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WINTER PHILOPATRY OF HARLEQUIN DUCKS IN PRINCE WILLIAM SOUND, ALASKA

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Abstract. We used capture-mark-recapture data to assess winter philopatry by Harlequin Ducks (*Histrionicus histrionicus*) in Prince William Sound, Alaska, during winters 1995–1997 and 2000–2001. Philopatry was quantified using homing rates, which were estimated as the proportion of birds recaptured at their original site out of all recaptured birds. Between-year homing rates of 0.95 (95% CI: 0.87–1.00) and 1.00 (0.92–1.00) were estimated for females and males, respectively, at three locations on Montague Island. Similar homing rates were measured in western Prince William Sound, where estimates were 0.92 (0.80–0.98) for females and 0.96 (0.79–1.00) for males, with a scale of detected movements for all recapture birds ranging from 3–52 km. Our results indicate that wintering aggregations may be demographically independent at a much finer spatial scale than genetic data indicate, and that conservation efforts should recognize this degree of demographic separation among population segments.

Key words: demographic independence, Harlequin Duck, *Histrionicus histrionicus*, homing rate, seaduck, site fidelity, winter philopatry.

Filopatría Invernal de *Histrionicus histrionicus* en Prince William Sound, Alaska

Resumen. Utilizamos datos de marcaje y recaptura para determinar la filopatría de *Histrionicus histrionicus* en Prince William Sound, Alaska, durante los inviernos de 1995–1997 y 2000–2001. La filopatría fue

cuantificada utilizando la tasa de retorno, estimada a partir de la proporción del total de aves capturadas que se recapturaron en su sitio original. Las tasas de retorno entre años, estimadas en tres localidades en la isla Montague, fueron de 0.95 (95% IC: 0.87–1.00) y 1.00 (0.92–1.00) para hembras y machos, respectivamente. En Prince William Sound se midieron tasas de retorno similares, donde las estimaciones fueron 0.92 (0.80–0.98) para las hembras y 0.96 (0.79–1.00) para los machos, y para todas las aves recapturadas se detectó una escala de movimiento entre 3 y 52 km. Nuestros resultados indican que las agrupaciones de invierno pueden ser demográficamente independientes a una escala espacial mucho más fina de lo que los datos genéticos indican, y que los esfuerzos de conservación deberían reconocer este grado de separación demográfica entre segmentos de poblaciones.

Breeding philopatry among North American waterfowl is typically female biased, and much attention has focused on the social and genetic consequences of this particular sex-biased dispersal pattern (Greenwood 1980, Rockwell and Barrowclough 1987, Rohwer and Anderson 1988). To date, comparatively little attention has been given to the consequences of philopatric behavior during other stages of the annual cycle. However, for most species the winter period encompasses a majority of the annual cycle and can be a considerable source of annual mortality. Furthermore, because most migratory waterfowl form pair bonds on wintering areas, the strength of individual affiliations to specific wintering grounds plays an important role in determining the genetic and demographic structure of populations (Robertson and Cooke 1999).

For example, geese and swans (tribe Anserini) typically exhibit high levels of philopatry to both breeding

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and wintering areas. As a result, their populations tend to be among the most genetically and demographically substructured of any migratory bird (Robertson and Cooke 1999), with geographically distinct subpopulations often forming at one or both stages. A classic example is that of the Canada Goose (*Branta canadensis*), for which 12 or more subspecies have been recognized (Van Wagner and Baker 1990, Scribner et al. 2003). In contrast, dabbling duck species (tribe Anatini) exhibit extremely low rates of winter philopatry, particularly among males (Robertson and Cooke 1999). Anatini populations tend to be much more genetically panmictic and demographically interconnected despite high rates of breeding site fidelity (Anderson et al. 1992). The Northern Pintail (*Anas acuta*) offers an extreme example, as they have very low rates of winter philopatry (Fedynich et al. 1989, Hestbeck 1993), with almost no genetic population structuring even at a continental scale (Cronin et al. 1996), and demographic rates that are thought to be correlated across broad geographic regions (Hestbeck 1993).

