

THE TIMING OF ARRIVAL AND MOULT CHRONOLOGY OF HARLEQUIN DUCKS *HISTRIONICUS HISTRIONICUS*

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The timing of arrival and moulting chronology of a population of post-breeding Harlequin Ducks was studied over a three year period in south-western British Columbia. Males first arrived on the moulting and wintering grounds in mid-June and most had returned from the breeding areas by the end of July. Females first arrived in late July and continued to arrive until the end of September. The flightless period for the males ranged from late July to late August. Flightless females could be seen throughout August and September. Wings took 30-31 days to regrow, compared to 26 days for tails. Assuming birds can fly at 70% remex growth this corresponds to a flightless period of about 21 days. Yearlings of both sexes exhibited moulting chronologies similar to adult males. All birds initiated moulting as soon as they arrived on the non-breeding grounds, suggesting an advantage for early moulting. The reasons for this are likely to be different for the two sexes. Males probably initiate moult quickly to be able to return to their alternate plumage and begin courting females. Females may moult early to complete wing growth before the onset of winter.

Key words: Harlequin Duck, Timing of Arrival, Moul Chronology, Flightless Period.

The post-breeding period is important in the life history of waterfowl (Hohman *et al.* 1992). After breeding, birds must undergo a number of activities before the onset of winter. These include recovering from the stress of breeding, possibly migrating to a moulting location, undergoing at least one body moult, a wing moult and a tail moult, and migrating to the wintering grounds.

Compared to other holarctic waterfowl very little is known about Harlequin Ducks *Histrionicus histrionicus*. Most studies of this species have been carried out during the breeding season (Bengtson 1966, 1972, Inglis *et al.* 1989), with the exception of some non-breeding studies of their diet composition and foraging behaviour (Vermeer 1983, Goudie & Ankney 1986, Gaines & Fitzner 1987). After breeding, little is known of their migration pattern and habitat use. Most information on

post-breeding movements and behaviour comes from the well studied populations in Iceland, where the breeding grounds are adjacent to their coastal wintering areas and the birds can simply swim down the rivers to reach the non-breeding grounds (Bengtson 1966, 1972). In western North America, where over half of the Harlequin Duck population resides, some birds breed hundreds of kilometres away from their non-breeding grounds, so substantial migrations must occur in these populations (Palmer 1976).

A detailed account of the moulting chronology for Harlequin Ducks is not available. Wing moult is an important activity for seaducks. They often take part in extensive migrations to moulting grounds, which are thought to allow the ducks to moult in isolated and, presumably, safe locations (Salomonsen 1968). Sometime after the body and wing

moult is complete courtship begins. Harlequin Ducks (Gowans *et al.* 1997), along with other duck species (Wishart 1983), do not initiate vigorous courtship until they have completed moulting. Therefore, the moult chronology and the timing of pair bond formation could be related.

In this study we describe the annual return of a population of Harlequin Ducks to their non-breeding grounds on the west coast of North America. We also describe the chronology of their subsequent moult, in both sexes, and in yearling and adult birds. Finally, we calculate the length of time for the wing and tail to be shed and regrown.

Methods

This study was carried out from August 1994 to November 1996 near White Rock, in coastal south-western British Columbia. A population of about 100 Harlequin Ducks moult and winter along a 5.5 km stretch of rocky shoreline. Once or twice a week the study area was surveyed and the sex and age composition of all groups of Harlequin Ducks were recorded. A proportion of this population is marked with individually coded leg rings (see Cooke *et al.* 1997 for details), and an effort was made to read the code for all ringed individuals. While the ducks were moulting all individuals were visually assessed to determine their moult status. For the body moult, males were categorized as either: still in old alternate plumage, undergoing pre-basic moult, in basic body plumage, undergoing pre-alternate moult or in full alternate plumage. Body moult in females could not be identified as most feathers are not visibly different in basic and alternate plumages. For males and females the wing (remex) and tail (rectrix) moults were classified as either: feathers old and present, feathers not present, feathers visible but not yet full grown, or feathers new and full grown. Observations of all ducks were made from close distances (< 50 m) and individuals were observed intently to determine the stage of their moult (see Cooke *et al.* 1997 for details). This method allowed us to identify moult in only those feather tracts that were visible to observers.

