Apparent Survival and Local Movements of Harlequin Ducks Wintering at Isle au Haut, Maine

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Abstract.—Capture-recapture data from a five-year field study of individually marked Harlequin Ducks (*Histrionicus histrionicus*) wintering at Isle au Haut, Maine was used to examine patterns in age- and sex-specific apparent survival and local movements. Adult females had lower annual apparent survival probabilities than adult males. Survival probabilities for adult females were lower during the summer season than the winter season. Adult males showed no differences in apparent survival between the summer and winter intervals and survival during the winter season was similar for adult males and females. There was little evidence to suggest differences in apparent survival between first winter males and females, although sample sizes, especially for first winter females, were small. Annual apparent survival rates were lower for first winter males than adult males and likely reflected a combination of greater dispersal and higher mortality. Adult males captured in April in the study area disappeared from the study area more than adult males captured in November and may represent spring dispersal of unpaired males searching for mates or individuals from other wintering sites gathering before spring migration. Greater dispersal of adult and first winter males to adjacent wintering sites in subsequent winters was noted than for adult females.

Key words.—age, Harlequin Duck, *Histrionicus histrionicus*, Maine, sex, survival, wintering.

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Despite concern over the status of Harlequin Duck (*Histrionicus histrionicus*) populations in eastern North America (Goudie 1991), little information exists on what factors are responsible for long or short-term fluctuations in numbers. For a long-lived species, such as the Harlequin Duck (Goudie *et al.* 1994), adult survival may have a greater influence on population growth than annual fecundity (Mertz 1971; Nichols *et al.* 1980; Lebreton and Clobert 1991; Beissinger 1995). Understanding and monitoring seasonal differences in survival and how these influence populations is essential for effective conservation and management (Likens 1989; Pollock *et al.* 1990; Nichols 1992; DeSante 1995; Newton 1998; Bennetts *et al.* 1999; Green 1999) and may provide insights into factors responsible for the low numbers of Harlequin Ducks in eastern North America.

The coast of Maine is a key wintering location for Harlequin Ducks in eastern North America and Isle au Haut is an important wintering site in Maine (Mittelhauser 2000; Mittelhauser *et al.* 2002). Birds were individually marked in the late 1990s to gain preliminary estimates of apparent survival, although small sample sizes and dispersal of birds hampered earlier results (Mittelhauser 2000). The objectives of this paper were to examine seasonal, sex, and age specific patterns of apparent survival that accounted for local movements in Harlequin Ducks wintering at Isle au Haut, Maine. Results from this study were also compared to survival and movement estimates for this species based on recent studies in western North America (Cooke *et al.* 2000; Esler *et al.* 2000; Robertson *et al.* 2000; Regehr *et al.* 2001; Regehr 2003).

METHODS

Patterns in local movements and apparent survival were examined in a population of 150-250 Harlequin Ducks that winter along a 10 km stretch of rocky shoreline at Isle au Haut, Maine. Isle au Haut is a 2,600 ha island situated 18 km off the Maine coast between outer Penobscot and Jericho Bays (Fig. 1) and is one of several important wintering islands for this species in the area (Mittelhauser *et al.* 2002). The study population was defined as those birds present along the southern shore of Isle au Haut, between Eastern and Western Heads (Fig. 1).

Harlequin Ducks were captured and banded at Isle au Haut and adjacent areas in the region (Fig. 1) from November 1997 to March 2002. Birds were caught during three to five days of trapping each fall and spring with mist-nets strung above an array of floating platforms (Mittelhauser 2000; Brodeur *et al.* 2008a). Six standard 3.0 × 18-m mist nets of 10-cm 4-ply mesh (210 denier) (Avinet, Inc. Dryden, New York) supported by aluminum tubing (18.8-mm × 3.0-m) mounted above

