

Movement Rates and Distances of Wintering Harlequin Ducks: Implications for Population Structure

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Movement Rates and Distances of Wintering Harlequin Ducks: Implications for Population Structure

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Abstract. Population structure of Harlequin Ducks (*Histrionicus histrionicus*) wintering in the Strait of Georgia, British Columbia, was evaluated by generating age, sex, paired status and distance-specific movement rates with multi-stratum mark-recapture analyses, and age and sex-specific movement distances through surveys of marked individuals. Annual movement distances and rates did not differ by sex, but only 2-4% of adults (third year and after-third year) compared to 7-11% of subadults (hatch year and second year) moved among locations per year and distance moved decreased with age. Adults were highly site faithful regardless of sex and paired status. The stepping stone gene flow model estimated the among population component of genetic variance (F_{ST}) at 0.005, suggesting that winter movement by subadults was sufficient to explain results of previous genetic analyses that detected no fine scale genetic structuring. Seasonal movement rates indicated that at least 95% of individuals molt and winter in the same location, and that annual aggregation at Pacific Herring (*Clupea pallasii*) spawning sites facilitates demographic mixing and gene flow. Low annual movement rates (0.001) between the northern and southern Strait of Georgia and dispersal by both sexes suggest that a metapopulation distribution may function within the Pacific Coast range, which is relevant to the geographic scale of management. Movement rates and distances suggest that subadult survival rates are particularly vulnerable to underestimation. Received 28 February 2010, accepted 3 June 2010.

Key words. age, dispersal distances, Harlequin Ducks, *Histrionicus histrionicus*, movement rates, paired status, population structure.

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The relationship between spatial distribution and population structure can be complex for species that have separate breeding and wintering distributions, especially when mates are chosen at wintering areas (Cooke et al. 1995; Scribner et al. 2001). Many waterfowl species migrate between breeding and wintering areas, and many form pair bonds during winter (Rohwer and Anderson 1988; Rodway 2007a). For species with a dispersed winter distribution and winter pairing, genetic differentiation could potentially develop among wintering populations regardless of whether or not they contain individuals from multiple breeding areas. If individuals pair at wintering areas, and if no genetic exchange outside of the pair bond occurs at breeding areas, then the distribution, movement and pairing choices of individuals at wintering areas would be important to genetic population structure (Robertson and Cooke 1999), whereas the location of breeding areas and geographical mixing of conspecifics there would be unimportant. Demographic population structure, on the other hand, needs to be defined for breeding and wintering areas separately (Esler 2000). Knowledge of genetic and demographic connections between groups of wintering birds is important for informed conservation decisions (Moritz 1994; Esler et al. 2006).

For Harlequin Ducks (*Histrionicus histrionicus*), genetic studies of wintering populations in western North America have detected no fine scale genetic structuring (Lanctot et al. 1999). However, family migration from inland breeding to coastal wintering areas (Regehr et al. 2001), high levels of philopatry

identified as paired or unpaired during behavioral observations conducted for other purposes (Rodway 2007b), and 2) if unpaired records were from 1 March or later.

Multi-stratum Models

Multi-stratum models in the program MARK (White and Burnham 1999) were used to estimate movement rates. Multi-stratum models permit estimation of transition probabilities (ψ_{ij}) in addition to estimates of survival (S) and sighting rates (p) by separating the joint probability of surviving and making a transition between two states (ψ_{ij}) into a survival component (S_i^r , the probability that an animal survives in location r from time i to time $i + 1$) and a transition component (ψ_{ij}^{rs} , the probability that an animal alive in state r at time i is in state s at time $i + 1$, given that the animal is alive at time $i + 1$). In this study, transitions between states represent movement among geographic locations.

Multi-stratum models, $T_w(r)$ models (2 an 0.28 0 TDic locations.) 1 Tf 3.4091 0 TD 0 Tw (i)Tj /F1 1 an a57 1 1 an 239

were used to estimate the variance inflation factor, c , by comparing observed frequencies of encounter histories to 1,000 simulated values generated by model parameters and the binomial distribution (Roff and Bentzen 1989). QAIC

SOG, the two highest ranking models (of 23) received similar support ($QAIC_c = 0.62$) and both included an age effect in the estimation of movement rates (Table 2). Models without an age effect on movement received virtually no support. Model-averaged movement rates among locations ranged from 0.072 to 0.105 per year for subadults, and from 0.022 to 0.037 per year for adults, and were best parameterized as equal regardless of the direction of movement (Fig. 3).

