

Population structure of breeding Harlequin Ducks and the influence of predation risk

J.P. Heath, G.J. Robertson, and W.A. Montevecchi

Abstract: Landscape features can have an important influence on the characteristics of populations, often resulting in heterogeneity in demographic processes. Therefore, local measurements of population parameters may not reflect regional characteristics. We studied populations of Harlequin Ducks (*Histrionicus histrionicus* L., 1758) breeding in 11 river canyons in northern Labrador in relation to biophysical habitat characteristics and abundance of avian predators. Density and stability of Harlequin Duck populations varied among river canyons and were positively related (mean of 4.7 survey years per river). Both density and stability were negatively related to densities of raptorial birds. Raptor density was related to availability of suitable cliff ledges for nesting. Comparison of rivers with stable, high-density Harlequin Duck populations and those with variable, low-density populations revealed no detectable differences in habitat or prey availability. In a high-density population, observed stability but positive projected growth suggested the system was at carrying capacity and a source of emigrants. In contrast, unstable, low-density populations approached local extinction in some years, while large increases in subsequent years were suggestive of immigration. These findings demonstrate that breeding aggregations in different river canyons could represent an important unit of demographic structure. The abundance of raptors appears to be an important factor influencing local characteristics of Harlequin Duck populations. We discuss the potential influence of local demographic differences on regional population dynamics and their importance for conservation management strategies for migratory species.

Résumé : Les éléments du paysage peuvent influencer de façon marquée sur les caractéristiques des populations, produisant souvent une hétérogénéité des processus démographiques. En conséquence, les mesures locales des paramètres démographiques peuvent ne pas refléter les caractéristiques régionales. Nous avons étudié des populations d'arlequins plongeurs (*Histrionicus histrionicus* L., 1758) qui se reproduisent dans 11 cañons de rivière du nord du Labrador en relation avec les caractéristiques biophysiques de l'habitat et l'abondance de prédateurs des oiseaux. La densité et la stabilité des arlequins plongeurs varient d'un cañon de rivière à l'autre et sont en relation positive l'une avec l'autre (moyenne de 4,7 années d'inventaire par rivière). La densité et la stabilité sont toutes deux reliées négativement à la densité des oiseaux de proie. La densité des oiseaux de proie est reliée à la disponibilité de rebords adéquats sur les falaises pour la nidification. La comparaison des rivières à densité stable/forte d'arlequins plongeurs aux rivières à densité variable/faible ne révèle aucune différence décelable dans l'habitat ou la disponibilité des proies. Dans une population à forte densité, la stabilité observée et l'accroissement positif projeté laissent croire que le système a atteint son stock limite et qu'il est une source d'émigrants. En contraste, les populations instables de faible densité s'approchent de l'extinction locale au cours de certaines années, alors que des accroissements importants les années suivantes font croire à une immigration. Ces résultats démontrent que les rassemblements de reproduction dans les divers cañons de rivière peuvent représenter des unités significatives de structure démographique. L'abondance des oiseaux de proie semble être un facteur important qui influence les caractéristiques locales des arlequins plongeurs. Nous discutons de l'influence potentielle des différences démographiques locales sur la dynamique démographique régionale et de leur importance pour les stratégies d'aménagement de la conservation des espèces migratrices.

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Introduction

Populations exhibit spatial structure that is often determined by landscape features (Wiens et al. 1993; Ritchie 1997). Subpopulations can be isolated to varying degrees by habitat patchiness and a species' dispersal characteristics. In situations where subpopulations exhibit some degree of connectivity (immigration and emigration occur, but not total mixing), regional population dynamics can result from changes within and interactions among subpopulations and cannot be properly understood from studies limited to local scales (Wiens et al. 1993; Kareiva and Wennergren 1995; Ritchie 1997).

