Differential use of similar habitat by Harlequin Ducks: trade-offs and implications for identifying critical habitat

Joel P. Heath and William A. Montevecchi

Abstract: Interactions between ecological processes operating at different scales are critical aspects of habitat suitability requiring careful consideration in conservation planning. Our previous research indicated that local abundance and demographics of subpopulations of Harlequin Ducks (*Histrionicus histrionicus* (L., 1758)), structured in 11 river canyons in northern Labrador, were influenced by predation risk from nest-site-limited raptors. At demographic extremes, where raptors were absent, Harlequin Ducks were stable at high densities, with positive-projected growth, suggesting that they were at carrying capacity and a source of emigrants. In contrast, where raptors were abundant, low density, highly variable populations of ducks approached local extinction in some years, with subsequent increases suggestive of immigration rescue effects. A comparison of resources for Harlequin Ducks indicated no differences in habitat availability among these putative "source" and "sink" subpopulations. In the present study, we used multivariate analysis to identify habitat characteristics important for home-range use within these river canyons and to develop habitat suitability indices (HSI). Despite similar habitat availability, different characteristics were locally important. In a sink where predation risk was high, only danger-reducing habitat characteristics (i.e., overhang vegetation) were identified as important, whereas invertebrates was a predominant characteristic of the source HSI. Despite similar habitat availability, HSI developed in source and sink habitats would, respectively, over- and under-estimate regional habitat availability. Informed conservation and management strategies will therefore require integrating individual trade-offs about predation risk and resources into a multiscale context.

Résumé : Dans la planification de la conservation, il est important de considérer avec soin les interactions entre les processus écologiques qui agissent à des échelles différentes comme des aspects essentiels dans la définition des habitats adéquats. Nos travaux antérieurs ont indiqué que l'abondance locale et la dynamique des sous-populations de canards arlequins (*Histrionicus histrionicus* (L., 1758)) établies dans 11 canyons fluviaux du nord du Labrador sont influencées par le risque de prédation de la part de rapaces qui sont eux-mêmes restreints par la disponibilité des sites de nidification. Dans des conditions démographiques extrêmes, en l'absence de rapaces, les canards arlequins atteignent des densités fortes et stables et leur croissance projetée est positive, ce qui indique qu'ils ont atteint le stock limite et qu'ils sont une source d'émigrants. En revanche, lorsque les rapaces sont abondants, les densités faibles et les populations très variables de canards s'approchent certaines années des conditions d'extinction locale et les regains subséquents semblent être le résultat d'un sauvetage par immigration. Une comparaison des ressources pour les canards arlequins dans ces sous-populations supposées « sources » et « drains » n'indique aucune différence de disponibilité des habitats. Dans cette étude, une analyse multidimensionnelle nous a servi à identifier les caractéristiques de l'habitat importantes dans l'utilisation de l'aire vitale dans ces canyons fluviaux et à développer des indices de convenance des habitats (HSI). Malgré des disponibilités d'habitats semblables, ce sont des caractéristiques différentes qui ont une importance locale. Dans les régions de type drain dans lesquelles le risque de prédation est élevé, seules les caractéristiques qui réduisent le danger (c.-à-d., une végétation en surplomb) ressortent comme importantes, alors que les invertébrés constituent la caractéristique prédominante des HSI des régions sources. Malgré des disponibilités d'habitats semblables, les HSI mis au point dans les habitats de type source et drain vont respectivement sur-estimer et sous-estimer la disponibilité régionale des habitats. Des stratégies de conservation et d'aménagement éclairées nécessiteront ainsi l'intégration des compromis individuels reliés au risque de prédation et aux ressources dans un contexte à échelles multiples.

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Introduction

Perhaps one of the most essential factors in developing comprehensive conservation and management strategies for any species is the identification and subsequent protection of critical habitat. As ecologists and conservation biologists have become increasingly aware, spatial scale and structure play critical roles in identifying and interpreting associations

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J.P. Heath[1,2] and W.A. Montevecchi. Cognitive and Behavioural Ecology, Departments of Biology and Psychology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

[1] Corresponding author (e-mail: jheath@math.ubc.ca).

[2] Present address: Mathematical Biology Program, The University of British Columbia, 121-1984 Math Road, Vancouver, BC V6T 1Z2, Canada.

