

Within-year fidelity of Harlequin Ducks to a moulting and wintering area

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Abstract

A small population of moulting and wintering Harlequin Ducks *Histrionicus histrionicus* was monitored between July 1994 and May 1995 near White Rock, British Columbia. Seventy-two of these birds were captured during the wing feather moult and banded with unique tarsal bands. Three patterns of habitat use over the nonbreeding season were observed: some individuals spent the entire period (August–May) in the study area; other birds permanently left the area in the fall, soon after the end of the moulting period (before 1 November); and, finally, some birds appeared to leave the study area in the winter (November–February), only to reappear in the spring (after 1 February). Unpaired males were seen at a greater variety of sites than paired males. Before pairing, males were seen at a greater variety of sites than females. Within-season observations of individuals show that individuals use very specific stretches of shoreline.

Résumé

On a observé une petite population d'Arlequins plongeurs (*Histrionicus histrionicus*) muant et hivernant entre juillet 1994 et mai 1995 près de White Rock, en Colombie-Britannique. Soixante-douze de ces oiseaux ont été capturés durant la mue des plumes des ailes et bagués d'une bague tarsienne unique. On a observé trois types d'utilisation de l'habitat au cours de la saison non reproductive : certains individus ont passé toute la période (d'août à mai) dans le secteur étudié; d'autres oiseaux ont définitivement quitté le secteur à l'automne, peu après la fin de la période de mue (avant le 1^{er} novembre); enfin, certains oiseaux ont semblé quitter le secteur étudié pendant l'hiver (de novembre à février), seulement pour réapparaître au printemps (après le 1^{er} février). On a observé des mâles non accouplés dans une plus grande variété de sites que les mâles accouplés. Avant l'accouplement, on a observé les mâles dans une plus grande diversité de sites que les femelles. Des observations d'individus au cours de la même saison montrent que ceux-ci utilisent des endroits très précis de la côte.

1.0 Introduction

Female philopatry to breeding grounds in waterfowl species is high. There is a tendency for female waterfowl to return to the same breeding area year after year and also to return to the area where they hatched for their first breeding effort (Anderson et al. 1992). Male waterfowl do not return to familiar breeding grounds with the same frequency as females, except in the case of males in long-term pair bonds such as geese and swans.

This pattern of female-biased philopatry is opposite that of other birds, where male birds exhibit higher rates of breeding and natal philopatry (Greenwood 1980; Greenwood and Harvey 1982). Male birds returning to familiar territories have an advantage over conspecifics (Pärt 1994). Waterfowl are assumed to be an exception to the rule of male-biased philopatry, because males cannot economically defend breeding territories. This inability to defend breeding territories results in males following females to the breeding grounds (Rohwer and Anderson 1988). Higher female mortality in waterfowl (Sargeant and Raveling 1992) results in populations with high proportions of males, thereby making females a limiting resource. Strong selection for males to pair early and retain their mates has led to the evolution of pairing in winter for some waterfowl and/or the maintenance of long-term pair bonds (e.g., geese and swans).

Waterfowl that pair in the fall or winter may not be expected to show the same patterns of sex-biased philopatry to the wintering grounds. In fact, if males can defend territories during the nonbreeding season, as is the case for Barrow's Goldeneye *Bucephala islandica* (Savard 1988), and there are fitness benefits for females in using these defended resources, a system of male-biased philopatry to the area where pairing occurs can evolve. To date, very few studies have looked at philopatry in waterfowl outside of the breeding period, particularly sex differences in winter philopatry (Robertson and Cooke 1999).

In this paper, we begin to examine the possibility that male sea ducks show higher levels of philopatry to their wintering grounds than females. To do so, we look at the within-year site tenacity of Harlequin Ducks *Histrionicus histrionicus* to their moulting and wintering grounds. Specifically, the objectives of this paper are 1) to document

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patterns of moulting and wintering area use by individual Harlequin Ducks, 2) to document within-site and between-site movements of Harlequin Ducks, and 3) to document relationships of movement patterns with the sex and/or pairing status of individual birds.