Genetics and morphology have often formed the basis for delineating populations of migratory birds, and finer scale

demographic structure has not generally been considered important (Esler 2000). Owing to the high mobility of migratory species and the expense of multi-site research, researchers and managers are often required to assume demographic panmixia when extrapolating locally measured parameters to regional population models. Even when spatial structure is considered and management units are identified, panmixia is still assumed within these (often coarse-scale) management units. However, Esler (2000) demonstrated that behavioural mechanisms such as natal philopatry and site fidelity (well documented among migratory birds; Greenwood and Harvey 1982; Weatherhead and Forbes 1994; Clarke et al. 1997; Rohwer and Anderson 1988; Robertson and Cooke 1999; Doherty et al. 2002) can limit dispersal and facilitate varying degrees of local demographic independence during periods of the annual cycle. Differences in subpopulation connectivity, in conjunction with spatial heterogeneity in resource availability, predation risk, or other factors that affect local demographic rates, can lead to more complicated regional population dynamics, such as source-sink structure (Pulliam 1988; Pulliam and Danielson 1991; Taylor 1991). In this context, the demographic processes of migratory species are likely structured over a range of spatial scales, across which different ecological mechanisms can be important (Wiens 1989; Kotliar and Wiens 1990; Orains and Wittenberger 1991). Effective conservation and management will therefore require careful consideration of population structure and demographic processes at various spatial scales, over the annual cycle (Moritz 1994; Esler 2000).

In northern Labrador, breeding populations of Harlequin Ducks (*Histrionicus histrionicus* L., 1758) are located within glacially carved river canyons that are separated by large areas of unsuitable habitat (high subarctic plateau; Fig. 1). These topographic features produce discrete habitat patches (river canyons) within a "featureless matrix", providing a simplified spatial structure in which to investigate population structure (Wiens 1997). Harlequin Ducks exhibit a high degree of natal philopatry and site fidelity, though both natal and adult dispersal occur, to some degree, among river systems (Robertson and Goudie 1999). Together these processes can provide a mechanism producing varying degrees of local demographic independence and regional connectedness during the breeding season (Esler 2000). Northern Labrador is presently an area practically unaffected by anthropogenic perturbation and, unlike human-induced habitat fragmentation, the patchiness of the 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 investigate whether populations of Harlequin Ducks breeding in different river canyons represent an important level of demographic structure by (i) comparing the demographic features of subpopulations breeding in 11 river canyons within a large, relatively homogeneous ecoregion in northern Labrador, (ii) evaluating the roles of the abundance of avian predators and the availability of prey and habitat features as ecological mechanisms underlying heterogeneity in local demographics, and (iii) considering the effects of local demographic differences on regional population structure and dynamics of Harlequin Ducks. We discuss the implications

of multiple levels of demographic structure for extrapolating local research to the landscape scale and for developing informed conservation and management strategies for migratory birds.

Materials and methods

Aerial surveys

Helicopter surveys for Harlequin Ducks and birds of prey (Peregrine Falcon, *Falco peregrinus* Tunstall, 1771, Golden Eagle, *Aquila chrysaetos* (L., 1758), Gyrfalcon, *Falco rusticolus* L., 1758, and Great Horned Owl, *Bubo virginianus* (Gmelin, 1788), all known predators of Harlequin Ducks (Heath et al. 2001)) were carried out between 1992 and 2000 on 11 river systems (total river length = 442.6 km) within the Kingurutik – Fraser River ecoregion (Ecological Stratification Working Group 1995) in northern Labrador (Fig. 2). Three experienced observers working together recorded bird locations on 1 : 50 000 maps, and locations were verified using GPS coordinates whenever possible. Surveys were conducted for an average of 4.7 years (range 4–7) per river for Harlequin ducks and 4.1 years (range 3–5) per river for birds of prey. Although survey accuracy has not been evaluated in this region, it is expected to be high owing to a lack of large trees (which are a primary factor influencing detectability; Gregoire et al. 1999). Given similar habitat characteristics among river canyons in this ecoregion, we expect that the probability of missing an individual is similar throughout the study area. Additionally, Harlequin Ducks' tenacity to rivers and their habit of flying along the middle of rivers when flushed make them highly amenable to aerial surveys.

