FACTORS INFLUENCING BREEDING DISTRIBUTIONS OF HARLEQUIN DUCKS *Histrionicus histrionicus* IN NORTHERN LABRADOR: A MULTI-SCALE APPROACH

JOEL P. HEATH

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ISBN: 0-612-84011-5

Factors influencing breeding distributions of Harlequin Ducks *Histrionicus histrionicus* in northern Labrador: a multi-scale approach

by

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A thesis submitted to the School of Graduate Studies
in partial fulfilment of the requirements
for the degree of Master of Science

Biopsychology Programme
Departments of Biology and Psychology
Memorial University of Newfoundland

December, 2001

St. John's Newfoundland

ABSTRACT

Considerations of spatial and temporal scales are important for understanding the distribution of highly mobile migratory birds, because habitat selection can involve hierarchical processes from the landscape to nest site scale. The aim of this thesis was to evaluate the importance of predation, intraspecific competition, biophysical habitat features and prey abundance in determining the distribution of breeding Harlequin Ducks *Histrionicus histrionicus* in northern Labrador. This was assessed at several spatial scales, both within and among years. Results indicate source-sink metapopulation structure at the landscape scale, with glacially carved river canyons containing sub-populations. Availability of cliff nesting habitat and, subsequently, abundance of birds of prey is a likely mechanism determining demographic differences among sub-populations of Harlequin Ducks along the source-sink gradient. Habitat and prey availability did not differ among source and sink populations, suggesting birds of prey may limit Harlequin Ducks from otherwise suitable habitat. A spatially explicit Geographical Information System (GIS) model supported these results, indicating spatial segregation of Harlequin Ducks and birds of prey at the landscape scale. Spatial segregation also was found at the home range scale within local populations where intermediate densities of both taxa were present. A variety of biophysical features and prey availability were important for home range selection within source populations. Tradeoffs among habitat quality and predation risk were important in sink and 'intermediate' populations. These results provide empirical support for aspects of several theoretical areas, including application of a metapopulation framework to migratory birds, coexistence of predators and prey through spatial dynamics, spatial and landscape influences on population dynamics and demographics, and the importance of considering multiple spatial and temporal scales in ecological research. Results also will be important for conservation and management of Harlequin Ducks, a species at risk in eastern North America, particularly for identifying key spatial areas in which to focus conservation efforts.

ACKNOWLEDGEMENTS

First and foremost, thanks to Bill Montevecchi, my supervisor, and to my committee members Greg Robertson and Joe Brazil for their comments, support, encouragement and knowledge throughout this degree. Special thanks to Dave Schneider and Ian Goudie for always making time to provide comments and guidance. Thanks also to Dan Esler and Joe Brown (my external and internal examiners, respectively) for their useful comments on the thesis. The group dynamics of the Biopsychology Programme provided a great collaborative atmosphere for research, learning, and support. Thanks to everyone in the program, particularly Gail Davoren, Ian Stenhouse and Keith Lewis, and all members of the Montevecchi lab, for consistently useful conversations and feedback throughout the thesis process. Thanks to all my ('school' and 'non-school') friends for helping me escape from my research when it was most needed! A big thanks to all administrative staff in both biology and psychology departments (particularly Craig Barnes, Roy Ficken, Maureen Howard, Gail Kenny, Brenda Noftle and Bernice St Croix) and to John Evans and Murray Colbo for both administrative support and thesis related conversations. Thanks to Dave Fifield for the invaluable technical support and to Shauna Ballie, Chantelle Burke, Greg Collier, Candice Kendell, Josh Pennell and Christina Snow for all their help. Thanks to Scott Gilliland, Pierre Ryan and Peter Thomas of the Canadian Wildlife Service and Fyzee Shuhood and Tony Power of the Newfoundland and Labrador Parks Division. Thanks also to Bill Duffet of the Provincial Wildlife Division for the logistical field support and the awesome care package after a month of isolation!

Thanks to Major Humphries and Tony Chubbs of the Department of National Defence, the Voisey Bay Nickel Company and Joe Brazil of the Provincial Wildlife Division for providing me with access to their survey data for both Harlequin Ducks and raptors in northern Labrador. Thanks to Perry Trimper and Kathy Knox of Jacques Whitford Environment Ltd. for their assistance throughout this process. These additional data sets had a significant influence of the scope and implications of this thesis, for which I am extremely grateful. Thanks to the Labrador Inuit Association (Nain) for their support and approval of this thesis project. Thanks to Geoff Goodyear of Universal Helicopters and the pilots of Canadian Helicopters for their expertise during surveys and getting us in and out of remote field sites. Thanks to Larry Nolan of DataSolutions for a great job programming the GIS routines exactly the way I wanted.

Financial Support for this thesis research was provided by the Newfoundland and Labrador Provincial Wildlife Division c/o Joe Brazil, and Endangered Species Recovery Fund of World Wildlife Fund Canada to William Montevecchi, Northern Scientific Training Program grants to JPH and William Montevecchi and Mountain Equipment Co-op Environment Fund and Canadian Society of Ornithologists (Taverner Award) support to JPH. Personal funding was provided by a Memorial University of Newfoundland graduate fellowship and a Natural History Society of Newfoundland and Labrador scholarship.

Finally, thanks to my family for their financial support, love and understanding throughout this degree.

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1.0. CHAPTER 1: INTRODUCTION AND OVERVIEW

1.1. INTRODUCTION

Many biophysical and ecological factors influence the distribution of breeding birds. Not only must essential proximate survival needs, such as food availability and shelter from predation and environmental conditions be met, but ultimate fitness considerations, including securing mates and finding an appropriate area for nesting and raising young, must also be achieved for successful reproduction (Cody 1985). It is these constraints and considerations which can influence behavioural aspects of habitat selection, and ultimately influence the distribution of a species across the landscape.

Of these behavioural aspects, social factors related to mate selection can often influence habitat selection. This is particularly true for territorial species in which habitat selection and mate selection may be synonymous (e.g., females of many territorial passerines, Cody 1985). For Harlequin Ducks *Histrionicus histrionicus* however, pair formation occurs on wintering grounds (Robertson 1997, Robertson et al. 1998) and mate defence, not territory defence, occurs during breeding (Bengtson 1966, Inglis et al. 1989, Robertson and Goudie 1999). Lack of territory defence does not imply that density dependent factors are unimportant, but their influence could be indirect through factors such as resource limitation (Newton 1998). Indirect evidence for density dependent intra-specific competition might be reflected in the low densities of pairs observed on breeding rivers across their range (Robertson and Goudie 1999). A major underlying premise of habitat selection theory is that areas differ in habitat quality, quality being defined as any feature that influences overall fitness and survival (Newton 1998). If habitat quality can be assessed, then the best locations are assumed to be selected first, or by competitively superior/dominant individuals, and density dependent competition or exclusion results in increasingly lower quality habitat patches being occupied as overall population numbers increase (Svardson 1949, Fretwell and Lucas 1969, 1970). If this is the case, densities may be a good indicator of habitat quality (Fretwell 1972). Widespread dispersion of Harlequin Ducks on breeding rivers might indicate that limited resources require use of relatively large home ranges, with a low density dependence threshold and carrying capacity for overlap on habitat patches (see e.g. Fretwell and Lucas 1969, 1970, Cody 1985). Adequate experience and competitive ability may therefore be important in selection of a home range, and ultimately in how Harlequin Ducks are distributed across the landscape of breeding regions.

Inter-specific competition is also an important aspect of habitat selection in many species (see Cody 1985), though coexistence is common (e.g. Rozenweig 1979, 1981, Pimm and Rosenzweig 1981). A particularly relevant example is of waterfowl breeding at Lake Myvath in Iceland where a variety of species are present and each species occupies different and discrete foraging patches (Bengtson 1971). Harlequin Ducks occupy a relatively unique niche on river systems, being primarily found in fast flowing sections of rapids and riffles (Robertson and Goudie 1999 and references therein, Section 1.2.1). Many of the other waterfowl species that breed on freshwater systems, particularly in my study area (see Section 1.2.2), occupy slower river sections or lakes and ponds. Mergansers are abundant, although their diet is restricted primarily to fish (Mallory and Metz 1999, Titman 1999). Although competition over evolutionary time may have produced differences in habitat selection among species (i.e. a competitive niche shift; e.g. MacArthur and Levins 1967), I do not expect direct interspecific competition with other waterfowl to be a major factor that influences breeding habitat selection of Harlequin Ducks in eastern Canada, although this is an area in which empirical data are lacking[1].

Quantifying habitat quality is important for both theoretical and conservation/ management concerns, and ideally the best method would be to measure fitness of individuals in each area over a long period of time (ideally for many generations). This is obviously not practical or even possible to measure in field situations, particularly within time constraints of conservation issues. In any case, if the species happens to exhibit an 'ideal free' type distribution, fitness is expected to be the same in each habitat and across the population (Fretwell and Lucas 1970), and would therefore not distinguish between good and

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[1] I do note, however, that fish could play two potentially competing roles in habitat selection decisions by Harlequin Ducks. 1) If fish consume adequate numbers of benthic invertebrates, they could potentially be food competitors with Harlequin Ducks, and/or 2) as Harlequin Ducks are known to eat fish eggs in coastal areas (see Dzinbal and Jarvis 1984, Robertson and Goudie 1999), they could potentially select breeding habitat in spawning areas of freshwater and/or anadromous fish. I note that for the first point, it is unlikely that benthic invertebrates in northern Labrador are in short supply (anyone who's been to northern Labrador without a bug jacket, personal communication). With respect to the second possibility, due to the phrenology of Harlequin Ducks and fish species, if this does occur it is most likely to influence habitat selection by Harlequin Ducks during brood rearing (which may or may not be mutually exclusive of habitat selection during the nesting season).

poor quality habitats. As mentioned previously, the fact that individuals (or pairs) may compete for habitat can allow densities to be an indicator of habitat quality (Fretwell 1972), although this may not always be the case (VanHorne 1983). Low variation in density among years (i.e. population stability) may be expected in higher quality areas and population variation may therefore provide a useful measure to help in this dilemma (VanHorne 1983, Howe et al. 1991).

Another feature population ecologists often quantify is natal and breeding philopatry (the latter is also often referred to as site fidelity), the re-use of the birth-place or former home range/nest site, by individuals (Greenwood 1980). Philoparty has been found to increase with density and reproductive success and may be related to nest site quality (Greenwood 1980, Skeel 1983, Jones 1988). Despite these features, I am unaware of any references in the literature that have attempted to use philopatry as an indicator of habitat quality. Perhaps this is because philopatry has almost exclusively been investigated based on return rates using mark-recapture techniques (see Anderson et al. 1992), and therefore has focussed on philopatric behaviour of individuals. One of the primary explanations for philopatry has been that previous experience and familiarity may be important aspects of fitness and therefore allowed selection for philopatry over evolutionary time (Lack 1966, 1968a, 1970, Greenwood 1980, McKinney 1986, Johnson and Gaines 1990, Bernstein et al. 1991). Perhaps because of these explanations, philopatry (especially natal philopatry) is often discussed as an innate characteristic that may limit free choice in habitat selection (e.g. Cody 1985). Alternatively, evidence has shown various degrees of philopatry between habitats and its relation to previous experience/success (Greenwood 1980, Skeel 1983, Jones

1988), thus philopatry may be considered a behavioural decision directly related to habitat selection. I therefore suggest that instead of focussing on individuals, if philopatry is reformulated in terms of the consistent use of habitat patches by the population, it may be an ideal indicator of habitat quality. Whether individuals of the population reuse the habitat or not may encompass a large variety of behavioural and ecological features relevant to habitat selection, including breeding success/fitness, predation risk, food availability, biophysical characteristics and even stochastic environmental events within the patch. Framing philopatry in terms of the population and habitat, instead of the individual will obviously require different quantitative techniques as philopatry is essentially being addressed at a different scale (i.e. population level). Development of such techniques and their usefulness as a currency of habitat quality is an important consideration throughout the present thesis.

A major development in ecology has been the immergence of the importance of scale (Levin 1992, Wiens 1989, Schneider 1994, 2001). Populations often exhibit spatial structure (Pulliam 1988, Pulliam and Danielson 1991, Wiens et al. 1993, Ritchie 1997) and both spatial structure and population dynamics may change with the scale of analysis (Kareiva 1990, Kolitiar and Wiens 1990, Wiens et al. 1993, Kareiva and Wennergren 1995). These considerations are particularly important in the relatively young sub-fields of metapopulation and landscape ecology (Wiens 1989, Hanksi and Gilpin 1991, Wiens 1997, Hanski 1999) A metapopulation may be defined as a set of sub-populations that interact by individuals moving among populations, without total mixing (Hanski and Gilpin 1991), or a population of populations (Levins 1969, 1970).

For migratory species such as waterfowl, habitat selection may be a hierarchical process from the landscape to nest-site level (Kaminski and Weller 1992, see also Kolitiar and Wiens 1990) and association with particular features may depend on the scale of analysis (Orians and Wittenberger 1991). In this regard, an important first step in investigating the importance of spatial scale is identifying the grain and extent relevant to the organism (Kolitiar and Wiens 1990). Grain and extent refer to the smallest and largest spatial scales containing heterogeneity relevant to the organism or study question (see also Andicott et al. 1987, Wiens 1989). Several spatial scales are likely important for habitat selection by Harlequin Ducks during the breeding season (Figure 1-1). At the geographic scale, Harlequin Ducks may have some degree of choice in the general area/direction they migrate to on their way from wintering grounds. For example, birds wintering in Maine, Nova Scotia or Cape St. Mary's, Newfoundland could potentially breed in south-east Quebec, Newfoundland or southern or northern Labrador, and birds wintering in Greenland might migrate to rivers in either Greenland or in northern Labrador and northern Quebec (Figure 1-1a; note that arrows in this figure are purely for illustrative purposes and do NOT all represent known migration routes of Harlequin Ducks). These possibilities are being studied with satellite telemetry (Brodeur et al. 1998, 1999, in press, M. Robert pers. comm.), and are not a direct aspect of the present thesis.

At the landscape scale (Figure 1-1b), Harlequin Ducks breed on river systems that are naturally patchily distributed, particularly in northern Labrador (see Section 1.1.2.). If each of these river systems show some degree of demographic independence, the overall population may be considered to function as a metapopulation (Esler 2000), with ducks on individual river systems functioning as sub-populations. Selection of a river system (or sub-population) may also be important as river systems may have different biophysical characteristics or prey availability. The presence of interspecific and conspecific competitors and predators also may be important to the ecology of each sub-population, and therefore to habitat selection decisions made by Harlequin Ducks. Of particular importance here, Harlequin Ducks often arrive on breeding streams in early spring (see Robertson and Goudie 1999), when rivers are mostly frozen over (staging occurs at open sections). This highlights the potential importance of the link between spatial and temporal scales; it is likely that the presence of snow and ice prevent home range selection based on information on prey abundance, vegetation and stream characteristics, and so landscape scale (sub-population) habitat selection may occur independently of habitat selection at finer scales (i.e. home range selection Fig 1-1c; see also Orians and Witternberger 1991). Home range selection may therefore occur later in the season after snow melt (and likely at high run-off; Bengtson 1972, Wallen 1987, Cassirer and Groves 1991, Diamond and Finnegan 1993). Within an established home range, selection of preferred feeding, loafing and brood-rearing habitat patches is likely to be important (Patch scale; Figure 1-1), with some areas within the home range being used more or less than others. It is at this scale that foraging theory (e.g. patch selection; Stephens and Krebs 1986) models may be most relevant. Even within these patches, some degree of selection must also occur (Micro scale; Figure 1-1), particularly with respect to the location of nest sites, which likely involve consideration of small scale vegetative structure, risk of flooding, microclimate, accessibility to nest predators, etc. (Cody 1985). Foraging decisions, particularly with respect to direct feeding on substrates where invertebrate prey are present, also will be based on fine scale/grain environmental variation that affect prey distributions (for example of factors influencing freshwater benthic invertebrates see Hynes 1970, Colbo and Wotton1981, Colbo and Porter 1981, Colbo 1985, McCreadie and Colbo 1992a,b,c).

It is within this multi-scale framework that this thesis is based. My major focus is on landscape and home range scales (i.e. within and between river systems), with consideration of features that are likely important at smaller (patch and micro) scales. Obviously many factors may influence habitat selection at each scale, often in different and sometimes competing ways. In chapter two I consider the landscape scale and investigate the importance of conspecifics, population dynamics, prey, biophysical features and predator densities in utilization of river systems. Landscape population structure, primarily from a spatially implicit source-sink metapopulation approach, is addressed. In chapter three, a spatially explicit Geographical Information System (GIS) approach is used to investigate spatial co-existence of Harlequin Ducks and avian predators at both landscape and home range scales. This is conducted both within and between years, and differences in this interaction among sub-populations along the source-sink metapopulation are investigated. Chapter four considers the importance of, and trade-offs between, prey, biophysical habitat characteristics, and predation risk on home range use within source and sink populations. This approach illustrates the importance of landscape considerations when investigating the importance of smaller scale habitat preferences. Multivariate analyses are used to determine the relative importance of various habitat characteristics and to generate a predictive habitat suitability index for Harlequin Ducks, a useful tool for environmental assessments and habitat conservation. Specifically, the goal of this thesis is to determine the factors that influence how Harlequin Ducks distribute themselves across habitats during the breeding season. More generally, the focus is to provide empirical insight into various theoretical aspects of habitat selection, source-sink, metapopulation and landscape ecology, and the role of spatial scale in each of these contexts.

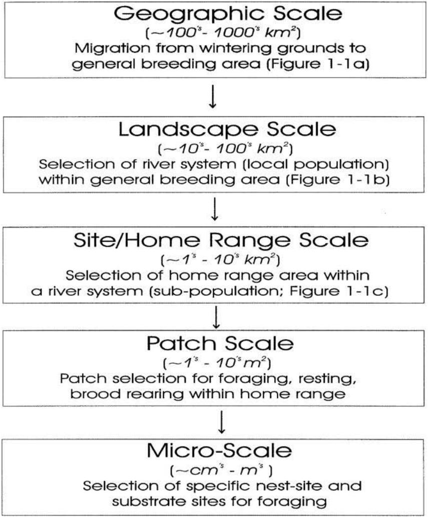

Figure 1-1. Schematic diagram of hierarchical spatial scales likely relevant to Harlequin Ducks during the breeding season. In each box, the scale of interest, approximate units and relevance to Harlequin Ducks is listed. Arrows indicate decreasing spatial scale.

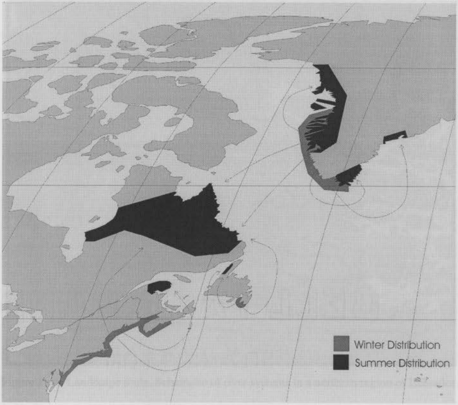

Figure 1-1a. Geographic scale. Schematic of the approximate winter and summer distributions of Harlequin Ducks in eastern North America and Greenland (adapted from Robertson and Goudie 1999). Within this scale, migration from wintering grounds involves 'selection' of a breeding grounds. A few of the possible choices are indicated by arrows (note that proper migration routes are not yet fully known [but see Brodeur et al. 1998, 1999, in press] and these arrows are purely for illustrative purposes).

