migrate to a breeding location. Although it is not been empirically shown for Harlequin Ducks, for birds in general, early breeding individuals enjoy a higher reproductive output than inexperienced breeders (Rohwer 1992). Impacts on the wintering grounds, such as disturbance or habitat alteration may have profound effects by delaying life history steps. By delaying one step, further steps may be delayed and ultimately reproductive output may be lowered. Harlequin Ducks are very sensitive to their body condition and foraging conditions before breeding, and will not breed if they are in poor body condition (Bengtson & Ulfstrand 1971). Any effect that may reduce the body condition of the female may reduce the possibility that she will breed. Therefore, a reduction in food quality and/or intake rates because wintering habitat is degraded or disturbed may have significant effects on populations, These impacts will not be immediately obvious as a dramatic population decline, and may continue for years before being detected.

The importance of philopatry on the population dynamics of a species is well known and has obvious impacts on the conservation of a species. In general, complete philopatry results in small populations existing in a fragmented (natural or artificial) landscape (Gilpin & Hanski 1991). In this case, small populations persist according to their own vital rates. Small, isolated, populations are prone to extinction through demographic stochasticity (Foley 1997). If populations are connected through some level of dispersal, a type of metapopulation results (Hanski & Simberloff 1997). If dispersal rates are low, sub-populations tend to follow their own trajectories, with some impact of immigration and emigration. If dispersal rates are high the sub-populations tend to behave more as a single population (Harrison 1994).

Some of the demographic consequences of philopatric behaviour, specific to Harlequin Ducks were examined in Chapter 5. An interesting result is that when two populations of equal size are connected, one that is maintaining itself and another that is declining, a relatively low level of dispersal between the sites will result in the population of both sites declining at the same rate as the population in the poor quality site. The implication of this result is that for a source-sink dynamic to maintain itself, the source population must be growing at a significant rate, or the source population must be significantly larger than the sink population. Populations that are maintaining themselves are likely to be common and they will suffer if they are connected to a sink. In this case small healthy populations must be protected, and unless true source population exist, sinks should be left alone to go to extinction instead of trying to increase population connectivity. Of course, and this point cannot be stressed enough, these interpretations are based on the parameter estimates that are currently available and as pointed out in detail in Chapter 5, estimates for some parameters are not yet available or are based on small sample sizes.

Stochasticity in vital rates reduces the realized population growth rate. Models that do not include stochastic elements will predict population growth rates that are biased high and should be interpreted with caution. Highly variable breeding conditions due to weather fluctuations and food availability are the norm for Harlequin Duck populations (Bengtson 1972, Reichel et al. 1997) and, as such, will need to be considered in further modeling attempts. The degree to which breeding and wintering populations are connected to each other via dispersal and the differences in vital rates between these populations will also need to be estimated in future field work of Harlequin Ducks. Estimating means for vital rates and dispersal rates are no longer sufficient, the variability in these elements also influences the populations dynamics and need to be incorporated in future modeling efforts.

The moulting and wintering periods are important in the life history of Harlequin Ducks. Harlequin Ducks must not only survive the winter, but perform a number of other life history events as well. Disruptions or delays at any one of these stages may reduce the productivity of the population. Philopatric behaviour tends to reduce the contact of populations and makes them susceptible to extinction. However, philopatric behaviour also ensures that individuals in good habitats do not move to poor quality habitats.

To ensure that healthy populations of Harlequin Ducks are maintained in the future adult survival must remain high. Protection on both the wintering and breeding grounds is essential. The impacts of habitat alteration and human disturbance on the wintering and breeding grounds needs to be quantified and efforts should be made to mitigate impacts that have serious deleterious effects. Since Harlequin Ducks are philopatric, preferred habitat must be conserved. Individuals that lose a preferred section of habitat will lose the benefits they have gained from having intimate knowledge of the local area. Environmental policies that call for the destruction of preferred habitat and then a subsequent habitat restoration effort are not likely to be successful in maintaining Harlequin Duck populations.

6.5. References

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