The unique life history and essentially linear habitat of Harlequin Ducks mean that survey methods require special consideration not typical for most waterfowl. Surveys for Harlequin Ducks were conducted between 7 and 23 June of each year, which was determined to be the best time for surveys in this region (Rodway 1998; Trimper et al. 2006). Primary rivers were located in discrete canyons, so most tributaries were unsuitable habitat (i.e., meltwater drainage located behind waterfalls on subarctic plateau; see Fig. 1); therefore, only primary rivers were surveyed. Consistent with previous surveys for Harlequin Ducks (Gilliland et al. 2006) and other migratory waterfowl (Dzubin 1969), lone individuals were considered to represent pairs. Lone males could indicate a pair in which the female is searching for a nest or incubating, while lone females could indicate a pair in which the male has departed for molting areas (see life history in Robertson and Goudie 1999). This method is considered the most conservative one for migratory waterfowl (Dzubin 1969). Further details of survey methods are given in Heath (2001).

Surveys for birds of prey were conducted by helicopter along both sides of river canyons and in surrounding lake areas between June and July of each year, following the methods of Lemon and Brazil (1990). Nest sites were considered to be active if (i) at least one individual was present and sitting on the nest, (ii) eggs or chicks were observed in the nest, or (iii) a pair or individual flushed from the cliff and acted territorial (Lemon and Brazil 1990). As all river systems in the study area are located in canyons, cliffs are

Fig. 1. Photograph of the Fraser River, northern Labrador, illustrating the location of river systems within glacially carved canyons (A) surrounded by extensive areas of high subarctic plateau (B). This provides a simple landscape structure for investigating demographic structure (see Wiens 1997).



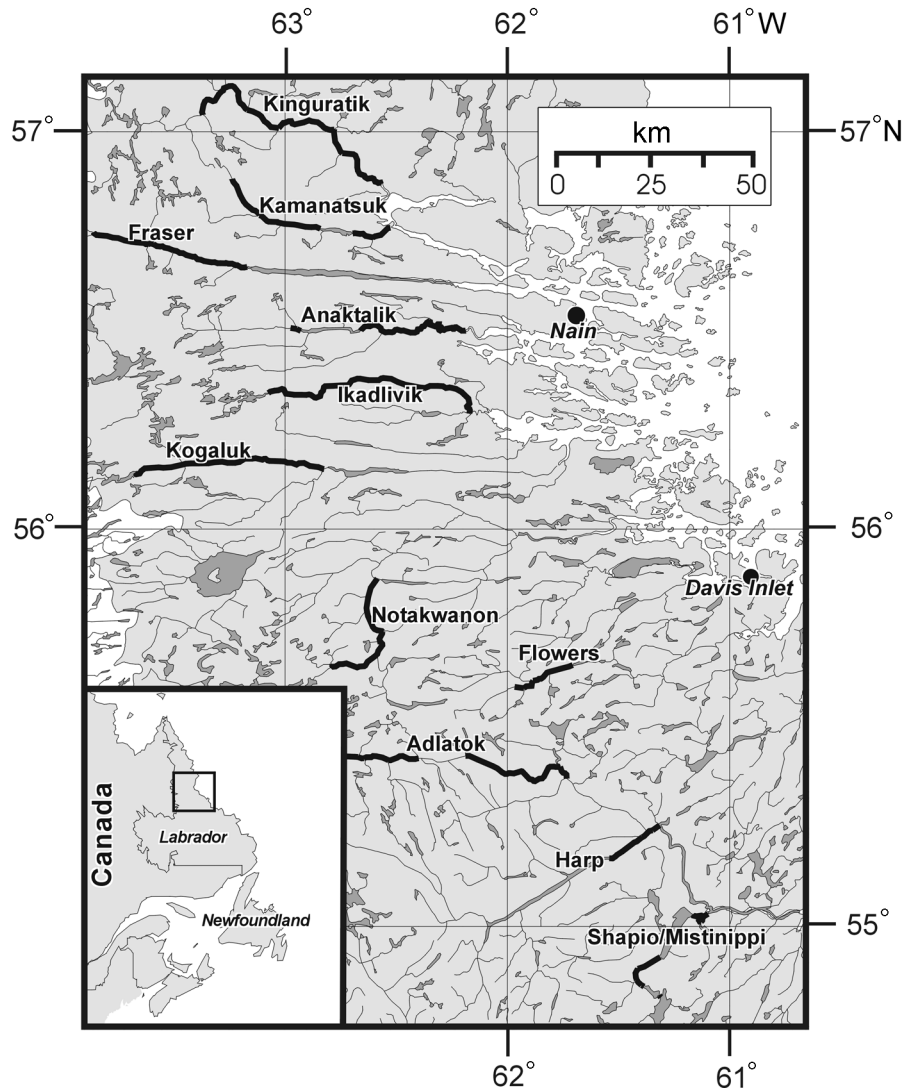
ubiquitous and differences in nest-site availability for raptors are primarily due to small-scale differences in cliff topology rather than the presence or absence of cliffs. Practically all ledges of adequate size contained stick nests, and old or empty stick nests and those occupied by ravens (*Corvus corax* L., 1758) were also recorded to index nest-site availability.