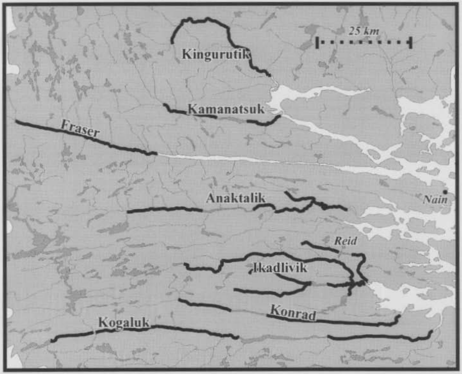

Figure 1-1b. Landscape scale. Schematic of river systems in a northern region of Labrador. Within this scale, selection of an appropriate river system for breeding is important. Major river systems are bolded and labelled. Due to isolation by terrestrial surroundings, river systems may be a landscape feature that plays a major role in population structure.

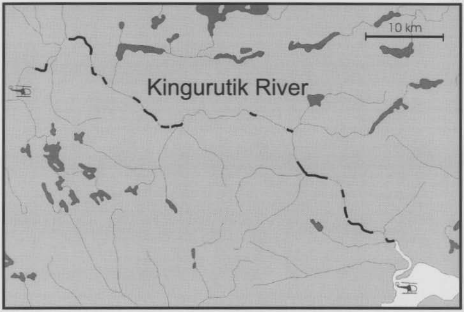

Figure 1-1c. Home range scale. A schematic of the Kingurutik River system, northern Labrador. Bold sections indicate areas that were used by Harlequin Ducks throughout four years of surveys. Helicopter icons illustrate the start/end points of the survey route. Within this scale, some sections of rivers are consistently used, while other sections are likely never used (for methods used to generate these used habitat polylines, see Chapter 2).

1.2. BACKGROUND

Harlequin Ducks occur in northeastern and northwestern North America, Greenland, Iceland, and along the northwestern Pacific coast (Palmer 1976, Robertson and Goudie 1999). They are a highly mobile migratory species that winters and molts along coastal rocky intertidal regions, and migrate to breed during summer on fast flowing sections of freshwater rivers and streams. In eastern north America, Harlequin Ducks are listed as a species of special concern. Across their range, habitat loss due to degradation of aquatic ecosystems, hydroelectric development and disturbance threatens breeders, while oiling and illegal hunting jeopardize wintering populations (see Montevecchi et al. 1995, Esler et. al 2000). It is therefore essential to develop a comprehensive understanding of habitat use by Harlequin Ducks in eastern North America, in order to determine which sites need to be protected and where to focus conservation efforts for the species' recovery.

1.2.1. *Breeding Ecology of Harlequin Ducks: a Review and Synthesis*

Pair formation occurs during winter (Kuchell 1977, Robertson et al. 1998). Following spring migration from the wintering grounds, birds may congregate at river mouths before moving up river (Bengtson 1966, Gudmundsson 1971). Immature birds often remain on the coast throughout the summer (Bengtson 1966, Bengtson and Ulfstrand 1971), while sexually mature birds migrate up river to their breeding grounds. It was previously reported that Harlequin Ducks swim most of the way upstream to their breeding grounds from the coast, only occasionally making brief flights (Bengtson 1966, Palmer 1976, Kuchel 1977); however, more recently, it has been noted that, in eastern North America (and likely for most birds travelling to inland river systems), breeding birds may fly directly to breeding streams

(Brodeur et al. 1998, 1999, in press).

In eastern Canada, eggs are laid and incubated between mid-May and mid-July, with males departing for the molting grounds between late June and mid-July. Broods hatch and are reared between July and September, upon which departure from the breeding grounds occurs and female molt begins (some variation between global populations; see review in Robertson and Goudie 1999). Variation in chronology may also be attributed to factors including differences in spring conditions, altitude and latitude, all of which may effect the timing of snow melt (Bengtson 1972, Wallen 1987, Cassierer and Groves 1991). Coordination of breeding events with local climatic conditions may be essential, as snow cover may reduce access to feeding and nesting areas, while high spring runoff may decrease productivity and juvenile survival through nest washout (Kuchell 1977, Wallen 1987, Diamond and Finnegan 1993). Harlequin Ducks may therefore initiate nesting during the period of maximum runoff (Kuchell 1977), decreasing further risks of flooding and allowing birds to nest as close to the water as possible, which may be important in the avoidance of terrestrial predators (Hunt 1998).

Site fidelity is strong across their range (Alaska: Crowley 1994 ; Idaho: Wallen and Groves 1989; Cassirer and Groves 1991, 1992; Oregon: Bruner 1997; Wyoming: Wallen 1987; Montana: Kuchell 1977; Iceland: Bengtson 1966, 1972), with individuals observed within 100 m of previous years sightings (Bengtson 1972), and nest locations often occur within 5-30 m of previous sites (Crowley 1994) or the same nest may be reused (Chubbs et al. 2000). Natal philopatry may also be important, as females are known to return to their natal breeding areas (Kuchell 1977). Although philopatry and site fidelity are high across their range, this is not absoulte. Although return rates less than unity may be partially due to mortality, there is direct evidence of limited dispersal to nearby river systems by banded birds among years (Robertson and Goudie 1999). Mate defence rather than territory defence occurs (Bengtson 1966, Inglis et al. 1989). Movement is often restricted within 1-2 km, although considerable overlap between pairs may occur at preferred feeding and loafing sites (Kuchell 1977, Bruner 1997; unpaired and unsuccessful individuals, however, may travel more extensively).

Research on habitat associations of Harlequin Ducks at a landscape level is generally lacking, although two general trends are recognized in western North America: coastal and inland breeding populations. Inland breeders feed primarily on insect larvae and pupae, which may be a limiting factor on productivity in some areas (Bengtson and Ulfstrand 1971, Gardarsson and Einarsson 1994). On coastal rivers, the majority of foraging has been reported to occur on marine invertebrates in intertidal regions, and breeding females may often fly down river to these areas to feed (Bengtson 1972, Dzinbal 1982, Crowley 1994). Upon arrival of spawning anadromous salmon, coastal Harlequin Ducks may move slightly upstream to feed on roe (Dzinbal and Jarvis 1984). Interestingly, although occurrence and densities of Harlequin Ducks may be higher at coastal sites, overall recruitment may be lower due to increased duckling mortality rates (Crowley 1999).

Other research relevant at a landscape level has indicated that breeding does not occur on glacially fed rivers (Bengtson 1972, Wallen 1987, Crowley 1994), where seasonal flow variability may be higher (Bengtson 1972) and productivity of invertebrate species may be decreased (Wallen 1987). In addition, Harlequin Ducks in Alaska used streams of greater width and discharge, which was related to a larger basin area and drainage network (Crowley 1994). These large scale features of used streams may maintain a more stable flow regime, even under periods of high precipitation (Verstrappen 1983). Effects of other landscape level features on the distribution of Harlequin Ducks have not been investigated, and further research is clearly needed.

Within river systems, Harlequin Ducks have frequently been associated with fast flowing turbulent waters. Many researchers have indicated that Harlequin Ducks often feed and inhabit sections of riffles and rapids (Bengtson 1966, 1972, Kuchell 1977, Wallen 1987, Inglis et al. 1989, Cassirer and Groves 1990, Bruner 1997, Hunt 1998), potentially due to an increased insect larvae and pupae abundance (Colbo and Wotton 1981, Inglis et al. 1989). Some slow moving water may also be important, especailly during brood rearing and periods of high water (Kuchell 1977, Dzinbal 1982, Inglis et al. 1989, Cassirer and Groves 1990, Crowley 1994, Rodway 1998b). Broods often avoid rapids during the first 2 weeks post-hatching, remaining in pools and backwaters, but after week four, begin using the main river, where the majority of feeding occurs by week six (Kuchell 1977). Areas containing heterogeneous flow regimes may therefore be important (Kuchell 1977), as requirements may change with environmental conditions and through different stages of the breeding season.

Other physical features of the river system may also be important to Harlequin Ducks. Shallow feeding areas may be preferred (Bengtson 1972), and black fly (Simulid) larvae may be more abundant in shallow water if velocity decreases with depth (Colbo and Wotton 1981). Low stream gradients (Wallen 1987, Cassirer and Groves 1990; but see

Chapter 4), and high pH and temperature (Rodway 1998a) have been found in used areas. Steeper shorelines may also be important (Crowley 1994, Bruner 1997, Rodway 1998a), potentially due to a decreased risk of flooding. Association with stream width are unclear as they may vary greatly in used areas (2-40 m; Bengtson 1972) or be wider (Cassirer and Groves 1990, Crowley 1994) or narrower (Rodway 1998a) than unused areas.

Substrate features may be particularly important. Larger grained substrates and bedrock have been consistently associated with Harlequin Duck habitat (Bengtson 1972, Kuchell 1977, Cassirer and Groves 1990, Bruner 1997, Rodway 1998a). Large grained substrates may increase insect abundance (Kuchell 1977, Colbo and Wotton 1981), and exposed boulders may provide resting sites (Kuchell 1977, Crowley 1994, Bruner 1997). Harlequin Ducks spend significant portions of time resting and preening on midstream boulders and islands throughout the breeding season (Bengtson 1972, Kuchell 1977, Dzinbal and Jarvis 1984, Inglis et al. 1989, Crowley 1994, Bruner 1997, Hunt 1998). Time spent preening may be important for feather maintenance due to diving in cold and turbulent waters (Inglis et al. 1989) and midstream areas may allow greater vigilance, reducing terrestrial predation (Kuchell 1977, Inglis et al. 1989). In addition, resting areas may be critical in order to reduce unnecessary energy expenditure due to swimming during non-foraging periods, especially if food is limited (as suggested by Bengtson 1972).

The location of Harlequin Duck nest sites is extremely variable (see Bruner 1997 and review in Robertson and Goudie 1999), however many may be located near the water, on instream islands, and under dense vegetative cover, such as willows and shrubs (Bengtson 1966, 1972, Wallen 1987, Crowley 1994, Bruner 1997, Hunt 1998, Rodway et al. 1998).

Dense overhanging vegetative cover also may be important during early brood rearing, hiding ducklings from potential predators (Bengtson 1966, Kuchell 1977). Bengtson (1970) has suggested that vegetative cover may be one of the most important factors in the habitat selection of waterfowl. Incidentally, the observed variation in nest site locations reported among populations of Harlequin Ducks may be due in part to variation in the type and amount of predation pressure. Cody (1985) notes that predation rates on nests may vary depending on the nest site, as certain predators may often select for specific habitats or nest types. In this manner, Harlequin Duck nest sites may vary with the respective pressure from terrestrial or avian predators or other factors, such as the risk of flooding.

A major factor influencing habitat use by many species food availability. Bengtson (1972) suggested that breeding success and therefore populations of Harlequin Ducks in Iceland may be limited by abundance of benthic invertebrates, in particular black fly Simulid larvae and pupae. Several lines of evidence support this hypothesis of food limitation across Harlequin Duck populations. Breeding frequencies and production of young have been shown to decrease in years of low benthic standing crops (Bengtson and Ulfstrand 1971, Gardarsson and Einarsson 1994). Low Harlequin Duck densities on breeding rivers and early male departure might be due to feeding conditions and might decrease the chances of food competition and depletion (Bengtson 1972, Kuchell 1977). Molt is delayed until arrival in coastal areas (Kuchel 1977). The period of hatching often corresponds with an increased abundance of insect larvae (Bengtson and Ulfstrand 1971, Kuchell 1977) and areas not used by Harlequin ducks often have fewer or no Simulids (Bengtson 1972, Rodway 1998a). Finally, Robert and Cloutier (2001) report that 87.2% of prey items taken by Harlequin

Ducks in eastern North America were Simuliidae, and Goudie (1988) has reported that Harlequin Ducks are absent on rivers above the northern limit of Simulid distribution. Habitat selection of Harlequin Ducks may therefore be related to factors of importance to benthic invertebrates, particularly Simulids, which may therefore indirectly drive Harlequin Duck habitat use. Simulid distributions and growth may be affected by variations in stream size and water chemistry, substrate, stream velocity and turbulence, water level and temperature (Colbo and Porter 1981, Colbo 1985, Colbo and Wotton 1981, McCreadie and Colbo 1992a, b, c), although different species and cytotypes may be best adapted to different conditions.

High invertebrate densities often occur at lake outlets (Hynes 1970, Bengtson and Ulfstrand 1971, Richardson and MacKay 1991, McCreadie and Colbo 1992c) and Harlequin Ducks may congregate in these areas during the breeding season (Hunt 1998). Simulids may not be the only important species however. Trichoptera, Plecoptera, Ephemeroptera, and Diptera:Chironomidae (Bengtson and Ulfstrand 1971, Kuchell 1977, Wallen 1987, Cassirer and Groves 1994, Rodway 1998a, Wright et al. 2000, Robert and Cloutier 2001) may also be important sources of food, and the importance of each could vary throughout the breeding season (eg. Rodway 1998a) and could be related to seasonal trends in emergence patterns of different invertebrate species.

Perhaps too much emphasis has been placed on abundance of prey as a limiting factor for Harlequin Ducks, as other factors that affect habitat use often have been glossed over. A growing number of incidental reports of predation on Harlequin Ducks exists (see Heath et al. [in press] for review; Appendix A), however its role in driving habitat utilization has not been considered. Potential terrestrial predators may include mink *Mustela vison* (Bengtson 1966, 1972, Kuchell 1977, Dzinbal 1982), arctic fox *Alopex lagopus* (Bengtson 1972) and river otter *Lutra canadensis* (Dzinbal 1982, Robertson and Goudie 1999), while suggested avian predators include Bald Eagles *Haliaeetus leucocephalus,* Gyrfalcon *Falco rusticolus*, Raven *Corvus corax*, and Arctic Skua *Stercocarius parasiticus* (Bengtson 1972, McEneaney 1997, Brodeur et al. 1998, Robertson and Goudie 1999). Attacks by a Golden Eagle *Aquila chrysaetos* and Gyrfalcon have been observed in northern Labrador (Heath et al. [in press], Appendix A; Rodway et al. 2000) while direct predation by Great Horned Owl *Bubo virginianus* and Red Tailed Hawk *Buteo jamaicensis* has been reported (Brodeur et al. 1998). Kuchell (1977) reports that exposure of female Harlequin Ducks when guarding their broods may make them particularly susceptible to avian predators, and female mortality may cause an entire brood to perish.

Interestingly, effects of predators could influence distributions in several competing ways. Raptors may often select breeding habitat where there are good nest-sites, eyries and prey availability (Janes 1985). Harlequin Ducks, on the other hand, may either select areas away from high densities of predators, or may be driven from otherwise ideal habitat due to predation. Interrelations between predators and prey could therefore influence the habitat utilized by both.

Several themes are apparent from a review of the existing literature on the breeding biology of Harlequin Ducks. Perhaps foremost is the often recurrent claim that the major limiting factor to Harlequin Ducks on the breeding grounds is prey availability, specifically the presence of blackfly Simulid larvae. This seems particularly over-emphasized as not only are experimental data testing this hypothesis non-existent, but Harlequin Ducks are known to be food generalists on the winter grounds (see Robertson and Goudie 1999). Recent diet analyses indicate that a variety of prey types may be taken (Robert and Cloutier 2001 and see above). This is not to say that prey are not a limiting factor, however other factors are likely more important than indicated by previous research.

Perhaps spatial scale of research studies is the major factor that has led to this focus on prey limitation. A large amount of the research on breeding ecology of Harlequin Ducks has been conducted, for logistical reasons, in areas of small spatial extent, on one or a few river systems, although recent work has investigated movements using satellite telemetry (Brodeur et al. 1998, 1999, in press). At small spatial scales, selection of foraging patches and nest-sites may dominate habitat use. The importance of predation, competition, inter-annual movements and population dynamics and especially population structure across river systems and the landscape, however, may be unapparent from results of small scale studies (eg. Orians and Wittenberger 1991). In migratory species such as waterfowl, habitat selection may be a hierarchical process from the landscape to nest-site levels (Kaminski and Weller 1992), and the importance of particular limiting factors may vary with the scale of analysis. It is therefore essential to consider multiple biophysical and ecological factors and multiple spatial and temporal scales when investigating factors influencing distributions of Harlequin Ducks.

1.2.2. *Study Area*

Northern Labrador is truly a unique ecosystem, and its features are particularly important to the framework of this thesis. The majority of the study area (approx. 51,000 km^2, Figure 1-2) is located in the Kingurutik-Fraser Rivers eco-region (Ecological Stratification Working Group 1995). Most of this region, particularly inland, is high sub-arctic plateau (Plate 1-1). There are many small ponds on this plateau that are sustained annually by snow melt. Glacial carved river canyons intersect this barren plateau (Plate 1-2). River canyons originate inland gradually widen as they approach the coast. Many river systems contain huge lakes (Plate 1-3). Within these river valleys are open black and white spruce (*Picea mariana, P. glauca*) forests that include some eastern larch *Larix laricina* and stunted balsam fir *Abies balsamea.* Riparian zones often include abundant willows (*Salix* spp.) and alders (*Alnus* spp.). Dwarf Birch *Betula glandulosum* and willow grow high in the valleys, above the tree line, on less stable scree.

Cliff and forest habitat around both rivers and lakes provide nesting sites for Ravens *Corvus corax* and a variety of raptors including Peregrine Falcon, Golden Eagle, Gyrfalcon, Great Horned Owl, Rough-legged Hawk *Buteo lagopus*, Merlin *Falco columbarius* and Osprey *Pandion haliaetus*. Forested regions also contain many species of small birds. In some years, small mammals, including Meadow Vole *Microtus pennsylvaticus*, are very abundant. Habitat in this region is particularly good for Caribou *Rangifer tarandus*. Other mammals include Moose *Alces alces*, Black Bear *Ursus americanus*, Wolf *Canis lupus*, American Marten *Martes americana*, Mink *Mustela vison*, Porcupine *Erethizon dorsatum*, River Otter *Lutra canadensis*, Beaver *Castor canadensis*, Arctic Hare *Lepus timidus* and Red

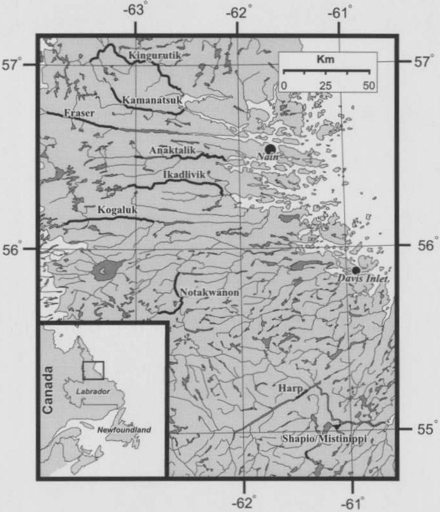

Figure 1-2. Study area in northern Labrador, Canada. River systems considered (bold lines) are located within glacially carved river canyons surrounded by sub-arctic plateau. All rivers considered are located within the Fraser - Kingurutik Rivers eco-region (as classified by the Ecological Stratification Working Group, 1995)

Plate 1-1. Sub-arctic plateau surrounds river canyons in the Fraser - Kingurutik Rivers Eco-region, Northern Labrador © Joel P. Heath 2001

Plate 1-2. The Fraser River, northern Labrador. River systems are fairly discrete patches, and this is particularly true in northern Labrador were rivers are located in glacially carved canyons, surrounded by sub-arctic plateau (see Plate 1-1). This landscape structure conforms well with the spatially implicit assumptions of a metapopulation framework, and is an important consideration throughout the present thesis. © Joel P. Heath 2001

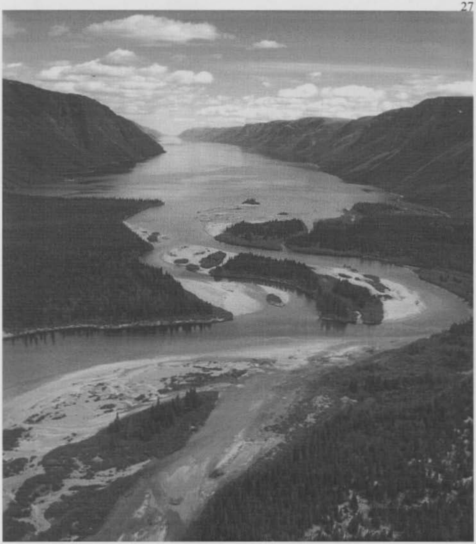

Plate 1-3. Large lake areas are present on many of the river systems in the Fraser - Kingurutik Rivers eco-region, northern Labrador. This plate illustrates where the Fraser River flows into Tasisuak Lake (over 50 km in length) before entering the Atlantic Ocean.

