Site fidelity and the demographic implications of winter movements by a migratory bird, the harlequin duck *Histrionicus histrionicus*

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Understanding the degree of demographic connectivity among population segments is increasingly recognized as central to the fields of population ecology and conservation biology. However, delineating discrete population units has proven challenging, particularly for migratory birds as they move through their annual cycle. In this study, radio telemetry was used to assess movement rates among habitats by harlequin ducks *Histrionicus histrionicus* during the non-breeding season in Prince William Sound, Alaska. A total of 434 females were outfitted with radio transmitters over six years of data collection, and their signals tracked by aircraft. Using a spatially nested design, it was determined that 75% of radioed females remained in the bay or coastline area where they were originally trapped, 94% remained on the same island or mainland region of Prince William Sound where they began the winter period, and 98% remained within the 4500 km^2 study area as a whole. Home range analyses corroborated these findings, indicating that the scale of individual movements was small, with 95% kernel home range estimates averaging only 11.5 ± 2.2 km^2. A simple demographic model, which incorporated estimates for population size, survival, and movement rates, was used to infer the degree of independence among population segments. Immigrant females were found to contribute little to population numbers in most areas, accounting for only 4% of the adult female population at a scale of approximately 100 km^2. These results have important implications for the scale of conservation action for the species and demonstrate that winter movements can have a strong influence local population dynamics.

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Movement and site fidelity patterns of individuals have important implications for the structure and dynamics of wildlife populations. High rates of movement promote gene flow and genetic homogenization, whereas site fidelity increases population genetic structure (Slatkin 1987). Rates of movement and site fidelity also determine the extent to which population segments are maintained by internal, or *in situ*, production, and what extent by immigration (Nichols and Pollock 1990). The exchange of individuals can link demographic rates across areas, whereas site fidelity produces regions wherein subpopulations have independent demographic processes (Ranta et al. 1997, Stacey et al. 1997). By determining the geographic origin of individuals and estimating the frequency of exchange between population segments, inferences can be drawn about the degree to which individuals in different locations are genetically and/or demographically connected. This knowledge is critical for delineating discrete subpopulations and managing them for sustainability (Dizon et al. 1992, Moritz 1994).

Migration poses additional challenges for understanding population structure because migratory species use a variety of geographically disparate habitats throughout their annual cycle. Migratory movements often confound efforts to delineate distinct population

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units (Esler 2000, Webster et al. 2002) and predict the consequences of habitat loss or modification during a given portion of the annual cycle (Sutherland 1998). To date, much attention has focused on use of genetic markers to delineate subpopulations for conservation purposes (Avise 2000), however, exclusive focus on genetic criteria for the delineation of management units has proven inadequate for many migratory bird species. Although numerous migratory species exhibit a high degree of site fidelity at specific stages of their annual cycle (Greenwood 1980, Anderson et al. 1992, Robertson and Cooke 1999), genetic differentiation has rarely been identified on a fine scale (Webster et al. 2002).

The absence of significant population genetic structure should not, however, be interpreted to indicate that populations lack biologically relevant spatial structuring (Paetkau 1999). There are several important questions to consider when delineating populations, including: how much movement is necessary to link demographic rates among local populations, does the existence of genetic panmixia preclude significant demographic structuring, and what is the relevance of site faithful behavior by individuals at various stages during their annual cycle? It is important to note that while a few immigrants per generation may be sufficient to homogenize subpopulations genetically (Slatkin 1985); similarly low rates of exchange might not be expected to have a significant demographic effect. Furthermore, demography is often of greater immediate importance than population genetics for determining minimum viable sizes of wildlife populations (Lande 1988), and for long-lived species in particular, differential survival and productivity among population segments can have important population dynamic consequences.

In order to derive movement probabilities at the spatial and temporal scales necessary to delineate demographically independent subpopulations, direct measurements of site fidelity and movement rates are necessary (Nichols and Kaiser 1999, Bennetts et al. 2001). Historically, inferences about movement and site fidelity have been restricted by limitations of data and methodology, however, advances in the use of satellite and radio telemetry have improved our ability to measure movement rates and evaluate population structure directly (Millspaugh and Marzluff 2001). Investigations of avian movement have most often focused on breeding individuals, in part due to the direct implications for measuring reproductive rates (e.g. Lindberg et al. 1998). However, for many species the winter period encompasses a large portion of the annual cycle and can be a considerable source of annual mortality (Marra et al. 1998). Further, in cases where pair bonds are formed on wintering areas and young recruit into the same local populations as their parents, wintering site fidelity can be a major determinant of population structure (Robertson et al. 2000). Thus, definition of

winter population structure and appropriately-scaled management of winter population units is highly relevant from a conservation perspective.

In this paper we consider the demographic implications of wintering site fidelity and movements by female harlequin ducks *Histrionicus histrionicus* in Prince William Sound, Alaska (60°N, 148°W). The research was part of a program initiated following the 1989 *Exxon Valdez* oil spill to evaluate the recovery process of harlequin duck populations. Previous studies have indicated that full recovery was likely constrained by a combination of chronic exposure to oil and the relatively long time frames needed for natural demographic processes to replace birds removed as a result of the spill (Esler et al. 2000a, 2002, Peterson et al. 2003). Our objective in this paper is to address the latter point in a theoretical context, using data on within-winter movements obtained from radio marked females to evaluate the degree of demographic structure at different spatial scales.