2.0 Study area

The main study area is a 5-km stretch of rocky shoreline located west of White Rock, British Columbia. This stretch of shore is bordered by a 4-m-high rock dike, along a railway line, which provides continuous access. The high intertidal sections are generally rocky with either cobbles or boulders as the dominant substrate. The lower intertidal sections vary along the shore; some areas are sandy with pebbles, whereas other sections are covered with cobbles, similar to the high intertidal. Large boulders, some of which are always exposed, are scattered about the shoreline. At the outer limits of this stretch of shore, the habitat becomes muddy and/or sandy. Harlequin Ducks have not been found locally with any regularity outside the main study site. Potential prey items present at the study site include green *Hemigrapsus oregonensis* and purple *H. nudus* shore crabs, hermit crabs (*Pagurus* spp.), isopods (*Idotea* spp.), periwinkles (*Littorina* spp.), and limpets (*Collisella* spp. and *Notoacmaea* spp.). Immature buffalo sculpins *Enophrys bison* are consumed in the fall season (B. Gowans, pers. commun.) and Atlantic herring *Clupea harengus* roe in the spring. Vermeer (1983) and Gaines and Fitzner (1987) provide further details of Harlequin Duck diets in the Pacific Northwest.

White Rock experiences warm dry summers and mild wet winters. Temperatures below 0°C can occur for short periods in the winter, but ice does not form at the study site. The maximum tidal amplitude is 6 m, resulting in an average exposure of 50 m of intertidal habitat at the lowest tides.

3.0 Methods

3.1 Capture of moulting Harlequin Ducks

Harlequin Ducks were captured using a drive trap erected along the shoreline. Moulting birds were corralled into the trap by 3–5 people in sea kayaks (see Clarkson and Goudie 1994 for details). In the first drive on 26 July 1994, 39 males and four females were captured. Two of the males captured had been previously banded at White Rock in 1986 (Breault and Savard, this volume). The second drive on 6 September 1994 netted 25 new females, four new males, and two males captured in the first drive. Birds were sexed by plumage. Age was determined by measuring the depth of the bursa of Fabricius using a blunt probe. The bursa of Fabricius is a small blind sac, posterior to the urogenital opening, and can be examined during standard cloacal examination (Peterson and Ellarson 1978). The bursa recedes during maturation and is absent in adult individuals (Petersen 1980). Birds were identified as second-year birds if the probe could be inserted over 20 mm. Birds with bursa depths of 5–10 mm were considered third-year birds. Birds with no bursa opening were considered adults (see also Petersen 1980). All birds were banded with standard U.S. Fish and Wildlife Service aluminum bands on one leg and a plastic

tarsal band bearing two unique alphanumeric characters on the other.

3.2 Survey data collection

Harlequin Ducks at White Rock were monitored for the entire nonbreeding season until the departure of the birds to the breeding grounds in spring. Data were collected by an observer with a pair of binoculars and a 15–60× zoom telescope walking along the entire shoreline. The observer recorded the time, the tidal stage, and the weather at the beginning and end of each survey. Observations of Harlequin Ducks were segregated by sex (and age for males in hatch year or after hatch year plumage; see Palmer 1976 for a description of these plumages) and whether the bird was paired. The banding status of the birds was recorded as 1) legs not seen (bird never left the water), 2) unbanded, 3) banded but not able to read band, and 4) banded with code read. The location of the bird(s) was recorded to the nearest tenth of a mile (160 m), using the mile markers already in place on the railroad tracks.

At least one survey per week was attempted. During poor weather conditions, especially windy days, birds did not haul out of the water, so band reading was not possible. Therefore, surveys were opportunistically done on fair-weather days. A minimum of three and up to nine surveys were done each month.