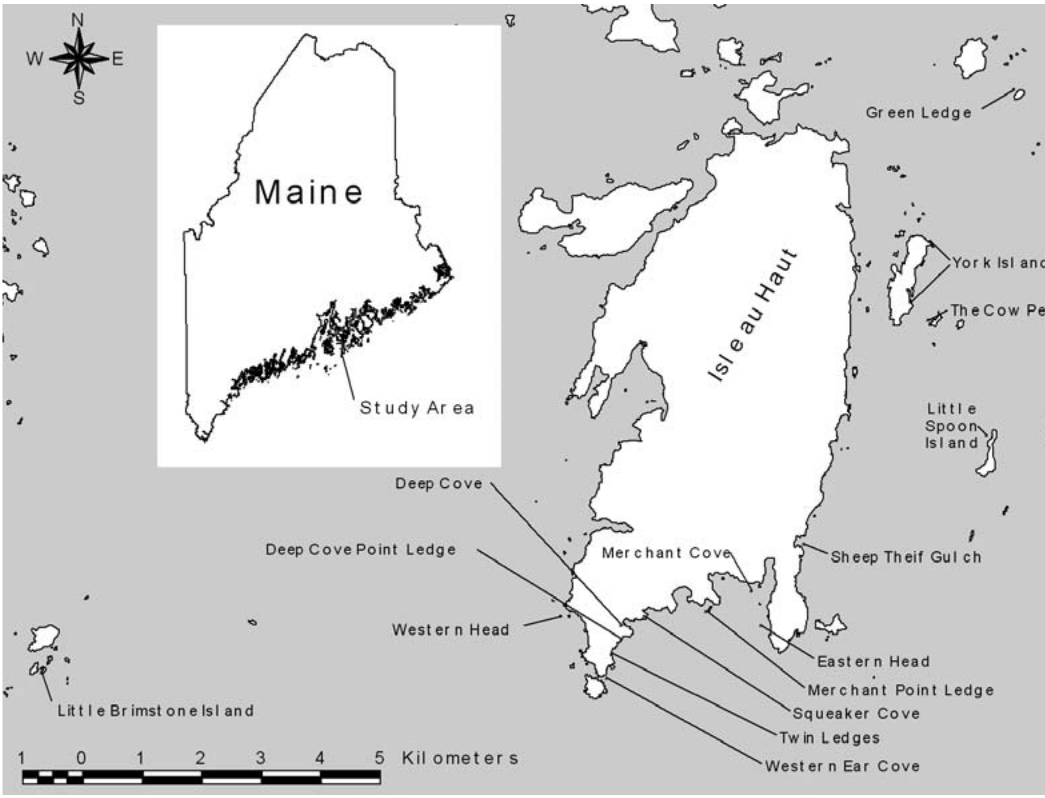

Figure 1. Banding locations of Harlequin Ducks in Maine since 1997.

floating platforms were used. Three to six nets were set in a line or a "T" formation adjacent to intertidal ledges. The near-shore platform was anchored as close to the shore as possible, ideally adjacent to a granite face extending at least three m out of the water. Thirty-six plastic Harlequin Duck decoys were anchored adjacent to the nets. Four to six people in two skiffs continuously monitored the setup and retrieved birds.

All birds were marked with an aluminum U.S. Fish and Wildlife Service leg band and an alphanumeric coded color band that uniquely identified each individual. These codes could be read with 20-60× spotting scopes when a bird was roosting on the shoreline. Captured males were aged by plumage characteristics (Smith *et al.* 1998) and female age was estimated by the depth of the bursa of Fabricius (Peterson and Ellarson 1978; Mather and Esler 1999). For fall captures, the criteria in Mather and Esler (1999) to age young (HY) females was used; for females captured during spring, a bursa depth criteria of 5 mm or greater was used to indicate young (SY) birds. Birds in their second fall after hatch (SY) and second winter after hatch (SY and TY) were considered adults.

During each fall and spring, when birds are most likely to haul out of the water, the study area on Isle au Haut and adjacent areas were searched for banded birds during two observation periods: from first arrival of individuals in October to the end of December, and from early March until the last birds departed in May. The middle of each observation period tended to be most productive for observing marked birds. Excessive waves or wind, cold temperatures, or other factors occasionally kept the birds from resting on the shoreline and hampered resighting efforts. Since 1997, band codes were read during 184 d of resighting effort at Isle au Haut and 18 d at adjacent islands, and seasonal effort ranged from 17 to 25 d.

From these seasonal resighting efforts, capture-recapture histories were compiled of individuals during five fall and spring sampling occasions from 1997 to 2002. The time between resighting efforts from December to early March is defined as the winter season and the time between resighting efforts from late May to early October as the summer season. Based on midpoints of these sighting periods, the winter interval lasted five months (0.42 y) and the summer interval lasted seven months (0.58 y). Seasonal survival estimates were adjusted to account for the unequal winter and summer intervals and all survival probabilities are presented as annual rates for ease of comparisons across analyses. A bird was denoted 'captured' if it was captured or resighted at least once during an observation period, after deleting questionable observations (e.g., recorded as a questionable or difficult read, or sex or leg band was incorrectly reported). Birds originally banded elsewhere were included if they were observed at least once within the study site on Isle au Haut (between Eastern and Western Heads) and the first observation of these individuals was used for the first entry into the capture history array. Once an individual was observed in the Isle au Haut study site, any observations at adjacent islands in the Isle au Haut region were included in the individual capture-recapture histories.