Harlequin ducks make a good study system for addressing the implications of winter site fidelity by a migratory bird for several reasons. Pacific harlequin ducks are short distant migrants that spend a vast majority of their annual cycle on wintering areas and do not undertake extensive molt or spring staging migrations (Robertson and Goudie 1999, but see Brodeur et al. 2002). Both males and females are known to exhibit extremely high rates of between-year site fidelity to specific molting/wintering areas (Cooke et al. 2000, Robertson et al. 2000, Regehr 2003a, Iverson et al. 2004), and pair bond formation occurs during winter (Bengtson 1972, Gowans et al. 1997, Robertson et al. 2000). Additionally, harlequin ducks are long-lived, exhibit low annual productivity, and there is some evidence that post-fledglings accompany their mothers to coastal areas during winter (Regehr et al. 2001). These traits make the survival and movement patterns of breeding age females particularly influential from a population dynamic perspective. Finally, due the large number of individuals that were radio tracked over an extensive study area, and an extensive body of previous research documenting population-specific distributions (Esler et al. 2000b), between year homing rates (Iverson et al. 2004), and survival rates (Esler et al. 2000a, Peterson et al. 2003), we believe this study is uniquely suited to address the demographic implications of individual patterns of site fidelity and movement by a migratory bird.

Methods

Capture and marking

Movement data were collected during six different winters (1995–1996 through 1997–1998 and 2000–2001

through 2002–2003) in Prince William Sound, Alaska (Fig. 1). During the first three winters (hereafter 1995, 1996 and 1997) female harlequin ducks were captured during wing molt (1 August to 17 September) by herding flightless birds into funnel traps using sea kayaks. During the last three winters (hereafter 2000, 2001 and 2002), floating mist nets were used to capture flighted birds (31 October to 2 December). Females were targeted because population sex ratios are male-biased and female survival and movement were considered of paramount importance from a population dynamic standpoint.

All birds were transported by skiff to a larger vessel where U.S. Fish and Wildlife Service bands were affixed, morphological measurements taken, and radio transmitters implanted. Sex determinations were made based on plumage characteristics and cloacal examination and age class was determined by probing bursal depth (Mather and Esler 1999). Radio transmitters were implanted surgically by experienced veterinarians using procedures described by Mulcahy and Esler (1999). During the first three years of the study only adult (after second year, ASY) females were implanted, whereas during the final three years second year (SY) and hatch year (HY) females also were implanted. The transmitters weighed 17.5 g (<3% average female body mass) and had external antennae (Holohil, Carp, Ontario, Canada). Each transmitter was equipped with a sensor that doubled pulse rate after a period of >12 hr of immobility to indicate mortality. Only birds that survived a 14-day post-surgery censor period (approximately 97% of all implanted birds) were included in analyses. Literature suggests implants are less disruptive than external methods for wild waterfowl (Esler et al. 2000c).

Radio tracking

Radio marked females were monitored at approximately weekly intervals from an airplane to determine mortality status and location. In total, over 1500 km of coastline was surveyed within the 4500 km² study area. Monitoring flights began after the first birds were released and continued until the end of March. All frequencies were monitored throughout the winter season, including those for which signals were lost.

During monitoring flights individual birds were located by *site*, which we defined as a bay, inlet, group of islets, or continuous section of coastline bounded by a prominent geographic feature (Fig. 1). Because we were interested in defining the spatial scale of movements, two additional geographic strata were created to evaluate movement probabilities. These were: *coastline sections*, which we defined as groupings of adjacent sites, separated from other coastline sections by >3 km of
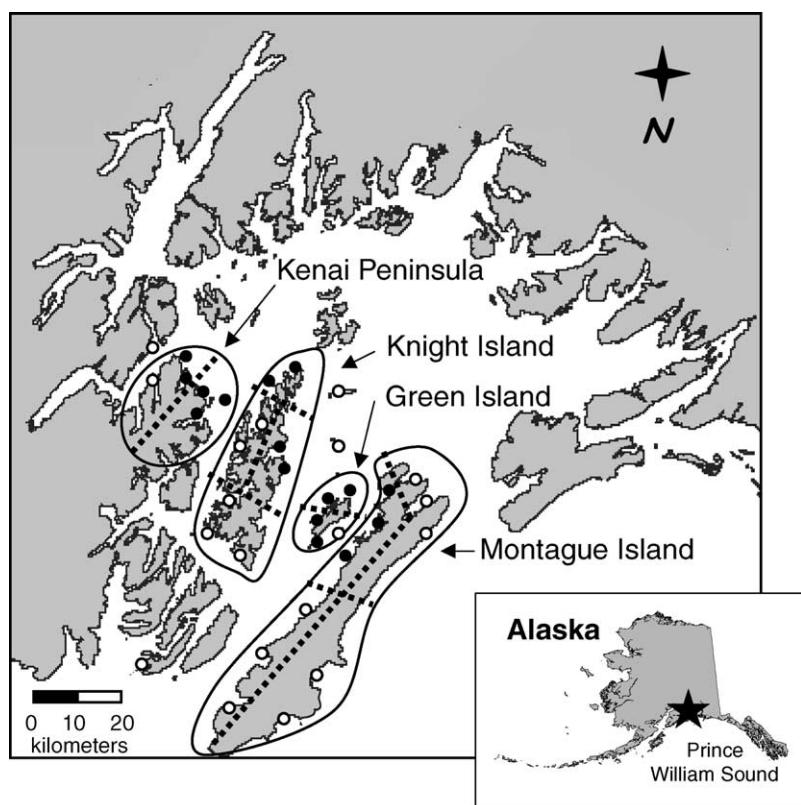
Fig. 1. Map of the study area in Prince William Sound, Alaska. Movement probabilities for radio marked female harlequin ducks were assessed at three different spatial scales: *sites* (indicated by points; black fills denote original capture locations and white fills locations to which birds moved); *coastal sections* (indicated by dashed lines); and *areas* (indicated by encircled areas). Descriptions for spatial scales are given in text.

habitat in which harlequin duck densities approached zero; and *areas*, which were islands or mainland regions separated from other areas by >5 km of open water (Fig. 1). Thus, each bird had a three level geographic strata location (e.g., *site*: Stockdale Harbor; *coastline section*: Northwest Montague Island, *area* Montague Island).

