

Survival of Female Harlequin Ducks During Wing Molt

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ABSTRACT Survival rates of waterfowl during wing molt have rarely been described, leading to uncertainty about the importance of this annual cycle stage for management. We quantified survival probability of 247 radiomarked female harlequin ducks (*Histrionicus histrionicus*) during wing molt in Prince William Sound, Alaska, USA. The daily survival rate (DSR) was extremely high (DSR = 0.999; 95% CI: 0.994–1.000) during the 37-day interval over which remiges were replaced and individuals were rendered flightless. Our DSR estimate corresponded to a cumulative survival probability of 0.99 (95% CI: 0.81–1.00) for the 20 August–15 October postbreeding period as a whole, which is appreciably higher than estimates that have been derived for breeding or overwintering stages. We conclude that wing molt is a comparatively safe stage of the annual cycle for harlequin ducks that does not constrain population growth rate, with the implication for wildlife managers being that, in the absence of anthropogenic influences, management prescriptions may be most effective when focused on other stages of the annual cycle. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1220–1224; 2007)

DOI: 10.2193/2006-433

KEY WORDS demography, harlequin duck, *Histrionicus histrionicus*, Prince William Sound, radiotelemetry, survival, waterfowl, wing molt.

Birds employ an array of strategies for balancing costs associated with molt. Replacement of flight feathers is particularly challenging and potentially costly because it requires high energetic and nutritional investment (Walsberg 1983, Hohman et al. 1992, Murphy 1996). Moreover, the temporary loss of flight feathers may impair locomotion (Hedenström and Sunada 1999, Bridge 2003, Williams and Swaddle 2003), which in turn can have adverse effects on foraging efficiency (Bridge 2004) and an individual's ability to evade predators (Swaddle et al. 1996, Swaddle and Witter 1997). A number of physiological, behavioral, and morphological adaptations have evolved to reduce costs associated with feather replacement and to minimize risks faced by birds while molting (King and Murphy 1985, Lovvorn and Barzen 1988, Hohman et al. 1992). One such adaptation is the simultaneous shedding of remiges, which are the flight feathers of the wing. Simultaneous replacement of the remiges occurs in 11 different avian families, the overwhelming majority of which are aquatic or marsh-dwelling birds. By shedding the remiges simultaneously rather than sequentially the duration of wing molt is shortened. However, simultaneous wing molt results in the temporary loss of flight capability and tends to be limited to species that occupy habitats where they can feed and escape predators even without the ability to fly (Hohman et al. 1992).

Waterfowl are the best studied among the families that undergo a simultaneous wing molt. Although several studies have shown that the nutritional and energetic demands of feather synthesis can be met without significant depletion of endogenous protein or fat reserves (Ankney 1979, 1984; Hohman and Crawford 1995; Thompson and Drobney 1996; Fox and Kahlert 1999), few studies have quantified

survival rates during the flightless period (Ringleman and Longcore 1983, Bowman and Longcore 1989, Miller et al. 1992), and we are aware of only one that has directly compared the survival rate during wing molt to survival rates during other stages of the annual cycle (Kirby and Cowardin 1986). This lack of information leads to uncertainty about the importance of this annual cycle stage for understanding variation in demographic rates and subsequently population dynamics.

We used a large sample of female harlequin ducks (*Histrionicus histrionicus*) implanted with radiotransmitters to estimate survival probability during wing molt. Apparent annual survival rates have been quantified for harlequin ducks using mark–recapture data (Cooke et al. 2000, Regehr 2003) and radiotelemetry data has been used to estimate breeding season (J. C. Bond, Simon Fraser University, unpublished data) and overwinter (Esler et al. 2000*b*) survival rates. However, survival during wing molt has never been directly quantified for the species.