Statistical and analytical treatment of survey data

Densities and temporal variability

The density of Harlequin Ducks on each river system was 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

Fig. 2. Location of study area in northern Labrador. Survey rivers are labelled and approximate survey routes along rivers are bolded. River systems in this region are located in glacially carved canyons separated by extensive areas of subarctic plateau, which is unsuitable habitat for Harlequin Ducks (see also Fig. 1; most unsurveyed rivers and tributaries are within subarctic plateau).



MapInfo (MapInfo Corporation 1998); step length = 0.05 km). Linear densities are the standard means of presenting counts of breeding Harlequin Ducks (Robertson and Goudie 1999) and provide a basis for comparing relative abundance between river systems. The density of birds of prey for each river system was calculated by dividing the average annual number of active nests (for all species combined) by the length of river surveyed (km). Active nests located on lakes within 5 km of the river were also included. Old and empty nests were used to calculate the density of available nest sites in the same manner.

To assess differences in variability (stability) among local populations of Harlequin Ducks, the coefficient of variation ($CV = \text{standard deviation} / \text{mean}$) was calculated to normalize for populations of different size (McArdle et al. 1990; Gaston and McArdle 1994; note that the same results were obtained in our analyses using either standard deviation of log-transformed abundances or a more robust measure of population variability (see Heath 2001)). We use the term stability to refer to $1/CV$.

Statistics

Relationships between density and stability of populations of Harlequin Ducks were evaluated across river systems using two-tailed product-moment correlation analysis. Regression analysis was used to evaluate the relationship, among river canyons, between densities of birds of prey and both densities and stability of populations of Harlequin Ducks. In several instances nonlinear relationships were most descriptive, so variables were log-transformed.

Comparison among selected river canyons

In-depth investigation of small-scale habitat features within river systems was not possible for all 11 river canyons, given the spatial extent of the study area (~450 km of river in a 40 000 km² area with no roads). We therefore focused this analysis on two river canyons, the Ikadlivik and Fraser river canyons, which represented extremes in Harlequin Duck demographic characteristics and, therefore, where differences in habitat availability would be most likely to occur if they were important in determining demographic

Table 1. Characteristics of Harlequin Duck (HADU) and raptor populations in 11 river canyons in northern Labrador (density is the average across survey years and CV is the coefficient of variation; see Materials and methods and Fig. 3 for further details).

River canyon	Length (km)	HADU density	HADU CV	Raptor density
Ikadlivik	46.7	0.3266	0.098	0.009
Shapio/Mistinippi	23.7	0.4822	0.495	0.0211
Harp Lake	11.1	0.4505	0.447	0.036
Notakwanon	29.5	0.2708	0.5	0.0169
Kingurutik	89.1	0.2048	0.255	0.0505
Anaktalik	46.4	0.1293	0.72	0.0575
Flowers	20.2	0.0988	0.707	0.0823
Kamanatsuk	28	0.0982	0.621	0.0643
Adlatok	43.2	0.0926	0.5	0.0579
Kogaluk	45.3	0.0773	0.645	0.1269
Fraser	59.3	0.054	0.839	0.1433

differences. The Ikadlivik River was selected because it had the most stable population of Harlequin Ducks, with one of the highest densities, and it also had the lowest density of birds of prey. The Fraser River was selected as the opposite extreme because it had the lowest density of Harlequin Ducks and the highest density of birds of prey (Table 1 and Fig. 3).