In addition to site locations, exact positions were recorded for a subset of 35 adult females in 1996 and 1997. For these individuals, precise locations were plotted on 1:80,000 marine charts. These records were taken only when weather conditions allowed the location of transmitting birds to be identified, and therefore, were as accurate as the pilot's ability to map them.

Statistical analyses

Three different analytical approaches were used to evaluate the spatial scale and demographic implications of harlequin duck winter movements. The first was designed to estimate the probability that an individual would emigrate from the location in which it had been trapped, and compared rates of site fidelity and movement at the *site*, *coastline section*, and *area* scales. The second quantified individual movements by calculating home ranges and distances traveled between successive observations. The final analysis incorporated spatially explicit transition probabilities among locations into a transition matrix model to evaluate the demographic consequences of the observed rates of movements. The three analyses are described below.

Transition probabilities: Kaplan-Meier analysis
A modified Kaplan-Meier procedure was used to estimate the probability that an individual would remain site faithful during the winter period. The Kaplan-Meier estimator is commonly used in telemetry studies, where the survival function (S[t]) calculates the probability that an arbitrary animal will survive from the beginning of the study to some specified time t (Pollock et al. 1989, Bunck et al. 1995). In our analysis we replaced the survival function with a fidelity function (F[t]) based on recommendations by Bennetts et al. (2001), using location assignments to infer movement probabilities at various spatial scales.

The geographic stratum in which an individual was originally trapped was defined as its reference location, and we considered consecutive observations in any location other than the reference location to be indicative of an emigration event. Emigration events could be detected only at discrete points in time a_1, a_2,...,a_g, therefore, r_1, r_2,...,r_g were defined as the numbers of individuals that could potentially move at these points and e_1, e_2,...,e_g as the number that actually emigrated. The probability of remaining site faithful from time zero

to time a_1 was estimated by $\hat{F}(a_1) = 1 - e_1/r_1$, where e_1/r_1 is the proportion that emigrated during that interval. The probability of remaining site faithful from a_1 to a_2 was $1 - e_2/r_2$, and $\hat{F}(a_2)$ was the product: $(1 - e_1/r_1)(1 - e_2/r_2)$. Thus, the cumulative fidelity function $\hat{F}(a_g)$ could be calculated, such that $\hat{F}(a_g) = (1 - e_1/r_1)(1 - e_2/r_2)\ldots(1 - e_g/r_g)$.

When organizing the data, *a priori* decisions were made to pool records over all six years, code encounter histories using monthly intervals, and permit staggered entry of individuals into the dataset (Pollock et al. 1989, Bunck et al. 1995). These actions were taken to ensure large sample sizes, wherein a minimum of one observation was obtained per individual per month. It was further stipulated that only one emigration event could take place per individual each winter, so the emigration rate would not be overestimated. Additionally, calculations were made to determine the frequency with which individuals returned to their original site after having been categorized as emigrants, as such movements would lead to underestimation of the fidelity function.

The assumptions for unbiased movement rate estimation are similar to those for survival in the Kaplan-Meier framework (Pollock et al. 1989, Esler et al. 2000c). They include: (1) radioed animals are representative of the population of interest, (2) movement probability is independent among individuals, (3) radio-marking does not affect movement during the study period, and (4) censoring of animals for which signals are lost is independent of the fate of those individuals. Little systematic bias was suspected with respect to susceptibility to capture and it was felt that the first two assumptions were met on the basis of capture technique and marking regime. The third assumption was explicitly tested with respect to survival by Esler et al. (2000c), and no effect was detected. The fourth assumption, however, required evaluation, which is described below.

Estimation of the fidelity function using telemetry data must allow for animals being censored due to death, radio failure, or movement outside the study area. Deaths could be identified by mortality signals, and such individuals censored from the dataset without systematic bias. However, overestimation of the fidelity function would result if failed radios could not be distinguished from those which had moved outside the study area. To determine the relative frequency of each event a subset of recaptured females that had been tracked during the winters of 1995 and 1996, and were recaptured the following year with radios still implanted, was used. These birds allowed the radio failure rate to be determined, and by assuming recaptured individuals had remained in the study, the probability of movement outside the study area to be inferred.

Two samples were of interest for making these calculations. The first sample was composed of females tracked during the winters of 1995 and 1996. Radios in

the tracked bird sample fell into one of four possible categories, which summed to $N_{tracked}$. These categories were: (1) S_{in}^+—the radio functioned normally and remained in the study area; (2) S_{in}^-—the radio failed, but remained in the study area; (3) S_{out}^+—the radio functioned normally and left the study area; or (4) S_{out}^-—the radio failed and the left the study area. Independent estimates for S_{in}^-, S_{out}^+, and S_{out}^- could not be made for the tracked bird dataset, because the three conditions were not distinguishable during monitoring flights, however, the sum of the three conditions was known: $(S_{in}^- + S_{out}^+ + S_{out}^-) = N_{tracked} - S_{in}^+$. The second sample was a subset of the first, composed of recaptured birds. There were two conditions of interest in the second sample: (1) $S_{in}^{+\prime}$—recaptured birds with radios that had functioned normally during the previous winter; or (2) $S_{in}^{-\prime}$—recaptured birds with radios that had during failed the previous winter. $S_{out}^{+\prime}$ and $S_{out}^{-\prime}$ were not considered because long distance emigrants were not recaptured.

From these samples the probability that a female harlequin duck moved outside the study area could be estimated using equations 1–3, below:

$$S_{in}^- = [(S_{in}^+)(S_{in}^{-\prime})]/(S_{in}^{+\prime}) \qquad (1)$$

$$S_{out}^+ + S_{out}^- = N_{tracked} - (S_{in}^+ + S_{in}^-) \qquad (2)$$

$$p[S_{out}^{+/-}](S_{out}^+ + S_{out}^-)/N_{tracked}, \qquad (3)$$

where equation (1) uses the proportion of failed radios in the recaptured bird data subset to estimate the number of failed radios, which remained in the study area from the full tracked bird data set, equation (2) estimates the number of long distance emigrants by subtracting the number of birds that remained in the study area from the total number of tracked birds, and equation (3) calculates $p[S_{out}^{+/-}]$, the proportion of females that emigrated from the study area.