STUDY AREA

We captured postbreeding adult female harlequin ducks during 3 molt seasons (20 Aug–17 Sep 1995–1997) in Prince William Sound, Alaska, USA (60°N, 148°W). Prince William Sound is characterized by extensive rocky shoreline and submerged reef habitats with which harlequin ducks are commonly associated (Robertson and Goudie 1999). During the nonbreeding season, harlequin ducks are closely linked to near-shore marine environments, with adults leaving coastal areas only for a few summer months when they migrate to fast-moving inland streams to nest and raise broods (Robertson and Goudie 1999). Pacific harlequin duck populations are unique in that they undergo wing molt in the same areas where they winter, rather than on breeding grounds or on separate molting areas (Robertson et al. 1997, 1999; Iverson and Esler 2006).

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METHODS

We herded flocks of flightless harlequin ducks into funnel traps using sea kayaks. We determined sex of captured birds based on plumage characteristics and estimated age class by probing bursal depth (Mather and Esler 1999). We affixed unique United States Fish and Wildlife Service metal bands to each individual and recorded morphological measurements, including wing cord and ninth primary length. A wildlife veterinarian surgically implanted radiotransmitters into adult (after third yr) female harlequin ducks using modifications (Mulcahy and Esler 1999) of the procedure described by Korschgen et al. (1996). The transmitters weighed 17.5 g (<3% of \bar{x} body mass of an ad F) and had external antennas. Previous research has suggested that implanted transmitters are an appropriate method of attachment for wild waterfowl (Hupp et al. 2003, Iverson et al. 2006) and can be used to derive an unbiased estimate of survival probability of harlequin ducks (Esler et al. 2000a). Following surgery, we held radiomarked birds for 1 hour before release and applied a 14-day postrelease censor period to the data to control for potential negative effects of the surgery (Esler et al. 2000a). Methods for capture, handling, and transmitter attachment were approved by appropriate animal care review (Simon Fraser University Permit No. 743B-05).

Our pilot monitored radiotransmitter signals from an airplane at approximately weekly intervals (\bar{x} = 6.5 d, range 1–12 d) to determine mortality status and location. Monitoring flights began after we released the first birds and continued through spring, when birds left the study area to migrate to breeding grounds. We restricted our analysis to the postbreeding period (20 Aug–15 Oct), when wing molt occurred. Esler et al. (2000b) previously estimated overwinter survival rates for this population. We confirmed all mortality events (indicated by a mortality sensor in the transmitter) by recovery of the transmitter and carcass or location of the signal in upland habitats, which harlequin ducks do not use during the nonbreeding season.

We used a modified version (Bart and Robson 1982) of the Mayfield method (Mayfield 1961, 1975) to estimate daily survival rate (DSR). To determine the duration of wing molt and the number of exposure days for each individual we used data on feather length and daily growth rate from captured birds. We estimated the average length of a fully grown ninth primary using a sample of adult females that were captured either before initiating or after completing wing molt (\bar{x} length). We calculated daily growth rate of the ninth primary using a sample of adult females that we captured and measured on ≥ 2 occasions before completing wing molt within the same year (daily growth rate = Δ length/no. of d). From these values we inferred the duration of wing molt (molt duration = \bar{x} length/daily growth rate) and the number of exposure days remaining for each individual [exposure d = molt duration – (length/daily growth rate)].

In addition to our estimate of DSR during remige replacement, we also estimated DSR over the course of

the entire 20 August–15 October postbreeding period. Postbreeding DSR was estimated to facilitate comparison of survival probability across annual cycle stages, irrespective of molt initiation date. Mayfield models require estimates of the number of individuals that live or die for each encounter history. Following the recommendations of Bart and Robson (1982), we assumed that mortality events occurred mid-way between monitoring flights ($b = 0.5$); however, because we calculated DSR using a likelihood procedure, end results are identical regardless of initial model parameterization (Bart and Robson 1982). Our models assumed constant survival throughout the monitoring period, and cumulative survival rate (CSR) was estimated as DSR^n , where n = number of days in the remige replacement and postbreeding periods, respectively. We computed a standard error for each estimate and calculated 95% confidence intervals as $DSR \pm 1.96$ standard error. We computed confidence intervals for CSR estimates by raising the 95% confidence interval for DSR to the n power (Johnson 1979).