Harlequin Ducks tend to haul out onto rocks, enabling observers to read the rings and identify individuals. Observations on these individually marked birds were used to calculate the total length of time individuals took to shed and regrow their wings and tails. Sufficient data were available only for 1995, from the birds that were marked in 1994 and returned in 1995. Harlequin Ducks exhibit high levels of winter philopatry, so many of the birds marked in 1994 returned in 1995 (we did not have a sufficient number of sightings in 1996 to perform the following analysis). The method used to calculate these periods relied on estimating the minimum and maximum length of time the bird could have been undergoing a particular moult. For each individual the interval in which a particular moult sequence began (eg the last day the bird was seen with their old wing to the first day the bird was sighted after it lost its wing) and ended (similar calculation) was determined. The minimum and maximum number of days a moulting sequence spanned was calculated with these intervals. This information was summarized for all birds and a probability density function was derived to estimate the mostly likely number of days a particular moulting sequence took for the population (see Cooke *et al.* 1997 for further details). The 95% confidence intervals were extracted from this probability density function. Errors around these estimates are quite large and reflect variation from: 1) sampling, because birds were not seen every day so the exact day of shedding or complete regrowth of feathers was not known, and, 2) to a lesser extent, natural variation among birds in the time it takes them to shed and regrow different feather tracts.

Results

Timing of arrival and moult

Males began returning to White Rock in June and most males had returned by late June (**Figure 1**). Males started to enter the pre-basic body moult almost as soon as they arrived. Some males were flightless by the end of July, with most able to fly again by early

September. The entire moult (the pre-basic and pre-alternate body moults, and the wing and tail moult) was complete by the end of September for most males (**Figure 1**). Arrival and moulting chronologies appear similar in the two years, 1995 and 1996, for which we have complete data.

Females began returning in late July or early August (**Figure 2**). The small number of females present during July (approx. 5 birds) were yearling females which may have been present in the area throughout the summer. The flightless period for females began in August and continued into early October. As a population, females had a longer flightless period than males, a reflection of their more protracted arrival chronology. Females appeared to complete the moult earlier in 1996 (**Figure 2**) than in the other two years. Their return to the non-breeding grounds was relatively synchronous in this year with most females returning in the first weeks of August.

Length of wing and tail moult

The estimated length of time for individual males and females to moult their wings and tails were very similar (**Table 1**). In both sexes it took, on average, about one month for a complete set of remiges to regrow and 26 days for the tail to regrow, although there is considerable variation in these estimates.

Young birds

A small sample of yearling ducks were caught during moult drives in late July in all 3 years. All of the nine yearling females captured over the three years (two in 1994, five in 1995, two in

1996) exhibited a wing and tail moult chronology similar to the adult males. All were flightless by late July and early August, well in advance of the adult females. All three yearling males captured (two in 1995, one in 1996) had moulting chronologies similar to the adult males. Additionally, all three were seen in complete definitive alternate plumage in the following fall, suggesting that males have a full breeding plumage by the beginning of their second pre-alternate moult.

Discussion

Chronology of arrival

Harlequin Ducks show some similarities in arrival patterns to the non-breeding grounds to that seen in most ducks (Palmer 1976, Bellrose 1980). Males arrive first and relatively synchronously, females arrive later and their arrival occurs over a longer time period. Males do show some variation in their timing of arrival, probably due to the fact that the timing of breeding may vary considerably for Harlequin Ducks in a single wintering population. Harlequin Ducks breeding in high elevation streams in the Rocky Mountains may initiate breeding up to six weeks later than birds nesting in low elevation coastal streams. Male Harlequin Ducks abandon their mates once incubation begins and then form 'clubs' on the streams where they breed (Bengtson 1966). They remain in these clubs for only a few days and then migrate to the coast. Females that have failed as nesters, or simply have not bred, also form groups on the breeding grounds, and then migrate to the ocean

Table 1. Estimated times for individual Harlequin Ducks to complete their wing and tail moult in 1995.