Scale of individual movements: kernel home range estimates
Individual home ranges and movement patterns were estimated using geographic information system software (GIS; Arcview, ESRI Inc., Redlands, California). Bird locations were plotted on a digital base map of Prince William Sound and analyzed using the Animal Movements extension for Arcview 3.2 (Hooge and Eichenlaub 1997), with an *a priori* decision made to pool data among years. A number of home range methods were considered, including fixed kernel, minimum convex polygons, and bivariate ellipses. Based on recommendations by Seaman et al. (1999), sample size considerations, and distributions of the data, use of fixed kernels with smoothing selected by least squares cross validation (LSCV; Silverman 1986) was deemed most appropriate for the dataset. We present 95% and 50% kernel home range (khr) areas, which are the two probabilities most commonly used in the literature, with 95% khr estimates

considered to be the area of active use and 50% khr estimates the core area of activity. The average and maximum distances traveled between successive observations also was calculated for each bird.

Kernohan et al. (2001) identified several potential sources of error that can bias home range estimates that we considered prior to our analysis. They included: (1) uneven sampling over distance and truncated dispersal distances through failure to detect long distance movements—which aerial survey methodology and a large study area minimized; (2) induced behavioral changes—which were explicitly tested with respect to survival by Esler et al. (2000c) and shown to have no effect; (3) serial correlation of successive observations—which was controlled for by the frequency of surveys (>5 days between all surveys), and (4) sample size—which was evaluated by regressing the number of locations obtained per individual against its kernel home range size to determine the minimum number of detections per individual required for unbiased home range estimates.

Demographic independence: transition matrix model
The final analysis used a simple matrix modeling approach to consider the effects of movement on the seasonal dynamics of wintering harlequin duck populations. Our objective was to evaluate the relative contributions to population size by site faithful and immigrating females, given observed variations in bird densities, survival rates, and movement probabilities. The analysis focused on the four mainland/island *areas* where female harlequin ducks were trapped: Kenai Peninsula, Knight Island, Green Island, and Montague Island (Fig. 1), which are coded as a–d, respectively, below. The matrix model was restricted to after hatch year (AHY) females, and allowed exchange of individuals among compartments, using the following model structure:

$$\begin{bmatrix} N_a^{t+1} \\ N_b^{t+1} \\ N_c^{t+1} \\ N_d^{t+1} \end{bmatrix} = \begin{bmatrix} \phi_a\psi_{a\to a} & \phi_a\psi_{b\to a} & \phi_a\psi_{c\to a} & \phi_a\psi_{d\to a} \\ \phi_b\psi_{a\to b} & \phi_b\psi_{b\to b} & \phi_b\psi_{c\to b} & \phi_b\psi_{d\to b} \\ \phi_c\psi_{a\to c} & \phi_c\psi_{b\to c} & \phi_c\psi_{c\to c} & \phi_c\psi_{d\to c} \\ \phi_d\psi_{a\to d} & \phi_d\psi_{b\to d} & \phi_d\psi_{c\to d} & \phi_d\psi_{d\to d} \end{bmatrix} \times \begin{bmatrix} N_a^t \\ N_b^t \\ N_c^t \\ N_d^t \end{bmatrix},$$

where N_i represents the number of AHY females in each *area*, t and t+1 are the start and end of the winter period, ϕ_i is the probability of surviving the winter period, and $\psi_{i\to j}$ is a transition probability between any two *areas*.

Parameter estimates for N_i and ϕ_i were obtained using an unpublished Alaska Department of Fish and Game report (Daniel Rosenberg and Michael Petrula), and results from published manuscripts on harlequin duck survival (Esler et al. 2000a) and distributions (Esler et al. 2000b), in Prince William Sound. Spatially explicit transition probabilities among *areas*, $\psi_{i\to j}$, were calculated using the encounter history data described for our Kaplan-Meier analysis. For each bird a starting

area—where it was originally captured, and a final *area*—where it was last detected alive, was recorded. A minimum of three monthly location assignments were required for inclusion in the dataset, with the same decision rules as those described for the Kaplan-Meier analysis used to make location assignments. Cumulative transition probabilities were estimated for each of the 16 putative transitions ($\psi_{a \to a}, \psi_{a \to b}, \psi_{a \to c} \ldots \psi_{d \to d}$) by dividing the number of females making each transition by the total number present. For example, if 50 individuals began the winter period in *area* a, and 40, 7, 2, and 1 of those individuals ended the winter in *areas* a-d respectively, then $\psi_{a \to a} = 0.80$, $\psi_{a \to b} = 0.14$, $\psi_{a \to c} = 0.04$, and $\psi_{a \to d} = 0.02$. Finally, the relative contributions to population size at time $t+1$ by site faithful (p_i) and immigrant (q_i) females were calculated as ($p_i = [(N_i^t)(\phi_i \psi_{i \to i})]/N_i^{t+1}$) and $q_i = (1 - p_i)$, respectively.

Results

Capture, marking and radio tracking

Table 1 presents data on sample sizes, survey date ranges, and the frequency with which female harlequin ducks were detected in aerial surveys. A total of 434 female harlequin ducks were outfitted with radio transmitters over the six years of data collection. Among these, 31 were SY females and 31 were HY females, all of which were marked during the 2000–2002 non-breeding seasons. Detections were made in 35 different *sites* over the course of the study, which ranged in size from 6.2–44.0 km², with a mean of 16.7 ± 1.5 km² (SE). At the *coastline section* scale, detections were grouped into 12 different locations, with mean size $= 42.5 \pm 5.5$ km² (SE), and at the *area* scale there were four locations, with mean size $= 127.5 \pm 39.1$ km² (SE).