3.3 Estimating the number of banded and unbanded birds present

As the banding status of all birds could not be directly observed, the proportion of banded birds present in the study area each month was modelled using a generalized linear model of a binomial distribution. Maximum likelihood estimates of the proportion of banded birds present in each month were obtained from PROC GENMOD using a binary distribution and a logit link function (SAS Institute Inc. 1993). Model fit was assessed from the significance of the model deviance; insignificant values reflect good model fit. The importance of explanatory variables was assessed by log-likelihood ratio testing; a significant log-likelihood ratio test indicates that the variable explains a significant portion of the variation in the data. The parameter estimates and 95% confidence interval for each month were back-transformed from a logit transform to obtain the proportion of banded birds present in each month. The absolute number of banded birds present in a month was obtained by multiplying this proportion by the mean number of birds sighted that month.

3.4 Identifying resident and transient birds

If an individual bird is not seen in the study area for a period of time, it could be because the bird has left the study area (or died) or the bird is present but not seen. Therefore, we calculated monthly probabilities of missing individually banded birds. The resight probability for each survey was estimated by dividing the number of birds whose legs were seen (the potential for an identification) over the total number of birds present during the survey. For example, if three birds could have potentially had their bands read and the legs could not be seen for seven birds, 70% of all banded

Table 1
Probabilities of missing a particular individually marked bird that is actually present in each month over the study period for each sex. These probabilities are based on the number of birds that could be identified at each survey and the total number of birds present.

Month	Number of surveys	Females	Males
August	9	0.034	0.004
September	8	0.009	0.003
October	7	0.004	0.038
November	4	0.316	0.359
December	3	0.743	0.745
January	7	0.318	0.400
February	5	0.604	0.572
March	7	0.043	0.071
April	9	0.001	0.001
May (until 16th)	9	0.003	0.012

birds present would have been missed (see Robertson et al. 1997 for further details). Monthly probabilities of missing a particular individually banded bird are a product of the values for each survey (Table 1). A cumulative probability for missing individuals over the winter is the product of the monthly probabilities for November through February. This method assumes that there is no difference in the probability of any particular individual bird hauling out. This value corresponds to 0.045 for females and 0.061 for males. Therefore, 95.5% of females and 93.9% of males present over the winter should have been resighted. Birds not sighted in any of these four months are considered to have left the study area for at least a part of this period, with 95.5% and 93.9% confidence, respectively. As a result of good weather conditions, the probabilities of missing birds in March and April were very low, and birds not seen in these two months were considered to be absent from the study area, with over 99.9% confidence. Individuals were classed into three categories: birds present throughout the entire study, birds present in fall and again in the spring, and birds that permanently left in the fall.

3.5 Assessing within-site movement patterns

As the study site is linear (5 km of shoreline), the variance in the location of the sightings of individuals was used as an index of relative amount of movement. Individuals seen at a greater variety of sites would have a higher variance. The variance calculated for each individual was used in comparisons between sexes and between paired and unpaired birds. A randomization approach (Manly 1997) was used to test whether individuals were using only specific sections of shore. We used the distribution of sightings of all marked birds over the winter as the null distribution (Fig. 1). To test whether an individual was using the habitat randomly, the variance in location calculated for each bird was compared with a distribution of pseudo-variances calculated from 1000 random samples from the sex-specific baseline distribution (Fig. 1). If the variance calculated for the individual was in the bottom 5% (one-tailed test) of observations of this distribution, then it was assumed that the individual was significantly underutilizing the available habitat and was showing site tenacity within the habitat.

4.0 Results

4.1 Population size and structure over the nonbreeding season

4.1.1 Males

The number of males present at the study site fluctuated around 40 birds for most of the winter (Fig. 2). There was a noticeable decline in the number of males present in late September, down to 30 birds; by October, however, the number of males returned to between 40 and 50 birds. A decline in the number of males is apparent from the middle of March onwards; however, large numbers of males appeared at the study site on some days in April (Fig. 2).

4.1.2 Females

Females began returning from the breeding grounds in August through September (Fig. 2). A departure of females occurred in late October. Afterwards, a slow increase in the number of females occurred until February. The number of females consistently declined after February, until the last birds were seen in late May (Fig. 2).

4.1.3 Both sexes

A fifth-order polynomial regression was fitted to the population counts of males and females. A fifth-order polynomial was used, as all terms of lower orders were significant, whereas the sixth-order term did not explain a significant amount of variation (Fig. 2). The model fit for females ($R^2 = 0.826$, $n = 68$) was significantly higher than for males ($R^2 = 0.392$, $n = 63$) ($Z = 5.58$, $P = 0.0001$), showing that male population numbers varied more than female numbers.