		Males		Females
	<i>n</i>	Estimated number of days (95% C.I.)	<i>n</i>	Estimated number of days (95% C.I.)
Wing moult	26	30 (14-44)	18	31 (12-47)
Tail moult	30	26 (10-47)	16	26 (4-54)

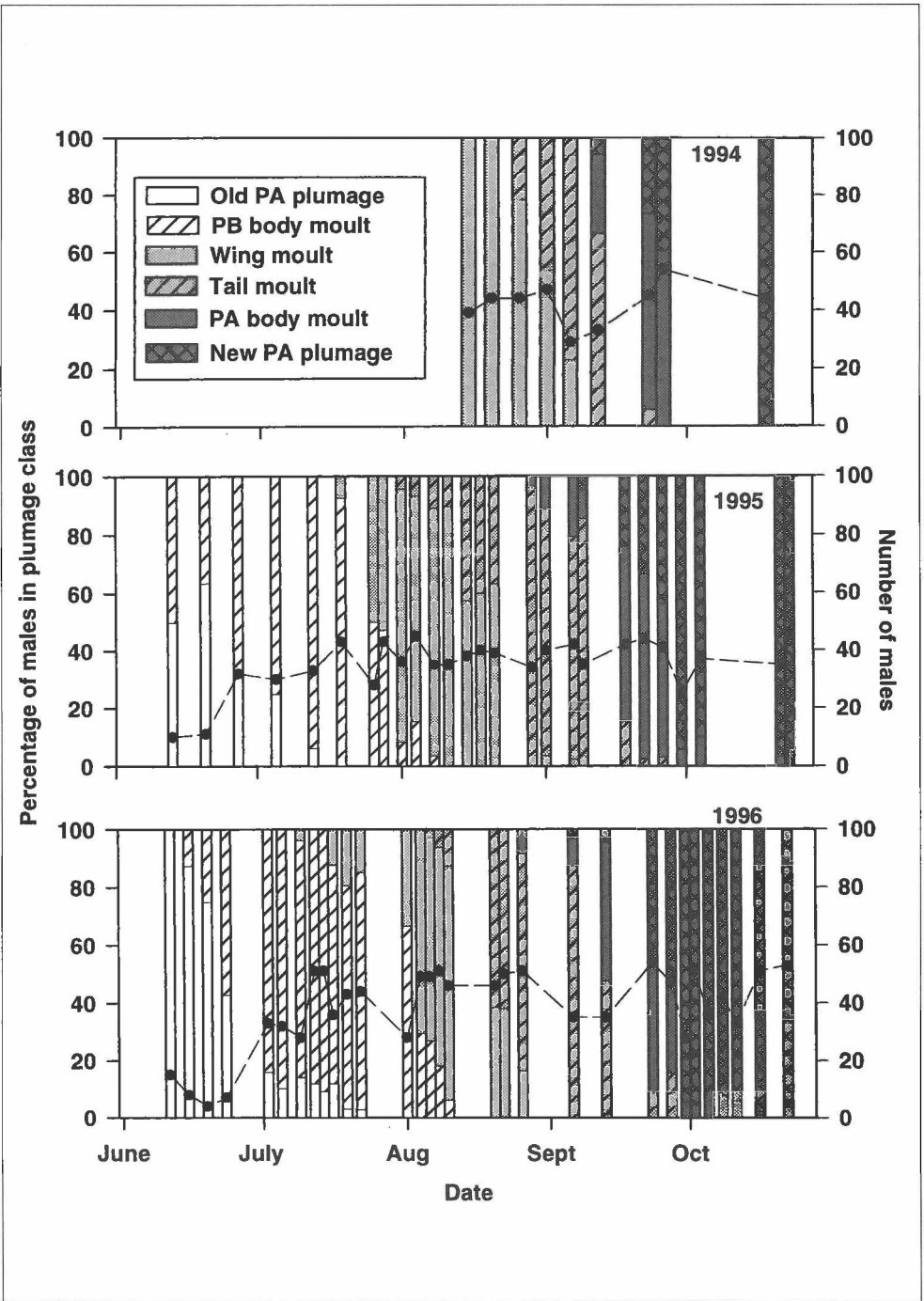


Figure 1. Percentage of male Harlequin Ducks seen in various plumage classes and the numbers of males present at White Rock, British Columbia.