Transition probabilities: Kaplan-Meier analysis

At the *site* scale, e_i/r_i, ranged between 0.02 and 0.08, with a cumulative fidelity function estimate for the winter period of $\hat{F}(a_g) = 0.74$ (95% CI: 0.72–0.77). A pulse of movement was evident during November and December (Fig. 2), indicating some post-molt disper-

sion. Movement at the *coastline section* scale occurred roughly half as frequently, with no seasonal movement pulse evident. Monthly e_i/r_i at the *coastline section* scale ranged from 0.01 to 0.04, with $\hat{F}(a_g) = 0.88$ (95% CI: 0.87–0.89). At the *area* scale, movement was infrequent, with e_i/r_i never exceeding 0.02, and $\hat{F}(a_g) = 0.96$ (95% CI: 0.96–0.97; Fig. 2). Fisher exact tests indicated that age-related variation in movement probability was not significant at the *site*, *coastline section*, or *area* scales (P = 0.19, 0.34, 0.58, respectively).

Few individuals moved back to their reference location after having been categorized as emigrants. At the *site* scale, 90 of the 434 radio marked females were detected away from their reference location for consecutive observations at some point during the winter. Among these, 14 subsequently moved back, leading to an underestimation of $\hat{F}(a_g)$ by approximately 3%. At the *coastline section* scale movement back to the reference location occurred 8 times, or in <2% of all cases, and at the *area* scale only a single occurrence was observed. Underestimation of $\hat{F}(a_g)$ due to back migration was partially offset by long distance movement events. In the sample of females tracked during the winters of 1995 and 1996 estimates for $N_{tracked} = 185$, $S_{in}^+ = 122$, and $S_{in}^- + S_{out}^+ + S_{out}^- = 63$ were obtained. In the sample of recaptured birds 33% of radios failed, with estimates for $S_{in}^{+\prime} = 27$ and $S_{in}^{-\prime} = 13$. Using equations 1–3, we estimated $S_{in}^- = 58.7$, $S_{out}^+ + S_{out}^- = 4.3$, and $p[S_{out}^{+/-}] = 0.02$].

After accounting for the underestimation bias that resulted from movements back to the reference location (*site*: 0.03; *coastline section*: 0.02; *area*: <0.01), and the overestimation bias that resulted from movement outside the study area (*site, coastline section,* and *area*: 0.02), corrected estimates for $\hat{F}(a_g)$ at the three scales were 0.75, 0.88, and 0.94, respectively.

Scale of individual movements: kernel home range estimates

95% kernel home range, 50% core area, and estimates for the mean distance traveled between successive observations by adult female harlequin ducks were generally quite small during the winter period (1 October–30 March). Estimation of home range and core area size was restricted to 26 individuals for which ≥ 15 precise

Table 1. Study periods, sample sizes, and the frequency with which female harlequin ducks were detected during aerial surveys.

| Year	Date range	No. females radioed	Age class	No. aerial surveys	Days between surveys ($\pm$SE)	Detections per individual ($\pm$SE)
1995	4 Oct 1995–30 Mar 1996	87	all ASY	21	7.7 ($\pm$0.8)	14.9 ($\pm$0.6)
1996	1 Oct 1996–29 Mar 1997	92	all ASY	24	7.8 ($\pm$0.4)	20.1 ($\pm$0.7)
1997	2 Oct 1997–18 Mar 1998	109	all ASY	23	7.6 ($\pm$0.6)	18.2 ($\pm$0.6)
2000	8 Nov 2000–2 Apr 2001	54	32 ASY, 15 SY, 7 HY	13	12.1 ($\pm$1.9)	9.6 ($\pm$0.5)
2001	19 Nov 2001–31 Mar 2002	49	29 ASY, 9 SY, 11 HY	15	10.3 ($\pm$0.9)	11.2 ($\pm$0.6)
2002	5 Dec 2002–2 Apr 2003	43	22 ASY, 7 SY, 13 HY	13	9.8 ($\pm$2.2)	10.2 ($\pm$0.7)
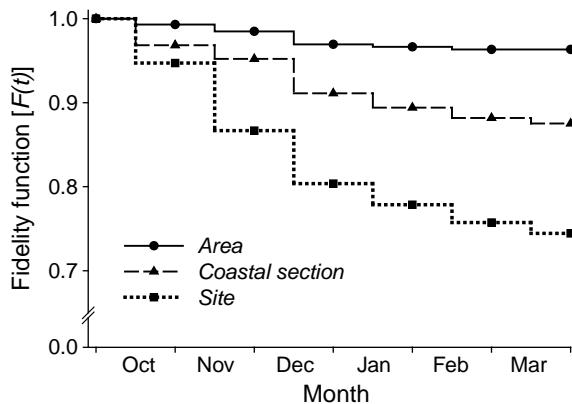
Fig. 2. Winter fidelity function F[t] estimates for radio marked harlequin ducks in Prince William Sound, Alaska, during winters 1995–1997 and 2000–2002, at *site*, *coastal section*, *and area* scales.

locations were obtained. Regression analysis suggested that, at that threshold, the slope of the regression line did not differ from zero, indicating home range size was independent of the number of samples obtained. Mean ($\pm$SE) home range size and core area sizes of 11.5 ($\pm$2.2) km^2 and 1.7 ($\pm$0.3) km^2 were estimated for the two variables, respectively. For these estimates an average of 18.9 ($\pm$0.4) locations were obtained per individual, with surveys conducted 8.9 ($\pm$0.2) days apart.

All 35 radio-marked adult females for which precise location data were collected were used to calculate the range of and mean distance traveled between successive observations. Two of the 35 adult females (6%) made moves which would have been considered emigration events at the *area* scale, with distances ranging from 30 to 40 km. The remainder of detected movements ranged from <0.1 to 9.2 km, and averaged 1.6 ($\pm$0.1) km.