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and Arctic Foxes (*Vulpes vulpes, Alopex lagopus*). Rivers and lakes contain high abundances of fish (Arctic Char *Salvelinus alpinus,* Atlantic Salmon *Salmo salar* and trout *Salvelinus fontinalis, S. namaycush*) and aquatic invertebrates, which are important for a number of waterfowl species. White-winged and Surf Scoter (*Melanitta fusca, M. perspicillata*), Long Tailed Duck *Clangula hyemalis* and Common Loon *Gavia immer* occur on lakes and ponds, and Canada Geese *Branta canadensis*, Black Duck *Anas rubripes*, Common and Barrows Goldeneye (*Bucephela clangula, B. islandica*), Red-Breasted and Common Merganser (*Mergus serrator, M. merganser*) and of course Harlequin Ducks occupy river areas.

Labrador has been described as "one of the last great wilderness regions in North America" (Anderson 1985, pg 1) and the relatively low levels of anthropogenic disturbance provide a unique opportunity to study the ecology of a natural system. Additionally, it is important to note that the niche of Harlequin Ducks is restricted to river systems for foraging, with nest sites in close proximity. This is particularly important from a landscape perspective as river systems themselves are naturally patchy, particularly in this eco-region as they are located in river canyons that are isolated by extensive areas of sub-arctic plateau. This situation meets the assumptions of several theoretical models of population ecology (e.g. island biogeography, metapopulation structure, source-sink dynamics). From a landscape ecology perspective, these habitats are discrete and therefore considerations of boundary effects, connectivity and patch context are likely irrelevant. With these features considered, the structure of the landscape in this eco-region is essential for understanding the distribution of Harlequin Ducks and provides the framework for the theoretical aspects of this thesis.

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CO-AUTHORSHIP STATEMENT

As the author of this thesis and principal author on all chapters (research papers) I have contributed the following:

i) *design and identification of the research proposal*

Study design and the formulation and writing of a research proposal were all conducted independently, with subsequent feedback from my thesis committee (see below)

ii) *practical aspects of the research*

I was responsible for planning and organizing field logistics and was involved in the direct collection of data, with the help of field assistants. Note that additional data were obtained from a variety of sources (see Acknowledgements), of which I was responsible for obtaining permission from all collaborative parties.

iii) *data analysis*

Model/index formulation and statistical design and analysis were conducted independently, with subsequent comments and validation from both my committee members and D.C. Schneider

iv) *manuscript preparation*

I researched and wrote all sections of this thesis. Comments both along the way and subsequent to complete drafts were provided by my committee members and other parties, as indicated in the Acknowledgements section of this thesis.

Co-Author Contributions

Greg Robertson is co-author on chapter 2 due to comments throughout manuscript preparation, and his role as a committee member. Joe Brazil is co-author on chapter 4 due to data contribution (see above), comments during manuscript preparation, financial contribution to field work, and role as a committee member. Bill Montevecchi is co-author on all chapters due to his role as supervisor throughout the thesis, and comments on and during design, analysis and manuscript preparation. Joe Brazil and Geoff Goodyear are co-authors on Appendix A due to their presence during this observation and comments during manuscript preparation.

2.0. CHAPTER 2. METAPOPULATION STRUCTURE OF BREEDING HARLEQUIN DUCKS AND THE ROLE OF PREDATION RISK[2]

2.1. ABSTRACT

Landscape considerations are essential for understanding the spatial distribution of many species, especially highly mobile ones. The structure, demography and dynamics of populations, measured at small spatial scales, may not reflect characteristics of the overall population across a landscape. In northern Labrador, Harlequin Duck (*Histrionicus histrionicus* L.) breeding populations are structured within glacially carved river canyons that are separated by broad areas of unsuitable habitat (high sub-arctic plateau). Strong natal philopatry and site fidelity, with limited dispersal among nearby river systems provides a mechanism for metapopulation structure among these highly migratory birds. I studied populations of Harlequin Ducks and four species of raptorial birds breeding on nine river systems in northern Labrador, 1992-2000. Density, stability and the degree of consistent patch use within sub-populations (site persistence) of Harlequin Ducks were positively related, indicating differences in habitat quality across river systems. Brood surveys within a high quality population of Harlequin Ducks indicated positive population growth, despite stability, implying a population at carrying capacity that produces emigrants. Trends in low quality populations approach extinction (1 breeding pair) in some years, and large increases in others (e.g. 700%), that can not be accounted for by local reproductive output, indicate

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[2] This chapter will be submitted for publication as Heath, J.P., Robertson, G.J. and Montevecchi, W.A. Metapopulation Structure of Breeding Harlequin Ducks and the Role of Predation Risk

an immigration rescue effect. These data supported my hypothesis of metapopulation structure and suggested source-sink dynamics. To identify an ecological mechanism underlying sub-population differences, I compared prey, biophysical habitat features and the presence of raptorial birds in putative source and sink sub-populations. I found no differences in prey availability and biophysical habitat features relevant to the ducks. Across river systems, however, Harlequin Duck density, stability and site persistence were negatively related to densities of raptorial birds. This relationship suggests raptorial birds reduce the value of potential breeding habitat for Harlequin Ducks and influence metapopulation dynamics, in areas where cliff nesting habitat for raptors is available. These findings hold critical implications for the conservation of both taxa and illustrate the importance of using landscape approaches to research and management of ecological systems.

2.2. INTRODUCTION

Population distributions often exhibit spatial structure, frequently determined by landscape features (Wiens et al. 1993, Ritchie 1997). Sub-populations can be isolated to varying degrees by habitat patchiness and a species' dispersal characteristics. In situations where sub-populations exhibit some degree of connectivity (immigration and emigration occurs), but not total mixing, the overall population can be described as a metapopulation (Levins 1970, Hanski and Gilpin 1991, Hanksi 1991, 1999). In this context, population dynamics result from changes within, and interactions between, sub-populations and cannot be properly understood by studies restricted to local scales (Wiens et al. 1993, Karieva and Wennergren 1995, Ritchie 1997).

Populations of migratory birds have generally not been considered to function as metapopulations, owing to high mobility. Esler (2000) has indicated, however, that behavioural mechanisms such as natal philopatry and site fidelity (which are both common among migratory birds; Greenwood and Harvey 1982, Clarke et al. 1997) can limit dispersal and allow metapopulation structure to occur during particular periods of the annual cycle. In northern Labrador, breeding populations of Harlequin Ducks (*Histrionicus histrionicus* L.) are structured within glacially carved river canyons which are separated by large areas of unsuitable habitat (high sub-arctic plateau). These topographic features therefore produce discrete habitat patches (river systems) within a 'featureless matrix', conforming well with the spatially implicit assumptions of a metapopulation approach (Wiens 1997). Harlequin Ducks exhibit a high degree of natal philopatry and site fidelity, however limited dispersal between nearby river systems has been observed among years (Robertson and Goudie 1999), providing a mechanism for metapopulation structure during the breeding season (Esler 2000). Northern Labrador is an area relatively unaffected by human activities, and unlike human-induced habitat fragmentation, the patchiness of Harlequin Ducks' habitat is a natural feature of the landscape, therefore providing a unique opportunity to study naturally occurring population structure.

The objectives of this study were to 1) compare the demographic features of Harlequin Duck populations on nine breeding rivers within a single eco-region in northern Labrador 2) to determine the applicability of a metapopulation approach, and 3) to evaluate the role of prey, habitat, and avian predators as potential mechanisms underlying sub-population differences. I subsequently discuss the relevance of my findings, and the importance of a landscape approach, to both ecological research and conservation and management strategies for migratory birds.

2.3. METHODS

2.3.1. *Life History Considerations*

Understanding how metapopulation theory can apply to migratory birds is more involved than in other species, and I therefore recommend reading the framework developed by Esler (2000). Harlequin Ducks in particular have several unique life history characteristics that are relevant (see Robertson and Goudie 1999 and references therein for review). In the northwest Atlantic, wintering Harlequin Ducks aggregate in marine intertidal areas. During this period, courtship and pair formation occurs (long term pair bonds common), and are therefore unlikely to influence breeding habitat selection. Migration occurs in spring to inland river system breeding areas. Mate defence, not territory defence occurs on river systems. Once incubation begins, the male migrates to marine areas to molt (this is particularly relevant to survey methods for determining pairs). Females and broods return to wintering areas upon fall fledging. High natal philopatry and site fidelity exist to winter, breeding and molting sites, however I emphasize that during the breeding season, limited natal and adult dispersal has been observed among years. Each of these life history/behavioural considerations are important in understanding population structure for this species, and the assumptions and arguments presented herein.

2.3.2. *Aerial Surveys*

Helicopter surveys for Harlequin Ducks and raptorial birds (Peregrine Falcon *Falco peregrinus* Tunstall, Golden Eagle *Aquila chrysaetos* L., Gyrfalcon *Falco rusticolus* L. and

Great Horned Owl *Bubo virginianus* Gmelin) were conducted between 1992 and 2000 on nine river systems within the Kingurutik - Fraser River eco-region (Ecological Stratification Working Group 1995), northern Labrador (Figure 1). An average of four (range 3-6) surveys (years) were conducted on each river system for each taxa. Each survey team included an experienced wildlife survey pilot and 2-3 additional observers and were flown at a height of 20-30 m above the river at flight speeds not exceeding 50 km/hr using a Bell 206L helicopter. Surveys for both Harlequin Ducks and raptors were only conducted when conditions allowed at least 6.5 km visibility, light winds, and a cloud ceiling >600 m.

Surveys for Harlequin Ducks were conducted between 7 - 23 June, which was determined to be the best time for surveys in this region (Rodway 1998, Robertson and Goudie 1999; with consideration given to timing of spring runoff). Consistent with previous surveys for Harlequin Duck (S. Gilland, pers. comm.) and other migratory waterfowl (Dzubin 1969), lone individuals also were considered pairs, as lone males may indicate a pair where the female is searching for a nest or incubating, while lone females may indicate a pair in which the male has departed for the molting grounds (Robertson and Goudie 1999). This method is considered the most conservative for migratory waterfowl (Dzubin 1969), particularly as the sex-ration in eastern North America is close to unity (Robertson and Goudie 1999).

Raptor surveys were conducted along river canyons and surrounding lake areas between June and July, in accordance with the methods of Lemon and Brazil (1990). Both sides of each river valley were flown at flight speeds not in excess of 50-100 km/hr. Particular attention was given to areas with suitable ledges, droppings and recent wash, and associated orange lichen. Raptor surveys were also conducted on cliffs surrounding large lake areas of the watersheds. Raptor nest sites were considered to be active if 1) at least one individual was present and sitting on the nest, 2) eggs or chicks were observed in the nest or 3) a pair or individual flushed from the cliff and acted territorial (Lemon and Brazil 1990; the last criteria, used for consistency with other research, was rarely employed and would not affect results).

2.3.3. Statistical and Analytical Treatment of Survey Data

Densities

Densities of Harlequin Ducks on each river system were calculated by dividing the average number of pairs observed per year by the length (km) of river surveyed (calculated using a polyline ruler on 1:50,000 topographic maps in Mapinfo v.5 (MapInfo Corporation 1998); step length = 0.05 km). Densities of birds of prey for each river system were calculated by dividing the average number of active nests (for all species) by the length of river survey (km). Active nests located on lakes that were within 5 km of the river were also included. Scrapes, old and empty cliff nesting sites were also recorded and used to calculate the density of available nest sites in the same manner.

Population Variability

Common measures of population variability over time can be badly biased (Stewart-Oaten et al. 1995). Statistical measures of variability (e.g. standard deviation, variance) rely heavily on the assumption that an average is the best way to describe a data set and deviation from this average reflects variability. While these assumptions may be fine for statistical analysis, their validity in reflecting stability/variation of biological populations are not as clear cut.

For example, for a population that is completely stable in all years except for one, the mean will not reflect population size in any year, and a classical statistical calculation of variability would imply deviation from the mean, and therefore variability in ALL years. Additionally, the presence of dates with zero counts can be problematic and the often arbitrary choice of a constant can bias results (McArdle et al. 1990, Stewart-Oaten et al. 1995). Spatial variation can also confound temporal variation when random sampling occurs (Stewart-Oaten et al. 1995); however, in the present situation each river system was consistently surveyed among years. I therefore defined population variability (V) between years as the average percent population difference between all years surveyed (y). To determine population variability V I first calculated Z, the number of ways to compare y years as:

$$Z = \binom{y}{2} = \frac{y!}{(y-2)!2!} \tag{1}$$

and define $\boldsymbol{List}_z$ as the list of these possible comparisons (where z identifies each comparison and therefore $z = 1 \ldots Z$). Labelling the two years compared for each z comparison as z_1 and z_2, population variability V was calculated as:

$$V = \frac{\sum^{List_z}\left(\frac{\mathrm{ABS}(z_1 - z_2)}{\mathrm{MAX}(z_1, z_2)}\right)}{Z} \tag{2}$$

Equation 2 treats populations of different size in the same manner (even dates with zero counts; although I note this was not an issue for this data set), and ensure population increases are weighted the same as decreases. Additionally, this method is free of the assumptions of selecting a 'best' measure of central tendency. Population variability V may therefore range from 0 to 1, a score of 0 representing completely stable population size between years (I herein use stability to refer to $1/V$). A value of 1 is approached as the differences in population size between years approach infinity (for the reader interested in the properties of this index, I note that a value of 1 can be obtained if only 2 years are considered [a rather nonsensical situation] and the sub-population goes to 0 [extinct] in only one of these years).

Site Persistence: A population/landscape perspective on philopatry and site fidelity

Mark-recapture techniques for individuals are highly unpractical at large spatial scales (Anderson et al. 1992), while radio/satellite telemetry methods are restricted to short temporal scales (only several months for Harlequin Ducks; M. Robert pers. comm). Additionally, both mark-recapture and radio telemetry methods do not accounts for populations change; dispersal outside of the study area may often be considered mortality and vice versa (Anderson et al. 1992). I therefore present an aerial survey/GIS based approach to understanding consistent patch use over time, from the perspective of a sub-population.

For Harlequin Ducks, utilized sites were defined by overlaying survey data from each year in Mapinfo v.5 and determining the area in which observations of pairs between years overlapped within a maximum distance of 2 km (equivalent to one home range size: Kuchell 1977, Bruner 1997, Robertson and Goudie 1999). A maximum distance criteria of 2 km is a conservative estimate as movements by individual birds of up to 8 km have been observed (MacCallum and Bugera 1998, Robertson and Goudie 1999). In some situations, Harlequin Ducks may have overlapping home ranges, as mate defence, not territory defence occurs

(Inglis et al. 1989, Robertson and Goudie 1999). Accordingly, the maximum distance criteria was increased to 3 km for areas where 2-4 pairs overlapped, and to 5 km where 5 or more pairs overlapped across years. This was a reasonable criteria as most pairs were resighted within much shorter ranges and observations not included by this criteria for a given site generally occurred at considerably greater distances from the site or were associated with other sites. This therefore split the river system up into used sites, surrounded by unused sections, with variable numbers of pairs over years on each site.

An index was developed to quantify the degree to which sites on a river are consistently reused by the sub-population, among years. This index is herein referred to as site persistence (*P*) and is expressed as a proportion between 0 and 1. The effects of natal philopatry and site fidelity across years are intrinsically incorporated, while accounting for sub-population change (e.g. birth, emigration, death, immigration) between years. $P = 1$ indicates that the sub-population consistently re-used the same sites on all years; $P = 0$ indicates that no sites were reused over the years surveyed (i.e. novel sites were used each year). Though movements of individual birds between years are unknown, this index is focussed on inter-annual changes in the distribution of the sub-population across the river system. As this index measures consistent patch use over time, I also expect it to be a good indicator of habitat quality. Although conceptually simple, this index is mathematically complex to describe. Details and an example calculation are given in Appendix A.

Statistics

Site persistence, population variability and density of Harlequin Ducks were compared across river systems using two-tailed product-moment correlation analysis and described using principal axes (Sokal and Rohlf 1995). One-tailed product-moment correlation analysis was used to investigate influences of avian predator densities on site persistence, densities and variability of Harlequin Duck populations, and Model II (functional) regression analysis (Ricker 1973, Sokal and Rohlf 1995) was used to describe these relationships. Relationships with Harlequin Duck densities were best described exponentially, so duck densities were log transformed for all comparisons.

2.3.4. Close Examination of Model River Systems

As in-depth investigation was not practical within all river systems, I selected two river systems to focus on, the Ikadlivik and Fraser Rivers. These were selected on the basis of high and low densities, stability and site persistence (Ikadlivik and Fraser rivers respectively; Table 2-1), in order to represent the two extremes of sub-population features observed in this eco-region.

Riverine Habitat Comparisons

I quantified habitat features relevant to Harlequin Ducks on both the Ikadlivik and Fraser rivers to evaluate differences in habitat availability. Twelve sites were randomly selected along each river system, and each site was visited in June/July 2000, after spring runoff had subsided. At each site habitat features relevant to Harlequin Ducks (Robertson and Goudie 1999, Rodway et al. 2000, Chapter 4) were measured within a 50 m section of the river. Stream depth was measured at center stream, mid-left and mid-right along three transects (25 m upstream, 0 m, 25 m downstream); stream width was measured at each transect and averaged for the 50 m section. Mid-stream velocity was measured as the time it took a small bobber to travel 10 m downstream, averaged over three trials. Percent composition of riparian (within 5 m of banks) and general (5-100 m from bank) ground/vegetation types (sand, rock, moss, shrub, alder, trees) were estimated visually in 10 m sub-sections along both banks, and averaged over these subsections to determine the overall percent composition for the site. Instream islands, boulders and debris were counted and islands were measured and categorized as gravel, alder or treed (conifers and hardwoods present). The percentage of exposed and vegetated banks, and banks that had overhanging alders were measured for each section. Substrate type of the stream bed (bedrock, large boulder [>1 m], small boulder [25 cm - 1 m], rubble [14 - 25 cm], cobble [6 - 13 cm], pebble [3 - 5 cm], gravel [20 mm - 3 cm], sand [0.06 - 20 mm] and mud [0.004 - 0.05 mm]) was quantified by visually estimating the percent cover in ten 5 m sub-sections and used to calculate percent cover for the entire 50 m section. Similarly, water characteristics (percent rapids, riffle, runs, slow water [back water eddies and pools], see Scruton and Anderson 1992) were estimated within five 10 m sub-sections and averaged to determine the percent composition for the site. Benthic invertebrates (the primary prey of Harlequin Ducks during the breeding season; see Robertson and Goudie 1999) were kick-sampled at three random sites within each 50 m section using a 46 cm by 25 cm rectangular kick net (see Frost et al. 1971). Invertebrates were identified to order (except Diptera also to family) and the total number of each taxa per sample was determined and averaged across the three samples for each site.