Seaducks (tribe Mergini) provide an interesting exception to the general pattern of low winter philopatry and male-biased dispersal characteristic of other ducks. Several seaduck species exhibit a high degree of philopatry to nonbreeding areas (Alison 1974, Spurr and Milne 1976, Limpert 1980, Savard 1985, Breault and Savard 1999, Robertson et al. 2000, Flint et al. 2000, Pearce et al. 2004), which makes them a potentially useful group for resolving the ecological mechanisms underlying philopatry, as well as deducing its genetic and demographic consequences. Furthermore, because of conservation concerns brought on by declines in seaduck population numbers (U.S. Fish and Wildlife Service 1993, Goudie et al. 1994), understanding how affinities to specific locations during the annual cycle may act to constrain population growth rates is extremely important.

In this paper we assess philopatry of Harlequin Ducks (*Histrionicus histrionicus*) wintering in Prince William Sound, Alaska (60°N, 148°W). Previous research on the wintering ecology of Harlequin Ducks has indicated that wintering habitats are stable and predictable (Esler, Bowman et al. 2000), and that within-winter site fidelity to specific stretches of coastline is high (Robertson et al. 1999, Cooke et al. 2000). Furthermore, Harlequin Ducks form pairs on wintering areas (Bengston 1972, Gowans et al. 1997, Robertson et al. 1998), re-pairing appears to be common (Smith et al. 2000), and there is evidence that postfledging broods are led to wintering areas by females (Regehr et al. 2001). While much research has been conducted to illuminate these characteristics, formal estimates of winter return rate are few. Winter philopatry has been studied in coastal British Columbia (Robertson et al. 1999, Cooke et al. 2000, Regehr 2003), but no studies have determined whether these patterns are consistent across the species' range. Thus, our objective was to quantify rates of winter philopatry by adult Harlequin Ducks in Prince William Sound, Alaska, and to consider the genetic, demographic, and conservation implications of the observed rates of movement.

METHODS

FIELD METHODS

Harlequin Ducks were captured during wing molt by herding flightless birds into funnel traps using sea kayaks. Unlike most waterfowl, Harlequin Ducks undergo wing molt on the same marine areas where they winter (Robertson and Goudie 1999, although more extensive molt migrations have been documented in the eastern North American population, Brodeur et al. 2002). Therefore, inferences drawn from molting birds are applicable to both molting and wintering stages. Three different trapping locations were used along northwestern Montague Island: (1) Stockdale Harbor, (2) Port Chalmers (3) West Montague (Fig. 1). Distances between sites ranged from 8.4 to 16.1 km. Capture sessions were conducted during five molt seasons: 1995, 1996, 1997, 2000, and 2001. Capture dates ranged from 1 August to 17 September in 1995–1997 and 6 to 12 September in 2000–2001. These capture dates encompassed the periods of peak wing molt by adult females. Adult males typically undergo wing molt before females, and were not targeted during 2000–2001. All captured individuals were marked with U.S. Fish and Wildlife Service aluminum bands. Sex determinations were based on plumage characteristics and cloacal examination. Age class was determined by probing bursal depth (Mather and Esler 1999). Our analyses were restricted to after-hatch-year birds because waterfowl do not undergo a wing molt during their first autumn and, as a result, hatch-year birds were not susceptible to our trapping methodology.

STATISTICAL ANALYSIS

We quantified philopatry by estimating homing rate, which is the probability an individual will return to the study area, given that it is alive. In studies that use multiple capture areas, homing rate can be estimated directly as the ratio of birds recaptured on their original capture site to those recaptured elsewhere (Robertson and Cooke 1999). This ratio considers only individuals alive at both time t and time $t + 1$, thus eliminating survival as a confounding variable. The method assumes that recapture probabilities are similar at all study sites, and will tend to overestimate the true homing rate if recapture effort outside the study area is low. We estimated homing rates and 95% CI for Harlequin Ducks banded and subsequently recaptured at the three capture sites on Montague Island. Contingency tests were used to assess variation in homing rate with respect to sex, trapping location, and year of recapture.