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of organisms with habitat features and ecologically limiting factors (Wiens 1989; Levin 1992; Schneider 1994, 2001). This is especially important when studying migratory birds, because habitat selection is a hierarchical process that integrates environmental information from landscape through to nest-site scales (Kaminski and Weller 1992; Jones 2001), with the relevance of particular habitat features dependent on the scale of analysis (Orians and Wittenberger 1991). Additionally, populations often exhibit well-defined scale-dependent spatial structure, and processes at local scales can influence regional distributions and dynamics (and vice versa; Schneider and Piatt 1986; Kareiva 1990; Hanski and Gilpin 1991; Kareiva and Wennergren 1995; Wiens 1997; Hanski 1999). Owing to logistic considerations, however, on-the-ground research is often conducted at small spatial scales, and this is frequently the case when conservation decisions require rapid responses (see Doak and Mills 1994).

Consideration of landscape and population features is essential for understanding local dynamics and their roles in ecosystem processes. For example, if the overall population exhibits demographic heterogeneity such as source–sink dynamics (Pulliam 1988; Pulliam and Danielson 1991), habitat studies in sink subpopulations could lead to incorrect or misleading information about the habitat requirements of a species (Watkinson and Sutherland 1995). While the implications of demographic heterogeneity are recognized, the mechanisms underlying heterogeneity are often poorly understood. Recent emphasis has been placed on bridging these gaps, by considering the role of behavioural mechanisms, including movement, site fidelity, and predator–prey interactions, in populations and landscape processes (Lima and Zollner 1996; Esler 2000). Understanding these relationships among levels of organization is a critical objective for interpreting pure research and for making informed conservation and management decisions.

Previously, we applied a framework for understanding demographic structure of migratory species across multiple scales (Esler 2000) to populations of Harlequin Ducks (*Histrionicus histrionicus* (L., 1758)) breeding in discrete river canyons in northern Labrador (Heath et al. 2006). We provided support for the hypothesis that Harlequin Ducks breeding in river canyons exhibit differences in local abundance and demographics, akin to source–sink population structure (emigration dispersal from a high density, stable population to low density, variable populations approaching extinction in some years, followed by increases suggestive of immigration rescue effects). Local demographic differences were strongly associated with the local abundance of nesting birds of prey, which in turn was related to the local availability of cliff-nesting sites. These raptor species (Peregrine Falcon, *Falco peregrinus* Tunstall, 1771; Golden Eagle, *Aquila chrysaetos* (L., 1758); Gyrfalcon, *Falco rusticolus* L., 1758; Great Horned Owl, *Bubo virginianus* (Gmelin, 1788)) are known to prey on adult and juvenile Harlequin Ducks (Heath et al. 2001). A comparison between a putative "source" with low densities of raptors and a putative "sink" with high densities of raptors indicated no differences in riparian habitat characteristics, suggesting that predation risk was likely a primary mechanism influencing Harlequin Duck population structure (Heath et al. 2006).

Our remote study area in northern Labrador provides an ideal situation to study habitat use under naturally occurring population structure, free of the often confounding effects of human-induced habitat fragmentation. Given the observed patterns of demographic structure and predation risk, the objective of the present study is to determine how these regional processes influence home-range use within river canyons. In particular, our aim is to evaluate Watkinson and Sutherland's (1995) prediction that habitat studies in sink populations can be misleading. We compare the use of riparian habitat among putative source and sink subpopulations, where habitat availability is similar (Heath et al. 2006), and evaluate the ability of locally derived habitat suitability indices (HSI) to predict site use in the other river system. We discuss the importance of our findings for understanding spatial heterogeneity in ecologically limiting factors and implications for making informed conservation and management decisions, particularly with respect to assessing and generalizing habitat suitability within and among spatial scales.

