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Title: Breeding Habitat of Harlequin Ducks in Prince William Sound, Alaska

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Breeding habitat of Harlequin ducks (Histrionicus histrionicus) was studied in eastern Prince William Sound, Alaska, during 1991 - 1993. Streams in Prince William Sound were surveyed for Harlequin ducks and monitored with mist nets. Physical characteristics of 24 Harlequin breeding streams were compared to those of 24 streams not used for breeding using 2 sample, principal components and logistic regression analyses. Nests were located using radio-telemetry of marked females.

Harlequin ducks resident in eastern Prince William Sound selected the largest anadromous salmon streams available for nesting. Volume discharge of breeding streams averaged 3.2 m^3/s and was the most important factor in habitat variation between streams used and not used by breeding Harlequins. Expansive estuaries and intertidal deltas present at the outflow of large streams were important foraging and loafing areas of Harlequin ducks. Although nesting females generally avoided smaller salmon streams their intertidal estuaries were often used for foraging by females and molting males. The largest streams

in Prince William Sound, glacially fed rivers, were not used by breeding Harlequins.

Ten nest sites of Harlequin ducks in eastern Prince William Sound were located on southwest facing, steeply sloping banks of small, first order tributaries near timberline elevation. Nests were associated with woody debris and shrubs, in shallow depressions or cavities, and were beneath the canopy of old growth forest. Microhabitat produced by a southwest aspect, snow shadow provided by the forest canopy, and sloping stream bank may provide nesting sites earlier in the spring compared to surrounding areas.

Breeding Habitat of Harlequin Ducks in Prince William Sound, Alaska

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INTRODUCTION

The Harlequin duck, (Histrionicus histrionicus), is a small, strikingly marked sea duck renowned for its use of turbulent, rushing streams as breeding habitat. Life history characteristics and habitat use of Harlequin ducks in Prince William Sound uniquely link upland forests, riparian ecotones, freshwater streams, estuarine and marine communities. Breeding Harlequins are essentially dependant on each community, either directly for food and cover, or indirectly for the regulatory function that each community or ecotone provides to its adjacent habitat (Petts 1990). Upland forests and riparian ecotones provide woody debris, tree cavities and shrubs used by Harlequin ducks for nesting cover (Bellrose 1980, Cassirer and Groves 1992, Crowley 1991). Riparian ecotones also regulate and maintain aquatic temperature, nutrients and structural habitat necessary for invertebrate production (Risser 1990, Gregory et al. 1989, 1991), an important food source for Harlequins. Harlequin ducks breeding in eastern Prince William Sound spend most of their lives in intertidal areas of estuaries and coastline.

Invertebrate populations on streams used by inland-breeding Harlequin ducks (i.e., those that migrate inland and remain away from the coast during the breeding season) must be adequate to meet nutritional needs for survival and successful reproduction (Bengtson and Ulfstrand 1971). Low breeding frequency of adult Harlequin females in interior Iceland coincided with decreased populations of aquatic invertebrates, suggesting that Harlequin duck populations were limited by food resources on inland breeding areas (Bengtson and Ulfstrand 1971).

Unlike inland-breeding Harlequins of Iceland (Bengtson 1972, Inglis et al. 1990), Wyoming (Wallen 1987), Idaho (Cassirer and Groves 1991) and Montana (Kuchel 1977, Diamond and Finnegan 1993), coastal-breeding Harlequins of Iceland (Bengtson 1972) and Prince William Sound fly downstream from nest sites to estuaries and adjacent, rocky intertidal zones where they forage on small crustaceans, invertebrates and polychaetes (Dzinbal and Jarvis 1982, Crowley 1991). Late incubation and brood rearing of Harlequin ducks in Prince William Sound corresponds with the annual anadromous salmon run. Salmon roe provides a substantial increase in available food for breeding hens and ducklings (Dzinbal 1982, Dzinbal and Jarvis 1982).

Although estuarine and marine communities inhabited by breeding Harlequin ducks probably produce a more abundant food supply than inland streams used by Harlequins, productivity of coastal-breeding Harlequins is similar to that of inland breeders (Bengtson 1966, 1972, Dzinbal 1982, Wallen 1987, Crowley 1991, Cassirer and Groves 1992).

Throughout their breeding range Harlequin females presumably do not breed until their second year, non-breeding frequency of paired females ranges from 31 - 53%, brood size is about 3.0 ducklings at fledgling age, and breeding density is low. Bengtson (1972) suggested that these characteristics may be adaptations for survival in less productive, subalpine to arctic communities. Only about 20% of anadromous salmon streams in Prince William Sound are used for breeding by Harlequin ducks, indicating that factors other than food resources may be limiting productivity of coastal Harlequin populations.

Knowledge of factors limiting Harlequin duck populations became important on March 24, 1989 when the Exxon Valdez ran aground on the charted Bligh Reef, spilling approximately 11 million gallons of crude oil into western Prince William Sound. Rocky intertidal communities were impacted first as oil washed ashore, and again when clean-up crews treated beaches with pressurized hot water and bioremediation compounds which contain chemicals potentially toxic to vertebrates (Patten 1993). Because Harlequin ducks inhabit intertidal areas year-round, exposure to crude oil through foraging and preening activities predisposes this species of sea duck to both lethal and sublethal effects of crude oil toxicity (Patten 1993).

Persistant oil contamination on intertidal habitat in western Prince William Sound has curtailed Harlequin duck reproduction in that area (Patten 1993) and is considered the probable cause for their population decline (Klosiewski and Laing 1993). In eastern Prince William Sound, an area not impacted by the oil spill, impending timber harvest threatened Harlequin duck nesting, foraging and molting habitat. These disturbances prompted a study of Harlequin duck physiology, productivity, habitat requirements for breeding and molting, and an inventory of breeding streams in eastern Prince William Sound by the Alaska Department of Fish and Game (ADFG). The objectives of my study were to determine which habitat characteristics, if any, differentiate streams used by Harlequin ducks breeding in eastern Prince William Sound from those not used for breeding, and to locate and describe habitat used by female Harlequin ducks for nesting.

STUDY AREA

Prince William Sound is a marine water body on the south-central coast of Alaska nearly enclosed and sheltered by large islands (Figures 1 and 2). Eastern Prince William Sound is characterized by fjord-like ports and bays with tides of up to 4.5 m (14 ft), and a landscape of steeply rising mountains and large glaciers. A narrow ecologic region of coastal rain forest occurs on the seaward side of coastal mountains of southcentral Alaska (Hultein 1968). A coniferous forest composed of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*) flourishes on mountain slopes and valleys. Regional climate is generally cool with high precipitation during summer months, and cold with snowfall often exceeding 7.6 m (300 in.) during winter.

The study area consisted of all shoreline, small islands, estuaries, and 75 anadromous fish streams along 630 km of coastline from Cordova to Valdez, Alaska and the protected, leeward shores of Hinchinbrook and Hawkins Islands (Figure 3). Hanning and MacLeod Creeks of southwest Montague Island (Figure 2), though disjunct from the main study area, were used by breeding Harlequin ducks and included in the habitat analyses. Compared to streams used by inland-breeding Harlequins, streams of Prince William Sound are short (averaging less than 15 km in length), of low volume discharge and are of low invertebrate productivity (Dzinbal 1982). At the outflow of most streams are small estuaries whose biological communities are influenced by both fresh water from streams, and by salt water from each rising tide. Estuaries expand downstream into alluvial deltas supporting a diversity of intertidal marine communities. I refer to the entire system from estuary to lower deltas (high to low tide) as an estuary, and to intertidal areas not influenced by stream outflow as intertidal coastline.

Oil spilled from the Exxon Valdez did not reach eastern Prince William Sound. Although it is unknown whether Harlequins move between eastern and western Prince William Sound, Harlequin ducks of the eastern study area were not perceptively impacted by oil (Crowley 1991, Patten 1993).

METHODS

Stream and Coastline Surveys

I identified potential breeding streams by the presence of Harlequin ducks on estuaries in late May, 1991 and 1992, during surveys of the study area. Surveys were conducted from a skiff piloted within 5 - 30 m of shore. The estuaries and lowest reaches of streams were surveyed on foot if not navigable by boat. All other estuaries of anadromous salmon streams (Alaska Department of Fish and Game 1993) within the same basin or bay of the potential breeding stream were surveyed at least 3 more times throughout the season to confirm presence or absence of breeding Harlequins. Brood surveys were conducted in mid- to late August (1991 - 1993); presence of ducklings on an estuary provided further evidence that the stream was used for breeding.

Based on results of survey visits, streams were grouped into 4 categories: (1) Harlequin breeding activity observed on stream; (2) no breeding activity observed but stream supported an anadromous fish run, and of apparently suitable volume and estuary size for breeding (based on known breeding streams); (3) small anadromous fish stream with low discharge, small estuary and no observed breeding activity by Harlequin ducks ; (4) large river of glacial origin having heavy siltation, extensive mud flats, and no

Harlequin activity. Streams of the first 2 categories were given priority for intensive monitoring using mist nets. Streams of category 4 were included in Harlequin duck surveys but were not intensively monitored.

Harlequin Duck Capture

Harlequin ducks were captured in mist nets suspended across streams. To avoid submerging nets at higher tides, nets were placed above the tidally influenced estuaries. Mist nets were heavy duty, with 10 cm (4 in) mesh and measured 1.8 m (6 ft) tall by 12 m or 18 m (40 or 60 ft) long. Mist nets were most effective when placed in pairs, 10 - 20 m apart, on bends in the stream channel where low-flying Harlequins often slowed to negotiate sharp turns.

We monitored streams during hours of peak Harlequin duck activity (2100 to 0100 and 0300 to 0800, 9 net hours) to determine whether Harlequin ducks were breeding on the stream. Breeding by Harlequins was confirmed either by actual captures of ducks or by observing flights of Harlequins (singly, or in pairs and small flocks) to and from upstream reaches. Breeding status of captured females was determined by presence or absence of a brood patch or cloaca distended from egg-laying. I trapped streams that were not conspicuously used by breeding Harlequins for 1 - 2 trap nights in an effort to determine if limited use of the streams was occurring. Captured Harlequin females were equipped with a 4.5 g radio transmitter glued to center tail feathers for tracking to nest sites (Crowley 1991, Quinlan and Hughes 1990).

Stream Data Collection

Streams were classified as breeding streams if they satisfied 1 of the following criteria: (1) Harlequin duck nests located, (2) breeding females captured, (3) solitary females observed flying upstream, or (4) broods observed upstream. Also classified as breeding streams were those that met 2 of the following 3 conditions: (1) Harlequin brood(s) observed in the intertidal area of the stream; (2) lone hen observed feeding in estuary; (3) Harlequin pairs (assumed to be breeding) observed near stream mouth in the spring. Streams meeting only 1 of the 3 conditions and having apparently suitable breeding habitat were designated as probable breeding streams. An unfortunate aspect of studying Harlequin breeding ecology is inherent small sample sizes resulting from low breeding frequency and low density of the species. Consequently, probable breeding streams and breeding streams were combined in my analysis to increase sample size of breeding streams.

Streams that had no observed breeding activity by Harlequin ducks after repeated surveys or trapping were designated as non-breeding streams (applicable to approximately 80% of the streams in the study area). I prioritized which non-breeding streams were to be included in the analyses, based first on use by Harlequin ducks for activities other than breeding, and secondly on resemblance to breeding streams in as many ways as possible. Consequently, I included in the analyses 2 groups of streams: (1) those streams whose estuaries had sporadic use by small flocks of post-breeding females and molting Harlequins, but that had no perceptible breeding activity were selected; and (2) the larger remaining streams (based on discharge and estuary size) because field observations suggested that Harlequins were breeding mostly on larger streams.

Because the structure and dynamics of stream habitat are determined by the surrounding watershed, many researchers (e.g., Lotspeich and Platts 1982, Frissell et al. 1986, Urban et al., 1987, Gregory et al. 1991) have recommended the integration of basin geomorphology, and aquatic and terrestrial characteristics of streams when describing stream habitat. To determine which habitat factors influence stream use by Harlequin ducks, I collected habitat data at 3 hierarchical levels: (1) local-level habitat characteristics at each stream mouth, (2) within-basin characteristics of each drainage network, and (3) landscape-level data describing basin morphology.

I collected 10 variables at each stream mouth near the marker of mean annual high tide (previously installed by ADFG fisheries workers). Channel width (m) was measured and divided into 3 equal segments; at the midpoint of each segment depth and rate of surface flow were measured. These data were used in an equation to calculate volume of discharge in m^3/s (Robins and Crawford 1954). I defined the riparian zone as the area along the stream having predominantly shrub and grass vegetation and measured its width (m). Channel gradient (%) was measured using a compass clinometer. The slopes of the adjacent uplands within 300 m of both banks of the stream mouth were determined using 1:63,360 USGS topographic maps, and the 2 slopes averaged for a measure of sideslope topography (%). Area of estuary (ha) was measured using a computer digitizer and USGS topographic maps. Water turbidity, channel substrate, channel configuration (e.g., straight, curved, or braided), and bank vegetation were described categorically (Cassirer and Groves 1991).