The data set used for the construction of models was based on 282 Harlequin Ducks banded or observed in the Isle au Haut study site between 1997 and 2002. By partitioning the resighting data, three separate survival analyses were conducted. A seasonal analysis, which allowed for simultaneous survival comparisons between summer and winter seasons, included resighting information on 203 adults (66% male, 34% female) and 70 first-winter birds (54% male, 46% female) for both fall and spring resighting occasions. To gain information on seasonal dispersal, two additional analyses were conducted: a fall analysis of 211 adults (62% male, 38% female) and 20 first winter birds (75% male, 25% female) that included only those birds captured or observed during the fall at Isle au Haut and a spring analysis of 180 adults (64% male, 36% female) and 62 first winter birds (52% male, 48% female) that included only those birds captured or observed during the spring at Isle au Haut. The separate spring and fall analyses were conducted to gain additional information on seasonal dispersal by comparing survival rates between these two analyses. Because very little resighting effort was conducted during the spring of 1998, the seasonal analysis was based on birds released between spring 1998 and spring 2002.

Apparent survival (φ) and resighting probabilities (p) was estimated from banding and resighting data using capture-mark-recapture models originally developed by Cormack (1964), Jolly (1965), and Seber (1965) following the analysis methodology outlined in Anderson and Burnham (1999). Program MARK (White and Burnham 1999) was used for conducting bootstrap goodness-of-fit tests, to obtain point estimates and confidence intervals for age and sex specific survival rates, and calculate weighted averages of survival probabilities among all models considered. Lack of model fit based on bootstrap goodness-of-fit tests was investigated using goodness-of-fit component tests in program RELEASE.

A set of biologically plausible models was constructed to examine variation in resighting and annual survival rates relative to sex, age, and season (Lebreton *et al.* 1992; Burnham and Anderson 1998; Anderson and Burnham 1999). Time-dependent models were not considered because of the number of additional parameters needed and small sample sizes. To select the most appropriate model for estimating survival and related parameters, Akaike's Information Criterion, adjusted for small sample size and overdispersion, was used ($QAIC_c$; Burnham and Anderson 1998). The models with $\Delta QAIC_c$ values, calculated by rescaling to a minimum relative $QAIC_c$ value of zero, <1 to 2 were considered to be the best approximating models. Model selection uncertainty was accounted for by deriving weighted estimates of survival parameters using model weighting procedures. Normalized Akaike weights (Burnham and Anderson 1998) were calculated for each model to provide an index of relative plausibility for all models considered.

Model selection began by first examining the fit of the most general seasonal, sex, and age specific model using a bootstrap goodness of fit test based on 100 simulations (Cooch and White 2003) to ensure that data met the model assumptions of independence of fates and identity of rates among individuals (Lebreton *et al.* 1992). To estimate the variance inflation factor ($\hat{c}$), the actual deviance of the global model was divided by the averaged deviances from 100 bootstrap simulations and model fit was adjusted for any overdispersion (Cooch and White 2003).

Local movements of individuals within a winter were monitored by marking 17 adult (59% male, 41% female) and seven first winter birds (71% male, 29% female) with nasal disks at Squeaker Cove on Isle au Haut (Fig. 1) during November of 1998 and recording the locations where these individuals were observed throughout the winter until departure the following spring. Observations were made regularly throughout the Isle au Haut study area until birds departed in April or May. In addition, occasional searches were made for these birds on islands adjacent to Isle au Haut. Nasal disks were attached through the nares with monofilament line and unfortunately these tended to fall off after one year or less.

To monitor dispersal of birds among years, 147 adult (61% male, 39% female) and 40 first winter birds (65% male, 35% female) captured and banded at varying distances away from the Isle au Haut study site between spring 1999 and spring 2001 (Fig. 1) were used to examine which birds were observed in the Isle au Haut study site during subsequent winters. Confidence intervals (95%) were used to quantify the magnitude of differences between proportions (Fowler and Cohen 1986).