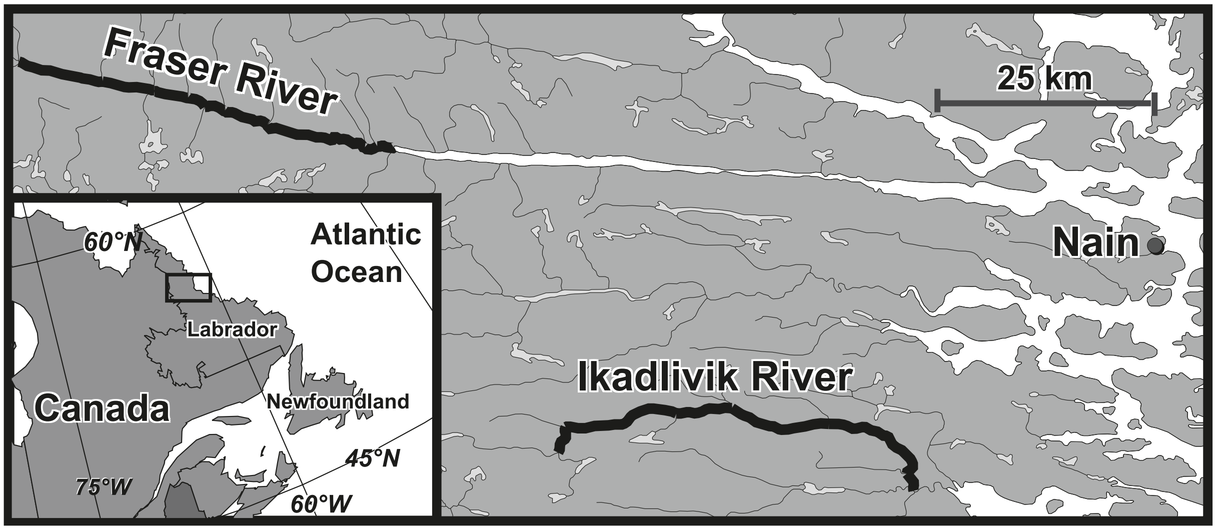
Materials and methods

Biophysical habitat characteristics and prey availability

Two river systems were selected for the study based on extremes in local demographics (Heath 2001; Heath et al. 2006). We chose a putative source (high density, consistent site use, stable population at carrying capacity with high productivity that is suggestive of emigration) and a putative sink (low density, inconsistent site use, variable population size approaching local extinction in some years with high population increases in other years that is suggestive of immigration). These are the Ikadlivik and Fraser rivers in northern Labrador (Fig. 1). The heuristic framework provided by source–sink population theory is a useful paradigm for discussing the observed demographic heterogeneity. Despite extreme differences in local demographics, these rivers did not differ in the availability of riparian habitat characteristics relevant to Harlequin Ducks (Heath et al. 2006).

Harlequin Duck home ranges were defined as 1 km stretches of river (Robertson and Goudie 1999), with survey locations at the centroid (for survey methods see Heath et al. 2006). Each river system was partitioned into used and unused sections by overlaying survey data from 4 years per river system in Mapinfo version 5 and considering a 1 km buffer around each annual sighting (for further details see Heath 2001; buffers that frequently overlapped among years were given high fidelity to breeding sites in this species (Robertson and Goudie 1999)). Twenty-six sample sites were randomly chosen along the Ikadlivik River (14 used, 12 from unused sections; total river length considered was 51.8 km) and 13 sites (5 used and 8 unused) on the Fraser River (total river length considered was 40.0 km; fewer sites were selected on the Fraser River because of a lower proportion of used habitat). Sites on the Ikadlivik River were sampled immediately after sites on the Fraser River, and all sites were visited between 29 June and 20 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.

Fig. 1. Location of the Ikadlivik and Fraser rivers in northern Labrador, Canada (inset), where we studied Harlequin Ducks (*Histrionicus histrionicus*). River systems in this ecoregion are located within glacially carved river canyons (the majority of tributaries are therefore vertical waterfalls), surrounded by the subarctic plateau.



Stream depth was measured centre stream, mid-left, and mid-right along each transect along with stream width, and both depth and width were averaged for the site to avoid replication (i.e., inflating degrees of freedom). Each site was then divided into five 10 m subsections in which we 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), water characteristics (percent rapids, riffle, runs, slow water (back water eddies and pools)), and overhang vegetation (the percentage of stream banks that were not exposed and were covered by vegetation that extended over the river; for definitions see Scruton and Anderson 1992). Percent composition of bank and vegetation characteristics also included that on in-stream islands. Measurements were averaged over all subsections to determine the overall percent composition for the site. In the same manner, but using ten 5 m subsections, we 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), and mud (0.004–0.05 mm)). The percentages of banks that had overhanging vegetation, and banks that were exposed (no hardwood or softwood vegetation within 1 m of stream banks), were also quantified for each site. In-stream islands and exposed boulders were counted, and islands were categorized as gravel, alder, or treed (conifers and (or) hardwoods present). Mid-stream velocity was measured as the time it took a 4 cm diameter 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 × 25 cm rectangular kick net (Frost et al. 1971). Invertebrates were identified to order (except Diptera, which was also identified to family), and total number of each taxa per sample was determined and averaged across the three samples for each site.