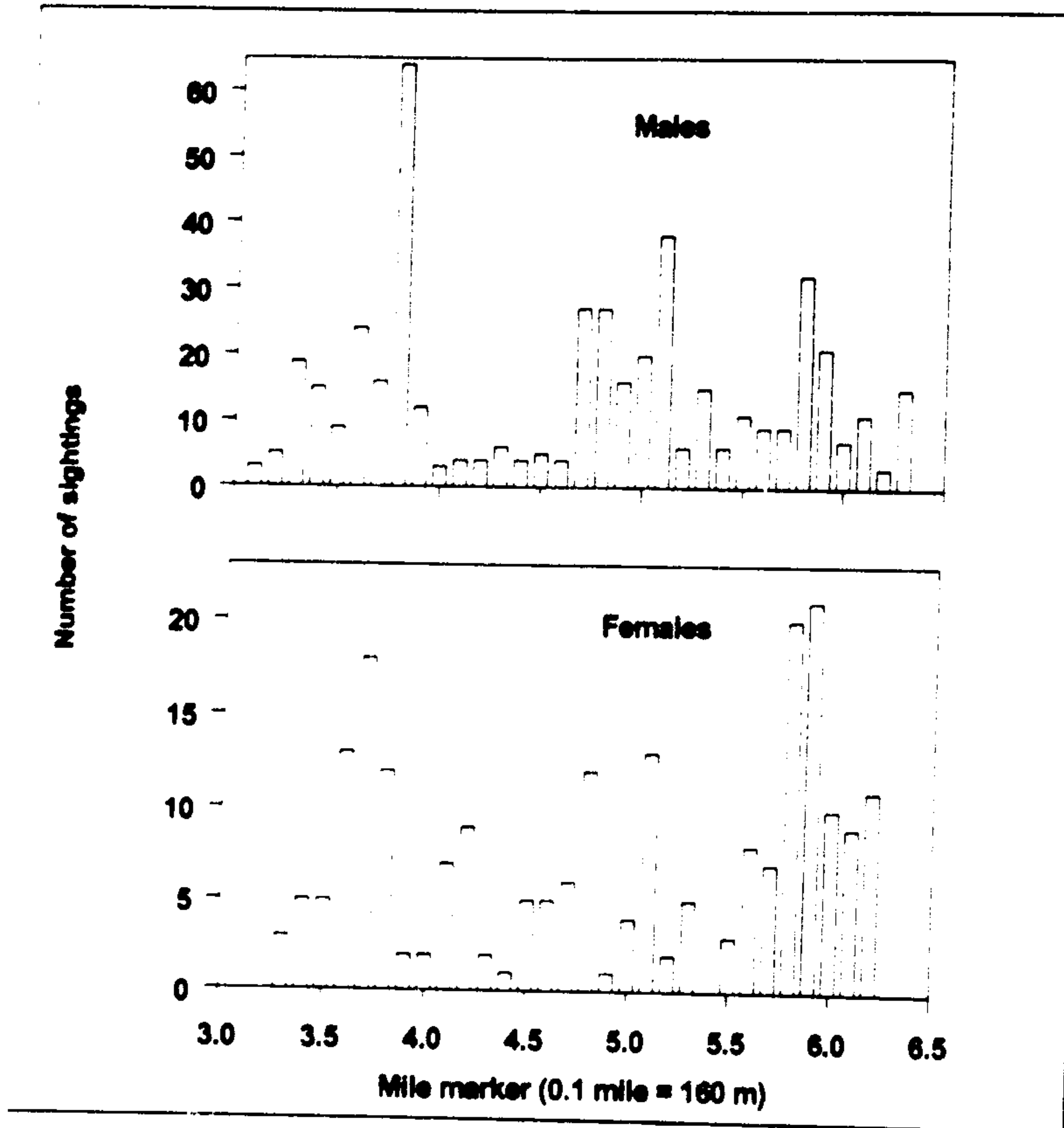
4.1.4 Banded and unbanded birds

Figure 3 shows the estimated number of banded and unbanded birds in the study area. Numbers of banded males fluctuated over the season. The number of unbanded males present in the study area increased sharply through September and October, afterwards, it remained stable until the decline in the spring. A departure of both unbanded and banded females appeared to occur in the fall. An arrival of unbanded females occurred in December. The estimated number of banded males in December is very high but represents a biased sample from only three surveys, on one of which seven banded males were seen and no unbanded males. The month in which a survey was conducted explained a significant proportion of the variation in the ratio of banded to unbanded birds in males ($\chi^2 = 125.5$, $df = 9$, $P = 0.0001$) and females ($\chi^2 = 37.0$, $df = 8$, $P = 0.0001$). The model including month as the explanatory variable to explain the proportion of banded birds in the population fit the data well for females ($\chi^2 = 47.3$, $df = 40$, $P = 0.198$), the fit for males was poor ($\chi^2 = 82.8$, $df = 50$, $P = 0.0024$), suggesting that other factors exist to explain the variation in the proportion of banded males present at the study site.

4.2 Residency patterns of individuals

Individually marked birds exhibited three general patterns of habitat use: some birds left after the moult, not to be seen again; other birds were seen consistently throughout

Figure 1
Number of individually marked Harlequin Ducks identified at each location from August 1994 to May 1995 at the study area near White Rock, B.C.



the fall, winter, and spring; and, finally, some birds were not seen over the winter, but were seen again in the spring. Table 2 presents the numbers of birds, of each sex, exhibiting each habitat use pattern. There is a significant difference between the sexes in their habitat use patterns ($G = 6.1$, $df = 2$, $P = 0.047$). A higher proportion of females remained at the study site after they moulted, although the number of birds wintering at the study site after they moulted was less than half for both sexes. Of the birds that left the study site in fall, a higher proportion of males returned in the spring (Table 2).

4.3 Within-site movements

Unpaired males were seen at a greater variety of sites than paired males once pair formation was under way (by 1 November) (Robertson et al. 1998) ($U = 179$, $n = 9$, 20 , $P = 0.0004$). Before pairing, males were seen at a greater variety of sites than females ($U = 357$, $n = 28$, 20 , $P = 0.005$).

Using the randomization approach described above, 20 of 25 (80%) females and 32 of 42 (76%) males