Prey abundance and biophysical habitat features were compared between the Ikadlivik and Fraser rivers using 2-tailed t-tests for unequal variance, and I adjusted alpha levels using a sequential bonferonni test (Rice 1989). Additionally, I entered all variables

Table 2-1. Harlequin Duck density (pairs/km), population variability (*V*), site persistence (*P*) and avian predator density (active nests/km) for the Ikadlivik (high quality, putative 'Source') and Fraser (low quality, putative 'Sink') river systems.

	Ikadlivik	Fraser
Harlequin Duck Density (pairs/km)	0.322	0.042
Population Variability (*V*)	0.12	0.50
Site Persistence (*P*)	0.627	0.074
Avian Predator Density (active nests/km)	0.031	0.149

into a discriminant function analysis and tested for equality of group means using a Chi-square transformed Wilks' Lambda in SPSS v.10 (SPSS Inc., 1999).

Population Trends

Brood surveys were conducted on the Ikadlivik River watershed in 1996 - 1998. Aerial surveys covered 33.2km, while more intensive ground surveys re-covered 20.8 km. I note that these surveys are conservative, representing minimum production as additional broods are likely missed. This information was entered into a population projection model previously developed for Harlequin Ducks (Goudie et al. 1994, Robertson 1997, but survival rates updated with values from Cooke et al. 2000) to obtain a projected population growth rate (λ). Population trends on the Fraser river and Kogaluk river (another river system with low density/stability/site persistence of Harlequin Ducks) were investigated by observing population changes between individual years.

2.4. RESULTS

Harlequin Duck density, population variability and site persistence varied across river system sub-populations. As predicted, Harlequin Duck density and population variability were negatively correlated ($r = -0.708$, $df = 7$, $p = 0.032$; Figure 2). Site persistence was positively correlated with Harlequin Duck density ($r = 0.906$, $df = 7$, $p < 0.001$; Figure 3a) and negatively correlated with population variability ($r = -0.679$, $df = 7$, $p = 0.044$; Figure 3b). This indicated the presence of some large stable populations, in which habitat patches are consistently reused (herein referred to as 'high quality' populations), some small populations that are variable in size among years and in which patch use is inconsistent (herein 'low quality' populations), and some intermediate populations between these two extremes.

A population projection model on a high quality river system (Ikadlivk) indicated a positive projected population growth rate (λ) of 2.1% per year, despite stability, indicating this river system is likely at carrying capacity with emigration of excess individuals. I also note that winter population surveys (Mittlehauser 2000) indicate an overall increase in the entire population, providing additional, albeit indirect support for this result. On two low quality river systems (Fraser and Kogaluk rivers) population size came extremely close to extinction (i.e. only 1 pair) in some years, while increases of up to 700% were observed in subsequent years - increases unaccountable to local reproductive output, therefore implying immigration in some years (e.g. Fraser River: one pair in 1993, five in 1994; one pair in 1999 and a minimum of 7 pairs in 2000 [this 2000 survey was late and therefore not included in other analyses]; Kogaluk River: one pair in 1993, three in 1994; one in 1997, [no survey 1998], six in 1999).

To identify a potential mechanism underlying differences among river systems, I compared habitat and prey availability on high (Ikadlivik) and low (Fraser) quality river systems. This comparison indicated no differences in habitat or prey availability, from both a univariate (see Appendix B) and multivariate approach (Discriminant function analysis: Wilks' Lambda Chi-Square = 20.734, df = 21,p = 0.475). Among all nine river systems, Harlequin Duck density (r = -0.821, df = 7, p = 0.003; Figure 4a), stability (i.e. $1/V$; r = -0.596, df = 7, p = 0.045; Figure 4b), and site persistence (r = -0.915, df = 7, p < 0.001; Figure 4c) were negatively related to the density of avian predators, indicating that high quality river systems had low densities of avian predators and vice versa. Densities of birds of prey were related to the availability of cliff nesting sites ($r = 0.838$, $df = 7$, $p = 0.005$) indicating nest site limitation for birds of prey is likely the underlying feature influencing the distribution and dynamics of Harlequin Duck population across the landscape.

2.5. DISCUSSION

2.5.1. *A metapopulation framework for Harlequin Ducks*

At the landscape scale, breeding Harlequin Ducks are structured within glacially carved river canyons. Positively related differences in population density and stability were observed across river systems. The consistent use of habitat patches (site persistence) also varied among river systems. Although site persistence is a measure of consistent patch use over time at the population/landscape scale, it reflects philopatry and site fidelity, which have been shown to be related to density, reproductive success and the quality of breeding areas (Greenwood 1980, Skeel 1983, Jones 1988). This suggests differences in the quality of river systems, particularly as site persistence was positively related to both density and stability, which are also considered indicators of habitat quality (Fretwell 1972, Howe et al. 1991).

These differences among sub-populations across the landscape indicate a degree of demographic independence among river systems. Despite vagility, Harlequin Ducks exhibit high natal philopatry and site fidelity across their range (Reichel et al. 1997, Robertson and Goudie 1999, Robertson et al. 2000; including Labrador: R. I. Goudie, personal communication) providing a mechanism for demographic independence and therefore metapopulation structure (Elser 2000). Given large migration distances from the wintering grounds, inter-river distances are likely irrelevant upon arrival at the breeding grounds.

Additionally, landscape features conform well with the spatially implicit assumptions of metapopulation theory, leaving little room for consideration of edge effects, connecting corridors, and patch context (see Wiens 1997). The situation for Harlequin Ducks, however, is distinct from the majority of previous metapopulation studies, as they are migratory and are only present on the breeding streams for 2 - 4 months of the year. Interestingly, they aggregate on wintering grounds and therefore individuals from different breeding sub-populations intermingle (Smith et al. 2000). Therefore, there is population structure on both breeding and wintering grounds, but these structures are not carried over between these seasons (see Esler 2000). Satellite telemetry data (Brodeur et al. in press) indicates that Harlequin Ducks breeding in the study area likely winter in southwest Greenland. In this case I expect similar wintering conditions and overwinter survival rates for birds breeding in northern Labrador. Therefore, demographic differences between sub-populations during the breeding season are most likely related to processes on individual breeding rivers.

In order for metapopulation dynamics to occur, some degree of dispersal of individuals among sub-populations must occur, but not total mixing (Hanski and Gilpin 1991). Although Harlequin Ducks exhibit high philopatry and site fidelity, this is not absolute, and there is direct evidence of dispersal to nearby river systems among years (Robertson and Goudie 1999). As site persistence varied among river systems, I anticipated differences in the specific dispersal characteristics of these sub-populations. Newton (1998) noted that carrying capacities may be reached when population numbers have stabilized between years, despite large numbers of potential settlers. These features were observed on a high quality (Ikadlivik) river system, indicating some emigration dispersal. Conversely, two low quality river systems showed population increases not accountable to local reproductive output, indicating immigration in some years. These low quality river systems also approached local extinction in some years. Other research indicates small populations are susceptible to local extinctions due to stochastic events alone (Schoener and Spiller 1987, Hanski 1999), however the observed increases suggest that immigration may provide a 'rescue effect' in some years (Brown and Kodric-Brown 1977, Hanski 1985). Decreases in these sub-populations could be due to either mortality or emigration (see Morris 1991).

These features are not only consistent with a metapopulation framework, but suggest that high and low quality populations may function as 'Sources' and 'Sinks', respectively (see Pulliam 1988, Pulliam and Danielson 1991). That population variability was higher in putative source than in putative sink populations is also consistent with demographic models of source-sink dynamics that incorporate stochastic variation (Howe et al. 1991). Demonstrating that a metapopulation exhibits source-sink dynamics is difficult and empirical evidence in limited (Davis and Howe 1992, Watkinson and Sutherland 1995, Ritchie 1997). Given the large spatial scale of this study, it would be practically impossible to measure all demographic features in every sub-population, however I argue that the present results conform well to the conceptual ideas envisioned by Pulliam and Danielson, and I therefore avoid semantic arguments over when it is appropriate to use the terms 'source' and 'sink'. I note that river systems with intermediate densities, population variability and site persistence were also observed, and may not fit into discrete high/low quality or source/sink categories. Discrete categories are likely irrelevant in natural ecological systems, and I therefore suggest that the overall population may be more accurately described as a source-sink gradient of sub-populations (for example, intermediates could be pseduosinks; see Watkinson and Sutherland 1995).

Although source populations are of primary importance, sink populations could still play an important role in overall population dynamics. Morris (1991) has argued that emigration from sources to sinks is only evolutionally stable if reverse migration back to the source occurs. Birds in secondary (sink) habitats may therefore provide a buffer of potential immigrants that can fill gaps in primary, source habitats (Brown 1969, Fretwell 1972). Models of this pattern of sequential habitat occupancy predict greater stability in primary as compared to secondary habitat (Newton 1998), again consistent with results. It is therefore possible that inexperienced birds may be restricted to sink populations until adequate experience is gained (e.g. see Gauthreaux 1988); if this is true, then these seemingly poor quality areas may be critical for recruitment into the breeding population (Davis and Howe 1992, Kacelnik et al. 1992). An assessment of Harlequin Duck age structure between potential source and sink rivers would effectively test this prediction.

2.5.2. *The Influence of Predation Risk on Population Structure*

In my opinion the most convincing argument when applying source-sink metapopulation theory to natural systems should involve identifying an underlying ecological mechanism responsible for differences among sub-populations. Avian predator density varied considerably among river systems, and was correlated with available cliff nesting sites, suggesting that nest sites are a limiting factor to birds of prey in this region (see also Janes 1985). Results of this study suggest that avian predators are a major limiting factor that influence Harlequin Duck habitat quality and demographics among river system sub-populations. Population density, stability and site persistence all decreased with increasing avian predator density. Several avian species nest at low densities near nests of birds of prey (Newton 1998), and predators can maintain some populations below the carrying capacity dictated by resource levels (Lack 1954, Martin 1991, Newton 1993, 1998). A comparison of habitat variables relevant to Harlequin Ducks between putative source and sink river systems (with respective low and high densities of raptors) indicated no differences in biophysical habitat features or prey availability. This provides support for the hypotheses that birds of prey can limit Harlequin Ducks in areas of otherwise suitable habitat, and influence population dynamics at the landscape scale (see Chapter 4 for further evidence for exclusion from suitable habitat).

There has been much interest in the stabilization of predator-prey dynamics through spatial sub-division (Vandermeer 1973, Karieva 1990, Taylor 1990, 1991, Karieva and Wennergren 1995). Predators and prey or competing species may coexist through spatial segregation (Comins and Noble 1985, Hassell et al. 1994) and top predators have been shown to influence densities of island sub-populations of prey species (Schoener and Toft 1983). The fact that predation risk may limit Harlequin Duck populations has important implications for understanding the species' demographics, in particular as a small increase in adult mortality can substantially affect overall population stability (Goudie et al. 1994, Pulliam et al. 1992). Incidental reports indicate raptorial birds can kill Harlequin Ducks (see summary in Heath et al. in press; Appendix A-1); however, even if predation rates are low, the perceived threat may be adequate to influence habitat selection. I suggest that the presence of avian predators may be a major factor that determines source and sink habitats for Harlequin Ducks within this eco-region, with sources for Harlequin Ducks occurring in refuges from predation risk, where nest sites for raptors are limited. Alternate prey for raptors can allow their stability and may permit Harlequin Ducks to function as a single species metapopulation (see Harrison and Taylor 1997).

2.5.3. *Conservation and Management Implications*

The suggestion that breeding Harlequin Ducks display metapopulation structure and exhibit source sink dynamics has important implications for the conservation and management of this species at risk. Conservation of source populations and their habitats is critical in maintaining regional stability of populations at the landscape level (Howe et al. 1991, Pulliam et al. 1992), while sink populations could also be important transition habitat and/or increasing the size and persistence of the overall population (Howe et al. 1991, Morris 1991, Pulliam and Danielson 1991, Kacelnik et al. 1992). Conservation efforts must therefore be based on a landscape approach, as habitat loss on one river system can disproportionally influence the overall population. The results of this study are particularly important in understanding population demographic processes and gene flow for this species and provides a new understanding of how populations of migratory and riparian species may function across the landscape.

2.6. ACKNOWLEDGEMENTS

Many people contributed to different aspects of this research. Thanks to Joe Brazil of the Newfoundland and Labrador Wildlife Division, Major Humphries and Tony Chubbs of the Department of National Defence (DND) and the Voisey's Bay Nickel Company (VBNC), all of whom contributed to significant portions of the survey data that made this study possible. Thanks also to Perry Trimper and Kathy Knox of Jacques Whitford Environment Ltd. for providing the raw data from surveys for both DND and VBNC. Thanks to Shauna Ballie for assistance collecting the habitat data. Funding for research in Labrador (habitat and aerial surveys) was provided by the Provincial Wildlife Division of Newfoundland and Labrador c/o Joe Brazil, an Endangered Species Recovery Fund grant of World Wildlife Fund Canada to WAM, a Northern Scientific Training Program (NSTP) grant to JPH, S. Ballie and WAM, an NSERC Individual Operating Grant to WAM, and support from the Mountain Equipment Co-op Environment Fund to JPH. Thanks also to Ian Goudie and Dave Schneider for commenting on various drafts of this manuscript, and to Geoff Goodyear of Universal Helicopters who is by far the best survey pilot a researcher could hope for.

Plate 2-1. Photograph of the Fraser River, northern Labrador, illustrating the location of river systems within canyons (A) surrounded by high sub-arctic plateau (B).

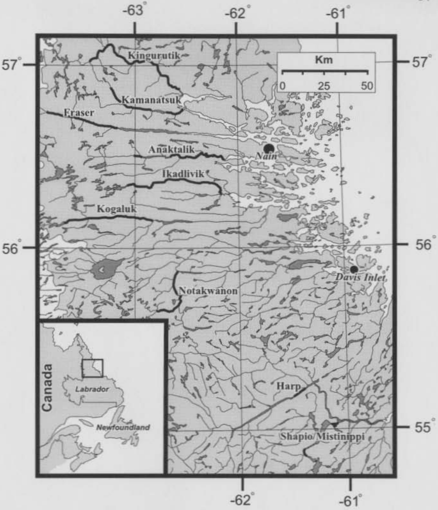

Figure 2-1. Location of study area in northern Labrador. Survey rivers are labelled and approximate survey routes along rivers are bolded (surveys for birds of prey were also conducted along adjacent lakes). River systems in this region are generally located in canyons, which are separated by extensive areas of sub-arctic plateau.

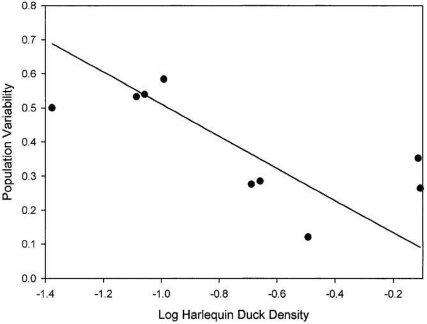

Figure 2-2. Relationship between Harlequin Duck densities (log) and population variability for nine river systems (circles) in the Fraser-Kingurutik eco-region, northern Labrador. The line is a principal axis (Sokal and Rohlf 1995).

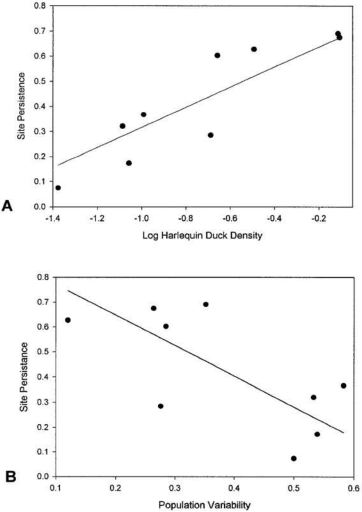

Figure 2-3. Relationships of site persistence with Harlequin Duck densities (log; A) and population variability (B) for nine river systems (circles) in the Fraser-Kingurutik eco-region, northern Labrador. Lines are principal axes (Sokal and Rohlf 1995).

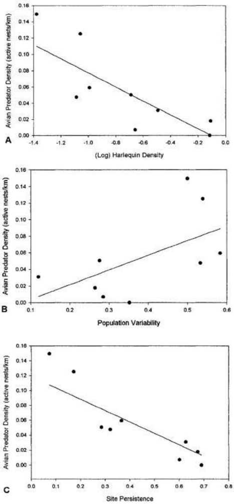

Figure 2-4. Functional relationship of densities of birds of prey and the density (log; A), population variability (B) and site persistence (C) of Harlequin Ducks on nine river systems (circles) in the Fraser-Kingurutik eco-region, northern Labrador. Lines were determined using functional regression (Ricker 1973, Sokal and Rohlf 1995).

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2.8. APPENDIX 2-A

The following is a description and example calculation of the index of site persistence (P) on a river system. Site persistence is defined as the consistent reuse of sites among years on a particular river system by members (pairs) of the sub-population present in each year. Descriptions and mathematical definitions are presented and refer to tables that contain relevant example calculations. Table 2-A1 summarizes the definitions of symbols presented in this appendix. A summary of the total number of pairs observed in each survey year, and the numerical symbol which will be used to identify each survey year are presented in Table 2-A2. Example survey data are in Figure 2-A1 for each site where a pair was ever observed. For example, at site 3 one pair was observed in 1996 and two pairs in both 1998 and 1999.

I first define y as the number of years a river was surveyed (see Table 2-A2), and $\boldsymbol{k}$ as the different possible ways of comparing y years (therefore $\boldsymbol{k} = 2 \ldots y$; e.g. if $\boldsymbol{k} = 2$, then compare two years at a time; if $\boldsymbol{k} = 3$, compare three years at a time, etc.). ${}_yC_k$, the possible ways of comparing years at level k is calculated as:

$$ {}_yC_k = \binom{y}{\boldsymbol{k}} = \frac{y!}{(y-\boldsymbol{k})!\,\boldsymbol{k}!} \qquad \text{(A-1)} $$

I further define $\boldsymbol{List_i}$ as the list of ${}_yC_k$ comparisons, where $\boldsymbol{i}$ identifies each individual comparison (and therefore $\boldsymbol{i} = 1 \ldots {}_yC_k$; see Table 2-A3). I then calculate the maximum possible number of site persistence events (M_k) for each comparison level (***k***) as:

$$M_k = \sum^{i=1\ldots{}_yC_k} S_{i,k} \qquad \text{(A-2)}$$

where $S_{i,k}$ is the smallest population size for the i^{th} comparison at level ***k*** (the smallest population size $S_{i,k}$ of the years being compared is obtained from Table 2-A2; see Table 2-A4 with reference to Table 2-A3 for further explanation). The observed site persistence (O_k) at each level ***k*** is taken from the raw data (Figure 2-A1; e.g. when $\boldsymbol{k} = 3$, O_k is the number of instances in which a site was reused by a pair between three survey years, i.e. $O_3 = 8$ in this case). Note, however, that lower levels of ***k*** are intrinsically included in higher levels of ***k*** (for example the level $\boldsymbol{k} = 3$ includes three comparisons at the level $\boldsymbol{k} = 2$). O_k must therefore be adjusted for site persistence included within higher levels of ***k***. This adjusted O_k (labelled O_k^*) can be calculated as (see Table 2-A5):

$$O_k^* = \sum^{q=0\ldots(y-k)} (R \cdot O_{(k+q)}) \qquad \text{(A-3)}$$

where ***q*** is added to ***k*** to describe higher levels of ***k*** (therefore $\boldsymbol{q} = 0\ldots(y\text{-}\boldsymbol{k})$; note that $(\boldsymbol{k} + \boldsymbol{q})$ can be considered as a single number that equals a value of ***k*** as originally defined). R is the number of ***k*** level comparisons included in the level $(\boldsymbol{k} + \boldsymbol{q})$ and is calculated as:

$$R = \binom{(k+q)}{k} = \frac{(k+q)!}{[(k+q)-k]!\,k!} = \frac{(k+q)!}{q!\,k!} \tag{A-4}$$

P_k, site persistence at level k, is then calculated as:

$$P_k = \frac{O_k^*}{M_k} \tag{A-5}$$

and the site persistence P for the entire river, over all comparison levels may be described as the average of the site persistence scores (P_k) at each level of k (see table 2-A6):

$$P = \overline{P_k} = \frac{\sum^{k=2\ldots y} P_k}{y-1} \tag{A-6}$$

P is therefore a proportion which represents the degree of consistent site-reuse between years by the pairs present on the river in each survey year, and is not biased by sub-population size or variability between years. It has often been difficult to find an appropriate currency for habitat quality that incorporates all ecologically relevant aspects. I suggest that this index is a good indicator of river system (i.e. sub-population) habitat quality, as it reflects the influence of a variety of ecological features that can affect philopatry and dispersal behaviour, and results of this index for the present study were related to both population density and stability (see text). The basic outcome of this method is an index of philopatry to home ranges, within sub-populations. Many studies of philopatry focus on return or homing rates of individuals, however, reformulated to a habitat perspective it may be defined as the consistent use of habitat (the essence of the above index).