RESULTS

We collected survival data for 297 radiomarked adult female harlequin ducks. Among these, 247 were included in our Mayfield model of survival probability during the remige replacement period. Fifty birds completed wing molt before the end of the 14-day postsurgery data-censoring period, allowing them to be included in the 20 August–15 October postbreeding survival model, but not the remige replacement model. Signals were lost before the 15 October end date for 7 of the 297 individuals we tracked.

The average length of a fully grown ninth primary for the birds in our study was 130.9 mm (± 0.3 SE; $n = 121$) and the daily growth rate was 3.5 mm per day (± 0.06 SE; $n = 68$). From these estimates, we calculated the duration of wing molt to be 37 days. In 1995, we did not measure ninth primary length, but we did measure wing cord. In 1996 and 1997 we measured both ninth primary and wing cord. Thus, we were able to use a predictive equation based on 1996 and 1997 data to precisely estimate ninth primary length for birds captured in 1995 [ninth primary = -68.2 mm (± 0.7 SE) + 1.0 (± 0.01 SE) \times wing cord]; $r^2 = 0.99$; $n = 365$]. Most birds in our study were captured early in the molt process, with the average ninth primary length at the time of capture estimated as 29.2 mm (± 1.5 SE; $n = 247$) for the subset included in the remige replacement model and 40.9 mm (± 2.0 SE; $n = 297$) for all birds in the study.

Only one bird died during wing molt and we detected no additional mortalities over the course of the postbreeding period. The DSR of adult female harlequin ducks during the 37-day remige replacement period was estimated as 0.999 (95% CI: 0.994–1.000), and DSR for the full 56-day postbreeding period was 0.999 (95% CI: 0.996–1.000). From these estimates, we calculated CSR estimates of 0.99 (95% CI: 0.81–1.00) and 0.99 (0.88–1.00), for the remige replacement and the 20 August–15 October postbreeding periods, respectively.

DISCUSSION

Survival rates of waterfowl during wing molt have rarely been described, particularly for females, so the importance of this annual cycle stage for understanding variation in demographic rates is uncertain. Although simultaneous replacement of remiges could result in increased predation risk and reduced foraging efficiency during the flightless period, our data suggest that neither mechanism posed a significant mortality risk for female harlequin ducks in Prince William Sound, Alaska. Only 1 of the 247 birds tracked in our study died, indicating that wing molt is a comparatively safe stage in the annual cycle. However, it should be noted that most waterfowl can fly on a wing that is only 70% grown (Hohman et al. 1992), which would reduce the flightless period down from the 37 days estimated in our study. At the same time, flight capabilities are likely impaired for several days before remiges are shed, thus increasing the duration of the flightless period and shifting it forward in time.

The Mayfield method was originally conceived as an estimator of nesting success that has been generalized to telemetry studies and is particularly useful for “ragged” radiotracking data, wherein encounter occasions are irregular or not clearly delineated. Use of the Mayfield method required several important assumptions, including the assumption that survival rates are constant throughout the monitoring period. Although the sample size for birds tracked in the initial stages of their flightless period was small, owing to the necessity of capturing birds while flightless and application of a 14-day censor period to control for the effects of surgery, we believe the data that were available support this assumption. During 1997, we recaptured 11 birds with functioning transmitters that had been implanted the previous year and all 11 survived wing molt during their second molt season. In addition, we captured 42 birds with ninth primaries measuring <1 mm and 21 others with ninth primaries <10 mm. Thus, a sufficiently large subset of birds was monitored early in the remige replacement process and variation over time was sufficiently small to confidently estimate survival probability during wing molt. When censoring data after the 14-day postrelease period, we assumed that signals that were lost were a result of transmitter failure rather than mortality, shedding, or emigration (Esler et al. 2000a).