Twelve geomorphic characteristics of each watershed were measured primarily from USGS topographic maps; 6 measured the drainage network within each basin, and 6 described basin size and shape. I collected the following measurements to describe geomorphology of drainage networks (Swanston et al. 1977 and Verstappen 1983). (1) Channel length (km) was estimated by measuring all permanently flowing tributaries within the basin as indicated on topographic maps. If a stream flowed through a lake, straight distance from inlet to outlet were included in the length measurement. (2) Stream density (km/km^2) was calculated by dividing channel length by area of the basin. (3) Channel frequency was determined by counting all first order streams in the drainage network. (4) Channel gradient (%) was calculated from elevation of stream origin divided by length of the main stream channel. (5) The number of lakes (wider than 5 stream channel widths) through which permanent streams flowed were counted. I included only lakes below 460 m (1500 ft) elevation because lakes above this elevation remained frozen and unavailable for Harlequin use for most of the summer. (6) Bifurcation ratio was calculated as number of first order streams divided by number of second order streams.

Basin characteristics were described using the following 6 variables (Swanston et al. 1977, Verstappen 1983). (1) Basin perimeter (km) was drawn by hand along the highest circumference and measured using a map-measure. (2) Basin area (km^2) was measured within the same perimeter using a digitizer. (3) Basin aspect (degrees from north) was determined by drawing a straight line along the approximate average direction of the main stream channel through the watershed and measuring degrees from north with a compass protractor. If basins were curved, the measurement was taken from the middle to upper part of the watershed because all Harlequin duck nests were found in the upper half of basins. (4) Basin relief (m) was measured from the highest point of the watershed to the outlet at sea level. (5) Basin shape was described using the Circularity Ratio, whose value decreases as shape becomes less circular: $R_c = A_d/A_c$, in which A_d is the basin area and A_c is the area of a circle having the same perimeter as the basin (Verstappen 1983). (6) Average basin slope (%) was calculated as the ratio of the difference in elevation between the most distant ridge (determined by map-measure) and watershed outlet at sea level, to the approximate average length of the watershed.

Nest Site Habitat

Nest sites of Harlequin ducks were located by radio-tracking incubating females first by Supercub airplane to locate the general vicinity within the watershed, then on foot to the nest site. Females were flushed from the nest, and eggs were measured and protected from the weather. Habitat data were collected as listed above for stream mouths. I also estimated percent occurrence of plant species in the overstory (greater than 1 m in height and within 3 m of the nest), understory (less than or equal to 1 m in height and within 1 m of the nest) and cryptic-cover (material or structure concealing the nest bowl).

Data Analysis

The data represented a census of streams potentially used for breeding by Harlequin ducks in eastern Prince William Sound and were not random. Inference should therefore be limited to eastern Prince William Sound.

Basin and drainage network variables and continuous variables from stream mouths were analyzed by first testing (at alpha = 0.05) for differences between the 2 stream groups (breeding and non-breeding) for each of the individual habitat variables. I used Student's t on normally distributed data sets, or Mann-Whitney Ranks test on nonparametric data. Aspect, collected as compass degrees, was compared using Watson's U^2 test for circular data (Zar 1984). Categorical data collected at stream mouths were compared using Fisher's Exact Test for contingency tables (Ramsey and Schafer 1993). Data were arranged in 2x2 tables whereby the explanatory factors (rows) were the presence or absence of each habitat category, and the binary response variables (columns) were the occurrence of the habitat on breeding or non-breeding streams.

I used a standardized principal components analysis (based on a correlation matrix) to test for combinations of variables that explained a substantial portion of variation within the data set (Morrison et al. 1992). I used 13 habitat variables in the analysis including all of the basin-level variables (except bifurcation ratio), and the continuous variables from stream mouths: discharge, area of estuary and sideslope gradient.

Logistic regression for binary responses was used to analyze basin, drainage network and stream mouth variables.

Each of the variables were first tested in individual models for their ability to explain breeding vs. non-breeding responses. Those variables not demonstrating a significant ($p <= 0.05$) effect on responses were eliminated from further modeling. The remaining variables were tested within hierarchical levels (i.e., stream mouth, drainage density and basin) by modeling the highest variable within each hierarchical level with each of the other remaining variables in that level (limiting models to 2 terms to maximize degrees of freedom). Finally, the remaining 3 variables were modeled together to determine which of the habitat characteristics most successfully explained the variation between breeding and non-breeding responses.

Nest site data which measured stream bank and channel aspects were tested for goodness of fit using Watson's U^2 test for circular distributions (Zar 1984). The remaining nest site variables were summarized in graphs.

RESULTS

Stream and Coastline Surveys

Harlequin duck surveys in 1991 and 1992 were conducted along 560 and 630 linear km of coastline, including 75 and 90 estuaries, respectively. Brood surveys only were conducted in 1993 covering the same areas surveyed in 1992. The sex ratio of observed Harlequin ducks during surveys was 1.3 males per female (56% males) and overall linear density of Harlequins was 1.4 ducks/km coastline. Nearly all Harlequins were observed along rocky or gravel beaches of shallow sloping bathometry, providing a substrate for emergent or intertidal islands, reefs and bedrock outcroppings. Because nest prospecting, courtship and feeding activities of Harlequin ducks were concentrated on estuaries in May and early June, it was usually obvious during spring surveys whether or not a stream was used for breeding. Although low numbers of Harlequin females and molting males were sporadically observed foraging in estuaries of smaller salmon streams (categories 2 and 3) during mid- to late summer, these streams were evidently not used for breeding.

Harlequin Capture

We captured 23 Harlequin ducks (16 females) in 1991 during 322 net hours of trapping on streams in eastern

Prince William Sound (Figure 2). In 1992 we captured 42 ducks (28 females) during 229 net hours of effort. Nine Harlequins captured in 1992 were previously captured in 1991. Our capture rate increased from 14 net hours per duck in 1991 to 5.4 hours per duck in 1992 probably because our equipment and efficiency improved. Breeding frequency of captured females was 9 of 14 in 1991 and 15 of 28 in 1992. Forty females were marked with radio tags in both years, combined. Of the 9 ducks recaptured in 1992, all 7 females and 2 males were captured on the same streams as in 1991.

Stream Habitat

I identified 22 Harlequin duck breeding streams, 2 probable breeding streams and 24 streams not used for breeding in eastern Prince William Sound (Figure 3) and western Montague Island. Summary statistics (Table 1) and graphing of numerical data determined that transformation of data to their natural logs was necessary to normalize distributions to meet assumptions of statistical tests. Two-sample testing of variables measured at stream mouths indicated that Harlequin breeding streams had significantly greater values for volume discharge ($p < 0.001$), area of estuary ($p = 0.003$), stream width ($p < 0.01$), and width of riparian zone ($p = 0.046$), than did non-breeding streams (Table 1). I did not detect significant variation between breeding and non-breeding streams in channel slope ($p = 0.50$), sideslope topography ($p = 0.23$), and aspects of stream mouths ($p = 0.86$, Table 1, Figure 4).

Fisher's exact test for homogeneity of the categorical variables collected at mouths of streams indicated no statistically significant differences between Harlequin duck breeding and non-breeding streams, except that deep slow water (pools) were more common on breeding streams, and shallow slow water was more prevalent on non-breeding streams (Table 2). There were no apparent differences in the composition of vegetation types on stream banks (Table 3). Those results reported as no test in Tables 2 and 3 had identical values in the response groups (breeding and non-breeding) for both rows of explanatory factors (presence or absence of the habitat feature).

Seven of 12 geomorphic variables measured were transformed to their natural logs, and average channel gradient to the logit scale to normalize distributions. Two-sample tests of area, perimeter, relief, average slope, bifurcation ratio, channel frequency and length, indicated significant differences ($p < 0.05$) between the stream groups (Table 4). All of these variables were greater on Harlequin breeding streams except average basin slope, which was higher on non-breeding streams. These data indicate that the number of stream channels available and basin size contributed to use of streams by breeding Harlequin ducks.

Most of the streams used by breeding Harlequins were of non-glacial origin. The two exceptions were streams having some tributaries of glacial origin, but whose silt burden was low enough to allow salmon to spawn in gravel beds.

Principal components analysis indicated that most variation among streams was explained in measurements of stream size and gradient. I interpreted the first principal (PC1), which explained 50% of the variation in my data, as representative of stream size because PC1 was primarily correlated with basin area (correlation coefficient = 0.98, $p < 0.0001$), perimeter (0.94, $p < 0.0001$), discharge (0.88, $p < 0.0001$), channel length (0.90, $p < 0.0001$) and channel frequency (0.78, $p < 0.0001$). PC1 was negatively correlated with the index of basin shape (-0.87, $p < 0.0001$) because the larger watersheds were generally long and narrow resulting in a lower value (less circular) for shape index.

The second principal component (PC2) explained an additional 15% of the variation in the data set. I interpreted PC2 as representative of stream gradient because it was correlated primarily with various measurements of gradient: overall channel gradient (correlation coefficient = 0.94, $p < 0.0001$), mean sideslope at stream mouths (0.79, $p < 0.0001$), and mean sideslope of basins (0.61, $p < 0.0001$). A scatterplot of the values from PC1 against those of PC2 separated most

Harlequin duck breeding streams from non-breeding streams along PC1 (Figure 5). Mean PC1 and PC2 values were tested by stream group using an analysis of variance and plotted with 95% confidence ellipses (Figure 6). The mean of PC1 values for breeding streams was significantly larger than mean PC1 values for non-breeding streams (F-ratio = 26.12, $p < 0.0001$). I detected no significant difference between mean PC2 values of breeding and non-breeding streams (F-ratio = 0.496, $p = 0.4925$).

Single-factor logistic regression eliminated 6 variables which did not significantly account for the binary responses of Harlequin breeding or non-breeding streams (Table 5). The second step, modeling variables within each hierarchical level, eliminated 9 more variables, leaving basin area, channel length and discharge representing each spatial scale. Final modeling determined that discharge was the single most important variable, and local stream mouth the most important level, in explaining the difference in response (Chi-square from maximum likelihood analysis of variance table = 11.74, $p = 0.0006$, Table 6).

Large basins in Prince William Sound had both long channel lengths and higher frequency of first order tributaries (Figure 7). Channel length and frequency of tributaries were also related (corr. coeff. = 0.73, $p < 0.0001$): long streams tended to have many first order tributaries flowing into them. The increased number of tributaries present in drainage networks of larger basins increased the availability of stream banks suitable for nesting. Of 10 Harlequin duck nests found, 8 were on first order tributaries or at the confluence of a first order tributary and main stream (usually second order) just below timberline elevation.

Nest Site Habitat

I found 10 Harlequin duck nests on streams of Prince William Sound by tracking telemetered hens to nest sites (Table 7). Five of the 10 nests, 2 active and 3 inactive nests (containing eggs or egg remains) from previous breeding seasons, were found within a 40 m stretch of stream bank on a small, first order tributary of Beartrap River (Figure 3). Nests from previous seasons were found incidentally while crawling under deadfalls in search of radio-marked nesting females. The 2 active nests (1 found each year) were made by the same Harlequin female that was captured and radio-tagged both years. One of the 10 nests was found on Hanning Bay of Montague Island (Figure 2).

Nests were located from 0.6 to 3.0 km upstream from the coast, in old-growth forest (trees greater than 75 cm diameter at breast height), and within 25 m or less of streams (Table 8). All stream banks used for nesting were southwest facing (218 - 241°) regardless of channel, stream mouth or basin aspect (Figure 7). A one-sample Watson's U^2

test indicated that aspects of nest banks differed significantly from a random distribution ($p < 0.001$ with all 5 Beartrap nests included, and $p < 0.01$ with only 1 Beartrap entry included to eliminate dependent sites, see Table 9). Stream channel aspects at nest sites differed from a random distribution with the full data set ($p < 0.001$), but not when only 1 Beartrap entry was used (Table 9).

Stream banks on which Harlequin nests were located were steep or vertical, allowing females to launch into flight directly from most nests. At stream level, banks used for nesting (Figure 9) were composed of bedrock (6 of 10), cobble and boulder (2) and grass/forbes (2). At mid-level stream banks were composed of tree/shrub mosaic (6 of 10) or shrubs (4). On the upper level of stream banks, composition was of old growth trees (10 of 10).