Twelve sites were randomly selected along each river system as follows: a random number generator was used to select (with replacement) a 1 km stretch of river, and a second randomly generated number was then used to select a 50 m section from the 20 available in the selected 1 km stretch. This provided a random set of sites well distributed across the entire river canyon. Each site was visited in June–July 2000, after spring runoff had subsided. At each site (50 m section) the following habitat features relevant to Harlequin Ducks (Robertson and Goudie 1999; Rodway et al. 2000; Heath 2001) were measured: stream depth and width, current velocity, percentage composition of riparian (within 5 m of banks) and general (5–100 m from bank) ground/vegetation types, presence of in-stream islands and boulders, bank characteristics (including overhanging vegetation), substrate composition, and water characteristics (e.g., rapids, riffle, runs, slow water). We sampled benthic invertebrates (the primary prey of Harlequin Ducks during the breeding season; see Robertson and Goudie 1999) using kick sampling (Frost et al. 1971) at three random locations per site. We acknowledge that high temporal variability in the distributions of benthic invertebrates over time scales shorter than the sampling regimes means a low signal to noise ratio, making extrapolation of significant differences to the between-site scale difficult. Spatial variability of benthic invertebrates is often associated with the riparian characteristics listed above (e.g., Hynes 1970), which may therefore provide a more accurate basis for assessment of habitat availability. Detailed sampling methods are given in Heath (2001).

Prey abundance and biophysical habitat features were compared between the Ikadlivik and Fraser rivers using a discriminant function analysis: equality of group means was tested using a χ^2 -transformed Wilks' Lambda in SPSS (SPSS Inc. 1999). A univariate approach was also used: two-tailed *t* tests for unequal variance were used to compare each characteristic separately; alpha levels were adjusted using a sequential Bonferroni test (Rice 1989). This additional univariate analysis is presented in Heath (2001).

Population trends

Brood surveys were available only for the Ikadlivik River watershed for 1996–1998; however, this allowed us to assess the productivity of this stable, high-density system. Aerial surveys covered 33.2 km, while more intensive ground surveys (consistent with the methods of Kuchell 1977) re-covered 20.8 km. For each detected brood, the number of young and the age class were recorded. All detected broods were at least 6 days old (i.e., age class 1B) and ranged up to 39–49 days old (age class 3A). Detected broods were divided by all the pairs observed during spring surveys, meaning our fecundity parameter was extremely conservative, representing minimum production. These data were entered into a population projection model previously developed for Harlequin Ducks (Goudie et al. 1994; Robertson 1997; survival rates updated with values from Cooke et al. 2000) to obtain a projected population growth rate (λ).

Results

Harlequin Duck density and stability varied among river system subpopulations (Table 1). Harlequin Duck density (log-transformed) and stability ($1/\text{CV}$) were positively related ($r = 0.678$, $df = 9$, $p = 0.022$). This indicated the presence of some stable, high-density populations, some small populations that were highly variable among years, and intermediate populations between these extremes. Heath (2001) also found that both local density and stability were positively related with how consistently particular stretches of river were used among years (an indicator of site fidelity).

A population projection model on a stable, high-density river system (Ikadlivik) indicated a positive projected population growth rate (λ) of 2.1% per annum, despite observed stability, suggesting that this river system was likely at carrying capacity during the study period and may have been a source of emigrants. On two highly variable, low-density river systems (Fraser and Kogaluk rivers), population size came close to extinction (i.e., only one pair) in some years, while dramatic increases were observed in subsequent years — increases that are unlikely to be accounted for by local reproductive output, therefore suggesting immigration in some years (e.g., Fraser River: one pair in 1993 and five

pairs in 1994; one pair in 1999 and seven pairs in 2000; Kogaluk River: one pair in 1993 and three pairs in 1994; one pair in 1997 and six pairs in 1999).