Most of these characteristics have been previously related to Harlequin Duck habitat use (Robertson and Goudie 1999; Rodway et al. 2000; Heath 2001). We screened each habitat parameter for relevance (separately for the Ikadlivik and Fraser rivers) before analysis. We used two-tailed t tests for unequal variance to compare each parameter and parameters not meeting a criteria of $p \leq 0.1$ were excluded from further consideration. Redundant variables were also excluded (i.e., each subcategory of invertebrates, subtypes of in-stream islands differed significantly ($p \leq 0.05$) between used and unused sites), therefore we used total invertebrates and total instream islands to avoid redundancy.

Given the highly inter-related nature of riparian habitat characteristics, we used a multivariate approach to determine differences underlying used and unused areas. Variables were entered into a principal component analysis (PCA) in SPSS version 10 (SPSS Inc. 1999) to evaluate the primary habitat variables underlying differences between used and unused sites in each river canyon. Only a single principal component (PC) was important in distinguishing used and unused areas in each canyon, and therefore further model selection (e.g., information–theoretic approach) was not required. A habitat suitability index (HSI) was generated for the Ikadlivik and Fraser rivers by using the locally derived PC equations and selecting a critical PC value that provided good separation between used and unused sites. Each HSI was then used to classify (used or unused) and quantify (PC value) the predicted suitability of sites on the other river system.

Results

Ikadlivik River

Principal component analysis on the Ikadlivik River indicated one PC as being important in describing habitat characteritics among sites (Table 1). This PC explained 61.5% of the variation in habitat characteristics, primarily owing to the abundance of invertebrates and vegetative characteristics. As indicated by Fig. 2A, a PC score of –0.1 provided

Table 1. Principal component analysis (PCA) of sites on the Ikadlivik River, indicating habitat characteristics entered into the analysis, amount of variation in each characteristic or parameter explained by the PCA (i.e., communalities), coefficient for the PC scores for each parameter, and the correlation coefficients of each characteristic with the extracted PC (which explained 61.5% of the variation in the data).

Habitat characteristic	Variance explained	Component coefficients	Component correlation
Invertebrates	0.523	0.294	0.723
Overhang vegetation	0.785	0.36	0.886
Riparian unvegetated	0.593	–0.304	–0.77
General unvegetated	0.558	–0.313	–0.747

maximum separation between used and unused sites and therefore provided a critical value for a HSI for the Ikadlivik River (85% correct classification: 2 unused sites classified as suitable, 2 used sites classified as unsuitable; in each case, misclassified sites were close to the critical value).

Fraser River

Principal component analysis on the Fraser River also indicated one PC as being important in describing habitat characteristics among sites (Table 2). This PC explained 74.5% of the variation in habitat characteristics, primarily owing to overhanging vegetation and in-stream exposed boulders. Notably, invertebrates were not an important component in distinguishing used and unused sites in this river canyon. The Fraser River PC provided complete separation (no misclassifications) between used and unused sites based on a PC score of 0.4 (Fig. 2B), and was therefore used as a critical value for a HSI.

Cross-validation

To determine the ability of source-derived HSI in predicting the suitability of sites in a sink, and vice versa, we applied the HSI developed for each river canyon to the other river canyon. When the Fraser HSI was applied to sites on the Ikadlivik (source) River, the Fraser HSI correctly classified 91% of unused sites but only 66.6% of used sites (Fig. 3A). Application of the Ikadlivik HSI to the Fraser River (Fig. 3B) indicated 100% of used sites were correctly classified, whereas 50% of unused sites were classified as suitable habitat.