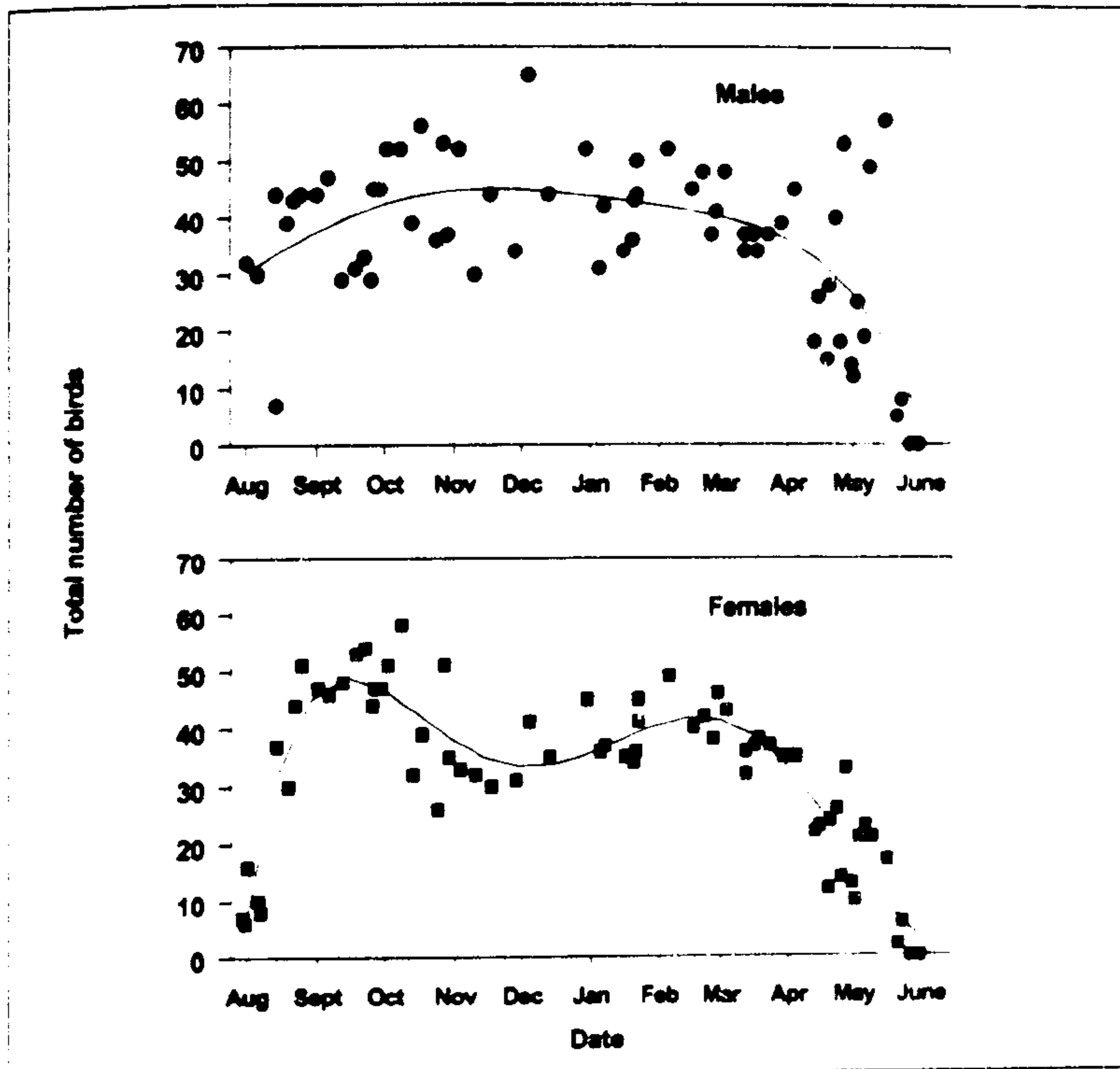
significantly underutilized the available habitat. Therefore, individual birds used specific areas of the shoreline for the entire winter. For example, a female that was seen 22 times over the winter was never seen outside a 1100-m stretch of the 5 km of available shoreline, and 18 of the 22 sightings were within a 320-m section of the shoreline.

5.0 Discussion

5.1 Population structure, turnover, and residency patterns

The number of males present at the White Rock study site showed considerably more variation from one survey to the next than did the number of females. Males may be more mobile within the nonbreeding season, on a day-to-day basis, whereas females may spend more time at an area once they arrive there. Counts of males on any particular day may represent only a portion of the males using the habitat. Observations that males are seen at a greater variety of sites within the study area also suggest that males are more

Figure 2
Number of males and females observed at each survey near White Rock, B.C., from August 1994 to June 1995



mobile. There are two likely places to which the males may go when not present at White Rock. There are other suitable sections of shoreline habitat within 50 km of the study site. A few banded Harlequin Duck individuals have been observed at these sites (Breault and Savard, this volume; G.J. Robertson, unpubl. data). Additionally, males may also spend time out on the open water, out of sight from shore. Recent observations of radio-marked male Harlequin Ducks have shown that they do, on occasion, move offshore to roost and feed (W.S. Boyd, unpubl. data). During April, large numbers of males were periodically seen at White Rock, whereas the numbers of females seen during this period steadily declined as birds left for the breeding grounds. This population of males was composed of unpaired adult and young males. Presumably, this was a population of bachelor males, possibly looking for potential mates or prospecting for a potential moulting/winter site for next season.