The average of estimated percent cover contributed to the overstory by plant species (Figure 9) was western hemlock (87%) followed by Sitka spruce (11%) and alder (2%). The average estimated understory composition (Figure 9) was primarily Vaccinium (62%) followed by fern (usually Athyrium filix-femina, 11%) and hemlock seedlings (9%). Woody debris concealed 8 of 10 nests; of these, 7 nests were situated beneath deadfalls and 1 was in a shallow cavity atop a rotting stump 2 m in height. One nest was in a shallow cavity at the base of a hemlock tree and 1 in a moss-lined rock crevice. Nest substrate was either conifer needles, moss or both (Figure 9) and all nests were lined with down.

DISCUSSION

Harlequin Site Fidelity

Harlequin ducks exhibited fidelity to nest sites and streams in eastern Prince William Sound. Site fidelity by Harlequins was also observed in Idaho (Wallen and Groves 1989, Cassirer and Groves 1991, 1992), Wyoming (Wallen 1987), Montana (Kuchel 1977) and Iceland (Bengtson 1966, 1972). All 9 Harlequin ducks recaptured in eastern Prince William Sound during 1992 were using the same streams on which they were captured in 1991. One female in 1992 nested within 5 meters of her nest site from 1991, and 3 other nest bowls were found within 30 m. Selection of a breeding stream by an individual Harlequin duck may thus be proximately influenced by where that individual was reared. The habitat differences I observed between Harlequin duck breeding streams and non-breeding streams, however, suggests that habitat characteristics influence some aspect of population dynamics (such as probability of survival, productivity or density of breeding ducks on a stream), and hence ultimately regulate use of streams by a population of Harlequin ducks.

Breeding Stream Habitat

Estuaries. I selected the stream mouth vicinity (at the annual high tide) for local-level habitat study for several reasons, both biological and practical. First, Harlequin ducks demonstrated an ecological dependency on the intertidal area where the streams met the sea. Feeding, courtship, resting and brood-rearing activities on streams were very high at or near the stream mouth, and absent elsewhere on the stream (Dzinbal 1982). Before salmon arrived to spawn, I observed Harlequins feeding on rising tides at or just below the confluence of tide and stream, following the tideline to the highest point and, unless suitable loafing sites were available (i.e., mid-stream boulders or open, trampled banks), retreating to the lower estuary or coastal rocks with the outgoing tide. During the salmon run Harlequins sometimes fed above the tideline in spawning beds, but generally within 50 m of the high tide area.

Second, the area where the stream meets the tide is unique from the entire length of the stream and therefore provided a standard location for measurements at each stream.

Finally, because it appears that the short, coastal streams in Prince William Sound are principally a travel conduit for Harlequin ducks between upper elevation nesting areas and the ecologically important area of the estuary, I believe that differences in breeding and non-breeding streams over their entire length are adequately described using basin geomorphology and drainage network measurements.

Use of Larger Streams. Two-sample tests (Table 5), PCA, Discriminant function analysis (see Appendix) and logistic regression of basin geomorphology and drainage network data all indicated that streams used by breeding Harlequin ducks were larger than those streams not used for breeding. Basin area was correlated with higher elevations (Figure 6, corr. coeff.= 0.73, $p < 0.0001$). Larger, higher basins retain more melting snow through the summer, and capture more precipitation than lower elevation, smaller basins, thus providing a more stable source of water flow (Verstrappen 1983). Large basins may also buffer against sudden flooding caused by heavy precipitation (Verstrappen 1983). Flooding probably reduces brood survival of Harlequin ducks (Kuchel 1977, Diamond and Finnegan 1993, and Wallen 1987).

Habitat variables collected at stream mouths also indicated that Harlequin ducks used larger streams for breeding. Stream widths and discharge were significantly higher on streams used by breeding Harlequin ducks than on those streams not used for breeding (Table 1). Discharge emerged as the most meaningful variable, probably because it was strongly linked both to basin area, to which it is exponentially related (Verstappen 1983), and to measures of drainage networks. Furthermore, stream discharge described a local habitat feature (depth, expanse and flow of water) that is of ecological importance to foraging Harlequins. Categorical variables, which were generally not precise enough to discriminate between groups, also indicated that more water (greater frequency of deep pools) was present in Harlequin breeding streams than in non-breeding streams, in which a greater frequency of shallow slow water occurred (Table 2).

Estuary size and width of riparian zone, functions of stream size (Verstappen 1983) were also greater on breeding streams (Table 1). Grassy riparian areas were large, and braided channels were more common at the mouths of Harlequin breeding streams, whereas the mouths of smaller streams were often closed in by forest or dense riparian or forest vegetation. The riparian meadows of grass and shrubs, prevalent on larger streams, were heavily used by brown bears (Ursus arctos) for travel and feeding along spawning beds. Once grass was trampled flat by bears, groups of Harlequin females used exposed banks for loafing between feeding bouts. Loafing areas were occupied by females sitting side by side, often in physical contact. The same behavior occurred along gravel spits on braided channels, and on large boulders both mid-channel and intertidal. Perhaps wider and more open stream mouths, generally found on larger streams, provided better loafing areas with good visibility against potential predators.

Foraging Habitat. Gravel beds used by spawning salmon and intertidal areas were generally larger on breeding streams. These characteristics provided more prey and foraging habitat for Harlequins. Habitat selection theory suggests that larger or richer foraging patches promotes selection of those patches (Rosenzweig 1985). As intertidal specialists, breeding Harlequins in Prince William Sound use shallow sloping, boulder-strewn shoals and estuaries for feeding and resting (Dzinbal 1982). Foraging patches within the selected intertidal areas are probably used opportunistically, i.e. in proportion to occurrence of prey items within a patch (Rosenzweig 1985). Dzinbal (1982) and I observed Harlequins diving, dabbling, skimming, wading and gleaning prey items from the water's surface to the bottom, from marine coastline to freshwater spawning beds, consuming a variety of invertebrates, alevins and roe.

Although Harlequin ducks are not territorial, I often saw individuals defending small (1 m diameter) feeding areas directly above spawning salmon, which they located after much swimming about and peering under water. Defense of feeding areas is perhaps a mechanism limiting numbers of foraging Harlequins on any 1 stream. Larger streams, such as Beartrap River, had up to 30 Harlequin ducks present at their mouths. Smaller streams such as Control Creek in Port Gravina generally had late-summer hen flocks of 7 or less.

Brood Rearing Habitat None of the 30 Harlequin duck broods I saw on or near regularly surveyed streams in eastern Prince William Sound from 1991 - 1993 appeared with adult Harlequins foraging in estuaries until the age of 2 weeks or older. I suspect that avoidance of the estuary reduced chances of brood mortality on the predator-rich spawning beds (pers. obs.). Despite the possible avoidance of predators during the first 2 weeks of life, brood size at the estuary (3 - 4 weeks before fledgling) averaged 3.0 ducklings over 3 years whereas clutch size at hatching averaged 6.7 eggs. Though brood-rearing occurred somewhere upstream, telemetric observations indicated that during the first several weeks of brood-rearing, females often flew to the stream mouth area to forage. Overall invertebrate abundance of coastal streams is low (Dzinbal 1982); possibly Harlequin ducklings fed on terrestrial and flying insects which can be very abundant along streams (pers. obs.)

Alternately, Harlequin ducklings less than 2 weeks of age may have fed on locally abundant aquatic invertebrates within specific microhabitats. I suspect that, because of a young Harlequin duckling's diminutive size, high buoyancy and inexperience, foraging in slow water may be more energy efficient than in turbulent, fast-flowing water (Kuchel 1977). Regardless of invertebrate abundance, invertebrates may be less available to foraging ducklings in high energy water. There are yet no studies of time or activity budgets of Harlequin duck broods. Dzinbal (1982) reported that a Harlequin brood was reared on a lake near the origin of Stellar Creek (Valdez Arm), Prince William Sound. Harlequin ducklings were also reared on small beaver ponds in Montana (Kuchel 1977). Larger streams in Prince William

Sound provide more slow-water areas in upstream reaches than steep, small streams (pers. obs.).

I saw only 1 Harlequin brood upstream of an estuary. It was on a stepwise series of fast, turbulent runs and calm pools of Sheep River of Sheep Bay, in water 0.25 - 1.0 m deep with a substrate of cobbles and boulders, approximately 1.5 km downstream of the nesting area. Although dense alder lined both banks, there was little vegetation overhanging the stream and the south-facing channel was exposed to sunlight. A series of small beaver ponds were adjacent to the stream.

Nesting Habitat

Harlequin females exhibited the prospecting behavior, site fidelity and delayed sexual maturity typical of other hole-nesting ducks (Eadie and Gauthier 1985). A hole as perceived by a female Harlequin duck, however, may be a tree cavity (Cassirer et al. 1993); a depression or cavity in a stump, root wad (Latta 1993), elevated stream bank; or crevice in a cliff face (Flint et al. 1983), a space beneath a deadfall; a cave within a rock pile; or, for captive-raised Harlequins, a large nest box (Charles Pilling, pers. comm.). Woody debris, both as snags and blowdowns, were important to nesting Harlequins in Prince William Sound and throughout the Pacific Northwest (Cassirer et al. 1993, Latta 1993). Harlequin females in

Iceland searched for nest sites by carefully examining every crevice, bush and rock along stretches of stream bank (Bengtson 1966).

Aspect was an important component of nesting habitat. Nests were consistently located on southwest-facing, sunny and well-drained stream banks. Harlequins also nest on stumps, root wads (Jewett 1931), cliffs and in tree cavities (Cassirer et al. 1993) which probably function similarly to elevated stream banks by providing relatively dry sites that are protected from heavy snow and floods, and provide security from predators.

Harlequin duck nests in Prince William Sound were generally positioned under the canopy of old-growth forest up to 25 m from the stream (which may provide a snow shadow), but close enough to canopy gaps caused by stream channels to allow penetration of sunlight. Nest sites on Beartrap River from 1991 at 220 m elevation were emerging from the snow in late May while much of the area still remained blanketed. Because Harlequins nest in mid- to timberline elevations in a region of heavy snowfall (often greater than 7.6 m annually), snow-covered stream banks may delay or limit nesting on any particular stream. Wallen (1987) suggested that snow and lack of leaves on shrubs discouraged early nesting by Harlequins at upper elevations of Grand Tetons National Park.

To determine whether snow cover had an effect on breeding by Harlequin ducks in Prince William Sound, I compared snow depth during the early nest initiation period to indices of Harlequin breeding activity by year. In 1992 the spring thaw in Prince William Sound was delayed by cool weather, consequently most basins had snow cover at near sea-level elevation in late May. Snow depth at 180 m (mean elevation of Harlequin nests was 167 m) near Valdez, Alaska in early May was 56 cm in 1991, 104 cm in 1992 and 58 cm in 1993 (National Weather Service, unpub. data). The number of females captured per hour peaked 1 week later, and males remained on streams 2 weeks later in 1992 than in 1991 (Figure 10). (The overall capture rate was higher in 1992 because our techniques improved.) Breeding frequency of captured females in 1991 was 64% and linear brood density 2.9/100 km. In 1992 these were 53% and 0.9/100 km respectively (Patten and Crowley 1993). Five streams on which Harlequin broods were observed during surveys in 1991 were absent of broods in 1992. In contrast, the 1993 spring was similar to 1991, linear brood density was approximately 1.8/100 km (Figure 11) and I found broods on 5 streams on which broods were not observed in the previous 2 years. While these data are mostly observational and short term, they do indicate a possible extrinsic constraint by weather on Harlequin productivity, i.e., increasing snow depth in the spring may have decreased nesting attempts by Harlequin ducks.

Nesting by Harlequin ducks at higher elevations may improve nest success despite possible limitations of snow depth during the nest initiation period. Glaucous-winged gulls, crows, eagles, mink, river otters and coyotes were abundant at stream mouths in late June through September but were not encountered upstream (pers. obs.) In Iceland, Harlequins nesting on mid-channel islands on the River Laxa began nesting several km up small tributaries following the spread of mink into the region (Bengtson 1966).

Eight of the 10 Harlequin nests I found were on small, steep tributaries that had discharges of less than 0.5 m^3/s and were less than 3 m wide. All nests were far above stream reaches used by spawning salmon. State law regarding forest practices on private timberlands requires leaving forested buffer strips only on stream reaches used by spawning salmon (Alaska Department of Natural Resources 1990) which would not protect tributaries used by nesting Harlequin ducks. If timber harvest extends into the upper reaches of basins, forested buffers along first and second order streams will be necessary to protect nest sites of Harlequin ducks.

Alternative Breeding Habitat

While large streams had a higher probability of being selected for breeding in eastern Prince William Sound, there were exceptions. For example, Cloudman Creek on Bligh Island (Figure 3) has a discharge of only 0.53 m^3/s and is 4 m wide at the mouth, yet a Harlequin duck brood was present at the outflow of the stream's small intertidal lagoon. This was the largest stream for several km of coastline. I saw 2 other broods along the coast of western Bligh Island where streams were very small and steep. The nearest anadromous salmon stream was over 10 km distant (ADFG 1993).