RESULTS

Apparent Survival and Resighting Probabilities

Analysis using both Spring and Fall Captured Birds. The result of the bootstrap goodness-of-fit test on the global age model that combined both fall and spring resighting data suggested that all individuals, whatever age or capture history, did not have the same probability of capture or survival ($P < 0.01$). Program RELEASE goodness-of-fit tests confirmed this lack of fit for the global model (Test 2 + Test 3: $\chi^2_{41} = 59.97$, $P = 0.03$). Results showed that this model was rejected (although not systematically) for males but not females. For males, there was a greater tendency for test 2.Cm to be significant ($\chi^2_9 = 25.61$, $P = 0.002$), generally diagnostic of temporary emigration. Because birds were resighted by reading band codes at a distance and birds were rarely recaptured, disturbance was minimal and trap effects were unlikely. Males also showed some evidence of poor fit for test 3.Sr ($\chi^2_7 = 12.46$, $P = 0.09$) and test 3.Sm ($\chi^2_6 = 11.46$, $P = 0.07$), suggesting slight age or seasonal dispersal effects. Females conformed to the assumptions of the starting model as shown by test 2.Cm (χ^2_6 < 0.001, P > 0.99), test 3.Sr (χ^2_7 = 5.42, P = 0.61), and test 3.Sm (χ^2_6 = 5.02, P = 0.54). Because extra binomial variation was detected ($\hat{c}$ = 1.47), the standard errors of each parameter estimate were adjusted and model selection was based on a quasi-likelihood corrected version of Akaike' Information Criterion.

The most parsimonious model (Table 1) indicated that adult females during the summer season and young males and females during their first winter had lower survival (0.62 ± 0.06; 95% CI: 0.51-0.73) than adult males during both the summer and winter intervals and young birds during their second summer (0.80 ± 0.03; 0.74-0.85). This model was not greatly supported over other competing models (Table 1), and differences in apparent survival probabilities among sex and age classes were less evident based on averaging results across models (Table 2). Apparent survival probabilities were lowest during the winter season for young birds, and were lowest during the summer season for adults, especially adult females, although all confidence intervals overlapped. The probability of resighting males and females during the fall resighting period on Isle au Haut did not differ among all top models;

Table 1. Summary of competing models used to estimate seasonal (both spring and fall captured birds) and annual (fall captured birds and spring captured birds) survival and resighting rates of Harlequin Ducks wintering at Isle au Haut, Maine, 1997-2002. Only the most parsimonious models ($\Delta QAIC_c$ < 2) are shown.

Model Name	No. of parameters	$\Delta QAIC_c$	$QAIC_c$ weight	QDeviance
Spring and fall captured birds[1]				
$\varphi_{[1121\text{-}1212]}\ p_{[1111\text{-}2211]}$	4	0	0.10	407.28
$\varphi_{[1121\text{-}1313]}\ p_{[1111\text{-}2211]}$	5	0.24	0.09	405.49
$\varphi_{[1122\text{-}1212]}\ p_{[1111\text{-}2211]}$	4	0.52	0.08	407.80
$\varphi_{[1121\text{-}1212]}\ p_{[1111\text{-}2233]}$	5	1.13	0.06	406.38
$\varphi_{[1122\text{-}1212]}\ p_{[1111\text{-}2233]}$	5	1.65	0.04	406.91
$\varphi_{[1121\text{-}1314]}\ p_{[1111\text{-}2233]}$	6	1.74	0.04	404.97
$\varphi_{[1121\text{-}1313]}\ p_{[1111\text{-}2233]}$	6	1.80	0.04	405.03
$\varphi_{[1232\text{-}1313]}\ p_{[1111\text{-}2211]}$	5	1.98	0.04	407.23
Fall captured birds[2]				
$\varphi_{[1231]}\ p_{[1123]}$	6	0	0.22	56.46
$\varphi_{[1223]}\ p_{[1123]}$	6	1.47	0.11	57.93
$\varphi_{[1232]}\ p_{[1123]}$	6	1.48	0.10	55.88
$\varphi_{[1233]}\ p_{[1123]}$	6	1.58	0.10	55.97
$\varphi_{[1233]}\ p_{[1234]}$	7	1.58	0.10	55.97
Spring captured birds[2]				
$\varphi_{[1212]}\ p_{[1111]}$	3	0	0.06	92.61
$\varphi_{[1212]}\ p_{[1122]}$	4	0.15	0.06	90.72
$\varphi_{[1211]}\ p_{[1122]}$	4	0.56	0.05	91.13
$\varphi_{[1211]}\ p_{[1111]}$	3	1.26	0.03	93.87
$\varphi_{[1212]}\ p_{[1211]}$	4	1.42	0.03	91.99
$\varphi_{[1111]}\ p_{[1122]}$	3	1.44	0.03	94.05
$\varphi_{[1111]}\ p_{[1111]}$	2	1.55	0.03	96.18
$\varphi_{[1231]}\ p_{[1122]}$	5	1.61	0.03	90.14
$\varphi_{[1232]}\ p_{[1122]}$	5	1.62	0.03	90.15
$\varphi_{[1213]}\ p_{[1122]}$	5	1.70	0.03	90.23
$\varphi_{[1211]}\ p_{[1123]}$	4	1.77	0.02	90.30
$\varphi_{[1213]}\ p_{[1111]}$	4	1.92	0.02	92.50
$\varphi_{[1232]}\ p_{[1111]}$	4	1.99	0.02	92.57