To complement this fine-scale analysis, we used supplementary data from Harlequin Ducks captured in western Prince William Sound, to estimate the number of birds that moved outside the Montague Island study area (a requirement of unbiased homing-rate estimation), and to quantify the range of distances moved. The additional capture sites were located on the Kenai Peninsula (Foul Bay, Main Bay, Crafton Island), Knight Island (Bay of Isles), and Green Island (North Green, West Green, South Green; Fig. 1). All seven of the additional trapping sites were located within the Exxon Valdez oil spill zone, and ranged in distance from 8.0–62.4 km from Montague Island. Capture protocols were identical to those described above, and

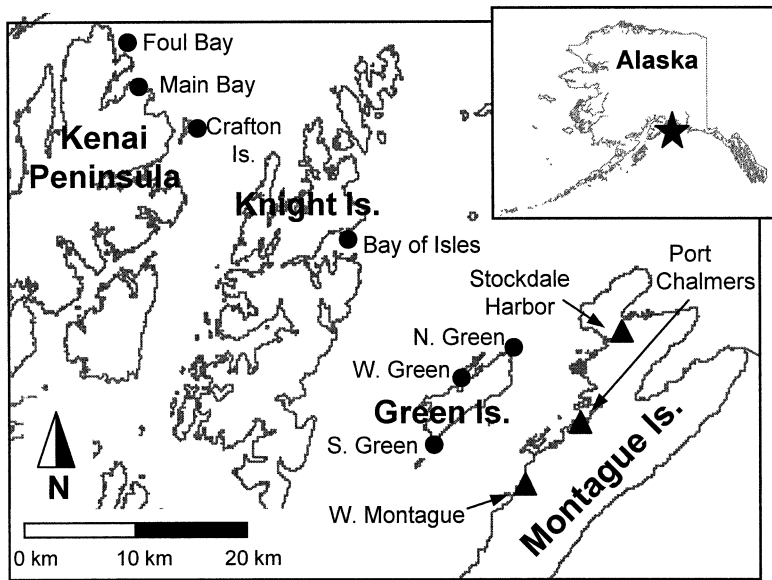


FIGURE 1. Map of the Harlequin Duck study area in Prince William Sound, Alaska. Triangles denote primary capture locations on Montague Island; circles denote supplementary capture sites on the Kenai Peninsula, Knight Island, and Green Island.

took place over the same date ranges as at Montague Island during 1995, 1996, and 1997.

RESULTS

In total, 799 captures were made during the 5 years of trapping on Montague Island, of which 348 were males and 451 were females. Among these, 102 were recaptures (28 males and 74 females). Homing rates to the three Montague Island capture locations were high, with estimates of 0.95 (95% CI: 0.87–1.00) and 1.00 (0.93–1.00) for recaptured females and males, respectively. Homing rate did not differ according to sex (Ta-

ble 1; Fisher exact test, $P = 0.57$), location ($\chi^2_2 = 3.0$, $P = 0.22$), or year ($\chi^2_3 = 3.0$, $P = 0.39$).

An additional 676 after-hatch-year birds, 334 male and 342 female, were captured at the seven trapping locations in western Prince William Sound, including 73 recaptures. Homing rates in western Prince William Sound were estimated at 0.92 ($n = 49$; 95% CI: 0.80–0.98) and 0.96 ($n = 24$; 0.79–1.00), for females and males, respectively. None of the birds originally banded on Montague Island during 1995 or 1996 were recaptured in outlying areas during 1996 or 1997. In the combined datasets, a grand total of 175 after-hatch-year Harlequin Ducks were recaptured, nine of which were at sites other than their original location. The maximum dispersal distance for any bird was 51.9 km, by a female dispersing from Foul Bay on the Kenai Peninsula to the north end of Green Island. The remaining eight recaptures in which movement was detected included one male and seven females, and ranged in distance from 3.1 to 8.9 km.