Table 2-A1. Definition of terms presented in calculating the index of site persistence.

Symbol	Definition
y	Number of years the river system was surveyed
$\boldsymbol{k}$	Possible ways of comparing y years ($\boldsymbol{k} = 2 \ldots y$)
${}_yC_k$	Number of possible ways of comparing years at level $\boldsymbol{k}$
$\boldsymbol{List_i}$	Listof ${}_yC_k$ comparisons ($\boldsymbol{i}$ identifies each individual ${}_yC_k$ comparison so $\boldsymbol{i} = 1 \ldots {}_yC_k$)
M_k	Maximum possible number of site persistence events for each comparison level $\boldsymbol{k}$
$S_{i,k}$	Smallest population size between years being compared ($\boldsymbol{List_i}$ at each level of $\boldsymbol{k}$)
O_k	Observed site persistence at each level $\boldsymbol{k}$
O_k^*	Observed site persistence at each level k adjusted for observed site persistence included within higher levels of k
$\boldsymbol{q}$	List of numbers [$\boldsymbol{q} = 0 \ldots (y-\boldsymbol{k})$] added to $\boldsymbol{k}$ to identify higher levels of $\boldsymbol{k}$
R	Number of level $\boldsymbol{k}$ comparisons included in the level ($\boldsymbol{k}+\boldsymbol{q}$)
P_k	Site persistence at level $\boldsymbol{k}$
P	Site persistence for the entire river (average of site persistence at each level $\boldsymbol{k}$)

Table 2-A2. Summary of number of pairs of Harlequin Ducks observed on hypothetical river surveys over four years. The numerical symbol will be used to identify each year in other tables within this appendix. Note that $y = 4$ and therefore $\boldsymbol{k} = (2,3,4)$.

Year	Symbol	Total pairs observed
1996	6	17
1997	7	14
1998	8	16
1999	9	10

Table 2-A3. Example calculation of equation A-1; e.g. at $\boldsymbol{k} = 3$, four comparisons can be made (${}_{y}C_{\mathbf{k}} = 4$) and these comparisons (***List***$_i$) are listed in the far right column (for ***List***$_i$ each numeral represents a survey year; see Table 2-A2).

$\boldsymbol{k}$	$\binom{y}{\boldsymbol{k}} = \frac{y!}{(y-\boldsymbol{k})!\boldsymbol{k}!}$	${}_{y}C_{k}$	***List***$_i$
4	$\frac{4!}{(4-4)!4!}$	1	6-7-8-9
3	$\frac{4!}{(4-3)!3!}$	4	6-7-8; 6-7-9; 6-8-9; 7-8-9
2	$\frac{4!}{(4-2)!2!}$	6	6-7; 6-8; 6-9; 7-8; 7-9; 8-9

Table 2-A4. Calculation of the maximum possible number of site persistence events (M_k) at each level of ***k***, is obtained by summing the smallest population size *S* between the years being compared (***i***, see ***List****ᵢ* in Table 2-A3, and refer to Table 2-A2 to obtain population sizes in each year.

k	$\sum^{i=1...,yC_k} S_{i,k}$	M_k
4	10	10
3	14+10+10+10	44
2	14+16+10+14+10+10	74

Table 2-A5. Calculation of the observed (O_k) and adjusted (O_k^*) number of site persistence events at each level of ***k***. O_k is calculated by counting the number of ***k*** - year resightings from Table 2-A2 and is adjusted (O_k^*) for level ***k*** observations included in higher level of ***k*** by equations A-3 and A-4.

k	O_k	$\sum^{q=0...(y-k)} (R \cdot O_{(k+q)})$	O_k^*
4	4	4(1)	4
3	8	8(1)+4(4)	24
2	4	4(1)+8(3)+4(6)	52

Table 2-A6. Site persistence P_k at each level of $\boldsymbol{k}$ is calculated using equation A-5 (see Tables 2-A4 and 2-A5), and overall site persistence P for the river is calculated as the average of each P_k, as per equation A-6.

$\boldsymbol{k}$	$\frac{O_k^*}{M_k}$	$\boldsymbol{P_k}$
4	36990	0.4
3	24/44	0.545
2	52/74	0.703

$P = \overline{P_k} = 0.549$

Site 1	Site 2	Site 3	Site 4	Site 5
67	678	89 689	69 6789	68 6789

Site 6	Site 7	Site 8	Site 9	Site 10
6 6 6789 6789	7	7 789	679	8 8 678 678

Site 11	Site 12	Site 13	Site 14
679	8 678	8	6

Figure 2-A1. Example data of survey results for each site at which Harlequin Ducks were observed. Each numeral represents a pair observation in the year indicated in Table 2-A2 (i.e. 6=1996, 7=1997 etc.).

2.9. APPENDIX 2-B [Formatted as a Digital Appendix fo Publication Purposes]

Comparison of the availability of habitat features between a suggested source (Ikadlivik) and sink (Fraser) river system in northern Labrador, based on 12 randomly selected sample sites per river. See Robertson and Goudie (1999) and Rodway et al. (2000) for summary of research on habitat features relevant to Harlequin Ducks. These results indicated no differences in habitat and prey availability between river systems, providing support for the hypothesis that birds of prey exclude Harlequin Ducks from suitable habitat. See the methods section of the text for a detailed description of habitat parameters.

Habitat Parameter		Fraser River		Ikadlivik River		Statistics		
		Mean	SE	Mean	SE	t	df	p
Riparian Vegetation	% Alder	49.17	6.82	44.17	5.85	0.39	22	0.698$_{NS}$
	% Mature Tree	39.17	11.71	9.17	2.17	1.78	12	0.100$_{NS}$
	% Non-Vegetated	19.58	7.35	22.08	5.96	-0.19	21	0.854$_{NS}$
General Vegetation	% Alder	7.50	1.54	8.75	2.92	-0.27	17	0.792$_{NS}$
	% Mature Tree	81.67	3.97	74.58	5.06	0.78	21	0.445$_{NS}$
	% Shrubs to Rocks	10.83	3.31	16.67	4.63	-0.72	20	0.477$_{NS}$
Discharge Characteristics	Mean Depth	88.78	4.93	66.77	3.39	2.60	20	0.017$_{NS}$
	Mean Width	34.06	2.59	33.89	1.71	0.04	19	0.970$_{NS}$
	Surface Velocity (m/s)	1.30	0.10	1.09	0.12	0.92	21	0.367$_{NS}$
	Mean Bank Gradient	26.88	2.94	26.67	4.13	0.03	20	0.977$_{NS}$
	Gradient	2.60	0.26	2.50	0.16	-0.67	17	0.512$_{NS}$
Water Characteristics	% Rapids	18.33	6.14	37.50	7.78	-1.37	21	0.186$_{NS}$
	% Riffles	6.25	3.34	4.17	1.37	0.41	15	0.689$_{NS}$
	% Runs	68.25	7.32	37.92	7.12	2.10	22	0.047$_{NS}$
	% Slow Water	7.17	2.86	14.58	5.86	-0.80	16	0.433$_{NS}$
Protection and Loafing Habitat	% Overhang Vegetation	47.00	7.17	35.83	4.62	0.93	19	0.366$_{NS}$
	Total Islands	0.67	0.29	0.50	0.14	0.36	16	0.721$_{NS}$
	Total Mature and Alder Islands	0.42	0.24	0.25	0.13	0.44	17	0.667$_{NS}$
	% Exposed Banks	22.25	5.58	5.42	3.00	1.88	17	0.078$_{NS}$
	Total Exposed Boulders	10.58	4.32	24.17	4.59	-1.52	22	0.142$_{NS}$
Substrate	% Large Boulders	6.50	2.93	2.92	1.11	0.81	14	0.433$_{NS}$
	% Small Boulders	21.67	4.73	24.17	3.19	-0.31	19	0.760$_{NS}$
	% Rubble	25.00	3.56	35.00	3.29	-1.46	22	0.159$_{NS}$
	% Cobble and Pebble	15.58	4.73	9.17	2.42	0.85	16	0.406$_{NS}$
	% Sand and Mud	9.17	2.75	10.00	4.13	-0.12	19	0.907$_{NS}$
Invertebrates	Total Invertebrates	42.00	4.73	55.00	8.47	-1.01	17	0.328$_{NS}$
	Total Trichoptera	0.67	0.25	0.83	0.41	-0.25	18	0.808$_{NS}$
	Total Plecoptera	6.17	1.72	4.58	1.45	0.50	21	0.623$_{NS}$
	Total Ephemeroptera	11.25	2.90	8.83	2.49	0.45	22	0.659$_{NS}$
	Total Diptera	20.42	2.48	36.75	4.89	-2.10	16	0.052$_{NS}$
	Total Simulids	2.00	0.48	11.50	3.10	-2.14	12	0.053$_{NS}$
	Total Chironomids	18.17	2.43	24.00	4.00	-0.88	18	0.390$_{NS}$

Note: All comparisons are 2-tailed t-tests for unequal variance. Significance was determined using a sequential bonferonni correction (Rice 1989); NS=not significant.

3.0. CHAPTER 3: CO-EXISTENCE OF PREDATORS AND PREY ALONG A SOURCE-SINK GRADIENT: A SPATIALLY EXPLICIT APPROACH[3]

3.1. ABSTRACT

The spatial nature of the environment can play an important role in population dynamics and coexistence of competitors, hosts/parasitiods and predators/prey, however effects may be scale dependent. In northern Labrador, river canyons structure Harlequin Duck populations across the landscape, however putative source and sink sub-populations were related to the presence of nest site limited raptorial birds. A spatially explicit GIS model is used to show spatial segregation of ducks and raptors at the landscape and within population scales over several years. Proximity to predators also influences inter-annual use of duck breeding sites, but the effect is dependent on the demographic status of the sub-population. Spatial coexistence theories can therefore be informative in natural systems if multiple scales and species specific ecological and behavioural constraints are considered.

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[3]

This chapter will be submitted as Joel P. Heath, Joe Brazil, and William A. Montevecchi. Co-existence of predators and prey along a source-sink gradient: a spatially explicit approach

3.2. INTRODUCTION

Consideration of scale and the spatial environment are important for both ecologists and land managers as patchiness or heterogeneity occurs at several spatial scales, organisms respond to ecological factors at multiple scales, and different scales of investigation can yield different results (Wiens 1989, Kotliar and Wiens 1990, Orains and Wittenberger 1991, Levin 1992, Amarasekare 1994, Schneider 1994, Turner et al. 1995). Theory indicates that spatial dynamics can allow coexistence and stabilize competitive, host-parasitoid and predator-prey interactions, however empirical evidence is generally lacking (Vandermeer 1973, Kareiva 1990, Taylor 1990, 1991, Hassell et al. 1994, Kareiva and Wennergren 1995, but see Schoener and Toft 1983). The landscape on northern Labrador provides an ideal situation for studying population structure in a spatially implicit metapopulation context; Harlequin Ducks are structured within glacially carved river canyons, interspersed within a featureless matrix of sub-arctic plateau, leaving little room for many landscape ecology paradigms (Wiens 1997), including boundary effects, connectivity and patch context. High vagility of Harlequin Ducks make inter-patch distances relatively insignificant upon arrival at the breeding grounds, however a high degree of philopatry and site fidelity(Robertson and Goudie 1999) can allow metapopulation dynamics to occur (Esler 2000, Chapter 2). Previous research indicated source-sink metapopulation dynamics among river systems. Putative source and sink populations did not differ in biophysical habitat features, but occurred in areas of high and low densities of raptorial birds, respectively. Raptor densities were directly related to the availability of cliff nesting habitat (Chapter 2).

Specific objectives for the present research were to investigate spatial segregation of birds of prey and Harlequin Ducks: 1) at the landscape scale by applying a spatially explicit approach to the spatially implicit metapopulation framework previously developed, 2) at the within sub-population scale, across the source-sink gradient, and 3) to evaluate if birds of prey influence the inter-annual use of breeding sites by Harlequin Ducks.

3.3. METHODS

Aerial surveys for Harlequin Ducks and birds of prey (Peregrine Falcon *Falco peregrinus*, Gyrfalcon *F. rusticolus*, Golden Eagle *Aquila chrysaetos* and Great-Horned Owl *Bubo virginianus*) were conducted on nine river systems in northern Labrador (Figure 3-1) between 1992 and 2000 (detailed methods are presented in Chapter 2). All active raptors nests, Harlequin Duck sightings and survey routes were analysed with MapInfo v.5 (MapInfo Corporation 1998). Considering breeding birds of prey as central place foragers from the nest-site, I used raptor home range (*HR*) sizes from the literature (Palmer 1988, Peery 2000) to calculate the foraging range (*FR*) of each species as:

$$FR = \sqrt{\frac{HR}{\pi}} \qquad (1)$$

where the foraging range *FR* represents the maximum linear travel distance, in all directions, from each raptor nest site (*FR* was 12.7 km for Peregrine Falcon; 13.6 km for Gyrfalcon, 3.48 km for Golden Eagle, and 2.82 km for Great-Horned Owl). The predator proximity (P_i) of each raptor pair (total raptor pairs/nests = i) to each Harlequin Duck pair, for each survey year (i.e. within years) was calculated as:

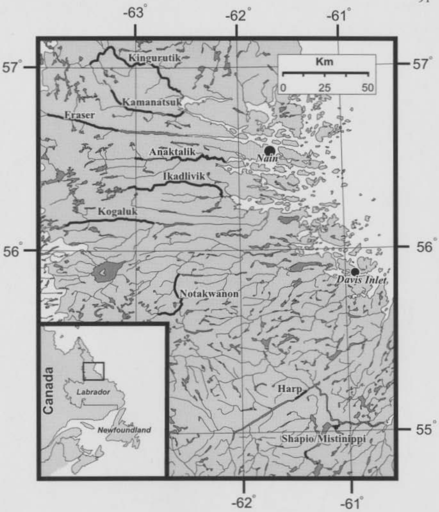


Figure 3-1. Location of study area in northern Labrador. Survey rivers/populations are labelled and approximate survey routes are bolded (surveys for birds of prey were also conducted along adjacent lakes). River systems in this region are generally located in glacially carved canyons, which are separated by extensive areas of sub-arctic plateau.

$$D \leq 1\text{km}, P_i = 1 \tag{2a}$$

$$FR_i \geq D > 1\text{km}, P_i = \frac{1}{(D / FR_i)^2} \tag{2b}$$

$$D > FR_i, P_i = 0 \tag{2c}$$

where D is the observed linear distance between a Harlequin Duck pair and a raptor nest. P_i was assigned a value of 1 if the Harlequin Duck was observed within 1 km (half of the average Harlequin Duck home range size; see Robertson and Goudie 1999, Section 1.1.1) of the raptor nest (equation 2a) and a value of 0 if the observed distance D was greater than the raptor's i foraging range (FR_i; equation 2c). Between these extremes, predator proximity P_i was considered to decrease exponentially as distance D increased, i.e. a $(1/D)^2$ function, normalized for differences in each raptor species' foraging range (equation 2b). Overall predator proximity (PP) for each Harlequin Duck was calculated as the total P_i due to each raptor pair:

$$PP = \sum^{i} P_i \tag{3}$$

The objective of this analysis was to determine if Harlequin Ducks avoid areas with high predation risk when selecting breeding sites. This was assessed statistically by comparing the predator proximity PP at observed Harlequin Duck locations to the PP that would occur by random habitat selection. To determine PP due to random habitat selection with respect to raptors, river survey routes for Harlequin Ducks were partitioned into points at 100 m intervals (considered to be a fine enough resolution as survey results likely had an error of approximately 100 m based on plotting locations on 1:50,000 maps). Random sites were determined by randomly sampling from these points 5,000 times for each analysis, and an overall predation pressure *PP* score was calculated for each random site using equations 2 and 3. This calculation therefore produced *PP* scores in accordance with the null hypothesis that Harlequin Ducks were randomly distributed with respect to raptors. Absolute cumulative frequency distributions of overall predator proximity scores *PP* and the number of Harlequin Ducks were constructed for observed and random conditions, based on the number of Harlequin Ducks observed on that river(s). Bins for the frequency distribution were defined as $PP \leq 0$, 0.01, 0.01234, 0.01563, 0.02041, 0.02778, 0.04, 0.0625, 0.0111, 0.025, 1, and > 1 (i.e. 0, $1/(1...10)^2$, >1), in order to maintain consistency between comparisons and to correspond to the manner in which predator proximity scores were calculated (see equation 2). Cumulative frequency distributions were then compared using two-sample Kolmogorov-Smirnov tests in SPSS v.10 (SPSS 1999). Analyses were conducted within each river system in years that both Harlequin Ducks and birds of prey had been surveyed. River systems were categorized a priori as putative source, sink and intermediate, based on previous research (Chapter 2). I did not feel confident in placing the Kamanatsuk and Anaktalik populations into any category, and therefore left them unclassified. I also conducted the above analysis for the entire region (i.e. all sub-populations considered together), however for this landscape scale analysis, the resolution of random points was changed from 100 m to 1 km (half an average Harlequin Duck home range) to reflect coarser environmental grain at the landscape scale.

To assess influences of predator proximity on Harlequin Duck sites among years, I calculated the temporal persistence of each raptor nest (years present / years surveyed) and multiplied this proportion by the predator proximity score P_i for that nest (i) before summing in equation 3. 'Sites' used by Harlequin Ducks were determined by overlaying survey data for all years (as per Chapter 2; this is important as no distinct physical boundaries are present among patches at the home range scale. This method defines home range scale sites in terms of how the population occupies space over time, with consideration of movement behaviour/home range size from previous radio-telemetry studies). Polylines therefore represented sites, instead of points as in the within-year analysis. Distances D from raptor nests were therefore calculated as the mean of the centroid and minimum distances to each Harlequin Duck site polyline in order to consistently account for differences in the size and shape of sites. G-tests were used to evaluate if sites in source, sink and intermediate populations differed from the overall population, in terms of inter-annual use and predator proximity.