Most of the landscape of western Prince William Sound differs from that of eastern Prince William Sound. Naked, Peak, Story, and N. Story Islands (60° 40', 147° 25'), typical of those in western Prince William Sound, are of low area and elevation, and lack the larger, anadromous streams used by breeding Harlequin ducks in eastern Prince William Sound. Prior to the oil spill, however, up to 121 Harlequin ducklings were observed along the Naked Island group (Oakley and Kuletz 1979). A young brood was also observed swimming down Otter Creek (60° 25', 147° 40'), a small, anadromous salmon stream in western Prince William Sound, and into the Bay of Isles, Knight Island (Patten pers. comm.).

In addition to using small streams for nesting, there is both historical and circumstantial evidence that Harlequins nest on coastal bluffs or small islands that have no streams. Nesting by Harlequin ducks was observed on offshore, rocky islands in British Columbia (Campbell et al. 1990), Peter the Great Bay of coastal Siberia (Dement'ev and Gladkov 1967) and on offshore skerries (isolated bedrock islands, sometimes grass-covered, jutting out of the sea) in Greenland (Salomonsen 1950-I, cited in Bengtson 1966). One brood was observed off Squire Island (60°15', 148°'), a small island without permanent streams in south western Prince William Sound in 1992 (Patten 1993). These observations provide evidence that offshore islands may be used for nesting by coastal-breeding Harlequins where permanent streams are not available.

The largest streams in Prince William Sound, glacially fed rivers, were avoided by Harlequin ducks. My investigation of these rivers, however, were limited to boat surveys only. Breeding Harlequins used 2 smaller rivers that were only partially glacial and which had salmon spawning beds. One radio-tagged hen was tracked up Beartrap River, over the pass and, surprisingly, into the next valley of a silty, glacial river. The hen, which I had assumed was laying (indicated by a distended cloaca), had unfortunately pulled off the radio and dropped it in the river, so no nest was located. Breault and Savard (1991, p. 20) reported records of historical breeding on a glacial fed lake and stream in British Columbia.

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Table 1. Comparison of characteristics at the mouths of streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

Variable	BREEDING Mean	BREEDING S.D.	NON-BREEDING Mean	NON-BREEDING S.D.	Unit	Transf.	Test	p -value
Volume Discharge	3.18	2.11	0.80	0.58	m^3/s	Log	$t = 2.36$	< 0.001
Stream Width	16.56	9.82	9.58	4.08	m	Log	$t = 2.95$	< 0.010
Riparian Width	116.10	135.70	44.65	44.64	m	Log	$t = 2.06$	0.046
Area of Estuary	50.29	63.76	17.33	37.73	km^2	Log	$Z = 3.05$	0.003
Channel Aspect[a]	210-240	--	300-330	--	°	Ranks	$U^2= 0.18$	0.50
Channel Slope	2.85	1.81	5.53	12.92	%	Log	$Z = 0.23$	0.23
Mean Sideslope	13	8	14	12	%	Log	$t = 0.86$	0.86

[a]Reported values are most frequent occurrence (mode) in 30° category.

Table 2. Comparison of categorical variables measured at the mouths of streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993. Reported p-values are 1-tailed, n = 24 per group.

Fishers Exact Test for Homogeneity

	% OCCURRENCE Breed	% OCCURRENCE Non-Breed	p-value
HYDROLOGY			
Deep Fast	7	0	<0.01
Shallow Slow	10	45	<0.01
Shallow Fast	50	50	0.50
Deep Slow	1	0	0.50
Falls	0	1	0.50
Boulder Run	0	0	no test[a]
Pocket Water	0	0	no test
SUBSTRATE			
Gravel	20	35	0.24
Cobble	11	12	0.50
Boulder	4	1	0.05
Sand	1	0	0.50
Bedrock	0	0	no test
CHANNEL TYPE			
Straight	10	20	0.33
Slight Curve	36	65	0.06
Curve	30	10	0.12
Braided	25	5	0.09
SIDESLOPES			
Enclosing	15	20	0.50
Moderate	30	40	0.37
Distant	55	40	0.26

[a] Not tested because of identical parameters in response categories.

Table 3. Comparison of composition of banks at mouths of streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993. There were no significant differences between variables at p <= 0.05. Reported p-values are 1-tailed, n = 24 per group.

	Fishers Exact Test for Homogeneity		
	% OCCURRENCE		
LOWER HABITAT	Breeding	Non-breed	p-value
Grass/Forbes	48	60	0.185
Gravel	33	25	0.500
Shrubs	3	0	0.500
Tree/shrub Mosaic	10	8	0.500
Trees	3	3	0.500
Bedrock	5	5	0.692
Forest Debris	0	3	0.500
Sand	5	0	0.247
MID-BANK HABITAT			
Grass/Forbes	23	18	0.390
Gravel	0	0	no test[a]
Shrubs	43	35	0.323
Tree/shrub Mosaic	20	13	0.378
Trees	15	30	0.090
Bedrock	0	5	0.247
Forest Debris	0	5	0.500
Sand	0	0	no test
UPPER BANK HABITAT			
Grass/Forbes	0	0	no test
Gravel	5	0	0.247
Shrubs	25	20	0.395
Tree/shrub Mosaic	5	10	0.338
Trees	65	70	0.635
Bedrock	0	0	no test
Forest Debris	0	0	no test
Sand	0	0	no test

[a] Not tested because of identical parameters in response categories.

Table 4. Comparison of characteristics of basins and drainage networks from streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

Variable	BREEDING Mean	S.D.	NON-BREEDING Mean	S.D.	Unit	Transf	Test	p -value
Basin area	23.52	19.01	7.09	5.25	km^2	Log	t = -2.56	<0.0001
Basin perimeter	19.55	10.17	10.71	4.45	km	Log	t = 4.87	<0.0001
Basin relief	1141	388	810	225	m	none	Z = -3.25	0.0017
Average basin slope	15.51	5.34	21.73	10.18	%	Log	Z = 2.27	0.02
Channels length	13.20	9.44	4.64	2.99	km	Log	Z = -4.30	<0.0001
Bifurcation ratio	4.01	1.73	2.67	1.34	--	Log	Z = -3.61	<0.0001
Channel frequency	5.38	4.16	2.33	1.81	--	Log	Z = -3.54	0.0004
Basin Aspect	210-240	--	270-299	--	°	Ranks	U^2= 0.83	>0.30
Channel Slope	7.95	3.97	11.71	7.52	%	Logit	t = -1.69	0.10
Stream Density	0.67	0.26	0.73	0.32	km/km^2	none	t = -0.70	0.49
Basin Shape	2.15	1.07	4.04	2.22	--	none	t = -0.67	0.50
Number of lakes	0.67	1.05	0.75	1.19	--	Log	t = -0.42	0.68

[a]Reported values are most frequent occurrence (mode) in 30° category.

Table 5. Single factor, followed by multi-factor logistic regression analyses of habitat variables from streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

	SINGLE-FACTOR LOGISTIC REGRESSION			MULTI-FACTOR LOGISTIC REGRESSION			
		Maximum Likelihood			Maximum Likelihood		Likeli. Ratio
Hierarchy Level	Variables	Chi^2	p-value	Remaining Variables	Chi^2	p-value	p-value
	Basin Area	10.93	<0.01				
	Perimeter	9.53	<0.01	Area*	4.13	0.04	
BASIN	Relief	8.66	<0.01	Perimeter	0.73	0.39	0.48
	Shape	8.41	<0.01	Relief	0.64	0.43	0.50
	Mean Sideslopes	4.35	0.04	Shape	0.02	0.88	0.46
	Aspect	1.31	0.25	Sideslope	0.47	0.49	0.48
	Channel Length	10.67	<0.01				
	Channel Freq.	10.01	<0.01	Length*	4.59	0.03	
DRAINAGE	Gradient	3.86	0.05	Frequency	0.14	0.71	0.51
DENSITY	Stream Density	0.50	0.48	Gradient	0.52	0.47	0.42
	Bifurcat. Ratio	7.62	<0.01	Bifurcat.	2.54	0.11	0.50
	Number Lakes	0.18	0.67				
	Discharge	11.74	<0.01	Discharge*	10.18	<0.01	
	Stream Width	6.36	0.01	Estuary	6.95	0.33	0.90
STREAM	Riparian Width	3.71	0.05	Stream Width	0.14	0.74	0.68
MOUTH	Estuary Area	7.65	<0.01				
	Mean Sideslopes	0.03	0.86				
	Channel Gradient	0.02	0.89				

* The indicated variable remaining within each hierarchical level formed a reduced model that adequately explained a significant difference between stream groups.

Table 6. Logistic regression modeling of basin area, channel length and volume discharge; a reduced model with only discharge term adequately explained variation between streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

Hierarchical Level	Models Tested	Maximum Likelihood Chi^2	Maximum Likelihood p-value	Estimate	Likelihood Ratio p-value
BASIN	Area*	2.14	0.1431		
	Length	0.65	0.4185		0.4914
DRAINAGE DENSITY	Length*	0.05	0.8267		
	Discharge	7.28	0.0070		0.8714
STREAM MOUTH	Discharge*	6.14	0.0132		
	Area	0.35	0.5519		0.8796
COMBINED	Discharge	6.13	0.0133	-3.4917	
	Area	0.90	0.3426	1.3026	0.8796
	Length	0.60	0.0133	-0.8046	

*Variables remaining within each hierarchical level.

Table 7. Locations of 10 Harlequin duck nests on coastal, mountain streams in old growth forests of Prince William Sound, Alaska, 1991 and 1992.

Year	Stream Name	Location	Alaska Stream Catalog Number	Latitude Longitude	Elevation
1991 1992	Beartrap[a]	Beartrap Bay Port Gravina	221-30-10480	$60^{\circ}46'30''$ $146^{\circ}28'00''$	220 m 225 m
1991	East Cove	Jack Bay Valdez Arm	221-50-11230	$61^{\circ}00'30''$ $146^{\circ}34'45''$	46 m
1991	East Cove	Jack Bay Valdez Arm	221-50-11230	$61^{\circ}00'15''$ $146^{\circ}34'15''$	122 m
1991	Nuchek	Port Etches Hinchinbrook Island	228-60-18120	$60^{\circ}15'30''$ $146^{\circ}28'00''$	150 m
1992	South Fork Constantine	Hinchinbrook Island	288-60-18150	$60^{\circ}22'45''$ $146^{\circ}31'30''$	90 m
1992	Hanning	Montague	277-10-17110	$59^{\circ}59'05''$ $147^{\circ}35'30''$	150 m

[a] Five nests total were found, 2 and 3 during 1991 and 1992, respectively.

Table 8. Characteristics of habitat at 10 nest sites of Harlequin ducks in Prince William Sound, Alaska, 1991 - 1992.

Nest Site Variables	Mean	SD	Unit	Range
Volume Discharge	0.76	1.05	m^3/s	0.13-3.59
Stream Width	3.61	1.91	m	1.5-7.6
Riparian Width	7.35	2.88	m	1.0-12
Channel Slope	5.43	18.14	%	5.0-67
Nest bank slope	53.00	21.76	%	20-90
Channel Aspect	320	--	°	178-332
Nest bank Aspect	238	--	°	218-241
Elevation	167.3	65.73	m	46-225
Dist. to Coast	1.8	0.76	km	0.6-3.0
Dist. to Stream	9.76	8.18	m	1-25
Dist. to Forest	1.1	1.85	m	0-5

Table 9. Comparison (to a random distribution) of 4 groups of directional aspects from streams used for nesting by Harlequin ducks in Prince William Sound, Alaska, with the full data set (n = 10) and without 4 redundant nest sites on Beartrap River.

	FULL DATA SET			PARTIAL DATA SET		
Variable	U^2	p-value	Result	U^2	p - value	Result
Nest Bank	0.728	<0.001	Reject H_o*	0.427	<0.01	Reject H_o
Nest Channel	0.464	<0.001	Reject H_o	0.206	0.05<p<0.10	Do Not Reject H_o
Mouth Channel	--	--	--	0.223	0.02<p<0.05	Reject H_o
Basin	--	--	--	0.244	0.02<p<0.05	Reject H_o

*Rejection of H_o indicates that the sample did not come from a random distribution.