Paired Status. The most highly parameterized model among the four highest ranking models with similar $QAIC_c$ values (Table 2) estimated separate movement rates for each paired status group in the northern SOG: 0.000 ± 0.000 for paired males, 0.050 ± 0.055 for unpaired males, and 0.018 ± 0.017 for paired females, for all locations combined. Similarly, 5% ($N = 39$) of unpaired males, 5% ($N = 138$) of paired females, and 0% ($N = 51$) of paired males (G_2

monious model (of 21), which included only distance in the estimation of movement rates, received six times the support of the second highest ranking model which included the effect of sex in addition to distance (Table 2). Movement rates ranged from 5 in 100 individuals per year to 1 in 1,000 individuals per year (Table 3). Sex-specific movement rates generated by the second highest ranking model indicated that point estimates for males were slightly higher than those for females for all distance classes (Table 3).

Age. When models with and without age effects on annual movement rates were compared between locations within the northern

Table 4. Model selection statistics for effects of sex and age on seasonal movement rates (molt to winter and winter to spawn seasons) for Harlequin Ducks in the northern Strait of Georgia, 1994-2000. Effects of time (t), sex (s), location (l), age (a) and season (s) are indicated for survival (s), sighting (p) and movement (m) rates; the */* notation separates time effects (time dependence [t*], or time held constant [t~]) for subadult and adult age classes, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction, and indicates that the location effect on survival rates are specific to the subadult age class. Highest ranking models up to QAIC_c

ation are higher than the annual rates used. F_{ST} estimates from gene flow models are typically considered rough order of magnitude only due to simplifying model assumptions, potential for sampling error in movement statistics, and limited study time scale (Rockwell and Barrowclough 1987; Slatkin 1987). Sensitivity analyses concluded that F_{ST} was robust to potential error in factors used in the estimation of N_e and m_{adj} .

F_{ST} increased substantially when the number of colonies was increased to roughly approximate the entire western species range ($F_{ST} = 0.11$). Birds typically have low F_{ST} values, likely due to their extensive dispersal capabilities (Evans 1987). However, Kimura and Weiss (1964) demonstrated that populations diverge rapidly with increasing number of steps in a single dimension, and Barrowclough (1980) found that the one species most likely to show any genetic differentiation was the Silver Gull (*Larus novaehollandiae*) with a one-dimensional distribution

along the Australian coastline. Similarly, genetic differences could develop in Harlequin Ducks because they are distributed along an extensive stretch of the western coastline of North America. Some indication of genetic structuring at this scale has been reported (Goatcher et al. 1999).

The lack of detectable difference in movement by sex was unexpected. Although the observed extreme philopatry (100%) of paired males likely reflects requirements of maintaining a multi-year pair bond and its value to the male (Savard 1985; Robertson and Cooke 1999), dispersal of unpaired males was expected to drive an overall difference between the sexes. Rather, unpaired males also showed high rates of philopatry (95%). Unpaired males may choose to court familiar females persistently rather than search for mates widely, especially because ecological benefits of philopatry and costs of dispersal are likely (Greenwood 1987; Anderson et al. 1992). Development of liai-

sons to improve chances of future pairing has been suggested for males in other waterfowl species (Anderson 1985; McKinney 1992). Courtship of paired females by unpaired males is common in Harlequin Ducks

sites by individuals from different locations would lead to a change in wintering location by at least one partner, and therefore, pending successful reproduction, to gene flow. In fact, higher annual movement rates for subadults than adults may partly reflect the fact that half of subadult females pair in spring, whereas most mature females pair during winter (Rodway 2007b). Further, the potential for demographic independence, which implies no correlation in vital rates (Hanski 1991), is reduced if normally separate populations mix at some time. In the northern SOG herring spawn likely is an important late winter food source (Rodway and Cooke 2002) that may benefit survival, and thus demographic independence is unlikely. Where no such seasonal aggregation occurs, demographic independence is more likely (e.g. Esler et al. 2006; Iverson and Esler 2006). At the scale of the entire study area, low but quantifiable movement rates between the northern and southern SOG (Table 3), little mixing between these regions during the spawn season (Rodway et al. 2003a), and dispersal by both sexes (Aulsebrook 1995; Regehr 2003) suggests that a metapopulation distribution (MacArthur and Wilson 1967; Lande 1988) may function for Harlequin Ducks between the north and south ends of the study area and at a larger scale within the Pacific Coast of North America.

Conservation concern exists for Harlequin Ducks partly due to increasing human disturbance to their wintering and breeding areas. In addition, there appears to be an imbalance between recruitment and mortality; however, some uncertainty remains as estimates of apparent survival are likely biased low due to emigration (Rodway et al. 2003b). Higher movement rates and distances for subadults than adults in this study suggest that subadult survival rates are more likely to be underestimated and are best generated using radio telemetry or large search areas. Further, survival rates estimated from paired individuals, because they were thought most likely to be philopatric (Cooke et al. 2000), are likely to be accurate for males but may be underestimated for females. Although many variables, such as the spatial and temporal

distribution of suitable habitat, likely influence movement rates, age and distance-specific movement rates estimated in this study should aid in the correction of local survival rates due to emigration in future studies.

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