Demographic independence: transition matrix model

Estimates for N_i, as well as measurements of surveyed coastline length, bird densities, and sex/age ratios, for all four *areas* are summarized in Table 2. Winter survival

estimates were obtained from Esler et al. (2000a), wherein mortality rates were shown to be higher in oil affected portions of Prince William Sound (Kenai Peninsula, Knight Island, and Green Island), $\phi_a = \phi_b = \phi_c = 0.78$, than in unaffected portions (Montague Island), $\phi_d = 0.84$. Site fidelity estimates were similar to those obtained using the Kaplan-Meier analysis. The lowest estimate was for Knight Island, $\psi_{b \rightarrow b} = 0.88$ (95% CI: 0.72–0.95), where harlequin duck linear densities were lowest, *HADU density* = 1.5 birds per km. Site fidelity estimates were higher for Kenai Peninsula, $\psi_{a \rightarrow a} = 0.96$ (95% CI: 0.87–0.99), Green Island, $\psi_{c \rightarrow c} = 0.98$ (95% CI: 0.92–1.00), and Montague Island, $\psi_{d \rightarrow d} = 0.97$ (95% CI: 0.93–0.99), where harlequin duck densities were higher, 11.2, 10.8, and 7.5 birds per km, respectively (Fig. 3). As expected, transition rates were higher between adjacent *areas* than more distant ones, with the most frequent transition being from Knight Island to Kenai Peninsula, $\psi_{b \rightarrow a} = 0.09$ (95% CI: 0.03–0.24). Transition rates >0.03 also were evident for Kenai Peninsula to Knight Island, $\psi_{a \rightarrow b} = 0.04$ (95% CI: 0.01–0.13), and Knight Island to Green Island, $\psi_{b \rightarrow c} = 0.03$ (95% CI: 0.00–0.17; Fig. 3).

Incorporation of estimates for N_i, ϕ_i, and $\psi_{i \rightarrow j}$ into the transition matrix model indicated that little mixing existed at the *area* scale during winter (Table 3). For Montague Island we estimated $p_i = 0.98$, meaning that 98% of AHY females present at the end of the winter period had begun the winter there. Estimates for p_i were ≥ 0.96 for Green Island and Kenai Peninsula as well. The only *area* for which immigrant females contributed a considerable portion of the population was Knight Island, where $p_i = 0.83$. An overall estimate of $\bar{p}_i = 0.96 \pm 0.02$ was calculated, weighting *area* estimates by population size.

Discussion

Relatively few studies have been able to empirically address the population level consequences of inter-patch movements at a landscape level (Bowne and Bowers 2004). This deficiency limits our ability to formulate

Table 2. Parameter estimates for harlequin duck densities and total numbers on island/mainland *areas* of Prince William Sound, Alaska. Estimates for N_i are for adult females, and were derived from measures of the length of coastline surveyed, harlequin duck densities along those coastlines, and age/sex ratios within each *area*.

Area	Length of coastline surveyed (km)	Harlequin duck density (birds km^{-1})	Sex ratio[a]	Female age ratio[b]	N_i
Kenai Peninsula	33.6[†]	11.2[†]	1.5[†]	0.14[†]	216
Knight Island	75.7[‡]	1.5[‡]	1.5[†]	0.14[†]	65
Green Island	51.5[†]	10.8[†]	1.5[†]	0.14[†]	319
Montague Island	74.1[‡]	7.5[‡]	1.4[†]	0.12[†]	349

[a]No. of males/No. of females.
[b]No. of HY females/No. of AHY females.
[†]Daniel Rosenberg and Michael Petrula (unpubl. data), winter 1997 survey.
[‡]Esler et al. (2000b), winter surveys 1995–1997.
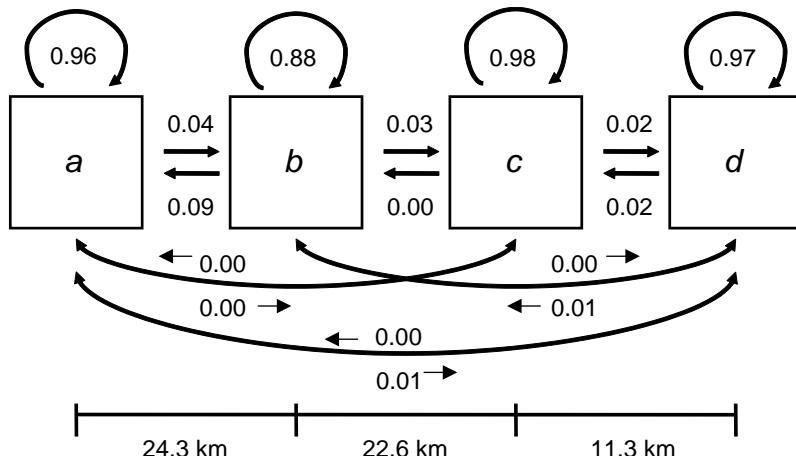
Fig. 3. Transition probabilities among island/mainland *areas* in Prince William Sound, Alaska. Kenai Peninsula, Knight Island, Green Island, and Montague Island are denoted by a–d, respectively. Distances between adjacent areas are given in km.

effective area-specific conservation strategies for wildlife populations. Given the high degree of philopatry exhibited by both male and female harlequin ducks to molting sites in Prince William Sound (Iverson et al. 2004), and the rates of within-winter site fidelity documented in this study, it is clear that spatial structure exists at a fine spatial scale among female harlequin ducks during the non-breeding season. Our data indicate that at the *site* scale (16.7 ± 1.5 km^2), which we defined as distinct bays, inlets, groups of islets, or continuous sections of coastline where female harlequin ducks were captured and released, approximately one in four birds emigrated over the course of the winter period. However, as the scale of reference was increased, exchange of individuals became much less frequent. At the *area* scale (127.5 ± 39.1 km^2), defined as island or mainland regions separated from other *areas* by >5 km of open water, the movement rate was approximately one in twenty, and only about 2% of all females emigrated from the 4500 km^2 study area as a whole. Home range analyses corroborated these findings, with the mean adult female winter home range among the smallest documented for any migratory bird species.