Discussion

Despite similar habitat availability for Harlequin Ducks, there were differences in the habitat characteristics identified as being important on the Ikadlivik and Fraser rivers. On the Ikadlivik River, a putative source population with high stable densities of Harlequin Ducks and low densities of avian predators, benthic invertebrates, and the presence of riparian and general vegetations were identified as the primary factors distinguishing used and unused areas. Benthic invertebrates (specifically simuliids) have been emphasized as a primary limiting factor for breeding Harlequin Ducks (Bengtson and Ulfstrand 1971; Bengtson 1972; Gardarsson and Einarsson 1994; Rodway 1998; Rodway et al. 2000, Robert and Cloutier 2001). Bengtson (1970), however, also suggested that vegetative cover could be a primary important factor in habitat selection by waterfowl. Dense vegetative cover can conceal nest sites and ducklings from potential predators (Bengtson 1966; Rodway et al. 1998; Robertson and Goudie 1999). This could explain why overhanging vegetation was the predominant factor identified as distinguishing used and unused sites on the Fraser River, where avian predators occurred in high densities. Exposed midstream boulders could provide suitable locations to facilitate vigilance (e.g., Bengtson 1972; Dzinbal and Jarvis 1984; Inglis et al. 1989), and were also indicated as important on the Fraser River. Notably, benthic invertebrates were not indicated as an important characteristic distinguishing used and unused sites on the Fraser River. This result does not imply that benthic invertebrates or other habitat features are unimportant, but rather that factors associated with reducing predation risk were more important in distinguishing used and unused areas (see Bengtson 1966, 1970; Grand and Dill 1997; Rodway et al. 1998; Robertson and Goudie 1999).

The Ikadlivik River is a high density and productive system that is likely at carrying capacity for Harlequin Ducks (Heath et al. 2006). The habitat characteristics identified as important on this system (invertebrates, vegetation) likely represent the primary factors important to Harlequin Ducks in the absence of predation risk. Application of the Ikadlivik HSI to sites on the Fraser River (Fig. 3B) correctly classified all used sites as being highly suitable habitat, and further identified 50% of the unused sites as being suitable. This substantial misclassification error can be understood ecologically as the result of a risk–resource trade-off, where birds of prey exclude Harlequin Ducks from otherwise suitable habitat, as suggested by Heath et al. (2006). Predation risk is high across the Fraser River (0.143 active nests/km) and ducks utilizing this putative sink population appear to have alleviated predation risk by utilizing sites with substantial overhanging vegetative cover that could provide a refuge for both adults and broods. These sites on the Fraser River also had other characteristics important to Harlequin Ducks, as indicated by their classification as suitable habitat based on the Ikadlivik HSI.

In contrast, application of the Fraser HSI to sites on the Ikadlivik River (Fig. 3A) indicated the opposite type of classification error. While the majority of unused sites were correctly classified as unsuitable habitat, 33.3% of used sites were classified as unsuitable habitat by the Fraser HSI. This misclassification was likely because overhanging vegetation was not as important on the Ikadlivik River (where predators were at low abundance) as on the Fraser River, and because invertebrates were not a component of the Fraser HSI.

To summarize, despite similar habitat availability, differences in habitat use between the Ikadlivik and Fraser rivers indicate that different limiting factors can be important in determining habitat use within different subpopulations. Trade-offs between biophysical habitat characteristics and predation risk are important for Harlequin Ducks when selecting sites on the Fraser River. On this, and likely similar river systems, birds of prey exclude Harlequin Ducks from otherwise suitable habitats, and biophysical factors relevant to reducing predation risk are predominantly important in site selection. On the Ikadlivik River (and likely other sys-

Fig. 2. Principal components (PCs) for the Ikadlivik (A) and Fraser (B) rivers, indicating sites used and unused (○ and ●, respectively) by Harlequin Ducks (*Histrionicus histrionicus*). The variation explained by each component and associated habitat characteristics are also indicated. In each case the extracted component provided good separation between used and unused sites, and were used to derive a habitat suitability index (HSI) by selecting a value that minimized classification error (indicated by the vertical gray arrows: –0.1 for the Ikadlivik River, 0.4 for the Fraser River). Values above these critical HSI values can be considered suitable habitat, while those below can be considered unsuitable habitat.