[1]Model notation codes for seasonal, sex, and age effects with two sets of numbers for φ (summer interval-winter interval) and p (fall occasion-spring occasion) with each four-digit placeholder representing adult male, juvenile male, adult female, and juvenile female respectively; identical numbers within φ or p indicate no effect.

[2]Model notation sex and age effects with four numbers with each placeholder representing adult male, juvenile male, adult female, and juvenile female respectively; identical numbers within φ or p indicate no effect.

Table 2. Akaike weighted averages of seasonal and annual survival and resighting rates of Harlequin Ducks wintering at Isle au Haut, Maine, 1997-2002. Apparent survival and resighting rates (±SE) were calculated as weighted averages across all models to account for model selection uncertainty. Unconditional 95% C.I. are presented below survival estimates. All survival rates, even in the seasonal analysis, are presented as annual rates for ease of comparisons.

	Adults		Young	
Season	Males	Females	Males	Females
Spring and fall captured birds				
Survival (φ)				
Summer	0.79 ± 0.03 (0.71–0.85)	0.65 ± 0.05 (0.52-0.76)	0.79 ± 0.04 (0.70-0.86)	0.76 ± 0.04 (0.60-0.86)
Winter	0.80 ± 0.03 (0.72-0.87)	0.79 ± 0.04 (0.68-0.87)	0.57 ± 0.13 (0.20-0.88)	0.52 ± 0.12 (0.14-0.88)
Resighting (*p*)				
Fall	0.79 ± 0.02 (0.74-0.84)	0.79 ± 0.02 (0.74-0.84)	0.79 ± 0.02 (0.74-0.84)	0.79 ± 0.02 (0.74-0.84)
Spring	0.62 ± 0.04 (0.54-0.69)	0.81 ± 0.03 (0.73-0.87)	0.62 ± 0.04 (0.54-0.69)	0.81 ± 0.03 (0.71-0.88)
Fall captured birds				
Survival (φ)				
Annual	0.86 ± 0.03 (0.78–0.91)	0.66 ± 0.04 (0.57-0.74)	0.48 ± 0.13 (0.21-0.76)	0.52 ± 0.15 (0.19-0.84)
Resighting (*p*)				
Annual	0.76 ± 0.04 (0.67-0.83)	0.94 ± 0.04 (0.79-0.98)	0.74 ± 0.10 (0.48-0.90)	0.09 ± 0.02 (<0.01-0.83)
Spring captured birds				
Survival (φ)				
Annual	0.72 ± 0.03 (0.65–0.79)	0.71 ± 0.03 (0.64-0.78)	0.88 ± 0.08 (0.52-0.98)	0.80 ± 0.06 (0.57-0.92)
Resighting (*p*)				
Annual	0.77 ± 0.04 (0.66-0.85)	0.82 ± 0.04 (0.70-0.91)	0.75 ± 0.07 (0.57-0.87)	0.84 ± 0.06 (0.65-0.94)

however, females had greater resighting probabilities than males during the spring. Although sample sizes for young birds were low, especially for first winter females, young males and young females had similar resighting probabilities as adults during fall and spring field work.

Analysis using Fall Captured Birds. The results of the goodness-of-fit tests on the fully time-dependent CJS model considering only fall resighting data since the fall of 1997 suggested independence of fates and identity of rates among individuals (P = 0.38). There was no evidence of overdispersion ($\hat{c}$ = 0.94) so the standard errors were not adjusted.