DISCUSSION

Harlequin Ducks in Prince William Sound, Alaska, exhibited a high degree of philopatry to specific wintering areas. The homing rates calculated in this study were >90% for both sexes, making them among the highest documented of any waterfowl species (Anderson et al. 1992, Robertson and Cooke 1999). The longest recorded dispersal distance was 52 km. Our results corroborate previous work on Harlequin Duck site fidelity and winter philopatry in coastal British Columbia (Robertson and Cooke 1999, Cooke et al. 2000, Robertson et al. 2000, Regehr 2003), and add to the growing body of evidence suggesting that strong affil-

TABLE 1. Homing rates for adult Harlequin Ducks captured in Prince William Sound, Alaska, during winter. Homing rate was calculated as the number of individuals recaptured at their original banding location divided by the total number recaptured. See Figure 1 for locations of main and supplementary capture sites.

	Number captured	Number recaptured	Homing rate	95% CI
Montague Island capture sites ^a				
Males	348	28	1.00	0.92–1.00
Females	451	74	0.95	0.87–1.00
Supplementary capture sites ^b				
Males	334	24	0.96	0.79–1.00
Females	342	49	0.92	0.80–0.98

^a Operated 1995–1997 and 2000–2001.

^b Operated 1995–1997.

iations to nonbreeding areas are common among sea-duck species (Alison 1974, Spurr and Milne 1976, Limpert 1980, Savard 1985, Breault and Savard 1999, Robertson et al. 1999, Flint et al. 2000).

Several ecological mechanisms have been proposed to select for philopatric behavior by wintering waterfowl. Primary among these are knowledge of local food resources, experience with the movements and habits of predators, and advantages conferred when acquiring mates (Robertson and Cooke 1999). Seaducks have high rates of annual survival, relative to other duck species (Livezey 1995), and hence may acquire considerable experience at particular locations. In addition, some seaducks form pairs during fall and early winter, and there is evidence that pairs reunite from one year to the next (Harlequin Ducks: Gowans et al. 1997, Robertson et al. 1998, Smith et al. 2000; Common Eiders [*Somateria mollissima*]: Spurr and Milne 1976, Tiedemann et al. 1999; Barrow's Goldeneye [*Bucephala islandica*]: Savard 1985). High rates of winter philopatry might result from selective pressure to facilitate re-pairing (Robertson et al. 1998). Finally, environmental variability is thought to be linked to philopatry, with philopatry being more likely in birds that use temporally consistent habitats (Flint et al. 2000). The intertidal prey resources Harlequin Ducks rely on are stable and predictable (Esler, Bowman et al. 2000, Esler et al. 2002), and this dependability likely contributes to the fine-scale homing that we observed.

Molecular data have indicated that genetic structure is evident among wintering populations of Harlequin Ducks only on a continental level, with regional populations being effectively panmictic (Lancot et al. 1999, K. Scribner et al., unpubl. data). However, our results suggest that from a demographic standpoint wintering subpopulations are independent on a much finer scale. We believe it is important to recognize that a lack of genetic differentiation does not necessarily imply demographic panmixia. Population genetic structure reflects a complex interplay between current and historical population size and movements (Avisé 2000), and while only a few immigrants per generation can homogenize the genetic variance within a population, similarly low exchange rates would not necessarily link them demographically. Given the homing rates that we estimated and the movements we observed, demographically important levels of isolation may occur within Harlequin Duck populations at a scale of tens to hundreds of kilometers.

The primary implication of philopatry by a migratory species from a conservation standpoint is that habitat perturbations occurring in a location where seasonal affiliations are strong may have long-lasting effects on local populations. From this perspective, actions such as the recent downlisting of the Eastern population of Harlequin Ducks from Endangered to Special Concern status in Canada (Thomas and Robert 2001) appear less well supported. The species was downlisted because new survey data identified a larger, previously unknown wintering population in Greenland. However, the possibility that the populations in eastern North America and Greenland are demographically isolated should be considered. Along the same lines, previous research has shown that recovery of

Harlequin Duck populations in areas affected by the 1989 *Exxon Valdez* oil spill was slowed by the high degree of demographic structure among population segments in south-central Alaska (Esler, Schmutz et al. 2000, Esler et al. 2002). In the absence of immigration of adult females from surrounding populations, full recovery of Harlequin Duck populations in oiled areas was likely delayed, even after immediate spill effects had ended (Esler et al. 2002). We conclude that efforts must be made to identify and manage populations primarily according to their degree of demographic separation, basing area-specific management actions on the demographic viability of population segments throughout the annual cycle.

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