To identify potential mechanisms underlying differences among rivers, we compared habitat availability between the Ikadlivik and Fraser river systems, which represented two demographic extremes where habitat differences would be most likely to be observed. This comparison indicated no detectable differences in habitat availability using either a univariate (see Heath 2001) or a multivariate approach (discriminant function analysis: Wilks' Lambda $\chi^2 = 20.734$, $df = 21$, $p = 0.475$).

Among all 11 river systems, (log) Harlequin Duck densities were strongly and negatively related to densities of birds of prey ($r^2 = 0.743$, $df = 10$, $p = 0.0006$; Fig. 3). Stabilities of Harlequin Duck populations were also negatively related to densities of birds of prey ($r^2 = 0.594$, $df = 10$, $p = 0.0055$). Densities of birds of prey were strongly related to the availability of cliff nesting sites ($r = 0.935$, $df = 9$, $p < 0.0001$).

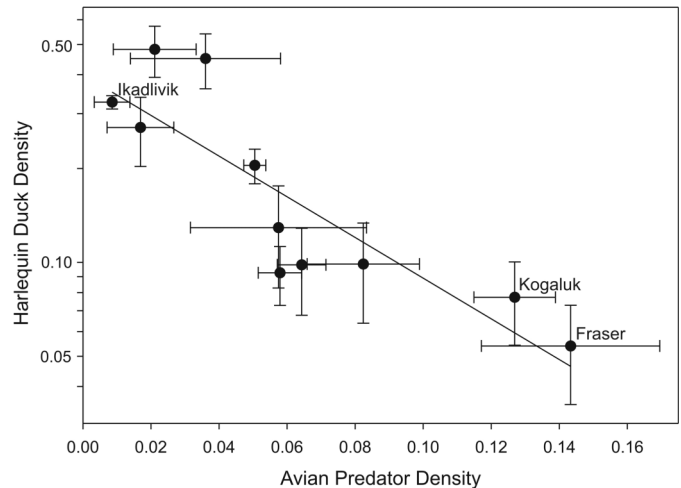
Discussion

River systems as demographically important units

At the landscape scale, subpopulations of breeding Harlequin Ducks are structured within glacially carved river canyons. Alone, this spatial structuring does not provide a conclusive basis for the treatment of river canyons as demographically important units, and the high mobility of Harlequin Ducks and other migratory birds has generally led many researchers to assume demographic panmixia at this spatial scale. Assuming demographic panmixia allows extrapolation of demographic parameters and other research results from logistically and financially constrained small-scale studies to the larger population across the landscape. This is a particularly risky assumption because if there are local differences in ecologically relevant factors such as resource availability and (or) predation risk, then local populations could differ markedly in their demographic characteristics. Therefore, despite high mobility, differences in demographic rates and fidelity to breeding sites of different quality could lead to local populations with varying degrees of demographic connectivity. In such a context, river systems could be an important demographic unit, with regional population dynamics resulting from changes within and interactions among subpopulations, precluding assumptions of panmixia and making the extrapolation of research and monitoring results from local study areas to large spatial scales a risky undertaking (Wiens et al. 1993; Kareiva and Wennergren 1995; Ritchie 1997).

Despite having high vagility, Harlequin Ducks often exhibit high natal philopatry and site fidelity across their range (Reichel et al. 1997; Robertson and Goudie 1999; Robertson et al. 2000). The degree of philopatry and fidelity, however, is not absolute, and there is direct evidence of both natal and adult dispersal between river systems among years (summarized in Robertson and Goudie 1999). This is important, as some degree of dispersal among subpopulations without total mixing can provide a mechanism producing varying degrees of local demographic independence that can have important implications for regional dynamics (Pulliam 1988;

Fig. 3. Relationship (regression line) between Harlequin Duck densities (logarithmic scale) and densities of birds of prey among 11 river canyons (circles) in the Kingurutik – Fraser ecoregion, northern Labrador. Error bars indicate standard error of the mean and therefore do not reflect population variability (see coefficients of variation in Table 1). River systems discussed in detail are labelled.