Considering only fall captures and observations of birds, annual survival probabilities showed sex and age related differences (Table 1). The most parsimonious model, having twice the support over the next competing model, indicated that adult males had higher apparent survival probabilities across winter and summer seasons (0.86 ± 0.03; 0.79-0.91) than adult females (0.67 ± 0.04; 0.58-0.74) and young birds (0.45 ± 0.14; 0.21-0.71). Adult females had higher resighting rates (0.94 ±

0.04; 0.81-0.99) than adult and juvenile males (0.76 ± 0.04; 0.67-0.83). Only three young females were captured and marked before the fall of 1999 and only one of these was observed after initial marking, resulting in an extremely low resighting rate (<0.001). Akaike weighted averages of survival and resighting probabilities, which accounts for model selection uncertainty, also support these differences (Table 2).

Analysis using Spring Captured Birds. The results of the goodness-of-fit tests on the fully time-dependent CJS model considering only spring resighting data suggests independence of fates and identity of rates among individuals (P = 0.51). Because extra binomial variation was detected ($\hat{c}$ = 1.26), the standard errors of each parameter estimate were adjusted.

Considering only spring captures and observations of birds, annual survival probabilities showed no sex or age related effects when assessed across winter and summer seasons (Table 1). The most parsimonious model indicated that adults had lower apparent survival probabilities (0.72 ± 0.03; 0.65-0.77) than young birds (0.87 ± 0.07; 0.67-0.96). Because this model was not greatly supported over other competing models, including a model with a constant survival probability across all groups (Table 1), model averages suggested no sex or age related differences in apparent survival probabilities (Table 2). Resighting probabilities were similar among all sex and age classes (Table 2).

Local Movements

Of 187 Harlequin Ducks banded from 2 to 10 km away from the Isle au Haut study site, 26% were observed at Isle au Haut in subsequent winters (Table 3). Fewer adult females (2%) than adult males (18%) moved 5 to 10 km from their original banding location to be observed in the Isle au Haut study area during subsequent winters. Although sample sizes for young birds were small, a greater proportion of first winter males (42%) than adult females (14%) banded ≥2 km away from the study area were observed in subsequent years in the study area.

Of 24 birds marked with nasal disks at Isle au Haut during November of 1998, 22 were observed at least once in the Isle au Haut region before spring migration. The maximum distance between resighting locations among individuals was not sex or age specific, although sample sizes were small throughout. Of seven adult females marked, all were observed later in the season in the study region. Maximum distance between resighting locations averaged 2.7 ± 0.1 km (95% CI: 0.7-4.7) based on an average of 29 resightings per bird (range = 3-59). Of ten adult males marked, only one bird was not observed later in the season in the study region, although this bird was observed back at Isle au Haut the following winter. Maximum distance between resighting locations for

Table 3. Age- and sex-specific movement probabilities (±1 SE, 95% in parentheses) of Harlequin Ducks originally banded on islands adjacent to Isle au Haut that were observed or recaptured in the Isle au Haut study area in subsequent years. Total number banded for each age class is listed as the sample size.

	Moved 2 km		Moved 5-10 km		
	N	Proportion	N	Proportion	Overall proportion observed in area
Adult male	16	0.81 ± 0.10 (0.61-1.00)	73	0.18 ± 0.05 (0.09-0.27)	0.29 ± 0.05 (0.20-0.38)
Young male	11	0.82 ± 0.12 (0.58-1.00)	15	0.13 ± 0.09 (0-0.31)	0.42 ± 0.10 (0.23-0.61)
Adult female	17	0.41 ± 0.12 (0.17-0.65)	41	0.02 ± 0.02 (0-0.06)	0.14 ± 0.05 (0.05-0.23)
Young female	4	0.50 ± 0.29 (0-1.00)	10	0.10 ± 0.10 (0-0.30)	0.21 ± 0.11 (0-0.43)
Total	48	0.65 ± 0.07 (0.51-0.79)	139	0.12 ± 0.03 (0.07-0.17)	0.26 ± 0.03 (0.20-0.32)

adult males averaged 2.6 ± 0.1 km (95% CI: 1.5-3.7) based on an average of 18 observations per bird (range = 0-53). Of five young males marked, all were observed later in the season in the study region. Maximum distance between resighting locations averaged 4.8 ± 1.3 km (95% CI: 1.3-8.4) based on an average of four observations per bird (range = 1-10). Two young females were marked, and only one was observed in the study region. This bird traveled 2.4 km between most distant resighting locations based on five observations between November and February.