Departure of birds from the moulting site probably reflects dispersion to the winter quarters. Therefore, a link between the moulting and wintering site exists for some, but not all, birds (Breault and Savard, this volume). All combinations of moulting and wintering habitat use were exhibited by Harlequin Ducks at the study site. More than half of the birds remained for the entire nonbreeding period. Other birds, especially males, used the area as something similar to a

migrational stopover site, spending the fall and spring, but not the winter. Other birds used the area only as a moulting site. Based on the influx of unbanded birds, a certain segment of the population used the study area as a wintering site but did not moult there. Finally, some males appeared to briefly stop over at the study area during the spring. Green-winged Teal *Anas crecca* wintering on the southern high plains of Texas showed a somewhat similar pattern of winter habitat use (Baldassarre et al. 1988). Birds captured after December had a higher chance of being resighted than those banded earlier. Presumably, the only birds in the area in December were those spending the entire winter

5.2 Winter territories and mating systems

Males may be more mobile than females and explore local areas to look for concentrations of females and or to assess the quality of other males. Regardless of the reasons, the fact that males do move around considerably before pairing suggests that they do not form a winter territory. Observations on the breeding grounds show that male Harlequin Ducks vigorously defend their mates, but not territories (Inglis et al. 1989). The observation that unpaired males move around more at the end of the season, presumably looking for females, also strongly suggests that males

Figure 3

Estimated number of banded and unbanded males and females present at White Rock, B.C., from August 1994 to May 1995. Point estimates and 95% confidence intervals were based on back-transformed binomial logit parameter estimates from a model with month as a nominal dependent term. See Table 1 for sample sizes.