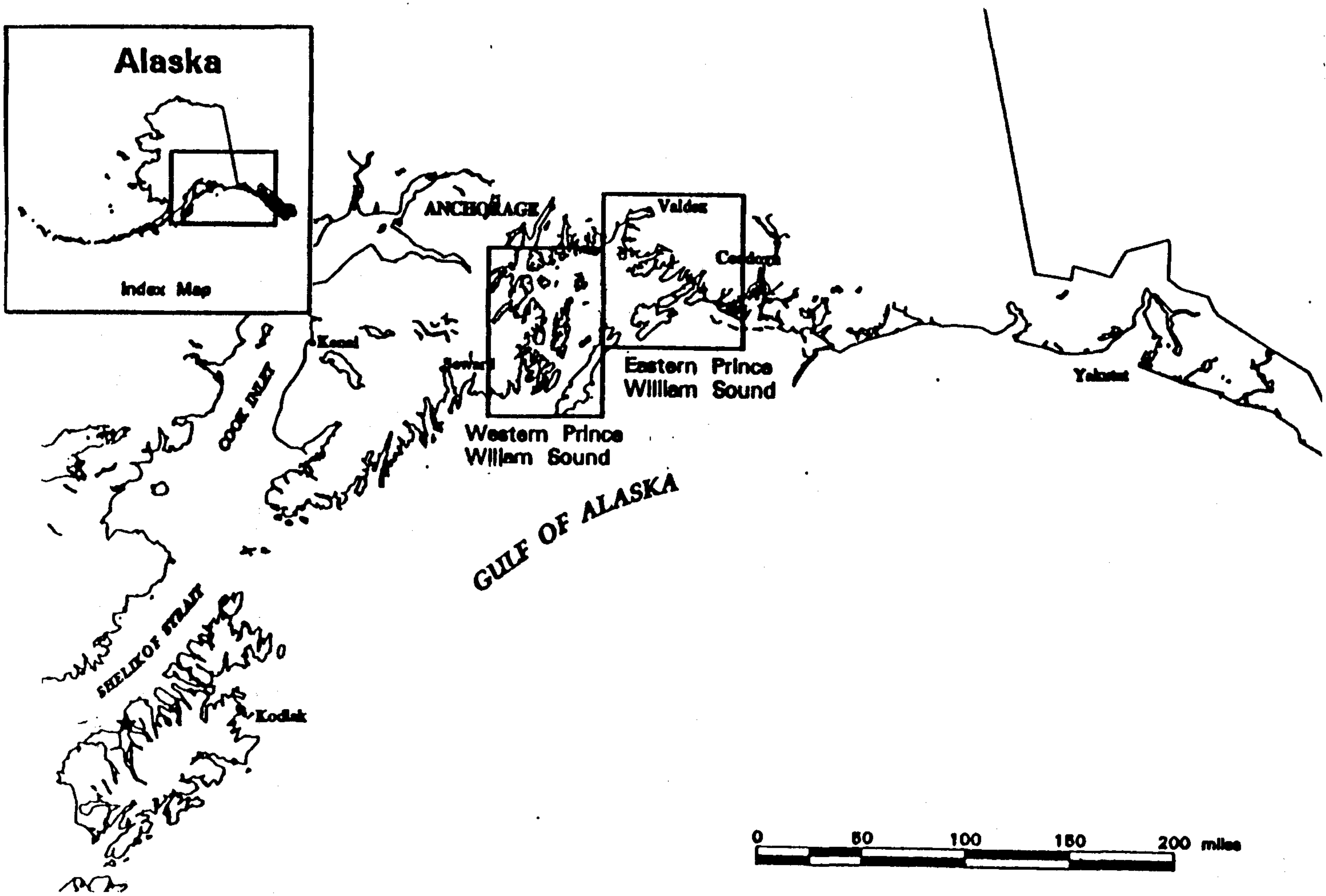

Figure 1. Western Prince William Sound (oil spill study area) and eastern Prince William Sound (breeding habitat study area) of south-central Alaska.

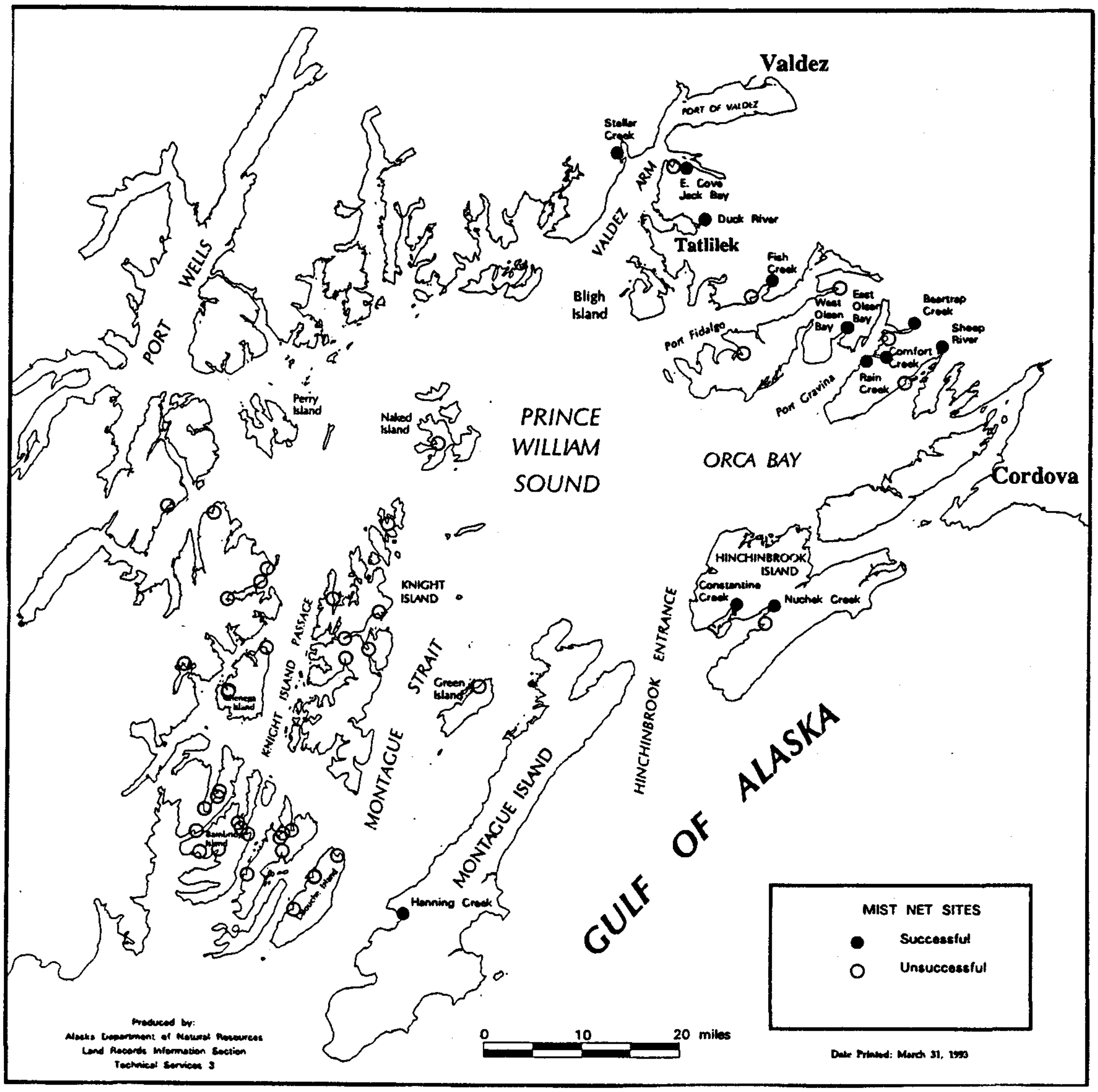

Figure 2. Area of study on Harlequin ducks in Prince William Sound, Alaska, 1991 - 1993.

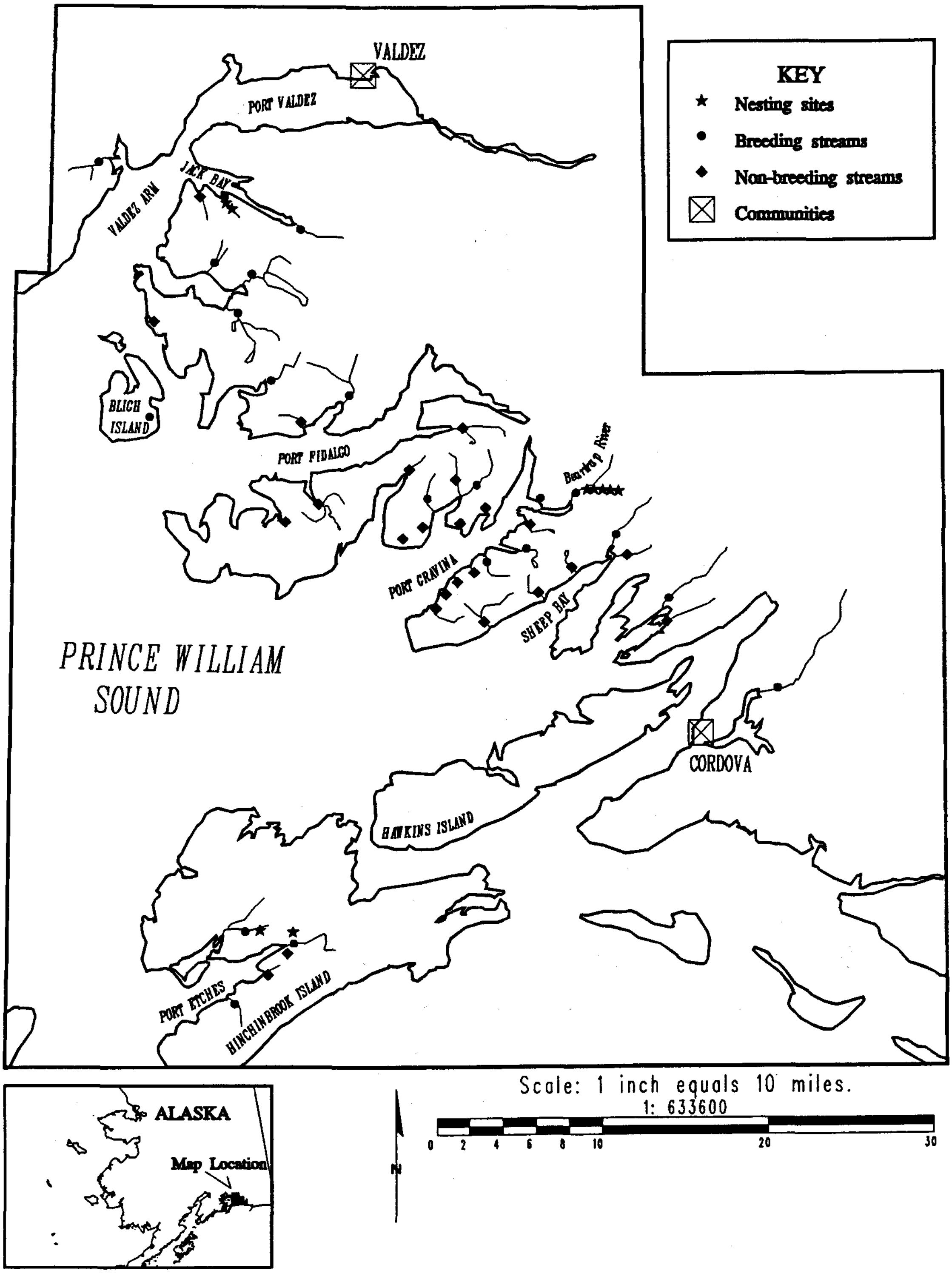

Figure 3. Area of study on habitat of breeding Harlequin ducks in Prince William Sound, Alaska 1991-1993.