3.3. RESULTS AND DISCUSSION

3.3.1. Within-Years Analysis

At the landscape scale, which considers all river systems, Harlequin Ducks occupied sites with lower predator proximity than expected by chance alone (1994, 384 km of river considered: Komologrov Smirnov Z [KS-Z] = 1.837, Most extreme difference [MED] = -0.75, $p < 0.001$; 1997, 397 km of river considered, KS-Z = 1.663, MED = -0.67, $p < 0.001$). This spatially explicit result supports previous research from a spatially implicit approach

(Chapter 2) that indicated spatial segregation from birds of prey and its influence on source-sink dynamics of Harlequin Ducks. Analyses were also conducted at the within river system (sub-population) scale, along the source-sink gradient (Table 3-1). For putative source populations, no difference was observed consistently, indicating that birds of prey had no influence on habitat use by Harlequin Ducks within these sub-populations. This result was driven by the low (sometimes 0) density of avian predators in these river systems. Overall, predator proximity appeared to play no major role in putative sink populations either, owing to low densities of Harlequin Ducks and relatively high predator proximity at all potential sites within these river systems. Birds of prey did not appear to influence home range selection within unclassified sub-populations either. In contrast, spatial segregation from birds of prey was consistently found within the intermediate sub-population (Kingurutik River), where intermediate densities of both birds of prey and Harlequin Ducks were present, implying that home ranges are selected in areas of low predator proximity.

3.3.2. Inter-Annual Analysis

In order to determine if inter-annual differences in predator proximity affected inter-annual use and abundance of Harlequin Ducks at each site, I plotted predator proximity among years (PP_a) against the average number of Harlequin Duck pairs per year, at each site in the study area (Figure 3-2; total sites = 67). Considering all sites together (Figure 3-2a) a distinct threshold effect can be seen. To facilitate interpretation, I partitioned this figure into quadrats based on high ($\geq$1.20 pairs/year) and low (<1.20 pair/year) inter-annual use and high ($\geq$0.22) and low (<0.22) predator proximity scores PP_a. (1.20 and 0.22 are the mean

Table 3-1. Results of the within year analysis, within each sub-population. MED = Most Extreme Difference, KS-Z = Komologrov-Smirnov Z score, p = probability of significance. Populations are grouped as putative source, sink and intermediate populations, based on previous research from a spatially implicit metapopulation approach (Chapter 2). Interpretation of results is avoidance [-], association [+] (lower or higher predator proximity scores than due to chance), or no difference [0] (no influence of predation risk on breeding site location).

Population (km considered)	Year	MED	KS-Z	p	Association
'Source'					
Ikadlivik	1996	0.333	0.82	0.518	0
(48.8 km)	1997	0.333	0.82	0.518	0
	1998	-0.33	0.82	0.518	0
Notakwanon	1994	0	0	1	0
(36.4 km)	1995	0	0	1	0
	1997	0	0	1	0
Harp	1992	0	0	1	0
(9.3 km)	1993	0	0	1	0
	1994	0	0	1	0
	1995	0	0	1	0
	1997	0	0	1	0
Shapio	1994	0.333	0.82	0.518	0
(16.4 km)	1995	0	0	1	0
	1997	-0.25	0.61	0.847	0
'Sink'					
Kogaluk	1994	0.167	0.41	0.996	0
(40.0 km)	1995	-0.1	0.2	>0.999	0
	1997	-0.33	0.82	0.518	0
	1999	0.583	1.43	0.034	+
Fraser	1994	-0.92	2.25	<0.001	-
(59.3 km)	1997	0.917	2.25	<0.001	+
	1999	-0.83	2.04	<0.001	-
'Intermediate'					
Kingurutik	1993	-0.83	2.04	<0.001	-
(89.1 km)	1994	-0.67	1.63	0.01	-
	1997	-0.67	1.66	0.01	-
Other (Unclassified)					
Kamanatsuk	1993	0.667	1.63	0.01	+
(28.1 km)	1994	0.333	0.82	0.518	0
	1997	-0.33	0.82	0.518	0
Anaktalik	1994	0.417	1.02	0.249	0
(55.0 km)	1996	-0.25	0.61	0.847	0
	1997	0	0	1	0
	1998	0.667	1.63	0.01	+

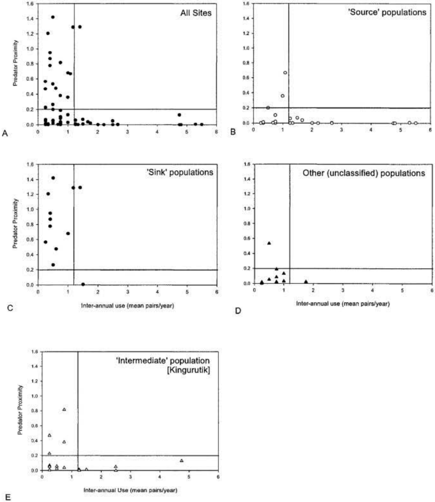
IAU and PP_a from the overall population (Figure 3-2a), respectively). High use sites had consistently low PP_a (bottom-right quadrat) and high PP_a sites showed consistently low use (top-left quadrat). The remaining sites (bottom-left quadrat) likely had low inter-annual use due to other factors influencing habitat quality, such as biophysical features and prey availability (see Chapter 4). This supported my hypothesis that proximity to birds of prey affects among-year site use by Harlequin Ducks.

The same procedure was conducted separately for sites within putative source, sink, unclassified and intermediate populations (Figure 3-2b-e, respectively). Sites in both source and sink populations were different from sites in all other populations combined ($G = 12.5$, $df = 3$, $p = 0.006$; $G = 32.9$, $df = 3$, $p < 0.001$; respectively). These relationships demonstrate that sink populations (Figure 3-2c) consist primarily of sites with low use and high PP_a (75%; top-left quadrat), while sites in source populations rarely had high PP_a (Figure 3-2b, 8%; top quadrats) and a high proportion were highly used among years (56%; bottom right quadrat). Most sites in unclassified populations showed both low use and low PP_a (Figure 3-2d, 85%; bottom-left quadrat). Interestingly, for the river system which had intermediate densities of both Harlequin Ducks and birds of prey, and which was classified as intermediate along the source-sink gradient (Kingurutik River; Figure 3-2e), the distribution of sites with respect to predator proximity and inter-annual use was the same as all remaining sites ($G = 1.05$, $df = 3$, $p = 0.789$) and therefore the overall population (Figure 3-2a). Results of the within-year analysis (Table 3-1) implied that spatial segregation of birds of prey and Harlequin Ducks occurs at the home range scale within this population. The similarity of the distribution of sites to that of the overall population raises the possibility that Harlequin Ducks within this population could demonstrate similar dynamics to that observed at the landscape scale. This can be more clearly illustrated by considering sites as 'populations' and the river system the 'landscape'. Although I have no further demographic data for sites on this river system, it is possible that source-sink structure could also apply at this within population scale (see also Amarasekare 1994). It is likely that the features of sites within populations influence population structure at the landscape scale, and (on average) determine the demographic status of each sub-population as a whole. This should not be a surprising conclusion, as small scale heterogeneity, by necessity, influences the degree of heterogeneity at larger spatial scales (Kolitiar and Wiens 1990).

Clearly there is a relationship between source-sink dynamics of Harlequin Ducks and predation risk from birds of prey in northern Labrador. Much of the research addressing this type of relationship has focused on the role of metapopulation (or spatial) dynamics in stabilizing predator-prey (or competitive/host-parasitoid) interactions. Although a valid approach, it may be equally valid to argue that it is the predator-prey interaction that influences spatial structure and metapopulation dynamics. On an otherwise homogenous ecological substrate, prey population structure could be the sole result of the predator-prey interaction (i.e. self-organized spatial dynamics; Hassel et al. 1994). Even if prey population structure is due to other factors (e.g. landscape structure, heterogeneity in biophysical habitat quality), observed metapopulation dynamics (e.g. sub-population demographic and dispersal characteristics) could be a sole result of the interaction. It may therefore be more precise to state that in some situations, metapopulation dynamics may be a prey response to predation risk, a response which may serve to stabilize the interaction and allow coexistence. It follows that predator removal may cause metapopulation effects and even population structure to decrease or disappear in some systems: a falsifiable prediction that may be tested by clever experimental design. Results of the present research imply spatial segregation of predators and prey at multiple spatial scales (landscape/metapopulation scale and within population/home range scale on the Kingurutik River), both within and among years. The role of refuges in allowing coexistence of predators and prey has long been realized (e.g. Vandermeer 1973, Sih 1987, Murdoch et al. 1989, Kareiva 1990 and references therein), and it is important to note that the refuge in the present interaction is of a purely spatial nature. Additionally, much of the theoretical research on spatial coexistence of competitors, host-parasitoids, and predators and prey consider situations analogous to a classical metapopulation framework, where both predators and prey disperse among populations (e.g. Holyoak and Lawler 1996 and see Taylor 1991). For Harlequin Ducks, a highly mobile migratory bird, inter-patch distances are likely of little relevance upon arrival at the breeding grounds, and philopatry can allow metapopulation structure (Esler 2000). Dispersal of birds of prey among years is likely limited by availability of suitable cliff nesting habitat (Chapter 2, Janes 1985), however it is unlikely that birds of prey rely on Harlequin Ducks populations, as other prey species are available. This, combined with the central place foraging behaviour of birds of prey from the nest-site, provides a spatial refuge (areas with a low probability of predator encounter) for Harlequin Ducks, which allows stability (and existence) of this predator-prey interaction at both the landscape and home range scales (see Vandermeer

1973, Kareiva 1990). Incorporation of such species-specific ecological and behavioural constraints will be important in applying spatial coexistence theories in natural populations (Kareiva 1987).

Figure 3-2. The relationship between predator proximity (among years) PP_a and inter-annual use (mean pairs/year) *IAU* of Harlequin Ducks breeding sites in northern Labrador for all populations (A), "source" populations (B), "sink" populations" (C), unclassified populations (D) and in an "intermediate" population (E). Horizontal and vertical lines indicate the mean for each axis from the overall population (A) and were used to classify sites as high or low PP_a and *IAU* respectively (see text).


All Sites
Predator Proximity
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0
1
2
3
4
5
6
A
'Source' populations
B
'Sink' populations
Predator Proximity
Inter-annual use (mean pairs/year)
C
Other (unclassified) populations
Inter-annual use (mean pairs/year)
D
'Intermediate' population
[Kingurutik]
Predator Proximity
Inter-annual Use (mean pairs/year)
E

3.4. ACKNOWLEDGEMENTS

Thanks to Major Humphries and Tony Chubbs of the Department of National Defence and the Voisey Bay Nickel Company for providing additional survey data on Harlequin Ducks and raptors, and to Perry Trimper and Kathy Knox of Jacques Whitford Environment Ltd. for assistance in providing the raw survey data. Thanks to the Labrador Inuit Association for their support. A special thank you to Larry Nolan of Datasolutions for a great job in programming the MapBasic randomization routines exactly the way I wanted. Thanks to Greg Robertson, Dave Schneider and Ian Goudie for comments and useful discussions at various stages of this research. Thanks to Dave Fifield for direction in programming databases and to Christina Snow for assistance with data entry, and to the Labrador Inuit Association (Nain) for their support. Funding was provided by the Newfoundland and Labrador Provincial Wildlife Division c/o JB, an Endangered Species Recovery Fund of World Wildlife Fund Canada to WAM, Northern Scientific Training Program support to JPH and WAM, Mountain Equipment Co-op Environment Fund support to JPH, a Society of Canadian Ornithologists research (Taverner) award to JPH and an NSERC individual operating grant to WAM.

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4.0. CHAPTER 4: FACTORS INFLUENCING HOME RANGE USE BY BREEDING HARLEQUIN DUCKS WITHIN SOURCE AND SINK SUB-POPULATIONS.[4]

4.1. ABSTRACT

Previous work indicated the importance of predation risk in determining population structure of Harlequin Ducks among, and within some, river system sub-populations in northern Labrador. For the present study, I evaluated the importance of small scale habitat features and prey availability within putative source (Ikadlivik River) and sink (Fraser River) populations, with respective low and high densities of avian predators. I use multivariate analysis to identify differences between used and unused sections of the Ikadlivik River and used this analysis to develop a habitat suitability index for breeding Harlequin Ducks. Habitat characteristics indicated as being important were generally consistent with previous research; however, these findings highlight the importance of a multi-scale approach and downplay the importance of prey limitation. A concurrent analysis on the Fraser River revealed that many habitat associations that were important on the Ikadlivik River were not significant for this sink sub-population. Additionally, when I applied the habitat suitability index to sites on the Fraser River, several unused sites were mis-classified, which was likely due to tradeoffs between habitat/prey quality and predation risk from nesting birds of prey. These results support the prediction of Watkinson and Sutherland that habitat studies in sink

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[4] This chapter will be submitted for publication as Heath, J. P. and Montevecchi, W.A. Factors influencing home range use by breeding Harlequin Ducks in source and sink sub-populations.

populations may be misleading. Findings also emphasized the importance of considering population structure across the landscape when investigating intra-population features, particularly for highly mobile species. These results and habitat suitability indices will be important in understanding distributions of Harlequin Ducks, and therefore in conservation and management strategies for this species.

4.2. INTRODUCTION

The selection of suitable habitat during the breeding period is essential as both proximate survival and ultimate fitness must be achieved. These considerations require selection of breeding sites with appropriate shelter from predation and environmental conditions, and sufficient food supplies for both parents and offspring (Cody 1985).

Scale has become an increasingly important consideration throughout the field of ecology (Levin 1992, Wiens 1989, Schneider 1994, 2001). This is particularly important when studying migratory birds, as habitat selection may be a hierarchical process from landscape through to nest-site scales (Kaminski and Weller 1992), and the importance of particular habitat features may depend on the scale of analysis (Orians and Wittenberger 1991). Additionally, in the related fields of landscape and metapopulation ecology, populations may exhibit well defined scale-dependent spatial structure that influences the distribution and dynamics of the overall population (Kareiva 1990, Hanski and Gilpin 1991, Kareiva and Wennergren 1995, Wiens 1997, Hanski 1999). Particularly for research conducted at smaller spatial scales, consideration of landscape and population features are essential for understanding local dynamics and their role in ecosystem processes. For example, if the overall population exhibits source-sink dynamics (Pulliam 1988, Pulliam and Danielson 1991), habitat studies in sink sub-populations could lead to incorrect information about a species' habitat requirements (Watkinson and Sutherland 1995).

A number of researchers have investigated habitat requirements of breeding Harlequin Ducks, in various parts of their global range (see Robertson and Goudie 1999 and Section 1.1.1.), but none have explicitly considered the importance of scale and population structure. In previous research (Chapters 2 and 3), I presented evidence that Harlequin Ducks breeding in northern Labrador exhibit source-sink metapopulation structure. This structure and habitat selection within some river systems is influenced by predation risk from breeding raptors (Peregrine Falcon *Falco peregrinus*, Golden Eagle *Aquila chrysaetos,* Gyrfalcon *Falco rusticolus,* Great Horned Owl *Bubo virginianus*). Despite the importance of spatial segregation from birds of prey (refuges are available where cliff nesting sites for raptors are limited; Chapters 2 and 3, see also Janes 1985), Harlequin Ducks consistently used specific areas (home ranges/sites) within source rivers (where the density of avian predators was low or absent) among years. Some river sections were never used. Even on rivers with intermediate densities of both Harlequin Ducks and avian predators, some sections with low predator proximity were unoccupied over the study period (3-6 years, mean = 4 years per river system between 1992 and 1999; Chapter 3). This suggests, not surprisingly, that within river systems (sub-populations), other factors besides predation risk are important (see also Rodway et al. 2000).

The objectives of the present paper are to 1) determine the habitat features relevant to Harlequin Ducks within a source population (Ikadlivik River), 2) develop a habitat suitability index, and 3) test Watkinson and Sutherland's (1995) prediction that habitat studies in a sink population (Fraser River) may be misleading. These objectives are important for understanding the influence of limiting factors within sub-populations, and 2) interactions and tradeoffs between limiting factors at different spatial scales in determining population structure across habitats in highly mobile species. Findings could also benefit the conservation and management of Harlequin Ducks, a Species at Risk in eastern North America.

4.3. METHODS

I measured small scale habitat features on a putative source (high density, stability and site persistence; at carrying capacity with positive population growth implying some emigration dispersal) and a putative sink (low density, stability and site persistence; population change implying 'rescue effect' immigration) river system in northern Labrador, the Ikadlivik and Fraser Rivers, respectively (see Chapter 2). Heath et al. (Chapter 2) also have shown that overall (a comparison of 12 random sites per river), these rivers had similar biophysical features and prey availability. For the present study, I divided each river system into used and unused sections by overlaying survey data from multiple years in Mapinfo v.5. (see Chapter 2 and Appendix 4-1). I then randomly selected 12 sample sites from both used and unused sections of the Ikadlivik (total river length considered = 51.8 km) and 5 used and 8 unused sites on the Fraser River (total river length considered = 40.0 km; fewer sites were selected on the Fraser River due to a lower proportion of used habitat). On the Ikadlivik River, I included three additional sites where Harlequin Ducks were directly observed during the study. One random unused site on the Ikadlivik was excluded from analysis because it occurred within a deep lake system and including it would have biased results. Each site was visited in June/July 2000, after spring runoff had subsided. At each site, habitat features were measured within a 50 m section of the river. Three transects perpendicular to the river banks (25 m upstream, 0 m, 25 m downstream) were established at each site. I measured stream width, and stream depth at center stream, mid-left and mid-right, along each transect, and averaged measurements for the site. I then divided the site into five 10 m sub-sections and visually estimated the percent composition of riparian (within 5 m of banks) and general (5 - 100 m from bank) ground/vegetation types (sand, rock, moss, shrub, alder, trees) and water characteristics (percent rapids, riffle, runs, slow water [back water eddies and pools], for definitions see Scruton and Anderson 1992) for each sub-section, and averaged over all sub-sections to determine the overall percent composition for the site. In the same manner, but using ten 5 m subsections, I visually estimated (using polarized lenses) the percent composition of each river substrate type (bedrock, large boulder [>1 m], small boulder [25 cm - 1 m], rubble [14 - 25 cm], cobble [6 - 13 cm], pebble [3 - 5 cm], gravel [20 mm - 3 cm], sand [0.06 - 20 mm], mud [0.004 - 0.05 mm]). The percentage of banks that had overhanging vegetation and the percentage of banks that were exposed (no hardwood or softwood vegetation present within the first 1 m of stream banks) were also quantified for each site. In-stream islands and exposed boulders were counted and islands were measured and categorized as gravel, alder, or treed (conifers and hardwoods present). Mid-stream velocity was measured as the time it took a small bobber to travel 10 m downstream, averaged over three trials. Stream gradient (angle from level) was estimated to the nearest degree for the 50 m section using a clinometer. Kick-sampling for benthic invertebrates was conducted at three random sites within each 50 m section using a 46 cm by 25 cm rectangular kick net (see Frost et al. 1971). Invertebrates were identified to order (except Diptera also to family) and the total number of each taxa per sample was determined and averaged across the three samples for each site.