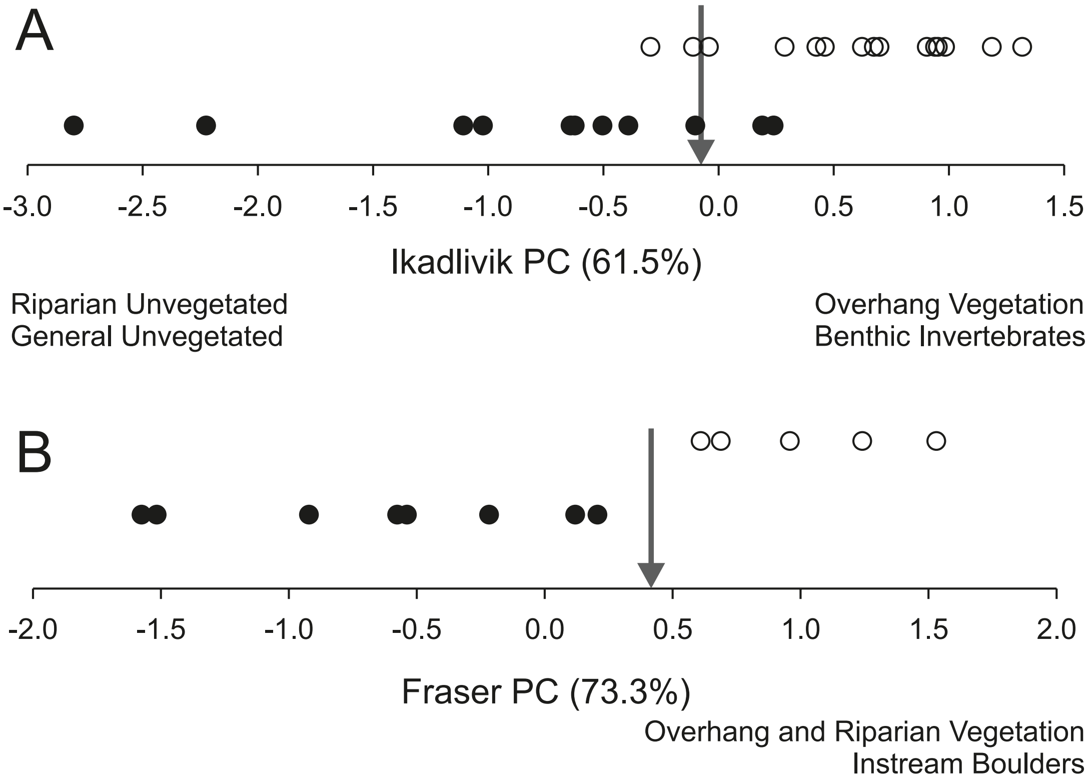


Table 2. Principal component analysis (PCA) of sites on the Fraser River, indicating habitat characteristics entered into the analysis, amount of variation in each characteristic or parameter explained by the PCA (i.e., communalities), coefficient for the PC scores for each parameter, and the correlation coefficients of each characteristic with the extracted PC (which explained 73.3% of the variation in the data).