Cumulative overwinter survival for the same cohort of radiomarked females was estimated as 0.84 (95% CI: 0.78–0.89; 1 Oct–31 Mar) in unoiled portions of Prince William Sound (Esler et al. 2000b). This estimate translates to a DSR of approximately 0.999, and a CSR of 0.95 over an equivalent 56-day period. In a separate set of studies, breeding-season survival estimates for female harlequin ducks have been shown to vary according to geographic area, with cumulative survival probability ranging from 0.76 (95% CI: 0.56–0.96) in the Canadian Rockies to 0.87 (95% CI: 0.71–1.00) in the Coast Mountains of British Columbia and 0.88 (95% CI: 0.72–1.00) in the Oregon Cascades for the interval 29 April–7 August (J. C. Bond, Simon Fraser

University, unpublished data). These estimates translate to breeding season DSR ranging from 0.997 to 0.998, and would correspond to CSR of 0.86–0.93 over a 56-day period. However, breeding season survival rates have not been estimated for populations in Alaska, nor have molt or overwinter survival estimates been derived outside Alaska. Therefore, our findings should be regarded as provisional until geographic variation in vital rates is more fully investigated for the species.

Harlequin ducks are relatively late nesters (Robertson and Goudie 1999). Thus, there may not be sufficient time or food resources for females to molt on breeding grounds before winter. Moreover, coastal locations likely provide better protection from predators during the flightless period than the rivers and streams used during breeding. Predation is high on Pacific breeding streams and is primarily by mustelids (J. C. Bond, unpublished data), which harlequin ducks would escape by flying. On coastal areas, predators are primarily avian, particularly bald eagles (*Haliaeetus leucocephalus*), which are usually escaped by diving, and which focus their foraging efforts on abundant salmon (*Oncorhynchus* spp.) during the harlequin duck wing-molt period. Extensive molt migrations have been documented in some sea duck species (Salomonsen 1968), however, Pacific harlequin ducks make only one migration to a coastal location where they molt and spend the winter (Robertson et al. 1997, 1999; Iverson and Esler 2006). Robertson et al. (1997) suggested that the climatic conditions faced by harlequin ducks in western coastal North America may be sufficiently benign during the nonbreeding season that a subsequent migration is not necessary, whereas in the Atlantic region of North America harlequin ducks must migrate south after molting (Brodeur et al. 2002).

In comparison to the other waterfowl species for which survival rates during wing molt have been documented, rates for harlequin ducks appear to be at the upper end of the range (Ringleman and Longcore 1983, Kirby and Cowardin 1986, Bowman and Longcore 1989, Miller et al. 1992). However, these studies are all for dabbling ducks, which tend to have life-histories characterized by higher fecundity and lower adult survival than would be expected for a sea duck. Preliminary data from one recent study suggests the survival rates may differ among habitats in relation to water management practices, with higher than normal predation rates documented among mallards (*Anas platyrhynchos*) in drying landscapes, where birds are concentrated in more confined areas (J. P. Fleskes, United States Geological Survey, unpublished data).

MANAGEMENT IMPLICATIONS

By pinpointing ecologically crucial stages or transitions in the annual cycle, and quantifying variation in vital rates, researchers are better equipped to identify mechanisms underlying population change and recommend conservation action. The limited movement capabilities of flightless birds have been raised as a potential conservation concern when predicting the effect of displacement caused by disturbance

and habitat loss, as well as when determining impacts associated with changing management practices (Lacroix et al. 2003, Flint et al. 2004). Our data suggest that mortality risk during wing molt is low in the absence of anthropogenic influences and that management prescriptions may be most effective when focused on other stages of the annual cycle. However, we caution that aggregative tendencies and lack of mobility during wing molt may render waterfowl vulnerable to anthropogenic disturbances to which they are poorly adapted and that the possibility of geographic variation in vital rates must also be considered.

ACKNOWLEDGMENTS

This research was supported primarily by the Exxon Valdez Oil Spill Trustee Council. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. We were assisted in the field by B. Baetsle, R. Ballas, B. Benter, T. Bowman, K. Burek, J. DeGroot, D. Mather, D. Monson, J. Morse, D. Mulcahy, D. Ruthrauff, D. Schaeffer, J. Schmutz, M. Stoskopf, J. Stout, K. Trust, and the crews of the motor vessels Auklet, Julia Breeze, Kittiwake II, and Waters.

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Associate Editor: Hall.