High rates of site fidelity are common among members of several waterfowl taxa, particularly swans, geese, and sea ducks (Anderson et al. 1992, Robertson and Cooke 1999). Postulated advantages of winter site fidelity include knowledge of local food resources, experience with the movements and habits of predators, and advantages conferred when acquiring mates (Robertson and Cooke 1999). The benefits of site fidelity tend to be strongest when environments are stable and predictable, which appears to be the case for harlequin ducks during the non-breeding season, when they forage intertidally on relatively abundant benthic marine invertebrates (Esler et al. 2002). Surveys designed to estimate harlequin duck densities and investigate habitat association patterns corroborate this finding, with harlequin duck numbers tending to be highly consistent across replicate surveys within and between years in Prince William Sound (Esler et al. 2000b) and elsewhere, including the Strait of Georgia, British Columbia (S. Iverson unpubl. data). We show that high rates of site fidelity by individuals can have important population level consequences as well. Using a transition matrix model to determine the relative contributions of site faithful and immigrant females for population numbers, we found that, in most cases, immigrant females contributed little to overall population size. For three of the four island/mainland *areas* studied: Montague Island, Green Island, and the Kenai Peninsula, immigrant females accounted for $<4\%$ of the adult female population. However, movement rates were notably higher on Knight Island, where 17% of the adult female population was composed of new arrivals by winter's end, suggesting some plasticity in habitat selection.

With respect to seasonal and age-related variation in winter movement, some patterns were apparent. We documented a previously unknown pulse in movement at the *site* scale during November and December, suggesting that the correspondence between molting and wintering areas is not absolute. However this trend was not evident at higher spatial scales, and we interpret the movements primarily as a spreading out of females after the completion of wing molt. In the Strait of Georgia significant seasonal movements have been documented by harlequin ducks taking advantage of abundant, but ephemeral Pacific herring *Clupea pallasi* spawn (Rodway et al. 2003). While such movements suggest the species has flexibility in habitat use patterns during winter, similar movements were not observed in Prince William Sound during the November–March monitoring period. Age-related variation in movement probability was not apparent in our study at the *site*, *coastal section*, or *area* scales. This finding also differs from previous reports in coastal British Columbia, where Regehr (2003b) found that radio marked juvenile harlequin ducks had a greater movement probability than adults during winter,

although sample sizes were very small in the British Columbia study.

For species like the harlequin duck, with high rates of site fidelity and subsequent reliance on intrinsic demographic properties to maintain population numbers, perturbations to local habitats may have important, long lasting population level effects. For example, previous research has speculated that harlequin duck population recovery in areas affected by the 1989 *Exxon Valdez* oil spill was slowed by the high degree of demographic structure in south central Alaska (Esler et al. 2000a, 2002). This study confirms that, in the absence of immigration by adult females, full recovery of harlequin duck numbers in oiled areas was likely constrained by the relatively long time frames required for recruitment to replace birds removed as a result of the spill, even after immediate spill effects had ended (Esler et al. 2002). Managers charged with conserving migratory species are often interested in knowing how fluctuations in numbers are related to changes in local habitat conditions (Nichols and Pollock 1990). To answer these questions it is imperative to know the degree to which aggregations in disparate geographic areas are interconnected and how affiliations to specific locations affect the dynamics of populations.

Finally, these movement patterns raise an important issue relating to the relative importance of demographic and genetic population structure when attempting to delineate management units for migratory bird populations. Molecular studies have indicated that genetic structure is absent within harlequin duck populations at a regional scale, and limited even at a continental scale (Kim Scribner unpubl. data, Lanctot et al. 1999). However, it would be erroneous to infer from these genetic data that demographic population structure is also absent. It is imperative that the degree of demographic separation between putative populations be considered when adopting management strategies, because in many cases it is the demographic rather than genetic consequences of rarity or isolation that pose the most imminent threat to species or subpopulations (Lande 1988). There is no one-to-one correspondence between demography and genetics and while a few immigrants per generation may result in genetic panmixia (Slatkin 1985), similarly low rates of exchange would not link subpopulations demographically. We suggest greater emphasis on collecting and interpreting movement and fidelity data in the context of demography, which will provide a broader temporal and spatial perspective that will shed light on the biology of organisms, and improve the prospects for their conservation.

References

Anderson, M. G., Rhymer, J. M. and Rohwer, F. C. 1992. Philopatry, dispersal and the genetic structure of waterfowl populations. – In: Batt, B. D. J., Afton, A. D., Ankney, C. D., Johnson, D. H., Kadlec, J. A. and Krapu, G. L. (eds). Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, pp. 365–395.

Avise, J. C. 2000. Phylogeography: the history and formation of species. – Harvard University Press, Cambridge.

Bennetts, R. E., Nichols, J. D., Lebreton, J.-D., Pradel, R., Hines, J. E. and Kitchens, W. M.. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. – In: Clobert, J. E., Danchin, E., Dhondt, A. A. and Nichols, J. D (eds). Dispersal: causes, consequences and mechanisms of dispersal at the individual, population and community level. Oxford University Press, pp, Oxford, pp. 3–17.

Bowne, D. R. and Bowers, M. A. 2004. Interpatch movements in spatially structured populations: a literature review. – Landscape Ecol. 19: 1–20.

Bengtson, S. A. 1972. Breeding ecology of the harlequin duck *Histrionicus histrionicus* L. in Iceland. – Ornis Scand. 3: 25–43.

Brodeur, S., Savard, J.-P. L., Robert, M., Laporte, P., Lamothe, P., Titman, R. D., Marchand, S., Gilliland, S. and Fitzgerald, G. 2002. Harlequin duck *Histrionicus histrionicus* population structure in eastern Nearctic. – J. Avian Biol. 33: 127–137.