DISCUSSION

Analysis of resighting data of a marked population of Harlequin Ducks wintering at Isle au Haut confirmed that apparent survival rates differed between adult males and females. Adult females had a slightly lower apparent survival probability during the summer season compared to the winter, whereas adult males showed no differences between these seasons. Survival during the winter was similar for adult males and females. Annual survival estimates based on a subset of fall-captured birds also indicated lower survival rates for adult females. This lower annual survival rate of adult females compared to adult males is consistent with the male-biased sex ratio recently observed in the Isle au Haut area (Mittelhauser *et al.* 2002) and may be related to female mortality during the nesting season in Labrador and Québec (Heath *et al.* 2001; Brodeur *et al.* 2008b). These results are consistent with observations of this species in western North America. Cooke *et al.* (2000) reported no differences in winter survival probabilities of adult male and female Harlequin Ducks in British Columbia, however, lower survival probabilities of females than males during the summer season was associated with increased predation risks to the female during incubation and brood rearing.

It is unusual for survival in the first year of life to be as high as in older birds (Dobson 1990) and apparently holds for male Harlequin Ducks. Because of small sample sizes for first winter females, results were not conclusive. Annual survival rates of first winter males were lower than for adult males based on a subset of fall-captured birds. In a seasonal analysis that allowed survival rates to differ between summer and winter months, this difference was not detected, although first year males had slightly lower survival rates than adults during their first winter. This is consistent with results in western North America where survival of young males is lower than adult males and likely reflects both greater dispersal and higher mortality (Cooke *et al.* 2000; Regehr 2003).

Mortality and permanent emigration are confounded in estimates of survival (Lebreton *et al.* 1992) and local movements of Harlequin Ducks may be significant (Regehr *et al.* 2001; Regehr 2003). An attempt to reduce the effects of permanent emigration in this study was made by searching for banded birds at locations up to 10 km away from the Isle au Haut study site and including these observations in the individual capture histories. Although the study was not designed to model movement as a separate parameter in the analysis, some insights into permanent emigration of adults by comparing annual survival rates derived from analyses based on fall banded or spring banded birds was gained. Annual survival rates for adults should be similar between these two analyses in the absence of permanent movements of birds out of the study area after banding. Survival probabilities of adult females were similar between these two analyses, but annual survival of adult males captured in April was lower than annual survival of fall captured adult males. This suggests that adult males captured in April in the study area disappear from the study area more than adult males captured in November. Adult males in spring at Isle au Haut may represent spring dispersal of unpaired males searching for mates (Robertson *et al.* 2000) or individuals from other wintering sites gathering before spring migration.

Age and sex related differences in local winter movements of birds among years were detected, although sample sizes were small. Of 187 birds marked at sites from 2 to 10 km away from Isle au Haut, adult and first winter males dispersed greater distances and more were observed at Isle au Haut during subsequent winters than adult females. Few first winter females were marked, thus results were inconclusive for this group. This is consistent with results for this species in western North America where first-winter birds have been known to disperse up to 48 km between September and February (Lanctot *et al.* 1999; Esler *et al.* 2000; Regehr 2003) and both young males and unpaired adult males move over greater distances than females within a 5.5 km stretch of rocky shoreline (Robertson *et al.* 2000).

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LITERATURE CITED

Anderson, D. R. and K. P. Burnham. 1999. Understanding information criteria for selection among capture-recapture or ring recovery models. Bird Study 46: 14-21.

Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. Ecological Applications 5: 618-631.

Bennetts, R. E., V. J. Dreitz, W. M. Kitchens, J. E. Hines and J. D. Nichols. 1999. Annual survival of Snail Kites in Florida: radio telemetry versus capture-resighting data. Auk 116: 435-447.

Brodeur, S., G. H. Mittelhauser, J.-P. L. Savard, P. Thomas, R. D. Titman and D. Comeau. 2008a. Capture methods for migrating, wintering, and molting sea ducks. Waterbirds 31 (Special Publication 2): 133-137.

Brodeur, S., J.-P. L. Savard, M. Robert, A. Bourget, G. Fitzgerald and R. D. Titman. 2008b. Abundance and movements of Harlequin Ducks breeding on rivers of the Gaspé Peninsula, Québec. Waterbirds 31 (Special Publication 2): 122-129.

Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference: a Practical Information Theoretic Approach. Springer-Verlag, New York.

Cooch, E. and G. C. White. 2003. MARK: a gentle introduction. Available: http://www.biol.sfu.ca/cmr/mark, accessed August 2003.

Cooke, F., G. J. Robertson, C. M. Smith, R. I. Goudie and W. S. Boyd. 2000. Survival, emigration and winter population structure of Harlequin Ducks. Condor 102: 137-144.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51: 429-438.