Hanski and Gilpin 1991; Esler 2000). Given that migration distances from the wintering grounds are large, inter-river distances are not likely to pose movement barriers at breeding grounds. In this study, positively related differences in population density and stability were observed among river systems, suggesting heterogeneity in demographics among river systems for Harlequin Ducks breeding in northern Labrador (Fretwell 1972; Howe et al. 1991). Heath (2001) also demonstrated that stretches of river were used more consistently among years in river canyons with stable, high-density Harlequin Duck populations. Together, these features suggest that Harlequin Ducks breeding in different river canyons could have different demographic characteristics. This indicates that fine-scale population structure within river canyons could represent a demographically important unit of analysis and could have implications for understanding regional dynamics.

Newton (1998) noted that carrying capacities may be reached when populations have stabilized between years despite large numbers of potential settlers. These features were observed on a high-density river system that was highly stable in size among years despite projected growth (Ikadlivik River). This suggests emigration and dispersal of individuals in excess of the carrying capacity. Conversely, two low-density, highly variable river systems (Fraser and Kogaluk) showed population increases that are unlikely to be accounted for by local reproductive output, suggesting immigration in some years. These low-density river systems also approached local extinction in some years. Small populations are susceptible to local extinctions due to stochastic events (Schoener and Spiller 1987; Hanski 1999), though the population increases observed in this study suggest that immigration could provide a rescue effect in some years (Brown and Kodric-Brown 1977; Hanski 1985). These findings not only suggest that populations in river canyons are demographically important units, but also indicate that demographics cannot be generalized across areas.

Interactions among local populations could therefore have important implications for regional dynamics.

Predation risk as a mechanism for population structure

Previous research on Harlequin Ducks has focussed almost exclusively on the role of biophysical habitat features in determining site use within river systems (see Robertson and Goudie 1999; Heath 2001). However, a large and growing number of reports indicate that the role of direct predation on Harlequin Ducks by birds of prey may be severely underestimated in the current literature (reviewed in Heath et al. 2001). Densities of birds of prey varied considerably among river canyons and were highly correlated with availability of cliff nesting sites, suggesting that nesting sites are a limiting factor for birds of prey in this region (see also Janes 1985). Our results show a strong negative relationship between densities and stability of local populations of Harlequin Ducks and the abundance of birds of prey nesting in each river canyon. Observed differences in local demographic characteristics of Harlequin Ducks could therefore be related to predation risk from birds of prey.

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 determined by resource levels (Lack 1954; Martin 1991; Newton 1993, 1998). A comparison of habitat characteristics between two demographic extremes indicated no detectable differences in the availability of features relevant to Harlequin Ducks. Obviously cliffs are present throughout river canyons, but canyons did differ in the availability of cliff nesting sites for birds of prey. This is most likely due to small-scale differences in cliff topology and not factors of direct importance to Harlequin Ducks. Together these findings support the hypothesis that birds of prey could limit Harlequin Ducks in areas of otherwise suitable habitat. Heterogeneity in predation risk among river canyons therefore appears to be an important factor influencing demographic structure of Harlequin Ducks in this study area.

There has been much interest in the stabilization of predator-prey dynamics through spatial subdivision (Vandermeer 1973; Kareiva 1990; Taylor 1990, 1991; Kareiva and Wennergren 1995). Predators and prey or competing species can coexist through spatial segregation (Comins and Noble 1985; Hassell et al. 1994), and top predators have been shown to influence densities of island subpopulations of prey species (Schoener and Toft 1983). The possibility that predation risk may limit Harlequin Duck populations has important implications for understanding the species' demographics, especially because a slight increase in adult mortality can substantially affect overall population stability (Pulliam et al. 1992; Goudie et al. 1994). Although a variety of reports indicate that all the birds of prey investigated in this study do indeed kill adult Harlequin Ducks (Heath et al. 2001; Brodeur et al. 2006), even if predation rates are low, the risk of predation and its associated costs could be sufficient to influence habitat selection (Lima and Dill 1990). While a number of ecological factors are no doubt important, we suggest that through direct mortality and (or) risk of predation, the local abundance of raptors is an important influence on local demographics and the suitability of particular habitats for

Harlequin Ducks within this ecoregion: stable, high-density, and productive populations of Harlequin Ducks often occur in potential refuges from predation risk, where nest sites for raptors are limited.