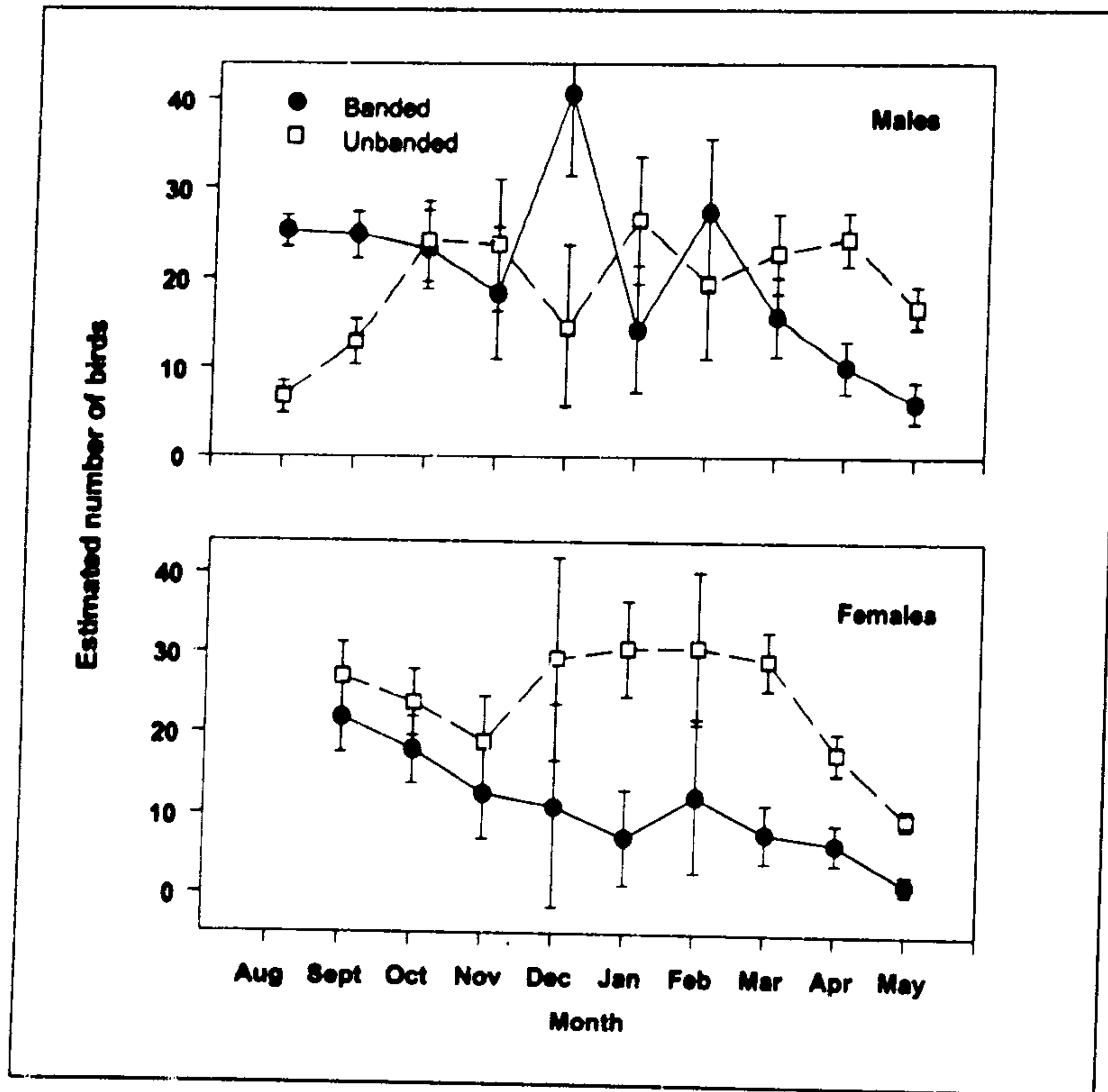


Table 2
Patterns of winter habitat use by the 72 marked Harlequin Ducks over the 1994-1995 winter season at White Rock, B.C. Actual numbers and percentages are presented.

	Winter resident	Leave in fall, return in spring	Depart in fall
Males	15 (35%)	15 (35%)	13 (30%)
Females	13 (45%)	3 (10%)	13 (45%)

are not establishing territories to attract mates; rather, a scramble type of mating system exists, where males search for less abundant females (Emlen and Oring 1977).

5.3 Within-site fidelity

Individual birds, even within a relatively small area (5 km of linear habitat), show strong site tenacity. This observation strongly suggests that local knowledge of an area is valuable and may help ensure high survival of individuals remaining in a familiar site. Potential benefits of local knowledge of an area may include 1) location of high-quality or

abundant food sources, 2) location of predator refugia, 3) knowledge of local predators and their movements, and/or 4) knowledge about neighbouring conspecifics. Rocky coastal habitats are very stable, with little change, or at least predictable changes, in food abundance and habitat structure between and within years. Philopatry to these stable habitats would be favoured once a good-quality site was found. Of all waterfowl, those species whose populations are highly sensitive to adult mortality and use stable habitats would be expected to have higher philopatry rates than short-lived species using more ephemeral habitats.

6.0 Conclusions