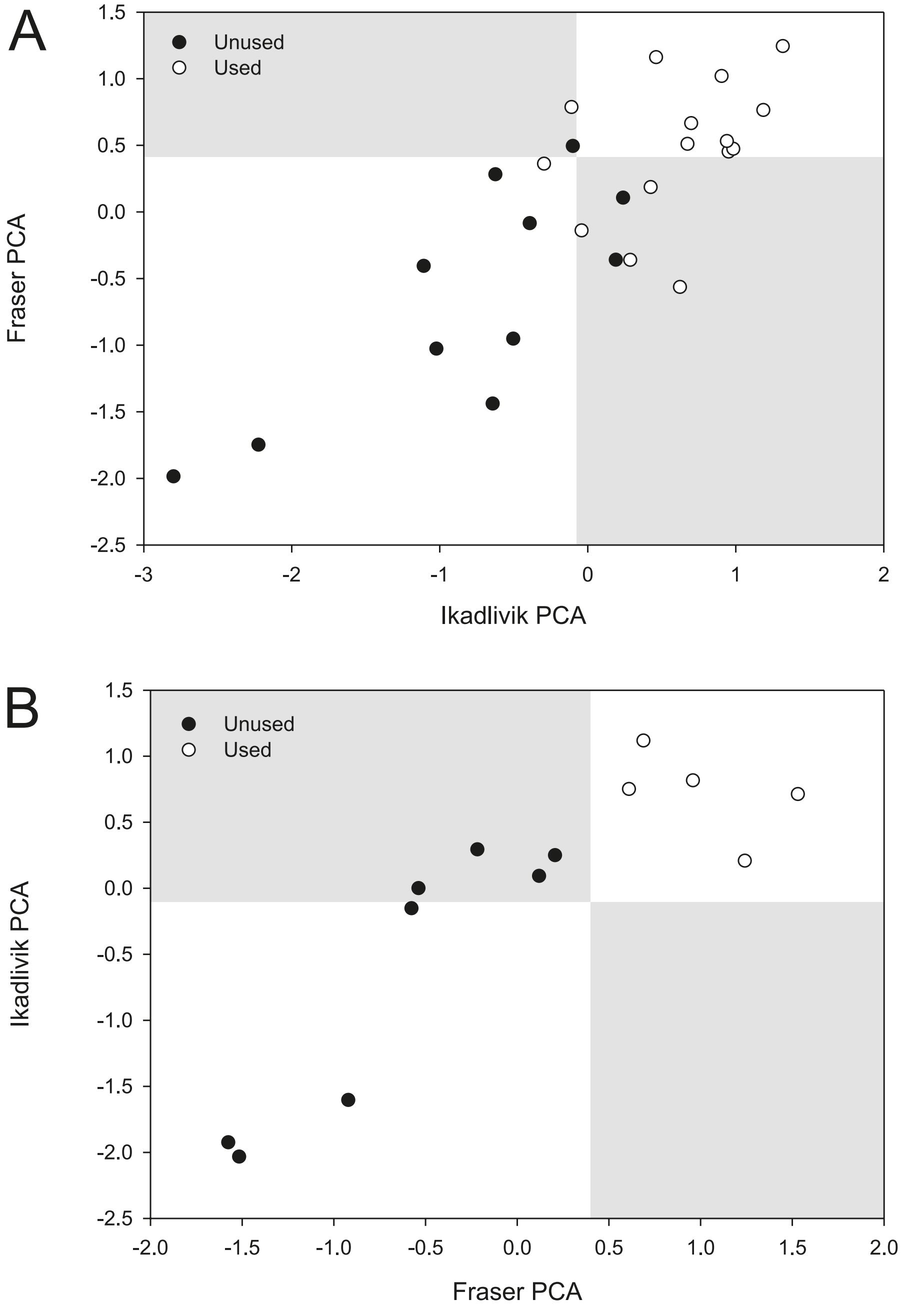
Habitat characteristic	Variance explained	Component coefficients	Component correlation
Overhang vegetation	0.917	0.435	0.958
Riparian alder	0.739	0.391	0.86
Boulders	0.544	0.335	0.737

tems where predation risk is low), a variety of biophysical habitat features are important in determining carrying capacity.

Our results support Watkinson and Sutherland's (1995) prediction that habitat studies in sink populations can be misleading. Furthermore, as demographic structure will be influenced by heterogenity in ecological mechanisms like predation risk, habitat studies in source populations or other demographic units can also be misleading about habitat suitability elsewhere in the landscape. Had this study been limited to only one of these two river systems, either the role of important biophysical habitat parameters (e.g., benthic invertebrates) or the influence of predation risk would have been overlooked. Had this study been restricted to the landscape or regional scale, biophysical habitat features would have been considered unimportant relative to predation risk (see Heath et al. 2006). Our results suggest that limiting factors cannot necessarily be generalized among different subpopulations, even within the same region, despite similar habitat characteristics and availability within the ecoregion. Ecologically limiting factors play different roles at different spatial scales, and even among different demographic units within the same spatial scale. Habitat choice and resulting species distribution will therefore be influenced by interactions among these limiting factors and demographic processes across a range of spatial scales, and local processes may therefore not directly reflect those in other areas (Wiens 1989; Schneider 1994, 2001).