Effects of local heterogeneity on regional dynamics

We have intentionally avoided use of the term "metapopulation" owing to an increasing dichotomy in its precise definition (see Pannell and Obbard 2003) that is making the concept relatively uninformative in applied contexts. However, our results strongly support the importance of the multi-scale demographic framework developed for migratory birds by Esler (2000), and source-sink theory could be an important consideration (Pulliam 1988; Pulliam and Danielson 1991). Demographic models of source-sink dynamics incorporating stochastic variation (Howe et al. 1991) indicate that stability may be an important indicator of these dynamics. Our observations appear suggestive of source-sink-type dynamics: high stability was observed in high-density populations, despite projected positive growth, whereas unstable, low-density populations approached extinction in some years but subsequently showed increases suggestive of immigration. Demonstrating that a spatially structured population exhibits source-sink dynamics is difficult, and empirical evidence is limited (Davis and Howe 1992; Watkinson and Sutherland 1995; Ritchie 1997). Given the large spatial extent of our study area, it would be practically impossible to measure all demographic and habitat features in every subpopulation. Additionally, we observed river canyons with intermediate densities and stability of Harlequin Ducks and raptors, and discrete categories (e.g., source-sink) are likely rare in natural ecological systems. However, source-sink theory is fundamentally about differences in demographics among subpopulations and how these differences can influence regional population dynamics. This could be an important consideration for Harlequin Ducks, although further work incorporating movements of known individuals and detailed demographic analysis is clearly needed.

Many conservation and management implications arise when regional dynamics are influenced by local demographic differences, although this framework has seldom been considered for migratory birds (Esler 2000). Because of connectedness among subpopulations, habitat alteration such as hydroelectric development on a single "source" river could have severe consequences not just locally but also for the regional persistence of Harlequin Ducks in our study area. Although protecting "source" populations would be important, "sink" populations can also play important roles in population dynamics. The extent to which individuals move into and utilize "sink" populations can relate to lifetime fitness trade-offs, depending on costs and gains in low-quality sink habitats versus not breeding at all in a particular season (e.g., Kokko et al. 2001). Morris (1991) argued that emigration from "source" to "sink" subpopulations is an evolutionarily stable strategy only if reverse migration back to the "source" also occurs. Birds in secondary ("sink") habitats may therefore provide a buffer of potential immigrants that can fill gaps in primary ("source") habitats at certain times (Brown 1969; Fretwell 1972). It is therefore possible that seemingly poor-quality "sink" populations could provide important transition habitat and at times be important

for regional recruitment and persistence (Howe et al. 1991; Davis and Howe 1992; Kacelnik et al. 1992).

The implication that breeding Harlequin Ducks exhibit heterogeneity in local demographics, the influence of local raptor abundance on these patterns, and the subsequent possibility of source–sink-like regional dynamics provides an important framework with critical implications for conservation and management of migratory species. Of particular importance is the fact that demographic characteristics and limiting factors quantified in one area may not generalize to other subpopulations or the regional population across the landscape. In such cases, subpopulations will be an important demographic unit to consider. In the case of Harlequin Ducks in our study area, populations in different river canyons appear to have different demographic characteristics that may be influenced by movement among canyons, so assuming demographic panmixia in this landscape can be risky and misleading. Typically both research and conservation/management studies must select a study site based on increasing the sample size of individuals (Doak and Mills 1994). Selecting a high-density (putative “source”) population of Harlequin Ducks would mean that demographic parameters extrapolated to the region could drastically overestimate population viability. Our findings therefore have important consequences for the development and application of conservation and management tools for similar migratory birds, including habitat suitability indices, viability analyses, and modelling population change in response to human perturbation. Effective conservation and management of migratory birds will require both precaution and a detailed understanding of population structure and demographic processes occurring across multiple spatiotemporal scales.

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