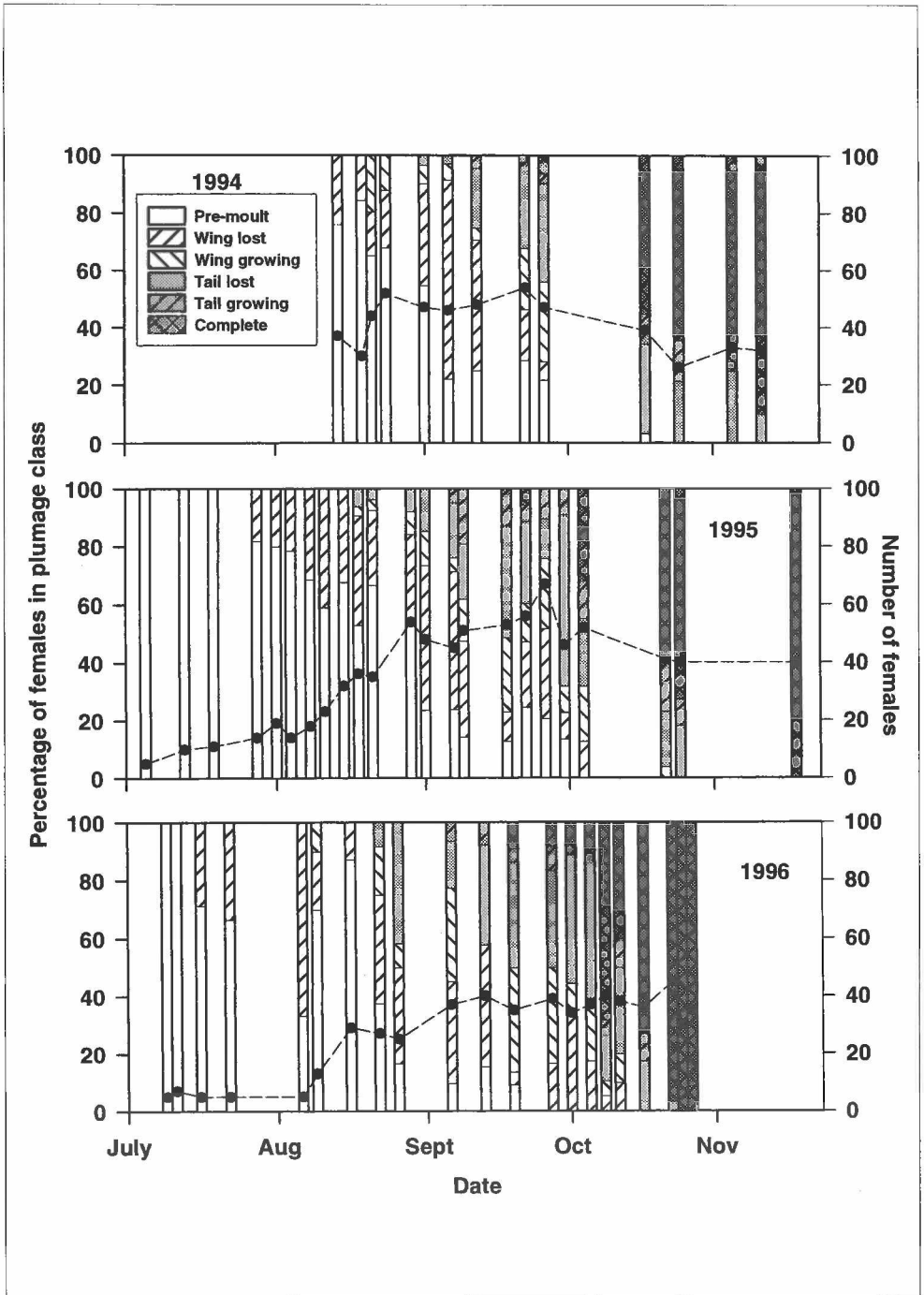


Figure 2. Percentage of female Harlequin Ducks seen in various plumage classes and the numbers of females present at White Rock, British Columbia.