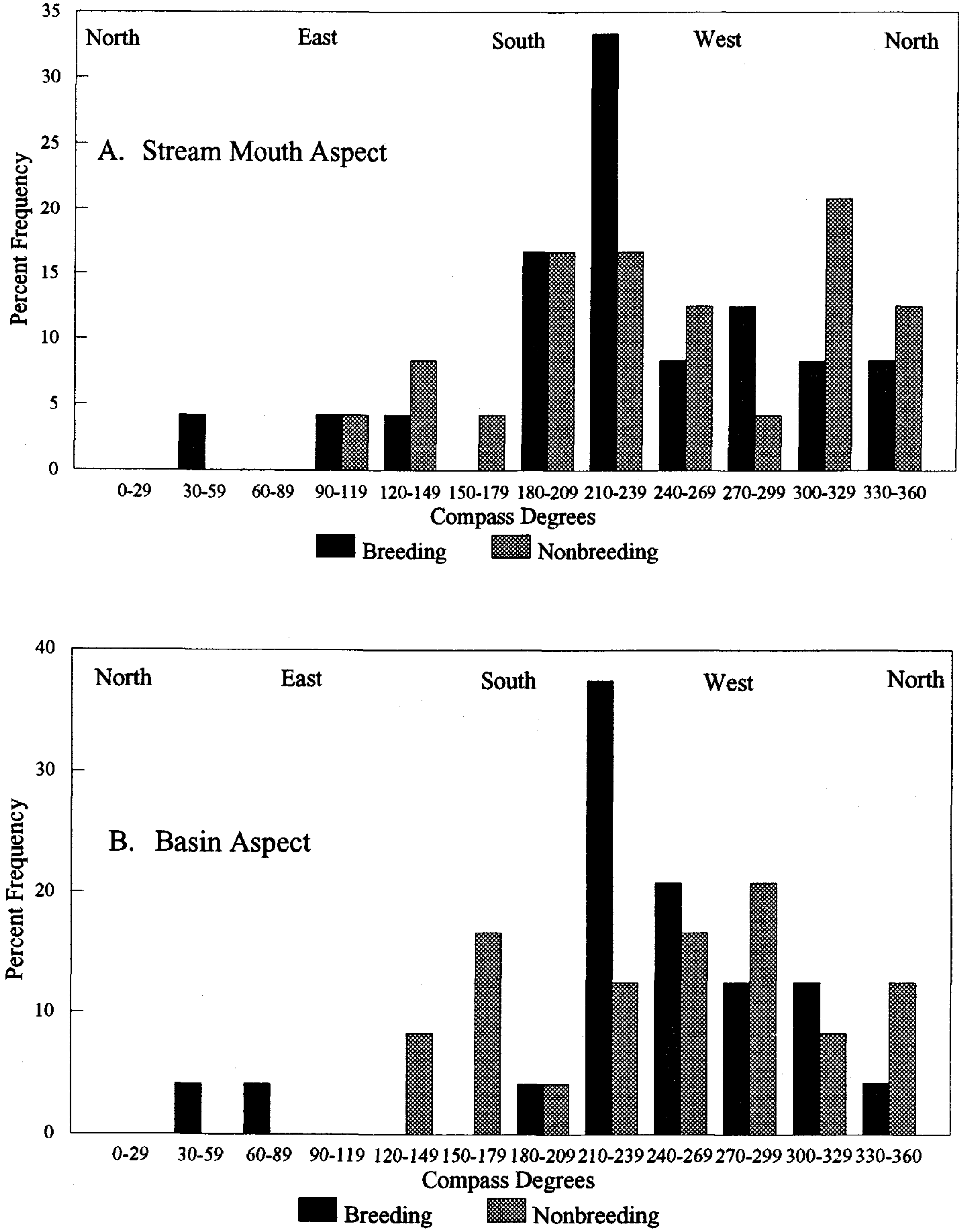

Figure 4. Comparison of the aspects of stream mouths (A) and basins (B) of streams used and not used by breeding Harlequin ducks in Prince William Sound, Alaska, 1991 - 1992.

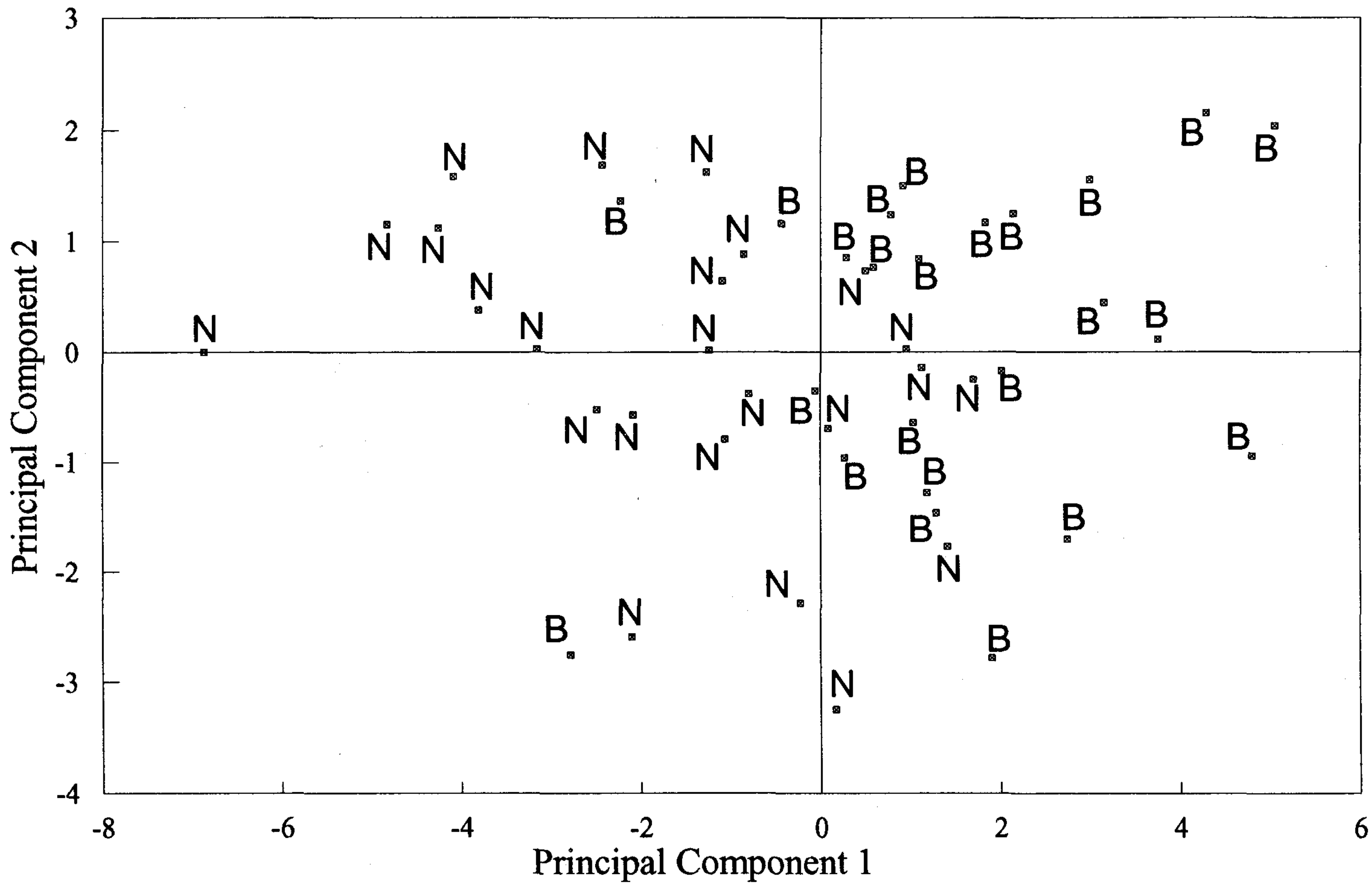

Figure 5. Separation of streams used (B) and not used (N) by breeding Harlequin ducks in Prince William Sound, Alaska, 1991 - 1993, along PC1 and PC2, which are weighted by measurements of size and gradient respectively.

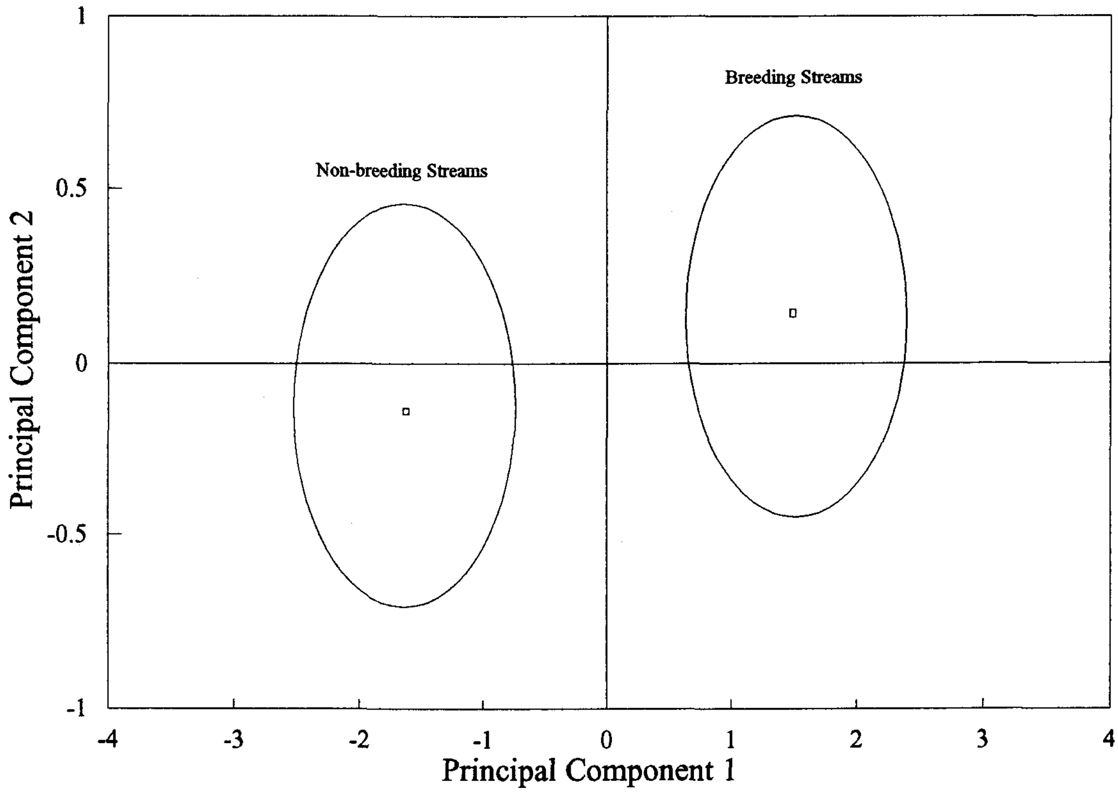

Figure 6. Means and 95% confidence ellipses indicating separation along PC1 of streams used and not used by breeding Harlequins in Prince William Sound, Alaska, 1991 - 1993.

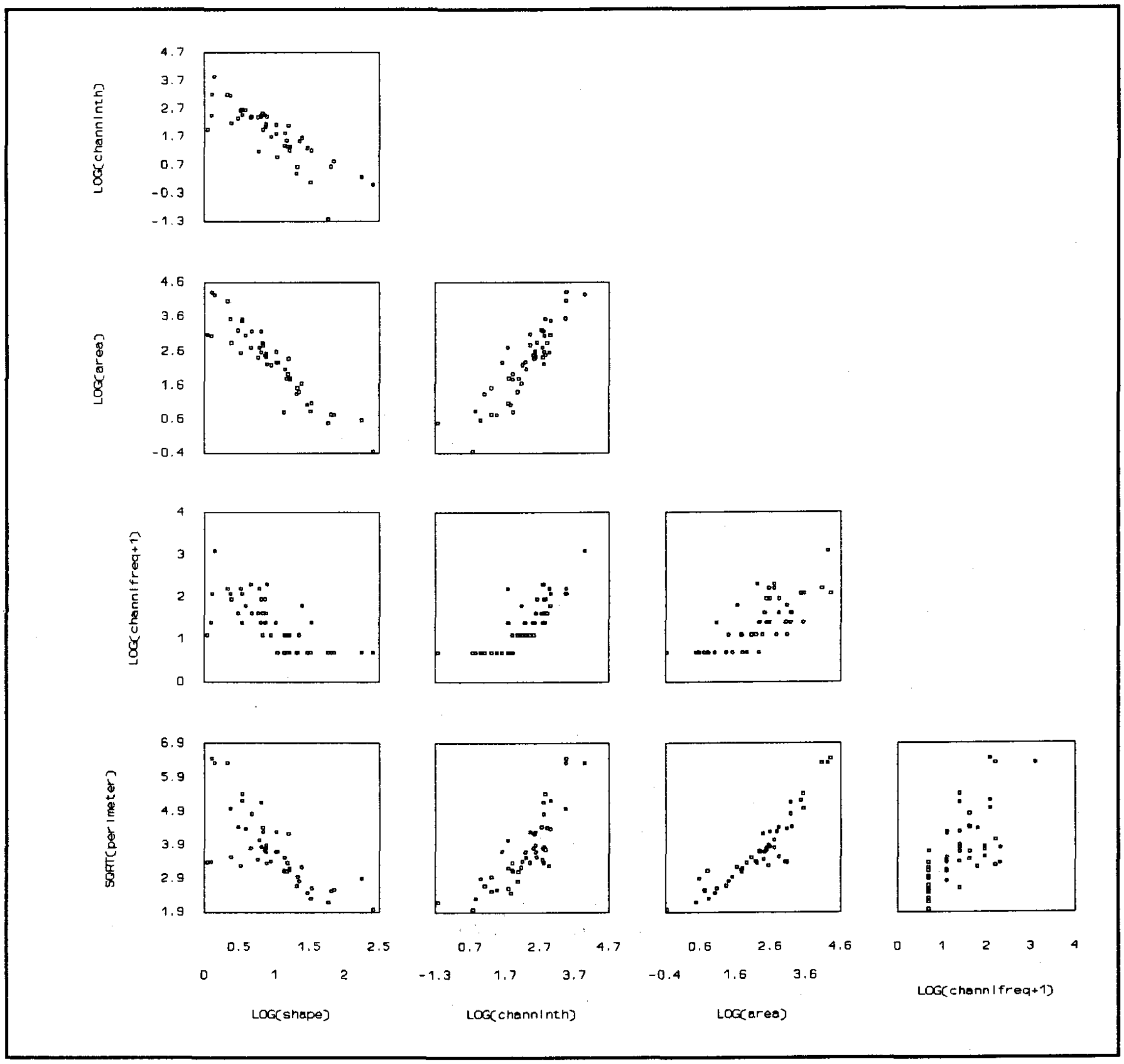

Figure 7. Correlation among 5 geomorphic variables important in discriminating between streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