DeSante, D. F. 1995. Suggestions for future directions for studies of marked migratory landbirds from the perspective of a practitioner in population management and conservation. Journal of Applied Statistics 22: 949-965.

Dobson, A. P. 1990. Survival rates and their relationship to life-history traits in some common British birds. Current Ornithology 7: 115-146.

Esler, D., J. A. Schmutz, R. L. Jarvis and D. M. Mulcahy. 2000. Winter survival of adult female Harlequin Ducks in relation to history of contamination by the Exxon Valdez oil spill. Journal of Wildlife Management 64: 839-847.

Fowler, J. and L. Cohen. 1986. Statistics for Ornithologists. BTO Guide 22, British Trust for Ornithology, United Kingdom.

Goudie, R. I. 1991. The status of the Harlequin Duck (*Histrionicus histrionicus*) in eastern North America. Unpublished report to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa.

Goudie, R. I., S. Brault, B. Conant, A. V. Kondratyev, M. R. Petersen and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. Transactions of the North American Wildlife and Natural Resource Conference 59: 27-49.

Green, R. E. 1999. Applications of large-scale studies of demographic rates to bird conservation. Bird Study 46: 279-288.

Heath, J. P., G. Goodyear and J. Brazil. 2001. Observation of a Golden Eagle, *Aquila chrysaetos*, attack on a Harlequin Duck, *Histrionicus histrionicus*, in northern Labrador. Canadian Field-Naturalist 115: 515-516.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247.

Lanctot, R., B. Goatcher, K. Scribner, S. Talbot, B. Pierson, D. Esler and D. Zwiefelhofer. 1999. Harlequin Duck recovery from the Exxon Valdez oil spill: a population genetics perspective. Auk 116: 781-791.

Lebreton, J.-D. and J. Clobert. 1991. Bird population dynamics, management, and conservation: the role of mathematical modeling. Pages 105-125 *in* Bird Population Studies: Relevance to Conservation and Management (C. M. Perrins, J.-D Lebreton G. J. M Hirons, Eds.). Oxford University Press, Oxford.

Lebreton, J.-D., K. P. Burnham, J. Clobert and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.

Likens, G. E. (Ed.). 1989. Long-term Studies in Ecology. Springer-Verlag, Berlin.

Mather, D. D. and D. Esler. 1999. Evaluation of bursal depth as an indicator of age class of Harlequin Ducks. Journal of Field Ornithology 70: 200-205.

Mertz, D. B. 1971. Life history phenomena in increasing and decreasing populations. Pages 361-399 *in* Statistical Ecology, volume 2 (G. P. Patil, E. C. Pielou and W. E. Waters, Eds.). Pennsylvania State University Press, University Park, Pennsylvania.

Mittelhauser, G. H. 2000. The winter ecology of Harlequin Ducks in coastal Maine. MSc thesis, University of Maine, Orono.

Mittelhauser, G. H., J. B. Drury and P. O. Corr. 2002. Harlequin Ducks (*Histrionicus histrionicus*) in Maine, 1950-1999. Northeastern Naturalist 9: 163-182.

Newton, I. 1998. Population Limitations in Birds. Academic Press, New York.

Nichols, J. D. 1992. Capture-recapture models: using marked animals to study population dynamics. Bioscience 42: 94-102.

Nichols, J. D., G. L. Hensler and P. W. Sykes, Jr. 1980. Demography of the Everglade Kite: implications for population management. Ecological Modeling 9: 215-232.

Peterson, S. R. and R. S. Ellarson. 1978. Bursae, reproductive structures, and scapular color in wintering female Oldsquaws. Auk 95: 115-121.

Pollock, K. H., J. D. Nichols, C. Brownie and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 100: 1-87.

Regehr, H. M. 2003. Movement patterns and population structure of Harlequin Ducks wintering in the Strait of Georgia, British Columbia. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia.

Regehr, H. M., C. M. Smith, B. Arquilla and F. Cooke. 2001. Post-fledging broods of migratory Harlequin Ducks accompany females to wintering areas. Condor 103: 408-412.

Robertson, G. J., F. Cooke, R. I. Goudie and W. S. Boyd. 2000. Spacing patterns, mating systems, and winter philopatry in Harlequin Ducks. Auk 117: 299-307.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52: 249-259.

Smith, C., F. Cooke and R. I. Goudie. 1998. Ageing Harlequin Duck *Histrionicus histrionicus* drakes using plumage characteristics. Wildfowl 49: 245-248.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120-138.