Most population projection models and habitat classification indices used in management scenarios are based on underlying assumptions that include spatial homogeneity in habitat quality and demographics. It is becoming increasingly clear (Schneider 2001) that, because of spatial heterogeneity and interscale processes, such simplifications can be misleading. Unfortunately, conservation issues increasingly involve crisis management that require rapid decision-making (Doak and Mills 1994). This pressure (usually economic) promotes decisions based on short-term studies, usually over small spatial scales. It is likely a fair assumption that when researchers select a study site that they are

Fig. 3. Application of locally derived habitat suitability indices (HSI) to the other river system. Critical HSI values are indicated by borders between shaded and unshaded areas of the figure. Unshaded regions indicate where both HSIs make the same classification, whereas shaded regions indicate the parameter space in which the two HSIs differ. (A) For sites on the Ikadlivik River, the Fraser HSI correctly classified 66.5% (10/15) of the used sites and 91% (10/11) of the unused sites. The Fraser HSI misclassified 33.3% (5/15) of used sites as unsuitable and 9% (1/11) of unused sites as suitable for Harlequin Ducks (*Histrionicus histrionicus*). (B) For sites on the Fraser River, the Ikadlivik HSI correctly classified 100% (5/5) of used sites as suitable for Harlequin Ducks, whereas 50% (4/8) of the unused sites were classified as suitable habitat and the other 50% were classified as unsuitable habitat. Therefore, the Fraser HSI was prone to misclassifying suitable habitat, while the Ikadlivik HSI was prone to misclassifying unsuitable habitat. These differences can be understood in the context of a predation risk – resource trade-off (Heath et al. 2006), the resulting predominant selection of danger-reducing habitat characteristics on the Fraser River, and the effective exclusion of Harlequin Ducks from otherwise suitable habitat by predation risk. See text for details.



interested in areas with high numbers of species of interest to assess optimal habitat and increase sample sizes. Such a practice can bias research findings to being (*i*) only appropriate to particular types of demographic units (e.g., source populations; Watkinson and Sutherland 1995), (*ii*) unable to generalize to large spatial scales (where conservation impacts are often most important; Schneider 2001), and (*iii*) to underestimating the importance of many ecological factors in determining a species' distribution and population dynamics. These biases will be of particular concern if a species exhibits heterogeneity in demographics among local populations (e.g., source–sink population structure). In our study area, application of locally derived HSI could either over- or under-estimate habitat availability at the regional scale.

Many conservation and management decisions are based on predictions of generalized habitat suitability and population projection models, which are frequently based on locally specific demographic parameters. Informed decision-making and the identification and protection of critical habitat could be more effective if they are additionally based on a precautionary consideration of the role of interacting ecological processes and their influence on population dynamics within and among a hierarchy of spatial scales. Such approaches will be particularly relevant for highly mobile species for which habitat selection is a hierarchical process (Kaminski and Weller 1992). In particular, the present study emphasizes the importance of considering the behavioural ecology of trade-offs, such as those between predation risk and resources, in a population and landscape context. This is clearly an area that requires extensive development (see Lima and Zollner 1996). It is inevitable that conservation and management decisions will have to be made under the constraints of limited available information (Doak and Mills 1994), but consideration of the role of inter- and intra-scale processes and above all a precautionary approach will be essential in developing effective protection, preservation, and conservation strategies.

Both Harlequin Ducks and Peregrine Falcons (a predominant avian predator in northern Labrador) are considered species at risk in Canada (Harlequin Ducks wintering in eastern North America were classified as endangered in 1995 (Montevecchi et al. 1995) and are currently considered a species of concern in eastern Canada and threatened in Maine, USA). Peregrine Falcons are classified as Threatened in Canada (Johnstone 1998). The possibility of predatory interactions between different species at risk is an important consideration for multispecies conservation and management strategies. Although Harlequin Ducks are unlikely to play a major role in the population dynamics of birds of prey (numerous, more abundant alternate prey types are available), management decisions and predictions about the effects of perturbations within any of these river systems could carry potentially conflicting impacts for each species at risk.

Conservation strategies for a given species require careful consideration of the behavioural and population ecology of predators and competing species. When expanding multiscale approaches to include multiple species, it is important to consider that different scales of investigation may be appropriate for different species (Wiens 1989; i.e., different species have different ecological neighbourhoods). For example, in the present study the foraging range and behaviour of avian predators are important considerations for evaluating predation risk to Harlequin Ducks. Although Harlequin Ducks are a highly mobile species, they remain within home ranges that are considerably smaller than those of raptors during the nesting season. Applying and understanding multiscale, multispecies approaches to conservation issues will no doubt be difficult. Perhaps the most important factors to incorporate are the spatial scales relevant to anthropogenic impacts, as ultimately the preservation of ecological integrity will primarily involve management of humans.

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