For the Ikadlivik and Fraser Rivers, separately, I used two-tailed t-tests for unequal variance to compare each habitat parameter between used and unused sites. Given the extensive number of habitat parameters considered, this analysis was used to remove irrelevant variables, and all habitat parameters not meeting a criteria of $p \leq 0.2$ were excluded from further consideration. Redundant variables were also excluded, i.e. each sub-category of invertebrates, in-stream islands and fast water (rapids, riffles, runs) differed significantly ($p \leq 0.05$) between used and unused sites, therefore I used total invertebrates, total islands and percentage fast water to avoid replication. All remaining variables were then entered into a discriminant function analysis in SPSS v.10 (SPSS 1999) to evaluate differences between used and unused areas. Principal component analysis was used to determine the relative importance of each habitat variable. Predation pressure scores for each sample site on the Fraser river were calculated using the 'among years' method outlined by Heath et al. (Chapter 3). Additionally, a habitat suitability index was generated using discriminant function data from the Ikadlivik River analysis (see Appendix 4-2) and was used to classify (used/unused) and quantify the relative suitability of sites on the Fraser River.

4.4. RESULTS

Discriminant function analysis indicated a significant difference between habitat characteristics at used and unused sites on the Ikadlivik River (Wilks' Lamda Chi-Square = 24.603, df = 12, p = 0.017; see frequency distribution of canonical discriminant function scores, Figure 4-1). Principal component analysis was conducted to determine the relative importance of each habitat parameter. Principal component (PC) 1 accounted for 36.9% of the variance among sites, and gave the best separation between used and unused sites (Figure 4-2a; Table 4-1). All habitat parameters considered were significantly correlated with PC1 (Table 4-1), however the negative contribution of RIPUNVEG and GENUNVEG and the strong positive contribution of OVERHANG, GRADIENT and FSTWATER suggest overall vegetative cover and fast water characteristics are most important (abbreviations for all habitat parameters are described in Table 4-2). The same analysis of the Fraser River (a putative sink population) also revealed a significant difference between used and unused areas (Wilks' Lambda Chi-Square = 25.324, df = 9, p = 0.003), although many variables that were important for the Ikadlivik analysis were not significant in the Fraser River Analysis. Principal component analysis indicated that PC1 accounted for 45.9% of the variance among sites, and was the only component that gave good separation between used and unused sites (Figure 4-2b, Table 4-3). This component was driven primarily by vegetative cover (RIPALDER, RIPUNVEG, EXPBANKS).

Additionally, I developed a habitat suitability index (*HSI*) for Harlequin Ducks using the discriminant function equation from data on the Ikadlivik River (see Appendix 4). Applying this index to the Fraser River, 61.5% of sites were correctly classified as used or unused. Classifications, suitability (*HSI*) and predator proximity are presented for each site on the Fraser River in Figure 4-3. All used sites were correctly classified as being used ($HSI > 0$) and of high quality ($HSI > 20$). These high quality sites were used regardless of variation in predator proximity, although a relatively high quality site that had high predator proximity was unused. Medium quality habitats with low to medium predator proximity were unused. Not surprisingly, unsuitable ($HSI < 0$) sites were unused, despite extremely low predator proximity.

Table 4-1. Correlation coefficients of each habitat parameter with each of the principal components (PC) generated from sites on the Ikadlivik River. Eigenvalues and the percentage of variance explained by each component are presented. PC1 was the only component that produced good separation of used and unused sites (Figure 4-2a) and is therefore the only component considered in detail (see Table 4-2 for definitions of habitat parameters).

Habitat Feature		PC1	PC2	PC3	PC4
	Eigenvalue	4.42	2.53	1.35	1.23
	% of variance	36.9	21.1	11.2	10.2
OVERHANG		0.723**	-0.492*	0.165	0.064
GRADIENT		0.723**	0.583**	0.217	0.076
FSTWATER		0.637**	0.447*	-0.386	0.187
RIPUNVEG		-0.626**	0.459*	0.126	0.429*
INVERTS		0.626**	-0.144	0.153	0.444*
GENUNVEG		-0.616**	0.429*	0.353	-0.022
BOULDERS		0.615**	0.401*	0.36	-0.400*
RIPALDER		0.601**	-0.504**	0.228	-0.388*
VELOCITY		0.570**	0.613**	-0.1	0.299
LRGSUBST		0.547**	0.558**	-0.253	-0.434*
ISLANDS		0.479*	-0.235	0.591**	0.392*
GENTREE		0.463*	-0.420*	-0.597**	0.248

* significant at $\alpha = 0.05$; ** significant at $\alpha = 0.01$

Table 4-2. Summary of definitions for abbreviations of habitat parameters discussed in the text and appendix. Further descriptions are given in the methods section.

Abbreviation	Habitat parameter
BOULDERS	Number of in-stream exposed boulders
EXPBANKS	Percentage of exposed banks (i.e. no hard or softwood vegetation within 1 m of banks)
FSTWATER	Percentage composition of waterway that was rapids, riffles or runs
GENTREE	Percentage composition of general vegetative zone (~100 m from banks) that consisted of mature softwood and hardwood trees.
GENUNVEG	Percentage composition of general vegetative zone that was bare (rocks/lichen) or consisted only of small plants/grasses/mosses
GRADIENT	Stream gradient of the 50 m section
INVERTS	Total number of benthic invertebrates from kick samples
ISLANDS	Total number of in-stream islands
LRGSUBST	Percentage composition of river substrate that was large and small boulders
OVERHANG	Percentage of banks containing overhanging vegetation
PEBBGRAV	Percentage composition of river substrate that was pebble and gravel
PLECOPTE	Total number of benthic invertebrates that were Plecoptera (stonefly)
RIPALDER	Percentage composition of riparian zone that was alder and immature willow
RIPUNVEG	Percentage of riparian zone (~5 m from bank) that was unvegetated or consisted of only small plants/grasses/mosses
VEGISLND	In-stream islands that contained alder/willow and/or hard/softwood trees
VELOCITY	Mid-stream velocity (m/s)

Table 4-3. Correlation coefficients of each habitat parameter with each of the principal components (PC) generated from sites on the Fraser River, a putative sink population. Eigenvalues and the percentage of variance explained by each component are presented. PC1 was the only component that produced good separation of used and unused sites (Figure 4-2b) and is the only component considered in detail (see Table 4-2 for definitions of habitat parameters).

Habitat Parameter		PC1	PC2	PC3	PC4
	Eigenvalue	4.13	1.83	1.2	1.02
	% of variance	45.9	20.4	13.4	11.3
RIPALDER		0.854**	0	-0.286	-0.079
RIPUNVEG		-0.852**	0.406	-0.01	0.151
EXPBANKS		-0.797**	0.176	0.335	0.388
PEBBGRAV		-0.759**	0.519	-0.153	-0.04
BOULDERS		0.702**	0.590*	0.203	0.157
VEGISLND		0.597*	0.552	0.414	0.34
PLECOPTE		0.55	0.649*	-0.07	-0.339
LRGSUBST		0.546	-0.398	-0.118	0.698**
VELOCITY		0.107	-0.363	0.868**	-0.31

*significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$

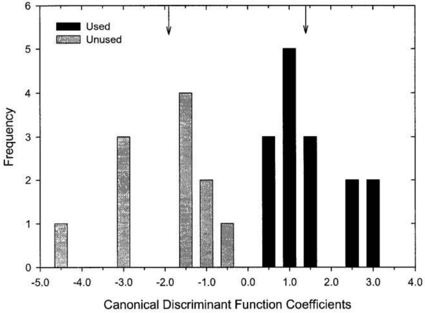
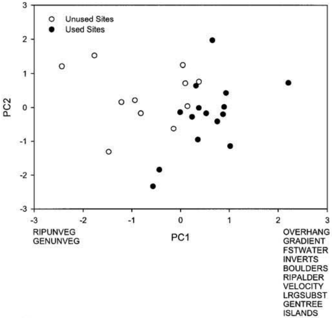
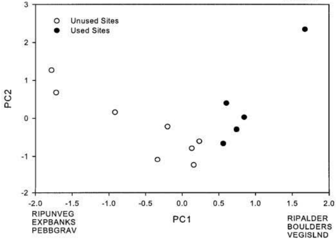


Figure 4-1. Frequency distribution of canonical discriminant function scores showing the separation of used and unused sites on the Ikadlivik River. Arrows indicate centroids for each group.

Figure 4-2. Principal components PC1 and PC2 accounted for (A) 36.9 and 21.1% of the variation in all sites on the Ikadlivik and (B) 45.9 and 20.4% of the variation among sites on the Fraser River (see Tables 4-1, 4-3). PC1 gave the best seperation of used and unused sites for both river systems, and was therefore the only component considered in detail. Habitat parameters that were significantly correlation with PC1 are presented in order of decreasing correlation coefficients (Tables 4-1 and 4-3; positive and negative correlations are presented at the respective ends of each axis)

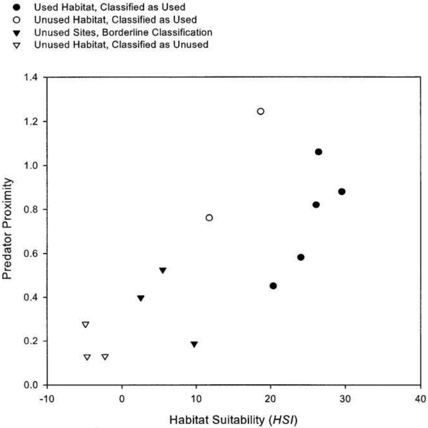

○ Unused Sites
● Used Sites
PC2
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
PC1
RIPUNVEG
GENUNVEG
OVERHANG
GRADIENT
FSTWATER
INVERTS
BOULDERS
RIPALDER
VELOCITY
LRGSUBST
GENTREE
ISLANDS

A


○ Unused Sites
● Used Sites
PC2
3
2
1
0
-1
-2
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
PC1
RIPUNVEG
EXPBANKS
PEBBGRAV
RIPALDER
BOULDERS
VEGISLND

B

Figure 4-3. Habitat suitability scores and classifications (*HSI*; see Appendix 4-2) applied to sites on the Fraser River (a putative sink population), plotted against the proximity of birds of prey (Predator proximity, among years method, Chapter 3). Of the high quality sites (*HSI* > 10), the best ones were used by Harlequin Ducks regardless of predator presence, with the exception of one high quality site with high predator presence, and one with medium predator presence that was of lower quality. Sites indicated as being unsuitable (*HSI* < 0) were not used by Harlequin Ducks in any years, despite low predator presence. Borderline quality habitats (10 > *HSI* > 0) that had medium to low predator presence were also unused


● Used Habitat, Classified as Used
○ Unused Habitat, Classified as Used
▼ Unused Sites, Borderline Classification
▽ Unused Habitat, Classified as Unused
Predator Proximity
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
-10
0
10
20
30
40
Habitat Suitability (*HSI*)

4.5. DISCUSSION

4.5.1. Importance of Habitat Heterogeneity within a Source Population

Association of Harlequin Ducks on the Ikadlivik River with habitat features including vegetative cover, large substrates, in-stream islands and benthic invertebrates are in general concordance with previous research on Harlequin Ducks in eastern and western North America and in Iceland (see Robertson and Goudie 1999 and section 1.1.1.). Association with rapids, riffles and large substrates (Bengtson 1966, 1972, Kuchell 1977, Wallen 1987, Inglis et al. 1989, Cassirer and Groves 1990, Bruner 1997, Hunt 1998, Rodway 1998b, Rodway et al. 2000) may be important due to an increased abundance of insect larvae and pupae (Kuchell 1977, Colbo and Wotton 1981, Inglis et al. 1989). Exposed midstream boulders and islands may be important for resting and preening (e.g. Bengtson 1972, Kuchell 1977, Dzinbal and Jarvis 1984, Crowley 1994, Bruner 1997, Hunt 1998), which may be particularly important for feather maintenance due to diving in cold, turbulent water (Inglis et al. 1989). Midstream resting sites may also allow avoidance of terrestrial predators and greater vigilance (Kuchell 1977, Inglis et al. 1989). In-stream islands and a dense vegetative riparian zone are important for nesting sites (Bengtson 1966, 1972, Wallen 1987, Crowley 1994, Bruner 1997, Rodway et al. 1998). During early brood rearing, dense vegetation overhanging stream banks can conceal ducklings from potential predators (Bengtson 1966, Kuchell 1977). Bengtson (1970) suggested that vegetative cover may be one of the most important factors in the habitat selection of waterfowl, consistent with the observed importance of vegetative characteristics in the principal component analysis for the both the

Ikadlivik and Fraser Rivers. In contrast with these results, other research has suggested that low stream gradients are important in used areas (Wallen 1987, Cassirer and Groves 1990). I expect that the association with high gradient river sections in northern Labrador are likely related to associations with fast water and large substrates, although it is likely a threshold exists for this relationship. Associations with both wider (Cassirer and Groves 1990, Crowley 1994) and narrower (Rodway 1998b) stream widths, and large variation (2 - 40 m) in width in used areas (Bengtson 1972) have been reported, and I found no difference in stream width between used and unused sites.

Many authors have emphasized the importance of benthic invertebrates as a limiting factors to breeding Harlequin Ducks (Bengtson and Ulfstrand 1971, Bengtson 1972, Kuchell 1977, Gardarsson and Einarsson 1994, Rodway 1998a, Rodway et al. 2000). These results suggest that a variety of classes of invertebrates may be important (see also Robertson and Goudie 1999, Robert and Cloutier 2001 and Chapter 1 for review), but their status in the principal component analysis, and the importance of predation risk (Chapter 2, 3) suggest that other factors are likely more important limiting factors for Harlequin Ducks in northern Labrador. Observations of low rates of foraging behaviour in southern Labrador (R.I. Goudie personal communication) also support this conclusion.

4.5.2. Comparison with a Sink Population

In the habitat analysis for the putative sink population (Fraser River), several features identified as important for the source population (Ikadlivik River) were excluded (e.g. all water characteristics, GRADIENT, GENUNVEG, total and all sub-categories of invertebrates, GENTREE, LRGSUBST, VELOCITY). Additionally, application of the habitat suitability index (*HSI*) to sites on the Fraser River classified several unused sites as being highly suitable. As previous work indicated the importance of avian predators in underlying source-sink dynamics and population structure between and within some rivers (Chapter 2,3), I plotted among year predator proximity against habitat suitability (*HSI*) scores for sites on the Fraser River. The highest quality sites were all used, regardless of predator proximity, and unsuitable habitat was unused regardless of low predator proximity. Other sites with relatively suitable habitat ($HSI > 0$) were also unused, likely due to predator proximity (see also Chapter 3). These differences between the Ikadlivik and Fraser Rivers suggest that tradeoffs between biophysical habitat characteristics and predation risk are important for Harlequin Ducks when selecting sites in sink populations, and birds of prey may exclude Harlequin Ducks from all but the highest quality habitats in sink river systems. These results support Watkinson and Sutherland's (1995) prediction that habitat studies in sink populations may be misleading. That only high quality sites were used on this river is likely the reason for the high degree of separation among used and unused sites in the Fraser River PCA. Interestingly, this may mean that the biophysical features indicated as being important on the Fraser river may be characteristic of high quality habitat, while features indicated as important on the Ikadlivik River (and source populations in general) may represent characteristics that are important across a broader spectrum of habitat quality. On the other hand, had this study been restricted to a source population, the role of predation risk would not have been apparent. It is likely a common trend throughout ecological research to select 'good' study areas with a large sample size of individuals. This is likely true for any study that requires capturing individuals (e.g. banding, radio telemetry, etc.), however as illustrated here, this may limit the generality of many studies, particularly if source-sink metapopulation structure exists. Habitat, and other research studies, should therefore be conducted in both source and sink populations.

Overall, these results stress the importance of considering large scale population structure when identifying small scale habitat requirements of species. Had I not considered overall source-sink metapopulation structure, and restricted this study to only the Fraser River, the results would have been confusing and misleading. Predation pressure may be important at the landscape/metapopulation level (Chapter 2, 3), however biophysical habitat features likely predominate at and within the home range scale, although tradeoffs between predation risk and habitat quality (biophysical features) are important within some sub-populations (e.g. Fraser River; see also Chapter 3). Consideration of multi-scale hierarchical habitat selection is likely important for the majority of highly mobile species (Kaminski and Weller 1992). The importance of smaller scale habitat features (heterogeneity within sub-populations) in determining overall population structure and dynamics across the landscape should also receive greater attention. More specifically for Harlequin Ducks, the results and habitat suitability indices presented, in combination with previous work (Chapter 2,3) provide important insight into how Harlequin Ducks use habitat throughout and within the landscape, and will be important in the conservation and management of this species at risk in eastern North America.

4.6. ACKNOWLEDGEMENTS

Thanks to Joe Brazil of the Newfoundland and Labrador Wildlife Division, Major Humphries and Tony Chubbs of the Department of Nation Defence, and the Voisey Bay Nickel Company for providing additional survey data on Harlequin Ducks and raptors. Thanks to Perry Trimper and Kathy Knox of Jacques Whitford Environment Limited for their assistance in providing raw survey data. Thanks to the Labrador Inuit Association (Nain) for their support. Thanks to Shauna Ballie fo assistance collecting habitat data, Bill Duffet for logistical field support, to Greg Robertson, Dave Schneider and Ian Goudie for useful comments on this manuscript, to Dave Fifield for direction in programming databases and to Amy Todd for data entry. Funding was provided by the Newfoundland and Labrador Wildlife Division c/o Joe Brazil, a World Wildlife Fund of Canada Endangered Species Recovery Fund to WAM, Northern Scientific Training Program grants to JPH, S. Ballie and WAM, Mountain Equipment Co-op Environment Fund support to JPH, a Society of Canadian Ornithologists research (Taverner) award to JPH, and an NSERC individual operating grant to WAM.

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4.8. APPENDIX 4-1

Properly assessing habitat availability is problematic. Several authors argue that comparisons of habitat usage versus availability are preferable to used versus unused comparisons (e.g. Johnson 1980, Jones 2001). Yet, because used areas are also areas of available habitat, this can compromise statistical analyses owing to issues of independence and replication. Comparisons of used versus available unused habitat can be informative (Jones 2001), and I affirm that unused river sections considered in the present study are available to Harlequin Ducks. Comparison of used versus unused habitat is also appropriate for the analyses used in this chapter for the following reasons: 1) multiple years of survey data were used to distinguish used and available unused habitat, with consideration of the species' life history characteristics, 2) within both used and available unused habitats, sample sites were selected in an a priori randomized manner, and 3) data in Chapter 2 suggests the Ikadlivik River system is at carrying capacity and therefore used and available unused habitats likely reflect suitability to the population.