(Bengston & Ulfstrand 1971). Females which successfully hatch their eggs remain with their brood until fledging, at which time they depart for the coast (Bengston 1972). Evidence for whether or not the brood migrates with their mother is ambiguous, and both strategies may exist (Kuchel 1977, Wallen 1987). A protracted chronology in the arrival of breeding females occurs because females may lose their nests or broods to predation at any time during breeding, after which they presumably migrate to the coast.

In some species of ducks, females moult on, or close to, the breeding grounds. In others they join the males on separate moulting grounds (Hohman *et al.* 1992). Usually it is only young, failed-breeding and non-breeding females that participate in a moult migration and moult with the males at these sites. Female Harlequin Ducks, at least in our population on the west coast of North America, migrate to the moulting grounds before they initiate the wing moult, regardless of their success in rearing young. Female Harlequin Ducks probably moult at the same location as the males because the moulting and wintering grounds overlap in this population. There are a number of reasons why females leave the breeding areas to moult on the coast. Harlequin Ducks are relatively late nesters; pre-fledging broods in western North America are seen well into September (Hunt 1995, Smith 1996). There may not be time, or sufficient food, for females to moult on the breeding grounds before the winter, so they must migrate to the coast before wing moult. Alternatively, coastal moulting locations may provide better protection from predators during the vulnerable moult period than narrow rivers and streams. Females may also moult on the coast to begin the process of selecting a high quality male before they are all paired or reuniting with her former mate as soon as possible. Pair reunion commonly occurs in Harlequin Ducks (Gowans *et al.* 1997). Finally, females may moult on the coast so that they can bring their offspring with them to their coastal wintering grounds. Any or all of these explanations could explain why females migrate to the coast to moult.

Timing of moult

Males initiate the pre-basic body moult soon after they arrive on the moulting grounds. This contrasts with patterns seen in King Eiders *Somateria spectabilis* (Frimer 1994) and Steller's Eider *Polystica stelleri* (Petersen 1980) where males arrive at the moulting grounds undergoing, or already having completed, the pre-basic body moult. In these species, wing moult is initiated soon after they arrive. Harlequin Ducks on the west coast make only one known migration to a coastal location where they moult and spend the winter season, as opposed to making a moult migration and then a second autumn migration to their wintering grounds; such as that exhibited by other sea ducks (Salomonsen 1968). Some individual Harlequin Ducks may move to other sites after the moult, but these movements are not extensive and do not represent a true migration (Robertson *et al.* in press). Conditions or food resources in western coastal North America may be sufficiently benign during the non-breeding season that a subsequent migration after moulting is unnecessary to avoid harsh conditions. Harlequin Ducks in the Atlantic region of North America do migrate south after moulting (Goudie 1991).

Females also initiate a moulting sequence (wing and tail moult) as soon as they arrive at the non-breeding grounds. For females we cannot visually detect body moult. Unlike males which tend to undergo the pre-basic moult after breeding, females in other species of ducks initiate the pre-basic moult before breeding (Lovvorn & Barzen 1988, Hohman & Crawford 1995), making the wing moult the next feather tract for moult in the sequence.

Females appeared to complete moulting slightly earlier in 1996 than in the other two years, and their arrival was relatively more synchronous than in 1995. In 1995, the number of females gradually increased from mid July to late August, in 1996, a large number of females arrived in the second week of August, and a few more arrived in early September. An earlier arrival and moult of the female population may suggest something about conditions on the

breeding grounds. If breeding conditions were good then it would be expected that many females would be successful and all females should return later to the non-breeding grounds after raising their young. Otherwise, if conditions were very poor on the breeding grounds, then many females may fail in their attempt to nest or not attempt at all, leading to an early and synchronous return of females to the non-breeding grounds. Conditions during the spring of 1996 were not favourable for Harlequin Ducks in the Rocky mountains. It snowed periodically during the month of May, temperatures were cold, and the spring run-off was very high (R. I. Goudie, *pers. obs.*). We suggest that the early and more synchronous return of females in 1996 was a result of a poor breeding effort, where many females did not succeed or did not attempt to nest. Interestingly, the males appeared to follow a similar arrival and moult chronology in all three years. Males return to the coast after the nesting attempt has been made, thus their arrival chronology is not greatly influenced by the reproductive effort or failure made by the females.