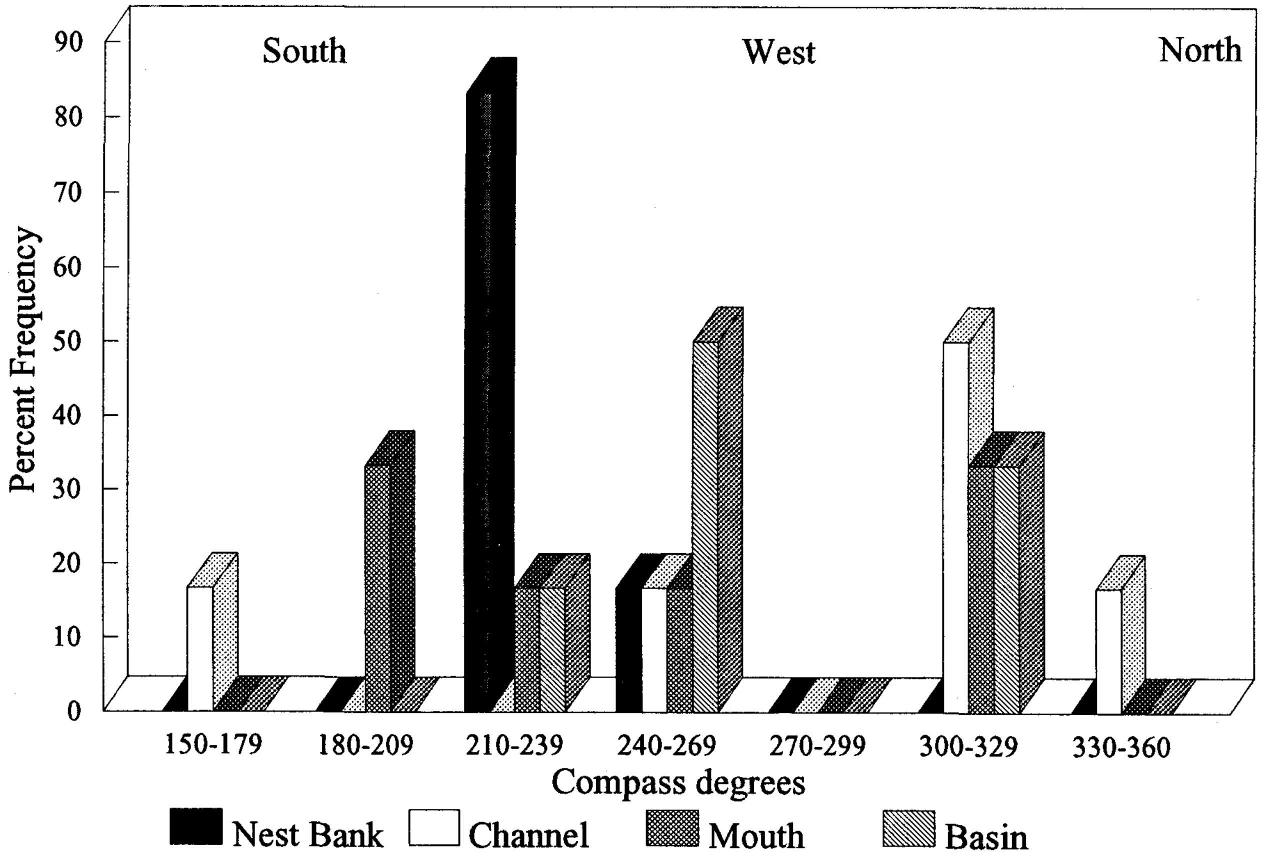

Figure 8. Distribution of 4 directional aspects: nest bank, channel adjacent to nest site, stream mouth, and basin, from 10 nest sites of Harlequin ducks in Prince William Sound, Alaska, 1991-1992. All nest bank aspects occur between 218 and 241°.

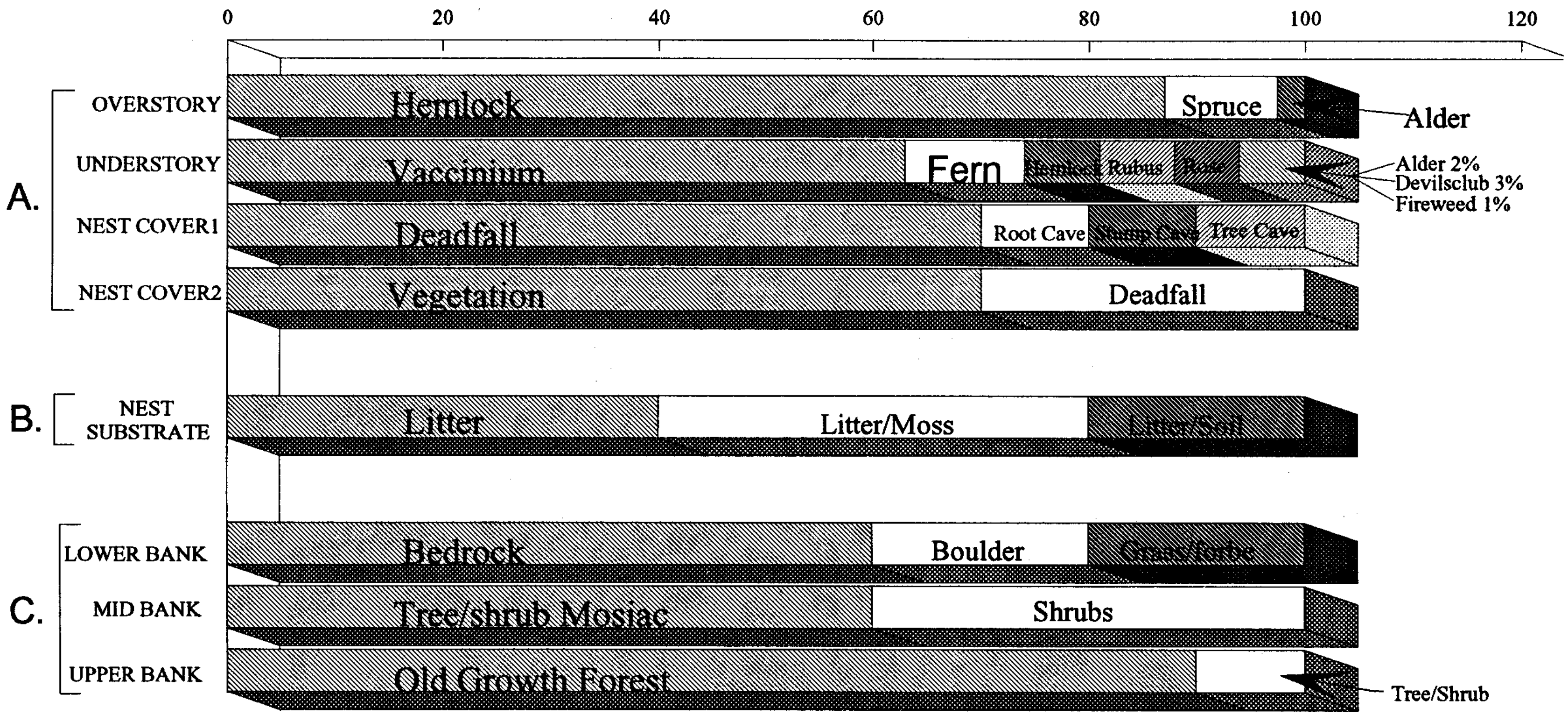

Figure 9. Vegetation (A), substrate (B) and stream bank composition (C) at 10 Harlequin duck nests in Prince William Sound, Alaska, 1991 - 1992. Units of measure are average percent occurrence.

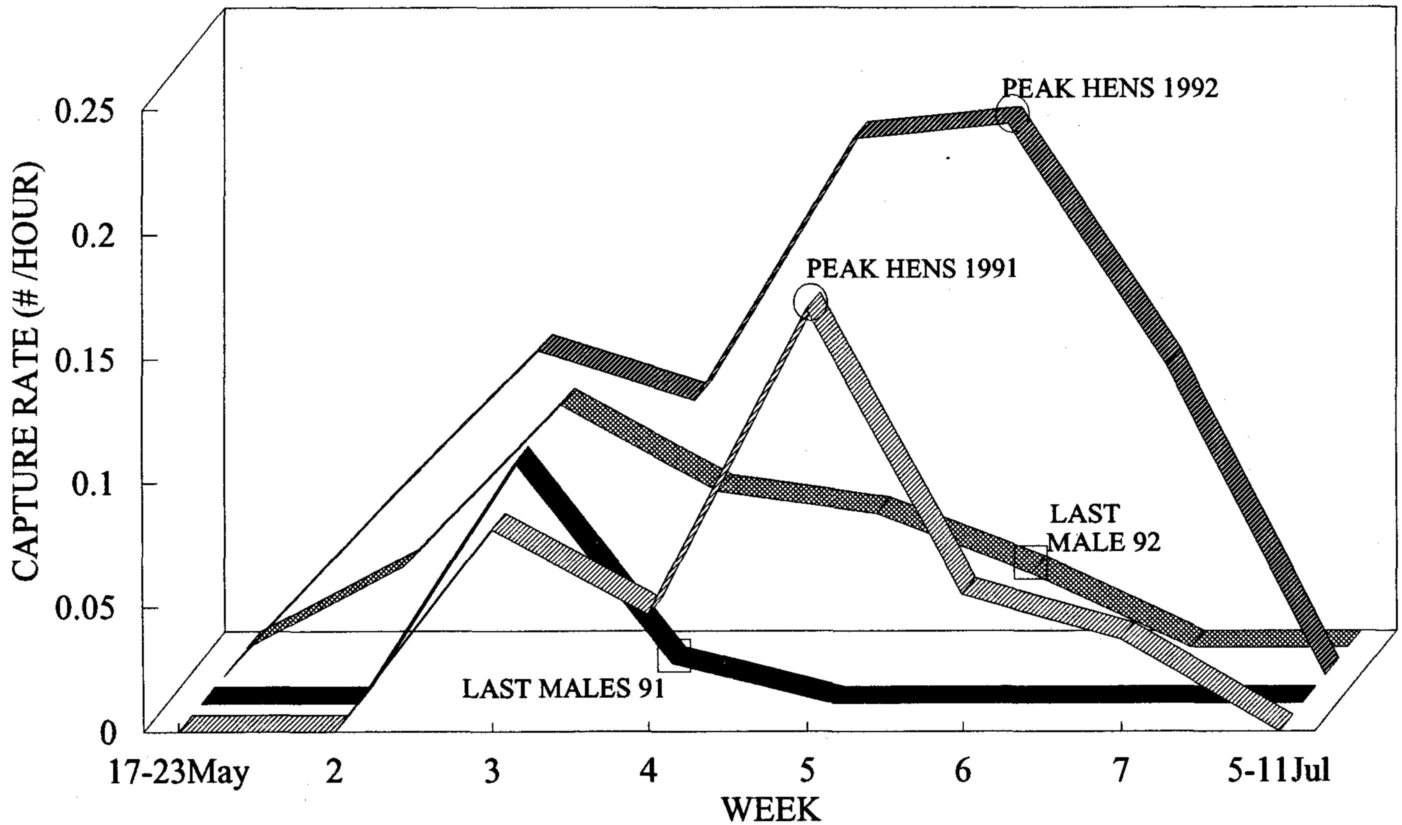

Figure 10. Weekly capture rates of Harlequin duck, 1991 and 1992, in Prince William Sound, Alaska.