4.9. APPENDIX 4-2

The discriminant function from the Ikadlivik River analysis was used to develop the following habitat suitability index (*HSI*):

$$\begin{aligned}\mathit{HSI} = {} & -3.09 + 0.029\mathit{OVERHANG} + 0.005\mathit{INVERTS} - 0.006\mathit{RIPALDER} + \\ & 0.678\mathit{ISLANDS} - 0.03\mathit{GENUNVEG} + 1.029\mathit{GRADIENT} + 0.001\mathit{GENTREE} - \\ & 6.24\mathit{VELOCITY} - 0.019\mathit{BOULDERS} + 0.067\mathit{LRGSUBST} - 0.028\mathit{FSTWATER} \\ & -0.001\mathit{RIPUNVEG}\end{aligned}$$

(see definitions of parameters in Table 4-2 of the text). When *HSI* is > 0, a habitat can be classified as used, and unused when *HSI* is < 0. This correctly classified 96.2% (25/26) of the sites on the Ikadlivik River, the misclassified case being extremely close to zero (-0.254). Additionally, all used sites on the Fraser River were correctly identified (but note some unused sites were incorrectly classified, likely due to the fact that this is a sink population; see text). This suggests that the above index *HSI* may be useful in identifying suitable Harlequin Duck breeding habitat, although I caution that sub-population demographic features and predation risk also should be considered (see text). Additionally, caution should be used in categorizing sites that have *HSI* scores close to zero, as is apparent from the borderline misidentified used site on the Ikadlivik River and borderline sites on the Fraser River (again, see text). I realize that in the majority of situations, due to the extensive logistics and effort required, all of the habitat parameters required for *HSI* may not be feasibly quantified, particularly over extensive regions. A habitat suitability index that uses habitat features that can be quantified from topographic maps, aerial photographs and/or satellite imagery (i.e. remote sensing) would be most useful in many situations. I therefore redid the discriminant function analysis using only BOULDERS, ISLANDS, OVERHANG, RIPALDER, RIPUNVEG, GENTREE, GENUNVEG and FSTWATER. This analysis still indicated a significant difference between used and unused sites (Wilks' Lamda Chi-Square = 19.297, df = 8, p = 0.013), and led to the following Remote-Sensing Habitat Suitability Index (*RSHSI*):

$$\begin{aligned}&RSHSI = -0.705 + 0.003BOULDERS + 0.260ISLANDS + 0.035OVERHANG -\\&0.002RIPALDER + 0.007RIPUNVEG - 0.008GENTREE - 0.044GENUNVEG\\&- 0.004FSTWATER\end{aligned}$$

which correctly identified 88.5% (23/26) of all sites on the Ikadlivik (again, mis-classified sites were extremely close to zero) and still correctly classified all used areas on the Fraser River. These indices may be particularly useful in identifying suitable Harlequin Duck breeding habitat in a variety of conservation and management contexts, including environmental monitoring and assessments, and may therefore be an important tool in protecting this species at risk in eastern North America. I encourage researchers with existing habitat data for breeding Harlequin Ducks, from different locations across their global distribution, to test the accuracy of these indices within their study areas.

5.0. SUMMARY

5.1. FACTORS INFLUENCING DISTRIBUTIONS OF HARLEQUIN DUCKS

The research presented in this thesis provides new perspective on several aspects of habitat selection and population structure of breeding Harlequin Ducks, and more generally to the ecology of northern Labrador. Figure 5.1. summarizes these findings in a schematic format. At the landscape scale, results imply source-sink metapopulation structure of breeding Harlequin Ducks, with individual river systems functioning as sub-populations. This structure appears to be primarily influenced by distribution of nesting birds of prey, whose distribution is limited by availability of cliff nesting sites (see also Janes 1985). Overall availability of biophysical habitat features relevant to Harlequin Ducks did not differ between a putative source and sink population, suggesting birds of prey could exclude Harlequin Ducks from otherwise suitable habitat. Although beyond the scope of this thesis, previous research has suggested metapopulation structure of nesting raptors (e.g. Peregrine Falcon: Wooton and Bell 1992; Northern Spotted Owl *Strix occidentalis* Lande 1988, McKelvey et al. 1992). It is therefore possible that raptor populations in northern Labrador may also exhibit metapopulation structure, the size of each sub-population being primarily determined by nest site availability. It is feasible that a type of (uni-directional) competing metapopulation dynamic could exist, with sources for raptors being sinks for Harlequin Ducks, and vice versa (e.g. see Danielson 1991). Instead of both predators and prey shifting among sub-populations (as is often the situation considered in theoretical studies), predators are constrained by habitat limitation providing patches of spatial refuge for Harlequin Ducks, outside the foraging range of raptors. Although birds of prey may limit Harlequin Ducks in otherwise suitable habitat (see Chapter 2), it is unlikely Harlequin Duck distributions will have a direct effect on populations of birds of prey, as a variety of alternate prey are available (Section 1.2.2). It is therefore also possible that, if alternate prey for raptors exhibit inter-annual cyclicities (e.g. voles), then sites within sink populations may allow Harlequin Ducks an increased probability of survival and reproduction in years of alternate prey peaks (see Pehrsson 1986, Underhill et al. 1993). Although there was inadequate data for statistical quantification, sinks also may be suitable in years of low raptor densities. For example, in 1999 I observed only one pair of Harlequin Ducks on the Fraser River, and high numbers of raptors (19 pairs). In the subsequent year, however, remarkably low numbers of birds of prey were present (total pairs = 4, only 1 Peregrine Falcon, the lowest number on record; J. Brazil unpubl. data), while a minimum (late aerial survey) of 7 pairs of Harlequin Ducks were present, the highest number yet recorded for this river system. It is therefore possible that Harlequin Ducks respond to predation risk from birds of prey in each season, although rigorous experiments would be required to properly test this hypothesis.

Results indicate Harlequin Ducks can reduce predation risk from birds of prey by spatial dynamics at the metapopulation/landscape level. Although several sub-populations were identified as potential source and sink populations, a number of intermediate populations also existed, and I termed the overall matrix of sub-populations a 'source-sink gradient'. A spatially explicit GIS analysis was applied to this framework, providing additional support for the hypothesis that segregation from nesting birds of prey is important at the landscape scale. Spatial segregation was also important within some sub-populations (i.e. home range scale; Figure 1-2), particularly where intermediate densities of Harlequin Ducks and birds of prey were present. This dynamic was not detected in putative source and sink populations, likely due to relatively constant low and high predator presence within these sub-populations, respectively. In both source and sink populations, the distribution of Harlequin Ducks was influenced by biophysical habitat parameters, although tradeoffs with predation risk are likely important in sink populations (see Chapter 4). Biophysical habitat parameters were not quantified in an intermediate population (Kingurutik River), but the fact that some areas with low predator proximity were never used suggest that other factors are also important in these populations. At this home range (within-river system) scale, Harlequin Ducks consistently used some river sections (sites) among years, and some overlap among pairs also occurred within these sections. An interesting possibility here is that a smaller scale source-sink metapopulation structure could also exist at this scale, that is, among sites within a river system. High production at a few high quality sites could allow dispersal into less suitable sites within the same river system. Although there are inadequate data to test this hypothesis, the similar distribution characteristics (i.e. interannual use, predator proximity) of sites on the Kingurutik river to that of the overall population are highly suggestive (see Chapter 3). This dynamic could also occur within source populations, although site quality is probably more influenced by biophysical features and prey availability than predation risk. This is particularly interesting as population dynamics and structure among sites within a population likely play an important role in population structure at the landscape scale (Kolitiar and Wiens 1990)

5.2. CONSERVATION IMPLICATIONS

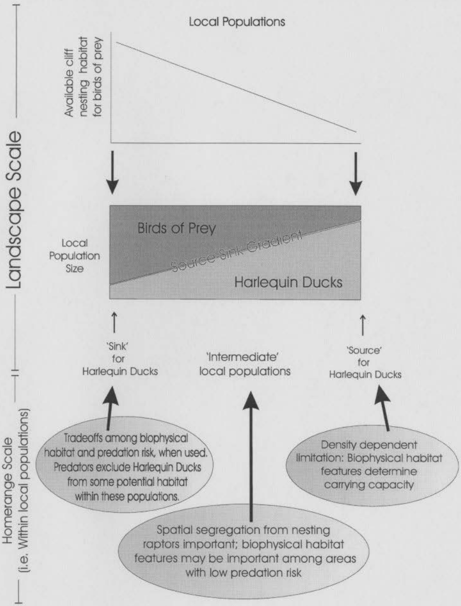
Although the majority of this thesis may appear to be from a more theoretical and basic science perspective, there are a number of direct applied implications inherent in the ecological processes described by this research. Understanding how landscape patterns influence population and ecological processes is essential to conservation and management efforts, particularly in situations where habitat destruction occurs on a large scale, therefore altering landscape structure (Kareiva and Wennergren 1995, Turner et al. 1995). Results of this research could be particularly important to conservation and management of Harlequin Ducks and birds of prey in northern Labrador, and even other migratory species elsewhere. Harlequin Ducks are a species at risk in eastern North America, and an understanding of habitat use has been identified as a priority consideration for recovery (Montevecchi et al. 1995); this being the initial motivation for this thesis project. A recent issue has resulted from the implication that Harlequin Ducks breeding in northern Labrador winter in Greenland, and therefore belong to a different regional population than Harlequin Ducks that winter in eastern North America (see Brodeur et al. 1998, 1999, in press, Thomas and Robert 2001). The spatial dynamics and population structure implied by this thesis could therefore play an important role in delineating these two populations on the breeding grounds (if such a delineation actually exists), as population structure and dynamics at the regional scale will likely be influenced by that at the landscape and home range scales. Together with the presented habitat suitability indices, the framework presented in this thesis will be important for understanding population dynamics, identifying key spatial areas in which to focus conservation efforts, and in evaluating the potential effects of future landscape change/perturbation on habitat use from the home range to landscape scale.

5.3. REALITY CHECK

It is often easy to fall deep into one's scientific niche, and the complexity of ecological phenomenon often require excruciatingly indepth examination on even relatively simplified interactions. To prevent mental implosion, it is often critical to step back from one's research for a 'reality check'. I therefore wish to conclude this thesis with an over-simplified summary statement:

"Food and shelter are important to ducks, good areas are used more than bad ones, and it's pretty stupid to nest near a predator. In order to save the ducks, we should protect areas with lots of ducks."

Figure 5.1. Schematic diagram summarizing factors influencing distributions of Harlequin Ducks in northern Labrador, at the landscape and home range scales. Bold arrows indicate influencing factors, smaller arrows are labels. The two spatial scales are separated vertically, while the horizontal represents a continuum of sub-populations (river systems), among which dispersal may occur among years.


Landscape Scale
Homerange Scale
(i.e. Within local populations)
Local Populations
Available cliff nesting habitat for birds of prey
Local Population Size
Birds of Prey
Source-Sink Gradient
Harlequin Ducks
'Sink' for Harlequin Ducks
'Intermediate' local populations
'Source' for Harlequin Ducks
Tradeoffs among biophysical habitat and predation risk, when used. Predators exclude Harlequin Ducks from some potential habitat within these populations.
Spatial segregation from nesting raptors important; biophysical habitat features may be important among areas with low predation risk
Density dependent limitation: Biophysical habitat features determine carrying capacity

5.4. LITERATURE CITED

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A-1.0. APPENDIX A. OBSERVATION OF A GOLDEN EAGLE *Aquila chrysaetos* ATTACK ON A HARLEQUIN DUCK *Histrionicus histrionicus* IN NORTHERN LABRADOR.[5]

A-1.1. ABSTRACT

During an aerial survey on the Kingurutik River, northern Labrador, a Golden Eagle (*Aquila chrysaetos*) was observed attacking a female Harlequin Duck (*Histrionicus histrionicus*). Although the attack ended unsuccessfully, I believe this was only a result of disturbance by the presence of the helicopter. I overview previous reports of predation on Harlequin Ducks, and emphasize the need for further research investigating the importance of the influence of predators on populations of Harlequin Ducks.

[Keywords] Harlequin Duck, *Histrionicus histrionicus*, Golden Eagle, *Aquila chrysaetos*, Predation, Labrador

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[5] This appendix is currently in press as Heath, J.P., G. Goodyear, and J. Brazil. Observation of a Golden Eagle attack on a female Harlequin Duck in northern Labrador. Canadian Field-Naturalist.

A-1.2. ARTICLE

On 21 June 1999, we conducted a survey for Harlequin Ducks on the Kingurutik River system (57° 0.5' N, 63° 4.0' W) in northern Labrador using a Bell 206L helicopter. This river system is known to hold moderate densities of both Harlequin Ducks and various raptor species (Heath 2001). During this survey, we observed a Golden Eagle, *Aquila chrysaetos,* attacking a female Harlequin Duck, *Histrionicus histrionicus,* in mid-stream. It appeared that the Golden Eagle had captured the female; however, she managed to escape as the Golden Eagle, presumably startled by the helicopter, flew away. We believe that this would have been a successful predation event had the birds not been disturbed. We were unable to determine if the Harlequin Duck had been injured in the encounter; however, this is the first documented interaction between a Golden Eagle and Harlequin Duck.

Current literature on birds of prey as predators of Harlequin Ducks is limited to incidental reports, but indicates that predation can occur on both adults and broods. In Forillon Park, Quebec, Brodeur et al. (1998) located two adult female Harlequin Ducks (carrying satellite radios) killed and consumed by a Red-tailed Hawk (*Buteo jamaicensis*) and Great Horned Owl (*Bubo virginianus*). In Hebron Fiord, northern Labrador, a white-phase Gyrfalcon (*Falco rusticolus*) was observed circling and stooping on 2 adult female Harlequin Ducks (Rodway et al. 2000); however, the females avoided capture by diving (J. Gosse, personal communication). Bald Eagles (*Haliaeetus leucocephalus*) have been reported as a threat on both breeding and winter grounds (Dzinbal 1982, McEneaney 1997, Robertson and Goudie 1999). Smith (2000*) reports that 10 of 13 predation events on ducklings were most likely by raptors (4 by Red-tailed Hawk, 1 by Northern Goshawk *Accipiter gentilis*, 1 by unknown Owl spp., and 4 by unknown raptor spp.), and that fledging by Harlequin Ducks coincided with high numbers of raptors and their fledged young. Raven (*Corvus corax*), Arctic Skua (*Stercorarius parasiticus*) and several mammalian predators including Mink (*Mustela vison*), Marten (*Martes americana*) and Arctic Fox (*Alopex lagopus*) have also been identified as potential predators during the breeding season (Bengtson 1966, 1972, Kuchell 1977, Bruner 1997, Smith 2000) and numerous Mink attacks have been observed on Harlequin Duck broods in southern Labrador (K. Squires and R. I. Goudie, personal communication).

Despite these incidental reports, the influence of predation on breeding populations of Harlequin Ducks has yet to be addressed in the literature. Previous studies have emphasized that Harlequin Ducks may be primarily limited by prey availability on the breeding grounds (Bengtson and Ulfstrand 1971; Gardarsson and Einarsson 1994; Rodway 1998); however, the growing list of direct predation encounters suggests that the role of predation should receive further attention.

A-1.3. ACKNOWLEDGEMENTS

Funding for this project was provided by the Newfoundland and Labrador Provincial Wildlife Division via. JB, a Northern Scientific Training Program grant to JPH and W. Montevecchi, and a World Wildlife Fund of Canada Endangered Species Recovery Fund grant to W. Montevecchi. Thanks to John Gosse (Parks Canada), Kelly Squires (University of British Columbia) and R. Ian Goudie (Memorial University of Newfoundland) for providing information on their observations of predation encounters in Labrador.

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A-2.0. APPENDIX B. OBSERVATION OF MALE HARLEQUIN DUCK *HISTRIONICUS HISTRIONICUS* PRESENCE DURING BROOD REARING IN NORTHERN LABRADOR.

A-2.1. ABSTRACT

Female Harlequin Ducks (*Histrionicus histrionicus*) incubate and rear broods, while males normally depart the breeding grounds at the onset of incubation. On 27 July 2000, I observed a male Harlequin Duck in association with a female and brood of 5 ducklings on the Ikadlivik River in northern Labrador. The male maintained some distance (~100 m) from the female and brood; however, upon appearance of a researcher, the group amalgamated and the male influenced the behaviour of the female and brood. Possible explanations for early male departure and this exception are discussed.

A-2.2. ARTICLE

Previous research on the breeding chronology of Harlequin Ducks (*Histrionicus histrionicus*) has indicated that pair formation occurs during the winter (Kuchell 1977; Gowans et al. 1997; Robertson et al. 1998) and breeding birds are therefore usually paired prior to arrival at the nesting area (Kuchell 1977; Lazaras et al. 1979; Dzinbal 1982; Wallen 1987). Harlequin Ducks arrive on breeding rivers between late April and early May (Idaho, Montana, Wyoming, south Canadian Rockies, and Iceland; see Robertson and Goudie 1999 for review), and males depart upon the onset of female incubation in late June and early July (Iceland: Bengston 1966; southwest Alberta: Smith 1996; Idaho: Cassirer and Groves 1994; E. North America: Brodeur et al. 1998, 1999, in press). The male and female are therefore separated for at least two to four months, females being solely responsible for incubation and brood rearing. Broods hatch and a reared between July and September, upon which departure from the breeding grounds occurs and female molt begins at the coast (Robertson and Goudie 1999).

Few explanations for early male departure have been provided, however low densities of birds and early male departure may decrease the chances of food depletion on breeding rivers (Bengston 1972; Kuchell 1977). Alternatively, the striking appearance of male alternate plumage may increase detection of nests and broods, whereas females are cryptic.

Contrary to previous reports, on 27 July 2000, during a habitat survey of the Ikadlivik river (56°21.7' N x 62°20.9' W) in northern Labrador, a male Harlequin Duck was observed sleeping on a gravel section of a midstream island, approximately 100 m downstream from a female Harlequin Duck with a brood of five young (≤1 week old). The male was in distinctive alternate plumage, indicating he had not yet molted, and the deep colouration of his flanks suggested he was not immature. Upon sighting the approaching researcher (wading upstream), the male entered the water and swam upstream towards the female and brood, at which point the latter were detected by the researcher. Upon sighting the researcher, the female and brood initially attempted to swim upstream against the current, while remaining close to the river bank. During this time, the female remained partially submerged beneath the water, with only her head visible, while calling to and chasing the brood to encourage them to move upstream (opposite direction from researcher). After a seemingly futile attempt to swim against the current, the female regained positive buoyancy and moved into the current with the brood, letting it carry them quickly downstream (similar to previous reports of predator avoidance behaviour [e.g. Bengtson 1966]). Upon reaching the male, approximately 100 m downstream, the group amalgamated and floated downstream for approximately 400 m, before entering a backwater eddy (~200 m downstream of another concealed researcher). Within the eddy, the female followed the male, being followed herself by the brood. They remained here for approximately 1 min, before being lead by the male out into the river and continued to drift downstream an additional 500 m. They were subsequently spotted hauled out on an exposed gravel bank at a sharp turn in the river, the male being on the opposite side of the river than the female and brood. After 5-7 min, they again entered the water continuing downstream and out of sight.

The interesting aspect of this observation was the fact that the male was present on the breeding grounds this late in the summer, during brood rearing. Additionally, he appeared to influence the behaviour of the female and brood after a predator encounter (presence of the researcher). Perhaps most surprising was the female's tolerance of the male's presence in proximity to the brood and the fact that she followed him. In both instances when the group was resting while hauled out of the water, the male maintained his distance from the female and brood. This distancing of the male may have served to prevent detection of the brood by potential predators, or alternatively (but not mutually exclusive) the male may have been excluded by the female.

In the only other report of a male present during this period of the breeding season (Harrison 1967), damage to primary feathers was reported. We were unable to determine the flight capabilities of the male observed in this report, however no injuries were detected and he appeared healthy. As Harrison (1967) points out, even if the male had lost flight capabilities, there is no reason he could not have swam downstream to molt along the coast.

Although reasons for the male remaining this late in the season are unknown, he was seen to play a role in warning and assisting the female and brood in escaping. Conversely, however, the distinctiveness of the male may have allowed detection of the brood by the researcher in the first place, despite the fact that he was initially a considerable distance (100 m) downstream from them. Documentation of these type of rare exceptions may be important in providing insight into the evolution of early male departure strategies in Harlequin Ducks and other waterfowl.

A-2.3. ACKNOWLEDGEMENTS

Funding for the project, during which this observation occurred, was provided by the Newfoundland and Labrador Provincial Wildlife Division via Joe Brazil, a World Wildlife Fund of Canada Endangered Species Recovery Fund grant to William A. Montevecchi, Mountain Equipment Co-op Environment Fund support to JPH and a Northern Scientific Training Program grant to JPH and William A. Montevecchi. Thanks also to S. Ballie who assisted field research and who's keen observation of this brood contributed to the detail of this report.

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