Harlequin Ducks use coastal habitats in a variety of ways and for different purposes. Although general censuses of ducks at the study site showed relatively constant population sizes, observations on individually marked birds revealed considerable population turnover. To adequately assess the importance of any given patch of habitat to Harlequin Ducks, the habitat must be monitored throughout the entire nonbreeding season. As adult survival has the greatest impact on the population dynamics of Harlequin

Ducks (Goudie et al. 1994), care must be taken to protect nonbreeding habitats and ensure high annual adult survival.

Individual Harlequin Ducks show strong site tenacity, even within a relatively small study area; hence, conservation must be applied at the local level. The mating system of Harlequin Ducks appears based on scramble competition and mate defence. This allows the less abundant females to remain in preferred locations, and unpaired males must disperse to search for available females. Once males are successful in establishing a pair bond, they remain with the females in traditional locations.

Acknowledgments

We thank Eric Reed, Saul Schneider, Barbara Pohl, Ken Wright, and especially Carl Hofbauer for assistance in the collection of the data. Billie Gowans kindly provided unpublished data. Frances Cassirer, Sean Cullen, and Billie Gowans kindly reviewed an earlier draft of the manuscript. Evan Cooch provided excellent ongoing statistical advice. This project has received generous funding from the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service, Simon Fraser University, the Research Network Program (Chair of Wildlife Ecology), the Institute for Wetland and Waterfowl Research, and the B.C. Waterfowl Society.

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