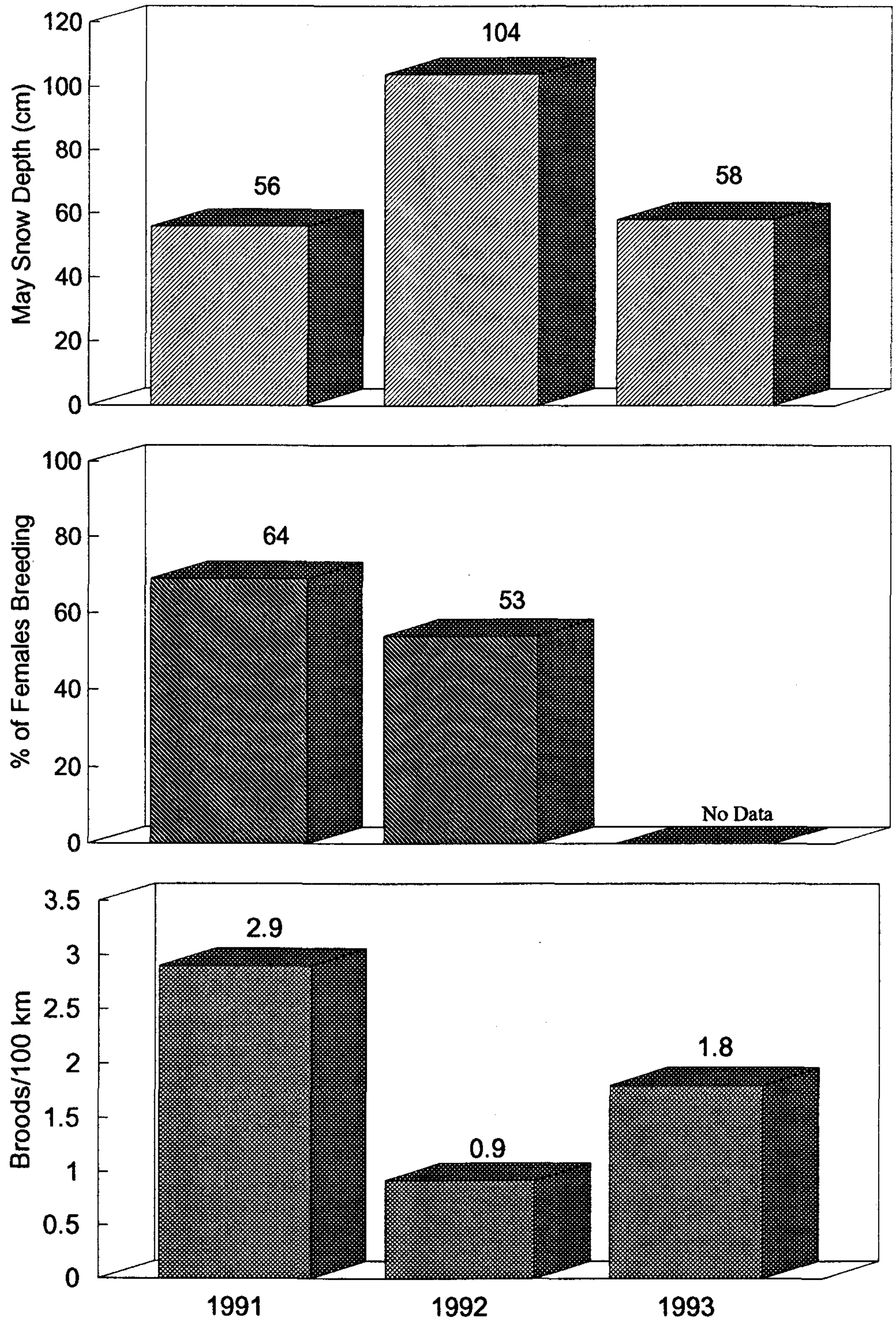

Figure 11. Relation of increased breeding frequency and breeding index of Harlequin ducks, with snow depth in May in Prince William Sound, Alaska, 1991-1993.

APPENDIX

APPENDIX

Discriminant function analysis (DFA) was used to determine which of the landscape variables were most important in discriminating between groups (Martinka 1972, Anderson and Shugart 1974, Conner and Adkisson 1976, Swanston et al. 1977, Rice et al. 1983, Ramsey and Schafer 1993).

Discriminant function analysis of landscape variables indicated that numerous stream channels and the contribution of basin area to the number of stream channels was important determinants of breeding habitat. A discriminant function (DF) containing all twelve variables classified 79.2% (19 of 24) of non-breeding streams and 83.3% (20 of 24) of breeding streams correctly at $p = 0.002$ (Appendix Fig. 1). By using DFA in a stepwise procedure, I determined that perimeter, area, channel length, channel frequency and discharge were most important in discriminating between stream groups. There was much intercorrelation occurring between variables (Fig. 5) in main Thesis). The DF most successful in separating stream groups contained perimeter and stream density: Crimcord = 1.131 (LOGperimeter) + 0.411(streamdensity), $p = 0.00003$. Although a t-test indicated that stream density was not significantly different between stream groups (Table 5), the linear combination formed by perimeter and stream density correctly classified 79.2% of non-breeding streams and 91.7% (22 of 24) of breeding streams (Appendix Fig. 2).

This discriminant function should be used with caution to predict streams used and not used by breeding Harlequin ducks because the formulation and testing of the DF was done with the same, small data set. Classification rates are likely overestimated and could be much lower when used on an independent data set.

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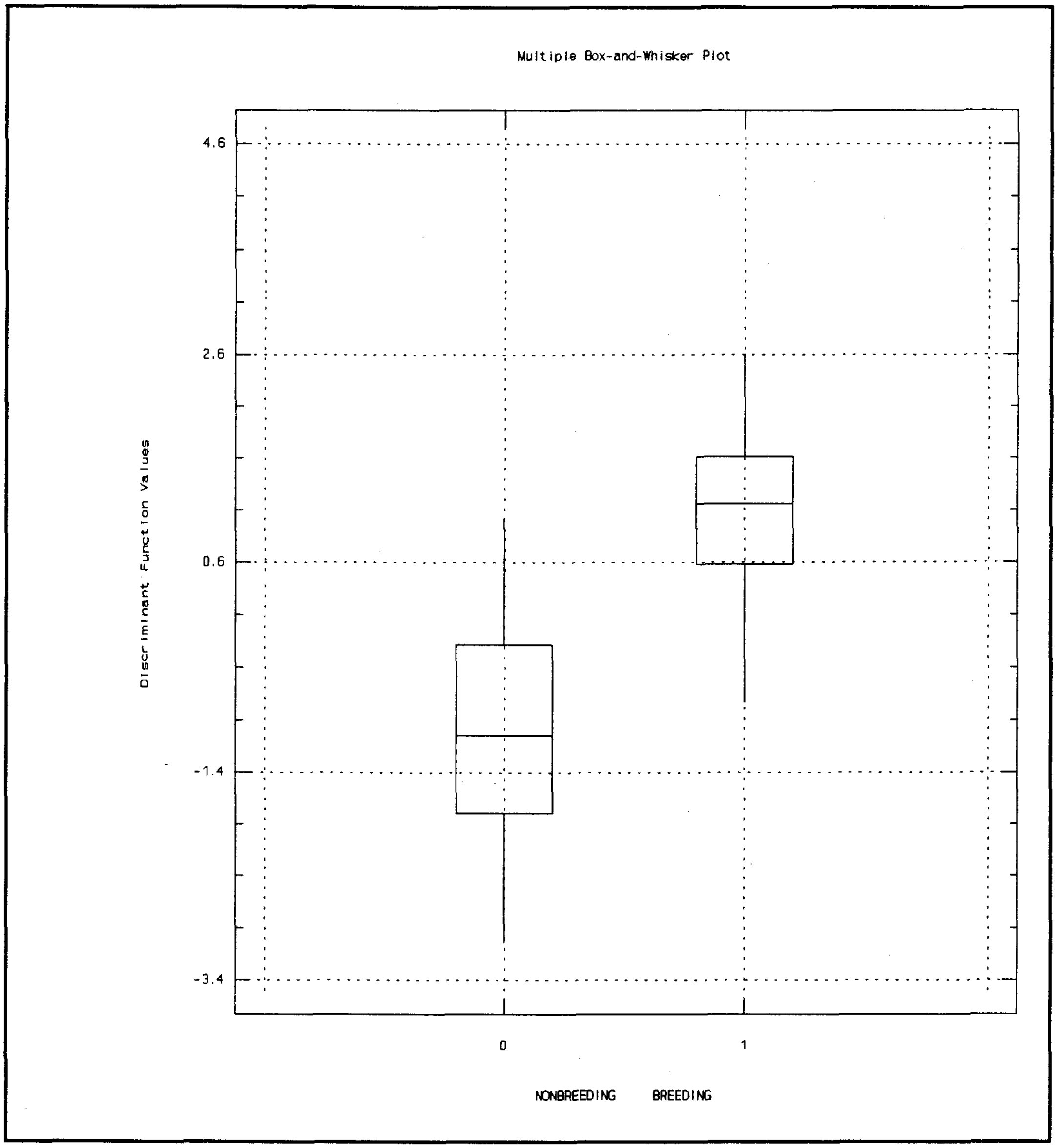
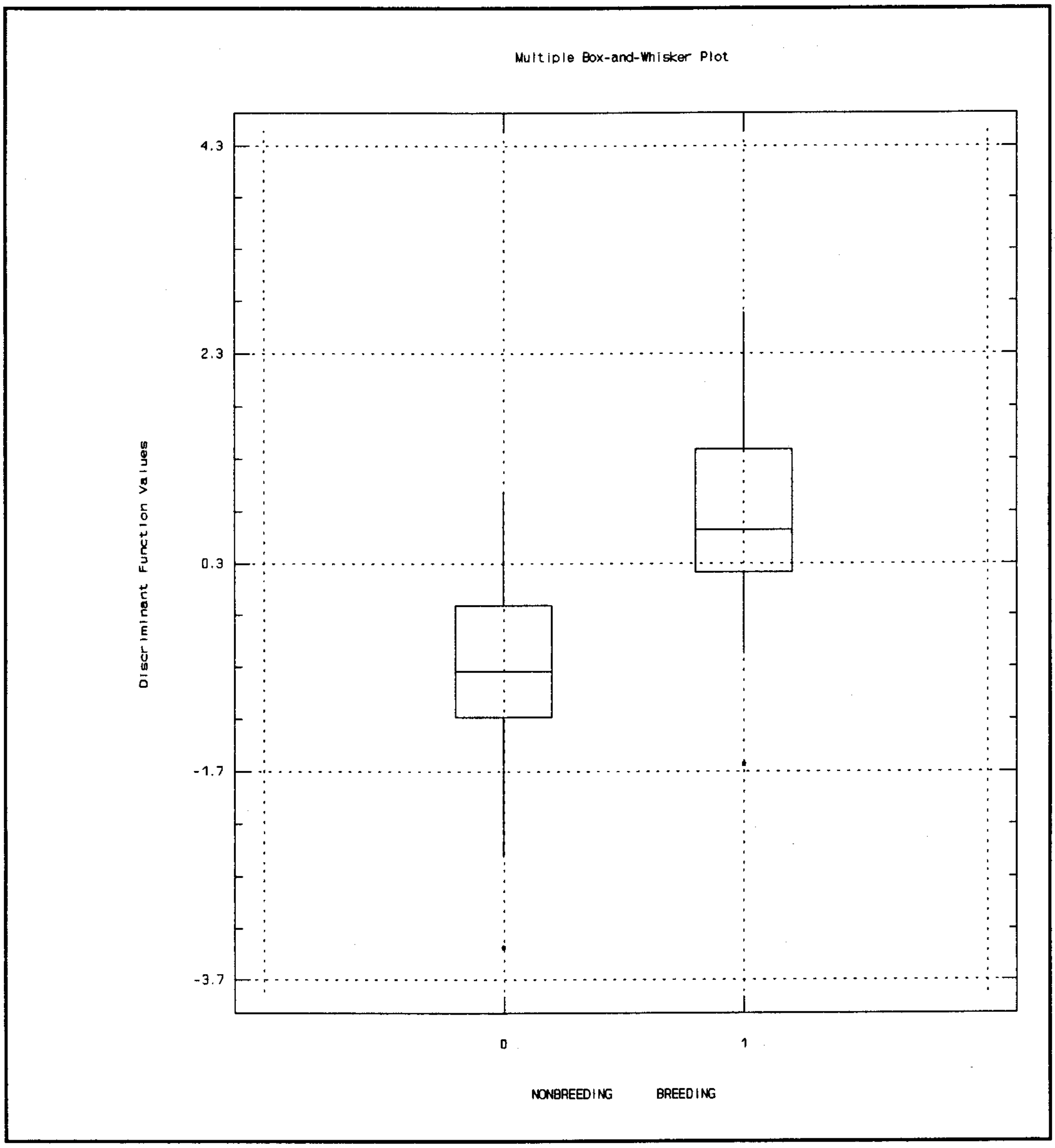


Appendix Figure 1. Discrimination between Harlequin breeding and non-breeding streams in Prince William Sound, Alaska, 1991 - 1993, using a function with all geomorphic variables included.



Appendix Figure 2. Discrimination, using a function with basin perimeter and stream density, between streams used and not used by Harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.