Bunck, C. M., Chen, C. L. and Pollock, K. H. 1995. Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. – J. Wildl. Manage. 59: 790–794.

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

Dizon, A. E., Lockyer, C., Perrin, W. F., Demaster, D. P. and Sisson, J. 1992. Rethinking the stock concept: a phylogeographic approach. – Conserv. Biol. 6: 24–36.

Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. – Conserv. Biol. 14: 366–372.

Esler, D., Schmutz, J. A., Jarvis, R. L. and Mulcahy, D. M. 2000a. Winter survival of adult female harlequin ducks in relation to history of contamination by the *Exxon Valdez* oil spill. – J. Wildl. Manage. 64: 839–847.

Esler, D., Bowman, T. D., Dean, T. A., O'Clair, C. E., Jewett, S. C. and McDonald, L. L. 2000b. Correlates of harlequin duck densities during winter in Prince William Sound, Alaska. – Condor 102: 920–926.

Esler, D., Mulcahy, D. M. and Jarvis, R. L. 2000c. Testing assumptions for unbiased estimation of survival of radio-marked harlequin ducks. – J. Wildl. Manage. 64: 591–598.

Esler, D., Bowman, T. D., Trust, K. A., Ballachey, B. E., Dean, T. A., Jewett, S. C. and O'Clair, C. E. 2002. Harlequin duck population recovery following the 'Exxon Valdez' oil spill: progress, process and constraints. – Mar. Ecol. Prog. Ser. 241: 271–286.

Greenwood, J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140–1162.

Gowans, B., Robertson, G. J. and Cooke, F. 1997. Behaviour and chronology of pair formation by harlequin ducks *Histrionicus histrionicus*. – Wildfowl 48: 135–146.

Hooge, P. N. and Eichenlaub, B. 1997. Animal movement extension to Arcview Version 1.1. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage.

Iverson, S. A., Esler, D. and Rizzolo, D. J. 2004. Winter philopatry of harlequin ducks in Prince William Sound, Alaska. – Condor 106: 711–715.

Kernohan, B. J., Gitzen, R. A. and Millspaugh, J. J. 2001. Analysis of animal space use and movements. – In: Millspaugh, J. J. and Marzuff, J. M. (eds). Radio tracking and animal populations. Academic Press, pp, San Diego, pp. 126–168.

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

Lande, R. 1988. Genetics and demography in biological conservation. – Science 241: 1455–1460.

Lindberg, M. S., Sedinger, J. S., Derksen, D. V. and Rockwell, R. F. 1998. Natal and breeding philopatry in a black brant (Branta bernicla nigricans) metapopulation. – Ecology 79: 1839–1904.

Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – Science 282: 1884–1886.

Mather, D. D. and Esler, D. 1999. Evaluation of bursal depth as and indicator of age class of harlequin ducks. – J. Field Ornithol. 70: 200–205.

Millspaugh, J. J. and Marzluff, J. M. 2001. Radio tracking and animal populations. – Academic Press, San Diego.

Moritz, C. 1994. Defining 'evolutionarily significant unit' for conservation. – Trends Ecol. Evol. 9: 373–375.

Mulcahy, D. M. and Esler, D. 1999. Surgical and immediate post release mortality of harlequin ducks (Histrionicus histrionicus) implanted with abdominal radio transmitters with percutaneous antennae. – J. Zoo Wildl. Med. 30: 397–401.

Nichols, J. D. and Kaiser, A. 1999. Quantitative studies of bird movement: a methodological review. – Bird Study (Supplement) 46: 289–298.

Nichols, J. D. and Pollock, K. H. 1990. Separate estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. – Ecology 71: 21–26.

Paetkau, D. 1999. Using genetics to identify intraspecific conservation units: a critique of current methods. – Conserv. Biol. 13: 1507–1509.

Peterson, C. H., Rice, S. D., Short, J. W., Esler, D., Bodkin, J. L., Ballachey, B. E. and Irons, D. B. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. – Science 302: 2082–2086.

Pollock, K. H., Winterstein, S. R., Bunck, C. M. and Curtis, P. D. 1989. Survival analysis in telemetry studies: the staggered entry design. – J. Wildl. Manage. 53: 7–15.

Ranta, E., Kaitala, V. and Lundberg, P. 1997. The spatial dimension in population fluctuations. – Science 278: 1621–1623.

Regehr, H. M. 2003a. Movement patterns and population structure of harlequin ducks wintering in the Strait of Georgia, British Columbia. – PhD. Thesis, Simon Fraser University, Burnaby, British Columbia.

Regehr, H. M. 2003b. Survival and movement of postfledging juvenile harlequin ducks. – Wilson Bull. 115: 423–430.

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

Robertson, G. J. and Cooke, F. 1999. Winter philopatry in migratory waterfowl. – Auk 116: 20–34.

Robertson, G. J. and Goudie, R. I. 1999. Harlequin duck (Histrionicus histrionicus). – In: Poole, A. and Gill, F. (eds). The Birds of North America, No. 466. The Birds of North America, Inc, Philadelphia.

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

Rodway, M. S, Regehr, H. M., Ashley, J., Clarkson, P. V., Goudie, R. I., Hay, D. E., Smith, C. M. and Wright, K. G. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. – Can. J. Zool. 81: 504–514.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. and Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. – J. Wildl. Manage. 63: 739–747.

Silverman, B. W. 1986. Density estimation for statistics and data analysis, 1st edition. – Chapman and Hall, London.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. – Evolution 39: 53–65.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. – Science 236: 787–792.

Stacey, P. B., Johnson, V. A. and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. – In: Hanski, I. A. and Gilpin, M. E. (eds). Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, pp. 267–291.

Sutherland, W. J. 1998. The effect of local change in habitat quality on populations of migratory species. – J. Appl. Ecol. 35: 418–421.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. 2002. Links between worlds: unraveling migratory connectivity. – Trends Ecol. Evol. 17: 76–82.