Length of wing and tail moult

We estimated that individual Harlequin Ducks require 30-31 days for their remiges to be lost and re-grown. For male Harlequin Ducks the ninth primary is the longest primary (Cramp & Simmons 1977) and grows to a length of about 130 mm; female primaries are slightly shorter at about 120 mm (G. J. Robertson, *unpubl. data*). Assuming a constant growth rate this feather is growing at 4.33 mm/day (or 3.33 % of remex length/day) for males and 3.87 mm/day (or 3.23% of remex length/day) for females. These values are slightly faster than the average of 2-3% of remex length/day reported for other species of waterfowl (Hohman *et al.* 1992). This consistency among species in remex growth rates lead Owen & King (1979) to speculate that 2-3% remex/day may be the physiological maximum for waterfowl and all species are attempting to regrow their remiges as fast as they can. Given the disadvantages to waterfowl

in remaining flightless (predation risk, the inability to quickly change location if resources become depleted, and/or search for mates) it would be expected that birds would regrow their flight feathers as fast as possible.

Assuming that Harlequin Ducks can fly at about 70% wing regrowth (Hohman *et al.* 1992) we calculate a flightless period of 21-22 days. This period is relatively fast for waterfowl which have flightless periods from about 20 to over 49 days (Hohman *et al.* 1992). Smaller species, such as the Wood Duck *Aix sponsa* (Bellrose 1980) and Green-winged Teal *Anas crecca* (Sjöberg 1988), have estimates of 21 days for the flightless period (Hohman *et al.* 1992), so our values do not appear unreasonable for Harlequin Ducks. Additionally, seaducks and Pochards have shorter wings relative to body size so they may not take as long to grow as in the dabbling ducks. Our estimate of 21-22 days may be biased low if 70% wing growth is not valid for Harlequin Ducks. Seaducks have a high wing loading capacity and shorter remiges. They may need a more developed wing before being able to fly again. Unfortunately, information on the true duration of flightlessness for seaducks is not available.

The tail moult took an estimated 26 days to complete, slightly shorter than the wing moult. The seventh and the eighth rectrices are the longest at 70 mm in males and 65 mm in females. Considering that there are only 14 tail feathers, compared to 40 primaries and secondaries which are much longer, tail feathers grow much slower than rectrices. This suggests that regaining flight capability is important and has led to selection for growing remiges as fast as physiologically possible. Not having a complete tail for a period of time is not as crucial. The rate of rectrix growth is much slower than the rate of remex growth. The nutritional cost of moulting rectrices is spread over a longer period of time and is possibly coupled with simultaneous moulting of other feather tracts.

The importance of rapid moulting

Males moulted through the pre-basic body

moult, remex, rectrix, and, pre-alternate body moult within a three month period with no obvious breaks between the different body, wing, and tail moults. They also moulted as soon as they arrived on the moulting grounds and regrew their wing feathers relatively quickly. This information suggests that males are moulting as rapidly as possible. Harlequin Ducks pair very early compared to most ducks, beginning in late September and over 50% of adult females are paired by December (Gowans *et al.* 1997). Although, males which have not completed the pre-alternate body moult do engage in some courtship behaviour, it is less than males which have completed this moult (Gowans *et al.* 1997). No male still in pre-alternate body moult was seen successfully paired; pairing began soon after this moult was completed. This suggests that selection may favour those males which leave the breeding grounds early and complete moult quickly, as it would allow them to compete more effectively for females.

Females may initiate their wing moult rapidly and immediately when they arrive at the coast to avoid being flightless during the approaching winter. Although recent opinion suggests that the nutritional costs of moulting are not very high (Hohman *et al.* 1992), it may be disadvantageous to moult wing feathers during the short, cold days of winter for a number of reasons. If local conditions become unsuitable then late-moulting females may not be able to fly to another location. Additionally, Harlequin Ducks feed almost continuously during the winter period (G.J. Robertson & R. Torres, *unpubl. data*), the further nutritional demands of wing moult may not be tolerable at this time of year.

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